

Food, song and speciation

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It is said that you are what you eat. Diet can also determine how you sound and perhaps even what species you are — if you are one of Darwin's finches.

According to the standard view of how new species arise, populations become geographically isolated and adapt to local conditions, and the communication systems used to recognize mates diverge¹. Surprisingly little is known about how mate-recognition systems diverge during speciation². On page 185 of this issue, however, Jeffrey Podos³ describes a clear and direct interaction between ecological adaptation and the divergence of signals that might be used in mate recognition.

Podos's study subjects were Darwin's finches, which inhabit the Galápagos Islands. The diversity of feeding adaptations in these birds, seen in their differing beaks, has been scrutinized by some of the most eminent of evolutionary biologists^{4–6}—first, of course, by Darwin himself. Beaks are adapted to different feeding tasks, from crushing large seeds to using cactus spines as spears (Fig. 1). Yet beak structure not only affects what goes into the bird but also what comes out. Movements of the beak during singing modify both the rate of trills and the range of the frequencies in the song⁷. Does the size of the beak influence its vocal performance? Podos shows that it does. Species with larger beaks have a more restricted vocal performance, or a greater 'vocal deviation'; that is, they have a narrower frequency range for their trill rate or a slower trill rate for their frequency range. This same pattern was found in a within-species analysis of the medium ground finch, a bird in which both beak and song structure vary widely.

For many songbirds, the female's preference for the songs of males of the same species, rather than of other species, results in strong pre-mating reproductive isolation⁸. Species stay separate because they don't reproduce with each other successfully. Such reproductive isolation can occur if the two species never mate in the first place because they don't recognize each other as potential mates; or, if mating does occur, because the partnership does not result in fertile offspring (such as the mule, the sterile offspring of a horse–donkey mating).

In Galápagos finches it now appears that when beaks become adapted to different food sources, they might simultaneously acquire a vocal signature that distinguishes them from other types of beaks. Females could use this signature in mate choice because natural selection should favour their

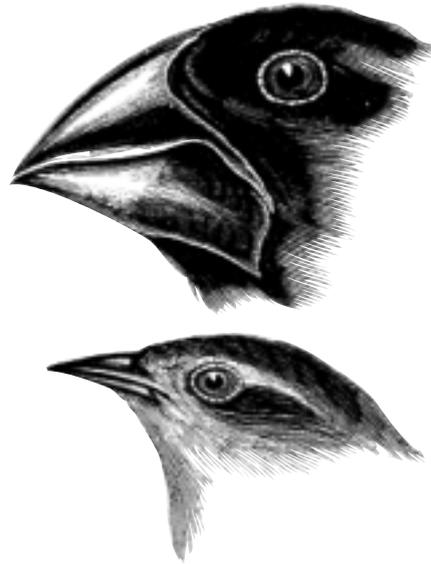


Figure 1 Eating adaptations. Two species of Darwin's finches, *Geospiza magnirostris* (top) and *Certhidea olivacea*, have very different forms of beak that stem from their different diets. Podos³ argues that song evolution has also been affected, and is a further factor influencing speciation in these birds.

recognition of males with the same beak type — intermediate beaks that result from hybrid matings might be less efficient for dealing with either food type on which their parents specialize. The role of the acoustic structure of trilled song elements in mate choice, however, is not known; this seems to be the next piece of the puzzle which the author needs to address.

The interplay between ecological adaptation, a correlated change in signal structure, and its potential influence on speciation reported by Podos is unusual. Other species, such as cichlid fishes in African lakes, have evolved extremely specialized diets and jaws, together with strong pre-mating isolation that has resulted in an astounding diversity of species⁹. But in cichlids the mate-recognition signal, or at least one of them, is colour pattern¹⁰. So we assume that the more standard pattern of species divergence occurs in circumstances such as these, when signal divergence is apparently not affected by other ecological adaptations.

During the process of speciation, mate-recognition signals can diverge by genetic drift; that is, by chance mutations. But signals can also adapt to local habitat condi-

tions as other aspects of the organisms' behaviour and morphology adapt to other aspects of the environment. For example, birds on the forest floor produce songs of lower frequency than those in open fields¹¹; chingalos (sparrows) show changes in call structure that match habitat changes with increasing altitude¹²; and a subspecies of cricket frog produces calls that transmit better in its forest environment than do the calls of the other subspecies that inhabits open fields¹³. Similar situations are found in some fishes. The light available for visual displays varies according to the fishes' preferred habitat in, say, its depth on a coral reef, and certain species evolve colours and patterns to exploit the prevailing light conditions¹⁴. But the Galápagos finches are unusual in that the ecological adaptation itself is constrained to cause a change in a signal.

Podos suggests that the inextricable link between beak structure, feeding and song has been partly responsible for the Galápagos finches' rapid speciation. But this is an assertion that requires more evidence before it can be accepted. In a larger context, this study further emphasizes how constraints on signals or receivers involved in mate recognition can influence signal or receiver divergence, and thus the probability of speciation. The large number of songbird species might result from the combination of a complex voice box and song learning; the complex voice box allows the production of a greater range of sounds, and song learning promotes cultural evolution of song due to copying errors¹⁵. Variation in the sound-reception organ in the frog's inner ear matches frog species number¹⁶, perhaps because it influences the extent of signal diversity that can evolve^{16,17}.

Podos has revealed an unusual pattern in which ecological adaptation, signal divergence and (perhaps) the opportunity for speciation are linked. It adds a critical piece to our already detailed understanding of natural selection and evolution in this hallmark group of species. But its implications are more far-reaching and general. Podos's study should warn us of the danger of trying to understand adaptation and evolution from a myopic perspective. An organism's phenotype is a complex nexus with different components specialized for different tasks, but in which the degree of optimization of one component is dependent on others. Perhaps

this is why you shouldn't speak with food in your mouth. ■

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1. Mayr, E. *Animal Species and Evolution* (Harvard Univ. Press, Cambridge, MA, 1963).
2. Rice, W. R. & Hostert, E. E. *Evolution* **47**, 1637–1653 (1993).
3. Podos, J. *Nature* **409**, 185–188 (2001).
4. Darwin, C. *The Origin of Species* (Murray, London, 1859).
5. Lack, D. *Darwin's Finches* (Cambridge Univ. Press, 1947).
6. Grant, P. *Ecology and Evolution of Darwin's Finches* (Princeton Univ. Press, 1986).
7. Hoese, W. J., Podos, J., Boetticher, N. C. & Nowicki, S. *J. Exp. Biol.* **203**, 1845–1855 (2000).
8. Searcy, W. A. & Marler, P. *Science* **213**, 926–928 (1981).
9. Fryer, G. & Iles, T. D. *The Cichlid Fishes of the Great Lakes of Africa* (T. F. H. Publications, Neptune City, NJ, 1972).
10. Seehausen, O., van Alphen, J. J. M. & Witte, F. *Science* **277**, 1808–1811 (1997).
11. Morton E. S. *Am. Nat.* **109**, 17–34 (1975).
12. Nottebohm, F. *Condor* **71**, 299–315 (1969).
13. Ryan, M. J., Cocroft, R. B. & Wilczynski, W. *Evolution* **44**, 1869–1872 (1990).
14. Marshall, N. J. in *Animal Signals: Signalling and Signal Design in Animal Communication* (eds Espmark, Y. Amundsen, T. & Rosenqvist, G.) 83–120 (Tapir Academic, Trondheim, 2000).
15. Vermeij, G. *Syst. Zool.* **37**, 69–71 (1988).
16. Ryan, M. J. *Proc. Natl Acad. Sci. USA* **83**, 1379–1382 (1986).
17. Lewis, E. R., Hecht, E. I. & Narins P. M. *J. Comp. Physiol. A* **171**, 421–435 (1992).