IJHSR
ijhighschoolresearch.org
■ REVIEW ARTICLE

Migration-Driven Adaptations in Avian Species

Arshi Aggarwal

International School of Beaverton, 7770 SW Blanton St, Beaverton, OR 97078, USA; arshiraleigh@gmail.com

ABSTRACT: Avian migratory flight is one of the most extreme endurance feats in the animal kingdom, requiring highly optimized physiological and cellular systems. This review synthesizes current research to evaluate how migratory pressures have driven adaptations in cellular, musculoskeletal, cardiovascular, and digestive systems in avian species. Details of these adaptations are discussed and compared with those of non-migratory birds to highlight the tradeoffs of traits selected for migration. The role of geographical and migratory constraints in shaping convergent or divergent evolution in avian species is also discussed. Finally, by linking structure, function, and performance, this work proposes a distinct migratory phenotype shaped by ecological pressures and offers insight into avian evolution.

KEYWORDS: Ecology, Avian Biology, Evolution, Migration, Migratory Phenotype.

■ Introduction

"Bird" (class Aves) is an umbrella term that encompasses more than 10,000 species of warm-blooded vertebrates, distinguishable by their unique feather-covered bodies and lightweight, aerodynamic physiques.[1,2] Their fused skeletal structure and high metabolic rates have enabled them to evolve the most sophisticated flight capabilities in the animal kingdom, supporting an extraordinary ecological and evolutionary diversification of the species.[1,2] Historically, this diversity was even greater, including species now extinct due to natural and anthropogenic causes.[3,4]

Migration is a behavior observed across animal taxa, involving a periodic, large-scale relocation in response to predictable environmental variation.[5] In birds, however, migration represents more than movement alone; it constitutes a coordinated syndrome of behaviors, physiological, and morphological traits that together enable survival under extreme energetic and ecological demands.[6] Migratory movements are often categorized as short-distance when occurring within a continent and long-distance when spanning continents. However, avian migration is best understood as a continuum of migratory distances rather than discrete categories. Along this continuum, short-distance migration likely evolved from local foraging expansions. In contrast, long-distance migration arose across evolutionary timescales through strong selection on genetic, physiological, and behavioral mechanisms that support endurance flight.[7,8]

Zugunruhe (derived from the German words *Zug*, meaning "migration" or "movement," and *Unruhe*, meaning "restlessness") describes a seasonally timed increase in nocturnal activity and agitation that occurs even in captive birds.[9,10] Research on *Zugunruhe* has provided key insights into the endogenous control of migration and established that migratory behavior is partially hardwired and regulated by internal circannual and circadian clocks.[9,10] While the precise migratory triggers are not fully understood, migration is thought to be initiated through the interaction of photoperiod, weather patterns, food availability, and endogenous hormonal signaling.[8,11]

Migratory flight imposes extreme physiological challenges that exert strong selective pressure across multiple biological systems. Sustained flapping requires continuous aerobic ATP production, lipid-based metabolism, and optimized oxygen delivery.[12-15] Birds must accumulate and efficiently mobilize large fat reserves, remodel digestive organs for rapid nutrient assimilation, and maintain muscle performance while minimizing oxidative damage.[14,16,17] Simultaneously, migratory species face tradeoffs between weight reduction and fuel storage, and the need for precise navigation and timing to exploit favorable atmospheric conditions.[18,19] Migratory distances can be extreme, exemplified by the Arctic tern (*Sterna paradisaea*), whose lifetime flight distance has been estimated as equivalent to three round-trips to the moon. Such feats are possible only through highly specialized and finely tuned biological systems that function in concert.[20] Migratory pressures distinguish migration from other forms of movement and necessitate integrated, whole-organism adaptations.

While there is extensive literature focused on individual traits associated with migration, there are relatively few reports examining how these traits are integrated across skeletal, muscular, cellular, cardiovascular, and digestive systems to form a unified migratory phenotype.[14,15] This review builds on earlier foundational work by synthesizing literature across levels of biological organization to frame migration as a distinct phenotype rather than the optimization of isolated traits.

■ Discussion

Skeletal Adaptations:

Axial Fusion:

Birds have a specialized axial skeleton characterized by extensive vertebral fusion that enhances rigidity and stability during flight, thereby limiting axial deformation and mechanical energy loss during wingbeats.[21,22] While vertebral fusion is a general feature of avian flight anatomy, this trait may be more

DOI: 10.36838/IJHSR810.83

pronounced in species adapted for sustained aerial activity, including many long-distance migrants.[21-24] Fusing multiple vertebrae into a single structure reduces both bone count and the amount of soft tissue and muscle needed to move individual segments.[21,25,26] This structural adaptation likely contributes to reduced body weight and the energy required per wingbeat.[27] In contrast, many non-migratory birds retain greater axial flexibility, which enhances terrestrial maneuverability and perching agility.[23,24,28]

A central component of axial fusion in birds is the synsacrum, a rigid structure formed from the fusion of the thoracic, lumbar, and sacral vertebrae.[29] The synsacrum plays a critical role in stabilizing the trunk and pelvis and in resisting mechanical stress generated from continuous flapping.[30] In addition to stabilizing posture, the synsacrum contributes to a rigid axial framework that indirectly anchors the pectoral girdle, supporting the pectoralis and supracoracoideus muscles.[31,32] In birds adapted for sustained aerial activity, the synsacrum is often elongated and tightly ossified, increasing axial stiffness and reducing the need for continual postural adjustments to maintain stable flight alignment over long distances.[26,29] Together, these features illustrate how skeletal fusion in migratory birds integrates structural stability and muscular support, enabling efficient long-distance flights.

Pneumatized Bones:

All birds have hollow, pneumatized bones, which are lined with spongy, lightweight trabeculae that reinforce the internal walls.[23] Some migratory taxa show increased or strategically redistributed pneumatization in related bones, such as the humerus (upper wing bone), sternum (breastbone), and vertebrae; these bones are also under the most strain during sustained flight.[23,24] A study by Machado *et al.* on avian bone mass distribution confirmed that pneumatization in bones is strategically concentrated in areas to reduce wing loading and optimize energy efficiency, supporting migratory endurance.[27] Another study by Louis *et al.* comparing the skeletons of resident and migratory subspecies of Dark-eyed juncos (*Junco hyemalis*) observed that the humeri of the migratory subspecies were thinner and wider, with a higher geometric stiffness. This feature helps support increased weight during migration. Furthermore, the femora (thigh bone) of the migratory birds were shorter and thinner, with lower geometric stiffness than those of resident juncos, reducing skeletal leg mass.[24] Stiffer wing bones support increased weight associated with migratory fattening and also key flight muscles.[24] Lighter and weaker thigh bones in migratory birds demonstrate an adaptive compromise, reflecting the importance of optimizing essential migratory components.[23,24]

Both the body and cranium of migratory birds show specialized adaptations that enhance flight efficiency, including centralized mass distribution and lightweight skeletal structures.[23,24] This centralization reduces rotational inertia, increasing aerodynamic control during prolonged flights.[24] Furthermore, mass centralization of the avian skull in migratory species demonstrates evolutionary specialization for flight. Migratory birds possess cranial morphologies that differ significantly from those of non-migratory species, with migration being an important predictor of skull shape across a broad comparative sample of birds. In addition, migratory lineages show faster rates of skull shape evolution than non-migratory birds, consistent with directional selection on cranial anatomy associated with long-distance movement.[33] Comparative morphometric work on specific passerines further supports this pattern. Migratory Yellow-breasted bunting (*Emberiza aureola*), resident House sparrow (*Passer domesticus*), and Eurasian tree sparrow (*Passer montanus*) differ in skull and cranial indices, with resident species exhibiting larger cranial indices than the migratory bunting, indicating distinct structural adaptations tied to migratory versus resident lifestyle.[23] In contrast, non-migratory species are more likely to maintain their robust cranial structures due to less evolutionary pressure to adapt to long-distance flight energy efficiency.[23]

While pneumatization decreases bone marrow space and calcium storage capacity, migratory birds compensate for these limitations through increased dietary calcium absorption during breeding or from medullary bone formation in females.[12] Such adaptations reflect an evolutionary tradeoff in which migratory performance is prioritized over skeletal mineral storage, highlighting the skeletal system's role as a flight-specialized structure.

Appendicular Modifications:

The appendicular skeleton of migratory birds (legs and wings) has undergone evolutionary refinement to ensure endurance and efficiency.[24,34-37] Wing morphology is an excellent example of this evolution. A comparative study of Eurasian barn swallows (*Hirundo rustica*) revealed that populations with the longest migrations had longer and more pointed wings than resident or short-distance counterparts in Israel and Spain.[36] These adaptations reduce drag and enhance the lift-to-drag ratio, allowing for greater energy conservation over long flights. This study also found that wingtip concavity, a measure related to aspect ratio (the ratio of wing length to wing width), did not differ significantly between short-distance and long-distance migrants.[36] This suggests that migratory adaptations target traits with the greatest payoff for endurance while other features remain stable, possibly due to biomechanical constraints or the need to preserve maneuverability.

More broadly, migratory birds typically have a higher wing aspect ratio (wingspan^2/wing area) in comparison to resident birds.[34] A higher aspect ratio signifies longer and narrower wings, enhancing endurance and energy efficiency while reducing drag.[34] This contrasts with the shorter and rounder wings of resident birds, which allow for quick takeoffs and maneuverability desirable for more frequent and shorter flights. Additionally, migratory birds typically have lower wing loading (weight/wing area) than resident or short-distance migratory birds.[36] A lower wing loading results in a lighter body relative to wing area, contributing to a greater lift and more efficient flight.[36] Feather structure, too, reflects migratory stress: primary feathers of long-distance migratory birds often have a thicker dorsoventral rachis and shorter barbs. These features improve feather durability during long flights.[37]

Beyond wings, avian leg morphology reflects trade-offs among flight performance, habitat use, and terrestrial locomotion rather than migration alone. Comparative analyses across birds demonstrate that relative leg length, commonly measured as tarsus length, is strongly associated with ecological function. Species that rely heavily on terrestrial locomotion or ground-based foraging tend to have longer leg elements, whereas species adapted for more efficient flights often exhibit relatively shorter tarsi.[24,38,39]

In this context, some migratory birds, particularly aerial specialists such as long-distance passerine migrants, may exhibit reduced hindlimb length compared with highly terrestrial species. This pattern is consistent with a shift in locomotor emphasis toward sustained flight rather than ground movement.[40,41] However, this trend is not universal across migratory taxa. Many long-distance migrants, including shorebirds and cranes, retain elongated legs that are functionally important for wading or terrestrial foraging.[38,39] Collectively, these findings suggest that there appears to be a trend toward relatively reduced leg length in some migratory lineages with limited terrestrial locomotion, but leg morphology in migratory birds remains highly variable and shaped primarily by ecological niche rather than migration distance alone.

Muscular Adaptations:

Seasonal Hypertrophy of Flight Muscles:

In preparation for migration, the pectoralis major (the primary downstroke muscle) and the supracoracoideus (the upstroke muscle) undergo seasonal hypertrophy, which is increased muscle growth through muscle fiber enlargement.[42] Studies show that these muscles can increase by 20-30% in mass in just a few weeks.[43-46] The pectoralis major and supracoracoideus muscles are specialized for prolonged aerobic metabolism, enabling birds to sustain flight for hours or even days without fatigue.[1,31] In small migratory songbirds, these muscles are predominantly composed of fast oxidative glycolytic (Type IIa) fibers, rather than Type I fibers found in larger waterfowl such as ducks and geese.[47-49] Type IIa fibers provide a balance of high contractile power and aerobic endurance, supporting both sustained light and daily movement requirements.[49] Seasonal modulation of fiber-type composition, coupled with increases in oxidative enzyme activities, enhances the oxidative capacity of these muscles during migration.[48,49] In addition, the fibers are densely packed with mitochondria and supported by a rich capillary network, allowing efficient oxygen delivery and near-exclusive reliance on fat metabolism during long-distance flights.[50]

Hypertrophy is not simply passive weight gain. It is an actively regulated process, shaped by hormones and physiology. Hormonal and molecular signals play a key role in triggering these changes. Research has shown that Insulin-like Growth Factor 1 (IGF1) mRNA expression significantly increases during pre-migratory weight gain, promoting protein synthesis and muscle fiber growth.[44] Simultaneously, myostatin mRNA (a negative regulator of muscle development) is suppressed.[44] This dual mechanism removes molecular constraints on growth, priming the muscles for the extreme workload of migration. Beyond molecular regulation, environmental and behavioral factors also influence hypertrophy. Photoperiod changes, food availability, and fat deposition all act as signals that coordinate muscle growth for migration readiness.[8,12,51] Even exercise outside the migratory window can partially activate these pathways, suggesting that flight muscles retain a year-round ability for remodeling, though migration amplifies the effect.[43,52]

Seasonal hypertrophy of migratory birds is distinct from that of non-migratory birds. Resident species exposed to similar photoperiods and environmental cues show little to no increase in flight muscle mass or fiber-type remodeling.[48] For example, comparative studies in White-crowned sparrows (*Zonotrichia leucophrys*) show significantly higher pre-migratory pectoralis mass and oxidative enzyme activity in migratory individuals relative to resident conspecifics.[48] This reinforces that this plasticity is a migratory adaptation rather than a general response to seasonal changes. However, not all migrants follow the same muscular hypertrophy pattern. Comparative studies on sparrow species suggest that long-distance migrants may exhibit greater seasonal shifts in muscle mass and fiber type composition than short-distance migrants or resident species.[48] However, these patterns are not universal. In some species, including short- and medium-distance migrants, the pectoralis muscle transverse area may decrease during the migratory season while fiber density increases, as shown in Yellow-rumped warblers (*Setophaga coronata*).[53] This change may improve oxygen and nutrient delivery to individual fibers rather than increasing absolute force production.[53] Migration timing and ecological context further influence these traits, with individuals departing earlier or facing more demanding routes often showing higher proportions of oxidative fibers and elevated aerobic enzyme activity.[49]

Once migration begins, hypertrophied muscles enter a delicate balancing act. They must sustain continuous wingbeats without fatigue while minimizing excess weight that could hinder flight.[1] After prolonged flights, post-migratory atrophy occurs as a controlled, adaptive response.[13] Studies show that after long-distance flights, the cross-sectional area of flight muscles such as the pectoralis can decrease, with altered contractile properties that reflect strategic remodeling rather than damage.[44] This reduction is part of a broader muscle adaptation that includes the breakdown of muscle proteins, providing amino acids for energy and metabolic water, which are crucial during hydration-stressed flights.[7] Experimental work on species like Yellow-rumped warblers further supports this, showing that flight-induced pectoralis atrophy occurs at a rate of about 4 mg dry mass per hour with minimal immediate loss in force production or aerobic capacity.[52] This indicates a balance between reducing tissue mass and maintaining function. Similarly, research on Black-necked grebes (*Podiceps nigricollis*) reveals that during migration, flight muscles can lose up to 50% of their mass, yet the mitochondrial density remains relatively high, suggesting that muscle reduction is a controlled adaptation.[54] At the same time, the lighter musculature reduces overall body mass, balancing the trade-off between force production and metabolic efficiency until the bird can replenish energy stores.[55] This cycle of muscle growth and reduction reflects an extraordinary flexibility in avian physiology, allowing birds to optimize their flight performance while adapting to the demands of migration.

Fiber Composition and Enzymatic Function:

The flight muscles of migratory birds rely primarily on fast oxidative-glycolytic (FOG) fibers, which combine high fatigue resistance with the contractile speed necessary for sustained flapping flight.[53] These fibers are characterized by high mitochondrial density, elevated myoglobin content, and extensive capillarization, supporting efficient oxygen delivery and high rates of aerobic metabolism.[53,56] Comparative studies of migratory and resident sparrows demonstrate that while FOG fibers dominate the pectoralis muscle in both groups, migratory species exhibit substantially greater seasonal plasticity in muscle phenotype than resident species.[48,57]

Rather than undergoing major shifts in fiber type, migratory birds enhance the oxidative capacity of existing FOG fibers during migration through coordinated biochemical and metabolic changes. Activities of key aerobic enzymes, including citrate synthase (CS), a marker of mitochondrial abundance, and β-hydroxyacyl-CoA dehydrogenase (HOAD), a central enzyme in fatty-acid β-oxidation, rise significantly during migratory periods.[16,48] These enzymatic changes are accompanied by the seasonal upregulation of fatty acid transporters in flight muscle, which enhances lipid uptake and supports sustained reliance on fat as a primary fuel source for long-distance flight.[58] Similar seasonal increases in CS activity have been documented in Yellow-rumped warblers, indicating elevated mitochondrial oxidative capacity relative to non-migratory states.[50,59] In contrast, resident sparrows show little to no seasonal variation in muscle fiber morphology, enzyme activity, or lipid transport capacity, maintaining relatively stable metabolic profiles year-round.[48]

This suggests that migratory birds undergo a reversible, migration-triggered metabolic reprogramming that optimizes endurance capacity when needed. Early-departing individuals often display larger mitochondrial densities and greater oxidative capacity, suggesting that intra-species variation is tuned to individual migratory schedules.[60,61] This muscle-level plasticity aligns with broader seasonal modulation across the oxygen transport cascade, including coordinated changes in oxygen delivery, diffusion, and utilization documented in migratory songbirds.[53]

Cellular Specialization:

One particularly striking adaptation is how flight muscles handle water balance during long flights. When Blackpoll warblers (*Setophaga striata*) fly thousands of kilometers over the Atlantic, muscle catabolism during extreme dehydration appears to create metabolic water: a critical survival mechanism under low-humidity conditions.[52,55] This dual use of muscle tissue, as both a power source and an emergency water reservoir, illustrates the versatility of migratory physiology.

Migratory birds also show structural adaptations at the myofibrillar and extracellular matrix (ECM) level. High-endurance species have tightly packed sarcomeres, increased elasticity, and optimized cytoskeleton anchoring, which together enhance contractile efficiency.[56] These specializations allow muscles to sustain repeated contractions with minimal energy loss. The ECM further contributes to mechanical stability by transmitting force laterally, supporting the integration of individual fibers, resisting fatigue, and reducing the risk of micro-tears during repetitive wingbeats.[1,56,62] Collagen composition, cross-linking, and alignment with the ECM are critical for minimizing mechanical stress and preserving structural integrity in vertebrate skeletal muscles, including those of birds.[62] Together, these structural adaptations provide stiffness and help distribute force efficiently across the muscle.

Mitochondrial Adaptations:
Increased Aerobic Energy Production:

Migratory birds have much higher mitochondrial density in their flight muscles than resident species, as indicated by enhanced mitochondrial enzyme activity and respiratory performance in migratory individuals.[50] This is crucial to fueling the intense, energetic demands of long-distance flight. In the pectoralis muscles of White-crowned sparrow subspecies, migratory Gambel (*Zonotrichia leucophrys gambelii*) showed greater markers of mitochondrial remodeling and enhanced capacity for mitochondrial oxidative metabolism compared with non-migratory Nuttall (*Zonotrichia leucophrys nuttalli*), supporting the link between mitochondrial adaptations and migration energetics.[63] This spatial arrangement minimizes diffusion distance for both oxygen and fatty acids, ensuring efficient delivery of fuel and oxygen directly into the oxidative machinery of the cell.[13,59]

In Yellow-rumped warblers, flight mitochondria have about 60% higher citrate synthase activity than non-migratory phenotypes, reflecting a stronger capacity for sustained aerobic metabolism.[50] Additionally, State 3 respiration rates, indicative of phosphorylating respiration, are approximately 70% higher in migratory birds when oxidizing palmitoylcarnitine.[50] Palmitoylcarnitine is an intermediate in mitochondrial fatty acid oxidation, a process that generates significant amounts of ATP required for high-powered flight.[64]

Interestingly, ROS (reactive oxygen species) emission rates are similar between migratory and non-migratory phenotypes, despite the higher metabolic rates in migrants.[13,50,65] Normally, elevated oxidative metabolism increases ROS production because oxygen partially reduces to superoxide at complexes I and III of the electron transport chain.[66] The maintenance of low ROS levels in migratory birds indicates adaptations that allow enhanced oxidative capacity without incurring oxidative damage.[67] These adaptations include the upregulation of redox-sensitive signaling pathways and redox-balancing proteins such as SIRT1, SOD1, and NF-κB.[67] Evidence for this comes from migratory Redheaded buntings (*Emberiza bruniceps*), which display tissue-specific control of oxidative stress during long-distance flights.[67]

Furthermore, in migratory species, flight muscles show mitochondrial adaptations that enhance ATP production, including changes in mitochondrial morphology and electron transport chain activity that optimize oxidative phosphorylation.[68] Such structural and functional optimization reduces metabolic bottlenecks and supports the extreme endurance required during migration.[7,13,68]

Seasonal Remodeling and Phenotypic Flexibility:

Mitochondrial adaptations in migratory birds are highly plastic. Seasonal cues, such as photoperiod, trigger the proliferation of mitochondria and increase oxidative enzyme activity in preparation for migration.[50,61,63] After migration, seasonal mitochondrial remodeling regresses, conserving energy during non-migratory flights.[57] This plasticity entails fine-tuned adjustments based on migratory distance and environmental conditions. For example, White-crowned sparrows and many boreal-breeding bird species have higher respiratory capacity and CS activity during migratory periods than at other times of year, indicating flexible mitochondrial performance across seasons.[57,69] This suggests that even subtle differences in ecological demands can shape cellular bioenergetics.[50,70] Such remodeling emphasizes the cost-benefit tradeoff inherent in maintaining high-performance mitochondria. While sustaining them year-round would be energetically expensive, repeatedly rebuilding mitochondrial machinery before and after migration also carries an energetic cost. This suggests that birds balance the benefits of high oxidative capacity during migration with the energetic demands of seasonal remodeling.

Fuel Utilization and Metabolic Efficiency:

Migratory birds predominantly fuel long-distance flight with fatty acids, as fats contain substantially more energy per gram than carbohydrates and are the dominant substrate for aerobic metabolism.[7,71] In flight muscles, mitochondria are closely associated with intramyocellular lipid droplets, allowing immediate access to fat stores without the delay of mobilizing distant reserves.[13,45,46] Fatty acids derived from stored triacylglycerides are transported to flight muscles, where they undergo β-oxidation and oxidative phosphorylation to meet high ATP demands.[1] Seasonal increases in fatty acid transporters and catabolic enzymes such as carnitine palmitoyltransferase (CPT) and HOAD support enhanced lipid uptake and oxidation in flight muscles during migration.[13,45,46,62] The upregulation of these enzymes and transport proteins ensures that the oxidative machinery can continuously process large amounts of lipid fuel during hours of intense aerobic flight.[62] Migratory birds also exhibit tighter coupling in oxidative phosphorylation, minimizing proton leak and maximizing ATP yield per unit oxygen consumed.[44] This combination of high-energy-density fats, enzyme specialization, and increased mitochondrial oxidative capacity enables migratory birds to maintain prolonged flights while meeting their energetic demands.[44,59]

Cardiovascular Adaptations:

Compared to resident species, migratory birds typically exhibit larger hearts relative to body size, a pattern that reflects evolutionary adaptation for the higher circulatory demands of endurance flight.[2,72,73] Migratory taxa such as Arctic terns and Blackpoll warblers show consistently greater relative heart mass than short-distance or resident species, suggesting selection for enhanced cardiovascular capacity.[12,20,72,73] Increased heart mass enhances stroke volume, particularly through left ventricular hypertrophy, elevates systemic cardiac output without disproportionately raising pulmonary circuit pressures.[1,74,75] Seasonal phenotypic flexibility also contributes to this process. In migratory passerines such as Yellow-rumped warblers and Warbling vireos (*Vireo gilvus*), heart mass is higher in spring before migration and declines after the migratory period.[73] This demonstrates reversible cardiac remodeling in preparation for and recovery from long flights. The cardiovascular system is tightly linked to muscle and mitochondrial performance. Hypertrophied flight muscles demand a higher oxygen influx, which drives selection for larger hearts and increased capillarization.[44,46] In turn, efficient mitochondrial networks utilize this oxygen effectively, converting it into ATP to sustain continuous wingbeats.[13,59]

Oxygen delivery is further facilitated by higher capillary density in the flight muscles of migratory birds, which reduces diffusion distances and supports robust oxygen supply to active fibers during flight.[1,53] While the capillary-to-fiber ratio may not change uniformly across all seasons or species, seasonal modulation in multiple components of the oxygen cascade has been documented in migratory songbirds.[53] This improves oxygen uptake and transport under migratory conditions.[53] Hemoglobin concentration and oxygen-binding properties also vary across migratory states, though the specific mechanism remains an area of active research.[53] Anatomical features such as specialized pneumatic bones and extensive air sac systems complement these cardiovascular traits. They increase respiratory efficiency and oxygen availability for sustained aerobic metabolism during long flights.[1] Together, these cardiovascular adaptations illustrate how migratory birds fine-tune heart morphology and function, both evolutionarily and seasonally, to meet the circulatory requirements for long-distance flight.

Digestive System Adaptations:

Migratory birds exhibit remarkable plasticity in their digestive system, allowing them to adjust gut structure and function in response to changing energetic demands. In waders (*Charadrii*), Kovtun *et al.* demonstrated that pre-migratory individuals significantly increase their intestinal length, mass, and absorptive surface area relative to non-migratory periods.[76] Supporting this, Western sandpipers (*Calidris mauri*) show increases of up to 25% in small intestine mass before migration, a change that coincides with peak fat deposition and maximized energy storage.[76,77] Comparable digestive flexibility has also been documented in migratory songbirds. Studies of passerines such as Garden warblers (*Sylvia borin*) and other long-distance migrants reveal reversible enlargement of digestive organs during fueling phases at stopover sites, facilitating the processing of energy-rich foods encountered during frequent migratory stops.[11,78]

In addition to structural remodeling, liver mass and digestive enzyme activity increase prior to migration, enhancing lipid processing and carbohydrate assimilation during periods

DOI: 10.36838/IJHSR810.83

of hyperphagia.[14,77] These changes are reversible: post-migratory birds exhibit regression of gut size and reduced digestive enzyme activity, minimizing maintenance costs once maximal digestive performance is no longer required.[11,17,46,76] Digestive plasticity is not exclusive to migratory species. Experimental studies in White-throated sparrows demonstrate that increased seasonal demands, such as cold exposure, can induce reversible enlargement of intestinal and hepatic tissues.[79] This suggests that gut flexibility is a generalized adaptive response to fluctuating energetic constraints rather than migration alone.[11,17]

Pre-migratory fattening is crucial to migratory success. Across multiple passerine and wader species, fat stores can reach 30-50% of body mass before departure, providing the primary fuel for sustained flight.[13,46,80] This fat accumulation is driven by pronounced hyperphagia and selective feeding, with birds preferentially consuming lipid and carbohydrate rich foods.[14,76] Experimental studies in migratory buntings and sparrows show that caloric intake can increase up to 60% above baseline during fueling periods, with the majority of assimilated energy directed towards subcutaneous and visceral fat stores.[13,14,80]

Hormonal regulation plays a central coordinating role in these digestive and metabolic changes. Cornelius *et al.* showed that pre-migratory corticosterone peaks coincide with elevated foraging activity, gut growth, and food intake, while rising thyroid hormone levels enhance metabolic rate and lipid mobilization.[8] Together, these endocrine shifts synchronize behavior, digestive organ remodeling, and nutrient assimilation, ensuring that energy acquisition and storage are optimally aligned with the timing and energetic demands of migration.[8,13]

The digestive system also undergoes molecular adaptations that facilitate rapid and efficient energy transfer from dietary intake to aerobic power output. In Western sandpipers, Guglielmo *et al.* found that fatty acid binding proteins (FABPs) are upregulated in both intestinal tissue and flight muscle during pre-migratory fattening, enhancing intracellular transport of absorbed fatty acids toward sites of oxidation.[45] By accelerating fatty acid trafficking from the gut to mitochondria, elevated FABP expression supports sustained lipid oxidation during flight and reduces dependence on carbohydrate metabolism.[13,14] This ensures that the high-energy demand of sustained wingbeats is met without delay, conserving limited muscle glycogen reserves.[13,14]

Seasonal shifts in digestive enzyme activity further reinforce this fuel-delivery system. Kovtun *et al.* reported pre-migratory increases in intestinal lipase and amylase activity in waders, reflecting enhanced capacity to process both lipid-rich and carbohydrate-rich diets during periods of rapid mass gain.[76] Comparable patterns of enzyme modulation and digestive upscaling have also been documented in migratory passerines.[11,46] This indicates that the biochemical flexibility of the gut is a general feature of migratory preparation rather than a shorebird-specific phenomenon. Together, these molecular and enzymatic adjustments tightly synchronize energy storage and utilization across organ systems during migration.

Convergent and Divergent Migratory Adaptations:

While the preceding sections emphasize shared physiological solutions to migration, not all migratory adaptations evolve uniformly. The interaction between geography, ecology, and phylogenetic history can result in both convergent and divergent evolution (Figure 1). On one hand, distantly related species often converge on similar morphological, physiological, and behavioral traits when exposed to the shared demands of long-distance flights. On the other hand, closely related lineages may diverge when ecological, geographical, and genetic variations impose distinct selective pressures. Together, these patterns highlight migration as both a unifying force shaping shared solutions and a diversifying driver promoting lineage-specific adaptations.[18]

On a generalized level, unrelated species frequently converge on similar migratory strategies when constrained by geography and atmospheric conditions. For example, many Western Hemisphere migrants undertaking trans-Gulf flights adopt looped or seasonally asymmetrical routes that exploit prevailing wind systems to reduce energetic costs.[81,82] In Central America and Northern South America, the narrowing of land corridors and the orientation of major mountain ranges channel migrants into partially overlapping pathways, promoting convergence in route selection across phylogenetically diverse lineages.[19] However, migration in the Americas does not follow a single uniform pathway. North American birds move through multiple north-south flyways that may diverge, merge, or shift seasonally depending on destination, weather, and ecological context.[83] This complexity highlights that convergence is strongest where geographic and atmospheric constraints are most restrictive, whereas divergence dominates in regions that offer multiple viable migratory options.

Behavioral strategies illustrate divergence under different ecological contexts. Within the wide-ranging songbird Northern wheatear (*Oenanthe oenanthe*), contrasting stopover and departure tactics have been documented between populations facing different onward migration distances.[84] Scandinavian wheatears (*Oenanthe oenanthe oenanthe*), crossing relatively short distances of up to 500 kilometers, typically depart stopover sites quickly regardless of immediate weather conditions. In contrast, Greenlandic and Icelandic conspecifics undertaking flights of up to 25,000 kilometers often prolong stopovers and time departures in relation to favorable conditions such as tailwinds and clear skies.[84] This intraspecific divergence in behavior underscores how ecological context can lead to distinct stopover and departure strategies within a single species. Moreover, divergent migratory strategies are linked to physiological performance at stopover in other songbirds as well. Long-distance migrating Gray catbirds (*Dumetella carolinesis*) exhibit a higher increase in plasma triglyceride concentration per unit increase in body mass compared to short-distance migrants during spring refueling.[85] This indicates variation in refueling performance tied to migratory distance within a species.

At the cellular level, high-performance mitochondrial traits have repeatedly evolved across distant species. Long-distance shorebirds, passerines, and high-altitude sparrows independently show increased mitochondrial density, elevated oxidative enzyme activity, and optimized cristae organization to increase ATP production efficiency.[44,86] This convergence highlights the intense selective pressures imposed by migration and demonstrates that natural selection can generate similar cellular "solutions" in unrelated lineages.[13,59] Convergent traits extend beyond energy output. For instance, species performing overwater migrations show reduced ROS emission even under high mitochondrial flux, suggesting that selection favors not only endurance but also cellular resilience to oxidative stress.[13,55,63] It is important to note that most of these studies are taxonomically concentrated toward passerines, shorebirds, and a few model species such as white-crowned sparrows and blackpoll warblers, with a strong emphasis on extreme long-distance migrants. Intermediate strategies, such as those employed by partial or short-distance migrants, remain poorly characterized, leaving gaps in understanding the spectrum of mitochondrial adaptations across the avian phylogeny. Expanding research to include diverse migratory behaviors and lineages could clarify the evolutionary and functional limitations of these cellular adaptations.

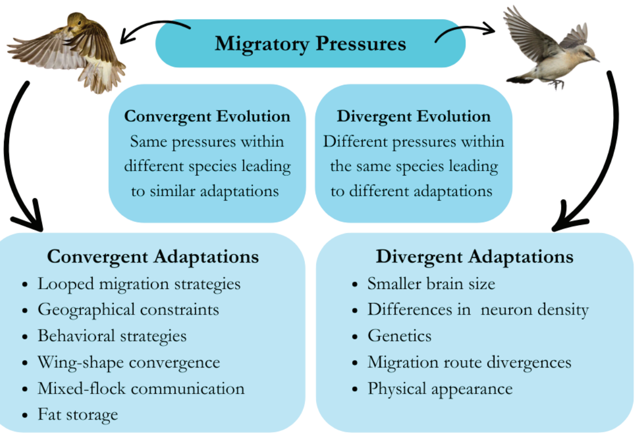

Figure 1: Schematic showing convergent and divergent evolution in migratory birds. Same migratory pressures promote similar traits across different species, while different migratory pressures can result in different traits in the same species.

At the genetic level, Common yellowthroats (*Geothlypis trichas*) with both migratory and resident populations illustrate how convergence and divergence can occur simultaneously within a single species. Eastern and western clades are genetically distinct, each carrying unique sets of single-nucleotide polymorphisms (SNPs) that reflect lineage-specific divergence.[87] Yet despite these differences, 27 out of 42 candidate genes overlap across populations, and these loci are associated with migratory timing, morphology, and metabolism.[87] Functionally, both migratory lineages have converged to have a similar adaptive response through different genetic routes. Moreover, resident populations in both clades show strong selection signals, suggesting that residency has independently evolved as a convergent response to year-round ecological pressures.[87] The Common yellowthroats therefore demonstrate that migration can drive both divergence in genetic pathways and produce convergence in phenotypic features.

Divergence is also evident in neurological evolution. Migratory Dark-eyed juncos have significantly higher hippocampal neuron density and superior spatial memory compared to their resident conspecifics, supporting advanced navigation during long-distance migration.[88] Similarly, adult sparrows show elevated hippocampal neurogenesis associated with migratory behavior, whereas juveniles do not, suggesting that neural plasticity is linked to both experience and the demands of migration.[89] Across passerines, migratory species may have smaller overall brain sizes compared to resident birds, which may reflect an energetic tradeoff in favor of specialized navigation and reduced developmental costs.[90] Hippocampal volume is also influenced by seasonal experience. Studies in warblers demonstrate that individuals exposed to migratory challenges exhibit larger hippocampi, highlighting the combined effects of environmental demands and age-related plasticity.[91] These findings illustrate how divergence and convergence in neurological structures enable migratory birds to balance spatial memory, cognitive demands, and energetic efficiency relative to resident species.

Morphological convergence further demonstrates the interplay of convergent and divergent evolution. Ficedula flycatchers show predictable scaling of wing pointedness and body size with migratory distance, within intermediate forms among short-distance migrants.[28,92] Long-distance migratory *Ficedula* species from different breeding and wintering grounds also display similar morphologies that have evolved independently.[28] These patterns highlight the sliding scale of migratory pressures that sculpt wing morphology in proportion to distance. Comparisons in shorebirds further reinforce this trend: among *Charadriidae* and *Scolopacidae*, long-distance migrants consistently evolve more pointed wings with reduced roundness and enhanced fat stores.[92] Quantitative analyses indicate that migration distance alone can explain up to 53% of the variation in wing shape.[92] These findings confirm a predictable, convergent relationship between wing pointedness and migration strategy, while interfamily differences emphasize lineage-specific divergence in achieving flight efficiency.

Convergence extends beyond morphology and physiology to communication and flight behaviors. Among North American wood warblers, migration has also shaped vocal behavior. Gayk *et al.*'s study on 36 species of wood warblers (*Parulidae*) found that birds with overlapping migratory ranges, breeding latitude, or migration distances had more acoustic similarities in their flight calls. In contrast, species with distinct migratory routes exhibited divergent calls. This suggests that acoustic convergence can be shaped by migratory pressures for communication within mixed flocks, increasing migratory success with a mixed variety of predator detectability and navigational knowledge.[93]

Together, migratory adaptations reveal the multi-layered strategies birds employ, linking molecular, cellular, and systemic changes into a unified migratory phenotype.

Conclusion

Migration has shaped more than isolated traits; it has forged a specialized, whole-organism phenotype finely tuned to the extreme demands of long-distance flight. This migratory phenotype represents a tightly integrated unit of anatomical, physiological, and molecular traits honed by natural selection to optimize endurance and efficiency. It is the coordination of skeletal, muscular, mitochondrial, cardiovascular, and digestive systems, and neural systems that underpins migratory success. The components of these adaptations that create the migratory phenotype are summarized in Figure 2.

At the core of the migratory phenotype is precise cross-system coupling. Lightweight, fused skeletal structures reduce mechanical stress and enhance flight stability. But this is only advantageous when paired with hypertrophied, oxidative-rich flight muscles capable of sustaining continuous wingbeats. These muscles rely on high mitochondrial density, optimized enzyme activity, and perfected oxygen delivery systems to maintain aerobic demands. Cardiac remodeling, including seasonal left ventricular hypertrophy, adjusts circulatory capacity to muscular workload, while digestive organs showcase pronounced phenotypic flexibility to maximize nutrient absorption during pre-migratory fattening. Even at the cellular scale, mitochondrial positioning ensures synchronized delivery of oxygen and lipid fuel, and endocrine signals trigger coordinated remodeling across muscle, heart, and gut. Collectively, these systems operate as an integrated network in which performance emerges from alignment rather than the sum of isolated traits.

Understanding the migratory phenotype has critical implications for conservation. Migratory success depends on tight cross-system coordination, and disruptions at any single stage can cascade across the migratory phenotype. Climate change has already been shown to alter photoperiod-temperature relations, leading to mistimed *Zugunruhe*, premature fattening, or departures that no longer align with peak food availability. This increases starvation risk and reduces reproductive success. Habitat loss at key stopover sites limits opportunities for refueling and digestive remodeling, resulting in incomplete migratory preparation and failed breeding attempts. Artificial light pollution further disrupts circadian and circannual cues, interfering with endocrine regulation of migration and increasing mortality through distortion and collision. These examples demonstrate that protecting migratory species requires conserving not only breeding and wintering grounds, but also the ecological corridors and environmental signals that allow the migratory phenotype to function as an integrated whole. Migration, therefore, stands as a powerful illustration of how evolution coordinates multi-level biological systems for extraordinary endurance and how vulnerable such calibrated adaptations are to anthropogenic change.

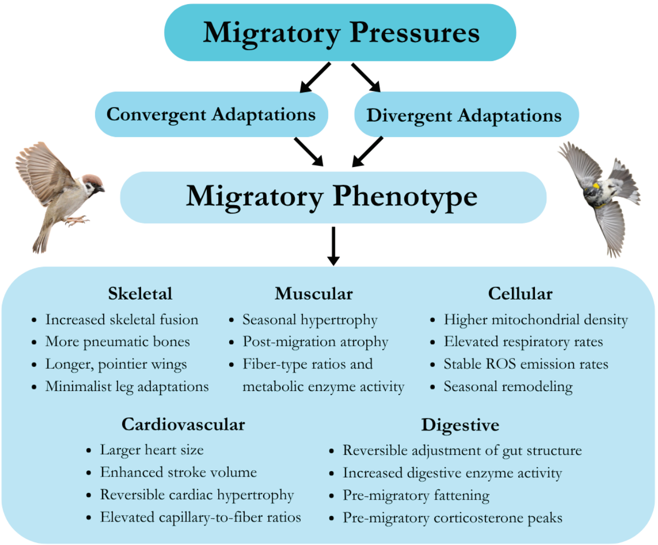

Figure 2: Schematic summarizing avian adaptations across skeletal, muscular, cellular, cardiovascular, and digestive systems in response to migratory pressures. These adaptations define the migratory phenotype, which is crucial for migratory success.

References

1. Butler, P. J. (2016). The physiological basis of bird flight. *Philosophical Transactions of the Royal Society B: Biological Sciences, 371*(1704), 20150384.
2. OBrien, S. J., Haussler, D., & Ryder, O. (2014). The birds of Genome10K. *GigaScience, 3*(1), 2047-217X.
3. Cooke, R., Sayol, F., Andermann, T., Blackburn, T. M., Steinbauer, M. J., Antonelli, A., & Faurby, S. (2023). Undiscovered bird extinctions obscure the true magnitude of human-driven extinction waves. *Nature Communications, 14*(1), 8116.
4. Matthews, T. J., Triantis, K. A., Wayman, J. P., Martin, T. E., Hume, J. P., Cardoso, P., ... & Sayol, F. (2024). The global loss of avian functional and phylogenetic diversity from anthropogenic extinctions. *Science, 386*(6717), 55-60.
5. Lennox, R. J., Chapman, J. M., Souliere, C. M., Tudorache, C., Wikelski, M., Metcalfe, J. D., & Cooke, S. J. (2016). Conservation physiology of animal migration. *Conservation Physiology, 4*(1), cov072.
6. Piersma, T., PÉREZ-TRIS, J. A. V. I. E. R., Mouritsen, H., Bauchinger, U. L. F., & Bairlein, F. (2005). Is there a "migratory syndrome" common to all migrant birds?. *Annals of the New York Academy of Sciences, 1046*(1), 282-293.
7. Jenni, L., & Jenni-Eiermann, S. (1998). Fuel supply and metabolic constraints in migrating birds. *Journal of Avian Biology*, 521-528.
8. Cornelius, J. M., Boswell, T., Jenni-Eiermann, S., Breuner, C. W., & Ramenofsky, M. (2013). Contributions of endocrinology to the migration life history of birds. *General and Comparative Endocrinology*, *190*, 47-60.
9. Helm, B., & Gwinner, E. (2006). Migratory restlessness in an equatorial nonmigratory bird. *PLoS biology, 4*(4), e110.
10. Pickett, S. M. (2021). *Zugunruhe (migratory restlessness)*. University of Kansas.
11. McWilliams, S. R., & Karasov, W. H. (2001). Phenotypic flexibility in digestive system structure and function in migratory birds and its ecological significance. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology, 128*(3), 577-591.

12. Mandal, S., Sant, S., Ahirwar, M. K., & Kumar, A. (2021). Migratory birds' physiology: A review. *Journal of Pharmaceutical Innovation*, *10*, 35-40.
13. Guglielmo, C. G. (2018). Obese super athletes: fat-fueled migration in birds and bats. *Journal of Experimental Biology, 221*(Suppl_1), jeb165753.
14. McWilliams, S. R., Guglielmo, C., Pierce, B., & Klaassen, M. (2004). Flying, fasting, and feeding in birds during migration: a nutritional and physiological ecology perspective. *Journal of Avian Biology, 35*(5), 377-393.
15. Piersma, T., & Van Gils, J. A. (2010). *The flexible phenotype: a body-centred integration of ecology, physiology, and behaviour*. OUP Oxford.
16. Marasco, V., Sebastiano, M., Costantini, D., Pola, G., & Fusani, L. (2021). Controlled expression of the migratory phenotype affects oxidative status in birds. *Journal of Experimental Biology, 224*(6), jeb233486.
17. Piersma, T. (2002). Energetic bottlenecks and other design constraints in avian annual cycles. *Integrative and comparative biology, 42*(1), 51-67.
18. Alerstam, T., Hedenström, A., & Åkesson, S. (2003). Long-distance migration: evolution and determinants. *Oikos, 103*(2), 247-260.
19. La Sorte, F. A., Fink, D., Hochachka, W. M., DeLong, J. P., & Kelling, S. (2014). Spring phenology of ecological productivity contributes to the use of looped migration strategies by birds. *Proceedings of the Royal Society B: Biological Sciences, 281*(1793), 20140984.
20. Egevang, C., Stenhouse, I. J., Phillips, R. A., Petersen, A., Fox, J. W., & Silk, J. R. (2010). Tracking of Arctic terns Sterna paradisaea reveals longest animal migration. *Proceedings of the National Academy of Sciences, 107*(5), 2078-2081.
21. James, H. F. (2009). Repeated evolution of fused thoracic vertebrae in songbirds. *The Auk, 126*(4), 862-872.
22. Aires, A. S., Reichert, L. M., Müller, R. T., & Andrade, M. B. (2022). Review of morphology, development, and evolution of the notarium in birds. *The Anatomical Record, 305*(9), 2079-2098.
23. Singh, N. S., Bamon, I., Dixit, A. S., & Sougrakpam, R. (2015). Structural variations and their adaptive significances in the bones of some migratory and resident birds. *The Journal of Basic & Applied Zoology, 70*, 33-40.
24. Louis, L. D., Bowie, R. C., & Dudley, R. (2022). Wing and leg bone microstructure reflects migratory demands in resident and migrant populations of the Dark-eyed Junco (Junco hyemalis). *Ibis, 164*(1), 132-150.
25. Schwarz, D., Kundrát, M., Tischlinger, H., Dyke, G., & Carney, R. M. (2019). Ultraviolet light illuminates the avian nature of the Berlin Archaeopteryx skeleton. *Scientific reports, 9*(1), 6518.
26. Skawiński, T., Kuziak, P., Kloskowski, J., & Borczyk, B. (2022). Phylogenetic Diversity of Ossification Patterns in the Avian Vertebral Column: A Review and New Data from the Domestic Pigeon and Two Species of Grebes. *Biology, 11*(2), 180.
27. Machado, J. P., Johnson, W. E., Gilbert, M. T. P., Zhang, G., Jarvis, E. D., O'Brien, S. J., & Antunes, A. (2016). Bone-associated gene evolution and the origin of flight in birds. *BMC genomics, 17*(1), 1-15.
28. Outlaw, D. C., & Nijman, V. (2011). Morphological evolution of some migratory Ficedula flycatchers. *Contributions to Zoology, 80*(4), 279-284.
29. Bui, H. N. N., & Larsson, H. C. (2021). Development and evolution of regionalization within the avian axial column. *Zoological Journal of the Linnean Society, 191*(1), 302-321.
30. Heers, A. M. (2023). Unexpected performance in developing birds. *Integrative and comparative biology, 63*(3), 772-784.
31. Biewener, A. A. (2011). Muscle function in avian flight: achieving power and control. *Philosophical Transactions of the Royal Society B: Biological Sciences, 366*(1570), 1496-1506.
32. Sullivan, S. P., McGechie, F. R., Middleton, K. M., & Holliday, C. M. (2019). 3D muscle architecture of the pectoral muscles of European Starling (Sturnus vulgaris). *Integrative Organismal Biology, 1*(1), oby010.
33. Hunt, E. S., Felice, R. N., Tobias, J. A., & Goswami, A. (2023). Ecological and life-history drivers of avian skull evolution. *Evolution, 77*(7), 1720-1729.
34. Norberg, U. M. (1995). Wing design and migratory flight. *Israel Journal of Ecology and Evolution, 41*(3), 297-305.
35. Vágási, C. I., Pap, P. L., Vincze, O., Osváth, G., Erritzøe, J., & Møller, A. P. (2016). Morphological adaptations to migration in birds. *Evolutionary Biology, 43*(1), 48-59.
36. Matyjasiak, P., López-Calderón, C., Ambrosini, R., Balbontín, J., Costanzo, A., Kiat, Y., ... & Rubolini, D. (2023). Wing morphology covaries with migration distance in a highly aerial insectivorous songbird. *Current Zoology, 69*(3), 255-263.
37. de la Hera, I., Hernández-Téllez, I., Pérez-Rigueiro, J., Pérez-Tris, J., Rojo, F. J., & Tellería, J. L. (2020). Mechanical and structural adaptations to migration in the flight feathers of a Palaearctic passerine. *Journal of Evolutionary Biology, 33*(7), 979-989.
38. Xu, Y., Price, M., Que, P., Zhang, K., Sheng, S., He, X., ... & Wang, B. (2023). Ecological predictors of interspecific variation in bird bill and leg lengths on a global scale. *Proceedings of the Royal Society B, 290*(2003), 20231387.
39. Zeffer, A., Johansson, L. C., & Marmebro, Å. (2003). Functional correlation between habitat use and leg morphology in birds (Aves). *Biological Journal of the Linnean Society, 79*(3), 461-484.
40. Kotnour, J., McPeek, S. J., Wedig, H., Dominguez, J., & Wright, N. A. (2022). Relative forelimb–hindlimb investment is associated with flight style, foraging strategy, and nestling period, but not nest type. *Ornithology, 139*(2), ukab084.
41. Heers, A. M., & Dial, K. P. (2015). Wings versus legs in the avian bauplan: development and evolution of alternative locomotor strategies. *Evolution, 69*(2), 305-320.
42. Evans, P. R., Davidson, N. C., Uttley, J. D., & Evans, R. D. (1992). Premigratory hypertrophy of flight muscles: an ultrastructural study. *Ornis Scandinavica*, 238-243.
43. Bauchinger, U. L. F., & Biebach, H. (2005). Phenotypic flexibility of skeletal muscles during long-distance migration of garden warblers: muscle changes are differentially related to body mass. *Annals of the New York Academy of Sciences, 1046*(1), 271-281.
44. Price, E. R., Bauchinger, U., Zajac, D. M., Cerasale, D. J., McFarlan, J. T., Gerson, A. R., ... & Guglielmo, C. G. (2011). Migration-and exercise-induced changes to flight muscle size in migratory birds and association with IGF1 and myostatin mRNA expression. *Journal of Experimental Biology, 214*(17), 2823-2831.
45. Guglielmo, C. G., Haunerland, N. H., & Williams, T. D. (1998). Fatty acid binding protein, a major protein in the flight muscle of migrating western sandpipers. *Comparative Biochemistry and Physiology Part B: Biochemistry and Molecular Biology, 119*(3), 549-555.
46. Biebach, H. (1996). Energetics of winter and migratory fattening. In *Avian energetics and nutritional ecology* (pp. 280-323). Boston, MA: Springer US.
47. Chang, R. M., Guglielmo, C. G., & Ivy, C. M. (2024). Seasonal modulation of pectoralis muscle fiber type composition in migratory songbirds. *Journal of Ornithology, 165*(4), 889-895.
48. Lewicki, L. M., Zhang, M., Staples, J. F., Guglielmo, C. G., & Ivy, C. M. (2025). A comparison of seasonal flexibility in pec-

toralis muscle fiber type and enzyme activity in migratory and resident sparrow species. *Journal of Experimental Biology, 228*(3), JEB249392.

49. Zhang, S., DuBay, S., Cheng, Y., Dong, Z., Liu, Z., & Wu, Y. (2025). Inter-and intraspecific variation in flight muscle fibers is associated with migratory timing. *Avian Research, 16*(1), 100223.
50. Coulson, S. Z., Guglielmo, C. G., & Staples, J. F. (2024). Migration increases mitochondrial oxidative capacity without increasing reactive oxygen species emission in a songbird. *Journal of Experimental Biology, 227*(9), jeb246849.
51. Dawson, W. R., Marsh, R. L., & Yacoe, M. E. (1983). Metabolic adjustments of small passerine birds for migration and cold. American Journal of Physiology-Regulatory, Integrative and Comparative Physiology, 245(6), R755-R767.
52. Groom, D. J., Black, B., Deakin, J. E., DeSimone, J. G., Lauzau, M. C., Pedro, B. P., ... & Gerson, A. R. (2023). Flight muscle size reductions and functional changes following long-distance flight under variable humidity conditions in a migratory warbler. *Physiological Reports, 11*(20), e15842.
53. Ivy, C. M., & Guglielmo, C. G. (2023). Migratory songbirds exhibit seasonal modulation of the oxygen cascade. *Journal of Experimental Biology, 226*(17), jeb245975.
54. Gaunt, A. S., Hikida, R. S., Jehl, J. R., & Fenbert, L. (1990). Rapid atrophy and hypertrophy of an avian flight muscle. *The Auk, 107*(4), 649-659.
55. Weber, J. M. (2009). The physiology of long-distance migration: extending the limits of endurance metabolism. *Journal of Experimental Biology, 212*(5), 593-597.
56. Cao, T., & Jin, J. P. (2020). Evolution of flight muscle contractility and energetic efficiency. *Frontiers in Physiology, 11*, 1038.
57. Rhodes, E. M., Yap, K. N., Mesquita, P. H., Parry, H. A., Kavazis, A. N., Krause, J. S., ... & Hood, W. R. (2024). Flexibility underlies differences in mitochondrial respiratory performance between migratory and non-migratory White-crowned Sparrows (Zonotrichia leucophrys). *Scientific Reports, 14*(1), 9456.
58. McFarlan, J. T., Bonen, A., & Guglielmo, C. G. (2009). Seasonal upregulation of fatty acid transporters in flight muscles of migratory white-throated sparrows (Zonotrichia albicollis). *Journal of Experimental Biology, 212*(18), 2934-2940.
59. Coulson, S. Z. (2024). *Effects of evolved migration strategy, seasonal flexibility, and endurance flight on songbird mitochondrial bioenergetics* (Doctoral dissertation, The University of Western Ontario (Canada)).
60. Toews, D. P., Mandic, M., Richards, J. G., & Irwin, D. E. (2014). Migration, mitochondria, and the yellow-rumped warbler. *Evolution, 68*(1), 241-255.
61. Trivedi, A. K., Malik, S., Rani, S., & Kumar, V. (2015). Adaptation of oxidative phosphorylation to photoperiod-induced seasonal metabolic states in migratory songbirds. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology, 184*, 34-40.
62. Gillies, A. R., & Lieber, R. L. (2011). Structure and function of the skeletal muscle extracellular matrix. *Muscle & nerve, 44*(3), 318-331.
63. Mesquita, P. H., Rhodes, E. M., Yap, K. N., Mueller, B. J., Hill, G. E., Hood, W. R., & Kavazis, A. N. (2024). Mitochondrial remodelling supports migration in white-crowned sparrows (Zonotrichia leucophrys). *Proceedings B, 291*(2036), 20242409.
64. Jenni-Eiermann, S., Liechti, F., Briedis, M., Rime, Y., & Jenni, L. (2024). Energy supply during nocturnal endurance flight of migrant birds: effect of energy stores and flight behaviour. *Movement Ecology, 12*(1), 41.
65. Bhardwaj, N., Kumar, A., & Gupta, N. J. (2023). Altered dynamics of mitochondria and reactive oxygen species in the erythrocytes of migrating red-headed buntings. *Frontiers in Physiology, 14*, 1111490.
66. Napolitano, G., Fasciolo, G., & Venditti, P. (2021). Mitochondrial management of reactive oxygen species. *Antioxidants, 10*(11), 1824.
67. Kumar, A., Bhardwaj, N., Rajaura, S., Afzal, M., & Gupta, N. J. (2024). Inter-organ differences in redox imbalance and apoptosis depict metabolic resilience in migratory redheaded buntings. *Scientific Reports, 14*(1), 20184.
68. Hood, W. R. (2024). Mechanisms that Alter Capacity for Adenosine Triphosphate Production and Oxidative Phosphorylation: Insights from Avian Migration. *Integrative and Comparative Biology, 64*(6), 1811-1825.
69. Pegan, T. M., Berv, J. S., Gulson-Castillo, E. R., Kimmitt, A. A., & Winger, B. M. (2024). The pace of mitochondrial molecular evolution varies with seasonal migration distance. *Evolution, 78*(1), 160-173.
70. Rhodes, E. M., Yap, K. N., Hill, G. E., & Hood, W. R. (2024). A comparison of the mitochondrial performance between migratory and sedentary mimid thrushes. *Integrative and Comparative Biology, 64*(6), 1859-1870.
71. Cornelius, J. M., Hahn, T. P., Robart, A. R., Vernasco, B. J., Zahor, D. L., Glynn, K. J., ... & Watts, H. E. (2021). Seasonal patterns of fat deposits in relation to migratory strategy in facultative migrants. *Frontiers in Ecology and Evolution, 9*, 691808.
72. Soriano-Redondo, A., Gutiérrez, J. S., Hodgson, D., & Bearhop, S. (2020). Migrant birds and mammals live faster than residents. *Nature Communications, 11*(1), 5719.
73. King, M. O., Zhang, Y., Carter, T., Johnson, J., Harmon, E., & Swanson, D. L. (2015). Phenotypic flexibility of skeletal muscle and heart masses and expression of myostatin and tolloid-like proteinases in migrating passerine birds. *Journal of Comparative Physiology B, 185*(3), 333-342.
74. Hahn, S., Emmenegger, T., Riello, S., Serra, L., Spina, F., Buttemer, W. A., & Bauer, S. (2022). Short-and long-distance avian migrants differ in exercise endurance but not aerobic capacity. *BMC zoology, 7*(1), 29.
75. Ramenofsky, M., Campion, A. W., Hwee, D. T., Wood, S. K., Krause, J. S., Németh, Z., ... & Bodine, S. (2024). Comparison of the phenotypic flexibility of muscle and body condition of migrant and resident white-crowned sparrows. *Ecological and evolutionary physiology, 97*(1), 11-28.
76. Kovtun, M. F., Lykova, I. O., & Kharchenko, L. P. (2018). The plasticity and morphofunctional organization of the digestive system of waders (charadrii) as migrants.
77. Stein, R. W., Place, A. R., Lacourse, T., Guglielmo, C. G., & Williams, T. D. (2005). Digestive organ sizes and enzyme activities of refueling western sandpipers (Calidris mauri): contrasting effects of season and age. *Physiological and Biochemical Zoology, 78*(3), 434-446.
78. Biebach, H. (1998). Phenotypic organ flexibility in Garden Warblers Sylvia borin during long-distance migration. *Journal of Avian Biology*, 529-535.
79. McWilliams, S. R., & Karasov, W. H. (2014). Spare capacity and phenotypic flexibility in the digestive system of a migratory bird: defining the limits of animal design. *Proceedings of the Royal Society B: Biological Sciences, 281*(1783), 20140308.
80. Biebach, H., Friedrich, W., & Heine, G. (1986). Interaction of bodymass, fat, foraging and stopover period in trans-Sahara migrating passerine birds. *Oecologia, 69*(3), 370-379.
81. Alerstam, T. (1979). Wind as selective agent in bird migration. *Ornis Scandinavica*, 76-93.

82. Buler, J. J., & Moore, F. R. (2011). Migrant–habitat relationships during stopover along an ecological barrier: extrinsic constraints and conservation implications. *Journal of Ornithology, 152*(Suppl 1), 101-112.
83. La Sorte, F. A., Fink, D., Hochachka, W. M., & Kelling, S. (2016). Convergence of broad-scale migration strategies in terrestrial birds. *Proceedings of the Royal Society B: Biological Sciences, 283*(1823), 20152588.
84. Dierschke, V., & Delingat, J. (2001). Stopover behaviour and departure decision of northern wheatears, Oenanthe oenanthe, facing different onward non-stop flight distances. *Behavioral Ecology and Sociobiology, 50*(6), 535-545.
85. Griego, M., Ramirez, M. G., & Gerson, A. R. (2025). Divergent migratory strategies lead to variable refueling performance amongst Gray Catbirds (Dumetella carolinensis) during spring stopover in the Gulf of Mexico. *Movement Ecology, 13*(1), 1-12.
86. Burskaia, V., Artyushin, I., Potapova, N. A., Konovalov, K., & Bazykin, G. A. (2021). Convergent adaptation in mitochondria of phylogenetically distant birds: does it exist?. *Genome Biology and Evolution, 13*(7), evab113.
87. Zamudio-Beltrán, L. E., Bossu, C. M., Bueno-Hernández, A. A., Dunn, P. O., Sly, N. D., Rayne, C., ... & Ruegg, K. C. (2025). Parallel and convergent evolution in genes underlying seasonal migration. *Evolution Letters, 9*(2), 189-208.
88. Cristol, D. A., Reynolds, E. B., Leclerc, J. E., Donner, A. H., Farabaugh, C. S., & Ziegenfus, C. W. (2003). Migratory dark-eyed juncos, Junco hyemalis, have better spatial memory and denser hippocampal neurons than nonmigratory conspecifics. *Animal behaviour, 66*(2), 317-328.
89. LaDage, L. D., Roth, T. C., & Pravosudov, V. V. (2011). Hippocampal neurogenesis is associated with migratory behaviour in adult but not juvenile sparrows (Zonotrichia leucophrys ssp.). *Proceedings of the Royal Society B: Biological Sciences, 278*(1702), 138-143.
90. Sol, D., Garcia, N., Iwaniuk, A., Davis, K., Meade, A., Boyle, W. A., & Szekely, T. (2010). Evolutionary divergence in brain size between migratory and resident birds. *PLoS One, 5*(3), e9617.
91. Healy, S. D., Gwinner, E., & Krebs, J. R. (1996). Hippocampal volume in migratory and non-migratory warblers: effects of age and experience. *Behavioural Brain Research, 81*(1-2), 61-68.
92. Minias, P., Meissner, W., Włodarczyk, R., Ożarowska, A., Piasecka, A., Kaczmarek, K., & Janiszewski, T. (2015). Wing shape and migration in shorebirds: a comparative study. *Ibis, 157*(3), 528-535.
93. Gayk, Z. G., Simpson, R. K., & Mennill, D. J. (2021). The evolution of wood warbler flight calls: Species with similar migrations produce acoustically similar calls. *Evolution, 75*(3), 719-730.

■ Author

Arshi Aggarwal is a senior at the International School of Beaverton in Oregon. She has been fascinated by birds and other animals since childhood. In college, she wants to pursue an understanding of human-animal interactions through an anthropology and ecology lens.

DOI: 10.36838/IJHSR810.83