

Altitudinal migration: ecological drivers, knowledge gaps, and conservation implications

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ABSTRACT

Animal migration has been the subject of intensive research for more than a century, but most research has focused on long-distance rather than short-distance migration. Altitudinal migration is a form of short-distance migration in which individuals perform seasonal elevational movements. Despite its geographic and taxonomic ubiquity, there is relatively little information about the intrinsic and extrinsic factors that influence altitudinal migratory behaviour. Without this information, it is difficult to predict how rapid environmental changes will affect population viability of altitudinal migrants. To synthesize current knowledge, we compiled literature on altitudinal migration for all studied taxa, and identified the leading hypotheses explaining this behaviour. Studies of animal altitudinal migration cover many taxonomic lineages, with birds being the most commonly studied group. Altitudinal migration occurs in all continents except for Antarctica, but about a third of the literature focused on altitudinal migration in North America. Most research suggests that food and weather are the primary extrinsic drivers of altitudinal migration. In addition, substantial individual-level variation in migratory propensity exists. Individual characteristics that are associated with sex, dominance rank, and body size explain much of the variation in migratory propensity in partially migratory populations, but individual-level correlates are poorly known for most taxa. More research is needed to quantify the effects of habitat loss, habitat fragmentation, and climate change on altitudinal migrants. Demographic studies of individually marked populations would be particularly valuable for advancing knowledge of the cascading effects of environmental change on migratory propensity, movement patterns, and population viability. We conclude our review with recommendations for study designs and modelling approaches that could be used to narrow existing knowledge gaps, which currently hinder effective conservation of altitudinal migratory species.

Key words: elevational movement, partial migration, seasonal migration, differential migration, birds, mammals, insects, reptiles.

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I. INTRODUCTION

Aristotle provided one of the first descriptions of animal migration by stating that fish migrated ‘in winter from the deep sea towards the land in pursuit of the warmth and in summer from inshore to the deep sea escaping the warmth’ and that birds ‘come down to the plains for warmth in winter and in frosts, and go back in summer to the mountains above because of the heat’ (Balme, Gotthelf & Peck, 1965, p. 133). The next 2000 years saw little progress in understanding of animal migration, as evidenced by Linnaeus’ treatise on avian migration, *Migrations Avium*, in which he explained that swallows and martins disappeared during the winter because they hibernated under the water in lakes until the next spring (Alerstam, 1990). Substantial progress in the study of animal migration began in the 19th century with discoveries of the physiology and proximate causes of this behaviour. Several books on avian migration were published detailing the timing and direction of bird migration and describing migratory flight (Harvie-Brown & Cordeaux, 1879; Whitlock, 1897). The 20th century saw an explosion of research on migration, with advances made using experimental studies of migration orientation strategies. For example, the indigo bunting (*Passerina cyanea* Linnaeus 1766) was shown to use the celestial system to navigate (Emlen, 1967). More recently, it was discovered that some species of sea turtles use magnetic fields to navigate during migration (Lohmann & Lohmann, 1996).

Despite centuries of observations and research on animal migration, researchers have yet to agree on a definition for this common behaviour, with most definitions applying to taxon-specific attributes. For example, entomologists have defined migration as large number of individuals ‘flying steadily in one definite direction’ (Williams, 1957, p. 168). Ornithologists, on the other hand, have defined migration as seasonal back-and-forth movements over geographic gradients (Baker, 1978). While acknowledging that no definition of migration can cover the migratory behaviour of all taxa, herein we will use the definition proposed by Rappole (2013, p. 1), who stated that migration is ‘an annually repeated, seasonal movement between the breeding range and those regions where breeding does

not occur... to exploit two or more environments whose relative suitability in terms of survival or reproduction changes over time’. This definition distinguishes migration from dispersal which occurs when animals make one-way movements away from their home range (e.g. natal dispersal). The evolution of migration is driven by natural selection acting upon animals seeking to exploit resources that vary over temporal and spatial scales (Milner-Gulland, Fryxell & Sinclair, 2011). Migration evolves when the fitness benefits of exploiting these resources outweigh the associated costs (Baker, 1978; Milner-Gulland *et al.*, 2011; Alves *et al.*, 2013). Benefits of migration include the ability to take advantage of seasonal availability of food, to avoid predation, and to seek mating and nesting habitats. Costs of migration include increased energetic expenditure during migration, potentially increased risk of predation *en route*, and shorter breeding seasons (Milner-Gulland *et al.*, 2011; Alves *et al.*, 2013; Boyle, 2017). Animal migration can be categorized based on characteristics such as frequency (e.g. number of moving bouts per year) and distance (Baker, 1978; Rappole, 2013). Rappole (2013) defined long-distance migration as movement of all individuals of a population over 2000 km, often to a different continent. Examples of long-distance migration include the leatherback sea turtle (*Dermochelys coriacea* Vandelli 1761) that can migrate approximately 7000 km between nesting attempts (Hughes *et al.*, 1998), and the Alaskan bar-tailed godwit (*Limosa lapponica* Linnaeus 1758) that can migrate 11000 km from Alaska to New Zealand (Battley *et al.*, 2012).

Altitudinal migration is a type of short-distance migration in which animals migrate seasonally between breeding and non-breeding grounds that differ in elevation (Rappole, 2013). Although widespread both geographically and taxonomically, studies of the patterns and causes of altitudinal migration are relatively uncommon. Numerous studies have examined movement patterns and migration routes of long-distance migrants (Hughes *et al.*, 1998; Fox, Glahder & Walsh, 2003; Luschi, Hays & Papi, 2003; Thirgood *et al.*, 2004; Block *et al.*, 2005; Stutchbury *et al.*, 2009; Horton *et al.*, 2011; Alves *et al.*, 2013; Trierweiler *et al.*, 2014), but similar studies on altitudinal migrants are much more limited (but see

Powell & Bjork, 2004, 2010; Poole & Mowat, 2005; Sawyer *et al.*, 2009; Blake *et al.*, 2013; Norbu *et al.*, 2013; Leopold & Hess, 2014). The trade-offs made by altitudinal migrants are similar to those facing long-distance migrants, although the costs may be lower because altitudinal migrants cover much shorter distances (Dingle & Drake, 2007). Consequently, most of the hypotheses used to explain altitudinal migration are similar to those explaining long-distance migration.

The objectives of this review are to provide a comprehensive summary of the existing hypotheses used to explain altitudinal migration in terrestrial animal taxa, to evaluate the supporting and conflicting evidence associated with each hypothesis, and to identify emergent patterns. In addition, we sought to highlight the potential for rapid environmental change to alter landscape composition and configuration in ways that could affect animal movement. The impacts of habitat loss on long-distance migrants have been well documented but are mostly unknown for altitudinal migrants. Even fewer studies have examined how landscape barriers affect movement of altitudinal migrants. The lack of knowledge of the effects of environmental change on their migratory behaviour makes it difficult to prevent population declines and extinction of altitudinal migratory species. Therefore, the final objective of our review is to identify knowledge gaps that hinder conservation efforts, and to propose future research directions.

II. PUBLISHED LITERATURE ON ALTITUDINAL MIGRATION

We conducted literature searches using the online database *Web of Science* and *Google Scholar* search engines. We searched for the terms ‘animal altitudinal migration’, ‘elevational movement’, and ‘altitudinal movement’, and combined each search term with different taxa (e.g. birds, bats, reptiles, ungulates, and insects). Additionally, we conducted searches combining either ‘altitude*’ or ‘elevation*’ and ‘movement’ or ‘migrat*’. Fish migration was not included in our review because nearly all anadromous fish migrations involve elevation changes and it would be unwieldy to include this large taxonomic group. We added additional sources including theses/dissertations or book chapters to our review when referenced by literature returned by our initial searches. We also included previous reviews of altitudinal migration, including two of birds (Barçante, Vale & Alves, 2017; Boyle, 2017), and one of bats (McGuire & Boyle, 2013).

We organized the literature by taxonomic class of the migrant species and the country/region in which the studies were conducted (Table 1). A total of 216 references were included in this synthesis with the earliest documentation of altitudinal migration dating back to Presnall (1935). Most studies and documentation of altitudinal migration were published within the last two decades (Fig. 1). Sixty-one per cent of the publications were on altitudinal migration of birds, 17.7% on ungulates, 7.4% on bats, 6% on insects, 6% on other mammals, and 1.9% on reptiles (Fig. 2).

The publications covered most of the world’s geographic areas, with the most publications in North America (31.3%) followed by Central America (18%), South America (16.6%), Europe (13.4%), Asia (9.2%), Africa (6%), Australasia (4.1%), and syntheses at a global level (1.4%) (Fig. 3).

III. HYPOTHESES FOR THE FACTORS DRIVING ALTITUDINAL MIGRATION

Seasonal variations in environmental factors such as climate and resource availability (e.g. food and nesting sites) along an elevational gradient alter habitat quality for animals, which may cause them to migrate in response to these changes. Furthermore, variations in characteristics such as sex, dominance rank, and body condition may cause individuals to respond differently to the same environmental variables due to varying reproductive needs and fitness pay-offs associated with each migratory strategy. Below we discuss hypotheses proposed and tested in the literature we compiled that explain how extrinsic (environmental) and intrinsic (individual-level) factors influence altitudinal migration.

(1) Extrinsic drivers of altitudinal migration

(a) Food-limitation hypotheses

Seasonal fluctuation of food resources is considered to be one of the major drivers of migration in general, and it is a common explanation for altitudinal migration. The production of food often varies seasonally over elevation gradients in response to fluctuations in temperature and precipitation throughout the year. Animals may move up and down in elevation in response to these variations. For example, the timing of altitudinal migration of elephants (*Loxodonta africana* Blumenbach 1797) in Kenya coincided with precipitation-driven changes in availability of vegetation consumed by the elephants at different elevations (Bohrer *et al.*, 2014). The elephants moved downslope to areas where there was more vegetation during the dry season and upslope when the vegetation at lower elevations senesced (Bohrer *et al.*, 2014). Galapagos tortoises (*Chelonoidis nigra* Quoy & Gaimard 1824) also make altitudinal movements affected by seasonal variation in vegetation availability in their lowland habitat (Blake *et al.*, 2013). The normalized difference vegetation index (NDVI), a measure of vegetation greenness, on Santa Cruz Island in the Galapagos indicated that forage vegetation in the highlands remained stable year-round, whereas vegetation availability decreased in the lowlands during the dry season, coinciding with the timing of uphill migration of the tortoises (Blake *et al.*, 2013). Fluctuations in food resources have also been identified as a major driver of altitudinal migration in ungulates. In the Rocky Mountains, bighorn sheep (*Ovis canadensis* Shaw 1804) ewes and yearlings migrated between a lower-elevation winter range and higher-elevation summer range to take

Table 1. Summary of literature pertaining to animal altitudinal migration arranged by taxa

Taxonomic group	Species	Common name	Location	References
Ungulates	<i>Oreamnos americanus</i>	Mountain goat	British Columbia, Canada Washington, USA	Poole & Heard (2003) Rice (2008)
	<i>Hemitragus jemlahicus</i>	Himalayan tahr	Southern Alps, New Zealand	Tustin & Parkes (1988)
	<i>Cervus nippon</i>	Sika deer	Japan	Takatsuki, Suzuki & Higashi (2000); Igota <i>et al.</i> (2004)
	<i>Capreolus capreolus</i>	Roe deer	Italy	Lamberti, Mauri & Apollonio (2004); Ramanzin, Sturaro & Zanon (2007) Carvalho <i>et al.</i> (2008) Mysterud (1999)
	<i>Ovis canadensis</i>	Bighorn sheep	Portugal Norway	Festa-Bianchet (1988)
	<i>Budorcas taxicolor bedfordi</i>	Golden takin	Alberta, Canada	Zeng <i>et al.</i> (2008); Wang <i>et al.</i> (2010); Yan <i>et al.</i> (2017)
	<i>Hippocamelus bisulcus</i>	Huemul deer	South-western China	Diaz, Marqués & Vila (2013)
	<i>Lama guanicoe</i>	Guanaco	Argentina	Puig <i>et al.</i> (2011)
	<i>Capra ibex</i>	Alpine ibex	Italy	Parrini <i>et al.</i> (2003); Aublet <i>et al.</i> (2009)
	<i>Odocoileus hemionus</i>	Mule deer	Wyoming, USA	Sawyer <i>et al.</i> (2009); Sawyer & Kauffman (2011)
	<i>Odocoileus hemionus columbianus</i>	Black-tailed deer	British Columbia, Canada	Poole & Mowat (2005)
	<i>Odocoileus hemionus sitchensis</i>	Sitka black-tailed deer	Colorado, USA	Gilbert, Wallmo & Gill (1970)
	<i>Odocoileus virginianus</i>	White-tailed deer	California, USA	Loft, Menke & Burton (1984)
	<i>Antilocapra americana</i>	Pronghorn	Alaska, USA	Schoen & Kirchoff (1985)
	<i>Cervus canadensis</i>	Pronghorn and mule deer Elk/wapiti	British Columbia, Canada Nevada, USA Wyoming, USA Canada	Poole & Mowat (2005) Collins (2016) Sawyer, Lindzey & McWhirter (2005) Morgantini & Hudson (1989); Poole & Mowat (2005) Hebblewhite & Merrill (2007, 2011); Hebblewhite, Merrill & Mcdermid (2008) Albon & Langvan (1992); Mysterud <i>et al.</i> (2001); Qviller <i>et al.</i> (2013) Zweifel-Schielly <i>et al.</i> (2009); Anderwald, Haller, & Felli (2016)
Bats	<i>Cervus elaphus</i>	Red deer	Norway	Poole, Serrouya, & Stuart-Smith (2007) Oosenbrug & Theberge (1980) Voigt <i>et al.</i> (2014)
	<i>Alces alces</i>	Moose	Switzerland	Bonaccorso <i>et al.</i> (2009); Menard (2001)
	<i>Rangifer tarandus caribou</i>	Woodland caribou	British Columbia, Canada	Neubaum <i>et al.</i> (2006)
	<i>Miniopterus natalensis</i>	Natal long-fingered bat	Yukon, Canada	Montalvo (1997)
	<i>Lasius cinereus</i>	Hawaiian hoary bat	Mount Kilimanjaro, Tanzania	Esberard <i>et al.</i> (2011)
	<i>Eptesicus fuscus</i>	Big brown bat	Hawaii, USA	Encarnação <i>et al.</i> (2005)
	<i>Leptonycteris curasoae</i>	Lesser long-nosed bat	Colorado, USA	Russo (2002)
	<i>Pygoderma bilabiatum</i>	Ipanema bat	Mexico	McCracken <i>et al.</i> (1997)
	<i>Myotis daubentonii</i>	Daubenton's bat	Brazil	Erzberger <i>et al.</i> (2011)
	<i>Lasius brachyotis</i>	Red bat	Germany	Timm & Laval (2000)
	<i>Lasius cinereus</i>	Hoary bat	Italy	Valiente-Banuet <i>et al.</i> (1997)
	Multiple species		Galapagos	
	Multiple species		Honduras	
	Multiple species		Costa Rica	
	Multiple species		Mexico	

Table 1. Continued

Taxonomic group	Species	Common name	Location	References
Bats	Multiple species		Nicaragua	Fraser, Mckinnon & Diamond (2010 <i>b</i>)
	Multiple species		Brazil	Pedro & Taddei (2002)
Other mammals	Multiple species		Worldwide	McGuire & Boyle (2013)
	<i>Canis latrans</i>	Coyote	Utah & Idaho, USA	Gantz & Knowlton (2005)
	<i>Felis concolor</i>	Mountain lion	Wyoming, USA	Logan & Irwin (1985)
	<i>Ursus thibetanus</i>	Asiatic black bear	Japan	Izumiya & Shiraishi (2004)
	<i>Tremarctos ornatus</i>	Spectacled bear	Northern Andes, South America	Kattan <i>et al.</i> (2004)
	<i>Rhinopithecus bieti</i>	Black-and-white monkey	China	Li <i>et al.</i> (2008)
	<i>Ailuropoda melanoleuca</i>	Giant pandas	China	Loucks <i>et al.</i> (2003); Wang <i>et al.</i> (2010); Liu <i>et al.</i> (2015)
	<i>Loxodonta africana</i>	African elephant	Kenya	Bohrer <i>et al.</i> (2014)
	<i>Sus scrofa</i>	Feral pigs	Australia	Mitchell <i>et al.</i> (2009)
	<i>Marmota marmot</i>	Alpine marmot	Pyrenees, Spain & France	Herrero, Garcia-Gonzalez & Garcia-Serrano (1994)
	<i>Pongo pygmaeus abelii</i>	Sumatran orangutans	Malaysia	Buij <i>et al.</i> (2002)
Birds	Multiple small mammal species		China	Wen <i>et al.</i> (2014)
	<i>Cinclus mexicanus</i>	American dipper	British Columbia, Canada	Morrissey (2004); Morrissey, Bendell-Young & Elliott (2004); Middleton, Morrissey & Green (2006); Gillis <i>et al.</i> (2008); Mackas <i>et al.</i> (2010); Green <i>et al.</i> (2015)
	<i>Junco hyemalis</i>	Dark-eyed juncos	California, USA	Garwood <i>et al.</i> (2009)
	<i>Junco phaeonotus</i>	Yellow-eyed junco	Southern Appalachians, USA	Rabenold & Rabenold (1985)
	<i>Sitta carolinensis</i>	White-breasted nuthatch	Arizona, USA	Lundblad (2014)
	<i>Cardellina pusilla</i>	Wilson's warbler	Arizona, USA	Dunning & Bowers (1984)
	<i>Camtocercus urophasianus</i>	Greater sage-grouse	California & Oregon, USA	Wiegardt, Barton & Wolfe (2017 <i>a</i>)
	<i>Dendrobagus obscurus</i>	Blue grouse	Wyoming, USA	Pratt, Smith & Beck (2017)
	<i>Tympanuchus phasianellus columbianus</i>	Columbian sharp-tailed grouse	Colorado, USA	Cade & Hoffman (1993)
	<i>Turdus migratorius</i>	American robin	Colorado, USA	Boisvert, Hoffman & Reese (2005)
	<i>Lagopus leucura</i>	Mountain quail	Colorado, USA	Inouye <i>et al.</i> (2000)
	<i>Poecile gambeli</i>	Mountain chickadee	California, USA	Brennan, Block & Gutierrez (1987)
	<i>Nucifraga columbiana</i>	Clark's nutcracker	Utah, USA	Dixon & Gilbert (1964)
	<i>Zonotrichia leucophrys</i>	White-crowned sparrow	Washington, USA	Lorenz & Sullivan (2009)
	<i>Pipilo chlorurus</i>	Green-tailed towhee	California, USA	Breuner & Hahn (2003); Hahn <i>et al.</i> (2004)
	<i>Strix occidentalis</i>	Spotted owl	California, USA	Morton (1991)
	<i>Leucosticte arda</i>	Black rosy finch	Western USA	Laymon (1989)
	<i>Branta sandvicensis</i>	Hawaiian goose	Western USA	French (1959)
	<i>Drepanis coracina</i>	'I'iwi	Hawaii, USA	Hess <i>et al.</i> (2012); Leopold & Hess (2014)
	<i>Chlorospingus ophthalicus wetmorei</i>	Wetmore's bush-tanager	Hawaii, USA	Guillaumet <i>et al.</i> (2017)
	<i>Chiroxiphia boliviana</i>	Yungas manakin	Veracruz, Mexico	Winker <i>et al.</i> (1997)
	<i>Metallura baroni</i>	Violet-throated metaltail	Bolivia	Villegas, Newsome & Blake (2016)
	<i>Eriocnemis nigrirostris</i>	Black-breasted puffleg	Ecuador	Tinoco <i>et al.</i> (2009)
	<i>Corapipo altera</i>	White-ruffed manakins	Ecuador	Guevara, Bonaccorso & Duivenvoorden (2015)
			Costa Rica	Rosselli (1994); Boyle (2008 <i>a,b</i> , 2010); Boyle, Norris & Guglielmo (2010); Boyle <i>et al.</i> (2011 <i>b</i>)

Table 1. Continued

Taxonomic group	Species	Common name	Location	References
Birds	<i>Procnias tricarunculatus</i>	Three-wattled bellbirds	Costa Rica	Powell & Bjork (2004); Papeş, Peterson, & Powell (2012)
	<i>Pharomachrus mocinno</i>	Resplendent quetzals	Costa Rica	Wheelwright (1983); Powell & Bjork (2010)
	<i>Cephalopterus glabricollis</i>	Bare-necked umbrellabird	Mexico	Solorzano <i>et al.</i> (2000)
	<i>Penelope purpuraceus</i>	Crested guan	Costa Rica	Chaves-Campos, Arévalo & Araya (2003)
	<i>Chamaepetes unicolor</i>	Black guan	Costa Rica	Chaves-Campos (2003)
	<i>Aburria aburri</i>	Wattled guan	Colombia	Rios, Londoño & Muñoz (2005)
	<i>Oryzopsis cristatus</i>	Sharpbill	Brazil	Da Silva (1993)
	<i>Columba plumbea</i>	Plumbeous pigeon	Brazil	Galetti (2001)
	<i>Platyichla flacipes</i>	Yellow-legged thrush	South-eastern Brazil	De Castro <i>et al.</i> (2012)
	<i>Turdus albicollis</i>	White-necked thrush	South-eastern Brazil	De Castro <i>et al.</i> (2012)
	<i>Catharus frontzii</i>	Ruddy-capped nightingale-thrush	El Salvador	Taylor & Komar (2010)
	<i>Amazilia cyanura</i>	Blue-tailed hummingbird	Nicaragua	Fraser, Diamond & Chavarria (2010a)
	<i>Muscipora vetula</i>	Shear-tailed gray-tyrant	Argentina & Paraguay	Areta & Bodrati (2008)
	<i>Euphonia cyanocephala</i>	Golden-rumped euphonia	Argentina & Paraguay	Areta & Bodrati (2010)
	<i>Thraupis bonariensis</i>	Blue-and-yellow tanager	Argentina	Ortiz & Capllonch (2008)
	<i>Pipraidea melanola</i>	Fawn-breasted tanager	Argentina	Ortiz & Capllonch (2008)
	<i>Zonotrichia capensis</i>	Rufous-collared sparrow	Argentina	Handford (1980)
	<i>Plectrophenax nivalis</i>	Snow bunting	North-eastern Scotland	Smith <i>et al.</i> (1993)
	<i>Serinus citrinella</i>	Citril finch	Spain	Borras, Cabrera & Senar (2010a,b)
	<i>Lullula arborea</i>	Woodlark	Italy	Brambilla & Rubolini (2009)
	<i>Sitta krueperi</i>	Krüper's nuthatch	Turkey	Albayrak, Bairlein & Erdoğan (2010)
	<i>Pinella collaris</i>	Alpine accentor	Southern France	Henry (2011)
	<i>Perdix perdix hispaniensis</i>	Pyrenean grey partridges	France	Novoa, Dumas & Resseguier (2006)
	<i>Pyrhula murina</i>	Azores bullfinch	Portugal	Ramos (1996)
	<i>Motacilla cinerea</i>	Grey wagtail	Switzerland	Klemp (2003)
	<i>Petroica phoenicea</i>	Flame robin	Australia	Green (2010)
	<i>Anthus novaeseelandiae</i>	Richard's pipit	Australia	Normant & Green (2004); Green (2010)
	<i>Tichodroma muraria</i>	Wallcreeper	Slovakia	Saniga (1995)
	<i>Gypaetus barbatus</i>	Bearded vulture	Crete, Greece	Xirouchakis & Nikolakakis (2002)
	<i>Andropadus virens</i>	Little greenbul	Eastern Tanzania	Werema (2014)
	<i>Poicephalus fuscicollis sudanicus</i>	Grey-headed parrot	South Africa	Symes & Perrin (2003)
	<i>Nectarinia famosa</i>	Malachite sunbird	South Africa	Symes, Downs & Mclean (2001)
	<i>Promerops gurneyi</i>	Gurney's sugarbird	South Africa	Symes <i>et al.</i> (2001)
	<i>Tragopan sabyra</i>	Satyr tragopan	Himalaya	Norbu <i>et al.</i> (2013, 2016)
	<i>Prunella fuscescens</i>	Brown accipiter	Tibet	Lu (2006)
	<i>Lanius tephronotus</i>	Grey-backed shrike	Tibet	Lu, Wang & Yu (2010)
	Rosy finches		Utah, USA	King & Wales (1964)
	Multiple species		Utah, USA	Presnall (1935)
	Multiple species		California & Oregon, USA	Wiegardt <i>et al.</i> (2017)
	Nectarivores		Hawaii, USA	Hart <i>et al.</i> (2011)

Table 1. Continued

Taxonomic group	Species	Common name	Location	References
Birds	Hawaiian waterbirds		Hawaii, USA	Engilis & Pratt (1993)
	Hummingbirds		California, USA	Grant & Grant (1967)
	Multiple species		California, USA	Grimmell & Miller (1944); McGrann & Fumas (2016)
	Multiple species		Mexico	Nocedal (1994); Ornelas & Arizmendi (1995); Olmos (1983)
	Multiple species		Costa Rica	Blake & Loiselle (1991, 2000, 2001); Boyle (2011); Levey & Stiles (1992); Slud (1964); Stiles (1988)
	Multiple manakin species		Costa Rica	Blake & Loiselle (2002)
	Neotropical frugivores		Costa Rica	Boyle, Conway & Bronstein (2011 <i>a</i>); Chaves-Campos (2004); Levey (1988); Loiselle & Blake (1991)
	Multiple species		Nicaragua	Fraser, Kyser & Ratcliffe (2008)
	Multiple species		Argentina	Capllonch, Ortiz & Soria (2007)
	Multiple species		Venezuela	Beebe (1947)
	Multiple species		Puna, Peru	Hughes (1984); Pearson & Plenge (1974); Roe & Rees (1979)
	Multiple species		Peru	O'Neill & Parker III (1978)
	Multiple species		Chile	Newsome <i>et al.</i> (2015)
	Multiple species		Ecuador	Hardesty & Fraser (2010)
	Hummingbirds		Ecuador	Hobson <i>et al.</i> (2003)
	Multiple species		Colombia	Hilty (1997)
	Multiple species		Colombia	Strewe & Navarro (2003)
	Multiple species		Brazil	Alves (2007)
	Multiple species		Southern Brazil	Bencke & Kindel (1999)
	Multiple species		Argentina	Rivera & Roman (2016)
	Multiple species		Spain	De la Hera <i>et al.</i> (2014)
	Multiple species		Tanzania	Werema & Howell (2016); Werema, Howell & Ndangalasi (2016)
	Multiple species		Africa	Burgess & Mingwa (2000)
	Multiple species		Southern Africa	Brooke (1994)
	Multiple species		South Africa	Johnson & Maclean (1994)
	Multiple species		South Africa	Berruti, Harrison & Navarro (1994)
	Multiple species		South Africa	Brooke (1994)
	Multiple species		South Africa	Brown (2006)
	Frugivores		Borneo, Malaysia	Kimura, Yumoto & Kikuzawa (2001)
	Multiple species		Taiwan	Chang <i>et al.</i> (2011); Ryan (2012); Wu (2008)
	Honeyeaters		Australia	Keast (1968)
	Multiple species		Snowy Mountains, Australia	Osborne & Green (1992)
	Multiple species		Australo-Papuan region	Dingle (2004)
	Neotropical raptors		Central and South America	Bildstein (2004)
	Multiple species		North America	Boyle (2017)
	Multiple species		Worldwide	Barçante <i>et al.</i> (2017)

Table 1. Continued

Taxonomic group	Species	Common name	Location	References
Insects	<i>Gonepteryx rhamni</i>	Brimstone	Spain	Gutiérrez & Wilson (2014)
	<i>Vanessa atalanta</i>	Red admiral butterfly	Spain	Stefănescu (2001)
	<i>Danaus erippus</i>	Southern monarch butterfly	Bolivia & Argentina	Slager & Malcolm (2015)
	<i>Euphilotes enoptes</i>	Pacific dotted blue	Washington, USA	Peterson (1997)
	Multiple butterfly species		California, USA	Shapiro (1973)
Reptiles	Multiple butterfly species		Costa Rica	Haber & Stevenson (2004); Henderson (2010)
	Multiple moth species		Costa Rica	Janzen (1987, 1988, 1993)
	Multiple wasp species		Costa Rica	Hunt, Brodie & Carithers (1999)
	<i>Agelais</i> wasps		Costa Rica	Hunt <i>et al.</i> (2001)
	Wasps and butterflies		Worldwide	Alcock & Dodson (2008)
	<i>Chelonoidis nigra</i>	Galapagos tortoise	Galapagos	Blake <i>et al.</i> (2013); Yackulic, Blake & Bastille-Rousseau (2017)
	Multiple <i>Chelonoidis</i> species		Galapagos	Bastille-Rousseau <i>et al.</i> (2016)
	<i>Crotalus oreganus</i>	Western rattlesnake	British Columbia, Canada	Gomez, Larsen & Gregory (2015)

[Correction added on 14 August 2018, after first online publication: In Table 1, under Bird Taxonomic group, Mexico has been added in location column and align the reference of Solorzano *et al.* (2000).]

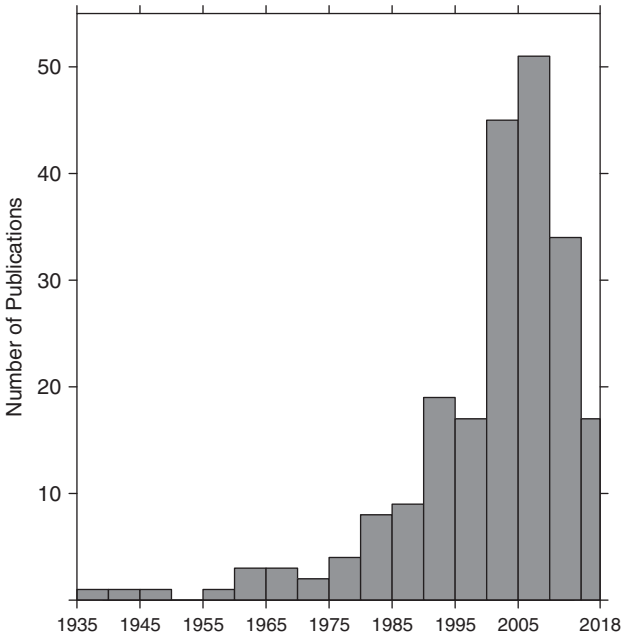


Fig. 1. Number of publications on animal altitudinal migration arranged by year of publication.

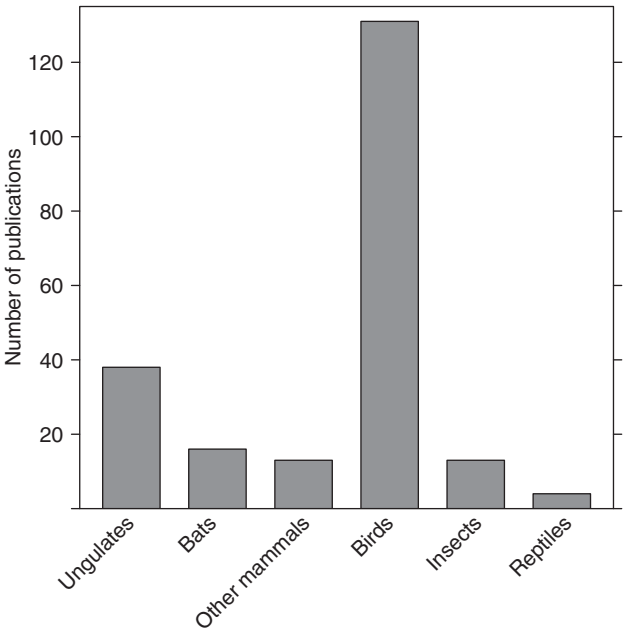


Fig. 2. Number of publications on animal altitudinal migration arranged by taxon.

advantage of higher forage availability in the latter during the breeding season (Festa-Bianchet, 1988). Sika deer (*Cervus nippon* Temminck 1838) in Japan are another altitudinal migrant that track forage (i.e. bamboo grass) availability downslope during the winter (Takatsuki *et al.*, 2000; Igota *et al.*, 2004).

Although food quantity is often used to explain altitudinal migration, forage quality may be equally important.

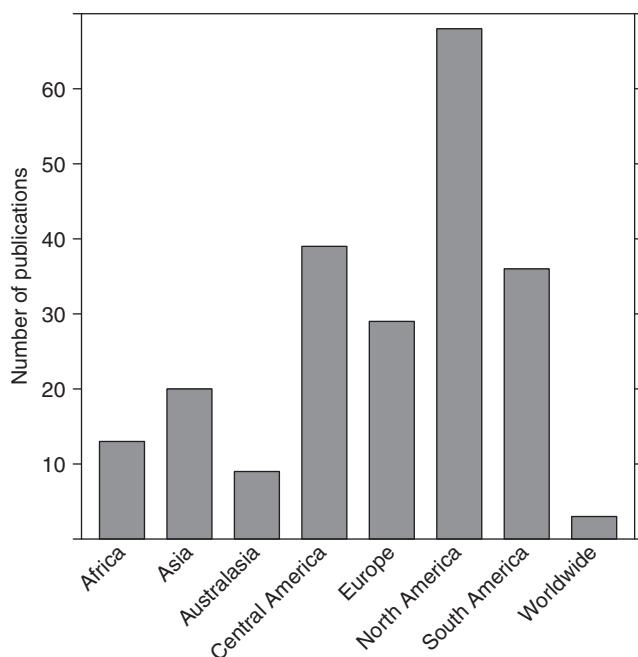


Fig. 3. Number of publications on animal altitudinal migration arranged by geographic area.

The Forage Maturation Hypothesis states that altitudinal migration of certain ungulates is driven by selection of younger vegetation with intermediate biomass that is of higher quality than more mature vegetation (Hebblewhite, Merrill & McDermid, 2008). Higher biomass in mature plants requires longer handling time and more effort to digest, thus the net energy intake for an animal decreases after plants reach an intermediate biomass (Hebblewhite *et al.*, 2008). One prediction of this hypothesis is that migratory individuals within a population will be able to track habitats with higher quality forage, or plants with intermediate biomass, better than resident individuals. In agreement with this prediction, migrant elk (*Cervus canadensis* Erxleben 1777) in the Canadian Rocky Mountains selected higher quality forage at both landscape and home-range scales, while residents selected vegetation with high biomass but low quality (Hebblewhite *et al.*, 2008). Female red deer (*Cervus elaphus* Linnaeus 1758) in Norway also migrated to higher elevation summer habitats when the vegetation there offered higher crude protein and migrated downslope to coastal habitats when the crude protein was higher there (Albon & Langvatn, 1992). Such tracking of seasonal variation in vegetation quality by ungulates often results in a phenomenon termed ‘surfing the green wave’ where individuals within a population employ different strategies for tracking peak vegetation quality (Fryxell & Avgar, 2012). For example, some individuals in a population of red deer in Norway moved to different locations seasonally following the ‘crest’ of the green wave where vegetation quality was highest, while other individuals moved ahead of the wave and arrived in anticipation of increase in availability of higher-quality forage (Fryxell & Avgar, 2012).

Food-limitation hypotheses have also found support in studies of tropical avian species, especially in frugivores and nectarivores whose food resources vary seasonally (Stiles, 1985, 1988; Levey, 1988; Blake & Loiselle, 1991; Solorzano *et al.*, 2000; Kimura *et al.*, 2001). Many of these studies examined changes in species diversity over elevation gradients over time and correlated them with seasonal changes in fruit abundance (Levey, 1988; Stiles, 1988; Blake & Loiselle, 1991). Several studies of birds in Costa Rica found evidence that the abundance of frugivorous birds tended to increase at higher elevations and decrease at lower elevations during the dry season (January–April), and exhibited the opposite pattern during the wet season (May–December) (Levey, 1988; Blake & Loiselle, 1991; Loiselle & Blake, 1991). This pattern coincided with the peak fruiting season of the plants that represent an important part of the diet of these species (Levey, 1988; Blake & Loiselle, 1991; Loiselle & Blake, 1991). However, in most of these studies, it remains unclear whether animals moved to elevations where they could locate relatively more food than at the elevations from which they departed. Seasonal variation in precipitation is similar along the whole elevational gradient, and the peak in fruit production is also similar along the same gradient (Loiselle & Blake, 1991). Thus, the role of food limitation in driving such movements is not clear.

Other support for the food-limitation hypothesis was found in several species of migratory bats. For example, the flowering of some columnar cactus species may shape the altitudinal migration of nectarivorous bats (Valiente-Banuet *et al.*, 1997). Furthermore, some insectivorous bats migrate to follow seasonal fluctuations of prey abundance at different elevations (McGuire & Boyle, 2013). Hawaiian hoary bats (*Lasiurus cinereus semotus* Allen 1890) migrate to higher elevations during the winter to coincide with an irruption in moth abundance (Menard, 2001). In insects, food availability explains altitudinal migration of certain butterfly species, such as the common brimstone (*Gonepteryx rhamni* Linnaeus 1758) in Spain where some individuals migrate downhill during the winter (Gutiérrez & Wilson, 2014). This downhill migration of the brimstone was best explained by the density of host plants along the elevational gradient; abundance of brimstone was highest at elevations with highest host plant density (Gutiérrez & Wilson, 2014).

Some tests of the food-limitation hypothesis suggest that food availability does not always shape altitudinal migration. A study of altitudinal migration of white-ruffed manakins (*Corapipo altera* Hellmayr 1906) in Costa Rica provided little evidence for the food-limitation hypothesis (Boyle, 2010). While the uphill migration of white-ruffed manakins coincided with peak fruiting season, neither fruit nor arthropod availability could explain downhill migration in this species (Boyle, 2010). Furthermore, a community-level study in Costa Rica revealed that both frugivores and insectivores migrated downhill during the wet season, suggesting that food availability is not the only driver behind altitudinal migration (Boyle, 2011). On the Island of Hawai‘i, changes in nectarivorous bird densities also did not track

seasonal variations in flowering density of ‘Ōhi’a (*Metrosideros polymorpha*) trees at mid and low elevations (Hart *et al.*, 2011). The lack of synchrony between bird and flower density (and hence nectar availability) could be a result of constrained bird movement during the breeding season, an increase in the availability of other species of flowering trees at the same time, or undesirable conditions at lower elevations, such as higher disease (e.g. avian malaria) prevalence (Hart *et al.*, 2011).

(b) Weather-driven hypotheses

Weather conditions can have both direct and indirect effects on altitudinal migrants. The direct effect of weather on altitudinal migration is largely due to physiological constraints on an animal's ability to cope with harsh weather. As temperatures drop, wind speeds increase, and exposure to precipitation increases, the energetic costs of maintaining optimal body temperatures increase in endothermic animals. Animals have some options to minimize these costs behaviourally or physiologically, including increasing energetic (food) intake or moving to a location with more tolerable weather. By contrast, for animals that are dormant during the non-breeding season (e.g. certain insects and bats), it may be better to migrate to a cooler elevation to reduce metabolic costs (Hunt *et al.*, 2001; Neubaum, O'Shea & Wilson (2006). Weather can also impact migration indirectly by affecting food supply. For example, in certain montane ungulate species at elevations receiving snowfall, lack of access to forage due to snow accumulation may explain why they migrate downslope during the winter (Takatsuki *et al.*, 2000; Parrini *et al.*, 2003). Additionally, the availability of above-ground vegetation will depend on the initiation and duration of the growing season, which are also affected by precipitation and temperature.

In birds, several species choose to migrate downhill to avoid harsh weather at higher elevations during part of the year. For example, tropical storms were proposed as a driver of downhill migration of white-ruffed manakins in Costa Rica (Boyle *et al.*, 2010). Further study at the community level revealed that the counts of known altitudinal migrants in Costa Rican lowlands during the wet season were positively correlated with the amount and severity of rainfall on the Atlantic slope (Boyle, 2011). In other words, increase in rainfall at higher elevations appeared to cause individuals to migrate to lower elevations. Downhill migrations driven by severe weather events at high elevations are sometimes short-term, only lasting a few days, and animals frequently make such short-duration movements. For example, birds in the Peruvian Andes (O'Neill & Parker, 1978) and white-crowned sparrows (*Zonotrichia leucophrys* Forster 1772) in the Sierra Nevada mountain range in the USA (Hahn *et al.*, 2004) responded to snow storms at high elevations by moving downhill to avoid the bad weather before returning to high elevations a few days later.

Snow cover drives altitudinal migration in many ungulate species, including roe deer (*Capreolus capreolus* Linnaeus 1758) (Mysterud, 1999; Ramanzin *et al.*, 2007), sika deer (Igota *et al.*,

2004), ibex (*Capra ibex* Linnaeus 1758) (Parrini *et al.*, 2003), and mule deer (*Odocoileus hemionus* Rafinesque 1817) (Sawyer *et al.*, 2005). The sika deer population in Japan consists of both upslope and downslope migrants during the winter (Igota *et al.*, 2004). Upslope migration during the winter is unusual and has not been documented in other cervids (Igota *et al.*, 2004). One explanation for this behaviour is that there is more coniferous cover at higher elevations during the winter, creating shelter from harsh weather elements and predators (Igota *et al.*, 2004). Furthermore, regardless of upslope or downslope migration, individuals selected winter home ranges within habitats that had less winter snow cover than their summer home ranges (Takatsuki *et al.*, 2000; Igota *et al.*, 2004).

Changes in temperature, both at high and low elevations, can also cause animals to migrate altitudinally. For example, although the downhill migration of giant pandas (*Ailuropoda melanoleuca* David 1869) in China appeared to be driven by availability of their preferred bamboo species, upslope migration during the spring and summer could be explained by the higher temperature at low elevations (Liu *et al.*, 2015). Migration due to heat stress has also been observed in an ibex population in Italy that migrated upslope during the summer in response to increased temperature in lower elevation habitats (Aublet *et al.*, 2009). Evidence of heat intolerance was demonstrated by individuals decreasing their feeding time during the day as temperature increased during the summer (Aublet *et al.*, 2009). In birds, American dippers (*Cinclus mexicanus* Swainson 1827) in Canada migrated from higher elevation breeding sites to lower elevation wintering sites, thereby avoiding cold stress (Morrissey *et al.*, 2004), although a decrease in food resources in high-elevation tributaries during the winter could be another explanation for downstream migration in this species (Morrissey *et al.*, 2004).

(c) Predation-risk hypotheses

The level of predation risk for animals can vary along both latitudinal and elevational gradients (Skutch, 1985; Martin, 2015). The needs of an animal differ between the breeding and non-breeding season, and in order to maximize fitness, it will benefit an individual to select an area for breeding with fewer predators of their nests or young. Therefore, if predation risk differs along an elevational gradient, animals may move to the elevation with lowest predation risk to breed, provided that the trade-off between predation risk and other factors such as food availability favour migration. Predation risk drives altitudinal migration in ungulates such as bighorn sheep in the Canadian Rockies. During the spring, pregnant ewes migrated upslope earlier than non-pregnant ewes to give birth to their lambs where the terrain provided more protection of young from predators, even though the forage quality was better at lower elevations (Festa-Bianchet, 1988).

In birds, the relationship between nest-predation rates and elevation is unclear. In the tropics, nest-predation rates have been observed to decline with elevation (Skutch, 1985). The

underlying mechanism is thought to be lower species richness and abundance of predators at higher elevations. Therefore, it may be advantageous in terms of nest success for birds to breed at higher elevations. However, other studies found no effect of elevation on nest predation (Badyaev & Ghalambor, 2001). Furthermore, artificial-nest-predation experiments have revealed more complex patterns. There was a negative relationship between artificial-bird-nest predation rate and elevation on the Atlantic slopes of Costa Rica, but the highest rates of artificial-nest predation occurred at middle elevations where many altitudinal migrants breed (Boyle, 2008a). In Cameroon, although survival of artificial cup-shaped nests placed in shrubs decreased at high elevation, there was no relationship between elevation and predation risk for nests placed about 10 cm above ground or nests placed directly on the ground (Djomo Nana *et al.*, 2015).

Predation risks for adults can also drive altitudinal migration. By moving to higher-elevation summer ranges, migrant elk in Banff National Park reduced their summer predation risk by 70% compared to resident individuals remaining at lower elevations (Hebblewhite & Merrill, 2007). However, migrant elk were also exposed to higher wolf predation risk during migration, thus facing a trade-off between decreased predation risk in their higher-elevation summer ranges and increased predation risk during migration (Hebblewhite & Merrill, 2007). Clearly, while predation risk could motivate animals to migrate, it could also be a cost of migration and select for sedentary behaviour.

(d) Synergistic factors affecting altitudinal migration

Multiple ecological processes often act in concert to influence altitudinal migration. One classic example is in the seasonal migration of many lepidopteran species to and from the dry forests of Guanacaste Province, Costa Rica. In these forests, the hot, dry conditions combined with a lack of food during the dry season make them inhospitable, and approximately 3100 lepidopteran species have evolved a variety of behaviours to adapt to these unfavourable conditions (Janzen, 1987, 1988, 1993). Many species spend the majority of the year in cooler, moister, higher elevation rainforests. Adults migrate to the lower elevation dry forests at the onset of the wet season, with the primary cue being a decrease in temperature at high elevations. The dry forest changes from largely brown and leafless (many tree species are deciduous) to green and fully leafed within a few weeks, providing ample food for newly emerged caterpillars. However, although the rainy season can last up to 6 months, and new vegetation continues to appear throughout this period, most of these species complete their reproduction within approximately 1–3 months, when vegetation is nearing its peak and the weather is still relatively cool and humid. Predators and parasitoids are also at their lowest annual abundance at the onset of the rainy season (Janzen, 1988, 1993). Their pronounced functional response but delayed numerical response to increased numbers of caterpillars is such that only the first half of the rainy season is optimal for reproduction by butterflies and moths. Thus, the

seasonality of reproduction interacting with weather-induced changes in food quantity (and perhaps quality) and predation risk likely all act together to determine patterns of altitudinal migration in these lepidopteran species.

Not surprisingly, predators of Lepidoptera exhibit some of the same patterns in the Guanacaste dry forests. Social wasps of the genera *Polistes* and *Mischocyttarus* migrated to high elevations during the dry season when food availability decreased in the lowlands; the colder temperature at high elevations providing an ideal climate for the wasps to become dormant (Hunt *et al.*, 1999). At the start of the rainy season, the wasps return to low elevations to reproduce.

(2) Intrinsic factors affecting altitudinal migration decisions

Individual traits can interact with extrinsic (environmental) factors to influence migratory propensity. The trade-offs migratory animals make differ among individuals with different traits, which can lead to differentiation in migratory strategies. In many cases, this results in partial migration, in which a population includes both migratory and resident individuals or differential migration which involves differences in migration distance among individuals (Ketterson & Nolan, 1979; Jahn *et al.*, 2010; Belthoff & Gauthreaux, 2013; Perez *et al.*, 2014). Ketterson & Nolan (1976, 1979) proposed three hypotheses to explain differential migration in dark-eyed juncos (*Junco hyemalis* Linnaeus 1758) based on individual-level traits: the 'body-size', 'dominance', and 'arrival-time' hypotheses. While these hypotheses have been tested for many long-distance migrants, little is known about their application to altitudinal migratory species (but see Lundberg, 1985; Boyle, 2008b; Jahn *et al.*, 2010; Norbu *et al.*, 2013).

(a) Body-size hypothesis

Variation in animal size results in differences in metabolic rates and energetic requirements (Lasiewski & Dawson, 1967; Nagy, 2005; White & Seymour, 2005). Weather will also affect individuals of different sizes differently. For example, a decrease in ambient temperature could be compensated by either reducing heat loss or increasing food intake. In general, larger individuals are better able to maintain body temperature than small individuals at low temperatures, primarily due to the difference in their mass to surface area ratio. Further, body size could affect an animal's ability to survive periods of fasting when food abundance is low. Thus, the body-size hypothesis posits that larger individuals are better able to withstand more severe weather and lower food abundance at higher altitudes than smaller individuals, and thus are predicted to have shorter migrations from higher-altitude breeding grounds (Ketterson & Nolan, 1976). Note that the energetic and metabolic requirements of endotherms differ from those of ectotherms, and thus the predictions of the body-size hypothesis may only apply to endotherms.

The body-size hypothesis has received equivocal support in altitudinal migration studies. In birds, larger individuals of yellow-eyed juncos (*Junco phaeonotus* Wagler 1831) in the mountains of Arizona were less likely to migrate compared to smaller individuals, regardless of sex (Lundblad, 2014). A similar pattern was observed in Carolina juncos (*Junco hyemalis carolinensis* Brewster 1886) in the southern Appalachians in the USA. However, female Carolina juncos are typically smaller than males; thus, the observed pattern could also be explained by sexually differentiated migratory strategies (Rabenold & Rabenold, 1985). Body size also failed to explain partial migration of a population of satyr tragopan (*Tragopan satyra* Linnaeus 1758) in the Himalayan mountains (Norbu *et al.*, 2013).

Physiological constraints associated with body size were related to individual migratory propensity of Galapagos tortoises. However, the migration patterns were opposite to those predicted based on capacity to tolerate cold temperatures and low food availability. Specifically, larger individuals moved longer distances than smaller individuals, consistent with the food-limitation hypotheses discussed in Section III.1a (Blake *et al.*, 2013; Bastille-Rousseau *et al.*, 2016). Thus, at least for these large-bodied ectotherms, the cost of a reduced food intake by remaining when food production is low outweighs the energetic cost of moving (Yackulic *et al.*, 2017).

The body-size hypothesis also includes the ability of an animal to maintain a positive energy balance during long periods of fasting when weather conditions do not allow frequent foraging. Boyle *et al.* (2010) proposed the 'limited foraging opportunities hypothesis' which posits that an increase in harsh climatic elements (e.g. precipitation) could lead to fewer opportunities for animals to forage, meaning that smaller individuals in a population would need to migrate to an elevation with more tolerable weather because they cannot withstand long periods of starvation (Boyle, 2008b). For example, white-ruffed manakins in Costa Rica exhibit partially migratory patterns where both migrants and residents bred at higher elevation sites, but migrants move downslope to the non-breeding grounds after the breeding season. Smaller individuals were more likely to migrate downhill during the wet season compared to larger individuals, and downhill migration of the manakins coincided with tropical storms in Costa Rica. As a result, there was a dramatic increase in manakins and other altitudinal migrants captured at lower elevation site following a storm (Boyle *et al.*, 2010). Birds remaining at higher elevations during the storm had higher circulating levels of the stress indicators corticosterone and β -hydroxybutyrate compared to birds that migrated downhill, indicating that higher-elevation residents did indeed fast during storms (Boyle *et al.*, 2010). This implies that smaller individuals may not have the metabolic capacity to endure the stress of harsh weather and decrease in foraging opportunities at higher altitudes during the non-breeding season and hence migrate to better conditions downhill.

(b) Dominance hypothesis

Habitat quality may vary along an elevational gradient, and competition for high-quality habitat could represent another driver of partial altitudinal migration: competition could drive subdominant individuals out of the best habitat occupied by dominant individuals. Thus, the dominance hypothesis posits that subdominant individuals are more likely to migrate between breeding and non-breeding grounds compared to dominant individuals due to competitive exclusion from high-quality habitats (Ketterson & Nolan, 1979). Habitat quality includes several factors: food availability, predation risk, and availability of nesting sites. Thus, it is important to identify the resources for which individuals within a population compete in order to establish the underlying ecological processes that force subdominant individuals out of high-quality habitat.

An example of social dominance and competition explaining partial migration is in American dipper in southeast British Columbia where migrants and residents overwintered together at low elevation, but migrants moved to higher elevation sites during the breeding season while residents remained at low elevations (Morrissey, 2004; Gillis *et al.*, 2008). Migrants of this partially migratory population had lower reproductive success than residents, implying that migrants were prevented from using the best breeding habitats due to competitive exclusion (Gillis *et al.*, 2008; Mackas *et al.*, 2010; Green *et al.*, 2015). High-elevation rivers in this area did not provide good breeding sites for the dippers during the summer because the snow/ice melt occurred later compared to low elevations, resulting in lower food abundance and a shorter breeding season. By contrast, low-elevation streams provided higher food quantity and quality to support breeding.

Like dippers, many montane ungulate species are partial altitudinal migrants where migrants and residents share a low-elevation wintering range, but migrants move upslope to their summer range to breed (Parrini *et al.*, 2003; Ramanzin *et al.*, 2007; Hebblewhite *et al.*, 2008; Hebblewhite & Merrill, 2011). The roe deer population in southern Norway exhibit this migratory pattern; migrants that move to higher-elevation summer grounds have larger home ranges compared to residents that stay at low elevations. Dominance may explain this pattern, as an increase in home-range size is often linked to decline in habitat quality. Consistent with this idea, higher-elevation summer grounds were of poorer quality compared to lower-elevation habitats, and individuals that migrated upslope were subdominants forced out of quality summer habitat (Myserud, 1999).

Daubenton's bats (*Myotis daubentonii* Kuhl 1817) in Europe have sex-differentiated roost sites in their summer habitat (Encarnação *et al.*, 2005). The nursery roosts of females are typically located at lower elevation compared to male roosts. The landscape surrounding these roosts differed between males and females; females roosted at sites with higher temperature, lower precipitation, and a greater foraging area (Encarnação *et al.*, 2005). Female Daubenton's bats may defend roosting sites with more forage availability, forcing

males to establish roost sites at higher elevations during the summer (Encarnação *et al.*, 2005). This hypothesis was consistent with the results of another study of sex-segregation of Daubenton's bats in Italy, where the body condition of males at low elevations during the summer was higher than the body condition of males at high elevations (Russo, 2002). This suggests that males that spent the summer at low elevations had access to better foraging compared to those at high elevations and that high-elevation habitats were occupied by individuals of lower competitive ability.

(c) *Arrival-time hypothesis*

The arrival time hypothesis posits that the sex that defends spatial resources for breeding will remain at or close to the breeding grounds during the non-breeding season because it will enable them to occupy better territories during the following breeding season (Ketterson & Nolan, 1976). Arriving earlier at the breeding grounds allows individuals to access breeding territories of higher quality compared to their late-arriving counterparts. As a result, early-arriving individuals will have better success at attracting and securing a mate.

Studies supporting the arrival-time hypothesis include the Carolina junco (*Junco hyemalis carolinensis* Brewster 1886), a subspecies of the dark-eyed junco, in North Carolina where males remain closer to the breeding grounds at higher elevations and females generally migrate further downslope during the winter (Rabenold & Rabenold, 1985). Columbian sharp-tailed grouse (*Tympanuchus phasianellus columbianus* Ord 1815) in Colorado perform altitudinal migrations between their summer and winter home ranges, with males migrating later from their lekking sites in the autumn and arriving earlier during the spring compared to females (Boisvert *et al.*, 2005). The arrival-time hypothesis has also been used to explain sex-biased partial migration in bats in temperate regions where females usually occur at lower elevations than males during the summer (McGuire & Boyle, 2013). Several bat species mate at higher elevations during hibernation, with the males that remain at these sites during the summer having a better chance of gaining priority access to females the following season (McGuire & Boyle, 2013). Conversely, female bats benefit from migrating downslope after mating at higher-elevation hibernacula because the lower temperatures and reduced food availability at high elevations do not provide enough resources for rearing young. Remaining at higher elevations during the summer would require females to go into torpor to reduce energetic costs which is detrimental to foetal development. By migrating downslope during the summer, females would not need to go into torpor to conserve energy because the temperature and food availability are generally higher (McGuire & Boyle, 2013).

Some studies provide only partial support for the arrival-time hypothesis. For example, female satyr tragopan in the Himalayas are more likely to migrate from higher-elevation summer to lower-elevation winter grounds compared to males, consistent with prediction of the arrival-time hypothesis. However, there was no difference

in the distances travelled between male and female migrants which is inconsistent with the prediction that females travel further during migration because they do not need to stay close to breeding territories (Norbu *et al.*, 2013). Further, the arrival-time hypothesis predicts that, by remaining close to the breeding ground, males are more likely to secure higher quality breeding territories and achieve higher reproductive success. However, this prediction was not supported by movements of yellow-eyed juncos in Arizona; even though females were more likely to migrate compared to males, the males that migrated further during the non-breeding season had higher nesting success, higher nestling growth rate, and higher clutch size during the breeding season (Lundblad, 2014).

IV. EMERGENT PATTERNS AND KNOWLEDGE GAPS

(1) *Biases in studies of altitudinal migration*

Our literature review revealed several important patterns in studies conducted on animal altitudinal migration. First, most studies were conducted in the Americas; few were conducted in Asia, Africa, or Australia. In temperate regions, most of the studies on altitudinal migration focused on ungulates and birds. In the tropics, most studies were conducted on birds and some on bats. The focus on ungulates may be partly due to their relationship with humans in terms of hunting and potential conflict (e.g. road collisions; Sawyer, Lebeau & Hart, 2012). The dominance of research on altitudinal migration of birds could be due to a higher proportion of migratory species within this group, or a strong history of research on bird migration in general. Our review revealed very few studies on altitudinal migration of ectotherms, such as amphibians, reptiles, and insects. Amphibians are not generally known for their migratory behaviour as their movements are typically restricted to ephemeral ponds and wetlands over short distances (<1 km) (Semlitsch & Bodie, 2003). However, the seasonal movements of certain salamander species suggest that they may be altitudinal migrants (Taguchi & Natuhara, 2009; Woolbright & Martin, 2014). There is some evidence for altitudinal migration in one species of terrestrial tortoise (Blake *et al.*, 2013; Bastille-Rousseau *et al.*, 2016) and our survey of the literature found only one study of altitudinal migration of snakes between winter hibernacula and summer habitats (Gomez *et al.*, 2015).

Studies on altitudinal migration are often focused on frugivorous birds (Chaves-Campos, 2003; Chaves-Campos *et al.*, 2003; Boyle, 2008b; Powell & Bjork, 2010), nectarivorous birds and bats (Valiente-Banuet *et al.*, 1997; Hobson *et al.*, 2003; Hardesty & Fraser, 2010), and herbivores (i.e. ungulates, Takatsuki *et al.*, 2000; Poole & Mowat, 2005; Sawyer *et al.*, 2005; Rice, 2008). More recent studies have found that most, if not all, feeding guilds contain species that engage in altitudinal migration (Bonaccorso *et al.*, 2009;

Mackas *et al.*, 2010; Boyle, 2011, 2017). For example, our review found few examples of altitudinal migration in carnivorous predators (but see Logan & Irwin, 1985). However, some carnivorous species such as mountain lions (*Puma concolor* Linnaeus 1771) are known to track the seasonal movements of their prey (Pierce *et al.*, 1999) and if their prey (e.g. ungulates) are altitudinal migrants, it is likely that such predators would also exhibit altitudinal migratory behaviour. The scarcity of empirical evidence of altitudinal migration in some feeding guilds could be a result of insufficient research focused on those taxa or authors of movement studies not framing their research in the context of altitudinal migration.

Most studies on altitudinal migration simply documented the behaviour and did not test extrinsic or intrinsic hypotheses of migration, especially with regards to individual migratory propensity as a result of fitness trade-offs. Of the studies that did test such hypotheses, most focused on only one driver of migration. Studies that simultaneously examine the validity of multiple hypotheses to explain altitudinal migration are rare (but see Boyle, 2008b; Gillis *et al.*, 2008; Mackas *et al.*, 2010; Norbu *et al.*, 2013; Lundblad, 2014). More studies testing multiple competing hypotheses for altitudinal migration drivers are needed to provide a more complete view of the trade-offs associated with different migratory strategies in a diversity of taxa and ecological contexts.

(2) Complexity of altitudinal migration

Long-distance migrations are often obligatory and complete, meaning that individuals retain migratory strategies from year to year, and usually the entire population migrates seasonally every year. By contrast, most cases of altitudinal migration are partial and facultative, so an individual's decision to migrate may differ from year to year depending on environmental conditions (Boyle, 2017). The drivers for uphill migration often differ from those of downhill migration, and they also differ among taxa because of differences in seasonal requirements. For ungulates and birds in temperate regions, uphill migration is often driven by the availability and quality of food resources and reduced predation risk at higher elevations during the spring and summer (Festa-Bianchet, 1988; Albon & Langvatn, 1992; Garwood *et al.*, 2009), while downhill migration is often driven by cold temperature and precipitation, especially snow (O'Neill & Parker, 1978; Parrini *et al.*, 2003). By contrast, several bat species in temperate regions migrate uphill during the autumn and winter because conditions at higher elevations are more suitable for hibernation and migrate downhill for breeding and rearing young (Esbérard *et al.*, 2011; Voigt *et al.*, 2014). Warm temperatures at low elevations during the summer may also drive uphill migration of animals in temperate regions because of desiccation of forage vegetation and heat stress (Aublet *et al.*, 2009). In the tropics, the timing of migration coincides with the transition between wet and dry seasons. During the dry season, the better quality of food resources at higher elevations drives upslope migration. Tropical storms may explain both uphill

and downhill migration in some tropical altitudinal migrants. For birds, storms at high elevations during the wet season appear to drive downhill migration (Boyle *et al.*, 2010), whereas storms in the lowlands drive uphill migration in certain bat species post-breeding (Bonaccorso *et al.*, 2009). Insects depend heavily on host plants during breeding, and studies have demonstrated that both uphill and downhill migration of several wasps and butterflies follows closely the availability of habitat and food resources such as density of host plants (Hunt *et al.*, 1999; Gutiérrez & Wilson, 2014).

While some partial migration hypotheses may explain this phenomenon in altitudinal migration of some species, considering the characteristics of individuals, such as body size, sex, and dominance rank, may not provide sufficient information to identify the underlying ecological processes because it can be difficult to disentangle the predictions of non-mutually exclusive hypotheses. For example, female roe deer in Norway typically migrate further upslope during the summer compared to males (Mysterud, 1999) but it is unclear whether the dominance or arrival-time hypothesis explains this best. Males of these populations are more dominant than females and could drive them out of quality summer habitat, consistent with the dominance hypothesis. However, the sedentary strategy of males could also be consistent with the arrival-time hypothesis. We could tease apart drivers for altitudinal migration by examining trade-offs between different migratory strategies. For example, by examining the benefits of staying at the breeding ground year-round for large individuals and the costs associated with harsher weather and reduced food availability during the non-breeding season, researchers could better understand the mechanisms by which body size affect migratory propensity.

V. CONSERVATION OF ALTITUDINAL MIGRATION SYSTEMS

Most altitudinal migratory behaviour is partial and facultative. Thus, altitudinal migrants are likely to be very responsive to environmental changes and can adapt their behaviour within a short period of time. As such, they could be important ecological indicators in today's rapidly changing environment. However, the degree to which recent environmental changes have impacted altitudinal migrants is largely unknown. Many studies have alluded to the potential negative impact of forest fragmentation on altitudinal migrants, especially in the tropics (Chaves-Campos *et al.*, 2003; Powell & Bjork, 2004, 2010). For example, three-wattled bellbirds (*Procnias tricarunculatus* J. Verreaux & E. Verreaux 1853) migrate between mid-elevation breeding areas in Costa Rica and non-breeding areas in Costa Rica and Nicaragua lowlands, relying on food resources provided by forested habitats in both areas. Recently, both montane and lowland rainforests within their range have experienced heavy deforestation outside of protected areas, leaving highly fragmented habitats for the bellbirds during all stages of their

annual cycle (Powell & Bjork, 2004; Papeş *et al.*, 2012). Rapid changes in human-modified landscapes may force altitudinal migrants to either alter their movement patterns or traverse areas where they are more susceptible to threats (Rappole, Ramos & Winker, 1989; Cohen & Lindell, 2004; Hadley & Betts, 2009). For example, ungulates in North America now face obstacles on their migration routes due to anthropogenic features such as fences and highways (Sawyer, Rodgers & Hart, 2016). Some Neotropical bird species have shown a reduced tendency to cross gaps between forest fragments, increased time to return to territory after relocation, and a higher tendency to stay close to remnant forests as distance between forest fragments increases (Hadley & Betts, 2009; Ibarra-Macias, Robinson & Gaines, 2011; Volpe *et al.*, 2014). Increased movement time could increase predation risk and decrease time for foraging, both of which could result in decreased survival.

In many regions of the world, native vegetation at low elevations has become highly degraded and fragmented due to urbanization and agriculture (Powell & Bjork, 2004; Bohrer *et al.*, 2014). Habitat conversion to agriculture can reduce food availability, increase predation risk, and increase human–wildlife conflict (Takatsuki *et al.*, 2000; Bohrer *et al.*, 2014). The ongoing encroachment of agricultural and residential developments near protected areas has resulted in conflicts such as when migrating deer and elephants damage crops through consumption and passage through croplands (Takatsuki *et al.*, 2000; Bohrer *et al.*, 2014). Increased anthropogenic activity at low elevations would also lead to a decrease in available breeding habitat, food resources, and nest sites for altitudinal migrants such as the Hawaiian hoary bat that breed at low elevations (Bonaccorso *et al.*, 2009). High-elevation habitats in certain parts of the world have also become increasingly threatened by anthropogenic development (Boyle & Martin, 2015). The loss of critical high-elevation habitats will have profound effects on altitudinal migrants depending on them for part of their annual cycle. For example, some Neotropical migratory birds perform a post-breeding upslope migration to moult, a time when they experience increased energetic costs and predation risk (Wiegardt *et al.*, 2017a,b).

Habitat fragmentation will result in smaller habitat patches potentially containing insufficient food and breeding habitat to sustain a viable population year-round. For example, nest success in wood thrush (*Hylocichla mustelina* Gmelin 1789) in North America was lower in small forest patches compared to contiguous forests due to higher nest predation (Hoover, Brittingham & Goodrich, 1995). A synthesis of studies on the relationship between population trends and associated habitat patch size demonstrated that the populations of migratory species generally declined less than resident species in response to smaller habitat patch size, indicating residents are less able to cope with decrease in habitat (Bender, Contreras & Fahrig, 1998). To our knowledge, no empirical study has examined how fragment size affects resource abundance and impacts altitudinal migratory behaviours of populations that depend on these fragments.

Altitudinal migratory species may respond differently to climate change compared to long-distance migrants. Because of their smaller range, changes in climate such as temperature could affect more or all of their year-round range. If they cannot adapt quickly enough, they could face dramatic range contraction, as has been observed in several sedentary species (Moritz *et al.*, 2008; Gibson *et al.*, 2010). Climate change could also have indirect effects on interactions between altitudinal migrants and residents. In Switzerland, red deer and alpine chamois (*Rupicapra rupicapra* Linnaeus 1758) occupy habitats at different elevations during most of the year except for summer when red deer migrate upslope to their breeding range where chamois also aggregate (Anderwald *et al.*, 2016). Interspecific competition between these two species has led to decreased offspring viability in chamois, which are outcompeted by red deer. Warmer temperatures in alpine regions could lead to longer growing seasons and thus attract a greater number of altitudinal migrants and further intensify interspecific competition. The observed downhill migration of birds in Costa Rica resulting from storms at high elevations provides another such example: not only did the number of altitudinal migrants increase in the lowlands but the number of individuals of resident species also increased, perhaps suggesting that some of these resident species also exhibit a partial migration strategy (Boyle, 2011). If the frequency or severity of tropical storms increases due to climate change, more individuals are likely to aggregate at low elevations in response, leading to increased competition (Webster *et al.*, 2005). By contrast, where climate change leads to increased drought in tropical regions (Karmalkar, Bradley & Diaz, 2011), a decrease in precipitation could result in reduced food resources at both low and high elevations, intensifying competition and potentially lowering survival of altitudinal migrants.

VI. FUTURE RESEARCH DIRECTIONS

Altitudinal migration offers a unique opportunity for advancing our mechanistic understanding of migration, yet relatively little attention has been paid to the potential impacts of rapid environmental change on altitudinal migratory behaviour. Below, we propose several research questions that future studies of altitudinal migration could use to gain a deeper understanding of the effects of environmental change on the behaviour of altitudinal migrants, as well as research tools and methods that can be used to answer these questions.

(1) How do changes in habitat composition and configuration within a landscape affect migratory behaviour?

To answer this question, we will require individual-level movement data which is currently lacking in studies of altitudinal migratory species. The lack of such data may be a result of the difficulty associated with conducting telemetry studies over elevational gradients, and thus most studies

have been conducted on species that are relatively easy to track with transmitters. Tracking individual migratory patterns in birds, for example, has been limited to species of larger body size, such as bare-necked umbrellabirds (*Cephalopterus glabricollis* Gould 1851) (Chaves-Campos *et al.*, 2003), resplendent quetzals (*Pharomachrus mocinno* De la Llave 1831) (Powell & Bjork, 2010), Hawaiian goose (*Branta sandvicensis* Vigors 1834) (Leopold & Hess, 2014), and satyr tragopan (Norbu *et al.*, 2013). Tracking movements of ungulates is also relatively easy because of their capacity to carry heavy radiocollars (Zweifel-Schielly *et al.*, 2009; Quyller *et al.*, 2013; Collins, 2016). However, recent advances in animal-movement-tracking technologies (e.g. GPS loggers and lightweight radio tags) now make tracking animals of smaller sizes attainable (Bridge *et al.*, 2011; Barçante *et al.*, 2017). Although telemetry may be the best option for studying individual movement behaviour, capture–mark–recapture methods are another viable option. However, thus far, most mark–mark–recapture studies have focused on seasonal changes in abundance along elevational gradients rather than individual movements, likely due to the difficulty of recapturing the same individuals at different elevations (Blake & Loiselle, 1991; McGuire & Boyle, 2013; Werema & Howell, 2016). Some researchers have used isotope analysis of fur or feather samples from birds and bats to detect altitudinal migration and this could be coupled with capture–mark–recapture methods (Fraser *et al.*, 2008; Erzberger *et al.*, 2011). While these methods can confirm the migratory status of individuals, they do not provide information regarding their shorter-term movement patterns.

Spatial and statistical modelling tools can be used to examine potential impacts of changes in landscape composition and configuration on altitudinal migratory populations. Spatial capture–recapture models have been developed to estimate landscape resistance coefficients and connectivity to understand how landscape composition affects animal movement (Royle *et al.*, 2013; Graves *et al.*, 2014; Fuller *et al.*, 2016). Similar methods could be applied to describe how habitat fragmentation influences movement patterns of altitudinal migrants in complex landscapes. However, the utility of these models will be contingent on a level of understanding of how altitudinal migrants move through the landscapes. Spatial capture–recapture models can be especially useful in analysing animal movement when telemetry is not possible. Research has demonstrated that, for elusive animals with large home ranges, spatial capture–recapture analyses of camera trap data can provide information regarding population size, density, and individual movement patterns (Sollmann *et al.*, 2011). Such methods could be useful in detecting altitudinal migratory behaviour of large carnivores that are difficult to study using other methods. Individual-based models (agent-based models) may also be useful. Recent advances in meta-population models linking the probability of colonization and extinction of habitat patches may also have applications in predicting the migratory propensity of altitudinal migrants (Howell *et al.*, 2018).

(2) How do migratory propensity and movement patterns affect population and meta-population dynamics?

To address this question, researchers should investigate how variation in migratory strategies affects individual survival and reproductive output, and the impacts of environmental changes on the population dynamics and viability of altitudinal migratory species. For example, in white-ruffed manakins, alpha (dominant) males typically have a higher reproductive success compared to beta males. In Costa Rica, males that migrate downslope after the breeding season decreased in lek status during the following breeding season and were less successful at attracting females (Boyle *et al.*, 2011*b*). Similarly, migrant American dippers in British Columbia had a lower reproductive success but higher survival compared to their resident counterparts (Gillis *et al.*, 2008), which combined to give the migrant strategy a lower lifetime reproductive success compared to residents. Combining studies of migration with population vital rates, such as survival and recruitment, would allow a better understanding of the mechanisms by which environmental changes influence population dynamics. Capture–mark–recapture data would allow us to document the migratory strategy, survival, and reproductive output of individuals to help illuminate fitness trade-offs and their consequences (Mackas *et al.*, 2010; Boyle *et al.*, 2011*b*). Modelling the relationship between individual fitness and migratory strategy while incorporating environmental and climatic variables could clarify the effects of habitat quality on an individual's decision to migrate and how this affects fitness (Hebblewhite & Merrill, 2011).

Field experiments coupled with observational studies may help to elucidate the mechanisms influencing individual migratory propensity. For example, in temperate regions, the provision of food supplements at higher elevations during winter (non-breeding season) could shed light on how animals balance the trade-off between enduring harsh weather and the benefit of additional food resources by remaining at higher altitude. Comparing the survival and recruitment of migrants and residents during the following breeding season would illuminate any carryover effect of the different migratory strategies. In one of the few examples of such manipulation, elk provided with supplemental food in winter in Wyoming travelled for shorter distances and arrived at summer ranges later compared to unfed elk (Jones *et al.*, 2014). Interestingly, supplemented elk did not follow the availability of quality forage as closely during migration, which could negatively impact their reproduction and survival during other parts of the year.

(3) What conservation practices could enhance the viability of altitudinal migrant populations?

To address this question, studies could examine the effects of different conservation and management strategies on altitudinal migrants. Altitudinal migrants that travel longer distances between breeding and non-breeding sites often

stop along their migration routes (Sawyer *et al.*, 2009; Sawyer & Kauffman, 2011; Leopold & Hess, 2014). Thus, the preservation of corridors between habitat patches is important for survival during migration (Chaves-Campos *et al.*, 2003; Powell & Bjork, 2004, 2010). Researchers should design their studies to inform conservation and make explicit recommendations for reserve and corridor designs to benefit not only altitudinal migrants, but also to preserve other forms of animal movement. When paired with post-implementation monitoring, such studies have great potential for concrete impacts on the persistence of altitudinal migratory populations within human-modified landscapes. For example, landscape-level conservation strategies to facilitate movements of altitudinal migratory ungulates by creating overpasses and underpasses on highways have resulted in frequent usage of these structures (Sawyer *et al.*, 2009; Sawyer & Kauffman, 2011). When combined with fencing, these underpasses reduced deer–vehicle collisions by 81% (Sawyer *et al.*, 2012).

VII. CONCLUSIONS

(1) Altitudinal migration exists in many species from diverse geographic areas and numerous taxonomic lineages, including mammals, birds, reptiles, and insects. With some notable exceptions, our knowledge of both the basic patterns as well as the underlying drivers of altitudinal migration is still extremely limited compared to research on long-distance migrants. Extrinsic causes of altitudinal migration include seasonal variation in food resources, weather, and predation risk. These external drivers frequently interact with intrinsic factors such as seasonality of requirements due to reproduction, differences in individual condition, and competitive asymmetries among individuals to produce flexible partial migration systems.

(2) The available literature is a biased towards certain taxa (birds and ungulates) and geographic regions (North America). In the species studied to date, drivers of uphill movements often differ from those of downhill movements. Additionally, the prevalence of partial migration implies that a combination of intrinsic and extrinsic drivers commonly shape migratory decisions at the individual level. Investigations of partial altitudinal migration patterns that focus on underlying mechanisms that lead to different individual responses to environmental factors could help elucidate how individual characteristics affect migratory propensity. However, detailed individual-level data are very scarce.

(3) Recent environmental changes, such as habitat fragmentation and climate change, could have profound effects on altitudinal migrants *via* multiple different pathways. Altitudinal migrants traverse multiple ecoregions that are under threat from anthropogenic development and climate change. Gaining an understanding of species-specific impacts is essential due to the dependency of altitudinal migrants on multiple regions over their annual cycle. Possible impacts of

habitat fragmentation and climate change on altitudinal migrants include reduction in food resources, barriers impeding movement, and changes in predation risk and competition.

(4) Altitudinal migration is often facultative and partial, offering a unique opportunity for researchers to examine factors that affect individual migratory propensity. Expanding our understanding of fitness trade-offs between migratory strategies and how they are reflected in the population dynamics of altitudinal migratory species could both help elucidate the mechanisms underpinning this behaviour and aid the development of strategies to protect species that are under threat from environmental change. Research methods including tracking devices, isotopic methods, and capture–mark–recapture or re-sighting methods should be combined with the development and application of spatial models to simulate animal movement across complex landscapes to allow us to target conservation efforts effectively. Population dynamics models should also be incorporated to estimate population vital rates over time to evaluate fitness consequences of different migratory strategies.

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