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International Journal of Molecular Zoology 2024, Vol.14, No.2, 111-127
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Feature Review **Open Access**

Chronobiology of Migratory Patterns in Animals

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International Journal of Molecular Zoology, 2024, Vol.14, No.2 doi: 10.5376/ijmz.2024.14.0012
Received: 13 Feb., 2024
Accepted: 25 Mar., 2024
Published: 16 Apr., 2024

Preferred citation for this article:
Li J.Y., and Chen M.Y., 2024, Chronobiology of migratory patterns in animals, International Journal of Molecular Zoology, 14(2): 111-127 (doi: 10.5376/ijmz.2024.14.0012)

Abstract This study synthesizes current knowledge on the chronobiology of migratory patterns in animals, focusing on the genetic, physiological, and environmental factors that influence these patterns. Key discoveries in the field highlight the role of endogenous circadian clocks in regulating migratory behaviors across various species. For instance, studies on North American monarch butterflies (*Danaus plexippus*) have shown evolutionary adaptations in clock genes that enable these insects to cope with different latitudinal environments. In birds, polymorphisms in clock genes such as *Clock* and *Adcyap1* have been linked to seasonal migratory timing, although these genes are not definitive markers for distinguishing migratory from sedentary species. Research on the American kestrel has identified multiple biological time-keeping genes that influence migratory timing, suggesting the existence of distinct migratory genotypes within populations. Furthermore, the interplay between circadian and circatidal rhythms has been observed in marine organisms, indicating a complex interaction between different environmental cues and endogenous clocks. The findings underscore the intricate relationship between endogenous biological clocks and migratory behaviors in animals. Understanding these mechanisms not only provides insights into the evolutionary adaptations of species but also has broader implications for conservation strategies and predicting the impacts of climate change on migratory patterns.

Keywords Chronobiology; Migratory patterns; Circadian clocks; Clock genes; Evolutionary adaptations; Environmental cues

1 Introduction

Chronobiology is the scientific study of biological rhythms and their mechanisms. It encompasses the investigation of periodic (cyclic) phenomena in living organisms and their adaptation to solar- and lunar-related rhythms. These biological rhythms, which include circadian (daily), infradian (longer than a day), and ultradian (shorter than a day) cycles, are crucial for the regulation of various physiological processes such as sleep-wake cycles, hormone release, and feeding patterns (Dominoni et al., 2017). The field of chronobiology has advanced significantly with the development of novel methodologies to measure rhythmicity at different levels of biological organization, from locomotor activity to gene expression (Dominoni et al., 2017).

The study of migratory patterns in animals is of paramount importance for several reasons. Migration is a complex behavioral adaptation that has evolved across the animal kingdom, allowing species to exploit different habitats and resources seasonally (Merlin and Liedvogel, 2019). Understanding the mechanisms underlying migration can provide insights into the evolutionary processes that shape these behaviors and the genetic and epigenetic factors involved (Liedvogel et al., 2011; Mueller et al., 2011; Merlin and Liedvogel, 2019). Moreover, migratory species face increasing challenges due to habitat fragmentation, climate change, and over-exploitation, making it essential to quantify migration parameters and predict migratory movements for effective conservation and management (Bunnefeld et al., 2011). Additionally, migration has significant implications for the life-history strategies of animals, influencing their survival and reproduction schedules (Soriano-Redondo et al., 2020).

This study investigates the chronobiology of animal migration patterns, focusing on the mechanisms regulating the timing and expression of migration. By integrating environmental cues and endocrine responses, this study aims to understand how different types of migration—obligatory, nomadic, and evasive—are regulated, and how these mechanisms vary among species; additionally, explores the genetic and epigenetic basis of migratory behavior; identifies candidate genes and regulatory elements that control these traits. By achieving these goals, this study will advance the understanding of the chronobiology of migration patterns, highlight the complex interplay of genetic, physiological, and environmental factors in shaping these remarkable behaviors, contribute to a broader understanding of migration biology, and inform conservation strategies for migratory species facing environmental changes.

2 Biological Rhythms and Migration

2.1 Types of biological rhythms

Biological rhythms are intrinsic cycles that regulate various physiological and behavioral processes within organisms. These rhythms can be classified into several types based on their periodicity, including circadian rhythms, circannual rhythms, ultradian rhythms, and infradian rhythms.

Circadian rhythms have a period of approximately 24 hours, synchronized with the Earth's rotation, and influence daily activities such as the sleep-wake cycle, feeding, and hormone release. Circadian rhythms are driven by internal biological clocks and are synchronized with external cues like light and temperature (Shochat and Tauber, 2021). Circannual rhythms follow an annual cycle, regulating seasonal behaviors such as migration, reproduction, and hibernation. Circannual rhythms help organisms adapt to the changing environmental conditions throughout the year (Clercq et al., 2023). Ultradian rhythms have periods shorter than 24 hours, such as the 90-minute sleep cycle in humans or certain feeding patterns in animals (Mazzoccoli, 2022). Infradian rhythms have periods longer than 24 hours but shorter than a year, such as the menstrual cycle in humans (Bellastella et al., 2021).

2.2 Mechanisms of biological clocks

Biological clocks are complex molecular mechanisms that generate and regulate these rhythms. The core components of biological clocks are highly conserved across different species, involving feedback loops of gene expression and protein interactions. At the cellular level, biological clocks are regulated by a set of core clock genes and proteins that produce rhythmic oscillations. In the circadian rhythm system, genes such as *CLOCK*, *BMAL1*, *PER*, and *CRY* form feedback loops, resulting in rhythmic gene expression and protein activity (Yuan et al., 2018; Clercq et al., 2023). In mammals, the suprachiasmatic nucleus (SCN) located in the hypothalamus acts as the master circadian regulator. The SCN receives light information from the retina and synchronizes peripheral clocks throughout the body, maintaining the coordination of circadian rhythms (Bellastella et al., 2021; Shochat and Tauber, 2021). These clocks exist in various tissues and organs, and while they can operate independently, they are usually synchronized by the SCN. Peripheral clocks regulate specific functions of tissues, such as metabolism and hormone secretion (Yeung and Naef, 2018; Costa, 2021).

Moreover, light is the primary environmental cue influencing biological rhythms. The photoperiod, or the length of daylight, is particularly important for circannual rhythms, as changes in daylight duration provide appropriate signals for migration, reproduction, or other seasonal behaviors. Hormones, such as melatonin and cortisol, play crucial roles in transmitting circadian and seasonal information to various physiological systems, thereby influencing the preparation and execution of migration.

2.3 Interaction between biological rhythms and migration

Migration is a complex behavior influenced by both circadian and circannual rhythms. These rhythms help migratory animals anticipate and prepare for seasonal changes, ensuring that they migrate at the optimal time to enhance their chances of survival and reproduction. Studies have shown that circadian rhythms can affect the timing of migratory activities, such as the initiation of flight in birds or the timing of feeding and resting during migration. Circadian rhythms help animals maintain energy balance and navigation during migration (Shochat and Tauber, 2021; Clercq et al., 2023).

Circannual rhythms are crucial for the timing of long-distance migrations. These rhythms ensure that animals' migrations are synchronized with seasonal changes in food availability, breeding conditions, and climate. For example, birds use circannual rhythms to align their migration timing with favorable conditions at their breeding and wintering grounds (Clercq et al., 2023). Research indicates that variations in clock genes can also influence migratory behavior. Polymorphisms in genes such as *Clock* and *Adcyap1* have been associated with differences in migration timing and distance in birds (Clercq et al., 2023).

In addition to the important role of internal clocks, external cues such as light, temperature, and food availability also influence migratory patterns. These cues help synchronize internal rhythms with the external environment, ensuring successful migration (Bellastella et al., 2021). Understanding these rhythms and their mechanisms provides crucial insights into how animals adapt to their environments and optimize their survival strategies.

3 Environmental Cues and Migratory Timing

3.1 Photoperiod and seasonal changes

Photoperiod, or the length of day, is a critical environmental cue that influences the timing of migration in many animal species. Birds, for instance, exhibit daily (circadian) and seasonal biological rhythms that are often synchronized with changes in day length. This synchronization helps them prepare for migration by inducing physiological and behavioral changes necessary for the journey. For example, in pine siskins, variation in chronotype, which is influenced by photoperiod, is associated with the timing of spring migration (Rittenhouse et al., 2019). Additionally, photoperiod-induced changes in behavior and physiology, such as body fattening and migratory restlessness, are crucial for the success of migration in Palearctic-Indian migratory buntings (Sharma et al., 2022).

3.2 Temperature and climatic factors

Temperature is another significant environmental cue that affects migratory timing. Birds often use local temperature conditions to decide when to start their migration. For instance, Asian houbara (*Chlamydotis macqueenii*) use local temperature cues to time their spring migration departure, with individual birds showing consistent responses to temperature across multiple years (Burnside et al., 2021). Similarly, climatic factors such as temperature and precipitation play a crucial role in shaping the migratory strategies of bird species like the Eastern Kingbird (*Tyrannus tyrannus*) and Fork-tailed Flycatcher (*Hemitriccus furcatus*). These species track temperature and precipitation patterns to optimize their migratory routes and timing (MacPherson et al., 2018). Furthermore, changes in temperature due to climate change have been shown to influence the timing of migration in wading birds, with some species migrating later in response to rising temperatures (Mondain-Monval et al., 2021).

3.3 Food availability and resource distribution

Food availability and resource distribution are also key factors that influence migratory timing. Animals often time their migrations to coincide with periods of high resource availability to maximize their chances of survival and reproductive success. For example, spatial and temporal fluctuations in resource availability have led to the evolution of varied migration patterns in different species. Obligate migrants, which undertake regular annual migrations, often move between locations where resources are predictable and sufficient (Watts et al., 2018). Intraspecific variation in migratory destinations among North American bird species suggests that access to resources during the breeding season is a significant driver of migration (Bonnet-Lebrun et al., 2020). Additionally, the availability of food resources during the non-breeding season, such as high precipitation areas that support abundant food, influences the migratory patterns of species like the Eastern Kingbird (*Tyrannus tyrannus*) and Fork-tailed Flycatcher (*Hemitriccus furcatus*) (MacPherson et al., 2018).

Environmental cues such as photoperiod, temperature, and food availability play crucial roles in determining the timing of migration in animals. These cues help animals optimize their migratory strategies to ensure successful navigation and survival across different habitats and seasons. Understanding these cues and their interactions is essential for predicting how migratory species will respond to changing environmental conditions.

4 Genetic and Epigenetic Regulation of Migration

4.1 Genetic basis of migration

Migration is a complex trait influenced by various genetic factors. Research indicates that migratory behaviors, such as timing and direction, are often under strong genetic control. Merlin and Liedvogel (2019) explored the genetics and epigenetics of animal migration and orientation, with a focus on the migratory behaviors of the European blackcap (*Sylvia atricapilla*) and the North American monarch butterflies (*Danaus plexippus*). Their studies revealed significant genetic differences in migratory behavior among species. For instance, the migratory direction and distance of the European blackcap are genetically controlled, whereas the migratory behavior of the North American monarch butterfly is triggered by seasonal environmental changes (Figure 1), indicating that epigenetic mechanisms play an important role in its migration process.

In the Yellow-throated Bunting (*Emberiza elegans*), genomic analyses revealed that genes related to energy metabolism, nervous system function, and circadian rhythms play crucial roles in regulating migratory behavior (Zhang et al., 2022). Additionally, in the American kestrel (*Falco sparverius*), genetic variations in metabolic and light-input pathway genes were found to be significantly associated with migratory timing, suggesting a polygenic basis for this trait (Bossu et al., 2022). The genetic architecture of migration is further exemplified by the presence of chromosomal inversions in rainbow trout, which maintain linked genes controlling migratory behavior (Arostegui et al., 2019).

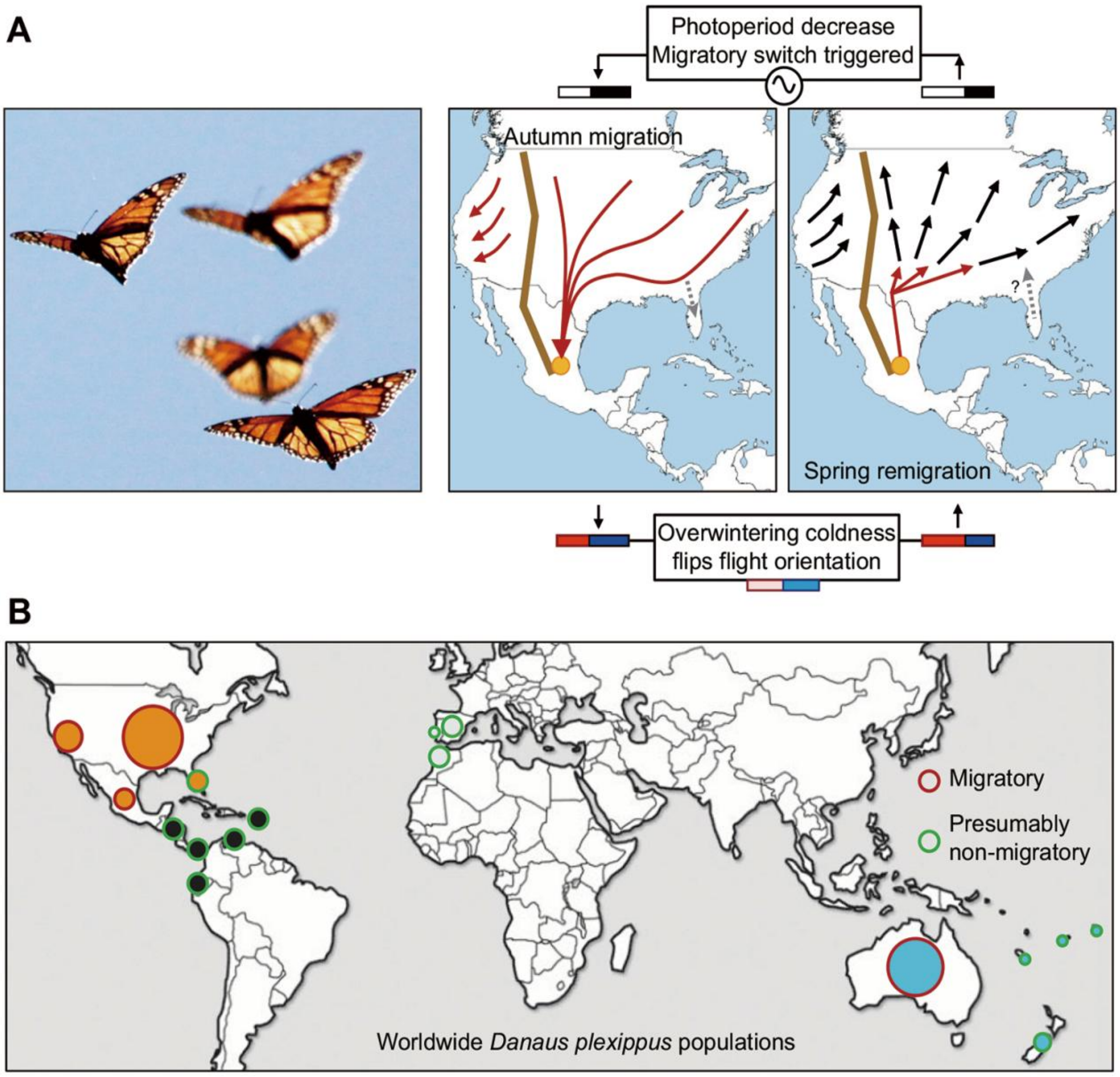

Figure 1 Annual migratory cycle of North American monarch butterflies (*Danaus plexippus*) and world-wide distribution of monarch populations (Adopted from Merlin and Liedvogel, 2019)

Image caption: Figure A describes the migration path of the North American monarch butterfly (*Danaus plexippus*), migrating from northern breeding sites to overwintering sites in Mexico during the fall and returning to breed in the southern United States in the spring. The migration behavior is influenced by photoperiod and temperature changes, indicating an epigenetic regulation of migration. Figure B shows the global distribution of monarch butterflies, where only populations in North America and Australia exhibit seasonal migration, while populations in other regions are primarily non-migratory. The image reveals the geographical and genetic diversity of migration behavior (Adapted from Merlin and Liedvogel, 2019)

4.2 Epigenetic modifications and phenotypic plasticity

Epigenetic modifications also play a critical role in the regulation of migratory behaviors. These modifications can influence gene expression without altering the underlying DNA sequence, thereby contributing to phenotypic plasticity. For example, Sharma et al. (2018) explored the physiological and gene expression changes in the red-headed bunting (*Emberiza bruniceps*) during spring and autumn migrations. The study hypothesized that birds employ different molecular strategies during spring and autumn migrations to meet varying environmental demands. By simulating photoperiods, the researchers investigated the changes in behavior, physiology, and gene expression in birds under migratory and non-migratory states. The study found that birds migrating in spring exhibited higher body fat and weight, as well as more intense migratory restlessness (Zugunruhe), compared to those migrating in autumn, which had lower body fat and weight. Additionally, the study revealed significant changes in the expression of epigenetic genes (such as *dnmt3a* and *tet2*) during migratory states, suggesting that epigenetics play a crucial role in seasonal migration. These findings provide an important molecular basis for understanding the adaptive mechanisms of migratory birds.

In the study of physiological and molecular changes in *Emberiza bruniceps* during spring migration, Sharma et al. (2021; 2022) focused on the changes in gene expression and protein levels related to fatty acid synthesis and transport in the liver and flight muscles. The research found that genes associated with fatty acid synthesis (*acc*, *dgat2*) and transport (*cd36*, *fabp3*, *cpt1*) were upregulated in the migratory state. Furthermore, increased expression of genes related to calcium signaling, cellular stress, and metabolic pathways was observed in the mediobasal hypothalamus, indicating that energy utilization during migration is epigenetically regulated.

4.3 Inheritance of migratory behaviors

The genetics of migratory behavior is a complex process involving genetic and epigenetic factors. In blackpoll warblers (*Setophaga striata*), it has been found that variations in the lengths of candidate genes such as *Clock* and *Adcyap1* are significantly correlated with migratory traits such as timing and duration. The maximum allele length of the *Clock* gene is significantly negatively correlated with spring arrival dates, while the minimum allele length of the *Adcyap1* gene is significantly associated with spring departure dates and fall arrival dates (Ralston et al., 2019). Additionally, the study found an interaction effect between the lengths of the *Clock* and *Adcyap1* genes on the duration of migration. These results indicate that specific genetic variations can be inherited and influence migratory behavior across generations.

Additionally, the study on European blackcaps demonstrated that the propensity to migrate, as well as the orientation and distance of migration, mapped to specific genomic regions, indicating a heritable component to these traits (Delmore et al., 2020). The retention of chromosomal inversions in rainbow trout (*Oncorhynchus mykiss*) also highlights the role of genetic inheritance in maintaining migratory behaviors within populations (Arostegui et al., 2019). The genetic and epigenetic regulation of migration involves a complex interplay of multiple genes and epigenetic modifications that contribute to the phenotypic plasticity and inheritance of migratory behaviors in animals. Understanding these mechanisms is crucial for elucidating how migratory species adapt to changing environments and for the conservation of migratory populations.

5 Physiological Adaptations to Migration

5.1 Energy metabolism and fat storage

Migratory animals exhibit a range of physiological adaptations that enable them to undertake long-distance journeys. These adaptations are crucial for optimizing energy use, enhancing endurance, and regulating the physiological changes necessary for migration. Energy metabolism and fat storage are critical for migratory animals, as these processes provide the necessary fuel for long-distance travel. Migratory birds, for instance, accumulate substantial fat reserves, which can constitute up to 50%-60% of their body mass. These fat stores are then oxidized at high rates to sustain prolonged flight (Guglielmo, 2018). The ability to store and utilize fat efficiently is supported by high capacities for fatty acid uptake, cytosolic transport, and oxidation in the flight muscles. Additionally, changes in energy intake, digestive capacity, and liver lipid metabolism contribute to migratory fattening.

Talal et al. (2023) discussed how high carbohydrate intake affects lipid storage and migratory flight capacity in locusts. The study found that locusts consuming high carbohydrates performed better in both total flight time and the longest single flight duration, with fewer pauses. These findings suggest that carbohydrates not only provide energy for migratory flights but may also extend flight time by reducing oxidative stress and minimizing water loss through various mechanisms. Similarly, migratory birds exhibit elevated levels of triglycerides and free fatty acids during migration, which are essential for meeting the high energy demands of flight (Sharma et al., 2022).

5.2 Muscle physiology and endurance

Muscle physiology and endurance are also vital for migration. Migratory birds undergo significant changes in their flight muscles, including hypertrophy and increased aerobic capacity, to support sustained flight. For example, DeMoranville et al. (2019) studied the physiological changes in gray catbirds (*Dumetella carolinensis*) throughout their annual cycle, particularly during the pre-migratory preparation and migration periods. The study found that the metabolic rate of gray catbirds was highest during migration, with significant increases in the heart and flight muscles during pre-migration and migration periods. Additionally, the research revealed the importance of transcription factors such as PPARs and ERRs in regulating the metabolism of the flight muscles and heart of gray catbirds, especially in the utilization and storage of fatty acids during migration. These findings suggest that migratory birds adapt to different stages of their annual cycle through metabolic and muscle flexibility. Furthermore, the hypertrophy of flight muscles is accompanied by changes in heart mass and mitochondrial content, further supporting the high metabolic demands of migration (DeMoranville et al., 2019).

In a study by Vernasco et al. (2021), it was found that the pectoral muscles of the nomadic migratory bird pine siskin (*Spinus pinus*) undergo significant changes during migration preparation, including hypertrophy and alterations in endocrine signaling components. These changes are crucial for regulating the entry into the migratory state and supporting the high energy demands of flight. Similarly, the light-bellied brent goose (*Branta bernicla hrota*) exhibits a strategic delay in migratory departure to enable the reorganization of its physiology into a flying phenotype, which includes the atrophy of non-essential organs and the growth of flight muscles (Handby et al., 2022).

5.3 Hormonal regulation

Hormonal regulation plays a crucial role in mediating the physiological changes associated with migration. Changes in photoperiod and environmental cues trigger neuroendocrine responses that regulate the timing and progression of migration. For instance, migratory birds exhibit elevated levels of triiodothyronine and corticosterone, which are associated with increased fattening and migratory restlessness (Sharma et al., 2022). The expression of genes involved in thyroid hormone signaling and dopamine biosynthesis also changes in response to migratory cues, highlighting the importance of hormonal regulation in migration (Sharma et al., 2022).

Studies have found that in the pine siskin (*Spinus pinus*), the expression of endocrine signaling components in the flight muscles changes during the transition into the migratory state. These changes indicate that the endocrine system plays a crucial role in regulating the physiological adaptations required for migration (Vernasco et al., 2021). Additionally, the regulation of appetite and fuel store set-points by neuroendocrine mechanisms is crucial for ensuring that migratory animals accumulate sufficient energy reserves for their journeys (Guglielmo, 2018).

In summary, the physiological adaptations to migration involve complex interactions between energy metabolism, muscle physiology, and hormonal regulation. These adaptations enable migratory animals to optimize their energy use, enhance their endurance, and regulate the physiological changes necessary for successful migration.

6 Navigation and Orientation Mechanisms

6.1 Magnetic compass and geomagnetic fields

Many migratory animals utilize Earth's magnetic field as a crucial navigational aid. This ability, known as magnetoreception, allows animals to detect the geomagnetic field and use it as a compass to determine their spatial orientation. Birds, sea turtles, fishes, crustaceans, and insects are among the diverse taxa that depend on this field for both short- and long-range navigation (Warrant, 2021).

Magnetoreception mechanisms are hypothesized to involve magnetically sensitive proteins called cryptochromes, located in the retina, which form magnetically sensitive chemical intermediates known as radical pairs when they absorb photons of light (Warrant, 2021). Additionally, some animals use the inclination or tilt of magnetic field lines as a component of their magnetic compass sense, which can help maintain migratory headings and even distinguish among different inclination angles to exploit inclination as a surrogate for latitude (Wynn et al., 2020; Taylor et al., 2021).

Experiments have shown that magnetic map cues can elicit homeward orientation in species like sharks and pink salmon, suggesting that these animals use a magnetic map to derive positional information (Putman et al., 2020; Keller et al., 2021). The study found that sharks can distinguish different positional cues from the geomagnetic field to navigate. This discovery is significant for understanding shark migration behavior and population structure in the marine environment (Keller et al., 2021). However, the magnetic sense is often considered 'noisy' and less reliable than other cues, which may explain why animals do not rely exclusively on geomagnetic fields for navigation (Johnsen et al., 2020).

6.2 Celestial navigation

Celestial navigation is another crucial orientation mechanism used by migratory species. The position of the sun during the day and the stars at night provide reliable directional cues. For instance, birds utilize the position of the sun in the sky and their internal circadian clocks to maintain a constant direction (Mouritsen, 2018). This solar compass mechanism requires birds to adjust their direction based on the time of day, and thanks to their internal clocks, they can do so accurately. Studies have shown that birds can adjust their flight path based on the sun's position during the day and maintain a stable direction during migration. For example, homing pigeons use the angle of the sun to calibrate their flight path during long-distance flights; even when encountering cloud cover or other environmental disturbances, they can rely on their internal biological clock to make corrections (Padget et al., 2018). This ability not only ensures that birds can complete their migratory tasks accurately but also demonstrates the optimization of navigational abilities through natural selection in the evolutionary process.

At night, many migratory birds switch to using the stars for navigation. They can identify constellations and use them to determine their position and direction (Mouritsen, 2018). Experiments on nocturnal migratory birds have shown that they can determine direction using simulated night skies, demonstrating their reliance on celestial navigation. In the Northern Hemisphere, the North Star (or Polaris) is particularly important because it provides a fixed reference point in the night sky. The constant position of Polaris makes it a reliable navigational marker, allowing migratory species to maintain the correct direction during long-distance migration (Tyagi and Bhardwaj, 2021). Research has found that some nocturnal migratory birds can remember the star patterns observed from their birthplace and use this memory during migration as adults, further enhancing their navigational accuracy. These findings not only deepen our understanding of animal migratory behavior but also provide scientific evidence for the conservation of migratory species.

6.3 Olfactory and visual cues

Olfactory and visual cues also play important roles in navigation and orientation, particularly for species migrating through complex environments. Olfactory navigation involves using scent trails and environmental odors to locate specific places. For example, salmon (*Salmo salar*) use olfactory cues to navigate back to their natal streams for spawning. They imprint on the unique chemical characteristics of their home stream during early life stages and use this memory to guide themselves during their return migration (Ueda, 2018). Visual cues, such as landmarks and landscape features, are crucial for the navigation of birds and mammals. Birds often use visual landmarks like mountains, rivers, and coastlines to orient themselves during migration (Mouritsen, 2018; Zhang and Pan, 2021). Additionally, they utilize the patterns of polarized light, which change with the sun's position, to maintain their direction. Mammals, such as *Connochaetes*, rely on visual and olfactory cues to move along established migratory routes across the savannah in response to seasonal changes in vegetation and water sources (Curtin et al., 2018).

The navigation and orientation mechanisms employed by migratory animals are diverse and highly adapted to their specific migratory challenges. The magnetic compass and geomagnetic field detection provide a fundamental navigational tool, especially in featureless environments. Celestial navigation using the sun and stars offers reliable directional cues that complement the magnetic compass. Olfactory and visual cues enhance navigation through familiar and complex landscapes, ensuring precise orientation and successful migration. These sophisticated mechanisms highlight the remarkable navigational capabilities of migratory species and underscore the importance of integrating multiple sensory inputs for successful long-distance travel.

7 Case Study: In-Depth Analysis

7.1 Case study 1: Migratory drop-offs in fork-tailed flycatcher

The fork-tailed flycatcher (*Tyrannus savana*) provides a compelling example of migration cessation, where individuals stop migrating and establish sedentary populations. Gómez-Bahamón et al. (2020) found that species differentiation in the fork-tailed flycatcher is closely related to changes in migratory behavior. Through detailed analysis of the genomic data and morphological characteristics of this bird, the research team revealed how the loss of migratory behavior contributed to species differentiation. The cessation of migration led the fork-tailed flycatcher to form distinct sedentary populations, which differ from migratory populations in terms of breeding time and geographic location, resulting in reproductive isolation. By analyzing numerous genetic markers, the study discovered significant genomic differentiation between migratory and sedentary fork-tailed flycatchers. Neighbor-joining tree and maximum likelihood analysis showed that the sedentary populations formed a monophyletic group, distinctly separated from the migratory populations.

Changes in migratory behavior have significant impacts on species diversity and evolution. This phenomenon not only affects the ecological habits of birds but can also promote new species formation through reproductive isolation and genomic differentiation (Figure 2) (Gómez-Bahamón et al., 2020). This finding underscores the crucial role of migratory behavior in avian diversity and species differentiation, providing new insights into the evolution of other migratory animals (Jahn et al., 2019; Gómez-Bahamón et al., 2020).

7.2 Case Study 2: Migration strategies of moose (*Alces alces*)

Borowik et al. (2021) explored the stability of moose (*Alces alces*) within their seasonal ranges and linked annual migration patterns to seasonal space use. The study found that some moose migrate between summer and winter ranges (partial migration), while others remain in the same area year-round. Migratory individuals showed significantly higher stability within their seasonal ranges compared to non-migratory moose, especially during summer. The home range size of migratory moose in summer was notably smaller than in winter, whereas non-migratory moose showed little difference in home range size between the two seasons.

In all seasons, the home range size of male moose was significantly larger than that of females. This is likely due to the greater energy and nutritional demands of males. Additionally, male moose are more active during the mating season, further expanding their range. During summer, moose have smaller, more stable home ranges because food resources are more abundant and evenly distributed, allowing moose to frequently revisit the same feeding sites. In contrast, winter food resources are scarce and dispersed, requiring moose to move more frequently to obtain sufficient food, resulting in larger, less stable home ranges (Borowik et al., 2021). Environmental changes (such as climate warming) could affect moose's annual migration strategies, thereby altering their seasonal space use and individual fitness.

The study results indicate significant differences in the home range size and behavior patterns of moose across seasons. Migration behavior significantly impacts the stability and size of seasonal home ranges. Future research should further explore the impact of food resource distribution and regeneration capacity on moose space use. Additionally, combining this with studies on animal adaptability can provide a comprehensive understanding of the effects of environmental changes on moose behavior and ecosystems.

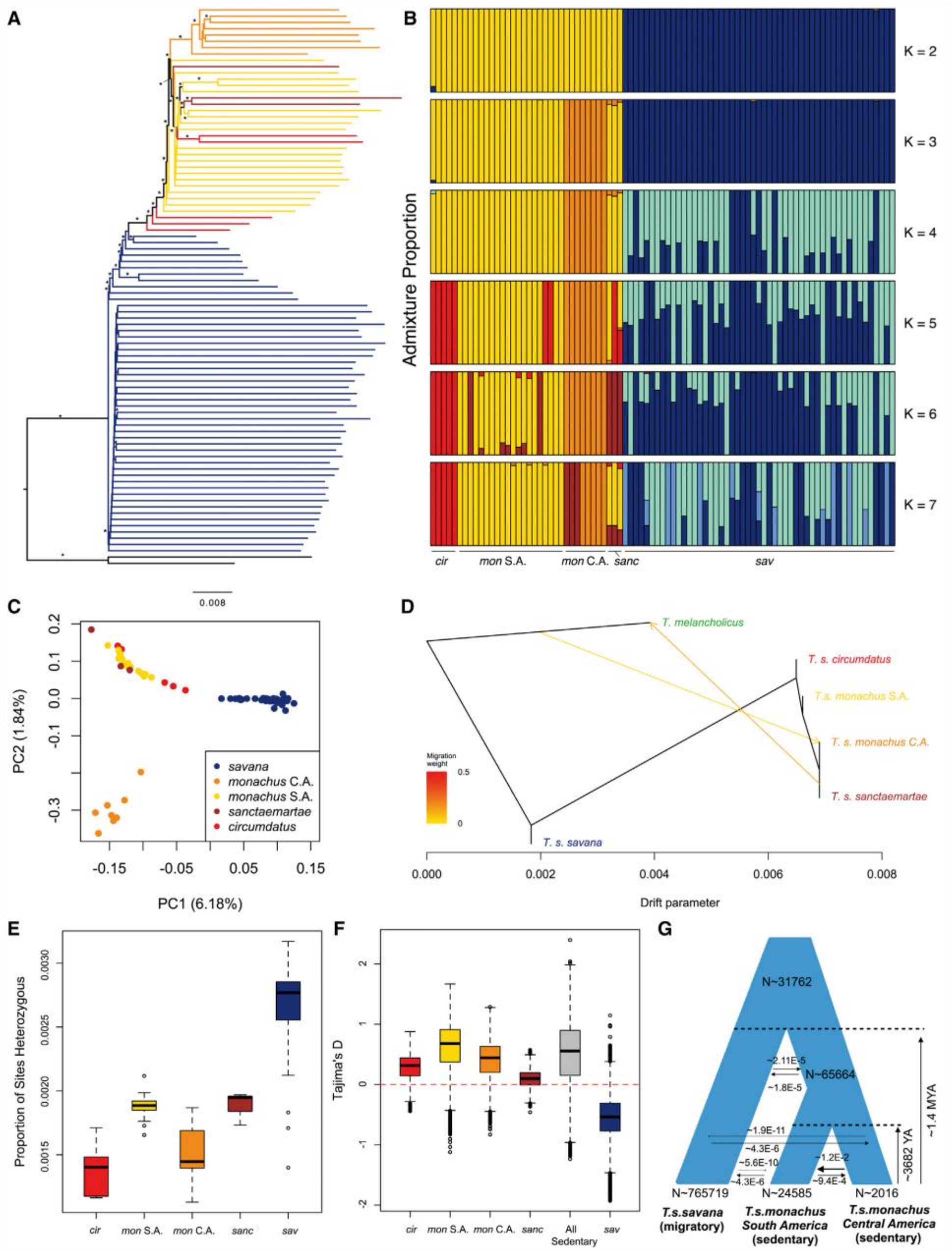

Figure 2 Population genetic analyses (Adopted from Gómez-Bahamón et al., 2020)

Image caption: The figure shows the population genetic analyses of the fork-tailed flycatcher (*Tyrannus savana*). Figure 2A displays a neighbor-joining tree based on genetic distances estimated from genotype likelihoods, where all sedentary subspecies (warm colors) form a monophyletic group associated with the migratory subspecies (blue), indicating that sedentary populations are derived from migratory ancestors. Figure 2B presents admixture proportions for different numbers of clusters, showing significant genetic differentiation between migratory and sedentary populations. The principal component analysis (PCA) in Figure 2C further confirms this genetic differentiation. The TreeMix model in Figure 2D shows no significant gene flow between sedentary and migratory populations. Figure 2E demonstrates lower genetic variability in sedentary subspecies, while Figures 2F and 2G indicate that sedentary populations have undergone a reduction in effective population size, supporting the scenario that sedentary birds evolved from migratory ancestors through a founder event (Adapted from Gómez-Bahamón et al., 2020)

7.3 Humpback whale migration patterns and their impacts

The study found that the Southern Hemisphere D population of humpback whales (*Megaptera novaeangliae*) migrates annually from Antarctic feeding grounds to the waters off Western Australia for breeding. Additionally, their arrival time in the Perth Canyon has been advancing each year. Based on passive acoustic monitoring data from 2002 to 2017, Gosby et al. (2022) used the hourly presence or absence of whale vocalizations as an indicator of changes in migration timing. They established trend models for arrival and departure times and linked these to environmental variables such as sea surface temperature (SST). The results showed that between 2002 and 2017, the arrival time during the northward migration advanced by approximately 1.4 days per year, while the departure time during the southward migration showed no significant change (Figure 3). Furthermore, SST was identified as the most significant factor affecting the acoustic presence of humpback whales; for each 1 °C increase in SST, the acoustic presence of whales decreased by approximately 4.4 hours per day. During the peak whale season, the average SST in the Perth Canyon was 19 °C. The analysis also indicated that humpback whales seem to leave the Antarctic feeding grounds at the end of the austral summer, as sea ice concentration increases and SST decreases.

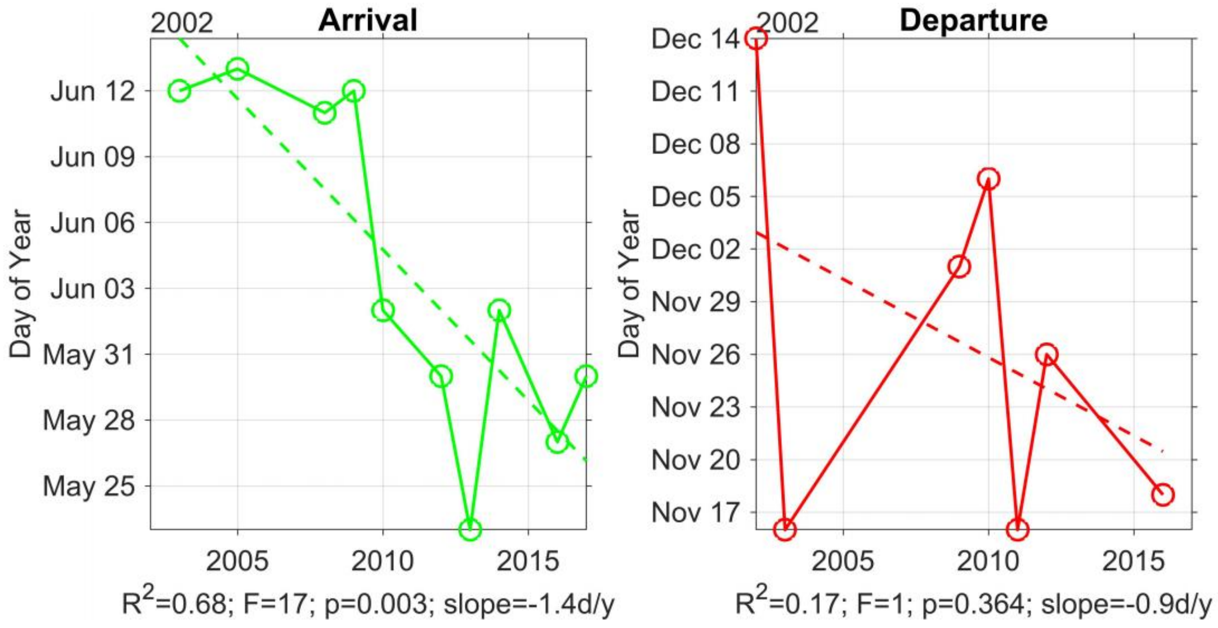

Figure 3 Scatter plots of humpback whale arrival (n = 10) and departure (n = 7) dates for the years of available passive acoustic monitoring data in the Perth Canyon. A linear trendline has been fitted; regression statistics (R2, F, and p-value) are noted beneath each plot (Adopted from Gosby et al., 2022)

Image caption: The figure shows the scatter plots and linear trendlines of humpback whale arrival (A25) and departure (D25) dates in the Perth Canyon from 2003 to 2017. The figure reveals that the arrival time has gradually advanced from mid-June to late May, advancing by approximately 1.4 days per year. The departure time, however, is less stable, showing greater annual variability without a significant overall trend. The linear regression analysis in the figure further validates the study's findings, indicating that the arrival time during the northward migration has significantly advanced, while the departure time during the southward migration remains relatively unchanged. These results highlight the impact of environmental changes on humpback whale migration behavior (Adapted from Gosby et al., 2022)

These findings suggest that the earlier arrival of humpback whales may be a response to environmental changes, particularly changes in SST. As global climate change continues, the migration patterns of humpback whales may further alter, affecting their adaptation to feeding and breeding grounds. Long-term passive acoustic monitoring provides valuable data for understanding humpback whale migration patterns. Future research should continue to monitor these trends and further investigate the potential impacts of climate change on humpback whale populations.

8 Impact of Climate Change on Migratory Patterns

8.1 Shifts in timing and routes

Climate change has significantly influenced the timing and routes of animal migration. For instance, studies have shown that migratory birds are adjusting their migration schedules in response to changing climatic conditions. In some cases, birds are migrating later in both spring and autumn, which contrasts with the earlier migration trends observed in other studies (Mondain-Monval et al., 2021). This shift in timing is attributed to changes in weather conditions, such as increased temperatures and headwinds, which affect the birds' migration patterns. Additionally, the timing of migration has been linked to large-scale climatic indices, with species showing earlier arrivals after winters with higher North-Atlantic Oscillation indices (Bókony et al., 2019). These shifts in timing and routes are crucial for understanding how migratory species are adapting to climate change and the potential consequences for their survival and reproduction.

8.2 Effects on population dynamics

The impact of climate change on migratory patterns extends to population dynamics. Changes in migration timing and routes can lead to mismatches between the availability of resources and the needs of migratory species, affecting their survival and reproductive success. For example, the Eurasian Reed Warblers (*Acrocephalus scirpaceus*) exhibited large-scale segregation within their African non-breeding range, with regions experiencing different interannual climatic variations. This variation was linked to population declines in the eastern European breeding population (Brlík et al., 2022). Similarly, the northern pintail (*Anas acuta*) populations have become more vulnerable to climate change due to intensified land use, which negatively impacts their productivity (Zhao et al., 2019). These findings highlight the complex interactions between climate change, migratory behavior, and population dynamics, emphasizing the need for integrated approaches to conservation planning.

8.3 Adaptation and resilience

Despite the challenges posed by climate change, some migratory species have shown remarkable adaptation and resilience. For instance, migratory birds have demonstrated changes in morphology, such as reductions in body size and increases in wing length, which may help them cope with the increased metabolic costs of migration (Weeks et al., 2019). Additionally, species with broader climatic niches have remained stable, while those with narrow climatic niches have experienced declines, suggesting that niche breadth plays a crucial role in determining the resilience of migratory populations (Ruegg et al., 2021). Furthermore, historical data indicate that migratory behaviors have been maintained through past climatic extremes, suggesting that these species possess inherent adaptive capacities (Doren, 2022). Understanding these adaptive strategies is essential for predicting how migratory species will respond to future climate change and for developing effective conservation measures.

9 Future Directions and Research Gaps

9.1 Emerging technologies in chronobiology research

The field of chronobiology, particularly in the study of migratory patterns, is poised to benefit significantly from emerging technologies. Recent advancements in miniaturized tracking devices, such as geolocators and archival GPS tags, have revolutionized our understanding of avian migratory behavior by providing unprecedented precision in tracking small landbirds over large spatial scales (McKinnon and Love, 2018). Additionally, automated radio-telemetry systems have enhanced our knowledge of migratory stopover biology, revealing previously unknown behaviors during these critical periods (McKinnon and Love, 2018). The integration of these tracking technologies with physiological and genetic measurements at key time points can offer deeper insights into the mechanisms underlying migratory behavior and its adaptability to environmental changes (Fudickar and Ketterson, 2018).

Moreover, the application of stable isotope analysis, particularly sulfur isotopes, has shown promise in tracing animal origins and understanding population trends in migratory species (Brlík et al., 2022). This method can overcome the limitations of traditional tracking techniques, especially in regions with high biodiversity like sub-Saharan Africa, and provide valuable data on the spatial segregation and climate variability affecting migratory populations (Brlík et al., 2022). The development of space-time isotope models (STIMPs) further enhances our ability to quantify habitat use and movement patterns of migratory fish across river basins, offering new insights critical to their conservation (Brennan et al., 2019).

9.2 Integrating chronobiology with conservation efforts

Integrating chronobiology with conservation efforts is essential for the effective management of migratory species. Understanding the genetic and epigenetic mechanisms underlying migratory behavior can inform conservation strategies by identifying key genetic markers and regulatory elements that influence migration (Merlin and Liedvogel, 2019). This knowledge can help predict how migratory species might respond to environmental changes and guide the development of targeted conservation actions. For instance, identifying the origin of individuals using pre-migratory sites through genetic markers can provide a better understanding of the impact of local threats on multiple breeding populations and inform the design of effective conservation actions (Bounas et al., 2018). Additionally, the integration of migration data with physiological and genetic measurements can help predict the capacity of migratory species to adjust to a changing planet, thereby aiding in the development of adaptive management strategies (Fudickar and Ketterson, 2018).

Furthermore, the study of partial migration in species like the wood stork (*Mycteria americana*) highlights the potential for plastic changes in migratory patterns in response to environmental heterogeneity and unpredictability (Picardi et al., 2020). This understanding can be leveraged to develop conservation strategies that account for the variability in migratory behavior and ensure the protection of critical habitats used by both resident and migratory individuals.

9.3 Identifying key areas for future study

Several key areas for future study have been identified to advance our understanding of the chronobiology of migratory patterns in animals. First, there is a need for more research on the intrinsic and extrinsic factors influencing altitudinal migration, particularly in the context of rapid environmental changes (Hsiung et al., 2018). Quantifying the effects of habitat loss, fragmentation, and climate change on altitudinal migrants is crucial for predicting their population viability and developing effective conservation strategies (Hsiung et al., 2018). A comparative approach across different migratory types, considering endocrine mechanisms, can provide new insights into the origin and diversity of migratory patterns (Watts et al., 2018). Understanding the hormonal mechanisms underlying migratory timing and behavior across various forms of migration can help elucidate the evolutionary and ecological drivers of migration. The integration of genetic and epigenetic studies with field research on migratory behavior can significantly advance the field of migration genetics (Merlin and Liedvogel, 2019). Identifying and functionally validating candidate genes and regulatory elements across different migratory species can provide a comprehensive understanding of the genetic architecture of migration and its adaptability to environmental changes.

Furthermore, the development and application of novel tracking and tracing technologies, such as stable isotope analysis and space-time isotope models, can enhance our ability to study migratory patterns at finer spatial and temporal scales (Brennan et al., 2019; Brlík et al., 2022). These technologies can provide valuable data on habitat use, movement patterns, and population dynamics, informing conservation efforts and management strategies for migratory species. By addressing these research gaps and leveraging emerging technologies, we can deepen our understanding of the chronobiology of migratory patterns and develop more effective conservation strategies to protect these vital species.

10 Concluding Remarks

The study of the chronobiology of migratory patterns in animals has revealed several critical insights into the mechanisms and consequences of migration. Firstly, migratory behaviors are influenced by a combination of genetic, epigenetic, and environmental factors, with significant variation observed across different species and populations. The timing and orientation of migration are often regulated by environmental cues and integrated through the endocrine system, which helps animals synchronize their movements with resource availability. Individual repeatability in migratory phenology suggests that consistent individual differences play a crucial role in population-level changes in migration patterns. Furthermore, migratory animals exhibit different life history strategies compared to their non-migratory counterparts, often leading to faster paces of life and distinct survival and reproductive schedules. The ontogeny of migratory strategies, particularly in long-lived species, is a progressive process influenced by age and experience, with younger individuals gradually refining their migratory behaviors over time. The use of advanced tracking technologies and isotopic analysis has also enhanced our understanding of migratory connectivity and the impact of climatic variability on population trends.

The findings from this body of research have significant implications for the conservation and management of migratory species. Understanding the genetic and environmental drivers of migration can inform strategies to protect critical habitats and migratory corridors, ensuring that animals have access to the resources they need throughout their annual cycles. The identification of key environmental cues and endocrine mechanisms underlying migration can also aid in predicting how species will respond to climate change and habitat alterations. Recognizing the life history trade-offs associated with migration, such as the increased mortality during migratory periods, highlights the need for targeted conservation efforts during these vulnerable times. Efforts to mitigate anthropogenic threats, such as habitat destruction and climate change, are essential to maintaining the delicate balance that allows migratory species to thrive. Additionally, the progressive nature of migratory behavior development in long-lived species suggests that conservation strategies should consider the different needs of individuals at various life stages.

The field of chronobiology offers a unique and valuable perspective on the study of migratory patterns in animals. As our understanding of the genetic, endocrine, and environmental factors that influence migration continues to grow, it is essential to apply this knowledge to conservation and management practices. Future research should focus on expanding our understanding of the molecular and genetic mechanisms underlying circadian rhythms and their role in migration. Additionally, interdisciplinary approaches that combine chronobiology with ecology, physiology, and behavioral studies will provide a more comprehensive understanding of migration and its adaptive significance. Conservation efforts should prioritize the protection of critical habitats and resources during key migratory periods, and consider the potential impacts of environmental changes on the timing and success of migration. By embracing the insights provided by chronobiology, we can develop more effective strategies to preserve the biodiversity and ecological integrity of migratory species and their habitats.

Acknowledgements

The AnimalSci Publisher extends sincere gratitude to the three anonymous peer reviewers who participated in the evaluation of this manuscript.

Conflict of Interest Disclosure

The authors affirm that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

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