

SONG DEVELOPMENT IN HAND-RAISED OREGON JUNCOS

PETER MARLER, MARCIA KREITH, AND MIWAKO TAMURA

THE song of wild Oregon Juncos, *Junco oreganus*, is a "loose quavering trill all on the same pitch" (Peterson, 1941). In comparison with many species the song is thus a simple one, which was the reason for selecting it as a subject for this study of song development. As a first step in the analysis we have taken young birds from the nest before they fledged and raised them in varying degrees of isolation. This paper describes the development of song under these conditions and compares the final results with the songs of wild Oregon Juncos.

METHODS

Eleven birds were raised by hand in 1958 and 1959. These were taken from nests as follows. 7 May 1958—one brood of four birds taken in Strawberry Canyon, Berkeley, California, at an age of about seven days after hatching. These will be described as the 1958 birds, and include three males, *green*, *yellow-blue*, and *white*. 5 May 1959—two birds taken in Tilden Park, California, about eight days after hatching, one, *blue*, a male. 22 May 1959—one bird taken on the Berkeley campus about 10 days after hatching, a male, *yellow*. 26 May 1959—a brood of four taken at Capitola, near Santa Cruz, California, at six days after hatching, including three males, *heliotrope-blue*, *black-white*, and *green-white*. These five males will be referred to as the 1959 birds. The three females, identified by dull plumage, the lack of song, and, in two cases, by the laying of eggs, will not be discussed in this paper.

The birds were fed with moistened nestling food, supplemented with hard-boiled egg, crushed seed, and meal worms. They were changed to soaked seed and subsequently maintained on mixed seed, dry nestling food, meal worms, and lettuce. All of the birds were raised successfully and are still in good health at the present time.

After removal from the nest none of the birds had an opportunity to hear any song or calls of wild juncos. However, they were exposed to songs of other species. The 1958 birds were kept at home in a large cage together with hand-raised House Finches, *Carpodacus mexicanus*. Through an open window they were also able to hear songs of the Rufous-sided Towhee, *Pipilo erythrophthalmos*, the White-crowned Sparrow, *Zonotrichia leucophrys*, and certain other species, but no juncos. In January 1959 they were separated from the House Finches and moved into the laboratory to a closed room, where they were isolated until the summer of 1959. Then they were moved to another room, with White-crowned Sparrows and

House Finches, where they have also been able to hear recordings of songs of many other species. The 1958 birds thus were raised in a rich and varied auditory environment, although in the period in their first spring, from January to June, they could hear only each other's songs and calls.

The environment of the 1959 birds was more restricted. By May 1959 we had constructed two soundproofed booths from heavy plywood and acoustic tile. The sound insulation from outside to inside was not perfect, and a person inside could hear songs played outside on a tape recorder. However, the insulation between boxes when both were closed was good. As soon as they became independent, the 1959 juncos were moved from the laboratory to one of these boxes and kept there in separate cages for 14 months until 29 July 1960, when they were transferred to a highly insulated, steel, soundproofed box, where further study is now continuing. During the 14-month period in the plywood booth, the adjoining booth was occupied continuously by hand-raised White-crowned Sparrows from May 1959 to October 1960, and intermittently after that. We had thought that the juncos were effectively separated from them. But it is clear from some of the songs which developed that they were able to hear White-crowned Sparrow songs, probably either while the door of one of the boxes was opened for cleaning, or while we were monitoring White-crowned Sparrow songs from another box. There was no opportunity for them to hear any other species.

Recordings of song and subsong were made at approximately monthly intervals, using either an Altec 633-A or an American D33 microphone, on a Wollensak T1500 tape recorder with a tape speed of $7\frac{1}{2}$ " per second. The recordings were then analyzed on a Kay Electric Company Sonagraph using the "high-shape" and "wide-band" filter settings in all cases.

We have also included an analysis of 12 song patterns from wild Oregon Juncos, all recorded in or near Berkeley, California, either on a Magnemite 610-E tape recorder at tape speeds of 15" or $7\frac{1}{2}$ " per second with an Altec 633-A microphone mounted in a parabolic reflector, or on a Midgetape 500 recorder at a tape speed of $3\frac{3}{4}$ " per second with an Electrovoice 644 unidirectional microphone. The faster recordings were played back on a Viking 75 tape deck and the slower tapes, directly on the Midgetape recorder.

THE SONG OF WILD JUNCOS

A sample of 12 song types of wild birds has been recorded and analyzed to provide a basis of comparison with the hand-raised birds. Time/frequency analyses are presented in Figure 1. A-H are taken from different birds singing in the vicinity of Berkeley. Each is a typical example from series of up to 70 songs that varied only in the number of syllables rep-

resented. At first we thought that each bird had only one theme, but this was probably not the case. A wild male, which was trapped and recorded shortly afterwards in an open-air aviary in Strawberry Canyon by Mark Konishi, used three distinct themes at different times (Figure 1, J1-3), each one given for long periods without a break. It is thus more difficult to determine the total repertoire of an Oregon Junco than of a Chaffinch (*Fringilla coelebs*) (Marler, 1952) or a Brown Towhee (*Pipilo fuscus*) (Marler and Isaac, 1960), which also have a repertoire of several types but switch more often from one theme to another.

The normal song usually consists of more or less identical repetitions of the same syllable type, as seen in Figure 1. This becomes significant in the comparison that follows since some of the hand-raised birds had more than one syllable type in a song.¹ Analysis of the sonagrams shown in Figure 1 reveals that the sample is relatively homogeneous in most respects. The mean over-all duration of the song is 1.40 seconds, and that of the individual syllables is 0.082 second (Figure 4). The mean interval between the start of successive syllables is 0.113 second, and the mean number of syllables per song is 12.9. The structure of syllables in the songs of different individuals is remarkably diverse. This is especially striking when we note that the recordings were all made in one restricted area, often from birds with adjacent territories.

FINAL FIRST-YEAR SONGS OF HAND-RAISED JUNCOS

During the course of development each hand-raised bird developed one or more songs, which, after a period of variability, then crystallized into more or less constant song types, which were used with little variation throughout the first spring and summer. We have described these as the "final first-year themes." To compile data comparable to those on wild birds, we have presented a typical sonagram of each theme from the date on which it was first recorded in its final, complete form. These sonagrams are reproduced in Figures 2 and 3. We have separated the results from 1958 and 1959 birds because of the different conditions under which they were raised.

The 1958 birds: first year. The three males, *yellow-blue*, *green*, and *white*, each developed two song types in their first year (Figure 2). Each bird had one abnormal type, in the sense that two syllable types were present in the song (Figure 2, *yellow-blue*, song 2; *white*, song 2; *green*, song 2). Of the other songs, those of *yellow-blue* and *green* would pass to our

¹ It should be noted that two-part songs with different syllable types in the first and second halves are known in wild Oregon Juncos. A. H. Miller (pers. comm.) has told us that they occur occasionally, and we have heard one example on the Berkeley campus, although it has not been recorded.

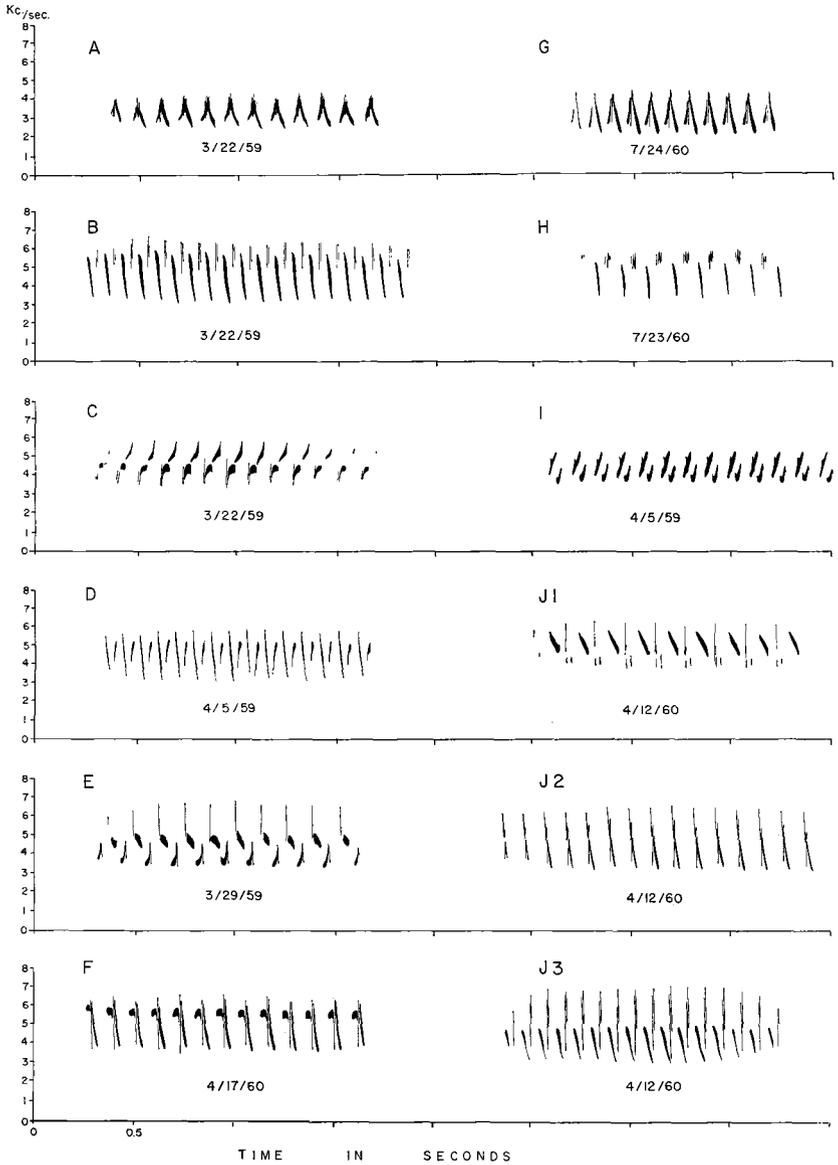


Figure 1. Wide band time/frequency analyses of 12 songs of wild Oregon Juncos. J1-3 are from a single bird, the others are from different individuals. The sonograms represented in this figure and in the other illustrations to this paper are ink tracings.

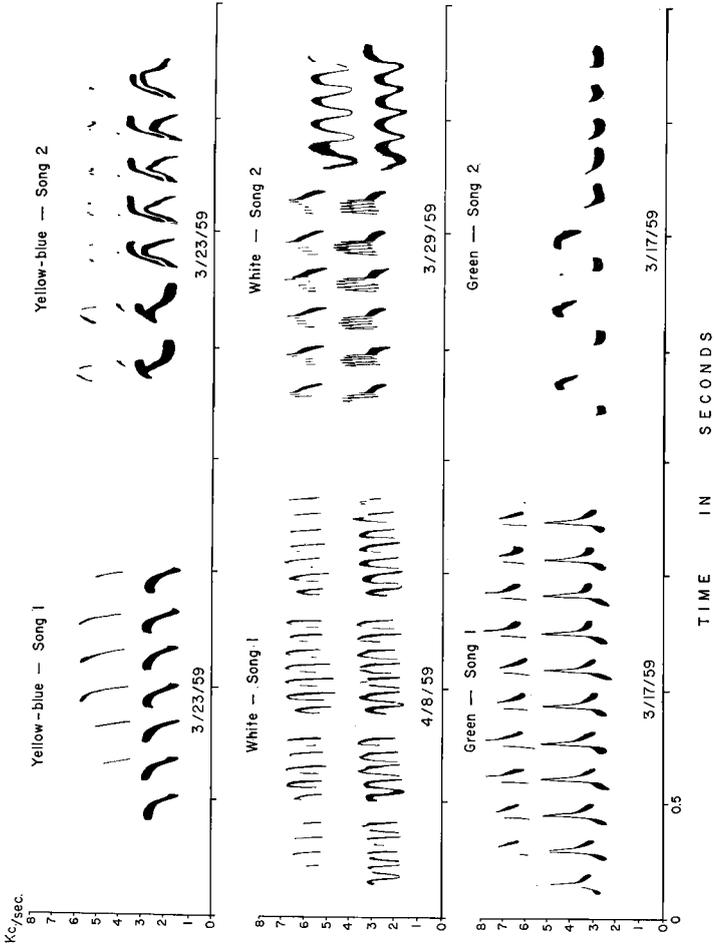


Figure 2. Time/frequency analyses of the final first-year songs of the three 1958 males: yellow-blue, white, and green.

ears as wild Oregon Junco songs. That of *white* had the normal timbre and an even pitch, but had an atypical division of the song into four parts (Figure 2, *white*, song 1). Perhaps the most striking aspect of these patterns is the lack of correspondence between syllable structure in the songs of these three sibling males. They were caged in close proximity to each other throughout the experimental period, exposed to the same alien species, and only had each other to listen to for much of the time. Nevertheless, they developed radically different syllable types.

The 1959 birds: first year. The five 1959 males developed the following numbers of song types: *green-white*, five; *black-white*, four; *blue*, four; *heliotrope-blue*, seven. Male *yellow* was treated differently from the others. Until 15 March he had produced only one song type, which is reproduced in Figure 3 together with all of those of the other four males. At this time he was removed from the group to a separate room containing one other junco, male *green* from 1958, and kept there for four months. His singing during this period is discussed in a later section.

The first point that emerges from Figure 3 is the greater proportion of apparently normal songs as compared with the 1958 birds. Of the 21 song types represented, 15 resemble those of wild birds, consisting of repetitions of more or less similar syllables. The other six sound quite unlike songs of wild juncos. In some cases there are two syllable types (*green-white*, songs B, E; *heliotrope-blue*, song C) or abnormally long and variable syllables (*heliotrope-blue*, song F; *blue*, song B). In one there is a complete absence of any syllable structure (*black-white*, song D).

In the 1959 birds we are again struck by the diversity of syllable types. However, in this case there is something in common between certain syllable types of the three siblings, *green-white* (Song A), *heliotrope-blue* (song A), and *black-white* (song B). We may also note the relatively simple syllable structure in most of these songs as compared with that in the wild birds and even with that in the 1958 hand-raised birds.

A summary of characteristics of the first-year songs. For the purpose of comparison with wild birds we have merged the data on the final first-year themes of the 1958 and 1959 birds. Figure 4 shows histograms of song duration, number of syllables per song, syllable duration, and the interval between the start of successive syllables. In all cases there is considerable overlap between the histograms for wild and hand-raised birds, although the data on the hand-raised birds are consistently more variable. The hand-raised birds have shorter songs with fewer syllables per song—8.4 as compared with 12.9. This deviation is partly caused by the abnormal songs of *blue* and *black-white* and by *white*'s problematical first song, which has been classified as having four syllables. However, if we

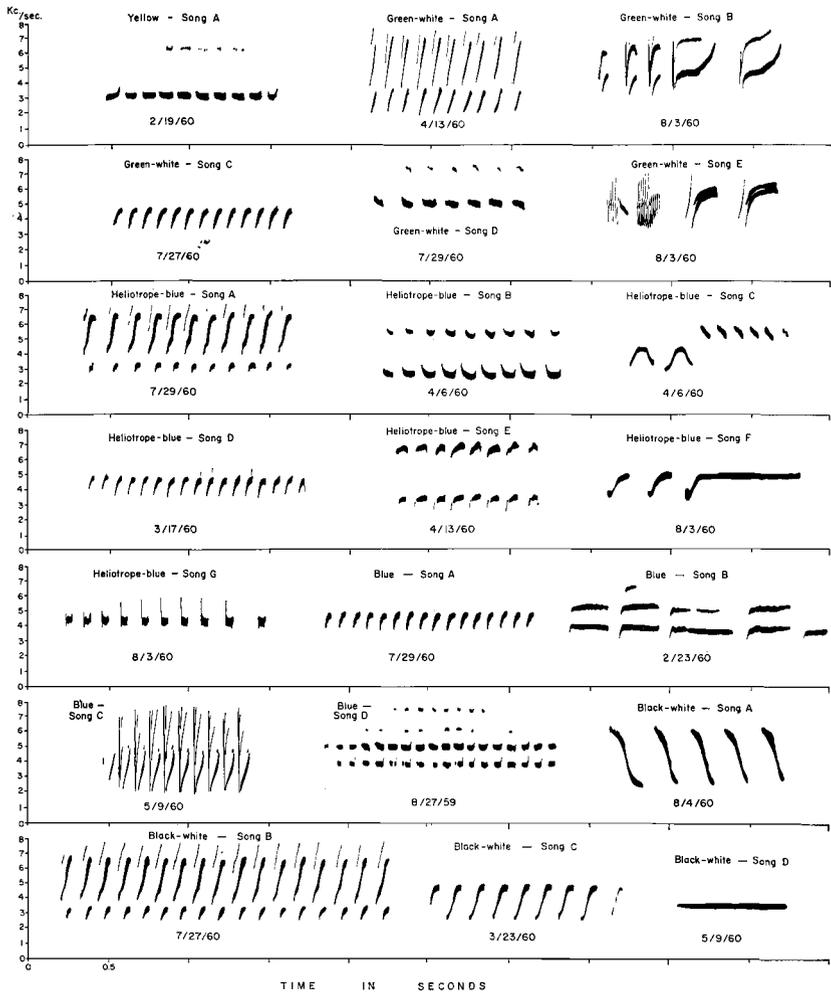


Figure 3. Time/frequency analyses of the final first-year songs of the five 1959 males: *yellow*, *green-white*, *heliotrope-blue*, *blue*, and *black-white*. The songs that bear least resemblance to those of wild juncos have been grouped to the right of the figure.

exclude these, the mean number only rises to a value of 10 syllables per song, which is still lower than that for the wild birds.

Correlated with this is the longer syllable duration of the hand-raised birds. Even if we exclude the four most obviously abnormal syllable types, which are off to the right of the histogram (the three listed above plus the terminal syllable of *white*'s second song), the reduction of the mean value

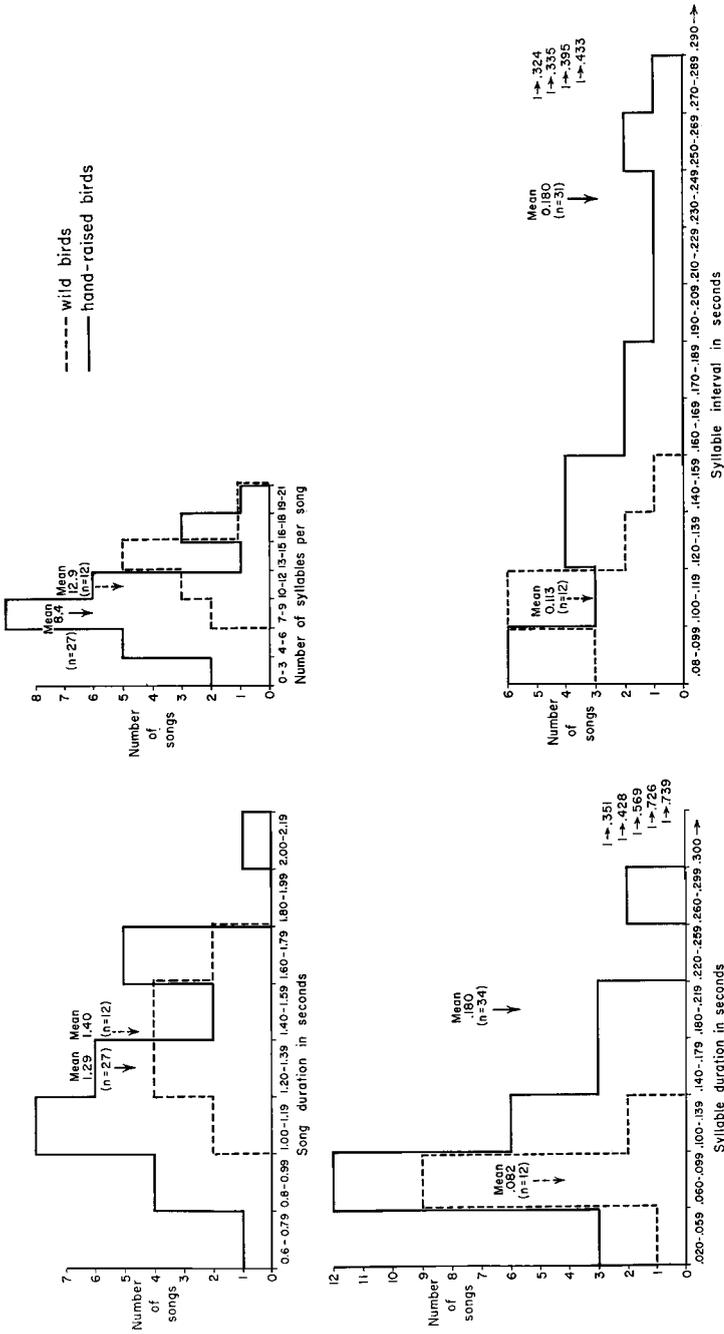


Figure 4. Histograms of song duration, syllable duration, syllable interval, and number of syllables per song in the songs of the wild juncos, and the final first-year songs of the hand-raised juncos.

from 0.180 to 0.107 second still does not achieve the lower value of 0.082 second for wild birds. Similarly, the intervals between syllables are longer in the hand-raised birds. We may conclude that there is a tendency for the songs of hand-raised birds to consist of a smaller number of syllables, and longer syllables as compared with wild birds, as well as being more variable in all of the measurements taken. However, there is considerable overlap, so that many of the hand-raised birds' songs are essentially indistinguishable from those of wild birds as far as these measures are concerned.

DEVELOPMENT OF SONG

The first year. The development of song in Oregon Juncos is intimately bound up with the so-called subsong, a long, rambling, and variable series of sounds, usually given at a lower intensity than the full song. Analysis of subsong on the sonagraph is very slow and tedious, and we are now applying the method described by Fish (1954), using a frequency meter and a pen-writing oscillograph, as an effective and quicker means of working with continuous vocalizations of this type. In the meantime we have made sonagrams of the separate, discontinuous songs of the 1959 birds that were interspersed in the subsong during the first winter and spring (or even in the first summer in one case) and later became the dominant form of song in spring and summer.

In several cases we have been able to trace the development of a song type during its winter and spring periods. Several themes, such as two from *black-white* and *heliotrope-blue* (Figure 5, top), passed through a phase with variable syllable structure, becoming more regular in the course of a few weeks. During these transitional phases, there was a tendency for the frequency of sustained notes to oscillate in an irregular manner. This can be seen in the two mentioned above, but is most obvious in the two abnormal songs of *blue* and *black-white* (Figure 5), where the long notes make the frequency oscillations most conspicuous. Thielcke-Poltz and Thielcke (1960) found a similar wavering quality in the developing songs of the European Blackbird, *Turdus merula*.

While development through a series of transitional phases in winter and spring seems to be common, it does not always occur. The most remarkable exception was *blue*, who produced, in August 1959, at an age of about three months, a fair version of what was to be his dominant song type throughout his first year. Several other song patterns seemed to appear more or less abruptly in their final form in the repertoire of different birds, although we cannot be sure that development through transitional phases may not have occurred in the subsong or even in full song. The hand-raised birds have the same habit as wild juncos of restricting

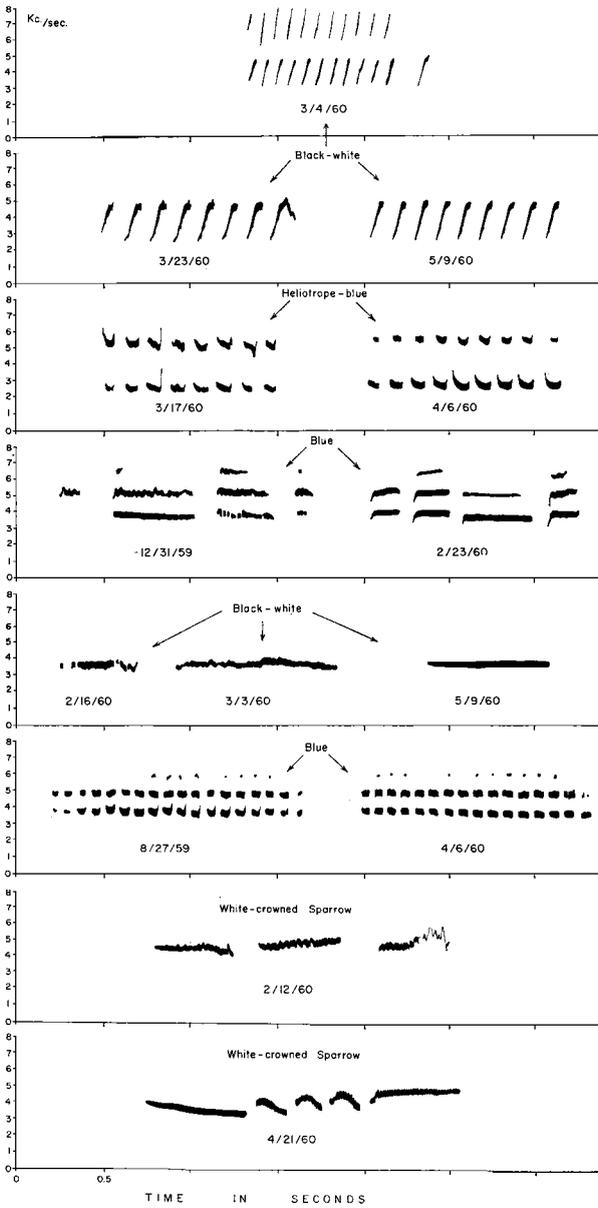


Figure 5. Time/frequency analyses illustrating changes in the songs of certain birds during the course of development. Two songs of hand-raised White-crowned Sparrows are illustrated at the bottom.

themselves to one theme from their repertoire for long periods, so that it is difficult to be sure that all existing themes are represented in recordings from any one date.

Learning from White-crowned Sparrows. As mentioned earlier, the 1959 birds were housed from May 1959 until July 1960 in an imperfectly insulated, soundproof booth. An adjacent booth contained a group of hand-raised White-crowned Sparrows of the same age. During this 14-month period the sparrows developed a variety of abnormal song types, sung with considerable volume. Two examples, selected to illustrate a characteristic developmental change in the White-crowned Sparrow songs, are shown at the bottom of Figure 5. The upper song, recorded in February, has a wavering quality resulting from irregular fluctuations in the frequency of the notes. In the lower song, from April, the frequency oscillations have become regular in the later part of the song and have disappeared from the early part. The disappearance of the irregular frequency fluctuations was seen in the course of development of most of the White-crowned Sparrow songs, although the change occurred at different times during late winter and early spring in different birds.

It appears that these songs must have been audible at times to the 1959 Oregon Juncos. Three of the six "abnormal" songs of the 1959 juncos bear strong resemblance to the White-crowned Sparrow songs and can probably be ascribed to learning from them (Figure 3, *heliotrope-blue*, song F; *blue*, song B; *black-white*, song D). We have no evidence that these are precise, complete copies of particular White-crowned Sparrow songs. Rather, the general characteristics of some of the individual notes seem to have been imitated. The complete lack of notes of this type in the songs of wild juncos and of the 1958 hand-raised birds reinforces our conclusion that they must have been acquired in this way. There are even parallels in the junco songs with the change from a wavering quality to a more steady tone, which we have described in the White-crowned Sparrows (Figure 5, *black-white* bottom). However, there is a suggestion of a similar change in the development of the normal junco songs (Figure 5, *black-white* top, *heliotrope-blue*) so that we cannot ascribe the effect to the influence of the sparrow songs alone.

Song development in yellow after exposure to green. The 1959 male *yellow* was removed from the soundproof box on 17 March 1960 and placed in a separate room with male *green* from 1958. Both birds were in full song and continued to sing against each other until the end of July when they were separated. At this time *green's* two themes from 1958 still persisted, and a third had been added before exposure to *yellow* (Figure 6, *green*, songs 1, 2A, B, 3A, B). *Yellow* at this time was using only one song type (Figure 3, *yellow*, song A) so far as we know.

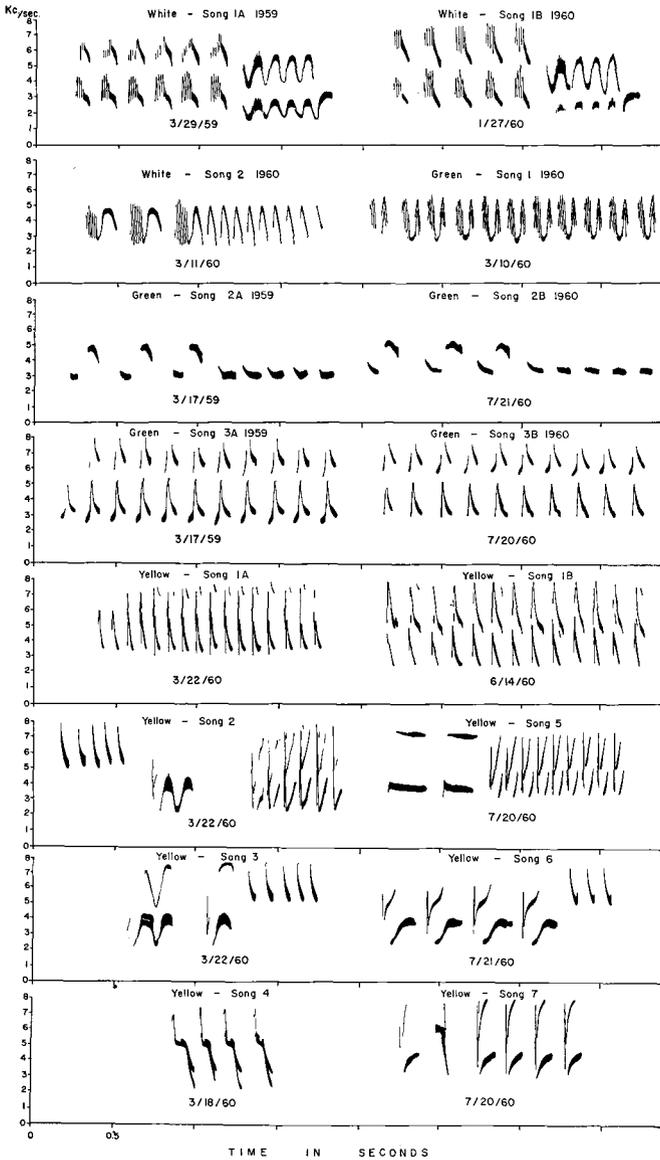


Figure 6. Top. Time/frequency analyses of songs of *white* and *green* in their first and second years. Bottom. Songs of male *yellow* that developed after removal from the soundproof room and exposure to the songs of male *green*.

Within a week *yellow* had produced several new song themes. Two of them settled down rather quickly to a regular pattern (Figure 6, *yellow*, song 1A, 4). Song 4 bore no resemblance to any of *green's* songs. Song 1A resembled *green's* song 3B and in the course of time came to match it even more closely (*yellow*, song 1B). In addition, *yellow* also began a series of variable songs in the first week containing several different components in a variety of arrangements; two of these are shown in Figure 6 (*yellow*, songs 2, 3). By July *yellow* had developed three more regular song patterns, each with more than one syllable type (*yellow*, songs 5-7). Several of these syllables seem to have been derived from the components of the variable March song, as suggested by comparison with songs 2 and 3 in Figure 6. There is no detailed correspondence between any of these and the syllable types used by *green*. If we are justified in ruling out maturation, or removal of the bird from a soundproof room to new environment as the significant factors, the implication seems to be that *yellow* was stimulated by *green* to develop new songs, perhaps partly through imitation of *green*, but mainly through renewed efforts at improvisation. We may note that these new songs of *yellow* reveal a greater frequency of elaborate syllable types than was characteristic of the 1959 birds in general (cf. Figure 3), and approach the degree of complexity seen in the wild birds (Figure 1).

Second-year song. We have been able to study the songs of the three 1958 males through a second year. *Green* retained both of his 1959 songs in 1960 with virtually no change (Figure 6, *green*, songs 2A, B; 3A, B). These remained his most frequent song types, but he did add another (Figure 6, *green*, song 1), presumably in the early spring of 1960. *White* retained one 1959 song in 1960 with only a slight change in emphasis of overtones in the second part of the song (Figure 6, *white*, songs 1A, B). The other 1959 song has either dropped out or, more likely, has become very uncommon. We think that we heard it several times in 1960 but have been unable to record it. *White* also added a new song in 1960, the first part of which bears some resemblance to *green's* new song (Figure 6, *white*, song 2; cf. *green*, song 2).

The third 1958 male, *yellow-blue*, showed more drastic changes in 1960. One song disappeared (Figure 2, *yellow-blue*, song 2). The other was modified by the increased emphasis of an overtone, and by the addition of a new second part (Figure 7C). Two new songs were also added, both with two syllable types (Figure 7A, B). The first part of song A resembles *green's* song 1 (Figure 2). The second part resembles the corresponding portion of one of *white's* songs (Figure 2, *white*, song 2; also Figure 6, *white*, songs 1A, B). This suggests that *yellow-blue* may have imitated these other birds. However, we have found that the same ele-

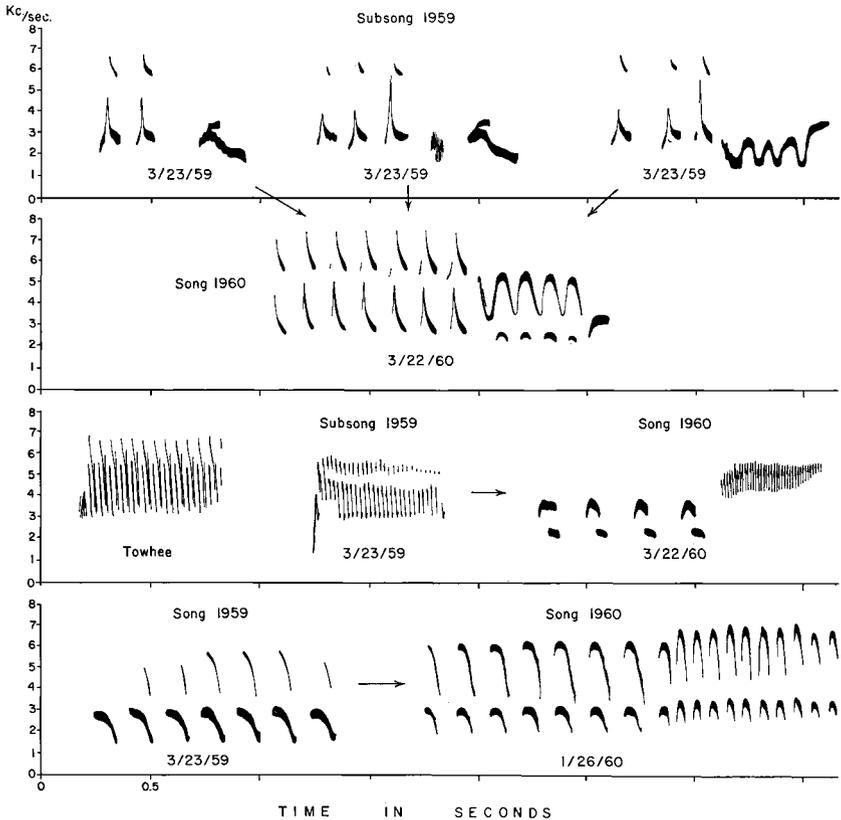


Figure 7. Time/frequency analyses of subsong and songs of male *yellow-blue* in his first and second years.

ments were also represented earlier in *yellow-blue*'s subsong, where we had the impression that they were acquired during the first winter through imitation of some phrases of House Finch song, which they resemble (Figure 7, line 1). Apparently they remained in the subsong in 1959 and only in 1960 appeared as a full song, perhaps partly under the stimulus of the rather similar song of *white*.

The other 1960 song of *yellow-blue* has a similar history. In the first winter, 1958-1959, this bird produced a clear imitation of a Rufous-sided Towhee singing in the garden (Figure 7, line 3). The original towhee song was not recorded, but Figure 7 shows an example from another part of California. In 1959 this imitation was restricted to the subsong. Only in 1960 was it incorporated into a regular full song (Figure 7, line 3), the original imitation still persisting in the subsong.

It is clear then that the song patterns are by no means fixed after the first year of life. While some themes remained virtually unchanged in the second year, others were modified, and new ones added or constructed in some cases from elements that were already present in the subsong of the first year.

DISCUSSION

The song of wild Oregon Juncos has several distinctive properties. It consists, with rare exceptions, of a trill of similar, repeated syllables. The length of the song, the number of constituent syllables, and the duration of those syllables vary relatively little. The fine structure of the syllables themselves shows great individual variability. Each individual has several song types, one of which may be given for long periods without interruption by another type. Our problem is to explain the ontogenetic basis of these various properties of the song.

Genetic factors. Until we have done controlled breeding experiments and raised birds of known parentage from the egg in strict isolation we cannot determine unequivocally the role of genetic factors in song development. A trill of normal, although more variable, over-all characteristics was produced by seven males raised out of hearing of adult birds of their own species after an age of six to 10 days from hatching. There is no reason to think that auditory experience of the song of wild birds before this age had any effect on subsequent song development (cf. Thorpe, 1959), but the possibility should be investigated.

Both the 1958 and 1959 birds were exposed to songs of alien species. However, the 1959 birds, which showed a greater incidence of "normal" songs, heard only hand-raised White-crowned Sparrows. The effect of these sparrow songs is evident in the abnormal songs of the 1959 birds, but cannot be seen in the normal songs. While the sparrow song may have had an unspecific stimulating influence on the juncos, it seems unlikely that the actual pattern of the normal junco singing was affected by it. Further experiments are needed to confirm that the over-all pattern of normal Oregon Junco singing is inherited. The developmental basis of the detailed syllable structure still remains to be explained.

Diversity of syllable structure is a prominent characteristic of wild Oregon Junco songs. It also occurs to a lesser extent in the hand-raised birds. Each of the three sibling 1958 males had a different syllable structure in all of his first-year songs, both normal and abnormal. In fact, in the 11 song types that these birds eventually produced in two years, comprising altogether 17 syllable types, there were only two cases of close correspondence between birds: the second parts of *white*, song 2 (Figure 2), and *yellow-blue*'s 1960 song (Figure 7, line 2); and between the beginning of the latter and *green*, song 1 (Figure 2). The diversity of syl-

lable types in the 1959 birds was less striking than in the 1958 birds, and, moreover, the three siblings, *black-white*, *green-white*, and *heliotrope-blue*, each share one common pattern, although different in other songs of their repertoires.

Basis of syllable diversity. The contrast in degrees of syllable diversity between the sibling males of 1958 and 1959 may give a clue to its developmental basis. The auditory environment of the 1958 birds was much richer than that of the 1959 birds. Some birds may have actually imitated some of the sounds that they heard. We have seen how male *yellow-blue* copied a Rufous-sided Towhee song and probably fragments of a House Finch song, and incorporated them into full songs in the second year. Male *yellow* from 1959 produced a much wider variety of complex syllable types after removal from the soundproof room and exposure to the songs of the 1958 male *green* (Figure 6). One of these closely resembled one of *green's* songs in syllable structure, and presumably was copied from him. Thus it seems clear that Oregon Juncos have the ability to learn to copy syllables of another bird's song rather closely.

However, this alone cannot explain the diversity of syllable types in the hand-raised birds. If syllable types developed only through imitation, we should have expected the two groups of 1958 and 1959 birds to have each converged on a common type, as described, for example, by Thorpe (1959) in the Chaffinch and by Thielcke-Poltz and Thielcke (1960) in the Blackbird. If different birds sang at different times or seasons, this could disrupt such a tendency to some extent, but surely not sufficiently to cause the great diversity we have observed.

It also seems unlikely that the different syllable types are under precise genetic control. The first results with the 1958 birds suggested the possibility of genetically controlled polymorphism, which would also explain the great diversity of syllable types in wild birds. The songs developed by the 1959 birds were not consistent with this interpretation. The three sibling males shared a similar song type (Figure 3, *green-white*, song A; *heliotrope-blue*, song A; *black-white*, song B). This might suggest an expression of a similar genotype. However, there was another song type shared by unrelated birds in the 1959 group (Figure 3, *green-white*, song C; *heliotrope-blue*, song D; *blue*, song A; and perhaps *black-white*, song C). Either the birds learned from each other, or, perhaps, this is a basic inherited song type.

Without further experiments we can only speculate about the probable basis of the syllable diversity. Genetic factors probably establish the broad, temporal pattern of the song as a sequence of similar, repeated syllables with a certain approximate duration. They may also lead toward the development of several themes, each of which is given in long series

without interruption. They may also set limits on syllable structure. These limits are approximate and appear to be exceeded under the artificial conditions of captivity in a soundproof room. By themselves they do not provide an adequate basis for development of completely normal syllables of wild Oregon Junco song. Instead, they result in the simpler, rather longer syllable types seen in many of the 1959 songs. A richer sound environment is required for normal development. Probably the song of other wild juncos is not an absolutely necessary component in the auditory environment for normal development, although songs of other juvenile juncos may play an important role. Whatever the components may be, their effect upon development is not normally achieved by direct, precise imitation of them by the young bird, although this can occur. Generally, the effect seems to be a less specific one, involving, as well as imitation, an encouragement of what may be called vocal "improvisation" or "invention."

If the auditory environment is greatly simplified, the few sounds that are heard seem to have a more dominant influence. The White-crowned Sparrow songs, which wild juncos in the Berkeley area hear constantly without obvious effect, evidently induced the development of grossly abnormal syllable types in some of the 1959 birds. This abnormality was expressed by long duration as well as by simplified internal structure. In the richer sound environment that occurs in nature, other sounds conforming more closely to the wild syllable type must assume a more dominating influence. This seems to imply a mechanism for focusing the Oregon Junco's attention on a certain limited range of external sounds during song development. The selection may be based on approximate conformity to the simple inherited song pattern or may involve other behavioral mechanisms at present unknown. A bond between father and son in the winter and early spring might play a role, as Nicolai (1959) noted in the Bullfinch (*Pyrrhula pyrrhula*), or the tonal quality of the sounds might be significant, as suggested for the Chaffinch (Thorpe, 1959).

The occurrence of songs with two syllable types. Two of the 1959 birds and all of the 1958 birds included within their repertoires songs that were abnormal in the use of two syllable types in the same song. It seems likely that the greater incidence of these two-part songs, especially in the 1958 birds, is the result of a crude kind of imitation. Many species include several trills in their songs at different pitches, and the House Finches, to which the 1958 birds were exposed, may well have had such an influence, without the juncos necessarily copying the exact syllable types that were used. Here the element of improvisation seems to come in again.

No critical period. These two capacities for improvisation and learning are evidently not restricted to any particular phase of the life history.

One bird developed a roughly normal song in August at an age of three months. Others produced new themes through the first spring of life. One 1959 bird, *yellow*, removed from the soundproof room in March 1960 and placed with an older bird, developed four new song types in the following three months. And we have seen that all of the 1958 birds produced new songs in their second year. There is thus no critical period in the life history for the development of song as seems to be the case, for example, in the Chaffinch (Thorpe, 1959). However, we have no idea whether wild birds retain the capacity to add new songs in this fashion. This is one of the several questions about Oregon Junco song that we hope to answer in the coming years.

ACKNOWLEDGMENTS

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SUMMARY

Eight male Oregon Juncos were taken from the nest and raised by hand in varying degrees of acoustic isolation. Each developed several song types. In comparison with wild juncos, the songs of the experimental birds were somewhat longer, with fewer, longer syllables. They were more variable. However, there was appreciable overlap, so that each male had at least one "wild-type" song. Some abnormal songs developed from imitations of other species. In addition, the birds raised in a rich auditory environment had more song types and a more elaborate syllable structure, derived not from imitations but from unspecific stimulation to improvise. Vocal inventiveness is established as a significant factor in the development of song in Oregon Juncos.

LITERATURE CITED

- FISH, W. R. 1954. A method for the objective study of bird song and its application to the analysis of Bewick Wren songs. *Condor*, **55**: 250-257.
- MARLER, P. 1952. Variation in the song of the Chaffinch *Fringilla coelebs*. *Ibis*, **94**: 458-472.
- MARLER, P., and D. ISAAC. 1960. Song variation in a population of Brown Towhees. *Condor*, **62**: 272-283.
- NICOLAI, J. 1959. Familientradition in der Gesangentwicklung des Gimpels (*Pyrrhula pyrrhula* L.). *J. Ornith.*, **100**: 39-46.
- PETERSON, R. T. 1941. A field guide to western birds. Houghton Mifflin Co., Boston. 240 pp.

THORPE, W. H. 1959. Talking birds and the mode of action of the vocal apparatus of birds. *Proc. Zool. Soc. Lond.*, **132**: 441-445.

THIELCKE-POLTZ, H., and G. THIELCKE. 1960. Akustisches Lernen verschiedener alter schallisolierter Amseln (*Turdus merula* L.) und die Entwicklung erlernter Motive ohne und mit künstlichem Einfluss von Testosteron. *Z. f. Tierpsychol.*, **17**: 211-244.

Department of Zoology, University of California, Berkeley, California.