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Passerine Morphology

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Passerines Share Many Traits with Other Types of Birds

In seeking to understand the traits that distinguish passerines from other types of birds, it is useful to consider them in light of the traits that distinguish birds from other groups of animals. Birds are warm-blooded (endothermic) vertebrates, meaning that they generate their own body heat rather than relying on the environment to maintain their body temperature, and their body structure includes a backbone. When we think of birds, features such as wings and eggs may leap to mind, but neither of those features is unique to birds. For example, bats and insects have wings, and egg laying is common across a wide range of animals such as fish and reptiles. When we consider the adaptations that define birds, many are associated with the demands of flight, such as reduced weight and efficient power. Feathers, pneumatic bones (such as those found in the wing), and a highly efficient respiratory system are all adaptations that facilitate birds' ability to fly (reviewed in Rodewald et al. 2018).

Highly adapted avian structures afford many useful advantages. For example, large flight feathers, such as the primary feathers on the wing, enable birds to generate lift and thrust while also controlling their direction in the air. Other types of feathers are collectively called "plumage" and are a form of ornamentation that plays an important role in courtship and mate choice for many species. Much smaller feathers are collectively called "down" and line the body to provide very efficient insulation to prevent heat loss. Despite their differences in size and appearance, each of these types of feathers is made primarily of a protein called keratin and consists of a hollow shaft with small barbs branching off on either side of that central structure (reviewed in Butler and Rohwer 2018). These highly adapted structures were once thought to be homologous to reptilian scales based on similar composition and development. However, more recent research suggests that feathers evolved through a series of changes in the follicle from which feathers grow (Prum and Brush 2002). The origin of feathers remains a topic of ongoing research, but it is clear that they provide important advantages in terms of flight, ornamentation, and insulation (reviewed in Butler and Rohwer 2018).

Forelimbs are also highly adapted in birds, so much so that they have received the specialized name "wings." At first glance, a bird's wing and a

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human arm might not appear very similar; however, the skeletal structure is very similar in wings, arms, and forelimbs observed across different species of vertebrates (reviewed in Shubin 2009). The most proximal portion of the wing consists of the humerus (from the Latin for "shoulder"), and the more distal portion is formed by the ulna (from the Latin for "elbow") and radius bones. Proceeding distally from those bones, they are connected to carpal (from the Latin for "wrist") bones that are in turn connected to the bones that compose the digits (from the Latin for "finger" or "toe"). The names given to these bones by anatomists make clear the parallels between the bones in an avian wing and those in your own arm.

In many species of birds, bones contain hollow spaces that are strengthened by networks of bony filaments called trabeculae (from the Latin for "beam") (reviewed in Voss and Pavia 2018). The hollow structure of these bones not only makes them lighter, it also makes them very resistant to bending and other forces that occur during the downstroke of the wing. This is important, as birds produce forces in excess of their body weight when they fly, and those forces are exerted by large muscles that attach to the bones of the wing. For example, contraction of the pectoralis muscle pulls on the humerus bone and causes the wing to be pulled down in the power stroke of flight. The joints that connect the bones of the wing also permit a wide range of movement, facilitating the power stroke, pulling the wing back up, and folding the wing to rest neatly against the body when the bird is not in flight (reviewed in Voss and Pavia 2018). These structural features of birds' wings – hollow, lightweight, agile, and strong – are ideal specializations for the challenges of flight in which weight is an obstacle and strength is essential.

The avian respiratory system is also highly specialized and adapted to meet the metabolic demands of flight. This system enables the movement of oxygen from air into the blood, and it performs this task very efficiently to enable the vigorous actions of flight. In humans, our lungs operate in a tidal system of air entering and leaving the lungs through inhaling and exhaling. The structure of avian lungs is very different, and air flows in a single direction across the surfaces that permit the exchange of gases (reviewed in Martinez Del Rio et al. 2018). Structures called air sacs and the muscles that control the movement of the rib cage act like bellows to move air through the avian lung, and the unidirectional movement of air across surfaces in the lungs enables birds to exchange nearly all the volume of their lungs in each breath. In contrast, humans and other mammals do not exhale all the volume of our lungs each time, leading to residual "stale" oxygen-depleted air that then mixes with fresh air in the next inhalation. Complete turnover of air in each breath means that birds have a greater content of oxygen-rich air available to them. The movements of flight further enhance the movements that drive respiration, pumping air through the respiratory system even more forcefully than when the bird is at rest (Jenkins Jr. et al. 1988). This is especially beneficial, as it provides even greater exchange of gases at the time when the metabolic demand for oxygen is greatest.

Together with additional specializations that are not described here (reviewed in Rodewald et al. 2018), the features described above are conserved across nearly all species of birds. These traits distinguish birds from other types of animals, and that is recognized by the taxonomic description of birds as belonging to Class Aves. However, there can be huge differences between different types of birds. For example, ostriches and hummingbirds are both birds, but there are vast differences in their size, shape, ecology, and metabolism. When we parse birds into more finely divided groups, the next level of taxonomic rank beyond Class is Order, and the largest group of birds is the Order Passeriformes. These birds are more commonly called passerines or "perching birds," and the properties that distinguish passerines from other birds are the focus of the next section.

Passerine Birds (Order Passeriformes)

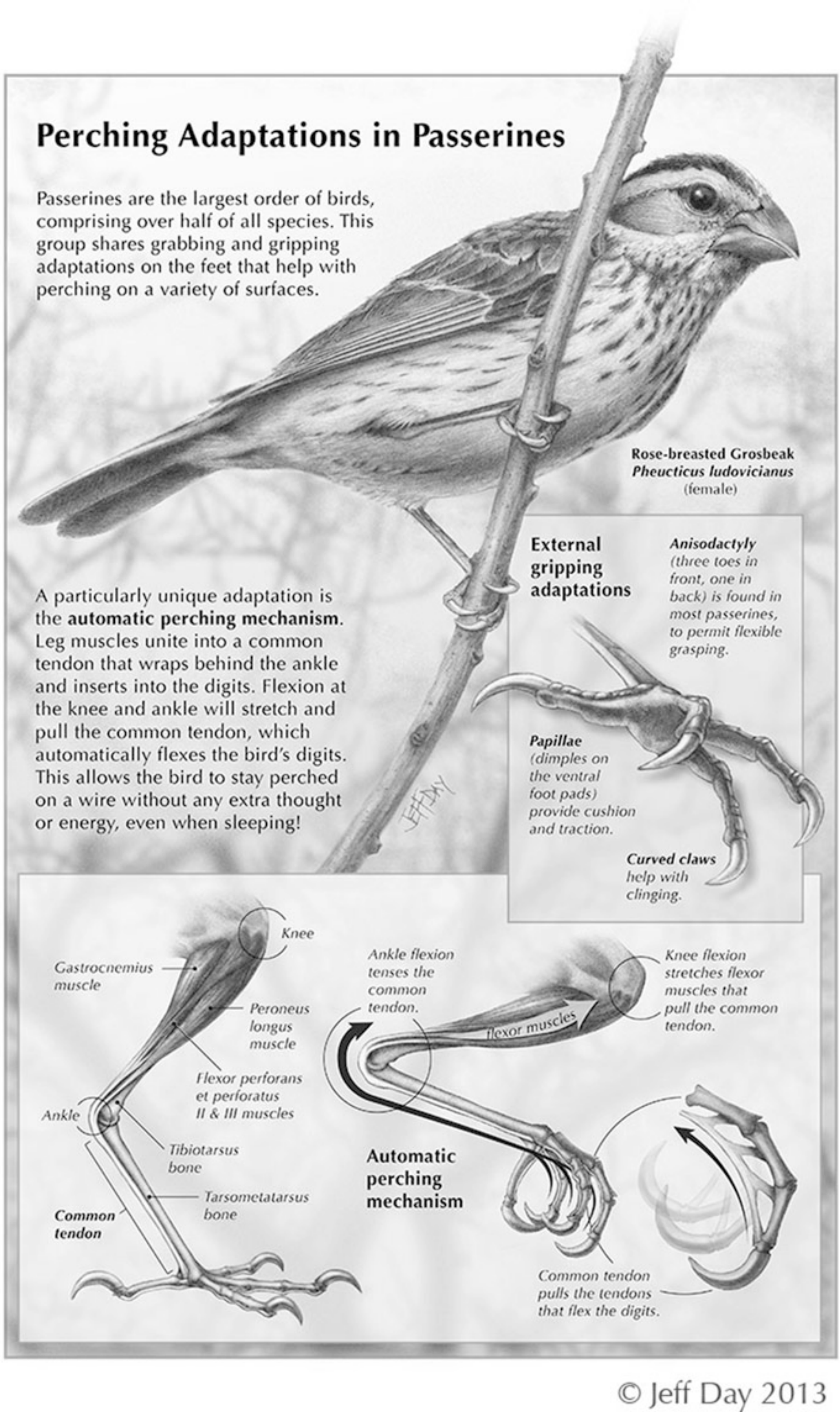
The group of birds called passerines includes approximately 140 families of taxonomic division and 6000 species, comprising approximately half of all species of birds that are alive today (Olalla-Tárraga et al. 2019; Raikow and Bledsoe 2000; Ricklefs 2012). These birds may be very familiar, as they are commonly active during the day and they include songbirds that are commonly seen in the wild, such as sparrows, finches, jays, chickadees, and wrens. Passerines take their name from the Latin name for sparrows and small birds like them (passer). They are a very successful group of organisms, flourishing in a very wide range of habitats and occupying remarkably diverse ecological niches (Olalla-Tárraga et al. 2019; Raikow and Bledsoe 2000). They are typically smaller than members of other orders of birds, with the largest passerines being lyrebirds and ravens (typically around 1.5 kg and 70 cm in height) and the smallest being pygmy tyrants (typically around 4 g and 6 cm in height) (Unwin 2011). Most passerines are small- to medium-sized land-dwelling birds that feed primarily on insects, fruit, seeds, or nectar, and their morphology is generally well suited to a variety of foraging techniques and prey items (Ricklefs 2012).

Unique Features of Passerine Morphology

Passerines are more commonly known as perching birds because the arrangement of their toes and hindlimb muscles facilitates them perching on twigs and branches. Across all groups of birds, the arrangement of toes on each foot is remarkably diverse (reviewed in Voss and Pavia 2018). Different groups can have not only different numbers of toes on each foot but also different arrangements of those toes. The arrangement in passerine birds includes three toes that point forward on the foot, one toe that points backward, and no webbing between any of the toes (Fig. 1). This arrangement is called anisodactyl (literally meaning "unequal digits"), and it facilitates birds grasping either horizontal or more upright perches such as branches and tree trunks.

Passerines are digitigrade, meaning that they walk on their toes rather than on the entire foot, so the point of contact with perching surfaces includes only the toes and not the rest of the foot (Fig. 1). The bones in the toes of passerine birds are attached to muscles that work together with the anisodactyl arrangement to facilitate the perching reflex. Those muscles include the flexor digitorum longus, which flexes the three forward-facing toes, and the flexor hallucis longus, which flexes the backward-facing toe (Fig. 1; as detailed in Raikow 1982). The flexor tendons run along the backward-facing (posterior) side of the main bone of the foot (tibiotarsus) and insert on the bottom (plantar) portion of the digits. The tendon from the flexor digitorum longus attaches to each of the three forward-facing toes, and the tendon from the flexor hallucis attaches to the single backward-facing toe (some birds have interconnections between these tendons; detailed in Raikow 1982 and Raikow and Bledsoe 2000). Because of this arrangement, the forward- and backward-facing toes can be controlled separately, but coordinated contraction of the two flexor muscles causes each of the four toes to flex (extension of the toes is controlled by other mechanisms). This is the same sort of action as what occurs when you close your hand around an object in your grasp.

The arrangement of passerine toes and the associated muscles has implications for the way that those birds can use their hindlimbs. Because the toes can be contracted in a grasping motion, passerines can use their feet to hold items such as food or nest-building materials. The wide range of motion in the movements of each toe enables the bird to adapt its grasp to accommodate a wide range of sizes and shapes of different perching sites. Passerines also commonly use their feet and toes in other ways such as aggressive encounters or the precisely controlled movements that occur in preening. Some passerines, such as the Family Corvidae within the Order Passeriformes, are especially adept at these sorts of movements. These birds have been shown to have impressive intellectual abilities, as they are able to solve challenges that require them to employ concepts such as analogy and problem-solving (Smirnova et al. 2015). Corvids have also demonstrated the ability to use the agility afforded by the arrangement of their feet and toes to create rudimentary



Passerine Morphology, Fig. 1 Perching adaptations in passerines. (Illustration by Jeff Day, copyrighted 2013. Accessed with permission from jeffdayart.com/illustration-1#/perching-adaptations/on June 19, 2020) tools such as hooklike structures to retrieve food from a location that would otherwise be inaccessible to them (Hunt 1996).

The arrangement of the muscles and toes also plays a key role in how the toes function even when the associated muscles are not being actively contracted. When a passerine bird assumes the posture that we refer to as perching, it results in the ankle being bent and the bird's body weight resting on that bent joint (Fig. 1). When the bird bends its ankle (the tibiotarsal joint), the tendons are pulled along the bottom portion of the foot. This is the same movement of the tendon that occurs when the muscles are contracted, but in this case the tendon moves because of a change in posture rather than an active contraction of the muscle. In either case, movement of the tendon causes the toes to flex. Therefore, when the bird is perched, it can relax its flexor muscles and yet still have the force of its body weight acting to bend the ankle and flex the toes. In that way, the bird is effectively gripping its perch even when it is not actively contracting its muscles. This anatomical arrangement gives rise to a very convenient advantage in that passerines can grip their perch, and this remain safely secured on their branch or other site, even when they are asleep.

Variability of Passerine Morphology

Just as there is great diversity across all birds (Class Aves), there is also diversity among passerines (Order Passeriformes). That diversity is commonly characterized by comparing specific measurements from each type of bird. For example, these measurements can include beak size and shape, properties of the pectoralis muscle, measurements of the bones in the hindlimb, features of wing shape, and the size of feathers at specific locations on the body. In addition to this anatomical diversity, there are also differences in the behavior and ecology of different kinds of passerines. Those differences are commonly characterized by features of a bird's diet, foraging strategy, and habitat (Kennedy et al. 2020). The following sections describe aspects of the diversity that is found among passerine species and how those differences are thought to have enabled these birds to thrive in a wide range of ecological environments.

Variability in Beak Morphology

The size and shape of beaks varies widely across passerine species. These differences are correlated with differences in diet and foraging modes, and they are thought to have played key roles in diversification of species (Mallarino et al. 2012). Differences in beak morphology, such as length or depth of the beak, can enable birds to adapt to diverse and changing ecological niches by enabling them to exploit different sources of a similar type of food. For example, seeds are important food sources for many passerine species, and beaks of different shapes and sizes may provide birds with varying degrees of success in accessing seeds such as those that are large and tough (for which a short and large beak may facilitate cracking those seeds) or that are hidden within the recesses of pinecones or other structures (for which a long and slender beak may facilitate access to those seeds) (Benkman 1993).

Similar patterns are also evident across species that exploit different food sources. Species that feed primarily or exclusively on small fruits (seed dispersers) tend to swallow those fruits whole, and those birds tend to have broader and flatter bills compared to other species (Herrera 2011). In contrast, species that feed on fruits only occasionally and rely on other food sources for most of their diet (seed predators) do not express those characteristics of bill shape (Herrera 2011). It is thought that the traits of beak morphology expressed by seed disperser species are advantageous in allowing them to feed primarily on fruit, whereas seed predator species do not express those specific adaptations and are therefore able to be dietary generalists that can exploit a greater range of dietary options.

Adaptations of bill morphology in association with diet and habitat are apparent even between closely related species. For example, long, flat bills are typical of birds that catch mobile prey, such as flying insects. In contrast, shorter, slightly curved bills are typical of birds that feed on more sedentary prey. In the case of warblers (Genus *Acrocephalus*), mobile prey are more abundant in marsh habitats, and the species of warblers that inhabit those areas tend to have long, flat bills. In contrast, less mobile prey are common in vegetation and undergrowth, and species of warblers that inhabit those areas tend to have shorter, slightly curved bills (Leisler et al. 1989). In perhaps the most compelling evidence in support of the idea that beak size and ecological opportunities are related, a correlation between changes in beak size and changes in habitat is evident within the seasonal transitions of an individual species. Within honeyeaters (Genus *Meliphagidae*), beak size increases during the summer months, becoming more elongated during a time when those birds also increase their reliance on nectar as a food source (Friedman et al. 2019).

Beak morphology is also related to activities other than feeding, such as thermoregulation, singing, and preening behaviors. Beaks are a primary means through which birds release heat into the environment; thus, smaller or larger beaks have consequences for not only feeding and the acquisition of energy but also thermoregulation and the release of energy (Friedman et al. 2019). A large bill might enable a species to fare better in a very warm climate than if it had a much smaller bill, opening the door to occupying a niche that the species might otherwise not inhabit. In singing, the beak is part of the vocal tract that influences the resonance of specific frequencies in calls or songs. If the beak is wide open, the overall vocal tract is shorter (favoring higher frequencies) than if the beak is more closed (favoring lower frequencies) (Huber and Podos 2006). This is similar to the musical phenomenon in which larger, longer tubes in a pipe organ produce lower notes than smaller, shorter tubes. Finally, beaks can also play an important role in the bird's ability to maintain its health through preening and removal of harmful parasites (Clayton et al. 2005). Thus, beaks can influence many aspects of a species' ability to thrive in different contexts, and demands and advantages such as these are thought to have acted as strong driving forces in shaping the evolution of beak morphology.

Variability in the Pectoralis Muscle

Flight is a very metabolically expensive behavior, and different species of passerines express different traits in the powerful muscles that enable flight (Welch and Altshuler 2009). The pectoralis muscle is the dominant muscle associated with powering flight as well as other aspects of survival such as thermoregulation by shivering, and it accounts for the majority of muscle mass in birds. Within the pectoralis, there can be different types of muscle fibers (e.g., DuBay et al. 2020). Some of those fibers can be glycolytic, meaning that they rely on cellular energy reserves such as glycogen that is immediately accessible. Other muscle fibers can be oxidative, meaning that they rely on oxygen obtained through respiration as their energy source. These differences can have functional consequences, as glycolytic fibers are excellent for producing rapid movements but they are more easily exhausted than oxidative fibers. Therefore, different composition of fibers in the pectoralis muscle may be better suited for different types of brief versus sustained behaviors.

Within the pectoralis of small-bodied birds, muscle fibers are often exclusively oxidative, whereas the pectoralis in larger species contain a much greater proportion of glycolytic fibers (Welch and Altshuler 2009). This is thought to reflect the different demands that species of different sizes face in takeoff and continued flapping during sustained flight. For example, large birds may be more dependent on the bursts of power that glycolytic fibers provide to lift them into the air. Interestingly, recent research has revealed that glycolytic fibers may be present in the pectoralis of small birds (DuBay et al. 2020). In most small species, the pectoralis is composed exclusively of oxidative fibers, and these new data suggest that species diversity in the composition of pectoralis fiber types may play important roles in not only powering takeoff but also other aspects of survival such as competitive interactions or predator avoidance (DuBay et al. 2020). In support of that idea, the proportion of glycolytic fibers is greater in socially dominant small birds than in less dominant members of the same species (DuBay et al.

2020). Together, these results reveal that diversity in pectoralis muscle fiber composition is evident not only across but also within passerine species. Those differences have functional consequences, and diversity may be influenced by not only evolutionary history but also experiences that accrue within an individual's lifetime.

Variability in Hindlimb Morphology

Different habitats place different demands on their inhabitants. For example, flat environments typically require little or no climbing, but habitats with steeper or perhaps even vertical surfaces could require very different patterns of locomotion. These differences in demand may be evident as structural differences between species that have adapted to each type of location. For example, warblers (Genus *Acrocephalus*) that live in environments where they commonly cling to vertical surfaces have long backward-facing toes, while those that live in habitats where they commonly run along the ground have adapted to express a longer version of a different toe (Leisler et al. 1989). In another example, species that are more reliant on hopping behavior for predator avoidance and takeoff tend to have longer foot bones (tarsus) than species who do not rely on those behaviors (Swaddle and Lockwood 1998). Adaptations of the hindlimb are also evident in the muscles that control flexion of the joints in the leg and foot. Anatomical differences associated with greater maximal force of contraction and flexion are evident in species that are more reliant on hanging behavior for their perching and feeding, and it is thought that these adaptations are helpful in counteracting the effects of gravity (Moreno 1990).

Variability in Wing Shape and Feather Size

Passerine species also vary in the shape and size of their wings, and those differences are thought to be associated with differences in behavior and habitat. In another example from warblers, species that exploit taller vegetation tend to have broader wings than those that move through shorter and more tangled vegetation (Leisler et al. 1989). It is thought that those differences are functionally significant because broader wings may facilitate takeoff from within tall vegetation, whereas more narrow wings may facilitate maneuverability through dense vegetation (Kennedy et al. 2020). Studies of other passerine species have revealed that species with rounded wingtips as opposed to pointed wingtips are at a lower risk for predation, and it is thought that rounded wingtips may enhance flight performance at slow speeds and thus allow individuals to take off more quickly and at steeper angles than birds with sharper wingtips (Swaddle and Lockwood 1998). The properties of these different types of wingtip are associated with differences in the lengths of the primary and secondary flight feathers on the wings of those species. Thus, passerine species express diversity in the features of the structures that power and control flight, and those anatomical differences are closely correlated with differences in habitat.

Variability in Behavior

In addition to anatomical differences between species, passerines also vary in their behavior. Some species have been characterized by the ability to learn the sounds they used in vocal communication (Suborder Passeri within the Order Passeriformes). These birds are commonly called "songbirds" or "oscines," named from the Latin word for singing birds. The ability to learn the sounds used in communication is a feature of human communication through speech, but it is otherwise rare across animal species (reviewed in Martins and Boeckx 2020). Therefore, songbirds have been the focus of research into not only the ways that song is used by those species but also how it may be informative as a means of understanding how we communicate through speech. Vocal learning is associated with the presence of specialized structures in the songbird brain, and a growing body of research is providing insight into how studies of songbirds may help us understand the mechanisms of human communication (reviewed in Mooney et al. 2008). In addition to the songbirds that comprise Suborder Passeri, other passerines (Suborders Tyranni and Acanthisitti) have long been thought to have little or no reliance on learning in their acquisition and performance of the signals they use in communication (e.g., Kroodsma 1984). That is reflected in the commonly used term “suboscines” to refer to those birds. However, recent research suggests that such a dismissive term may be inappropriate and that the differences between these groups are not as stark as was previously thought (reviewed in Martins and Boeckx 2020). Feedback-dependent effects on vocalizations are a hallmark of the vocal learning process, and suboscine species have been shown to modify their vocalizations based on sensory experience (Kroodsma et al. 2013; Martins and Boeckx 2020). The effects of experience on song performance are much greater in songbirds than the effects seen in suboscines, but research suggests that both groups may be at least somewhat dependent on learning in their vocal communication (Martins and Boeckx 2020). Thus, the difference between these groups may be one of degree rather than a categorical distinction. Ongoing research is seeking to understand these differences and their associated neural circuits more fully as a means of understanding how the brain enables perception and learning in not only these passerine species but also ourselves.

Passerine Success across Many Different Niches

As noted throughout this entry, passerines comprise a large number of species that are quite diverse in their morphology, life history, and behavior. They have adapted to occupy a broad range of terrestrial habitats and a similarly diverse range of ecological niches. Their characteristics such as relatively small bodies, large brains, arboreal living, reproductive success, behavioral flexibility, and ability to feed on a broad diversity of food sources have apparently provided them with abilities to colonize new areas better than any other group of birds (Olalla-Tárraga et al. 2019). This tolerance and adaptability may also explain how they have been able to thrive across diverse and widespread habitats. Changes throughout Earth’s history may also have played a key role in their success, as global climate changed during the Tertiary period and adaptive radiation among flowering plants and insects gave rise to a diversity of habitats that may have been especially well suited to support small birds (Oliveros et al. 2019).

Passerines also express many behaviors that are also thought to have helped them thrive throughout their history. For example, passerines have an extraordinary ability to create nests out of a wide range of materials, place them in a variety of areas, and conceal them effectively against threats from predators and the environment (Olson 2001). Those nests provide protection for not only the birds that construct them but also their offspring, and that is especially beneficial in light of how vulnerable hatchlings are during the earliest days of their lives. The ability of passerines to protect their young in this way may also have contributed to their success (Olson 2001). Additional aspects of reproduction such as rapid development to an early age of sexual maturity and the associated short generation times may have also contributed to successful adaptation to novel environments. Passerines are also behaviorally flexible and capable of complex learning, as shown by their mate choice strategies and vocal behavior. In addition, many species are capable of migrating over very long distances, enabling them to disperse over wide ranges and take advantage of resources present across those different locations (Olson 2001). Taken together, these features reveal that passerines express many anatomical and behavioral traits that have likely contributed to their ability to reach new environments, adapt to survive there, and evolve into the diversity of passerine species that we observe today.

Cross-References

- ▶ Aves (Birds)
- ▶ Birds of Prey
- ▶ Passerine Cognition
- ▶ Passerine Diet
- ▶ Passerine Life History
- ▶ Passerine Locomotion
- ▶ Passerine Navigation
- ▶ Passerine Sensory Systems
- ▶ Passerine Vocal Communication
- ▶ Skeletal System
- ▶ Songbird Duets
- ▶ Songbird Learning

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