

Drivers of animal migration and implications in changing environments

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Received: 19 May 2016 / Accepted: 6 September 2016 / Published online: 16 September 2016
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Abstract Migratory species are widespread in terrestrial, aquatic and aerial environments, and are important both ecologically and economically. Since migration is an adaptive response to particular conditions, environmental changes (climate or otherwise) will potentially alter the selective pressures on movement behavior. Such changes may also interfere with, or disrupt, a species' ability to migrate. In either case, environmental changes could lead to the reduction or total loss of a migration, yet we have little understanding of when to expect these outcomes to occur. Here, I argue that an understanding of both the proximate and ultimate drivers of migration is needed if we are to predict the fate of migrations under changing environmental conditions. I review what is currently known about the drivers of animal migration, but show that we also need a more complete synthesis of migratory patterns across diverse ecosystems and taxonomic groups. The current understanding of migration indicates that (1) drivers of migration vary across species and ecosystems, and (2) a species' ability to adapt to environmental change successfully depends in part on its migration drivers. Together, these findings suggest a way forward for studying and generating predictions of how changing environmental conditions will differentially impact species by taxonomic group and geographic region of the world.

Keywords Climate change · El Niño-Southern Oscillation index · Evolution · Life history · Migration · Movement ecology · Partial migration

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Introduction

Migration, the round-trip, seasonal movement of organisms among two (or more) locations, is ubiquitous. Migratory species are found around the globe, in aquatic, terrestrial, and aerial environments, and across all major vertebrate (birds, fish, mammals, reptiles, amphibians), and many invertebrate lineages (Dingle 2014). Many species of importance to humans are migratory, including insect crop pests (Holland et al. 2006), fisheries species (Harden Jones 1968), and ungulates that compete with domestic livestock (Talbot and Talbot 1963). This relationship between migratory behavior and economic impact is due in part to the fact that migration often allows a population to reach higher numbers than would be possible in a sedentary population (Fryxell et al. 1988). Migrants also play an important role in many ecosystem processes: as they travel between locations migrants can transport nutrients, toxicants, propagules, pathogens and parasites, linking habitats that otherwise might not be connected (Bauer and Hoye 2014). Given these ties, loss of migratory behavior in a particular species could have ramifications for their broader ecological communities. This observation in turn suggests the importance of conserving migration as a phenomenon, beyond solely conserving the organisms that migrate (Wilcove and Wikelski 2008).

Migratory species are often viewed as highly susceptible to environmental change: climate shifts, habitat destruction, or barrier creation in any of the habitats migrants rely on could negatively impact them (Wilcove and Wikelski 2008). However, migrants can also be viewed as highly adaptable in the face of change: they are often extremely mobile and expected to track changes easily (Robinson et al. 2009). This apparent contradiction can be resolved in part by recognizing that whether migrants are viewed as susceptible or adaptable depends on the magnitude and pace of environmental change. Gradual shifts in climate conditions (e.g., Pulido and Berthold 2010) or resource availability (e.g., Satterfield et al. 2015) can select for altered migratory behavior. Consequences of these changes include shifted migration timing, altered migration frequency, or even in the extreme case, loss of migration. In contrast to gradual shifts, abrupt changes are likely to constrain the ability of species to migrate, and lead to failed migration (e.g., new physical barriers that disrupt migratory routes; Bolger et al. 2008).

Given the relative importance of migratory species and their susceptibility to change, it is essential that we are able to anticipate how migratory patterns are likely to shift in the future. However, in order to do this, we must understand which changes will select for altered migratory behavior, and which will constrain migration. This in turn requires an understanding of both which ecological factors ultimately favor migration as a strategy in particular species, as well as which proximate cues individuals use to guide their migration. Below, I review the current understanding of: (1) the ultimate drivers of migration both generally and in the case of partial migration, (2) the proximate drivers of migration, and (3) ecological and evolutionary consequences of environmental change. In particular I note that our knowledge of migration and its interactions with environmental change is extremely taxonomically and geographically biased, which currently restricts our ability to draw broad conclusions about the general implications of environmental change for migration.

Ultimate drivers: why migrate?

Debate over the causes of migratory movement predates the earliest systematic studies of migration, which started in the 1800s (Williams 1957; Harden Jones 1968). It was proposed as early as 1786 that migration enabled fish to avoid extreme temperature conditions

(Gilpin 1786). In contrast, it was initially believed that insect migration served as a ‘safety valve’ to remove excess individuals from the population (Southwood 1962). The adaptiveness of bird migration was debated as late as the 1950s when Lack (1954) cautiously claimed “It may, I think, be accepted that migration is a product of natural selection.” Currently, migration is primarily considered adaptive for most organisms. The exception is species inhabiting areas with strong directional currents (e.g., streams and oceans); in these cases environmental constraint is also thought to be important (e.g., Schneider and Lyons 1993; Luschi et al. 2003).

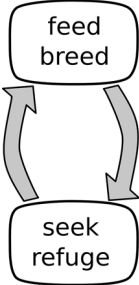
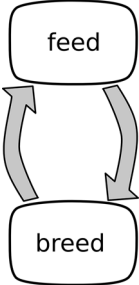
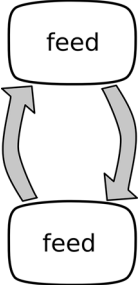
At a basic level, migration can be adaptive if it increases an organism’s growth, survival, or reproduction. Often movement in each migratory direction is driven by one of these three benefits, resulting in three forms of one-way movement described by Heape (1931) as “alimentary movement” (to increase access to food or water and aid growth or maintenance), “climatic movement” (to avoid unfavorable conditions, increasing survival), and “gametic movement” (to reproduce). Within the fish migration literature these types are often referred to as “feeding”, “wintering” and “spawning” movements, respectively (Nikolsky 1963; Lucas and Baras 2001). Not all species necessarily display all three types of movement; for example, in fish it is common for either the wintering and feeding grounds or the spawning and feeding grounds to coincide (Nikolsky 1963).

Throughout this review, I describe migration as falling into one of three types of round-trip movement: “refuge”, “breeding”, and “tracking” (Shaw 2012). These types build on the one-way drivers above to capture the common drivers for full round-trip migrations, which situates migration more explicitly within an organism’s life history cycle. Organisms with refuge migrations have one primary habitat (where they do most of their foraging and reproduction) that they migrate away from seasonally to seek refuge from temporarily unfavorable conditions (e.g., extreme abiotic or biotic factors such as temperature, precipitation, predation). In Heape’s terminology, this is effectively a “climatic” movement (although in my definition I also include non-climatic factors such as predators and parasites) in one direction and an “alimentary and gametic” movement in the other. Organisms with breeding migrations fundamentally rely on two different habitats: one where they forage and one where they breed, and migrate between these. This is equivalently a set of “alimentary” and “gametic” movements. Finally, organisms with tracking migrations typically do not have a primary location, but rather move continuously, following food resources (e.g., tracking vegetation gradients or migratory prey). This is a continuous “alimentary” movement. Categorizing migration in this way enables a focus on the factors driving the full migratory cycle and allows for a comparison of migration across distinct taxonomic groups. Although some species have aspects of more than one of these migration types, the majority of migrants fall into one of these three categories. Below I review migratory patterns by taxonomic group, using these terms (see Table 1 for summary).

Invertebrates

Insects are by far the most abundant of terrestrial migrants, yet, due to their size, they are less well studied than migratory vertebrates (Chapman et al. 2015). Bogong moths (*Agrotis infusa*) in Australia have refuge migrations: they breed along the coast, then migrate into the mountains to aestivate in caves over the hot summer (Common 1954). In the early fall, moths migrate back to the coast to breed. Other species, particular milkweed bugs and lady beetles (*Lygaeus equestris*, *L. kalmii*, *Coleomegilla maculata*) have round-trip migration to diapause sites during the winter months (Dingle 1996). The butterfly *Goneptyeryx rhamnii*

Table 1 Schematic of each round-trip migration pattern (refuge, breeding, tracking) and general trends based on current migration knowledge

	Refuge	Breeding	Tracking
Schematic			
Taxonomy	Insects, snakes, birds, bats, ungulates	Crustaceans, molluscs, amphibians, turtles, fish, whales [rare: birds]	Insects, sharks, ungulates, carnivores [absent: amphibians]
Geography	Temperate		Tropics
Habitat	Escape extreme temperature, rainfall, oxygen, predation, parasitoids	Aquatic/terrestrial gradient salinity gradient	Follow vegetation driven by rainfall follow migratory prey
Locomotion	Flying	Swimming, walking [rare: flying]	Swimming, walking

is one of the few insects for which the specific drivers of movement in each direction have been explicitly tested: uphill movements are driven by physiological constraints on temperature and downhill movements by food availability (Gutiérrez and Wilson 2014), supporting the idea of a refuge migration in this species. Climate is not the only factor driving refuge migrations; Stefanescu et al. (2012) suggest that painted lady butterflies (*Vanessa cardui*) migrate to escape parasitoids.

Although refuge migrations are the most common migration type in insects, some species display tracking or breeding migrations. Monarch butterflies (*Danaus plexippus*) migrate south and overwinter in Mexico then migrate slowly northward in the spring, tracking the availability of milkweed (Brower and Malcolm 1991). This process takes four generations and is a cross between a refuge and a tracking migration. Similarly, many armyworm moth species have latitudinal tracking/refuge migrations in North America, spending winters at low latitudes, then migrating northward in the spring, reinfesting cropping areas as vegetation becomes available (McNeil 1987; Westbrook et al. 2016). Many locust species have tracking migrations, moving in response to rainfall and changes in vegetation availability (Dingle 1996). Many grasshoppers have breeding migrations, moving between their oviposition and feeding habitats (Uvarov 1957). Some migratory dragonflies breed in temporary pond habitats (Southwood 1962), suggesting that these are potentially breeding migrations. One unique characteristic of insect round-trip migrations is that the majority occur across multiple generations. Unfortunately this had led to the few examples of single-generation insect migrations (e.g., bogong moths) to often be overlooked by summaries of migration (e.g., Holland et al. 2006).

There are a number of migratory groups within crustaceans. Both true land crabs (family Gecarcinidae) and land-dwelling hermit crabs (Coenobitidae) have breeding

migrations. Adults migrate seaward to reproduce seasonally (since larvae require high-salinity water to develop) and return inland for the rest of the year to decrease aggressive interactions (competition, cannibalism) and increase access to food (Wolcott and Wolcott 1985). In some species mating occurs prior to migration and only females migrate to the shore (e.g., *Gecarcoidea lalandii*, *Epigrapsus notatus*; Liu and Jeng 2005, 2007), while in other species, both females and males migrate and then mate at the shore (e.g., *Gecarcoidea natalis*, *Johngarthia lagostoma*; Hicks 1985; Hartnoll et al. 2006). Spiny lobsters display several migratory patterns (George 2005). In some species adults have breeding migrations and move from their main grounds to breeding sites, located either in shallow habitat (e.g., *Palinurus delagoae*) or in areas where the current will carry larvae to juvenile grounds (e.g., *Sagmariasus verreauxi*). Other species have refuge migrations: adults migrate seasonally to avoid winter storms (e.g., *Panulirus argus argus*) or to avoid oxygen depletion (e.g., *Jasus lalandii*). The copepod *Neocalanus plumchrus* has seasonal vertical breeding migrations: individuals are born around 250 m depth in winter and spring, then migrate to deeper water in late summer, before returning to shallower water to spawn the following year (Kobari and Ikeda 2001).

Of migratory molluscs, most marine species seem to have breeding migrations. Both the cuttlefish *Sepia officinalis* (Keller et al. 2014) and the squid *Loligo gahi* (Arkhipkin et al. 2004) migrate closer to shore to spawn, and then offshore during feeding and development. Squid species in both the North Pacific Ocean (*Todarodes pacificus*; Kawabata et al. 2006) and the Southwest Atlantic Ocean (*Illex argentinus*; Rodhouse et al. 1995) display latitudinal breeding migrations: individuals migrate pole-ward to feed and equator-ward to spawn. The bivalve *Macoma balthica* also has breeding migrations from tidal flats to higher nursery flats in spring, then back to the low intertidal in winter (Hiddink 2003). Migration is common in freshwater snails as well (Gorbach et al. 2012), although it is unclear what factors drive these movements. Food, predation, extreme climate, breeding, and a response to other constraints have all been proposed as drivers (Gorbach et al. 2012), but few have been explicitly tested. Furthermore, most studies pose an adaptive hypothesis for upstream movement while describing downstream movement as an artifact of the stream environment (e.g., Paulini 1963; Schneider and Lyons 1993).

Migratory species are found throughout other groups of invertebrates, although they are generally less systematically described than the above groups. Some arachnids like the spider *Haplodrassus dalmatensis* have breeding migrations, moving between habitat suitable for reproduction and habitat for development (Bonte et al. 2000). Although refuge migrations are more often described for temperate species, some tropical harvestmen also migrate to caves in winter (Chelini et al. 2011). Horseshoe crabs have breeding migrations: adults seasonally migrate from deeper water to shore in order to reproduce (Swan 2005). Although some copepods migrate seasonally (as mentioned above), daily vertical movements are much more common among marine invertebrates (typically referred to as ‘diel vertical migration’). These are not been described in detail here since the focus of this review is on seasonal migratory movements.

Amphibians and reptiles

Many amphibians have an aquatic larval stage and a terrestrial adult stage, so—according to the definition of migration used here—the majority of amphibians undergo breeding migrations as adults from terrestrial feeding grounds to aquatic breeding grounds (Russell et al. 2005). In many of these species, individuals migrate only every few years, each time they attempt reproduction (Bull and Shine 1979). Some amphibians have refuge migrations

from summer habitats where they feed and breed, to overwintering sites. For example, green frogs (*Rana clamitans*) migrate from summer breeding ponds to streams and other areas that do not freeze over the winter (Lamoureux and Madison 1999). Manitoba toads (*Anaxyrus* [previously *Bufo*] *hemiohryus*) overwinter in Mima mounds (Kelleher and Tester 1969) and the toad *Bufo bufo* overwinters either in holes or within the leaf layer (Sinsch 1988).

In contrast to amphibians, the majority of reptiles appear to be non-migratory. However, those that migrate do so for a variety of reasons: there are examples of refuge, breeding, and tracking migrations across reptiles. Female tuataras (*Sphenodon punctatus*) have breeding migrations, moving outside their forested home ranges to areas with higher temperatures that promote egg development (Moore et al. 2009). Most crocodylians nest within their home range but a few have breeding migrations to suitable nesting sites (e.g., *Crocodylus porosus*; Kay 2004). Other species have refuge migrations from swamps to permanent bodies of water in the dry season (e.g., *Caiman crocodilus crocodilus*; Ouboter and Nanhoe 1988).

Within Testudines (turtles) the most notable migrations are those of all seven sea turtle species: adults have breeding migrations between marine foraging areas and terrestrial nesting grounds (Luschi et al. 2003). A number of terrestrial (e.g., *Geochelone* spp.), freshwater (e.g., *Chelydra serpentina*, *Apalone spinifera*, *Podocnemis sextuberculata*) and estuarine (e.g., *Malaclemys terrapin*) turtle species also have breeding migrations (Southwood and Avens 2010). Other turtles have refuge migration to overwintering sites (e.g., *Chelydra serpentina*; Brown and Brooks 1994) or tracking migrations following seasonal shifts in food (e.g., *Chelonoidis nigra*; Blake et al. 2012).

Of migratory snakes, many temperate species (e.g., *Thamnophis sirtalis*, *Crotalus atrox*) have refuge migrations between summer areas and winter hibernacula whereas tropical species tend to having tracking migrations, driven by food and water availability instead of temperature (Russell et al. 2005; Southwood and Avens 2010). For example, water pythons (*Liasis fuscus*) track their prey, the dusky rat (*Rattus colletti*), from swamps to floodplains (Madsen and Shine 1996). Some snakes also have breeding migrations: gravid females move from summer foraging groups to thermally preferable nesting sites (Southwood and Avens 2010). Lizards are generally non-migratory, although a number of iguanas display breeding migrations (Werner 1983; Bock et al. 1985).

Fish

In general, fish migrations fall into three categories: diadromous migrations between fresh and salt water, potomadromous migrations within freshwater, and oceanodromous migrations within the ocean.

Diadromous migrations can be further split into three types: adults live and forage in salt water but migrate to spawn in fresh water (anadromy), adults live and forage in fresh water and migrate to spawn in salt water (catadromy), or movement between fresh and salt water that is not linked to breeding (amphidromy). Both anadromous and catadromous migrations are by definition breeding migrations, whereas amphidromous migrations are not. Anadromy (e.g., in lampreys, sturgeons, salmonids, osmerids, salangids, shads) is more common in temperate regions while catadromy (e.g., in eels, mullets) is more common in the tropics (McDowall 1987). This is thought to be due to the fact that in the tropics, freshwater productivity is higher (and so fish born in saltwater can increase their growth rate by migrating to feed in freshwater), and in the temperate zone, saltwater productivity is higher and anadromy is favored (Gross et al. 1988). In contrast, the motivations for amphidromous migrations are less commonly discussed (McDowall 2007)

and the reasons given are based on benefits of correlated life history traits (body size, dispersive ability) rather than on benefits of the timing of migration itself. However, the amphidromous migration of galaxiid fish in New Zealand seems to be a refuge migration, enabling individuals to seasonally escape parasites (Poulin et al. 2012).

Potomadromous fish migrations are often described as movements between three distinct habitats (instead of between two, as in many other migratory species): wintering, feeding, and spawning areas (Northcote 1978). However, there are still examples of species that move between two primary habitats. For example, cyprinids like the common roach (*Rutilus rutilus*) have refuge migrations, moving from lakes in the summer to streams in winter to avoid predation (Chapman et al. 2012). Arctic grayling (*Thymallus arcticus*) also have refuge migrations, moving to streams in summer to spawn, then back to areas that do not freeze for the winter (Craig and Poulin 1975). A number of tropical species have tracking migrations, moving between different feeding areas during the wet and dry seasons (Northcote 1978).

Most oceandromous migrations appear to be breeding migrations, although all forms of migration are present. Many pelagic fish such as western mackerel (*Scombrus scombrus*; Walsh et al. 1995) and Atlantic bluefin tuna (*Thunnus thynnus*; Stokesbury et al. 2004) feed in high-latitude waters and spawn in low-latitude waters. Other species like capelin (*Mallotus villosus*; Shackell et al. 1994) have onshore-offshore breeding migrations: they spawn in shallow waters but feed in deeper waters. Atlantic cod (*Gadus morhua*) also have onshore-offshore migrations, but these movements are driven primarily by water temperatures (Rose and Leggett 1988), and therefore are closer to tracking migrations. Both whale sharks (*Rhincodon typus*; Wilson et al. 2006) and basking sharks (*Cetorhinus maximus*; Sims et al. 2003) have tracking migrations, moving seasonally to locations of high prey abundance. However, like freshwater fish, some species of marine fish have distinct wintering, spawning, and foraging grounds, and thus do not fit neatly into any of the three types of round-trip migration (e.g., Norwegian spring spawning herring, *Clupea harengus*; Huse et al. 2010).

Birds

Approximately 4000 of the 10,000 species of birds are migratory (Bildstein 2006), the majority of which seem to have refuge migrations. By far most migratory birds breed in high-latitude high-productivity breeding sites in the summer and migrate to lower latitudes for the winter—a pattern typically studied in Northern Hemisphere species, but which also holds for Southern Hemisphere ones (Jahn et al. 2004). Many tropical species have refuge altitudinal migrations, breeding at high elevation and moving to lowlands (e.g., to avoid seasonal storms; Boyle et al. 2010). A number of waterfowl species have refuge migrations from nesting sites to more protected areas where they moult (Newton 2008).

However, there are also examples of bird species with tracking and breeding migrations. Red-billed queleas (*Quelea quelea*) have a form of tracking migration (referred to as ‘itinerant breeding’; Newton 2008): individuals forage on grass seeds and follow the rain belt as it moves across tropical Africa. Some penguins have breeding migrations: adults migrate to rookeries to breed and then make extensive trips back to ocean to forage (e.g., Emperor penguins, *Aptenodytes forsteri*; Pinshow et al. 1976).

Mammals

Mammals display a diversity of migration types (Avgar et al. 2014). Baleen whales have breeding migrations, while migration in toothed whales is less common and the drivers less

clear (Lockyer and Brown 1981). Temperate bats avoid harsh winter climate by having refuge migrations to the tropics (like birds), hibernating in place, or combining both strategies and migrating to hibernation sites (Fleming and Eby 2003). Migration patterns of tropical bats are less well documented than those of temperate species, but are often across altitudinal gradients, tracking food availability (McGuire and Boyle 2013). Many ungulates have tracking migrations, following seasonal flushes in food resources (Harris et al. 2009). Other ungulate species have refuge migrations, moving seasonally to escape deep snow, biting insects, or predators (Fancy et al. 1989; Harris et al. 2009; Hebblewhite and Merrill 2009). Finally, some carnivores also have tracking migrations, following prey that are themselves migratory, e.g., wolves (*Canis lupus*) follow migratory caribou (*Rangifer tarandus*; Walton et al. 2001), and cheetahs (*Acinonyx jubatus*) follow migratory Thomson's gazelles (*Gazella thomsonii*; Durant et al. 1988). See Gnanadesikan et al. (Evolution of mammalian migrations for refuge, breeding, and food, unpublished) for a systematic review of migration patterns across all extant mammals.

Ultimate drivers and partial migration

Many migratory species are 'partially migratory' where only a fraction of individuals migrate each year. This provides an ideal system for comparative studies on why individuals migrate. There are three primary forms of partial migration: non-breeding partial migration, breeding partial migration, and skipped breeding partial migration (Chapman et al. 2011; Shaw and Levin 2011).

The first type, non-breeding partial migration, was initially described in northern hemisphere temperate birds (Lack 1943, 1944) in which individuals migrate south to avoid harsh winter conditions, and migrate north in spring to take advantage of the food resources during breeding. Here, the decision to migrate or remain resident is based on a trade-off between potentially increasing overwinter survival or having the competitive advantage for nesting sites at the start of the breeding season. The first models of partial migration were developed for this migration type. These models predict that partial migration should occur when overwintering survival at the breeding grounds is uncertain, that full migration should occur when overwintering survival is predictably low, and that full residency should occur when overwintering survival is predictably high (Cohen 1967; Lundberg 1987). Although these models were developed with birds in mind, the results can be extended to any species for which migration is driven by the potential for increased survival (even if it is not specifically to escape from cold temperatures). Examples of this include: cyprinids that migrate from lakes to streams to avoid predatory fish (Brodersen et al. 2008), elk that migrate reduce wolf predation risk (Hebblewhite and Merrill 2009), and some tropical birds that migrate altitudinally from mountains to valleys to avoid decreased foraging opportunities during seasonal storms (Boyle et al. 2010).

The second type, breeding partial migration, occurs when individuals spend the non-breeding season together and breed apart. American Dippers (*Cinclus mexicanus*) spend winter in low-elevation streams, then some breed in place while the rest migrate to higher elevation streams to breed. Here, partial migration seems to be caused by competition for limited breeding sites forcing some individuals to breed elsewhere (Gillis et al. 2008). Pike (*Esox lucius*) in the Baltic Sea, either spawn in brackish coastal waters, or migrate to spawn in rivers (Engstedt et al. 2010). Here, partial migration may be related to competition among juveniles (e.g., via size-specific cannibalism) rather than competition among adults. A model by Taylor and Norris (2007) of this form of partial migration showed that partial

migration should be maintained as long as there is sufficient density-dependent regulation of individuals at the non-shared sites.

The third type, skipped breeding partial migration, occurs in species that migrate to breed in a specialized habitat. Here, since migration is tied to breeding, individuals that skip migration also skip reproduction for that year. This migratory pattern is taxonomically widespread, particularly in marine species such as sea turtles, baleen whales, and both anadromous and oceanodromous fish species (Table 1 in Shaw and Levin 2011), most of which have the ability to accumulate and store energy across seasons (i.e., are capital instead of income breeders; Stephens et al. 2009). Here, in contrast to the first two forms of partial migration, the decision to migrate or remain resident for the year is based on a trade-off between current and future reproduction. Models based on this form of migration predict that full migration should occur when there is little mortality cost to migration or when there is little risk of a bad year for juvenile survival (Shaw and Levin 2011, 2013). The degree of partial migration increases as migration cost and survival risk increase.

Partial migration systems can be used to generate prediction for how the tendency to migrate may respond to changing environmental conditions. In each of the above partial migration models, the authors determined what conditions influence the fraction of the population expected to migrate. Examining how the model outcomes change across ‘parameter space’ in each of these cases enables us to generate predictions for the effects of changing environmental conditions. For example, consider the consequences of increasing survival at the site shared by migrants and non-migrants for each type of partial migration. For non-breeding partial migration, increasing survival at the breeding site unilaterally favors a decreased fraction of the population migrating (Lundberg 1987). For breeding partial migration, increasing survival at the non-breeding site typically decreases the migration fraction, but can instead increase migration if migrants and residents are affected differentially by the environmental change (Griswold et al. 2011). For skipped breeding partial migration, increasing the survival at the non-breeding site decreases the frequency at which individuals migrate (Shaw and Levin 2011). However, here (unlike the first two cases) full residency is never a viable strategy: individuals must migrate in order to reproduce. The conditions that favor a reduced migration frequency will, in the extreme, lead to population collapse (Fig. 3 in Shaw and Levin 2011) since reproduction, and hence the survival of the population, is dependent on migration. Clearly, being able to predict the fate of migrations under changing conditions requires a careful understanding both of the ultimate drivers of migration as well as the types of environmental change that are likely to occur.

Proximate drivers and links to climate

Migration is triggered by a complex combination of proximate cues, both internal and external. An individual’s body condition, or level of internal energy reserves, may be particularly important for species with breeding migrations, such as salmon and sea turtles (Thorpe 1994; Hays 2000). Body condition can also be important in species with refuge migrations; timing of migration towards the refuge grounds can depend on individual reserve level (Brodersen et al. 2008). Photoperiod, the changes in day length over the course of a year, is commonly used as a cue for bird refuge migrations from temperate regions of the globe (Berthold 2001). Although photoperiod may drive broad life history changes associated with migration, the specific date of departure is often most closely correlated with local temperature for migrations in North American and European birds (Jenni and Kéry 2003; Van

Buskirk et al. 2009). Temperature is an important trigger for migrants from temperate regions in other taxonomic groups as well, including fish (Lehodey et al. 2006), insects (Chapman et al. 2015) and amphibians (Beebee 1995). In the tropics, changes in precipitation patterns often trigger migration in insects (Srygley et al. 2010), birds (Studds and Marra 2011), mammals (Boone et al. 2006), and crabs (Shaw and Kelly 2013).

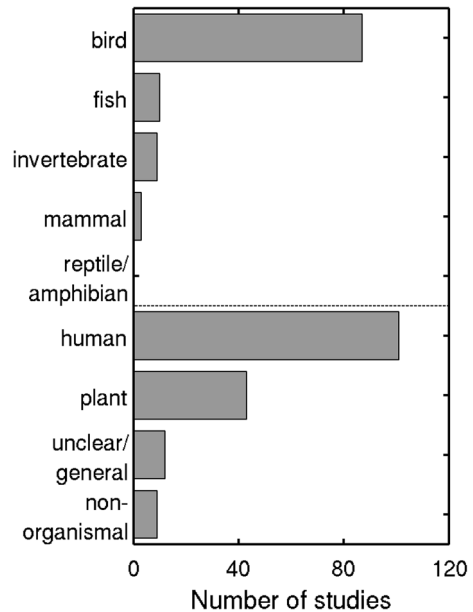
Once the proximate cues driving migration have been identified, they can be then linked to broader climate variables. Doing so can aid in the generation of predictions of whether and how changing conditions will impact proximate cues and, in turn, migration itself. For example the North Atlantic Oscillation (NAO) has been linked to migration timing in many species of North American and European birds (Lehikoinen et al. 2004; Macmynowski et al. 2007), veined squid *Loligo forbesi* (Sims et al. 2001), and European flounder *Platichthys flesus* (Sims et al. 2004), to migration condition in common eider *Somateria mollissima* (Lehikoinen et al. 2006), and to migration abundance in loggerhead sea turtle *Caretta caretta* (Báez et al. 2011). The El Niño-Southern Oscillation index (ENSO) has been linked to migrant abundance in a number of fish species (Lehodey et al. 2006) and whale sharks *R. typus* (Wilson et al. 2001), to migrant location in Pacific hake *Merluccius productus* (Smith et al. 1990), and the sea turtle *Chelonia mydas* (Quiñones et al. 2010), to migration timing in Christmas Island red crabs *Gecarcioidea natalis* (Shaw and Kelly 2013), and to migrant survival in black-throated blue warblers *Setophaga* (previously *Dendroica*) *caerulescens* (Silllett et al. 2000).

However, studies linking migration and climate are far from systematic; rather they tend to be biased towards certain regions and taxonomic groups. The majority of studies documenting climate change impacts in biological systems (in general) have been conducted in the northern hemisphere terrestrial regions of the world (Fig. 2 in Rosenzweig et al. 2008). This is true specifically for migration studies as well: birds are one of the few taxonomic groups that has been broadly studied with respect to migration and climate (Fig. 1), yet most work has focused on temperate northern hemisphere species, with relatively less known about either tropical or Australian species (Chambers et al. 2005; Studds and Marra 2011). Although migrants are found across most animal groups, comprehensive studies linking migration and climate in non-avian taxonomic groups are much less common (Fig. 1). A Web of Science search for studies with “migrat*” and “climate change” in the title returned 271 hits, of which 109 could be clearly classified by one of the taxonomic groups considered in this review. Of these 109 studies, 87 (80 %) were on birds, 10 (9 %) on fish, 9 (8 %) on invertebrates, 3 (3 %) on mammals, and none on amphibians or reptiles. As a consequence, we currently have a very narrow perspective of the impacts of climate change on migration. Given the ubiquity of migration taxonomically and across regions of the globe, it should be concerning that migration/climate studies focus on a limited set of species. Current climate projections predict that extremes of both temperature and precipitation will increase, and will have impacts across the globe (Pachauri et al. 2015). Restricting ourselves to a subset of migratory species, geographic regions or climate variables will greatly limit our ability to predict and mitigate these impacts.

Consequences of environmental change

Changing environmental conditions may have both ecological and evolutionary consequences for migrants. First, organisms that adapt aspects of their migratory behavior to local climate cues may face difficulties if changes in proximate cues are not matched with

Fig. 1 Web of Science entries that include “migrat*” and “climate change” in the title, sorted by taxonomic group (N = 271). Above the *dotted line* are studies that fall within the scope of this review (N = 109) and below the *line* are the rest (N = 163)



changes in ultimate drivers of migration. For example, changing phenology at low altitudes has triggered American robins to migrate earlier to higher altitudes, yet the date of snowmelt at higher altitudes has not changed, creating a mismatch between timing of migrant arrival and of food availability (Inouye et al. 2000).

Second, selective pressures may favor a reduced tendency to migrate altogether, which may have knock-on consequences. For example, increased average temperatures have favored blackcaps (*Sylvia atricapilla*) to migrate increasingly shorter distances, a pattern that is expected to eventually result in a fully non-migratory population within Europe (Pulido and Berthold 2010). Similarly, shifting spatial availability of milkweed has led to an increased number of non-migratory monarchs (*D. plexippus*) in the southern United States (Satterfield et al. 2015). A number of historically migratory ungulates have recently ceased to migrate (Harris et al. 2009), while other migratory ungulates have either suffered a local population decline or extinction, as a result of human activities (Bolger et al. 2008). Reduction (or discontinuation) of migration itself could have important ecological consequences. Loss of migration can lead to population decline and local (if not global) extinction (Bolger et al. 2008), to increased infection risk in a population (Satterfield et al. 2015), and to a decrease in important nutrient flow between areas (Gresh et al. 2000).

Finally, based on the classification presented in this review, clearly not all migrations are equivalent. A species' migration type (breeding, tracking or refuge) will determine, in part, its response to selective pressures. Since breeding migrants fundamentally rely on two environments, changes that interrupt migration (or favor its loss) should be difficult to adapt to. In the extreme, these can lead to extinction (e.g., poorer conditions for juveniles in the breeding habitat favor reduced adult migration, which can become unsustainable; Fig. 3 in Shaw and Levin 2011). In contrast, tracking migrants could survive interrupted migration, although likely at lower population sizes, as long as some food is available year-round (e.g., as in several ungulate species; Harris et al. 2009). Finally, refuge migrants are intermediate, able to survive certain types of environmental change, particularly if there is

a decrease in the severity of the poor conditions that they migrate to avoid (e.g., an increase in winter temperatures; Pulido and Berthold 2010). Given these patterns, it should be particularly worrisome that those migratory species that have been well-studied with respect to climate change (i.e., birds) do not represent this diversity of migratory consequences well, but instead are clustered within a single migration type (refuge).

Future directions

The broad overview of migration presented in this paper highlights a number of areas where future work should be directed. A systematic analysis of the factors driving migration of all species within each taxonomic group would be valuable and move towards evaluating the phylogenetic patterns of migration (e.g., Gnanadesikan et al. (Evolution of mammalian migrations for refuge, breeding, and food, unpublished)). To comprehend the expected impact of changing climate, we need an increased diversity of studies on the effects of climate change on migration, particularly focusing on precipitation-driven changes, and the impact of climate for tropical (and other non-temperate) and aquatic species. We also need more systematic reviews of the effects of non-climate environmental changes (e.g., habitat fragmentation) on migration. Finally, we need studies that explicitly link these two areas to see to what extent species' responses to environmental change are determined by the factors driving migration.

Conclusions

Here I have reviewed the current understanding of migration drivers across taxonomic groups. Although any conclusions drawn must be tentative, given the lack of systematic studies, some patterns do emerge (Table 1). Refuge migrations seem to be quite common among organisms that fly (particularly birds and bats). Breeding migrations are found among organisms that migrate between very distinct environments, e.g., between water and land (land crabs, amphibians, sea turtles), or across salinity gradients (fish). Tracking migrations occur in organisms that move relatively locally across a fairly constant environment where only the distribution of food is changing. This behavior is found both in herbivores that move to track vegetation patterns that change with rainfall (locusts, tortoises, ungulates) and in carnivores that move to track either patchy or migratory prey (snakes, sharks, birds of prey, mammals). Not all migrations fit cleanly into this trichotomy; in particular many insect species have a combination of refuge and tracking migrations. Although most taxonomic groups include species of all migration types (Table 1), tracking migrations are (to my knowledge) unknown in amphibians, and breeding migrations are quite rare in birds. In terms of geographic distribution, refuge migrations are more common among temperate species, while tracking migrations are more common among tropical ones. Species that migrate latitudinally by flying have refuge migrations, but those that migrate latitudinally by swimming have breeding ones. Few species migrate latitudinally by walking. Many altitudinal migrates have refuge migrations.

Environmental change is likely to have a diversity of effects for migrants that vary by species and location. Yet, studies linking migration and climate change (in particular) are biased towards a subset of species (Fig. 1). This mismatch suggests that our current expectation of the effect of environmental change on migration is skewed, and that we are

in need of balanced and systematic studies of migration drivers and the interactions with environmental change. This review indicates that species' round-trip migration types (refuge, breeding, or tracking) appear to be non-uniformly distributed both taxonomically and geographically and predict, in part, whether they can successfully adapt to changing conditions. As such, this framework of migration types offers one way forward to organize predictions of how environmental change will impact migratory species.

Acknowledgments I thank G. Gnanadesikan, A. Smith and D. Stanton for discussion of ideas, and K. Meyer, E. Strombom, L. Sullivan, and two reviewers for comments on previous versions. The general ideas were initially conceived under partial support by the National Science Foundation Graduate Research Fellowship under Grant No. DGE-0646086 (at Princeton University), and the manuscript was fully developed under partial support by startup funds from the University of Minnesota.

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