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CHANGES WITH TIME IN THE SONGS OF A POPULATION OF CHAFFINCHES

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ABSTRACT.—A comparison has been made between 23 song types recorded from Chaffinches in Stanmer Great Wood, Sussex, U.K. in 1960, and the total of 36 that were sung there in 1978. Eight of the earlier song types showed clear similarities with those present in 1978: in three of these the differences were minor, but in the other five they were substantial enough for the songs to have been classified as different types had they been found in the same population at the same time. With all other song types, the differences were too great for song types to be compared between the two sets of recordings. While at any one time some song types are shared in more or less identical form among many individuals in a population of Chaffinches, these results show that the form of song types changes through time. These changes may occur because rare song types are not copied by other birds and become extinct in the area, because new song types are introduced from elsewhere by birds moving into the area and because mistakes in copying may lead to new song types being generated.

All the songs of Chaffinches (*Fringilla coelebs*) have certain features in common. The first part, or trill, may be split into two to four phrases within which there are units, referred to here as syllables, that are repeated in more or less identical form. The songs shown in Figure 1 are an example in which the trill has three phrases, the syllable structure being the same within a phrase but differing among them. The final part of the song, after the trill, is the end phrase, a note complex in which the elements are not usually repeated.

Within this pattern there is much variation both among birds and among the songs in an individual's repertoire. In a study of the songs found in the Orkney Islands (Slater and Ince 1979) we found that this variation is discontinuous, the songs falling into discrete types. Within a song type the intervals between syllables and the structure of the syllables themselves are very similar among birds. On the other hand, the number of syllables in a phrase varies considerably both among individuals (see Fig. 1) and among repetitions by the same individual. The best criterion for distinguishing between song types is therefore the form of the syllables. In assigning songs to types, we have used any consistent difference in form, no matter how slight, to indicate that two songs should be classified as separate. Some song types are very similar to each other, but, as the variation is not continuous, they can be separated by playback at slow speed or by inspection of sonograms. Our criteria for classifying songs into types appear similar to those used by the birds, as the most similar of the song types we have found can appear as two separate types in the repertoire of one bird (see Slater and Ince 1979).

Young male Chaffinches learn the details of their songs from conspecifics during the first 13 months of life (Thorpe 1958). The fact that some of the song types in an area are very similar to each other indicates that new types may arise by mistakes being made during copying. Comparison between types suggests that such mistakes may involve gradual change as the song is passed down through several successive individuals or sudden major changes, such as the mixing up of phrases from two different song types (Slater and Ince 1979). By contrast, some of the song types in an area bear little relation to any others and have probably been introduced by immigration of individuals after their songs were learnt.

The reconstruction of changes in song by analyzing the similarities and differences among the song types found in a population at a particular time is analogous to tracing the probable course of genetic evolution by an examination of living species. However, as cultural evolution is a more rapid pro-

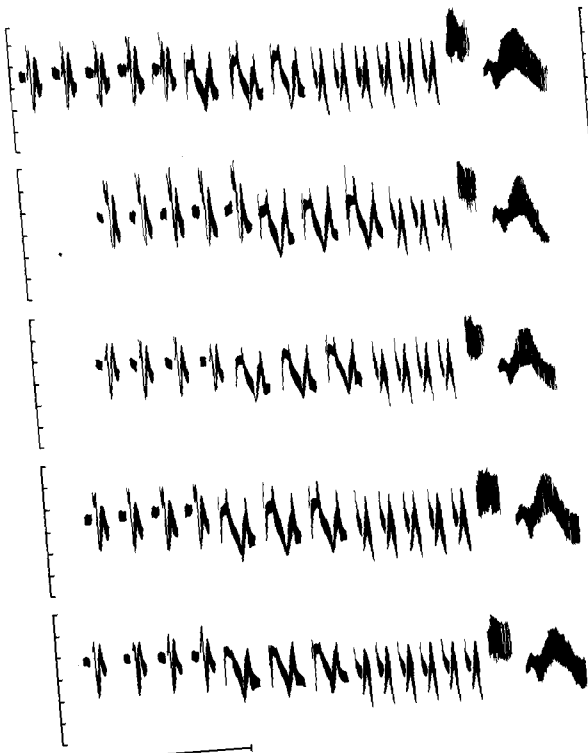

FIGURE 1. Five sonograms of the same song type (type B), as sung by five different Chaffinches in Stanmer Great Wood, Sussex in 1978. In this and the other figures the scale at the side runs from 1–7 kHz and the time bar beneath is 0.5 s long.

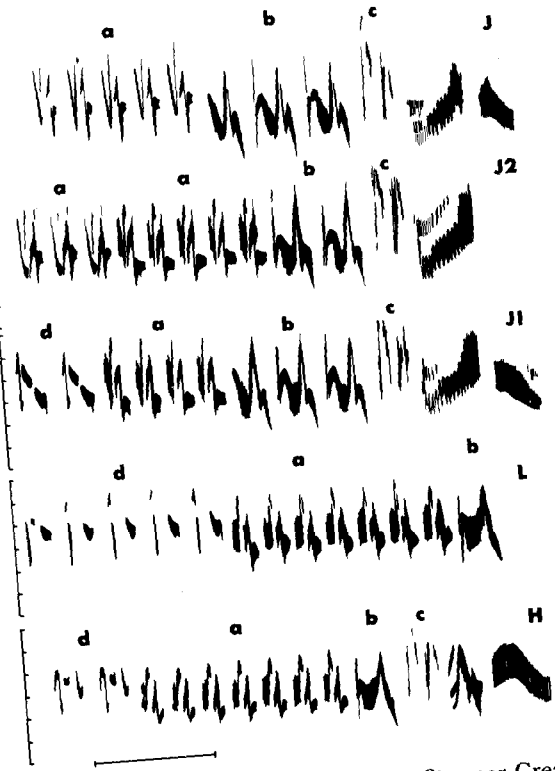

FIGURE 2. Five song types sung in Stanmer Great Wood in 1978. Compare with Figure 3.

cess, it is feasible to examine changes through time as well, to determine whether immigration and inaccuracies in copying lead to changes in the songs present in an area over time. This paper is concerned with a study of this latter type, made possible by two sets of recordings made at the same place 18 years apart.

METHODS

Between 30 May and 7 June 1960, C. W. recorded as many Chaffinch songs as possible in Stanmer Great Wood, Sussex, U.K. close to the site on which the University of Sussex was subsequently built. These recordings were made with an EMI L2A tape recorder and Sennheiser MD21 microphone mounted in a 90-cm parabolic reflector. The tape speed used was 38 cm/s but the recordings were copied at 19 cm/s before analysis. About 22 individuals were recorded. This survey was not complete and so cannot indicate the relative frequencies of different song types. Chaffinches usually have more than one song type in their repertoire (Marler 1956), and sonographic analysis showed that these recordings included 23 distinct song types: these were assigned numbers. Eighteen years later, in summer 1978, S. A. I. surveyed completely the songs of all the male Chaffinches in Stanmer Great Wood. These were recorded at 9.5 cm/s on a Uher 4000 tape recorder using a Grampian DP6 microphone and 50-cm parabolic reflector. The 42 birds present had an average of 2.9 song types each and, sharing of song types being common, the number of distinct types found was 36. These are labelled throughout this paper by letters, followed by numbers where necessary. With both samples, the classification of songs into types was based on any consistent difference in form that was found between them (see below).

The two sets of recordings were compared by taking each song type found in 1978 and finding the song type from 1960 to which it was most similar. Sonograms, prepared with a Kay-Electric Sonagraph No. 6061A using the wide band setting, were used in making these comparisons. The figures illustrating this paper are tracings from these sonograms; the quality of the original recordings, particularly those from 1960, was often not adequate to use the actual graphs. Each set of recordings was traced without reference to the other.

RESULTS

Figures 2 and 4 show two groups of song types recorded in 1978, within each of which there are strong similarities. The differences among the songs within these groups illustrate the differences in structure that allow song types to be classified as distinct. Lower case letters in these figures label syllables that have features in common and may therefore have evolved from a common original. In some cases the similarities are so strong that they have almost certainly done so. However, caution is required here because, for example, the *b* and *c* syllables in Figure 2 closely resemble elements we

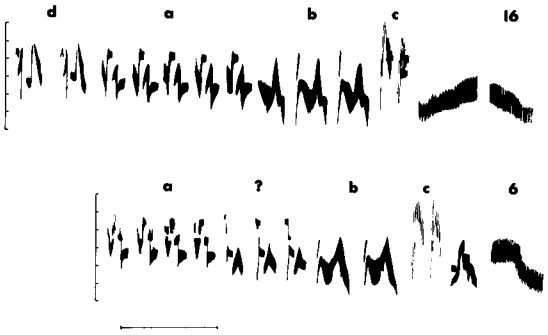

FIGURE 3. The two song types recorded in Stanmer Great Wood in 1960 that are most similar to those in Figure 2, which were recorded in 1978.

have found in Chaffinch songs in Orkney, about 900 km from Stanmer (see Slater and Ince 1979). Given the distance involved and the variation found in song over comparatively short distances, this is likely to be due to convergence rather than evolution from a common precursor. The mechanism of song production in Chaffinches may be particularly prone to generating elements of these types. For this reason, we restrict ourselves here to a comparison among songs that have more than one syllable type in common, a situation which, given the wide variety of syllable types, would be very unlikely to arise by chance.

Figure 3 shows the two song types recorded in 1960 that were most similar to those in Figure 2. Type 16 is most like type J1, the strongest differences between them being in the *d* syllable and the more drawn out end phrase in type 16. The last part of type 6, from syllable *b* onwards, is virtually identical to that of type H, but the earlier sections of these two songs are clearly distinct. Thus, although song types 16 and 6 include elements that are of the same form as those of the songs shown in Figure 2, no song type found in 1978 was identical with either of these earlier types.

A comparison of the song types shown in Figures 4 and 5 yields similar conclusions. Type 18 is most like type C or type S, but the end phrase differs from either, as does the detailed structure of syllables earlier in the song. Type 11 is like type A1, but A1 lacks a component in the end phrase and also in the syllable type *e*. Type 10 is perhaps most closely allied to type A in syllables *g* and *h*. However, there is again a difference in that type A has a very brief end phrase which lacks the two final components of that in type 10, and the introductory elements also differ between them.

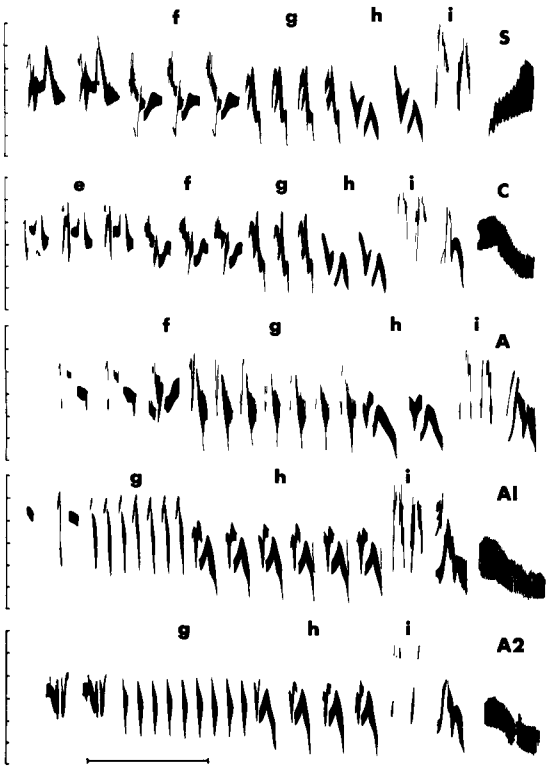

FIGURE 4. Five song types sung in Stanmer Great Wood in 1978. Compare with Figure 5.

Many of the other song types found in 1978 showed no clear similarity to any of those recorded in 1960. The only three other cases where resemblance was sufficient to suggest that the two types had a common derivation, or that the earlier type had evolved into the later, are shown in Figure 6. In each pair, differences between syllable types can be seen, although these are

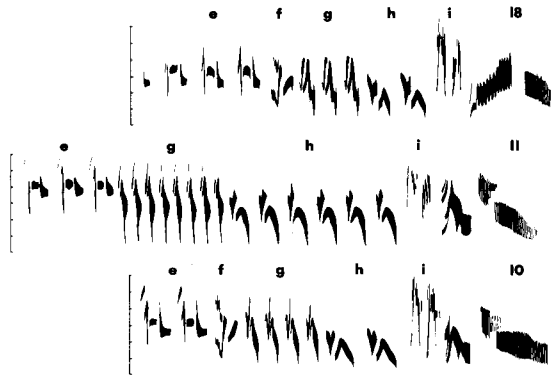

FIGURE 5. The three song types recorded in Stanmer Great Wood in 1960 that are most similar to those in Figure 4.

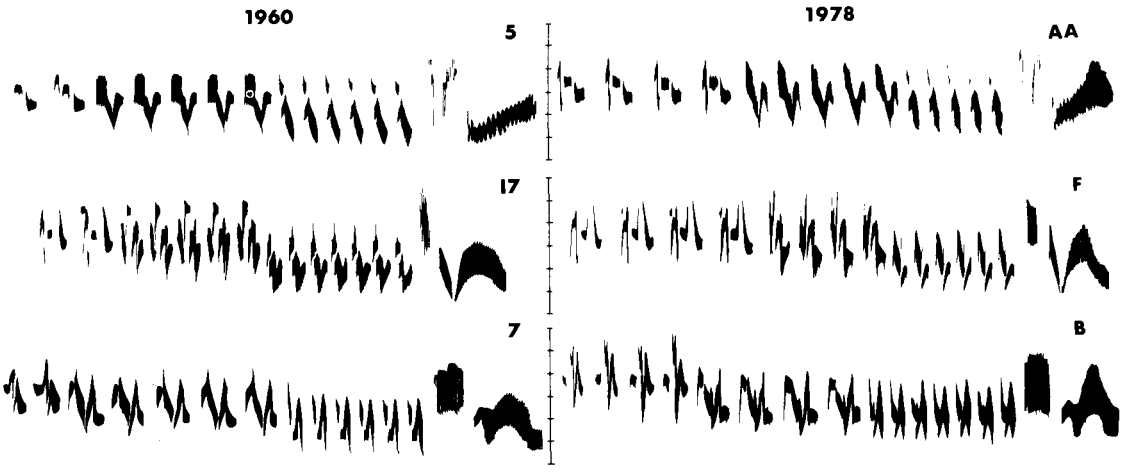

FIGURE 6. Three song types recorded in 1960 compared with their nearest equivalents recorded in 1978.

minor in some cases and could have resulted simply from small changes in amplitude modulation leading to different aspects of a particular syllable being emphasized. Types 5 and AA appear to be the most similar. The main difference lies in the second phrase, syllables of which are longer in type 5 than in type AA. This variation is greater than that usually found within a song type; measuring the intervals between equivalent points in the syllables of this phrase for these two songs yields a coefficient of variation of 10.6%, which is considerably greater than normal within a song type (see Table 1). Despite this quantitative difference, however, song types 5 and AA might well be classified as the same because of their overall similarity in form.

Types B and 7 look rather more different from the tracings in Figure 6 than comparisons of the original sonograms suggest; the recording of type 7 was particularly poor, with the result that small details could not be traced accurately. However, these two types can be compared in more detail by examining the interval between equivalent points in successive syllables of each phrase. This is possible here, and in comparisons with song types C and F, because these three types were recorded from several birds in 1978 so that the variation among them could be measured for comparison with the earlier song types. These data are shown in Table 1. The results confirm the similarity between type B and type 7, the intervals in the latter falling within

TABLE 1. Comparisons of the interval between the same points in successive syllables for each phrase of the three song types that were most common in 1978 with their nearest equivalents in 1960. Times given are in milliseconds; CV = coefficient of variation.

		Phrase			
Song type		1	2	3	4
B (N = 14)	Mean interval	139	182	89	
	Range	131–151	169–204	82–98	
	CV	4.94%	5.29%	4.96%	
7 (N = 1)	Interval	139	178	95	
F (N = 10)	Mean interval	184	122	84	
	Range	174–197	117–139	78–91	
	CV	5.17%	4.29%	4.53%	
17 (N = 1)	Interval	178	116†	86	
C (N = 10)	Mean interval	185	153	100	161
	Range	174–204	142–167	98–106	144–167
	CV	5.59%	5.66%	2.96%	4.24%
18 (N = 1)	Interval	201	*	121†	197†

* No comparison can be made here because there was only one syllable in the second phrase of song type 18.
† These figures fall outside the range of intervals given above. This may suggest some divergence, although with only a single sample of each song type from 1960, numbers are too small for statistical testing.

the range of those recorded from 14 birds singing the former. The elements in the second phrase of type 17 are repeated slightly more rapidly than any of those recorded for type F, suggesting a small divergence between these song types, though not one which would be likely to yield statistical significance with a larger sample. On the other hand, comparison of type C with type 18, shows a more substantial discrepancy in the timing of the third and fourth phrases which is in keeping with the greater difference in form between these types (see Figs. 4 and 5).

DISCUSSION

These results show that substantial changes have taken place in the song types found in a population of Chaffinches during the course of 18 years. Some individual syllables have remained very much the same over time (e.g., *b* in Figs. 2 and 3 and *h* in Figs. 4 and 5), but others have changed considerably, and there has also been reassortment of syllables between song types. Of the 23 song types recorded in 1960, eight showed clear relationships with those of 1978, and the three of these shown in Figure 6 had persisted with only minor changes. Even in these cases, however, the changes might have been sufficient for the earlier and later forms to be regarded as different song types if both had been found in the population at the same time. As with species of organisms, it is easier to classify forms present at one time than variants recorded at different times.

Both our observations on territory ownership and the analysis of banding recoveries by the British Trust for Ornithology (R. J. O'Connor, pers. comm.) suggested that about 60% of male Chaffinches survive from one breeding season to the next. The average duration of a cultural generation is thus approximately two years, so that 8–10 generations would be expected in the course of 18 years. However, in a population of 42 birds, one or two individuals would be expected to be over seven years old, meaning that some song types could have passed through considerably fewer generations, thus giving greater conservatism. Another factor countering change may be how common a particular song type is in the population. Not only are these types more likely to be included in the repertoire of long-lived individuals, but also young birds may have more than one model available to copy if two adults are singing the same type near them. Individual idiosyncrasies would therefore be less likely to pass on from one bird to another. It may be for these reasons that the two song types which were most common in 1978, B and F, sung by 22 and 16 individuals respectively, were also those most clearly related to types recorded earlier.

No previous study has examined cultural changes over the length of time covered by this analysis. Even so, the evidence suggests that the speed of cultural change differs considerably among species. For example, while Snow (1968) found no change in song types over a period of three years in the Little Hermit hummingbird (*Phaethornis longuemareus*), Thompson (1970) found two years to be sufficient for most song types to have changed from those previously found in a population of Indigo Buntings (*Passerina cyanea*). In Saddlebacks (*Creadion carunculatus*), cultural mutations are infrequent, but Jenkins (1978) was able to observe a number as they happened by following a small population through five years. The exact speed of change found by any study doubtless depends on mortality rates as well as on the exactitude of copying. If many individuals died in a particular year, as might have been the case in the present study for the unusually hard winter of 1962–63, the apparent speed of cultural change might have been enhanced by a subsequent influx of birds who had learnt their songs elsewhere. In general, however, male birds nest close to their natal area (Greenwood and Harvey 1976) and we have found that male Chaffinches tend to occupy the same territory in successive years. In our Sussex population of 42 birds, only one had a repertoire in which none of the song types were shared with any others; this again suggests that birds tend not to move long distances after song learning has ceased. Thus the introduction of song types from elsewhere is unlikely to be a major source of change; most of the differences observed have probably resulted because some song types that are sung by only one or a few individuals become extinct and because new ones are formed when copying is inexact.

The original intention of the 1960 recordings was to trace parallels between the songs of Chaffinches at Stanmer and those of the same species in New Zealand. The entire New Zealand population is known to be derived from 66 birds caught in Stanmer Park and transported there in 1870. The comparison would be interesting but, from our observations on the changes which can

occur over 18 years, it seems unlikely that close parallels would be found between two populations that have been separated for nearly a century. Thielcke (1974) reported no differences in song between European Chaffinches and those recorded in New Zealand. However, this is only in the general characteristics of song rather than in the details considered here.

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RECENT PUBLICATIONS

Estimation of density from line transect sampling of biological populations.—Kenneth P. Burnham, David R. Anderson, and Jeffrey L. Laake. 1980. Wildlife Monographs No. 72. 202 p. Paper cover. $4.00. Source: The Wildlife Society, Inc., Suite 611, 7101 Wisconsin Ave., N.W., Washington, D.C. 20014. "This monograph provides what we believe to be a rigorous, comprehensive, and practical reference on line transect sampling as it is used in estimating the abundance of wildlife populations." It combines theory and practice, and includes many illustrative examples. The work is addressed to both field biologists and biostatisticians, and offers a detailed Reader's Guide as a roadmap. Familiarity with applied statistics is expected before setting out. Diagrams, references, appendixes.

A working bibliography on the Peregrine Falcon in Washington State.—Richard L. Knight, Leray E. Stream, and Roger H. Harkins. 1979. Washington Department of Game. 25 p. Paper cover. **An annotated bibliography of Washington raptors and the Common Raven.**—Richard L. Knight. 1979. Washington Dept. of Game. 68 p. Paper cover. Source: free from the Washington Dept. of Game, 600 North Capitol Way, Olympia, WA 98504. The peregrine bibliography consists of an annotated list of references to the species in Washington and a list of selected articles on the biology of the species as studied elsewhere. The bibliography of raptors and the raven gives a list of references to these birds in Washington, each citation coded to show its nature (e.g., general article, checklist, thesis) and which species are mentioned. A species index follows. Much of the first bibliography is subsumed in the second, so it is not evident why they were published separately. Nevertheless, they will be useful to those involved with research or management of raptors and ravens in the Pacific Northwest.

Avian community structure of six forest stands in La Maurice National Park, Quebec.—J.-L. Desgranges. 1980. Occasional Paper No. 41, Canadian Wildlife Service. 32 p. Paper cover. The author studied avian communities in various successional stages of northern-coniferous forest. Similarity, feeding niches, dominance, equitability, and diversity were considered. The report provides useful data and tests some current ecological theories on community structure. Photographs, graphs, and references.

Census methods for murres, *Uria* species: a unified approach.—T. R. Birkhead and D. N. Nettleship. 1980. Occasional Paper No. 43, Canadian Wildlife Service. 24 p. Paper cover. Murres are said to be "probably the 'best' alcid species to serve as indicators of the quality of the marine environment." This report presents methods for estimating the size and status of their populations, as appropriate for the different types of breeding colony. The frequency of counts and potential sources of error are discussed. This is a practical manual of techniques for censusing colonial seabirds. Photographs, diagrams, appendixes, references.