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## Passerine Vocal Communication

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### Definition

Birds of the order Passeriformes, known as pas-
serines, include over half of the almost 10,000
known bird species (Mayr 1946). In comparison
to other orders under the class Aves, passerines
have a particular toe arrangement: three toes
pointing forward and one pointing back (Proctor
and Lynch 1993). This particular arrangement
aids in perching, which has lead to the name
"perching bird".

### Introduction

Passerines include many songbirds, a group of
more than 5,000 species that engage in vocal
learning, similar to how humans, cetaceans, bats,
elephants, parrots, and hummingbirds learn their
vocalizations (Doupe and Kuhl 1999). Passerines,
in general, are commonly referred to as songbirds,
but this is not entirely correct. The order can
instead be broken down into the Oscines and the
Suboscines. Oscines (i.e., songbirds or "true"
songbirds) have highly developed song and learn
their species-typical vocalizations via a model
(e.g., a parent) and have dedicated brain architec-
ture. Suboscines, however, do not require a model
to learn their species-typical vocalizations and
continue to produce and perceive vocalizations
even with damaged auditory brain regions; how-
ever, some species do have a rudimentary vocal
system, the structure(s) within the brain associ-
ated with production of vocalizations, which
appears to act in the same way as in the Oscines
(Kroodsma and Konishi 1991). These structures
include rudimentary forms of structures like the
robust nucleus of the arcopallium, which could
indicate an evolutionary predecessor to a true
vocal control system (see more details below;
Liu et al. 2013). In North America, there is only
one family of Suboscines: Tyrannidae, which
includes flycatchers, phoebes, and king birds. Pas-
serines primarily communicate using vocaliza-
tions, as acoustic signals are difficult to localize
(e.g., in the presence of a predator), can travel
across greater distances than visual cues, and are
advantageous in dense vegetation. Passerines
include a wide range of species found in both
temperate and tropical climates.

## Passerine Species

### Example Temperate Species

Temperate forests extend north from the Tropic of Cancer to the Arctic Circle and south from the Tropic of Capricorn to the Antarctic Circle. The Paridae family includes the tits, chickadees, and nuthatches. Titmice are widely distributed and can be found in North America (e.g., tufted titmouse, *Baeolophys bicolor*), Africa (e.g., African blue tit, *Cyanistes teneriffae*), Asia and Europe (e.g., Great tit, *Parus major*). Chickadees are a group of North American songbirds including seven different species: black-capped (*Poecile atricapillus*), mountain (*P. gambeli*), Carolina (*P. carolinensis*), Boreal (*P. hudsonicus*), chestnut-backed (*P. rufenscens*), mexican (*P. sclateri*), and gray-headed (or "Siberian tit"; *P. cinctus*). Nuthatches mostly reside in North America (e.g., red-breasted, *Sitta canadensis*), but few species live in Eurasia (e.g., Eurasian nuthatch, *S. europaea*). A few examples of common non-Paridae temperate species include cowbirds (*Molothrus*), jays (*Corvidae*), sparrows (*Passer*), thrush (*Turdidae*), warblers (*Sylvia*), and wrens (*Troglodytidae*; Cornell Lab of Ornithology n.d.).

### Example Tropical Species

Passerines living between the Tropic of Cancer and the Tropic of Capricorn are classified as tropical species. A few examples of these birds are the Andean cock-of-the-rock (*Rupicola peruvianus*), Wilson's bird-of-paradise (*Cicinnurus respublica*), Australia's regent bowerbird (*Sericulus chrysocephalus*), and multiple species of broadbill (*Eurylaimidae*). There are also multiple species of finches, such as the cut throat finch (*Amadina fasciata*), the Gouldian finch (*Erythrura gouldiae*), and the subfamily of Hawaiian honeycreepers (*Carduelinae*; Cornell Lab of Ornithology n.d.).

Zebra finches (*Taeniopygia guttata*) whose range extends from Eastern Indonesia throughout the arid regions of Australia, however, have such a large habitat that they cannot be considered only temperate or tropical. Zebra finches are one of the most widely studied bird species in avian neurobiology because they learn and memorize their song from a tutor bird, and this learning and

memory process is similar to how human infants acquire language (Konishi 1985).

## Vocalization Types

Bird calls are often distinguished from song by a variety of characteristics, although in some species this distinction may be somewhat blurred. Songs are usually multipart sounds produced primarily by males during the breeding season as acoustic ornaments (Marler 2004; Smith 1991). Songs are used for the purposes of reproduction and territoriality, are typically produced in a consistent manner, and primarily by males in many species. In comparison, calls are typically simpler (sometimes even monosyllabic), produced by both sexes in all age groups, and used daily for the purposes of communication. Thus, calls serve a variety of functions crucial for survival (Marler 2004).

**Song** Songs are elaborate and complex vocalizations that have two main purposes: (1) to advertise and defend territory from other males and (2) to attract potential females for mating and potentially stimulate female reproductive behavior and physiology (Kroodsma and Miller 1996). The acoustic structure of birdsong is fairly consistent in production, which encompasses the notes, syllables, and phrases, and also dictates the way in which songs and song repertoires are delivered (Marler 2004). Song repertoires can range in size from one simple song (as seen in the black-capped chickadee) to over a thousand complicated songs (as seen in the brown thrasher) (Kroodsma and Miller 1996). In order for birdsong to be acquired there has to be a predisposition to learning as well as being exposed to song (Brainard and Doupe 2002). Again, the learning process is generally divided into two phases, the sensory phase and the sensorimotor phase, which can overlap. During the sensory period, the songbird is in a sensitive state where the brain is prepared to receive auditory input. The songbird listens to the songs produced by adult songbirds (i.e., tutor birds) and their brain processes this auditory input, forming a memory template of song (Mooney 1999). This input leads to both neural and behavioral changes, which is followed by the sensorimotor phase. In

this phase, songbirds start to produce their own song based on the template that was formed or activated during the sensory phase. Initially, this song is fairly inaccurate and variable and is often compared to babbling in human infants (e.g., Marler 1970). The auditory feedback that the songbird receives allows them to assess their performance and make changes until the song they produce matches the song template they developed during the sensory phase (e.g., Konishi 1965).

These early life experiences are crucial for song learning, and this learning can be disrupted in a variety of ways. The length of exposure to a tutor bird can drastically affect birdsong (i.e., shorter exposures lead to less complex song structures; e.g., Thorpe 1958). Acoustically isolating a bird from others during the sensory phase can lead to songs that are simpler, shifted in their frequencies, and extremely variable (e.g., Shackleton and Ratcliffe 1993). Preventing auditory feedback during the sensorimotor phase by deafening birds can also negatively impact song by producing shorter songs, delaying singing behavior, or even eliminating song altogether (e.g., Konishi 1965). However, many species still maintain some of the features of their species typical songs, indicating that there is partial encoding of some song features or an inherent song template that initially directs song learning (e.g., Bolhuis and Gahr 2006).

**Calls** Birds must maintain their social groupings, whether it is in the context of a mated pair, flock, or family group. Most birds have some form of contact call, which allows them to remain in contact with one another during foraging. Separation calls may be a variation of a contact call and are produced when a bird loses contact with its group. Finding food is also crucial for a bird's survival; therefore, some birds emit food calls which announce the presence of a food source enticing other birds in the group to come feed. A subset of these calls, begging calls, is produced by chicks after hatching which coax parents into feeding their offspring. These calls often allow for nest or kin recognition by the parents, or for nest mates to recognize one another (e.g., Beecher 1982).

Aggressive calls are used in antagonistic interactions between individuals, whereas alarm calls are used to announce the presence of a predator or danger in the environment (e.g., distress and mobbing calls). Distress calls are typically produced when the individual is in the grips of a predator (e.g., Zachau and Freeberg 2012). Conversely, when a nearby predator is detected, mobbing calls are used to attract other members of the group to harass or "mob" the predator in order to scare them off. There are also variations of mobbing calls that tend to code for the type of predator or the threat level posed to the individual (e.g., Templeton et al. 2005).

Calls were long believed to be innate; however, this is not the case for all species. Many calls are learned or partially learned (for review see Marler and Slabbekoorn 2004). Learning calls, as with songs, is also accomplished through a process of vocal imitation (Vicario 2004). Unlike songs that are produced primarily during the breeding season, many calls are produced year round and are more easily elicited in laboratory conditions. Again, the male zebra finch distance call, like their song, is learned from a tutor bird, and, as such, the calls vary between individuals (Simpson and Vicario 1990, 1991). Also, many calls are produced by both sexes, unlike song which is primarily produced by males. This allows researchers to examine the learning and development of calls in both males and females. There is some evidence suggesting that the black-capped chickadee's namesake *chick-a-dee* call is partially learned (e.g., Hughes et al. 1998). Black-capped chickadees raised in social and acoustic isolation produce *chick-a-dee* calls; however, the quality of these vocalizations is poor in comparison to chickadees raised with a tutor (Hughes et al. 1998). Overall, this indicates that there is some evidence for learning calls in songbirds.

Unlike production of the *chick-a-dee* call, the ability to memorize, categorize, and discriminate *chick-a-dee* calls may not be learned. Whether or not birds were raised with their own species, they are able to discriminate between a foreign and familiar species typical *chick-a-dee* calls. Specifically, it appears as though chickadees' internal template for discrimination does not require input

from adults within their own species (Bloomfield et al. 2008). Therefore, memorization and discrimination of the *chick-a-dee* call is not learned, but production seems to be partially learned.

## Structures and Perception

Oscines are characterized by a specialized and embellished (compared to Suboscines, see below) sound-producing organ, the syrinx. The syrinx is complex, comprised of five pairs of muscles, and is located at the junction of two bronchi, which allows for each bronchus to act as its own independent sound source. Vocal production is therefore accomplished by a complex interplay between muscle movements in the syrinx, air flow, and beak articulation. Suboscine species also possess a syrinx; however, its role in song production is unclear; song production and frequency modulation do not seem to rely entirely on the syrinx, but primarily on air sac pressure modulation (Amador et al. 2008). Oscines also possess a set of discrete brain nuclei called the vocal control system that are specialized for the acquisition, production, and perception of vocalizations. HVC (proper name, previously referred to as the high vocal center) and the robust nucleus of the arcopallium (RA) are integral components of the vocal control system within the brain of Oscines, and we know that lesioning these structures can drastically impact song production (Nottebohm et al. 1976). It also appears as though these two structures may be involved in call learning and production. Lesioning HVC and RA in male zebra finches causes one of their vocalizations, the distance call, to become more female-like, and lose their male-typical characteristics (Simpson and Vicario 1990). Certain manipulations can cause females to be able to learn and produce male-like distance calls, such as estrogen treatment during development (Simpson and Vicario 1991). Early life exposure to estradiol causes a masculinization of vocal behavior in zebra finches; estradiol-treated females produce song-like vocalizations in adulthood, as well as being able to produce the male-typical aspects of the distance call. Eastern phoebes (*Sayornis phoebe*), a suboscine species, also possess a rudimentary RA-like structure (Liu et al. 2013). Since suboscine species, like the eastern phoebe, do not learn their song, this suggests that vocal learning may be an evolved trait.

Humans can hear sounds in the range of 20 Hz to 20,000 Hz, but best perceive sounds between 2,000 and 4,000 Hz (Dooling 1982). In comparison, birds have a more restricted hearing range, especially for higher frequencies where they do not detect sounds above 10,000 Hz (Dooling et al. 2000). Similar to humans, birds hear best between 2,000 and 5,000 Hz, with songbirds (i.e., Oscines) typically more sensitive to higher frequencies and non-songbirds typically more sensitive to lower frequencies within this range. Human perception thresholds tend to be lower than birds for all frequencies, meaning that birds can detect quieter sounds, but there are a number of exceptions, including many owl species. Although birds have a more narrow overall frequency perceptual range than humans, birds are more sensitive to absolute frequency, changes in frequency, and timing between sounds, which aid in perceiving and discriminating their own, and other species, complex vocalizations (Dooling 1982).

Even though birds and mammals are not closely related, the ears of both share a number of structural similarities (e.g., they both have inner and middle ear structures, though the avian ear lacks a pinna or outer ear). In all vertebrate species, the middle ear serves to mediate the transfer of sound from the environment to the inner ear, usually by way of tympanic membrane vibrations and movement of a varying number of small bones. The avian middle ear has little variation among species and takes up a large amount of space relative to head size compared to reptiles and mammals. Avian ears have a single bone, the columella, while mammalian ears have three bones, collectively called ossicles. The mammalian cochlea is longer and coiled, while the avian equivalent, the papilla, is shorter and straight or slightly curved (Dooling et al. 2000). Both cochlea and papilla have specialized hair cells which vibrate in response to sounds of specific frequencies. However, the avian tall and short hair cells serve the same function as, but are not

evolutionarily related to, the inner and outer hair cells in the mammalian cochlea. The orientations of these hair cells are fixed across mammalian species, but vary widely in avian species. Vibrations in hair cells are transferred to neurons, and certain hair cells are responsive to certain frequencies. Frequency and intensity are stored and passed into the auditory nerve. The pathway from auditory nuclei through the auditory areas of the brain is conserved across both birds and reptiles. From the auditory nerves, sound information projects to two cochlear nuclei which in turn project onto parallel pathways of auditory nuclei, one of which encodes information about sound loudness and the other which encodes timing. This auditory information eventually reaches Field L, which is involved in auditory processing. In songbirds, Field L projects to HVC and the RA in the vocal control system, allowing for recognition of and response to vocalizations (Dooling et al. 2000).

## Vocal Production

### Vocal Learning

Songbirds acquire some of their species-specific vocalizations through vocal learning; thus, songbirds must attend to the vocalizations of others and modify their own vocalizations to match these models. Vocal learning is thought to be relatively rare in the animal kingdom, but has been documented in a number of vertebrates (Doupe and Kuhl 1999). However, to our knowledge Suboscines have not shown evidence of vocal learning.

Songbirds can generally be separated into two broad groups based on how they learn their vocalizations: open-ended and closed-ended learners (Brainard and Doupe 2002). Open-ended learners pass through a sensory phase in which they are sensitive to the auditory input they receive and acquire a song template. Open-ended learners then experience a sensorimotor phase during which time they attempt to match their vocal production to that template, which ultimately results in a stable adult song. However, they are still able to continue to learn and modify their

song throughout their lifetime. Canaries (*Serinus canaria*) are a good example of an open-ended learner. Canaries learn their songs during the spring, practice throughout the fall, then sing a crystallized song during the following spring (Nottebohm et al. 1986). This process is repeated every year, and thus their song repertoires expand and change annually.

Vocal mimics, a type of open-ended learner (e.g., parrots, *Psittacines*; lyrebirds, *Menura*; etc.), possess highly complex syrinxes which allow for these passerines to produce their species-typical vocalizations. In addition to learning vocalizations produced by other species, including human speech, vocal mimics can also imitate noises from their environment (e.g., chainsaw sounds, camera shutter). These complex vocalizations are integrated into their song resulting in a more complicated repertoire, which many individuals use to attract potential mates (Cocker et al. 2013).

Closed-ended learners only pass through the sensory and sensorimotor phase once, then their songs become relatively fixed for the rest of the birds' lives (Brainard and Doupe 2002). For zebra finches, the sensory and the sensorimotor phases overlap. These birds only produce one song type, which is crystallized by 90 days posthatch (Slater et al. 1988). Another developmental path is that of the white-crowned sparrows (*Zonotrichia leucophrys*) which learn their song in the first few months of life, but do not actually sing until the following breeding season (Marler 1970).

## Conclusions

Passerines are the largest order of birds, encompassing more than half of all known avian species. Oscines' ability to learn vocalizations from adults is rare and has only been observed in a limited number of species. This ability contributes to the size of song repertoires, and occasionally calls, observed within this group. Oscines' auditory systems, including their specialized ears and neural pathways, are consistent across songbird species. Oscine and suboscine species differ in the number of vocalizations in their repertoire

(i.e., ranging from a few vocalizations to hundreds), the time during which vocalizations are acquired (i.e., during a single acquisition period, annually, or continually), and the underlying neural mechanisms used to produce these vocalizations. Overall, passerine communication is complex and critical for social dynamics, in particular for species that inhabit dense vegetation, communicate over long distances, and cannot rely on visual cues.

## Cross-References

▶ Aves (Birds)
▶ Critical Period for Song Learning
▶ Contact Calls
▶ Countersinging
▶ Dawn Solo
▶ Dialects
▶ Passerine Cognition
▶ Passerine Life History
▶ Passerine Morphology
▶ Passerine Sensory Systems
▶ Signaller
▶ Songbird Learning
▶ Subsong

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