Chapter 1
Adaptation and Evolution of Bird Migration

Abstract Migration in birds is a fascinating biological phenomenon. Migration denotes the annual predictable return movements among breeding and nonbreeding populations of birds. Over millennia, the migration in birds evolved with and by various adaptive mechanisms enabling them to survive in the harshest of the conditions. Migration helps in population differentiation by exposing various groups to different environmental conditions or restricting the chances for a genetic exchange through selection by hybridization or assortative mating. The bird migration routes, also known as flyways, are influenced by various ecological factors. There are broadly eight primary flyways worldwide which are followed for long-distance migration of birds often across continents and large expanses of land and water. Avian migration also impacts human health. In the course of annual migration, birds disseminate many bacterial, viral, fungal, and parasitic diseases or disease-causing agents that affect humans. Birds may act as natural reservoirs (viz. psittacosis, Newcastle disease, avian flu, etc.), may act as asymptomatic carriers (salmonellosis and mite diseases), may disseminate various arthropod vectors of diseases (eastern equine encephalitis, western equine encephalitis, St. Louis encephalitis, etc.) and might create new reservoirs for infections on through fecal pollution of the environment (histoplasmosis, cryptococcosis). Considering the importance of avian migration in spreading of human infections including the zoonotic ones, in this chapter, we look into the basics of avian migrations along with the role of birds in dissemination of zoonotic infections to humans.

Keywords Bird migration · Population differentiation · Flyways · Human health · Arthropod vectors · Zoonotic infections

1.1 Introduction

Among the animal taxa, birds are the most mobile creature. Their mobility has significantly affected different parts of ecology and evolution (Boyle 2017). Migration is a term that denotes the annual predictable return movements among breeding and nonbreeding populations. Regular bird migration comprises movements of all

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the individuals to long distances in a population to distinct areas of breeding and wintering (Terrill and Able 1988) through the movements which are naturally controlled (Berthold 1991). The majority of the bird migration studies are mainly based on the obligate, native, long-distance movements of large-scale ecological studies (Dingle 2008; Somveille et al. 2013) to field-intensive and population studies (Ydenberg et al. 2002; Stanley et al. 2012).

In the last few decades, many of the bird species have altered their migratory behavior. The most common changes noticed are the timing of relocation and the distance traveled during migration, the two of which are generally linked with climate changes (Newton 2008; Palacín et al. 2017). However, other reasons are not well known, especially for species found in the human-modified environments. Several different animals attempt seasonal migration among breeding and nonbreeding areas. These seasonal migrations in birds are due to many ecological benefits, like providing a favorable niche, allowing the migratory birds to escape competition and to escape parasites and predators (Milner-Gulland et al. 2011). In seasonal migration, birds need a group of various adaptions to survive in a different environment and take long-distance movements (Milner-Gulland et al. 2011). Thus, migration helps in population differentiation by exposing various groups to different environmental conditions or restricting the chances for a genetic exchange through selection by hybridization or assortative mating (Turbek et al. 2018).

1.2 Adaptation and Evolution of Bird Migration

Migration is a process that requires adaptation of different qualities like orientation, morphological adaptations of the locomotory framework, and metabolism (Berthold 2001; Hansson and Akesson 2014). Many studies recommend that major components of the migration, for example, the direction of migration or capacity to migrate, are genetically controlled (Berthold 1991; Pulido 2007; Liedvogel et al. 2011). Nevertheless, migratory behavior can unexpectedly change in a short time. This is shown in the case of blackcaps (*Sylvia atricapilla*) where a particular route of migration emerged in the twentieth century achieving frequencies of around 10% in 30 generations of the population (Helbig et al. 1994). Besides, it is related to adjustments in wing morphology (Rolshausen et al. 2009) that constructs a basis for selection and standing allelic variations being the main driving factor of the change.

Most of the researchers agree that birds have acquired most of their capabilities from their ancestors for migration as the migratory movements are a common and evolutionary feature among ancestral animals (Berthold 1999; Piersma et al. 2005). However, those explaining the evolution of migration does not explain the deep origin; instead, they explain capacities of migration of different lineages (Rappole et al. 2003). Three most essential questions in the bird migration are: (1) Whether migration evolved from wintering grounds to breeding grounds or vice versa? (2) Does the long-distance migrants have their phylogenetic origin in tropical environments or at low latitudes which generally have Palearctic region as their breeding ground? (3) Whether evolution is a characteristic of specific phylogenetic groups or the adaptive changes in a particular individual?

The population which is dispersed in seasonal breeding areas, and individuals among them having a high genetic predisposition of migration, has a selective advantage when migrating to less severe climate during the nonbreeding period. The term dispersal and migration should be clearly understood as the dispersal can be used in different linguistic ways (Salewski and Bruderer 2007). The summary of evolutionary theories of the historical development of bird migration highlights autumn departure from various severe conditions in northern ancestral homes (Dixon 1892), while further range expansion for the reproduction, considered the southern equatorial ancestral home (Dixon 1897). Thus, dispersal movements are regarded as an integral part of the evolution of bird migration (Gauthreaux 1982).

Diverse migratory birds have continuously evolved with a low level of genome-wide variation in a related population (Bensch et al. 2009; Lundberg et al. 2013). At the point when populaces contrasting in migratory behavior come into auxiliary contact, hybrid zones with intermediate and mixed migratory phenotypes can be formed (Delmore and Irwin 2014). Such migratory partitions will, in general, spatially overlap with hybrid zones of different organisms (suture zones) developing because of population separation amid glacial vicariance and resulting recolonization of deglaciated territory (Hewitt 2000; Møller et al. 2011). The regular example of clinal variety in extra quantitative characteristics crosswise over migratory divides underpins this hypothesis (Bensch et al. 2002; Ruegg 2008) and recommends that distinctions in migratory traits, for the most part, developed in allopatry.

Consequently, migratory divides work as natural research facilities where the evolutionary procedures related to hybridization and early speciation can be examined. The development of migratory divides may have a significant effect on the ecology and evolution of species. Sympatric reproducing populaces using diverse migratory routes can be presented to various selection pressures, for example, parasite networks (von Rönn et al. 2015), climate conditions (Newton 2007), or generally the distance required for morphological adaptations (Rolshausen et al. 2009; Alvarado et al. 2014). In the event of transgressive or intermediate hybrid phenotypes failure which may have the risk of high mortality or diminished condition, then disruptive selection can advance for reproductive isolation of parental populaces (Rolshausen et al. 2009) which inevitably can result in summed-up genome-wide differentiation (Shafer and Wolf 2013). The intermediate migratory phenotypes give rise to the selection, which has been supported indirectly in a different study (Helbig 1996; Delmore and Irwin 2014), but the pattern of selection may differ in different systems as a function of primary adaptive landscape (Irwin 2009). Furthermore, to the selection, assortative mating can altogether add to the stable support of the phenotypic dissimilarity against gene flow (Poelstra et al. 2014); however, proof here has likewise been mingled (Bearhop et al. 2005; Liedvogel et al. 2014). Further, in-depth and microevolutionary knowledge on mating and wellness segments connected with migration-related attributes is essential to comprehend the mode and quality of selection and the subsequent populace genetic concerns.

1.3 Route of Bird Migration

Migratory birds consistently perform migrations over the globe (Fig. 1.1), covering significant distances through long continuous flights (Klaassen et al. 2011; Åkesson et al. 2016). Bird migration routes generally develop in response to ecological factors like geology, accessibility of stopover destinations, favorable wind movements, and orientation signals (Alerstam et al. 2003). For better performance, the migration itself includes different adaptations to orientation, flight, timing, and fueling in the birds (Åkesson and Hedenström 2007). The geometry of worldwide routes pursued by birds during migration has been assessed for distances and courses, and for these, two different types of routes have been defined, i.e., orthodromes and loxodromes (Imboden and Imboden 1972; Gudmundsson and Alerstam 1998). The orthodrome route represents the big circular route, which is the shortest distance between the two points on the globe and needs constant changing of direction along the way. While the loxodrome (rhumb line) route is somewhat longer and is created, a consistent geographic course is kept all through the route, expecting a simple orientation mechanism. The two courses have been reflected in different studies assessing alternative compass routes in migratory birds (Muheim et al. 2003; Grönroos et al. 2010; Åkesson and Bianco 2016).

How the birds cross natural boundaries is the most exciting problem of bird migration. Aside from extensive waterways, highlands and arid zones, where no refueling is conceivable, may likewise be hindrances for temperate zone land fowls.

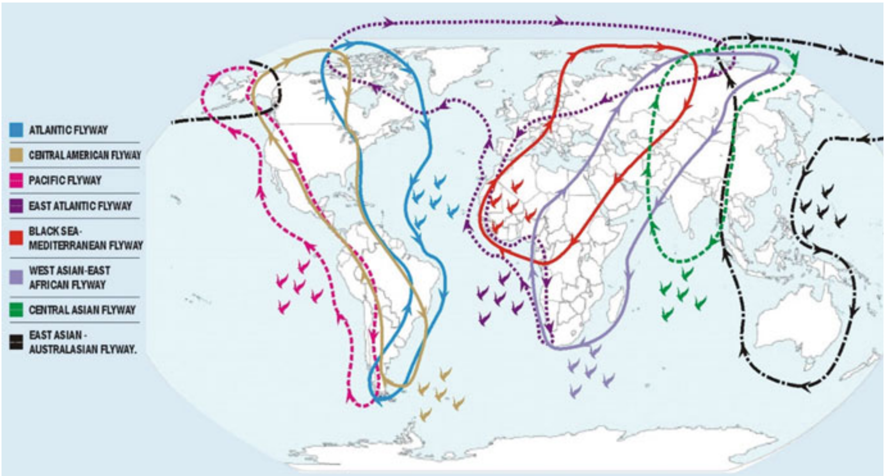

Fig. 1.1 The worldwide routes pursued by birds during migration are presented

Various studies have been done on the migration strategies of passerines crossing the Sahara (Bairlein 1988; Biebach et al. 2000; Biebach 1990; Biebach and Bauchinger 2003) and in the highlands and deserts of western Central Asia (Dolnik 1990; Bolshakov 2001). Studies in western Central Asia, together with moon-watching and catches at stopovers, recommended the speculation that nocturnal passerine migrants reproducing in Siberia and wintering in Africa abstain from crossing the deserts in autumn; instead, they make a reroute toward the north and northwest and fly north of the Caspian Sea (Bolshakov 2001, 2002). This theory is upheld by moon-watching information from the northwestern edge of the desert north of the Caspian Sea (Bulyuk and Chernetsov 2005). In light of cage experiments, a few compasses have been portrayed in birds that depend on data from the sun and the associated pattern of skylight polarization, stars, and the geomagnetic field (Able 1980; Wiltschko and Wiltschko 1995; Åkesson et al. 2014). The use of sun compass by which birds can gradually correct their apparent movement by a time-compensation mechanism, over the sky for the day generally equivalent to a move of 15° every hour of the sun azimuth for the horizon at high latitudes (Kramer 1952; Schmidt-Koenig 1990). While the star compass gives direction concerning the rotation center, i.e., geographic north of the night sky, without using a time-compensation mechanism (Emlen 1970), the geomagnetic field gives a universally accessible source of data, which might be used by migratory birds for compass orientation and route (Wiltschko and Wiltschko 1995, 2009).

The magnetic compass of birds is reliant on the angle of inclination by which the geomagnetic field lines cross the earth surface, and not on the polarity of the geomagnetic field (Wiltschko and Wiltschko 1972), giving a method to separate directions along a north-south axis driving toward the equator or poles. Young birds have an acquired ability to investigate alternative routes. However, they have to encounter a mix of characteristic compass data amid ontogeny to utilize the data for compass introduction (Able and Able 1996; Emlen 1975) and build up a populace-specific orientation (Weindler et al. 1996). Compasses may additionally be recalibrated amid movement (Cochran et al. 2004; Muheim et al. 2006; Åkesson et al. 2015). Despite significant aggregated information of compass components and calibration processes, we do not know precisely what and how compasses are utilized amid active flights of migration. However, the inquiry has been drawn nearer by foreseeing flight courses dependent on alternative compass mechanisms (Alerstam and Pettersson 1991).

1.4 Flyways and Stopovers

Mostly bird species undergo significant scale movement to protect them from unfavorable conditions or potentially use high-quality resources somewhere else. These movements can appear as migration (back and forth movements among breeding and wintering locations), partial migration when not all individuals in a populace are involved (Dean 2004). The large-scale movements of birds are a global phenomenon, and around 20% of bird species are migratory (Somveille et al. 2015). The three main migration system can be defined, the Nearctic–Neotropical system, the Palearctic–African system, and the Palearctic–Asian system (Rappole and Jones 2003). Nomadism is, for the most part, connected to semi-arid and arid conditions around the world (Dean 2004) with nomadism representing around 10% of all flying creature species in southern Africa (Dean 1997) and 26% of all flying creature species in Australia (Smith 2015).

A flyway is a flight way utilized in bird migration – flyways by and large range over landmasses and oceans. When going between their rearing and wintering grounds, feathered creatures do not pick their ways arbitrary. They pursue set courses that incorporate reasonable living spaces where they can stop to rest and refuel enroot. A wide range of animal groups bunch together to go along comparable courses, which have been inexactly part into eight primary flyways. (1) Atlantic Flyway, (2) Central Flyway, (3) Pacific Flyway, (4) East Atlantic Flyway, (5) Black Sea-Mediterranean Flyway, (6) West Asian-East African Flyway, (7) Central Asian Flyway, and (8) East Asian-Australasian Flyway.

Numerous migratory bird species having a wide geographic distribution are made out of various subpopulations following particular migratory routes. Thus, these flyways are delineated depending on mark-recapture information, while in numerous species like passerines, they are supported by the molecular data (Ruegg and Smith 2002; Clegg et al. 2003; Pérez-Tris et al. 2004), waterfowl (Scribner et al. 2001; Gay et al. 2004), and waders (Wennerberg 2001). The absence of genetic divergence among migratory flyways may recommend that the migratory behavior is commonly adaptable or the migration route has changed recently in specific populations. The different flyways are frequently deciphered as a heritage of the ice ages. Various subpopulations would have been bound to different refugia, which they held as wintering grounds following a postglacial range development (Ruegg and Smith 2002). These periods in allopatry would prompt some genetic divergence among subpopulations, then which may be disintegrated step by step through gene flow.

Long-distance migratory birds are under pressure to migrate rapidly. Stopovers need additional time than flying and are utilized by birds to refuel amid movement, yet the impact of fuel loads obtained at stopover destinations during the migration has not been measured or quantified (Gómez et al. 2017). As far as time is concerned, the maximum expense of migration is during stopovers rather than during times of flight (Hedenström and Alerstam 1997; Wikelski et al. 2003), and the birds depend on the time spent at stopover destinations to rest and refuel for the next leg of their journeys (Smith and McWilliams 2014). Optimal migration theory gives a system to examine stopover behavior and its outcomes by checking whether migrants are time or energy minimizers utilizing information on fueling rate, stopover length, fuel burdens, and potential flight ranges (Alerstam 2011). Individuals endeavoring to limit the total time spent on migration are relied upon to augment the measure of fuel they can obtain at every stopover in the briefest time conceivable. A key result of this procedure is that it expands the distances that can be flown between stopovers (Hedenström and Alerstam 1997; Weber and Houston 1997). Subsequently, the fuel loads (a measure of fat conveyed) of a period minimizer ought to be firmly connected to local conditions at stopover destinations just as to the conditions expected ahead because these conditions impact fueling rates (Hedenström and Alerstam 1997; Weber and Houston 1997). Besides, stopover lengths in time minimizers are relied upon to have been molded by or to react straightforwardly to experienced fueling conditions (Alerstam 2011; Hedenström and Alerstam 1997). Bigger takeoff fuel loads ought to take into consideration longer and quicker flights, large pace of migration since individuals securing adequate fuel in the briefest time conceivable should make less stopovers and have the option to take more straightforward routes to their destinations, including having the option to fly over physical obstructions or substantial zones of inadequate territory, for example, deserts or seas, as opposed to evading these areas (Alerstam 2001).

1.5 Significance in Disease Transmission

The birds can transmit infectious diseases to humans by several mechanisms. The infections caused by birds can be assembled into four groups. In group 1 infections, the birds act as natural repositories for the infection, which causes disease among them. The unhealthy birds at that point spread the infectious agent into nature, and people become infected as unintentional hosts. Instances of such infections are psittacosis, Newcastle sickness, avian flu, and yersiniosis. In group 2 and 3 infections, fowls are the characteristic reservoirs for the infection, yet do not turn out to be sick themselves. The infection from group 2 (for instance, salmonellosis and mite diseases) scatters from the colonized birds directly into the environment, while the agents of group 3, for instance, eastern equine encephalitis, western equine encephalitis, St. Louis encephalitis, and Japanese B encephalitis, are dispersed by the arthropod vectors and include humans as unintentional hosts. In group 4, the organism transmits through their fecal matter in the environment. Instances of infections of the last class are the fungal disease like histoplasmosis and cryptococcosis (Levison 2015).

The disease caused by fowls can be intense, chronic, latent, or asymptomatic. Infections that can be transported are the arboviruses (Eastern equine encephalitis, West Nile infection), Newcastle disease virus, Usutu virus, avian pox virus, duck plague virus, St. Louis encephalitis virus, and influenza A virus (Bengis et al. 2004; Hubalek 2004). Similarly, the causal agents of ornithosis, avian cholera, mycoplasmosis, avian tuberculosis, erysipelas, coxiellosis, campylobacteriosis, Lyme borreliosis, colibacillosis, cholera, salmonellosis, listeriosis, and yersiniosis can likewise be transferred. In the same manner, drug-resistant enteropathogens can also be dispersed (Bengis et al. 2004; Hubalek 2004; Chuma et al. 2000; Hudson et al. 2000; Rappole and Hubalek 2003) like fungi and endoparasites, for example, *Aspergillus* spp., *Candida* spp., *Haemoproteus* spp., *Leucocytozoon* spp., *Sarcocystis* spp., *Toxoplasma* spp., and *Cryptosporidium* spp. (Bengis et al. 2004; Hasle et al. 2004).

Mechanical carriers transmit either outer or interior microbial pathogens. Exterior pathogens, as fungal spores, are situated on the body of the fowl and can retain up to 12 days on the plumes of migratory swallows. Internal pathogens do not develop in the avian body but go through the digestive tract and are viable when discharged. Foot and mouth disease infection has been believed to be transmitted by mechanical carriers (Bengis et al. 2004; Hubalek 2004).

Migratory fowls can act as carriers of tainted hematophagous ectoparasites, which act as vectors for a few infections. In this way, the infected immature ixodid and argasid ticks are transported from one spot then onto the next and even from one continent to another (Hasle et al. 2004). Tick-borne pathogens can be viruses, for example, tick-borne encephalitis, Meaban, Hughes group, Crimean-Congo hemorrhagic fever virus, Bhanja, Great Island complex, Thogoto, and Dhori viruses; or the bacteria, for example, *Rickettsia* spp. and *Anaplasma phagocytophilum*; or then again protozoa-like *Babesia microti*. Further, bugs can be transmitted on migrating birds to long distances (Bengis et al. 2004; Hubalek 2004).

The method of transmission of all these microbes can either be direct or indirect. Direct transmission is brought about by the migratory fowl itself through close contact, contact by the inward breath of released respiratory droplets from sneezing or coughing, or by infectious feces. Indirect transmission happens using an arthropod, for example, a bug, mite, mosquito, sandfly, or tick, or a lifeless vehicle like water, soil, food, and so on. Likewise, the airborne infection spread by droplet nuclei, dust, and so forth is viewed as an indirect method of transmission (Hubalek 2004). The mode of transportation of pathogens by migratory birds relies upon the course of transmission (Hasle et al. 2004).

The agents in water-borne infections, for example, avian flu infection, *Chlamydia psittaci*, Newcastle sickness infection, *Escherichia coli, Enterococcus faecalis*, *Yersinia* spp., *Clostridium* spp., *Pasteurella multocida*, and *Candida* spp., are shed by tainted migratory fowls in excreta, in nasal release, and in respiratory exudate into water. In tick-borne contaminations, the infectious larval or nymphal tick is dropped into another geographic region amid relocation (Hubalek 2004).

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