

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

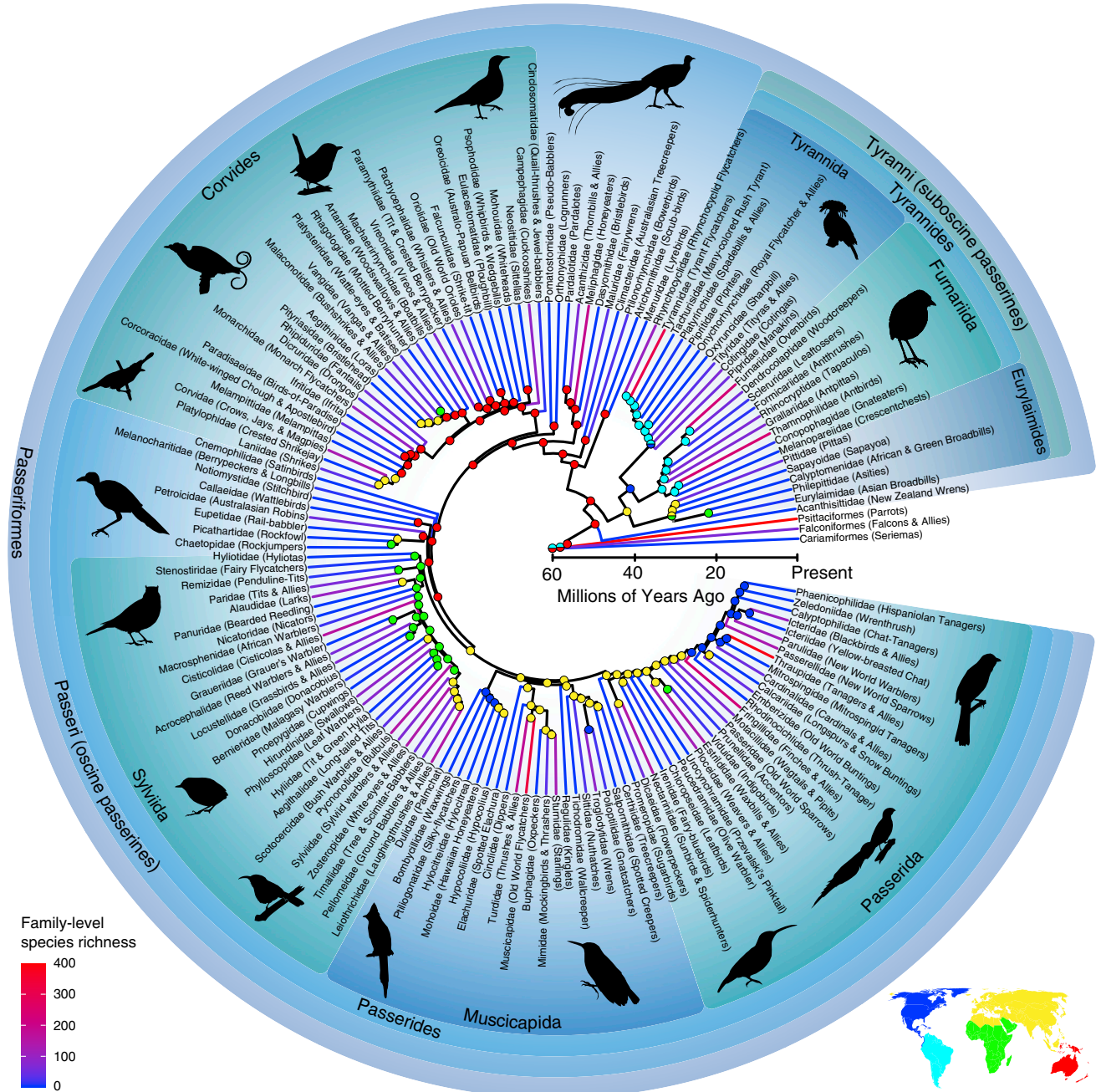
C. Jonathan Schmitt,  
and Scott V. Edwards\*

Passeriformes, more commonly known as perching birds or passerines, are the most species-rich group of birds. Totalling 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 (Paradisaeidae) 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



**Figure 1. Passerine phylogeny.**

Phylogeny of 147 currently recognized families of passerine birds, modified and simplified from Oliveros *et al.* 2019. A timeline appears along the phylogeny at right. The reconstructed ancestral biogeographic regions of each clade are indicated by circles on nodes and the color of each circle corresponds to the regions in the map at the bottom right. Family-level species richness, or the approximate number of currently accepted species in each family, is indicated by the color of terminal branches in the phylogeny, with color corresponding to the legend at bottom left. Silhouettes around the outside of the phylogeny highlight some of the morphological variation across Passeriformes.

140! Furthermore, these studies are changing our understanding of how, when, and where passerines diversified.

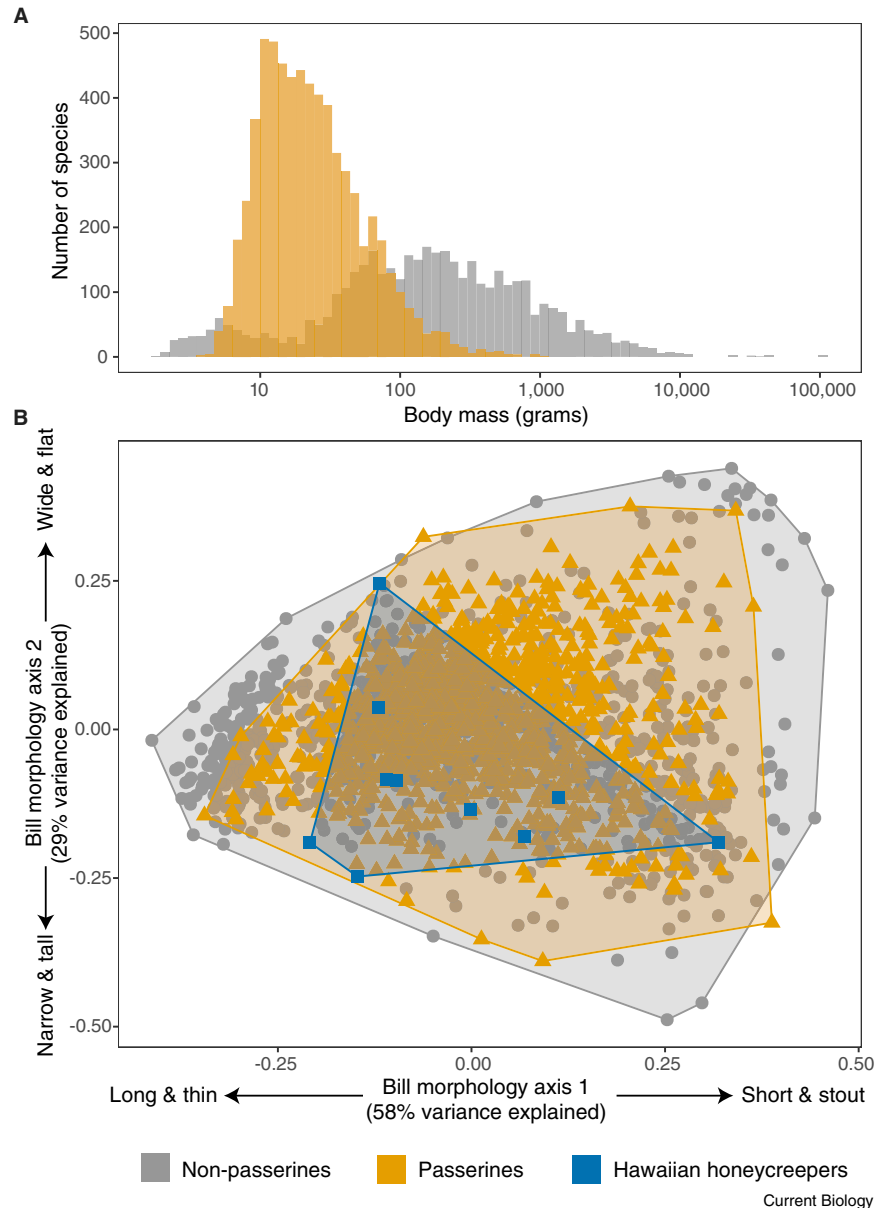
Although currently occurring on all continents except Antarctica, there is a general consensus that passerines

originated in the southern hemisphere. Specifically, most studies have inferred an Australo-Pacific origin for passerines as a whole, and one recent study incorporating DNA and fossil data suggests that passerines began

diversifying on the proto-Australian landmass around 47 million years ago, a hypothesis bolstered by the fact that one of the oldest passerine fossils was found in Eocene rocks of northeastern Australia, as well as the confinement

of the deepest passerine branch (Acanthisittidae) to New Zealand (Figure 1). However, recent evidence from two fossil passerines described from 52 million-year-old Eocene formations in Wyoming, USA, and Germany could suggest a Northern origin of the clade. Best estimates indicate that oscines, suboscines and passerines separated about 44 million years ago, with many independent colonizations by oscines of Eurasia, Africa and North America. Contrary to their current center of diversity in the Neotropics, suboscines appear to have originated in Eurasia approximately 39 million years ago, only later colonizing and diversifying in South America, likely from the West Antarctica segment of the Gondwanan supercontinent. While some uncertainties remain, these scenarios represent most-likely hypotheses based on available data and we suspect that the discovery of new fossils will further clarify our understanding of passerine biogeography and diversification.

The names passerine and Passeriformes are derived from the Latin word *passer* meaning ‘sparrow’. Indeed, sparrows and sparrow-like birds are some of the most familiar passerines; however, these names belie considerable morphological and ecological variation in the order. Although generally small compared to other birds, passerines exhibit a wide range of body sizes (Figure 2). For example, the largest passerines include several species of raven (Corvidae: *Corvus* spp.) that weigh more than one kilogram and, larger than many raptors, are over 250 times heavier than the smallest passerine, the Pygmy Bushtit of Java (*Psaltria exilis*; Aegithalidae), which weighs less than five grams and is smaller than many hummingbirds. While conical seed eating bills are typical of many well-known sparrow- and finch-like passerine families, there is great variation in bill morphology across Passeriformes (Figure 2). A strong correspondence between passerine bill morphology and ecology provides compelling evidence of an intricate and specific link between form and function — passerines provide many examples in which there appears to be a single optimal morphology for a specific ecological niche. Accordingly, passerines have figured prominently in understanding

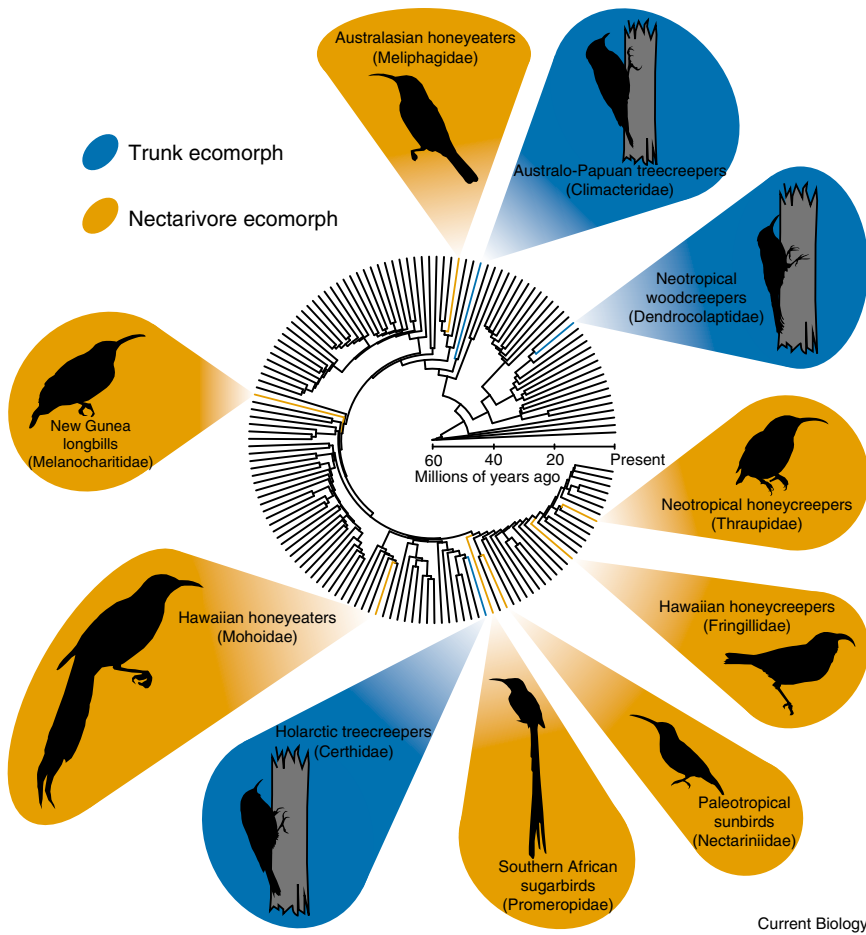


**Figure 2. Comparison of body mass and bill morphology between passerines and non-passerines.**

(A) is based on data from Tobias *et al.* 2022 and shows how passerine body mass is smaller yet broadly overlapping with that of non-passerines. (B) describes the distribution of bill morphology in Hawaiian honeycreepers, the remaining passerines, and non-passerines based on data from Cooney *et al.* (2017).

the celebrated evolutionary concept of adaptive radiation, the process by which an ancestral species evolves to exploit new ecological niches and rapidly diversifies into multiple species. The Darwin’s finches of the Galapagos islands, which are actually tanagers (Thraupidae), are the prototypical example of an adaptive radiation — natural selection to exploit novel niches

across the archipelago has driven the evolution of diverse bill morphologies and new species within an evolutionary blink of the eye, last estimated at less than a million years ago. Even more morphologically disparate are the examples of adaptive radiation seen in the Hawaiian honeycreepers (Fringillidae; for more, see the quick guide by Robert Fleischer and



**Figure 3. Examples of convergent evolution in passerine birds.** Patterns of inferred independent evolution of two ecomorphs, tree-trunk climbing and nectarivore, are shown on the passerine phylogeny. Silhouettes around the outside of the phylogeny illustrate examples of each ecomorph.

colleagues in this issue) and the vangas (Vangidae) of Madagascar, where each group has evolved bill morphologies nearly as diverse as those seen across the entirety of the Passeriformes (Figure 2).

**Convergent evolution in Passerines**

Passerines also provide many examples of the concept of evolutionary convergence. For instance, several passerine groups have independently evolved specialized ecomorphs, or body plans, associated with a particular ecological niche. One example is the trunk-climbing ecomorph (Figure 3), which has evolved independently in the Neotropical woodcreepers (Dendrocolaptidae), Eurasian treecreepers (Certhiidae) and Australo-Papuan treecreepers (Climacteridae). All three of these

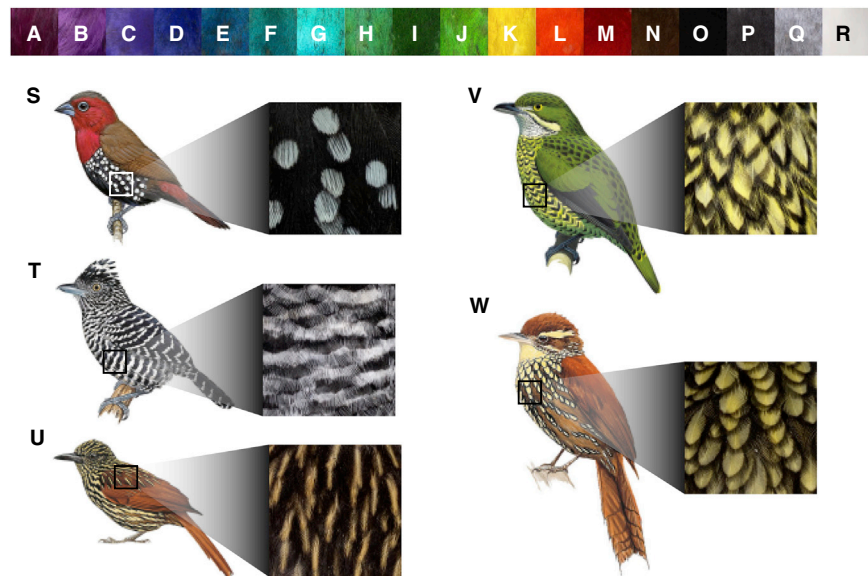
passerine families are characterized by streaky brown plumage — strikingly similar in its minute details in some cases — that camouflages them against tree bark, as well as strong toes, deeply curved claws and long, stiff tails facilitating locomotion on vertical tree trunks, converging in turn on the non-passerine woodpeckers (Piciformes). Other examples of convergent evolution in passerines can be found in the diversity of bill morphology that natural selection has repeatedly shaped to fit specialized diets. For example, long, thin, often downwardly curved bills adapted for feeding on floral nectar have evolved independently at least seven times (Figure 3). Specifically, this nectarivorous ecotype evolved once in the Australasian honeyeaters (Meliphagidae), once in the longbills of

New Guinea (Melanocharitidae), once in the now extinct Mohos or Hawaiian honeyeaters (Mohoidae), once in the sugarbirds of Southern Africa (Promeropidae), once in the sunbirds of the Paleotropics (Nectariniidae), once in the Hawaiian honeycreepers (sometimes called Hawaiian finches; Fringillidae) and at least once in the Neotropical honeycreepers (Thraupidae) — an example of convergence even in common names!

Perhaps the most visually striking aspect of bird diversity are their feathers, and passerines in particular have extravagant and highly colorful feathers. For example, birds-of-paradise (Paradisaeidae) are famous for their highly modified plumes and have been heralded as examples of the creative potential of runaway sexual selection. Bright coloration is generally more widespread in oscines compared to suboscines; however, notable exceptions include the Old World suboscines (Eurylamides), cotingas (Cotingidae) and manakins (Pipridae; Figure 4). Owing to this diversity in coloration and the availability of captive experimental populations for many species, studies investigating the genetic basis of plumage coloration have frequently used oscine passerines as model systems. Indeed, the link between plumage coloration and genetic variation in wild birds was first discovered in Bananaquit (*Coereba flaveola*; Thraupidae) by sequencing of the melanocortin-1 receptor (MC1R), a now well-known gene in the pathway producing brown and black melanin pigments. Other oscines have been the workhorses for understanding the genetic basis of carotenoid-based pigmentation typified by yellow, orange, and red colors in passerine birds. Leveraging color variation in captive Common Canaries (*Serinus canarius*; Fringillidae) and the Zebra Finch, a native to Australia and the Indonesian island of Timor (*Taeniopygia guttata*; Estrildidae), researchers have linked the genetic basis of yellow and red carotenoid coloration to two genes: scavenger receptor B1 (SCARB1) and cytochrome P450 (CYP2J19). In New World Warblers (Parulidae), another oscine group, carotenoid coloration also appears to be associated with variation at SCARB1, as well as the beta-carotene oxygenase 2 gene

(BCO2). The genetic basis of structural coloration, or non-pigment-based coloration responsible for white, blues, greens, purples, super blacks and iridescence, remains elusive; however, detailed biophysical studies are describing the micro- and nanoscale mechanisms that produce such structural colors.

Passerine birds also produce a diversity of sounds (for more on bird sounds, see the primer by Jeffrey Podos and Michael Webster in this issue), and efforts to study avian vocalizations and vocal learning have focused extensively on passerines. The German physiologist Johannes Müller recognized as early as 1847 that suboscines have simple musculature of the syrinx, the major vocal organ situated at the base of the trachea and named as such by Thomas Henry Huxley in 1871, whereas oscine syrinx musculature is often more complex (for more on the syrinx, see the primer by Franz Goller in this issue). Oscines and suboscines are further distinguished by the fact that oscines learn their songs, whereas the songs of suboscines are generally innately determined, with some suspected exceptions. Because of these differences, oscine passerines are often referred to as ‘songbirds’. Vocal learning is currently believed to have evolved independently in hummingbirds, parrots and oscine passerines, despite the close relationship of the latter two clades. Early evidence for song learning in oscines came from the observation of frequent vocal dialects in species such as the White-crowned Sparrow (*Zonotrichia leucophrys*) of western North America, as well as isolation experiments, in which it was found that juvenile oscines raised in isolation could not reproduce, or crystallize, their fully developed song. Like humans, oscine song learning generally involves hearing, copying and perfecting model sounds through repetition. In most oscines, the process of song learning occurs during an individual’s first two months of life, a time referred to as a ‘sensitive period’. Exceptions to this paradigm include ‘open-ended learners’, or species that continue to learn new songs throughout their lives, such as species in the mimid family (Mimidae), including Mockingbirds



**Figure 4. Examples of color diversity across passerines.**

Boxes A through R summarize some of the color variation seen across passerine birds. Each square represents a closeup image of a plumage patch from specimens in the Museum of Comparative Zoology at Harvard University: (A) belly of Banded Cotinga (*Cotinga maculata*; MCZ 141082), (B) breast of White-Browed Purpleuft (*Iodopleura isabellae*; MCZ 84322), (C) breast of Gouldian Finch (*Chloebia gouldiae*; MCZ 123392), (D) breast of Red-legged Honeycreeper (*Cyanerpes cyaneus*; MCZ 198639), (E) breast of Green Honeycreeper (*Chlorophanes spiza*; MCZ 103898), (F) breast of Green Honeycreeper (*Chlorophanes spiza*; MCZ 230825), (G) breast of Paradise Tanager (*Tangara chilensis*; MCZ 232794), (H) breast of Viridian Dacnis (*Dacnis viguieri*; MCZ 272491), (I) back of Grass-green Tanager (*Chlorornis riefferii*; MCZ 122988), (J) breast of Bay-headed Tanager (*Tangara gyrola*; MCZ 106329), (K) rump of Lemon-rumped Tanager (*Ramphocelus icteronotus*; MCZ 107435), (L) rump of Flame-rumped Tanager (*Ramphocelus flammigerus*; MCZ 103856), (M) breast of Brazilian Tanager (*Ramphocelus bresilius*; MCZ 273881), (N) back of Streak-breasted Treehunter (*Thripadectes rufobrunneus*; MCZ 108935), (O) breast of Lemon-rumped Tanager (*Ramphocelus icteronotus*; MCZ 107435), (P) back of Black-spectacled Brushfinch (*Atlapetes melanopsis*; MCZ 366294), (Q) back of Red-crested Cotinga (*Ampelion rubrocristatus*; MCZ 266742), (R) wing of Yellow-billed Cotinga (*Carpodectes antoniae*; MCZ 117066). S through W highlight common plumage patterns in passerines: (S) Peter’s Twinspot (*Hypargos niveoguttatus*; MCZ 263938), (T) Barred Antshrike (*Thamnophilus doliatus*; MCZ 366196), (U) Flammulated Treehunter (*Thripadectes flammulatus*; MCZ 331072), (V) Scaled Fruiteater (*Ampelioides tschudii*; MCZ 124421), (W) Pearled Treerunner (*Margarornis squamiger*; MCZ 366311). (Bird illustrations from Birds of the World (<https://birdsoftheworld.org/bow/home>) and reproduced courtesy of Cornell Lab of Ornithology (©).)

(*Mimus polyglottus*), New World Catbirds and Thrashers. Because of their experimental tractability oscine species, such as the Zebra Finch, Bengalese (or Society) Finch (*Lonchura striata*) or Common Canary, are the go-to commonly used models for the research on evolution and neurobiology of vocal learning (see the primer by Richard Mooney in this issue). Extensive studies of domestic Zebra Finches (Estrildidae: Taeniopygia guttata) have clarified the neurological basis of song and two brain pathways have been identified — the motor pathway and the anterior forebrain pathway. Both pathways are linked by a set of interconnected neurons, or song nuclei, that are concentrated in specific parts of the brain. The motor pathway

passes the instructions for producing song from the brain to the nerves of the syrinx and respiratory system, while the anterior forebrain pathway is responsible for processing and memorizing the sounds a bird hears.

Passerine birds, and particularly the oscine passerines, appear to represent a sort of biological ‘phase transition’ in avian biology, albeit one whose basis is still somewhat elusive. In a famous 1982 essay in *Systematic Zoology*, the systematist Robert Raikow suggested that there were no obvious key adaptations underlying the spectacular diversity of passerine birds. To be sure, passerines exhibit several morphological traits that both demonstrate their monophyly and provide possibilities for underlying key

adaptations. For example, passerine birds exhibit a uniquely simplified leg and foot musculature compared to non-passerines, underscoring their common name as ‘perching birds’. Specifically, they have lost several of the muscles controlling the three forward toes found in non-passerines, substantially reducing the possibility of detailed movements of individual toes. Passerines also possess sperm that are bundled with a large acrosome. But there appear to be few or only weak correlations between sperm morphology, including sperm length, and probability of paternity in those mating systems and species that have been studied. Thus, Raikow reasoned, the adaptive significance of the several classical synapomorphies distinguishing passerine birds is unclear. Other researchers responded to Raikow’s essay that a suite of morphological and behavioral traits could reasonably be suggested as key drivers of passerine diversification. For example, the small body size of passerine birds could have promoted speciation, as in rodents. Some major passerine radiations are distinguished by large relative brain size, with some of the largest passerine brains being driven by expansion of the hippocampus, a brain area associated with spatial memory and seed caching, as in nutcrackers and titmice. Accordingly, behavioral flexibility was also suggested as a driver of passerine diversification, and indeed, most of the research on one aspect of behavioral flexibility, variation in avian personalities, has been performed on passerines such as the Great Tit (*Parus major*). Recent work has also shown that rates of extra-pair paternity among chicks in the nests of passerines — due to extra-pair mating and cryptic departure from their typically monogamous and observable social mating system — is often higher in passerines than in non-passerines (for more on bird mating systems see the primer by Bart Kempenaers in this issue). At this point, all the links between these traits and passerine diversification are merely speculative, and further work is needed. However, few researchers would doubt that the suite of traits that come together in passerine birds have undoubtedly contributed to their extraordinary diversity, and that together they comprise the biological phase transition we allude to.

Early on in molecular phylogenetic studies it was recognized that the branch leading to the passerines was long, suggesting an accelerated rate of molecular evolution and an extensive opportunity for trait evolution that might distinguish the clade. Recent genome-wide and many gene-specific studies have confirmed this higher rate of substitution in passerines, although more extensive work is needed. This accelerated rate of molecular evolution is likely to be driven by short generation times and high metabolic rates typically found in passerine birds. Oscine passerines also exhibit some genomic traits that, thus far, appear to be unique among birds, such as a germline-restricted chromosome — a segment or segments of DNA of variable size that is present in the chromosomes of male and female gonads but lost in somatic tissues. The evolution and functional significance of the germline-restricted chromosome is currently a topic of intense interest among avian geneticists.

Owing in part to their global distribution, species diversity, importance in studies of song learning, and general accessibility as both field and laboratory model species, oscines have been more intensively studied than suboscines. Although some excellent neuroscience work has been performed on suboscines called Neotropical manakins (Pipridae), it has been challenging to develop any suboscine species as a model organism for laboratory-based studies because their highly specialized frugivorous or insectivorous diets are difficult to replicate in captivity. Furthermore, most suboscine diversity is concentrated in the Neotropics where it is often logistically difficult to conduct field studies of suboscines. Despite these challenges, many researchers, especially those from countries in the Neotropics, are making advances in the study of suboscine biology that will fill important knowledge gaps and provide useful comparisons to the biology of oscines. Increased research focus on suboscines will be essential to advancing our understanding of passerine birds generally.

#### DECLARATION OF INTERESTS

The authors declare no competing interests.

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