

Correlated evolution of morphology and vocal signal structure in Darwin's finches

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Speciation in many animal taxa is catalysed by the evolutionary diversification of mating signals¹. According to classical theories of speciation, mating signals diversify, in part, as an incidental byproduct of adaptation by natural selection to divergent ecologies^{2,3}, although empirical evidence in support of this hypothesis has been limited⁴⁻⁶. Here I show, in Darwin's finches of the Galápagos Islands, that diversification of beak morphology and body size has shaped patterns of vocal signal evolution, such that birds with large beaks and body sizes have evolved songs with comparatively low rates of syllable repetition and narrow frequency bandwidths. The converse is true for small birds. Patterns of correlated evolution among morphology and song are consistent with the hypothesis that beak morphology constrains vocal evolution, with different beak morphologies differentially limiting a bird's ability to modulate vocal tract configurations during song production. These data illustrate how morphological adaptation may drive signal evolution and reproductive isolation, and furthermore identify a possible cause for rapid speciation in Darwin's finches.

The avian vocal tract, comprised of the trachea, larynx and beak, acts as an acoustic resonance filter during sound production, attenuating harmonic overtones and emphasizing fundamental frequencies produced by the sound source^{7,8}. The vocal tract thus enables birds to produce songs that have a high tonal purity or a 'whistle-like' quality. While singing, songbirds (oscine Passeriformes) actively modify the configuration of their vocal tracts, in a manner closely coordinated with the sound source, so as to maintain the vocal tract's filtering function over a wide range of source frequencies⁷. Studies have shown that vocal tract reconfigurations are achieved largely through rapid changes in beak gape, with increases in beak gape accompanying increases in source frequencies, and vice versa^{9,10}. Beak movements are normally very rapid and precise, and when birds' beaks are either temporarily immobilized or hampered, the tonal purity of songs becomes compromised¹¹. These studies together suggest that limits on the dynamics of vocal tract movements during song production may shape patterns of vocal signal evolution^{12,13}. For example, constraints on vocal tract dynamics in emberizid songbirds probably cause trade-offs between temporal and frequency-based song features¹³, and may set limits on the development and evolution of syllable repetition rate¹⁴.

Vocal performance capacities are predicted to vary as a function of vocal tract morphology, and particularly beak morphology^{12,13}. Songbirds with comparatively large and strong beaks, such as those adapted for crushing hard seeds, should face relatively severe performance constraints on vocal tract dynamics. This is because of an intrinsic trade-off in jaw biomechanics between maximal force and velocity; as jaws become adapted for strength, they will be less able to perform the rapid movements required for the production of certain types of songs. By contrast, songbirds that have evolved smaller beaks, such as those adapted to probe for insects, should suffer less severe constraints on vocal performance. The objective of

this study was to assess, in Darwin's finches, the extent to which adaptive diversification of the beak has shaped the evolution of song features related to vocal performance capacities. Darwin's finches are a particularly appropriate songbird group for this study not only because they express extensive diversity in beak morphology¹⁵ and song¹⁶ (Fig. 1), but also because beak morphology in this group has been shown to adapt precisely and rapidly, through natural selection, to ecological conditions such as food type availability and interspecific competition¹⁷⁻¹⁹.

I conducted correlation analyses, at intra- and interspecific scales, between morphological features and a composite measure of the temporal and frequency structure of songs, the 'vocal deviation' (Fig. 2). High vocal deviations are indicative of poor vocal performance, and vice versa (see Methods). Intraspecific analyses were restricted to the medium ground finch, *Geospiza fortis*, for which the largest sample was obtained. *G. fortis* on Santa Cruz Island exhibits unusually high variation in morphological features relative to other Darwin's finches¹⁹, and produces a wide diversity of song types¹⁶. The vocal deviation correlated positively and significantly with all beak measurements and with body mass (Fig. 3; $P < 0.005$ for each correlation), but not with tarsus length ($P = 0.573$) or wing chord length ($P = 0.209$). For interspecific analyses, I calculated correlations between average values of morphological variables and minimal values of vocal deviations (Fig. 4a). These correlations were not tested for statistical significance, however, because of the likelihood of statistical non-independence among species samples²⁰. Correlations were thus re-evaluated in a phylogenetic context (Fig. 4b),

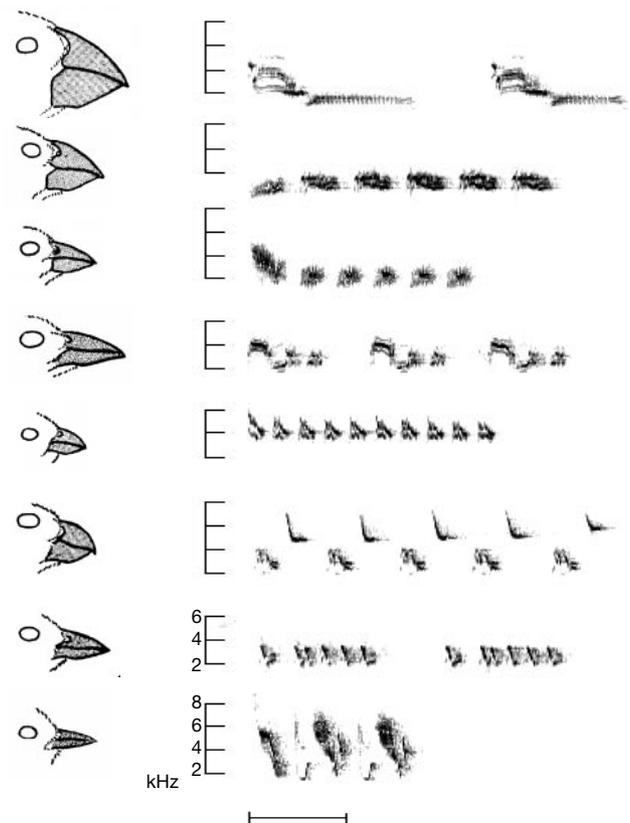


Figure 1 Beak morphology (sketches reprinted¹⁵) and representative sound spectrograms of songs from eight Darwin's finch species on Santa Cruz Island (from top to bottom: *G. magnirostris*, *G. fortis*, *G. fuliginosa*, *G. scandens*, *C. parvulus*, *C. psittacula*, *C. pallida*, *C. olivacea*). Interspecific variation is apparent in both morphology and song structure. Comparability of the songs of different species is supported by the young age of the clade¹⁹, and the striking uniformity among species in the structure of the syrinx and associated musculature²². See ref. 16 for a discussion of homology among Darwin's finch songs. Spectrogram frequency resolution, 98 Hz; scale bar, 0.5 s.

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using independent contrasts analyses^{20,21}. Vocal deviation contrasts correlated positively with contrasts of all beak measurements, wing chord length, and body mass (Fig. 4c; $P < 0.051$ for all variables and all phylogenies), but did not correlate with tarsus length contrasts ($P = 0.159\text{--}0.207$).

The intra- and interspecific analyses are consistent in illustrating that vocal deviations have evolved in correlated fashion with beak morphology, in the direction predicted by the vocal tract constraint

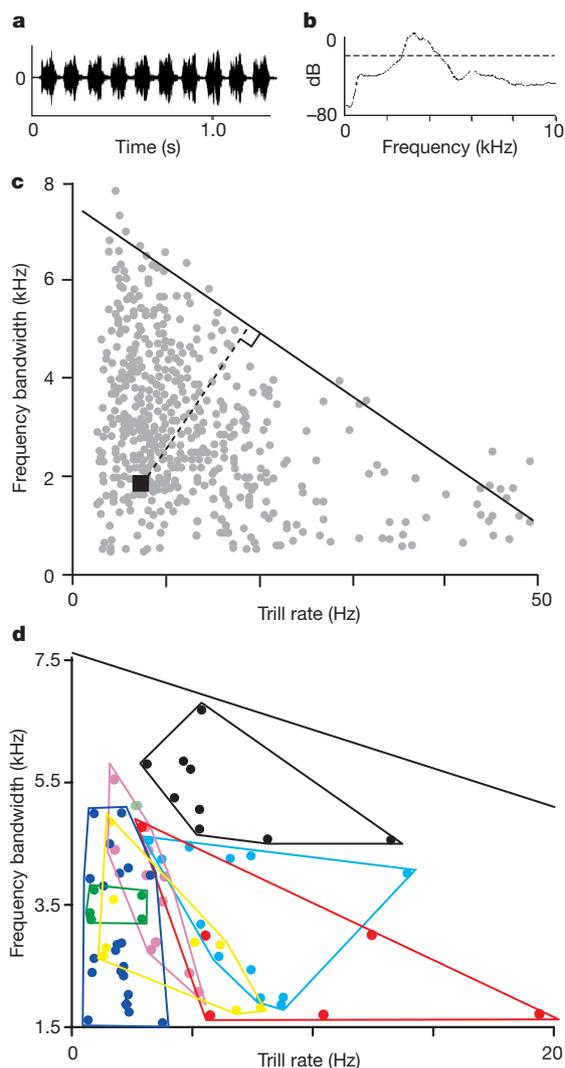


Figure 2 Acoustic analyses. **a–c**, Calculation of trill rate, frequency bandwidth and vocal deviation, illustrated for the *C. parvulus* song in Fig. 1. **a**, Oscillograms were used to measure trill rate, as the number of syllables produced per second (7.85 Hz here). **b**, Amplitude spectra were used to measure frequency bandwidth, the range of frequencies produced (1.97 kHz here), using a -24 dB amplitude cut-off criterion¹³ (dashed line). This criterion was chosen *a priori* to maximize the proportion of signal energy analysed while excluding background noise. Earlier analyses revealed that lower dB cut-off values (for example, -27 and -30 dB) regularly include background noise in spectral analyses, while higher cut-off values (for example, -21 and -18 dB) unnecessarily exclude signal energy. Amplitude spectra were computed at 32 kilopoints and smoothed to a frequency resolution of 300 Hz. **c**, For each trill type, average frequency bandwidth was plotted as a function of average trill rate (for example, filled square). Vocal deviations (dashed line) were calculated relative to an upper-bound regression (solid line)¹³, which was in turn calculated relative to the distribution of trill types across 34 emberizid songbird species (grey dots)¹³. **d**, Plot of all trill types for all species analysed, with minimum area convex polygons shown. Overlap in raw data among most species is apparent. *G. magnirostris*, green; *G. fortis*, dark blue; *G. fuliginosa*, pink; *G. scandens*, yellow; *C. parvulus*, light blue; *C. psittacula*, light green; *C. pallida*, red; *C. olivacea*, black.

hypothesis. Vocal deviations also correlated strongly and positively with body mass in both analyses, however, so the potential influence of body mass on vocal performance should be considered as well. Body mass varies positively and nearly isometrically with the size of the syrinx (the sound organ) in Darwin's finches²², and variation in syrinx size presumably influences the expression of fundamental frequency^{16,23}. By contrast there are no clear predictions about how variation in body mass might shape the expression of vocal deviations. As an indirect test of the body mass hypothesis, I assessed the relationship between body mass and minimum vocal deviations across 30 emberizid species¹³, which express a range of body size variation comparable to Darwin's finches. Minimum vocal deviations were found to regress negatively on body mass (slope = -0.028 , $r^2 = 0.038$), in the direction opposite to that predicted by the body mass hypothesis. Although the statistical significance of this regression could not be assessed (because of non-independence among species samples), the negative slope of the regression, along with the finding that body size does not influence emberizid upper-bound regression values¹³, suggest that the vocal tract constraint hypothesis offers a more reasonable explanation for the observed correlations. Body mass in both intra- and interspecific analyses, and wing chord length in the interspecific analyses, might covary with vocal deviations simply because beak and body size measures in Darwin's finches are generally highly correlated¹⁹.

The correlations between morphology (beak and body size) and song offer strong evidence that adaptation can drive signal evolution, as has been discussed in classical theories of speciation but for which little empirical evidence has been offered. Darwin's finches provide one of the premier examples of adaptation in nature, with the most pronounced adaptive diversification centring on beak evolution^{17–19}. Body mass in Darwin's finches also evolves through adaptive processes, both as a direct adaptation to divergent environments and as an indirect correlated effect of beak adaptation¹⁹. Studies of finch adaptation have advanced to the point where it is now possible to predict, with high accuracy, how ecological adaptation (for example, in response to changing food availability) will drive morphological evolution²⁴. The present findings extend this model by illustrating how morphological adaptation in turn drives the evolution of vocal performance capacities. The linkage between morphology and song results in part from the fact that two functional systems—that used for feeding and that used for singing—share a common morphology, the beak.

Morphological adaptation probably shapes finch song evolution in concert with other evolutionary factors, including adaptation to varying acoustic environments¹⁶ and drift caused by copying inaccuracies during song learning (that is, cultural evolution²⁵). The relative influence of these factors varies according to song feature, with, for example, copying inaccuracies exerting their greatest influence on the level of phonology²⁵ and with morphological constraints identified here exerting their greatest influence on higher-order timing and frequency features. A distinguishing feature of morphological influences on vocal evolution is that

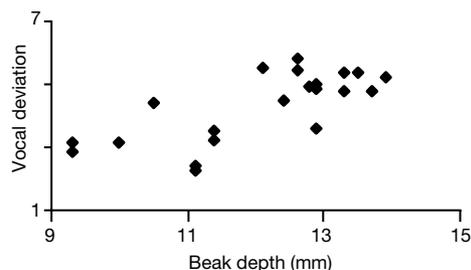


Figure 3 Vocal deviation as a function of beak depth in *G. fortis*. Pearson product moment correlations: beak length, 0.763; beak depth, 0.733; beak width, 0.727; tarsus length, 0.481; wing chord length, 0.549; body mass, 0.792.

they appear to evolve in step with the primary locus of finch adaptation.

Because song presumably has a central role in reproductive isolation in Darwin's finches^{19,26}, the linkage between morphology and vocal performance capacities holds important implications for the dynamics of finch speciation. In island songbird clades, including the Darwin's finches, speciation is driven primarily, if not exclusively, by prezygotic isolating mechanisms, as evident from the regular occurrence of viable and fertile hybrids²⁷. The effectiveness of prezygotic isolating mechanisms generally depends on the extent to which mating signals among incipient species are distinct, with more distinct signals increasing the probability of 'correct' matings and thus enhancing probabilities of speciation⁶. My data suggest that magnitudes of ecological and morphological diversification among incipient Darwin's finch species will directly determine magnitudes of diversification in vocal features, and thus determine probabilities of speciation (to the extent that trill rate and frequency bandwidth are used by birds in mate recognition). Taking this hypothesis one step further, the high diversity of ecological opportunities for Darwin's finches on the Galápagos Islands may thus have promoted, through extensive morphological adaptation and correspondingly large evolutionary changes in vocal signal structure, conditions suitable for rapid speciation and the marked radiation that has defined the group. □

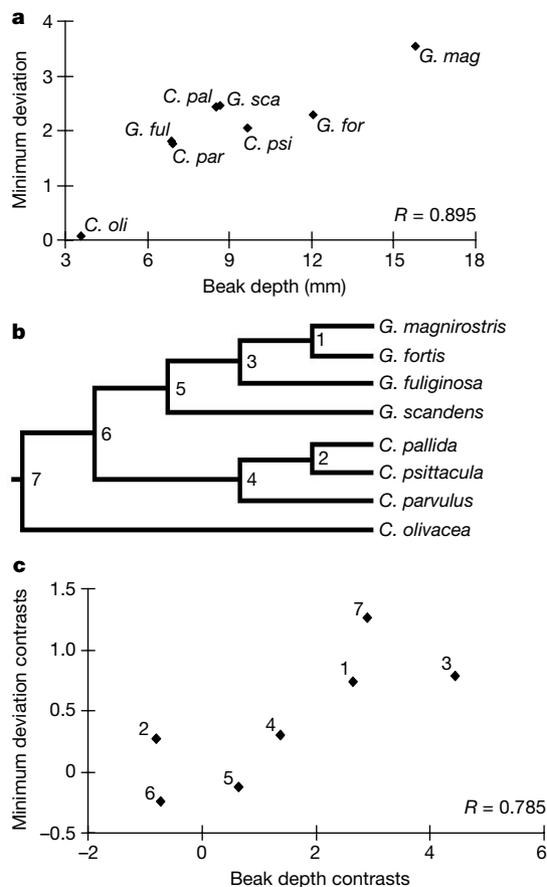


Figure 4 Interspecific analyses. **a**, Minimum vocal deviation as a function of beak depth across eight species of Darwin's finch. **b**, One of four phylogenetic hypotheses used in independent contrasts analyses. Additional hypotheses differ in classifying *G. fortis* as sister taxon to *G. fuliginosa* and/or *C. psittacula* as sister taxon to *C. parvulus*. **c**, Minimum vocal deviation contrasts as a function of beak depth contrasts. Labels refer to phylogenetic nodes from Fig. 4b. Across the four phylogenies, ranges of Pearson product moment correlations were beak length, 0.757–0.809; beak depth, 0.751–0.784; beak width, 0.750–0.794; tarsus length, 0.535–0.588; wing chord length, 0.847–0.869; body mass, 0.835–0.847.

Methods

Sample

I collected morphological and acoustic data from nine species of Darwin's finch. Field work was conducted at coastal and upland sites on Santa Cruz Island during February and March 1999. Male birds, captured in mist nets, were banded with unique colour combinations, measured and released. Morphological measurements included: beak length, beak depth, beak width, tarsus length, wing chord length and body mass¹⁹. Songs of banded birds were recorded using Sennheiser K6/ME66 microphones and Sony TCD-5ProII tape recorders. The number of individuals banded and recorded were as follows: *Geospiza magnirostris*, *n* = 4; *Geospiza fortis*, *n* = 18; *Geospiza fuliginosa*, *n* = 9; *Geospiza scandens*, *n* = 5; *Platyspiza crassirostris*, *n* = 2; *Cactospiza pallida*, *n* = 3; *Camarhynchus psittacula*, *n* = 2; *Camarhynchus parvulus*, *n* = 10; *Certhidea olivacea*, *n* = 7. All song figures were generated and acoustic analyses conducted using SIGNAL version 3.1 sound analysis software (Engineering Design, Belmont MA, 1999).

Acoustic analyses

Eight species in the sample produce songs with trilled sequences (Fig. 1; I define a 'trill' as a series of notes or note groups repeated in succession at a constant tempo). In emberizid songbirds, the family that includes the Darwin's finches, trilled sequences in particular are limited in their timing and frequency structure by constraints on vocal performance¹³. I thus focused on trilled sequences in Darwin's finch songs. For each recorded finch trill, I measured trill rate (rates of syllable repetition; Fig. 2a) and frequency bandwidth (ranges of frequencies produced; Fig. 2b). For each trill type, I then plotted average frequency bandwidth as a function of average trill rate (for example, Fig. 2c, filled square). Across the emberizids, trill rate by frequency bandwidth plots regularly yield triangular distributions at species, generic and family levels (Fig. 2c, grey dots illustrate the pattern at the family level¹³). These triangular distributions presumably occur because of motor trade-offs between rates and magnitudes of vocal tract reconfigurations during trill production¹³. Video analyses of vocal motor activity^{9–11} provide evidence that these triangular distributions also reflect a gradient in vocal performance, with trill types that plot near the origin requiring low levels of vocal activity (for example, only minor vocal tract modulations) and with trill types closer to the upper edge of the distribution requiring higher levels of vocal activity (for example, more vigorous vocal tract modulations¹³).

The realized extreme for trill rate and frequency bandwidth production across the family can be characterized using an upper-bound regression (Fig. 2c, solid line¹³). Minimum distances (Fig. 2c dashed line, referred to herein as 'vocal deviations') between each Darwin's finch trill type and the family-wide upper-bound regression were used as a composite indicator of relative vocal performance, with higher deviation values reflecting lower levels of vocal activity, and vice versa. Use of the emberizid upper-bound regression for determining vocal deviations for Darwin's finches is supported by the fact that Darwin's finches are nested phylogenetically within the emberizids. For interspecific analyses, minimum vocal deviations provided an appropriate indicator of a species' vocal potential, because only a subset of vocal renditions are expected to challenge a species' vocal production capacities. Other possible summary values, including average vocal deviations, include submaximal events and thus less precisely reflect the vocal production capacities of a species¹³.

Phylogenetic analyses

Independent contrast analyses used a punctuational or speciation assumption of evolutionary change, with all branch lengths set to unit length, as has been recommended for clades that have undergone adaptive radiations through the occupation of diverse niches^{5,28}. Phylogenetic hypotheses were based on studies using molecular data and microsatellite DNA variation^{29,30}, which have largely supported earlier hypotheses of branching relations among genera¹⁹. Within the constraints of available information four equally likely species-level phylogenies were identified (see Fig. 4b).

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- West-Eberhard, M. J. Sexual selection, social competition, and speciation. *Quart. Rev. Biol.* **58**, 155–183 (1983).
- Dobzhansky, T. *Genetics and the Origin of Species* 3rd edn (Columbia Univ. Press, New York, 1951).
- Mayr, E. *Animal Species and Evolution* (Harvard Univ. Press, Cambridge, MA, 1963).
- Rice, W. R. & Hostert, E. E. Laboratory experiments on speciation: what have we learned in 40 years? *Evolution* **47**, 1637–1653 (1993).
- Schluter, D. & Nagel, L. Parallel speciation by natural selection. *Am. Nat.* **146**, 292–301 (1995).
- Rundle, H. D., Nagel, L., Boughman, J. W. & Schluter, D. Natural selection and parallel speciation in sympatric sticklebacks. *Science* **287**, 306–308 (2000).
- Nowicki, S. Vocal tract resonances in oscine bird sound production: evidence from birdsongs in a helium atmosphere. *Nature* **325**, 53–55 (1987).
- Fletcher, N. H. & Tarnopolsky, A. Acoustics of the avian vocal tract. *J. Acoust. Soc. Am.* **105**, 35–49 (1999).
- Westneat, M. W., Long, J. H. Jr., Hoese, W. & Nowicki, S. Kinematics of birdsong: functional correlation of cranial movements and acoustic features in sparrows. *J. Exp. Biol.* **182**, 147–171 (1993).
- Podos, J., Sherer, J., Peters, S. & Nowicki, S. Ontogeny of vocal tract movements during song production in the song sparrow. *Anim. Behav.* **50**, 1287–1296 (1995).
- Hoese, W. J., Podos, J., Boetticher, N. C. & Nowicki, S. Vocal tract function in birdsong production: experimental manipulation of beak movements. *J. Exp. Biol.* **203**, 1845–1855 (2000).
- Nowicki, S., Westneat, M. W. & Hoese, W. Birdsong: motor function and the evolution of communication. *Sem. Neurosci.* **4**, 385–390 (1992).
- Podos, J. A performance constraint on the evolution of trilled vocalizations in a songbird family (Passeriformes: Emberizidae). *Evolution* **51**, 537–551 (1997).
- Podos, J. Motor constraints on vocal development in a songbird. *Anim. Behav.* **51**, 1061–1070 (1996).
- Bowman, R. I. Morphological differentiation and adaptation in the Galápagos finches. *Univ. Calif. Publ. Zool.* **58**, 1–302 (1961).

16. Bowman, R. I. in *Patterns of Evolution in Galápagos Organisms* (eds Bowman, R. I., Berson, M. & Leviton, A. E.) 237–537 (American Association for the Advancement of Science, Pacific Division, San Francisco, 1983).

17. Schluter, D., Price, T. D. & Grant, P. R. Ecological character displacement in Darwin's finches. *Science* **227**, 1056–1059 (1985).

18. Gibbs, H. L. & Grant, P. R. Oscillating selection in Darwin's finches. *Nature* **327**, 511–513 (1987).

19. Grant, P. R. *Ecology and Evolution of Darwin's Finches* 2nd edn (Princeton Univ. Press, Princeton, 1999).

20. Felsenstein, J. Phylogenies and the comparative method. *Am. Nat.* **125**, 1–25 (1985).

21. Martins, E. P. COMPARE, version 4.2. *Computer Programs for the Statistical Analysis of Comparative Data* (Univ. Oregon, Eugene, Oregon, 1999).

22. Cutler, B. *Anatomical Studies on the *Syrinx* of Darwin's Finches*. Thesis, San Francisco State Univ. (1970).

23. Ryan, M. J. & Brenowitz, E. A. The role of body size, phylogeny, and ambient noise in the evolution of bird song. *Am. Nat.* **126**, 87–100 (1985).

24. Grant, P. R. & Grant, B. R. Predicting microevolutionary responses to directional selection on heritable variation. *Evolution* **49**, 241–251 (1995).

25. Grant, P. R. & Grant, B. R. Cultural inheritance of song and its role in the evolution of Darwin's finches. *Evolution* **50**, 2471–2487 (1996).

26. Ratcliffe, L. M. & Grant, P. R. Species recognition in Darwin's finches (*Geospiza*, Gould). III. Male responses to playback of different song types, dialects and heterospecific songs. *Anim. Behav.* **33**, 290–307 (1985).

27. Grant, P. R. & Grant, B. R. Speciation and hybridization in island birds. *Phil. Trans. R. Soc. Lond. B* **351**, 765–772 (1996).

28. Mooers, A. O., Vamossi, S. M. & Schluter, D. Using phylogenies to test macroevolutionary hypotheses of trait evolution in cranes (Gruinae). *Am. Nat.* **154**, 249–259 (1999).

29. Petren, K., Grant, B. R. & Grant, P. R. A phylogeny of Darwin's finches based on microsatellite DNA length variation. *Proc. R. Soc. Lond. Ser. B* **266**, 321–330 (1999).

30. Sato, A. *et al.* Phylogeny of Darwin's finches as revealed by mtDNA sequences. *Proc. Natl Acad. Sci. USA* **96**, 5101–5106 (1999).

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Nitrogen limitation of microbial decomposition in a grassland under elevated CO₂

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Carbon accumulation in the terrestrial biosphere could partially offset the effects of anthropogenic CO₂ emissions on atmospheric CO₂ (refs 1, 2). The net impact of increased CO₂ on the carbon balance of terrestrial ecosystems is unclear, however, because elevated CO₂ effects on carbon input to soils and plant use of water and nutrients often have contrasting effects on microbial processes^{3–5}. Here we show suppression of microbial decomposition in an annual grassland after continuous exposure to increased CO₂ for five growing seasons. The increased CO₂ enhanced plant nitrogen uptake, microbial biomass carbon, and

available carbon for microbes. But it reduced available soil nitrogen, exacerbated nitrogen constraints on microbes, and reduced microbial respiration per unit biomass. These results indicate that increased CO₂ can alter the interaction between plants and microbes in favour of plant utilization of nitrogen, thereby slowing microbial decomposition and increasing ecosystem carbon accumulation.

Terrestrial ecosystems contain nearly three times more C (~2,060 Gt) than the atmosphere (~735 Gt C)⁶ and may be either a significant C sink or source under future CO₂ models⁷. CO₂ enrichment often enhances ecosystem C gain in the short term through the stimulation of photosynthesis². Over the long term, however, ecosystem C content depends on the balance between net primary production (NPP) and decomposition. Although increased CO₂ affects microbial processes by increasing C inputs to soil^{3,4} and soil moisture^{8,9}, future ecosystem C content has been considered primarily in terms of nutrient supply to plants (C inputs) rather than CO₂ effects on decomposition (C loss). A large source of uncertainty is the effect of increased CO₂ on N availability to plants and microbes¹⁰. Because plants are commonly N-limited in terrestrial ecosystems^{10,11}, any tendency for increased CO₂ to decrease N availability can suppress the stimulation of NPP by elevated CO₂. Microbes can also be N limited^{12,13}, and a decrease in N availability due to increased CO₂ could decrease decomposition and enhance C storage. Conversely, N stimulation of C fixation under increased CO₂ may not necessarily translate into ecosystem C storage because increased N availability can also stimulate microbial decomposition and C turnover¹⁴.

We used a sandstone grassland with moderate soil fertility to investigate the effect of increased CO₂ on microbial biomass and activity and on the interaction between plants and microbes in N acquisition. Experiments were conducted in an annual grassland at Stanford University's Jasper Ridge Biological Preserve in central California (37° 24' N, 122° 14' W; elevation 150 m) between 1992 and 1997. The climate is mediterranean with cool, wet winters and dry summers. Two CO₂ concentrations, ambient (360 p.p.m.) and increased (720 p.p.m.), were maintained for five years with open-top chambers (ten replicates for each treatment)^{15,16}. Soil samples were collected on 26 November 1996, 23 March and 23 April 1997, corresponding approximately to early germination, peak physiological activity, and peak biomass of plants, respectively.

Annual NPP was either stimulated or not affected by increased CO₂ (refs 15, 16). By the end of the sixth growing season, plots exposed to increased CO₂ exhibited a moderate increase (2,750 g C m⁻²) in the stock of below-ground organic C (soil, debris plus roots) compared with ambient controls (2,612 g C m⁻²). Although this increase is not significant at P = 0.05, it is consistent with a moderate increase in C inputs¹⁶. We studied organic C

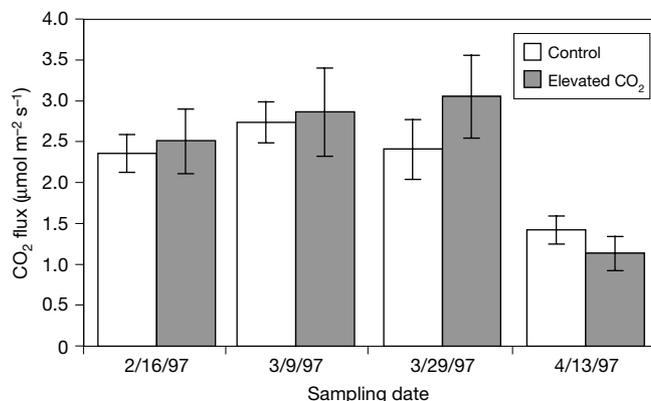


Figure 1 Below-ground respiration. Ambient (open bars) and elevated (filled bars) CO₂. Values are means ± standard error of the mean, s.e.m., n = 5–6 plots.

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Food, song and speciation

Michael J. Ryan

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 an analysis of a single species, 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 results in infertile 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

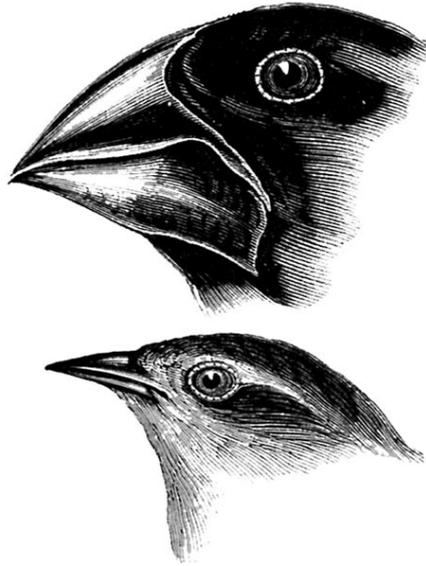


Figure 1 Feeding adaptations. Two species of Darwin's finches, *Geospiza magnirostris* (top) and *Certhidea olivacea*, have very different forms of beak that stem from their different diets. Podos³ argues that song evolution has also been affected, and is a further factor influencing speciation in these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

because natural selection should favour their 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 conditions 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 — say, its favoured 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 talk 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. *On 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, NJ, 1986).

7. Hoesle, W. J. *et al. 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* (TFH, 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).

Astronomy

The dark cradles of stars

Bo Reipurth

Stars are born in dark clouds of molecular gas, which remain shrouded in mystery. Astronomers have found a new way to peer inside these star factories.

One of the success stories of twentieth-century astronomy was the development of a physical understanding of the nature, evolution and death of stars — replacing thousands of years of mystical speculation with firm knowledge. But one piece of the puzzle is still missing: how stars are born. Hidden in the dark interiors of molecular clouds lie the birthplaces of stars, inaccessible at optical wavelengths to the probing eyes of astronomers. Technological breakthroughs in detectors operating at infrared and sub-millimetre wavelengths have improved our picture of stellar genesis in the past two decades, but it is still too early to declare that we understand how stars, including our own Sun, were formed. On page 159 of this issue, João Alves and colleagues¹ bring our knowledge of pre-stellar processes an important step forward.

It is widely agreed that most stars in the Galaxy are born in giant molecular clouds. Hundreds to several thousand stars are produced in these star factories, which convert tenuous gases into objects dense and hot enough to ignite nuclear processes. In the course of a few million years, roughly 10% of a molecular cloud may be turned into stars. But what conditions determine whether a particular clump of gas and dust will become gravitationally unstable and form a star? Such information is critical for calculations of the early stages of star formation.

Alves and co-workers imaged a type of dark cloud known as a Bok globule, at optical and infrared wavelengths, by using telescopes of the European Southern Observatory, including the world's biggest, the Very Large Telescope in the Chilean Atacama desert. Although most stars are born in giant molecular clouds, these enormous stellar nurseries are a mixture of complex environ-



Figure 1 A star-forming Bok globule (GDC1). GDC1 is similar to the B68 globule studied by Alves *et al.*¹, but it has already passed through the collapse phase and formed a Sun-like star in its interior. Although the newborn star is still embedded within thick layers of gas and dust, it reveals its existence by spewing a two-sided supersonic jet into the surroundings. Such jets rid the forming star of rapidly rotating material that would otherwise hinder its formation. Jets also help the newborn star to blow away the remnant cloud material⁸.

ments that are not readily disentangled. Bok globules, on the other hand, are relatively simple, tiny, dense blobs of gas and dust, which can completely blot out the visible light of background stars (see Fig. 1 on page 159). When the eighteenth-century astronomer Sir William Herschel first encountered a Bok globule in his telescope, he exclaimed: “Mein Gott, da ist ein Loch in Himmel” (“My God, there is a hole in the skies”)². Bok globules are thought to be the original dense cores of larger molecular clouds, which have been broken up by powerful radiation from nearby massive stars³. The destruction of the rest of the

molecular cloud allows us a clear view of the surviving cloud core.

There have been many previous attempts to probe the structure and physical conditions of pre-stellar cores of gas and dust by using modern radio telescopes operating at millimetre wavelengths, which are sensitive to emissions from complex molecules^{4,5}. These and other studies have shown that the main ingredient of such cores is molecular hydrogen (H₂) mixed with small but important traces of heavier molecules, along with a sprinkling of dust particles. We also know that temperatures are very low, of the order of 10 degrees above absolute zero. The gas densities of 10⁴–10⁵ cm⁻³ appear high relative to the interstellar environment, but are still at least twenty orders of magnitude smaller than that of their ultimate destination inside stars. Because hydrogen cannot be observed directly at millimetre wavelengths, other trace gases are used to infer gas densities. Unfortunately, this introduces uncertainties in the physical parameters of cloud cores derived from millimetre observations.

In their study, Alves *et al.*¹ have exploited the fact that at infrared wavelengths (a few micrometres) a Bok globule becomes more transparent, even though it is virtually opaque at optical wavelengths. By combining optical and infrared images they measure the degree to which dust particles in the Bok globule B68 block out the starlight of background stars seen through the cloud. They chose to study B68 because it is an almost spherical, isolated globule that is viewed against the rich stellar backdrop near the Galactic centre. So although it is small (0.4 light years in diameter), the light of thousands of stars is attenuated while passing through the dusty globule.

In the same way that the light from the setting Sun becomes redder as it passes through more of the Earth's atmosphere, starlight is reddened as it passes through B68. Alves *et al.*¹ construct a detailed map of how the reddening of light from nearly 4,000 stars changes across the globule, from which they determine the profile of the dust density through the cloud with unprecedented resolution and signal-to-noise ratio. By assuming that the dust is mixed throughout the gas in the cloud, and that the gas-to-dust ratio is 100:1, Alves *et al.* get a good picture of the internal structure of this gas globule. Remarkably, they find a close correspondence between the observed dust profile and theoretical predictions for the structure of a certain type of gas sphere that is stable but close to collapse⁶. With a total mass of only twice that of the Sun, B68 appears to be a prime candidate for a pre-stellar cloudlet.

The formation and evolution of stars represent a slow but inexorable effort by gravity to compress interstellar gas into the increasingly high densities encountered in stellar interiors, and ultimately into the

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