conditions that could be linked with downstream extreme weather events.

DECLARATION OF INTERESTS

The author declares no competing interests.

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Primer

The genetics of bird migration

Hannah Justen and Kira E. Delmore*

Bird migration is one of the most amazing biological phenomena exhibited by organisms today, with birds as small as three grams travelling thousands of kilometers twice each year. Most people are familiar with this behaviour; they likely recognize the seasonal movements of birds each year and may have even witnessed specific migratory events (e.g., geese flying in their characteristic V-formations). What many people may not know is that bird migration has a strong genetic basis, especially in groups like songbirds who migrate alone and at night, preventing juveniles from following more experienced adult birds on their first migration. Successful migration also requires the coordinated function of many traits, not only behavioural traits like timing and orientation but also morphological and physiological traits to permit these long distance treks. Together, these traits comprise what has been called the ‘migratory syndrome’. In this primer, we provide a broad overview of research on the genetics of migratory traits, from early experimental work to future functional assays and their importance for bird conservation. We focus primarily on songbirds as most work on the genetics of migration has been conducted with this group.

Early experimental work

Early work on the genetics of migration was dominated by experimental approaches testing if traits in this syndrome are genetically determined. One of the most influential experiments was conducted by Perdeck in the 1950s. Perdeck displaced 10,000 European starlings (*Sturnus vulgaris*, Figure 1A) from the Netherlands to Switzerland. These birds were in the middle of fall migration, heading southwest to their wintering grounds. Perdeck predicted that if migratory orientation is genetically determined in songbirds, juvenile starlings should maintain their initial headings and be recaptured southwest of Switzerland. This should not be the case for adults who should use knowledge from previous trips to re-orient themselves, navigating northeast to their intended wintering grounds. This is the pattern Perdeck observed; juveniles were recaptured southwest of Switzerland while adults compensated for the displacement and migrated northeast (Figure 2A).

Perdeck’s displacement experiment was followed by a series of lab experiments comparing the migratory behaviour of birds from different populations in a common environment and after interbreeding. Researchers predicted that if there is a genetic basis to migration, birds should exhibit population-specific values for migratory traits despite being raised in a common environment. If these traits are inherited additively (i.e., combine the effects of alleles at each loci), hybrids should exhibit intermediate values. Experiments with European blackcaps (*Sylvia atricapilla*, Figure 1B) supported these predictions. Blackcaps exhibit considerable variation in migration, including populations that do not migrate at all and others that migrate northwest, southwest, or southeast on fall migration. Nestlings from these populations were brought into the lab and continued to exhibit population-specific values for migratory traits in this common environment. Hybrids between these populations exhibited intermediate trait values (Figure 2B). These experiments relied on the fact that caged songbirds become restless during the migratory period, fluttering their wings and hopping in the direction of migration. This behaviour can be quantified with registration cages (cages with moveable perches linked to microswitches) and Emlen funnels (cylindrical cages with ink pads in the middle and print paper on the sides).

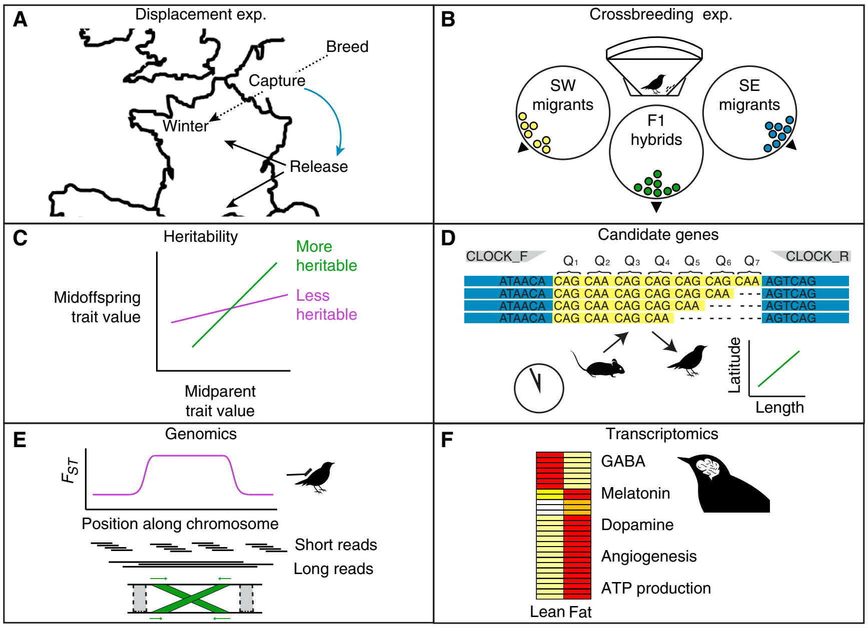
Once it was established that there was a genetic basis to migratory traits, there was a shift to determining exactly how much of the variation in these traits derives from genetic versus environmental variation. There are several reasons to decompose phenotypic variation into its component parts; primary among them is that genetic variation is essential for mounting a response to selection. The main parameter estimated by this work was heritability, the proportion of phenotypic variation attributed to (additive) genetic variation. Correlations between parents and offspring in migratory traits were used to estimate this parameter along with animal models that account for more complicated relationships among relatives (Figure 2C). Similar to earlier experiments, much of this work was conducted with European birds. Moderate to high values of heritability were documented suggesting a considerable amount of the variation documented in migratory traits derives from genetic variation. For example, values of 0.38–0.53 and 0.34–0.45 were documented for the intensity and onset of fall migration in the European blackcap, respectively. Interestingly, lower values of heritability were documented for the termination of fall migration in this species (0.16–0.44). Heritability estimates for morphological traits important for migration like wing measurements are also high (greater than 0.6) in European blackcaps and similar values have been documented for other species (e.g., 0.67 for the onset of spring migration in garden warblers, *Sylvia borin*, and 0.69–0.93 for wing length in Tristan warblers, *Nesospiza* ssp.).

Figure 1. Influential study species.
Photographs of some of the species upon which work on the genetics of migration has been conducted, including (A) European starlings, (B) European blackcaps, (C) Swainson's thrushes and (D) willow warblers.

Early work on the genetics of migration finished with examinations into genetic correlations among migratory traits. Recall, successful migration requires the integration of multiple traits. Moderate to high levels of heritability indicate genetic variation exists for migratory traits and could facilitate a response to selection but this response will also depend on correlations across traits; positive correlations could facilitate rapid responses to selection but negative correlations could have the opposite effects. Much of this work was conducted in the 1990s and used captive birds, where researchers selectively bred birds for one trait and tested for corresponding changes in additional traits. Much of this work focused on blackcaps again and documented high correlations among several traits, including positive correlations between the intensity and amount of migratory activity of fall migration and negative correlations between the onset and intensity of fall migration. Genetic correlations were not found for all traits (e.g., termination of fall migration was not correlated with any other traits) but, in general, these results provided the first evidence that many migratory traits are expressed as a genetically integrated syndrome.

Expansion of genetics and 'omics' techniques

The emergence of genetic tools in the late 1900s allowed researchers to quantify marker-based genetic variation (e.g., single nucleotide polymorphisms or microsatellites) and led to a flurry of studies aimed at identifying specific genetic variants linked to migratory traits. This work started with candidate genes; researchers identified genes that could have a function relevant for migration and surveyed natural populations for variation in this gene. One of the most common genes examined was *Clock*. The *Clock* gene was first identified in mice and is part of the circadian clock, a negative feedback loop that controls daily rhythms and is regulated by changes in photoperiod. Migration is initiated by changes in photoperiod and involves a transition to nocturnal behaviour and thus it was hypothesized that *Clock* could be important for migratory timing. In support of this hypothesis, variation in the length of a poly-glutamine repeat motif in the promoter region of this gene was associated with migratory timing in many birds (Figure 2D). These findings suggest that there



Current Biology

Figure 2. History of work on the genetics of migration.

(A) Displacement experiment using starlings. Trajectories before (dotted) and after (solid) displacement (blue) are shown. Juveniles continued along southwest routes and adults reoriented northwest. (B) Crossbreeding experiment using blackcaps and Emlen funnels in the lab. Each point represents the average orientation of a bird. F1 hybrids exhibited intermediate orientations to pure forms. (C) Estimating heritability using pedigrees, as the correlation between phenotypic traits of parents and their offspring. The steeper the slope of the regression, the more heritable the trait. (D) Examining variation at candidate genes like *Clock*. *Clock* was first identified in mice linked to circadian rhythms. Variation in the length of a glutamine repeat has been linked with breeding latitude (a proxy for migratory timing) in birds. (E) Genomic analysis using willow warblers. A region of elevated differentiation was originally identified by short reads/sequences and shown to be an inversion by long reads (reads map in reverse within the inversion [green] for some individuals). (F) Transcriptomic analysis using wheatears, comparing expression levels between lean and fat birds in the brain. Each row is a different gene (high expression = red, low = white).

could be a common genetic basis to migratory timing and that genetic machinery that was already present in birds was co-opted to facilitate this adaptation.

Genomics

Work with candidate genes advanced our understanding of migration's genetic basis but was associated with several limitations; results were not always consistent (e.g., when studying different populations of the same species) and these genes are often identified in genetic model organisms that do not migrate. In addition, candidate genes represent only a small proportion of the genome, precluding the identification of novel genes and answers to broader questions about the genetics of migration. For example, there is considerable interest in the genomic architecture of migration — the number, location and effect size of genes that control migratory traits and their interactions.

The recent advent of next-generation sequencing techniques and parallel advances in animal movement ecology are allowing researchers to expand beyond candidate genes. Next generation sequencing techniques produce millions of sequences in a short time and for a reasonable price. These techniques allow researchers to study thousands of marker loci at one time and are cost-effective enough for use in non-model organisms like migratory songbirds. Advances in animal movement ecology include the miniaturization of light-level geolocators and GPS tags. Early work on migration relied on registration cages and/or Emlen funnels in the lab. Work with candidate genes was conducted with natural populations but often used proxies for migration (e.g., breeding latitude as a proxy for migratory timing, assuming birds further north migrate earlier). Light-level geolocators and GPS tags are fitted to individual birds in the wild. These devices store near-daily location estimates for birds, providing far greater, individual-level resolution of migratory behaviour for a full year.

Some of the first work integrating next-generation sequencing techniques with advances in animal movement ecology was conducted in migratory divides, hybrid zones between closely related groups that breed adjacent to one another but use different migratory routes (Figure 3). For example, admixture mapping was used to study the genetic basis of migratory orientation in a divide between Swainson's thrushes (*Catharus ustulatus*, Figure 1C) in western North America. Admixture mapping uses natural recombination in hybrids to isolate the effects of specific genomic regions on a trait of interest, precluding the need to generate crosses in the lab. A single region on chromosome 4 was linked to migratory orientation in thrushes. Genetic variants in this region were additively inherited and effect sizes were high, suggesting they control a considerable amount of the variation seen in migratory orientation. Approximately 60 genes occurred in the region and, surprisingly, *Clock* was among them. This connection with *Clock* is intriguing to consider in light of the migratory syndrome. Specifically, this study was mapping migratory orientation but identified a gene that may be more important for timing. This finding suggests genes controlling multiple migratory traits may be in close proximity to one another in the genome and thus inherited together as a single 'gene package'.

There are several features of the genome that could facilitate the co-inheritance of genes controlling multiple traits, including structural variants like inversions (DNA segments that are reversed in some individuals and so experience lower levels of recombination). Until recently, it was very difficult to study structural variants because next-generation sequencing techniques

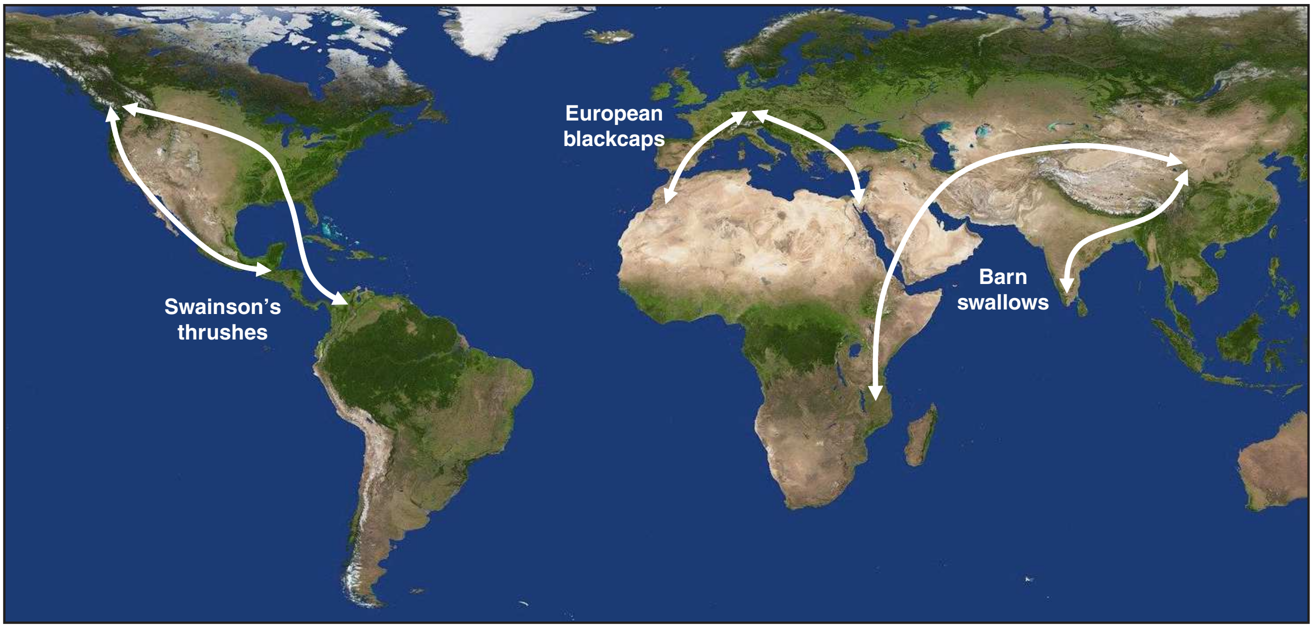


Figure 3. Migratory divides.

Each of the main migratory systems hosts several divides. One divide per system is illustrated here and based on light-level geolocator data presented in Delmore *et al*. (2012) Proc. R. Soc. B. *279*, Delmore *et al*. (2020) Proc. R. Soc. B. *287*, and Turbeck *et al*. (2022) Evolution *76*.

were limited to short sequences (75–250 bp) that do not span the full length of these variants. Many structural variants also have repeat-rich regions, making them difficult to map to unique locations in the genome. New platforms can sequence much larger sequences (5–30 kb), allowing us to study structural variants in earnest; this expansion was exemplified well in a migratory divide between two subspecies of willow warblers (*Phylloscopus trochilus*, Figure 1D) in Scandinavia. Short reads were used to estimate genomic differentiation between these subspecies and revealed two large regions of elevated differentiation (on chromosomes 1 and 5). Abrupt drops in differentiation were documented at the edges of these regions, suggesting they may be inversions. Long-reads were recently used to confirm the presence of these inversions and pinpoint their exact breakpoints (Figure 2E). Long-reads also showed that a different genetic variant that had previously been linked to migration in the system (WW2, an amplified fragment length polymorphism) is actually part of a transposable element. Transposable elements are segments of DNA that can move between locations in the genome, introducing genetic variation and affecting gene regulation. This particular transposable element occurs in several locations of the willow warbler genome. These locations are repeat-rich, making them difficult to assemble without long-read data.

Transcriptomics and beyond

So far we have focused on variation at the level of DNA sequences. A complete understanding of migration's genetic basis will require work at additional molecular levels as there are several steps between sequence variation and the final migratory phenotype. For example, sequence variants can occur in the regulatory regions of genes, affecting patterns of gene expression instead of the actual protein produced.

Similar to work on sequence-level variation, early work on gene expression focused on candidate genes but has since expanded to capitalize on next-generation sequencing techniques. For example, RNA was extracted from the brains of Northern wheatears (*Oenanthe oenanthe*) raised in captivity and at three different stages of migratory fuelling: lean, fattening and fat (Figure 2F). Eighty-four genes exhibited different patterns of expression across these stages, including those involved in neurogenesis (the formation of new neurons in the brain). Regions of the brain important for visual and spatial memory are often larger in migrants. Combined, these findings suggest bird brains prepare for migration by forming new neurons and connections. Genes involved in ATP production, lipid trafficking, anti-oxidative stress response and innate immune response were also differentially expressed in wheatears and are likely important for confronting the physiological challenges of migration.

There are several avenues where future work using genomic and transcriptomic tools can expand our knowledge of migration's genetic basis. For example, continued reductions in the cost of sequencing and tracking birds should allow us to expand to additional study systems and utilize larger sample sizes, especially when combined with new bioinformatic tools capable of genotyping birds using less sequencing data. Increased sample sizes will permit more fine-scaled

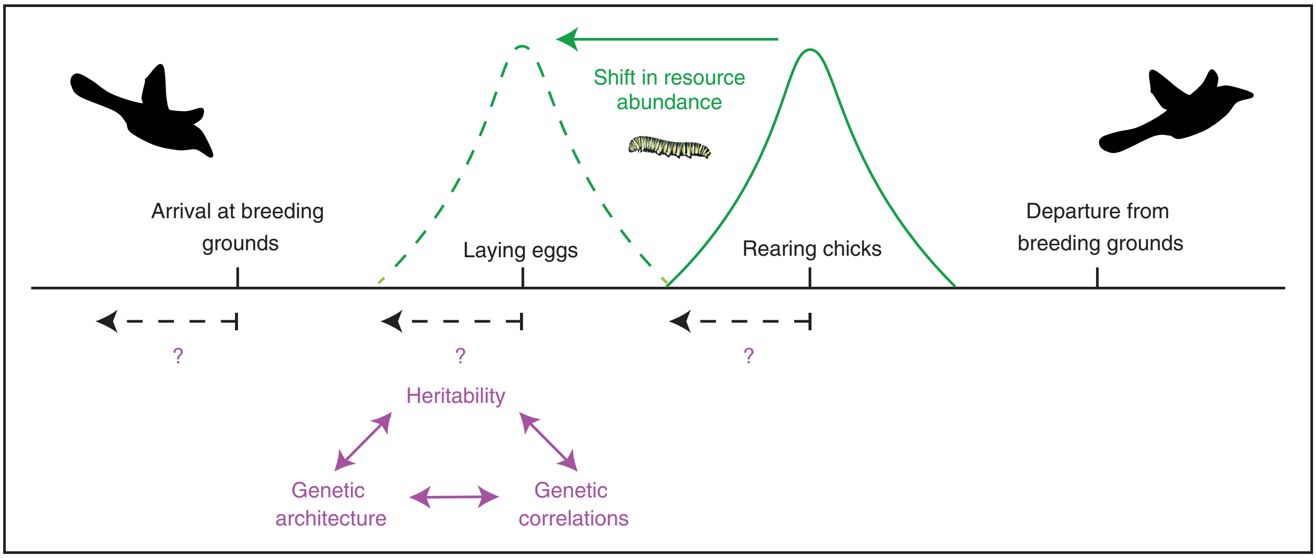


Figure 4. Climate change and migratory timing.
Warmer springs are causing resources (green) to peak earlier. Life history traits in birds (black) are timed so chick rearing will occur when resources are at their highest. It is unclear if the timing of these traits can shift to match their resources (dotted black lines). This shift will depend on several features of migration (and breeding) genetics (purple).

mapping, narrowing down lists of genes associated with migratory traits. Methods to functionally validate these associations are under active development in the community and include virus-mediated manipulations of gene expression that can be done locally (e.g., at specific brain regions) and isolate the effects of specific genes. Combined with earlier experimental designs (e.g., Emlen funnels), functional validation will allow researchers to make direct connections between genetic variants and migratory traits.

So far there has been little consistency in the experimental approaches used in transcriptomic studies, with differences in the tissues, sex and age of birds sampled and time when sampling is conducted. Future work using consistent experimental approaches across species will allow us to test long-standing hypotheses on the genetics of migration, including if there is a common genetic basis to migration as early candidate gene work suggested. Greater integration of genomic and transcriptomic studies from the same species will also allow us to directly connect sequence-level variation with differences in gene expression. This integration could involve additional molecular levels as well, including epigenetic markers (e.g., chromatin accessibility and DNA methylation) that determine whether or not genes are even accessible to be expressed. Epigenetic markers also interact with the environment to regulate behaviors. We already know that environmental cues like photoperiod and the Earth's magnetic field are important for migratory timing and orientation, making epigenetics a particularly promising new avenue of study.

Relevance to conservation

Huge population declines have been documented in birds; more than three billion birds have been lost since the 1960s in North America and similar declines have been noted worldwide. Population declines are likely higher for migrants whose ranges encompass several geographically distinct regions that face unique anthropogenic threats. Declines in migratory birds will have devastating effects on our ecosystems as they provide essential ecosystem services and their visibility makes them important sensors of ecosystem health. The genetic basis of migration is important to consider when establishing conservation strategies for this group. For example, the fact that there is a strong genetic basis to migratory routes means these routes are often repeatable. This repeatability could facilitate the identification of important areas for conservation but may only work over the short term as habitat loss and climate change will likely affect these locations and require future changes to migratory routes.

Comparable concerns about the future of migratory timing also exist. Warmer springs in the temperate region are causing breeding resources to become available earlier in the season. Corresponding advances in migratory timing have been documented in some songbirds but are not universal and may not occur fast enough to match changes in resource availability (Figure 4). Migrants spend much of the year away from their temperate breeding grounds where they are disconnected from environmental cues. The timing of migration is also more tightly linked to photoperiod, which is not affected by climate change, and there are critical differences in the life history traits of migrants and their resources that will affect their response to selection (e.g., generation times and number of offspring produced).

In the end, knowledge of how heritable migratory traits are, their correlations with other traits in the syndrome and genomic architecture will help determine if migrants can respond to future anthropogenic changes. Recall, the adaptive potential of traits increases with heritability and correlations across traits will affect their response to selection. In addition, traits controlled by a few genes of small effect may have fewer pleiotropic effects (e.g., interactions with other genes and traits), allowing more rapid changes to occur. Early work on the genetics of migration quantified heritability and cross-trait correlations but was limited to a small number of European songbirds and relied on data from multiple generations of related individuals. Multi-generational data can be difficult to obtain but new approaches using genomic data have been developed (e.g., genomic relatedness matrices) that do not need this information. This is just one example where new approaches using 'omic' techniques will inform our understanding of how migration is controlled and will respond to future selection pressures. This information can be used to develop data-driven conservation strategies for migratory birds and the ecosystems that depend on them.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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Primer

Passerine birds

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Passeriformes, more commonly known as perching birds or passerines, are the most species-rich group of birds. Totaling nearly 6500 species, approximately two out of every three bird species is a passerine. Passerines are globally distributed and are among the most abundant birds at nearly every terrestrial location on Earth. Owing to their diversity, abundance and cosmopolitan distribution, passerines are among the most familiar of all birds and have figured prominently in both human culture and science. For example, humans have long been captivated by the beautiful songs of many passerines (such as the Common Nightingale (*Luscinia megarhynchos*) in Europe and the Wood Thrush (*Hylocichla mustelina*) of North America), and it is common in some cultures — although globally discouraged as ecologically damaging, especially when birds are captured directly from the wild — to keep passerines as pets. Nevertheless, the vocal prowess and frequent ability to thrive in captivity have made passerines important models for lab-based research ranging from neurobiology to genetics. In contrast, the diversity and accessibility of many passerine birds in the wild continue to make them among the best animal models for field-based studies of behavioral ecology, evolution, mating systems, life history, disease resistance, ecological and evolutionary responses to climate change, among many other fields.

Passerine phylogeny

The relationship between passerines and other clades of birds has historically been challenging to establish; however, the development of DNA sequencing technologies has facilitated progress towards this goal and a clearer picture of passerine taxonomy and relationships is emerging. Beginning in about 2008, DNA-sequence studies yielded a surprising result that was not evident in even earlier DNA-hybridization studies, namely that passerines are most closely related to parrots (Psittaciformes), which are in turn most closely related to falcons (Falconiformes; Figure 1). Within passerines, three main clades are well established: the New Zealand wrens (Acanthisittidae; two species), the suboscines (Tyranni; ~1350 species) and the oscines (Passeri; ~5100 species). As we discuss in more detail below, the suboscines differ from the oscines primarily in the complexity of the syrinx, the avian vocal organ; additionally, whereas oscines typically learn their songs and require a tutor for doing so, suboscines in general are born with their vocalizations and can eventually produce them without a tutor. Although traditionally of debated phylogenetic and taxonomic affinity, molecular studies have consistently found New Zealand wrens to be the earliest branching passerine lineage. Although the division of the remainder of the passerines into the suboscines and oscines has long been accepted, elucidating the relationships of families within each of these two groups has proved challenging because of the difficulties of sampling deeply across taxonomic and genomic scales, as well as the high level of morphological and behavioral convergence. For example, the bowerbirds (Ptilinorhynchidae) and birds-of-paradise (Paradisaedae) were early on thought to be sister taxa — a conclusion that appears to have been driven by their centers of taxonomic diversity on the island of New Guinea, but also by their extreme levels of sexual selection, manifested in the form of elaborate bowers on the one hand and plumages and complex mating display behaviors on the other. We now know that these two groups are only distantly related, albeit both within a southern hemisphere subgroup of the oscines called the 'Corvides'. Based on genome-scale sequence data, a recent and well-resolved phylogeny detailing relationships among all passerine families provides the clearest hypothesis for the evolution of passerines thus far (Figure 1). One outcome of this and other recent phylogenetic studies has been an astounding increase in the number of recognized passerine families. For example, the past three decades have seen the number of passerine families skyrocket from 46 to over