

commonly occur in winter in large flocks that exploit similar patchy resources, for example locally abundant Toyon berry (*Heteromeles arbutifolia*) crops. Unlike the above pairs, some other pairs of significantly covarying species show no obvious ecological relationships. Examples of such pairs are the Cedar Waxwing with Dark-eyed Junco or the Hermit Thrush with Purple Finch. In fact, close study of the correlation matrix shows that about half of the significant relationships are between ecologically rather dissimilar species pairs.

The results of the randomization procedure for testing the "significance" of the various group structures are presented in Fig. 1. The most "realistic" ecological group structure, which incorporated information about diet and microhabitat association, was significant ($P = 0.049$). The simple foraging-site grouping and the rather arbitrary taxonomic structure did a poor job of combining concordant species. The simple migratory-habit group structure was highly significant ($P = 0.015$). This latter result probably reflects the overall "boreal/montane bird year" phenomenon.

If these results verify the existence of a boreal/montane bird invasion phenomenon, what does that pattern mean? One possible explanation for the pattern is that the fluctuations represent actual changes in boreal/montane bird populations. Perhaps years with excellent summer recruitment are followed by a widespread occurrence of these species in the lowlands of southern California during winter. This could explain why ecologically similar species tend to covary. Alternatively, co-occurrence patterns might result from similar responses to local food or weather

conditions. If the distribution of wintering density varies across the range of these species, certain years may be characterized by high densities in the Los Angeles basin. Such years need not be years with high recruitment but could represent years of locally favorable food supplies or weather conditions (or unfavorable conditions elsewhere). Identifying the relative influence of each factor on local population densities would require a broader scale analysis. Such a study should consider recruitment success, migratory pathways, and winter population densities across the entire range of the species in question.

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Chaffinch Imitates Canary Song Elements and Aspects of Organization

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The learning of certain aspects of song between bird species is a well-known phenomenon, and species vary from those that regularly imitate the sounds of many others to those in which inter-specific mimicry is rare or unknown. In cases in which the range of sounds normally copied is restricted, it is of great interest to discover the nature of the constraints that limit this learning. Marler (1976) suggested that young birds are born with a template and will only learn sounds that match its features. If this analogy is accurate, it is particularly interesting to know just what form the restrictions imposed by this template take and how they operate to ensure that most birds usually sing only the song typical of their

own species. Examples of cross-species copying in cases in which copying is unusual, such as the one reported here, may shed light on this problem and help us to understand the processes involved in song learning.

In May 1982, I heard a song coming from a cage containing British birds at London Zoo and recognized it to be that of a Canary (*Serinus canaria*), although it was very brief for that species. I was surprised to find that the singer was a Chaffinch (*Fringilla coelebs*). This species is not noted for its mimetic ability, although an individual singing Greenfinch (*Carduelis chloris*) song in the wild has been reported (Conrads 1977), and Thorpe (1958) trained one to sing

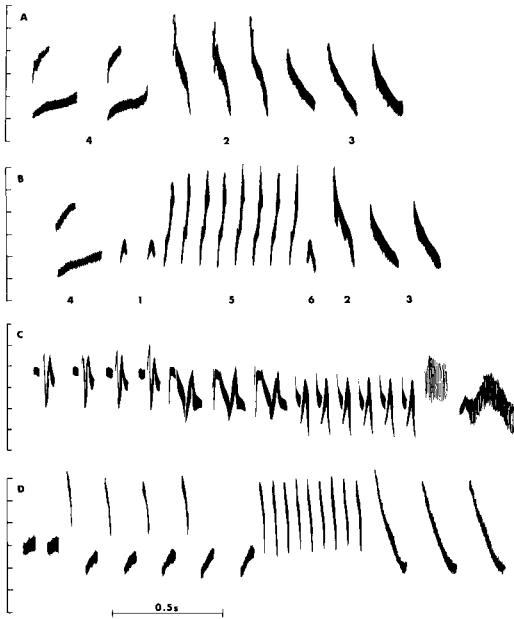


Fig. 1. (A) and (B) Sonograms of two songs produced by a Chaffinch at the London Zoo, which illustrate its six different element types. These are labelled by numbers under the sonograms. (C) Sonogram of a typical Chaffinch song recorded in Stanmer Park, Sussex, U.K. (D) Sonogram of a short section from a Border Canary song recorded in captivity. In each case the frequency scale runs from 1 to 7 kHz. The original sonograms have been traced, as there was considerable background noise from other species in the case of the captive birds.

Brown Tree-Pipit (*Anthus trivialis*) song in captivity. He also reported that Chaffinches raised by Canaries would produce Canary song when in subsong, although this was lost in full song. In areas of the Azores where their range overlaps that of Canaries, Chaffinches have been recorded as regularly imitating Canary syllables (Knecht and Scheer 1968). Chaffinch song and Canary song differ considerably in sequencing and length, however, as well as in the structure of the elements. The exact nature of the imitations was therefore of some interest, and I returned to record the bird on 10 July. On this occasion, as on the previous one, the bird was undoubtedly in full song rather than subsong; the individual songs were brief and loud, with silent intervals between them, rather than being quiet and less structured. I obtained recordings of 170 songs using a Marantz C-205 Professional cassette recorder, with an EC-3 microphone mounted in a 50-cm parabolic reflector. Sonograms were produced (Kay Elemetrics

TABLE 1. The frequency of different sequences of elements (see Fig. 1) in the songs recorded from a captive Chaffinch at the London Zoo.

Sequence	Number of occurrences
1-2	2
1-2-3	52
2-3	32
4-2-3	59
1-5	9
4-1-5-6-2-3	1
1-5-6-2-3	3
5-6-2-3	1
1-2-5	1
4-6-5	1
4-1-2-3	4
4-2	4
4-2-4-2-3	1
Total:	170

Digital Sonagraph No. 7800) from a selection of these songs, and the complete sample was examined and sequenced using the visual display of a Unigon Continuous Spectrum Analyzer.

Two songs are shown in Fig. 1A and 1B and illustrate the six different element types recorded from this bird. All the elements, with the exception of type 6, were usually repeated several times in succession within a song, a feature typical of both Chaffinch and Canary (Fig. 1C, 1D). The songs were of brief duration, none of them exceeding 2.5 s in length. This is also a characteristic of Chaffinch song, while the songs of Canaries are generally much longer. In several other respects, however, the songs were very unlike those of a normal Chaffinch. It is the quality of the individual elements that makes them recognizably those of a Canary: they have a purity and simplicity that diverges sharply from the rapid frequency modulations usually found within elements of Chaffinch song (Fig. 1C). The sweeping descent of types 2 and 3 is especially striking in its similarity to the Canary song shown in Fig. 1D.

In the wild, Chaffinch songs always have a complex ending, referred to as the terminal flourish, which consists of un-repeated broad frequency band elements. In none of the songs sung by this individual did any such feature appear. Normal Chaffinch songs are also deterministic in their sequencing, a particular song type always following exactly the same order of element types. Songs have between 2 and 5 different element types in the trill that precedes the flourish (there are 3 in the example shown in Fig. 1C). Songs sometimes terminate prematurely, but they always start with the first element type. Most birds have more than one song type, and usually each song type consists of a totally different sequence

of element types, although sometimes different song types have elements in common. The songs sung by the London Zoo individual are very different from this pattern. The sequences of elements that were recorded are shown in Table 1. Although certain sequences were very much more common than others and some elements were more likely to occur at the beginning (e.g. 4 and 1) and others at the end (e.g. 3 and 5) of songs, many different sequences were recorded. The bird could not be thought of as having a repertoire of a few stereotyped song types, nor was the variety simply generated because it started its songs in the same place but sometimes ceased before completing them. This feature is very unlike the song of a normal Chaffinch, and it is interesting that the bird was capable of introducing such varied patterning when this is outside the range of variation shown by this species in the wild. It is further evidence that Canary song is what the bird had learnt, as Canaries, while showing preferred sequences, do not tend to show fixed ones (Wolffgramm 1973).

This bird was probably reared by Canaries. It had been bred by a pet dealer and purchased by the Zoological Society in October 1980. While its history before that was uncertain, the dealer commented in correspondence that "as far as I can remember the bird was indeed reared by Canaries. It would probably not have heard another Chaffinch sing and, while I had it, it did not come into contact with another Chaffinch." The capacity of Chaffinches to memorize songs they have heard as fledglings has already been demonstrated by Slater and Ince (1982): this individual shows that in such circumstances Chaffinches can learn across species. This possibility is in line with the increasing evidence that one of the constraints on the song learning of young birds of many species is not so much a song template as a constraint making it more likely that learning will occur from individuals with which the bird has a social relationship. Thus, birds may learn from rivals, cage-mates, or foster parents, whereas they will not learn from hidden individuals or from tape-recordings (see Slater in press). Regardless of why this particular Chaf-

finch learnt Canary song, its learning illustrates the fact that cross-species copying can involve an intricate blending of the species-specific characteristics of tutor and pupil songs.

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