Z

Zebra Finches

J. P. Swaddle, College of William and Mary, Williamsburg, VA, USA

© 2010 Elsevier Ltd. All rights reserved.

Taxonomy, Distribution, and Morphology

The zebra finch, *Taeniopygia guttata*, is an estrildid finch common in Central Australia, which occurs in most of the Australian continent and up through parts of Indonesia. Populations of introduced birds, that presumably escaped from the pet trade, have also been reported in the United States (e.g., California and Oregon) and Europe (e.g., Portugal). Zebra finches commonly occupy low bushes and sparse, but dense, vegetation in relatively open areas and have quickly adapted to human-disturbed habitats in many areas. They are abundant in most parts of their range and are not of conservation concern.

Although the sexes are similar in overall size, males have distinctive red bills, orange cheek patches, chestnut flanking, and distinctive namesake black chest and throat barring. Females do not possess any of these traits (**Figure 1**). The sexes also differ in vocal traits in that males sing extensive songs, but females do not. Both sexes also make a number of calls that appear related to predatory threats, alarms, territorial defense, and pair-bond maintenance. Their vocal repertoire is fairly well understood from neural functioning and behavioral points of view.

There are two commonly recognized subspecies. *T. guttata* is found through Indonesia and coastal areas of Australia and is somewhat smaller and lacks some of the male throat banding patterns of *T. g. castanotis*. *T. g. castanotis* is much more common throughout the Australian continent.

Domestication and Genetic Variants

The zebra finch is a common pet trade and show bird. They are easily kept in captivity, breed readily (see below), and can be hand-trained to make excellent companion birds. Because of the extensive interest in this species from aviculturists, there are numerous well-documented genetic variants and phenotypic morphs that have been selectively bred over the years, resulting in a wide variety of phenotypes and genotypes that are available for study and comparison.

Life History, Mating, and Breeding

Zebra finches can live for up to 5 years in the wild, but life expectancy is commonly 5–10 years in captive conditions. Records of birds reaching their 'teens' are not uncommon among captive breeders.

They are primarily seed eaters, but will commonly eat fruits and vegetables in the wild (where available) and in captivity. Most aviculturists raise zebra finches on millet and fruit seed blends, supplemented with fresh fruits, vegetables, and protein and additional calcium mixes to promote egg laying. As anyone who has raised zebra finches can testify, they are messy eaters and seemingly quite inefficient seed dehuskers.

In nature, breeding is commonly cued by unpredictable heavy rains; hence zebra finches are commonly in a physiological condition to breed at any time of the year. This means that birds can easily be maintained on long-day photoperiods with adequate food and water so that they breed throughout the year in captivity. This physiological feature has contributed to the appeal of zebra finches in behavioral studies, as it is not necessary to phase birds through 'seasons' to induce mating and breeding behaviors – the birds are pretty much ready to breed at any time.

Courtship behaviors are fairly ritualized and are well-documented, including a sequence of neck stretching, body twists, hopping, and tail flicking as well as extensive vocalizations (see section 'Vocal Signaling and Song Learning'). Males and females seem to show the same sequence and range of courtship behaviors in captive and wild conditions, often meaning that behaviorists can assay courtship in the laboratory and infer future mating decisions based on the intensity of these behaviors.

Zebra finches nest in a wide variety of substrates, from natural cavities to shrubs, bushes, and even termite mounds. Hence, in captivity, nest boxes and artificial cups can vary in design yet stimulate successful breeding. Nests are most often comprised of dried grasses, woven into tight and domed cups. Zebra finches commonly breed in small

Figure 1 Typical wild-type female (left), her partner male (middle), and an extra-pair male (right).

colonies at reasonably high densities, hence breeding birds in captive aviaries and cages can often represent reasonably similar nesting densities to natural conditions.

They are unusual in that zebra finches mate for life; once paired, males and females are rarely out of contact with each other, except when incubating eggs. This may be one reason why extra-pair paternity rates are generally low, in comparison to many bird species, in wild populations (often around 5% extra-pair young).

Both sexes incubate their brood, and they lay 3–12 eggs per brood, most commonly 5 or 6. These eggs hatch after 14–16 days and chicks are fed by both parents for the 3–4 week nestling phase. Postfledging, the young are dependent on their parents for a further couple of weeks but mature quickly so that young males are capable of breeding just 70 days after hatching and females after around 100 days. Distinctive male plumage traits start to develop at around 8–10 weeks posthatching. Their rapid maturation, coupled with year-round breeding, means that zebra finches can attain tremendous individual and population productivity.

Zebra Finches as Model Organisms in Animal Behavior

The zebra finch has been extensively studied in numerous behavioral contexts, in the wild and in captivity. The following are a few of the areas that have received substantial attention, but this brief review in no way represents the true breadth to which the zebra finch has been studied.

Sexual Selection

One of the most appealing aspects of using zebra finches as a model system in sexual selection studies is that many of the mate preferences and mating behaviors shown in the wild can be solicited in controlled, captive situations. Hence, this species opens up opportunities to understand genetic, developmental, neural, physiological, and behavioral mechanisms that determine sexual selection processes in a complex vertebrate.

Both male and female zebra finches exhibit some degree of primary mate choice, with females preferring males with redder bills and those with longer more complex directed songs (see below). Males and females also prefer heterospecifics wearing specific colors and symmetric arrangements of plastic leg bands. Nancy Burley has also indicated that females possess several latent preferences for aesthetic traits that have not evolved in males, such as for certain colors of artificial plumage crests. With the documented preferences for bill color and artificial traits, it is possible to perform reversible manipulations of individual attractiveness, which allows numerous experimental behavioral studies of mate choice.

Postcopulatory mechanisms of sexual selection occur in zebra finches, including sperm competition even though extra-pair paternity appears relatively uncommon (often less than 5% young are extra-pair in natural colonies). Males appear able to vary the size of their ejaculates and engage in 'retaliatory' forced copulations with their partner after they observe her engaging in an extra-pair copulation. This is probably because there is a general pattern of last male sperm precedence, increasing paternity assurance of males who copulate with females closest to the time of egg laying.

Females are fertile for ~11 days before laying their first egg and can store sperm for almost 2 weeks, although a very small percentage of each ejaculate appears to reach the female sperm storage structures. However, because there is some form of sperm storage, there is some possibility for elements of cryptic female choice in zebra finches.

Even after eggs have hatched, zebra finches appear to selectively feed and possibly commit selective infanticide, to bias their brood toward the sex of attractive partners. Hence, there also appear to be postzygotic mechanisms of sexual selection in zebra finches.

Vocal Signaling and Song Learning

The vocal repertoire of zebra finches is extensive and functionally well understood. Among the most common calls, loud distance calls appear related to revealing individual identity (even perhaps age and geographic origin) and soliciting the other member of the pair to follow, whereas softer 'tet' calls may function to reinforce pair bonds and elicit close contact between a pair. Zebra finches also show an array of distress, alarm, and movement intention calls. Most of these calls can be recognized by ear (with a little experience) or by analysis of recorded sonograms.

Nestlings beg loudly for food from their parents and their calls can sometimes be heard as much as 100 m away from the nest. Accompanied with striking mouth coloration patterns, zebra finch adults are not short of sensory stimulation to induce chick feeding. As nestlings grow, begging calls increase in amplitude, length, and rate and decrease in pitch while gaining harmonic elements. Hungrier nestlings seem to call more rapidly. As we know a considerable amount about how nestlings beg from parents, zebra finches have also become a popular subject for studies of parent–offspring conflict and communication.

Male zebra finches produce directed and undirected song. Undirected songs are simpler, softer, not associated with any pronounced body movements and are often produced when the female is not in visual range. This type of song is most often produced during early nest building and egg laying stages and has been hypothesized to be important in mate guarding and paternity assurance.

Directed songs are classic courtship and precopulatory vocalizations that are reasonably complex in structure and associated with upright bodily posturing. These directed songs vary in structure among males in three sequential elements: (1) the number of introductory elements; (2) the structure and number of repeated song phrase elements (where some of these elements appear almost identical to their calls, whereas others appear novel and unique to a male), and (3) a terminal distance call. In preference tests, females tend to prefer males who sing with longer song phrases. Both rate and structure of song appear to influence mate preferences.

Along with the canary (*Serinus canaria*) and song sparrow (*Melospiza melodia*), the zebra finch has become a model species for song learning studies. As occurs in many songbirds, male zebra finches learn their songs from a tutor, most commonly their social father, and song is learned and crystallized during a critical period thought to be between days 35 and 80 posthatching. When kept in acoustic isolation, males develop only rudimentary song phrase elements, indicating that elements of song structure are hard-wired in some manner. Interestingly, song learning and final crystallization of the song is both age and experience related. In the presence of a tutor, the song is set by days 70–80; but without a tutor, the song can be modified for a period after this. The zebra finch is arguably the dominant laboratory model species for studying this form of song learning, and many researchers have drawn analogies between the communication learning processes in zebra finches to early communication learning in many other animals, including humans.

Song learning is more precise when auditory cues are accompanied by visual cues of the tutor male. Additionally, young males prefer to learn songs from mated tutors compared to unmated tutors and there is some evidence that females in the local population influence song learning, biasing males to learn attractive songs that may differ somewhat from their social father.

Males appear to learn their songs in a sequential unit structure, with introductory elements, song phrases, and the terminal distance call apparently learned in 'chunks' from the tutor. Hence, there may be a functional link between how songs are learned and how they are expressed as adults.

There are interesting sex differences in learning of vocalizations. Females do not sing, but they do show some of the calls of males. However, cross-fostering and deafening studies indicate that males fine tune their calls (particularly their distance calls) using environmental input. In contrast, females' calls are almost exclusively innate and are not influenced by their auditory environment early in life.

The neural pathways for song production, song perception, and song/call learning are fairly well described in both males and females. In general, the simpler vocalizations of females are associated with neural pathways predominately in the brain stem, whereas male vocalization pathways are more strongly associated with the telencephalon. Some of the calls produced by males are associated with song production centers.

There are two forebrain neural circuits associated with male singing, one related to song learning and the other to song production. Central to both circuits are the connectedness of the HVC (higher vocal center) and RA (robust nucleus of the archistriatum). Notably, similar to some other songbirds, new cells are continually added to the HVC during song learning and later sexual activity. Unlike other songbirds, the song production and learning in the zebra finch is dominated by the right hemisphere rather than the left, although the significance of this is not yet understood.

The zebra finch brain is anatomically and functionally different between the sexes, and this extreme sexual dimorphism is dependent on sex hormones. As estrogens that determine this sexual differentiation are potentially produced before hatching, anatomical studies have revealed marked brain sexual dimorphism in very early stages of development.

In summary, because of the availability of detailed neural atlases of the zebra finch brain, there is a large and growing body of literature that describes the neuronal basis of song learning in this species. With recent advances in functional neuroanatomy and high resolution magnetic resonance imaging (MRI; **Figure 2**) of the zebra finch brain, the links between neural anatomy and functioning with complex behavioral processes related to song learning promise to increase at a rapid pace. When you consider that there is also extensive functional genomic information being developed for zebra finches, I doubt that we are too far from being able to interpret song learning and production from gene expression all the way through to ecologically relevant behaviors.

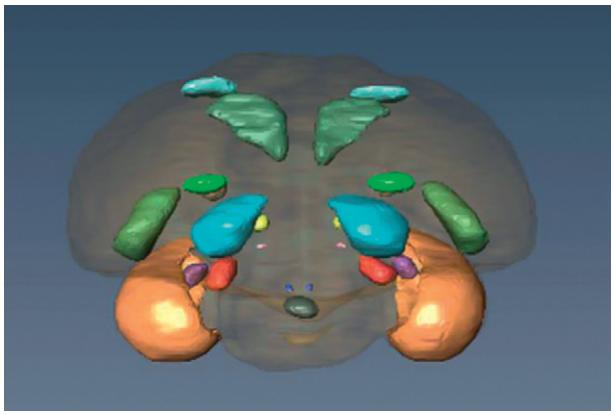

Figure 2 Digital three-dimensional MRI atlas of the zebra finch brain. The full interactive atlas is available free to the scientific community at: http://webh01.ua.ac.be/biomag/zebrafinch_mri_atlas.htm. Courtesy of Colline Poirier and colleagues.

Genomics and Genetics

The zebra finch genome was published in 2008 and became the second avian genome available, following the domestic chicken. Extensive cDNA libraries have also been compiled from neural materials of zebra finches. Hence, the possibility of linking complex behaviors and the neural mechanisms underlying these behaviors with a detailed understanding of gene functioning is now possible and is underway for several questions related to song learning and development. The availability of these genomic tools promises great advances in our mechanistic and evolutionary understanding of zebra finch behavior.

At a simpler genetic level, an array of microsatellite markers have been described in the literature that allow relative straightforward paternity/maternity analyses as well as measures of gene flow and phylogeography. Hence, the breadth of genetic tools now available for the zebra finch is starting to rival some of the invertebrate taxa that have long been the focus of behavioral genetic and genomic studies.

Summary

Overall, the level of mechanistic understanding from functional genomics to detailed neuronal and cognitive studies blended with the repeated observations that ecologically and evolutionarily relevant behaviors can be replicated and manipulated in various captive experimental designs; give the zebra finch extraordinary potential as a model system in evolution, ecology, and behavior. For a complex vertebrate, they have a relatively short generation time, with rapid sexual maturity, and are straightforward to maintain in breeding condition. Hence, zebra finches will continue to grow in popularity as model species for many forms of behavioral study, especially those that aim to elucidate genetic and neural mechanisms of breeding and mating behaviors.

See also: Acoustic Signals; Genes and Genomic Searches; Mate Choice in Males and Females; Mating Signals; Sperm Competition.

Further Reading

Adkins-Regan E (2002) Development of sexual partner preference in the zebra finch: A socially monogamous, pair-bonding animal. *Archives of Sexual Behavior* 31: 27–33.

Birkhead TR, Hunter FM, and Pellat JE (1989) Sperm competition in the zebra finch, *Taeniopygia guttata*. *Animal Behaviour* 38: 935–950.

Boumans T, Gobes SMH, Poirier C, et al. (2008) Functional MRI of auditory responses in the zebra finch forebrain reveals a hierarchical organisation based on signal strength but not selectivity. *PLoS ONE* 3: e3184.

Burley NT (2006) An eye for detail: Selective sexual imprinting in zebra finches. *Evolution* 60: 1076–1085.

Burley N, Krantzberg G, and Radman P (1982) Influence of colour-banding on the conspecific preferences of zebra finches. *Animal Behaviour* 30: 444–455.

Dawson DA, Chittock JC, Jehle R, et al. (2005) Identification of 13 polymorphic microsatellite loci in the zebra finch, *Taeniopygia guttata* (Passeridae, Aves). *Molecular Ecology Notes* 5: 298–301.

Holveck MJ and Riebel K (2007) Preferred songs predict preferred males: Consistency and repeatability of zebra finch females across three test contexts. *Animal Behaviour* 74: 297–309.

Immelmann K (1965) *Australian Finches in Bush and Aviary*. Sydney: Angus and Robertson.

London SE and Clayton DF (2008) Functional identification of sensory mechanisms required for developmental song learning. *Nature Neuroscience* 11: 579–586.

Naurin S, Bensch S, Hansson B, et al. (2008) A microarray for large-scale genomic and transcriptional analyses of the zebra finch (*Taeniopygia guttata*) and other passerines. *Molecular Ecology Resources* 8: 275–281.

Nottebohm F (1993) The search for neural mechanisms that define the sensitive period for song learning in birds. *Netherlands Journal of Zoology* 43: 193–324.

Replogle K, Arnold AP, Ball GF, et al. (2008) The Songbird Neurogenomics (SoNG) Initiative: Community-based tools and strategies for study of brain gene function and evolution. *BMC Genomics* 9: 131.

Swaddle JP, Cathey MG, Correll M, and Hodkinson BP (2005) Socially transmitted mate preferences in a monogamous bird: A non-genetic mechanism of sexual selection. *Proceedings of the Royal Society of London B* 272: 1053–1058.

Zann RA (1996) *The Zebra Finch: A Synthesis of Field and Laboratory Studies*. Oxford: Oxford University Press.

Relevant Websites

http://www.ncbi.nlm.nih.gov/genome/guide/finch/ – National Institutes of Health's zebra finch genome resource site.
http://titan.biotec.uiuc.edu/songbird/ – Songbird Neurogenomics (SoNG) Initiative.
http://www.ncbi.nlm.nih.gov/bookshelf/br.fcgi?book=atlas – Stereotaxic atlas of the zebra finch brain.
http://zebrafinch.info/science/ – Zebra finch info scientific links site.
http://webh01.ua.ac.be/biomag/zebrafinch_mri_atlas.htm – Zebra finch online MRI atlas.
http://www.zebrafinch-society.org/ – Zebra finch society, USA.
http://www.zebrafinch.org/ – Zebra finch song learning consortium.