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Conservation biology

Genomes to space stations: the need for the integrative study of migration for avian conservation

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Ongoing changes to global weather patterns and human modifications of the environment have altered the breeding and non-breeding ranges of migratory species, the timing of their migrations, and even whether they continue to migrate at all. Animal movements are arguably one of the most difficult behaviours to study, particularly in smaller birds that migrate tens to thousands of kilometres seasonally, often moving hundreds of kilometres each day. The recent miniaturization of tracking and logging devices has led to a radical transformation in our understanding of avian migratory behaviour and migratory connectivity. While advances in technology have altered the way researchers study migratory behaviour in the field, advances in techniques related to the study of physiological and genetic mechanisms underlying migratory behaviour have rarely been integrated into field studies of tracking. To predict the capacity of migrants to adjust to a changing planet, it is essential that we combine avian migration data with physiological and genetic measurements taken at key time points prior to, during and after migration.

1. Introduction

Each year billions of birds migrate across the planet, passing through varied habitats and creating marked changes in the structure of communities [1]. Birds migrate for many reasons but many migrate in anticipation of seasonal changes [2]. Regardless of the reason, in order to persist, migrants must time their movements accurately in relation to the environment, and accurate timing is highly dependent on the availability of resources at every stage of their journeys [3–5].

Owing to environmental change, the availability and predictability of resources on which migrants depend en route are rapidly changing [6]. Recent technological advances have provided novel opportunities to observe how migrants respond to changes in climate and resources [3,7,8]. However, understanding of the mechanisms underlying behavioural responses to change is still lacking. Here, we highlight opportunities for integrating cutting edge technologies for studying migration in free-living birds with easily attained genetic and physiological measures. Our goal is to convey how integrating behavioural and mechanistic aspects of avian migration with emerging patterns of how animals move over time and space will enhance our ability to predict the capacity of migrants to meet the challenges they will face under continued environmental change. It is our strong opinion that an integrative approach will provide critical information for prioritizing conservation efforts to preserve migratory birds.

Technological advances over the past decade have resulted in a wealth of discoveries about avian migration (e.g. [9–12]). Information gained from light-level geolocators, miniaturized GPS loggers, satellite transmitters, stable isotopes and large-scale radio-telemetry arrays has revealed how individuals moving from breeding sites to non-breeding sites and back again give rise to year-round geographical distributions that characterize a species or a population. Year-round studies have further shown that the breeding ranges of some migratory populations are tightly linked to specific, geographically restricted non-breeding ranges (high connectivity), while other migratory populations are loosely linked to non-breeding ranges that cover large geographical regions (low connectivity) [13]. Additionally, it is becoming exceedingly clear that correct timing of migration is critical and that timing and connectivity are inextricably linked [14].

Understanding the conservation implications of high versus low connectivity for the resilience of populations is a growing area of investigation [13,15]. If connectivity is high, loss of suitable habitat during the breeding or non-breeding seasons is likely to have greater negative impact on populations than if connectivity were low. We argue here that research on the physiological and genetic mechanisms underlying migratory behaviour will also be essential if we are to realize the potential conservation benefits to be derived from knowledge about connectivity. If, for example, connectivity is high and populations exhibit little variation in physiological or genetic mechanisms that time migration or reproduction, then extreme weather events during the breeding or non-breeding season are likely to have greater negative impact than if connectivity were low.

2. Combining tracking, logging, stable isotopes and connectivity with physiology to predict adaptive capacity

The unique vulnerability of migratory populations to environmental change is well established [6]. One of the many challenges faced by migrants is their restricted ability to monitor phenological shifts in breeding habitat prior to spring arrival. Consequently, many migrants depend on neuroendocrine mechanisms that respond to seasonal changes in day length (photoperiod) to time their transition from non-breeding physiology to migratory and reproductive physiology. Less appreciated is how neuroendocrine mechanisms may relate to connectivity and the capacity of populations to respond to environmental change. What is known about mechanisms is only just now being applied to connectivity, and several gaps in this knowledge become apparent when the attempt is made.

For example, we are just beginning to learn how migration distance might influence the timing of the events of the annual cycle, including when to migrate or when to breed. Similarly, cues experienced at non-breeding habitat such as day length in early spring may differ in their impact on timing, depending on migration distance. Studies of migrants in the field and in captivity indicate that reproductive development is more advanced in birds residing closer to their spring destinations. In the field, migrants caught during spring respond more strongly to stimulation of gonadal output if they are closer to their known breeding destination [16]. Also in the field, birds most prepared to breed when caught upon arrival at their breeding sites, as evidenced by higher circulating androgens, are known to have spent the non-breeding season nearby [17]. Among captives, birds exposed during the non-breeding season to natural variation in day length have stronger responses to stimulation of gonadal output if their breeding sites are closer as opposed to farther away [18]. Also based on studies of captives, birds experimentally exposed to photoperiods characteristic of non-breeding latitudes that lie closer to breeding latitudes develop migratory tendencies and reproductive physiology earlier [19].

Table 1. Minimally invasive methods for studying physiological, genetic and epigenetic mechanisms of migration in free-living birds. vi, visual inspection.

measure	method	tissue
condition	triglycerides	blood
	β-hydroxybutyrate	blood
	subcutaneous fat	vi
	pectoral muscle profile	vi
energetic state and stress	metabolic hormones	blood
regulatory mechanisms	DNA methylation	blood
	gene expression	blood
reproductive state	cloacal protuberance	vi
	reproductive hormones	blood
senescence	telomere length	blood

It follows that breeding populations with low connectivity will be made up of individuals that vary more widely in the photoperiods they experience during the non-breeding season than populations with high connectivity. As such, low connectivity breeding populations should exhibit greater ‘standing variation’ in arrival times and breeding dates than high connectivity populations. Early breeders are known to benefit in most years, but are selected against in harsh years [20]. Greater standing variation in arrival found in low connectivity populations should give them greater capacity to respond to environmental variability, and thus greater resilience as the environment changes. That is, populations with low connectivity should be more variable in timing of reproduction and migration, granting them greater potential to respond to environmental change. Conversely, high connectivity is predicted to lead to low variation in seasonal timing, which could constrain response to environmental change.

Future studies that integrate year-round tracking to determine connectivity with physiological and genetic measures of reproductive and migration phenology will contribute to the development of general principles for understanding vulnerability of specific populations and species to environmental change. We urge researchers who study migration to take measures of reproductive state (table 1) prior to, during, and/or immediately following spring migration, to help develop a more complete model of the relationship between connectivity and resilience.

3. Studying genetic and epigenetic mechanisms in free-living migratory birds

Gene expression studies have provided insight into regulatory gene networks underlying migratory behaviour [21–24]. Unfortunately, application of these methods to monitor free-living animals over time is limited because sampling is often terminal. However, recent studies have identified genes expressed in the red blood cells of migrants during the pre-migratory and migratory stages [21,22], making it possible to combine gene expression studies with behavioural data collected from free-living migrants to learn more about the mechanisms involved in migration. Genes associated with migratory fuelling, muscle growth, lipid synthesis and biological rhythms are upregulated in bird blood during migration [21,22,24]. Integrating knowledge of differential gene expression with behavioural information collected during migration will greatly increase our understanding about how metabolic constraints of migration may be influenced by environmental change.

In fact, methods using easily acquired blood samples have already led to many exciting new discoveries in avian migration. For example, Bauer *et al*. [14] found that migratory dark-eyed juncos (*Junco hyemalis*) have shortened telomeres compared to non-migrants, suggesting a measurable cost of migration [25]. Future tracking and logging studies that relate individual telomere length to migratory behaviours that vary across individuals and populations, like speed, duration, and distance of migration, will provide insight into the relative lifetime costs of migrating. Another exciting example of integrating genetic sampling with logging is the recent report that differences in methylation levels of the photoperiodic *Clock* gene are associated with migration phenology of barn swallows (*Hirundo rustica*) whose timing was measured using light-level geolocators [26]. These tantalizing results suggest potential for epigenetic mechanisms to regulate migratory phenology and hold promise that adjustment to environmental change by migrants might be achieved relatively rapidly through phenotypic flexibility.

4. Studying the impact of severe weather events on migratory birds

The behavioural response of migratory birds to extreme weather events during migration is a growing area of research due to logging and tracking. Drought, extreme storms and extreme temperatures can all alter the behaviour of migratory birds and their chances of surviving migration [3,27]. As the occurrence of extreme weather events increases and climate becomes less predictable [28], greater knowledge of how individual migrants respond to extreme conditions will be critical to our ability to assess vulnerability.

5. Toward the integrative understanding of avian migration

Over the past decade, the average researcher of avian migration has transitioned from primarily relying on ringing to a wealth of options for tracking individual birds throughout their annual cycles. We live in a time when an animal tracking system will soon be on-board the International Space Station and massive networked radio-telemetry arrays are being developed for automated tracking of animals over thousands of kilometres [29,30]. The resulting discoveries from these and other technologies have led to a renaissance in scientific interest in avian migration. Current developments in understanding avian migration behaviour and migratory connectivity are a required step in the effective conservation of avian migration. Efforts to conserve avian migration will be significantly aided by active integration of research on migratory connectivity with research on the physiological, genetic and epigenetic bases of variation in migratory behaviour. We strongly urge migration researchers to take the next steps towards achieving this integration.

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