SEASONAL CHANGES IN BILL LENGTH OF CERTAIN PASSERINE BIRDS

By JOHN DAVIS

Seasonal changes in bill length in passerines have been largely ignored by taxonomists. However, some workers have been aware of the possibility that seasonal changes in diet may be reflected in variation of bill length. For example, Miller (1941:183) noted that a Nevada population of the Gray-headed Junco, *Junco caniceps caniceps,* was significantly shorter-billed than a Utah population. He suggested that the difference in bill length might have been the result of diet, since the Nevada birds had been kept from their montane breeding grounds by late snows and were feeding on seeds on barren ground whereas the Utah birds were nesting and were feeding on insects. Marshall (1948:247) noted that bills averaged longer in older series of the Song Sparrow, *Passerella melodia,* taken at San Pablo Bay, California, than in recently collected series from that locality. He stated: "The old collections from San Pablo Bay contain many late summer specimens with long bills, which I believe have grown out due to changes in food utilized at that season." Clancey (1948) reported that bills of specimens of the European Tree Sparrow, *Passer montanus,* taken in late May, June, and July were noticeably attenuated, whereas the bills of specimens taken in autumn and winter were much shorter. Whereas Miller and Marshall implied a direct effect of diet on bill length, Clancey felt that the longer bills of summer specimens were "presumably . . . more advantageous in the rapid acquisition of insect larvae, imagines, etc., upon which the young are reared." He found evidence of the same type of seasonal change in the English Sparrow, *Passer domesticus,* but did not have enough summer specimens to prove this conclusively.

In this study, certain species of passerines were selected which ingest significant amounts of insect material during the spring and summer, and subsist almost entirely on vegetable matter during the autumn and winter. These species were: the Scrub Jay, *Aphelocoma coerulescens,* represented by the subspecies *obscura* and *insularis*; the English Sparrow, *Passer domesticus,* represented by samples drawn from the populations of Berkeley and Los Angeles, California; the Brewer Blackbird, *Euphagus cyanocephalus*; the Tri-colored Blackbird, *Agelaius tricolor*; the Red-winged Blackbird, *Agelaius phoeniceus,* represented by the subspecies *californicus* and *nevadensis*; the Brown Towhee, *Pipilo fuscus,* represented by the subspecies *carolae, petulans, senicula, albigula,* and *mesoleucus*; the Sierra Nevada Oregon Junco, *Junco oreganus thurberi*; the Chipping Sparrow, *Spizella passerina,* represented by the subspecies *arizonae* and *mexicana*; and the Song Sparrow, *Passerella melodia,* represented by the subspecies *morphna, gouldii, cooperi,* and *pectoralis.*

Since the diets of these species have been ascertained from detailed analyses of stomach contents, the records available represent the actual consumption of food by individuals regardless of what these individuals might feed to their young during the breeding season. The nature of the diets of the selected species was determined from analyses of stomach contents as reported by Barrows (1889), Beal (1910), Kalmbach (1940), and Soriano (1931).

Bills were measured from the anterior edge of the nostril to the tip in winter- and summer-taken samples of each population. The measurements were treated statistically in samples of 10 or more when seasonal averages differed so widely as to indicate possible significance. Winter samples were composed of birds taken in December and January when sufficient material was available. First-year and adult birds were not separated, since it was assumed that the bill is full-grown in first-year passerines by De-

cember. This is true of *Pipilo fuscus* (Davis, 1951:5) and *Passerella melodia* (Marshall, 1948:242). When winter specimens taken earlier than December were included, only adults were used. Summer samples were collected in May, June, and July.

In addition to species which change their diets seasonally, winter and summer samples of the House Finch, *Carpodacus mexicanus frontalis,* collected in California, were measured as a control. According to Beal (1907:17, 18) this species lives almost entirely on weed seeds and fruit in California, and does not ingest more than a trace of animal matter at any time of year. Further, analyses of the stomach contents of nestlings indicate that the adults feed the young a diet that is similar to their own. The measurements of all species are presented in table 1.

DISCUSSION

Examination of the figures presented in table 1 shows a definite tendency toward increase in bill length in summer in all species except *Carpodacus mexicanus* and *Aphelocoma coerulescens*. The latter species has dietary peculiarities which will be discussed later in this paper. Although many of the average differences between winter and summer samples are not statistically significant, the tendency toward increase in bill length in summer in nearly all samples is biologically significant. This biological significance is enhanced by the fact that seasonal changes in bill length are evident in samples of both males and females in the populations analyzed.

Two explanations for increase in bill length in summer may be suggested. First, it may be a secondary sex character. The bills of the English Sparrow, especially of the male, and of both sexes of the Chipping Sparrow undergo marked color changes during the breeding season. In the English Sparrow this color change has been demonstrated to be under the control of the male hormone (Keck, 1932), and it is possible that changes in bill configuration are under similar control. However, increase in bill length is more pronounced in the Song Sparrow than in any of the other species studied, and there is no seasonal change in bill color in this species. Therefore it seems unlikely that increase in bill length is associated with reproductive physiology.

Second, it may be that seasonal changes in bill length are associated in some way with seasonal changes in diet. Support is given this idea by the fact that, with the exception of the Scrub Jay, bills average longer in summer samples of all the species which ingest large numbers of insects in the spring and summer, but do not in the one species which never eats insects in large amounts, the House Finch.

If the bill does respond to seasonal variation in diet, three possibilities must be considered. First, increase in bill length in summer is of adaptive significance in that it enables parent birds to catch more easily the insects that are to be ingested, or fed to the young, as suggested by Clancey (1948). This seems unlikely because of the variability in the degree of seasonal differences between samples of the same species, or subspecies. Thus, in *Pipilo fuscus,* in the races *carolae* and *albigula,* the average differences between summer and winter males are of such low order that the samples may be considered identical. In *P. f. petulans* the average difference between summer and winter males is significant. In *Spizella passerina mexicana* the difference between seasonal samples of males is significant, whereas it is so low between the female samples that they may be considered identical. Such wide amplitude of variation suggests that seasonal variation in bill length is influenced by some variable environmental factor rather than by the genetic make-up of the individual. The seasonal appearance of insects, which make up most of the animal portion of the diets of the species studied, would be just such a variable factor, depending in large part on the time of onset of rising spring temperatures. A case in point is that of *Junco c. caniceps* as described by Miller (1941). Had it not been for late snows, the short-billed Nevada birds would have been on the

breeding grounds and subsisting on insects rather than on seeds. It is possible that had the unseasonal snows fallen in the Utah breeding grounds, the situation would have been reversed. If seasonal change in bill length were under genetic control, annual variation in environmental factors would be of little importance, and the degree of difference between seasonal samples would probably be less variable. In my opinion, any advantage given by longer bills in summer is purely coincidental.

A second possibility is that the bills elongate because of the higher intake of animal protein during the summer. This possibility cannot be dismissed until checked by controlled feeding experiments.

The third possibility is that seasonal change in bill length is merely a reflection of the mechanical wear on the constantly growing bill tip caused by different foods. When

Table 1

Seasonal Differences in Bill Measurements

Season	Sex	Number	Mean	Standard error	Number	Mean	Standard error
		Aphelocoma c. obscura			*Aphelocoma c. insularis*		
Winter, adults	♂	7	21.00	.....	20	23.86	0.22
April, adults	♂	14	20.04	0.16	13	22.85	0.17
April, 1st year	♂	10	19.10	0.32	18	23.07	0.19
Summer, adult and 1st year	♂	9	19.30	.....	15	23.49	0.28
Winter, adults	♀	8	18.31	.....	22	22.07	0.29
April, adults	♀	....	.....	.....	10	21.96	0.17
Summer, adult and 1st year	♀	16	17.76	0.21	6	22.88	.....
		Passer domesticus, Berkeley			*Passer domesticus*, Pasadena		
Winter	♂	12	9.29	0.10	15	9.41	0.13
Summer	♂	14	9.69	0.10	14	9.97	0.11
Winter	♀	11	9.21	0.10	14	9.29	0.11
Summer	♀	11	9.55	0.11	10	9.63	0.10
		Euphagus cyanocephalus			*Agelaius tricolor*		
Winter	♂	24	13.83	0.14	10	16.56	0.34
Summer	♂	22	15.01	0.18	20	17.05	0.20
Winter	♀	22	12.82	0.14	11	13.95	0.17
Summer	♀	22	13.30	0.17	26	14.26	0.16
		Agelaius p. californicus			*Agelaius p. nevadensis*		
Winter	♂	11	15.39	.....	20	16.23	0.18
Summer	♂	27	15.60	.....	25	16.74	0.18
Winter	♀	24	12.48	0.11	12	13.30	0.24
Summer	♀	24	12.92	0.14	25	13.92	0.12
		Carpodacus m. frontalis			*Pipilo f. carolae*		
Winter	♂	25	8.26	.....	25	10.96	.....
Summer	♂	25	8.20	.....	49	11.01	.....
Winter	♀	23	8.25	.....	19	10.73	0.12
Summer	♀	18	8.15	.....	27	10.96	0.09
		Pipilo f. petulans			*Pipilo f. senicula*		
Winter	♂	27	10.43	0.07	19	9.89	0.08
Summer	♂	16	10.89	0.10	17	10.15	0.13
Winter	♀	18	10.36	0.08	11	9.66	0.12
Summer	♀	12	10.67	0.12	10	10.17	0.12
		Pipilo f. albigula			*Pipilo f. mesoleucus*		
Winter	♂	12	10.63	.....	24	10.43	0.08
Summer	♂	21	10.64	.....	33	10.83	0.07
Winter	♀	12	10.43	0.10	20	10.37	0.07
Summer	♀	20	10.63	0.06	10	10.71	0.20

Table 1 *(continued)*

Season	Sex	Number	Mean	Standard error	Number	Mean	Standard error
		Spizella p. mexicana			*Spizella p. arizonae*		
Winter	♂	13	7.15	0.08	15	7.15	0.09
Summer	♂	26	7.49	0.06	26	7.44	0.06
Winter	♀	10	7.21	.....	13	6.99	0.07
Summer	♀	15	7.24	.....	25	7.29	0.07
		Passerella m. morphna			*Passerella m. gouldii*		
Winter	♂	17	8.74	0.08	20	8.41	0.07
Summer	♂	26	9.27	0.08	27	9.14	0.06
Winter	♀	20	8.65	0.08	14	8.49	0.07
Summer	♀	25	9.22	0.04	17	8.95	0.08
		Passerella m. cooperi			*Passerella m. pectoralis*		
Winter	♂	21	8.39	0.06	8	9.24	.....
Summer	♂	22	8.79	0.07	13	9.85	0.06
Winter	♀	6	8.10	.....	8	9.15	.....
Summer	♀	16	8.53	0.07	3	9.50	.....
		Junco o. thurberi					
Winter	♂	25	7.78	0.06	....	.....	.....
Summer	♂	25	7.98	0.06	....	.....	.....
Winter	♀	25	7.74	0.05	....	.....	.....
Summer	♀	25	7.92	0.06	....	.....	.....

foods with a highly abrasive effect are consumed in large amounts, the bill tip is worn down, and when such foods are taken in smaller amounts, the bill tip tends to elongate. Except for the Scrub Jay, all the species studied which consume insects in the summer subsist primarily on weed seeds and/or grain during the winter. During the summer appreciable amounts of insect material are eaten with a concomitant decrease in seed consumption. Increased consumption of insects could reduce wear on the bill tip in two ways. First, soft-bodied insects such as aphids, and soft-bodied insect larvae, would have less of a wearing effect on the bill tip than would hard-shelled seeds. Secondly, the individual items of food are larger when the birds are eating insects, and the bill tip would thus be used less frequently in the course of gathering food than when the birds are obtaining weed seeds or grain. These factors would be partially minimized during parts of the summer months when parents would be foraging for their nestlings or fledglings as well as for themselves. However, in most passerine species the young are fed a diet rich in animal matter. Foraging for the young would be of more importance in a species such as the House Finch, which feeds its young a diet composed almost entirely of weed seeds. Although this species never includes more than a trace of animal matter in its diet, it does have a seasonal change in diet. According to Beal (1907:18), fruit constituted between 13.4 and 27.4 per cent of the diet from June through October, and between 0.0 and 8.3 per cent from November through May. Since fruit would probably induce less wear on the bill tip than the weed seeds which made up almost the entire remainder of the diet, some increase in bill length might be expected during the summer and early fall, when consumption of fruit is increased. However, analysis of the stomach contents of 46 nestlings (*op. cit.*:21) indicated that 97.6 per cent of their diet was weed seeds. Although actual consumption of weed seeds by breeding adults and first-year birds may have been less from June through October, parents were gathering large quantities of this food for their young during much of this time, and this probably offset the reduced amount of wear put on the bill by the summer diet. Some increase in bill length might be expected in September and October, when fruit is still being eaten in significant amounts and the young are no longer dependent on the parents. The fact that bill length

averages very slightly longer in the winter samples of both sexes (table 1) may be a reflection of autumnal bill growth.

The peculiar pattern of seasonal change in bill length in the Scrub Jay lends support to the hypothesis of mechanical wear. In the analysis of bill length variation in this species, winter samples were made up of adults only, since Pitelka (1951:199) has indicated a tendency for the bills of adult *Aphelocoma* to measure longer than the bills of first-year birds. The measurements of April samples of adult and first-year male *A. c. insularis* indicate that first-year birds attain full bill growth by April at the latest, and first-year birds, when available, were included in spring and summer samples of *A. c. obscura* and in summer samples of *insularis*. It will be noted (table 1) that in the males of *obscura*, the bill steadily decreases in length from September through April, and begins to elongate in summer. In both males and females of this subspecies, the bill is longer in winter than in summer. In *A. c. insularis* the pattern is similar in both sexes in that the bill decreases from winter through April, and elongates in summer. In the males of *insularis*, the summer bill has not yet become as long as the winter bill, but in the females it is longer. The fact that the bill is longer in winter than in summer in three of four samples appears at first glance to reverse the trend established in those species with seasonal change in diet. However, this may very possibly be explained by the fact that the Scrub Jay subsists during the fall and winter primarily on acorns rather than on seeds, and during the late spring and summer primarily on fruit and animal matter. In the stomach contents analyzed by Beal (1910:54) acorns varied between 0.19 and 2.22 per cent of the total diet from May through August. In September acorns made up 31.65 per cent of the diet, from October through February between 66.29 and 88.57 per cent, in March 27 per cent, and in April, 24.75 per cent. Fruit was consumed mainly from May through August, forming between 44.94 and 61.41 per cent of the diet. These figures for fruit are probably high for the species in California, as Beal (*op. cit.*:51) stated that as many of his specimens as possible were collected near buildings and orchards. Consumption of animal food was greatest in April (70.25 per cent) and then gradually decreased to a minimum of 5 per cent in January. From May through August animal matter formed between 32.53 and 36.45 per cent of the diet.

The pattern of seasonal variation in bill length in the Scrub Jay may possibly be explained by the great amount of wear on the bill tip involved in pounding and cracking acorns and extracting the meats from the broken husks. When the diet is low in acorns and high in fruit and animal matter, the bill probably elongates. This period of growth would last from May through August, during which month the bill would presumably reach maximum size. In September, when acorns, animal matter, and fruit are consumed in significant amounts (31.65, 24.20, and 19.89 per cent, respectively) the bill probably remains at, or near, the maximum. Heavy wear is put on the bill starting in October and continues through the winter. Thus in male *obscura* the September-October sample averages longer than the winter sample. The bill probably reaches minimum length in February, the last month during which acorns are eaten in large amount. In March, the birds are on a diet which is still mainly vegetable, and the bill probably remains at, or near, the minimum. In April, with consumption of animal matter at its high for the year, there may be some elongation, although this would be slight because one-fourth of the diet is still acorns. Thus, the March-April samples in male *obscura* and in both sexes of *insularis* average shorter than the winter samples. Pronounced and steady bill growth presumably occurs from May through August, when acorns are eaten in small amounts and fruit and animal matter form the bulk of the diet. Thus, the summer samples in male *obscura* and in both sexes of *insularis* average longer than the March-April samples. In both sexes of *obscura*, and in male *insularis*, the summer sam-

ples, based on specimens taken in May, June, and July, do not average as long as the winter samples, although pure samples of late summer birds would probably average longer than the winter samples. In female *insularis* the summer sample has surpassed the winter sample in average length.

In brief, it appears as though the unusual amount of wear imposed on the bill tip by the acorn-rich winter diet postpones the attainment of maximum bill length in the Scrub Jay until late summer, whereas in the other species considered, in which the wear engendered by the winter diet is less severe, the bill surpasses the winter average earlier in the summer. The peculiar pattern of seasonal bill change in the Scrub Jay, and the probable correlation of this pattern with the unusually abrasive winter diet of this species, suggests that seasonal changes in bill length in the species treated in this paper result directly from the mechanical wear on the bill tip caused by different foodstuffs which are eaten at different times of the year.

Seasonal change must be taken into account in the analysis of geographic variation in bill length in species which change the diet seasonally. For example, Lack (1940) analyzed variation in bill length in *Passer domesticus* from various localities in North America, using the bills of black-throated males without regard for age or seasonal variation. This species is one in which there is marked seasonal change in bill length; and in order to be strictly comparable, samples should be composed of either winter or summer specimens. Lack found that bill length in a sample from southern California and Baja California averaged significantly longer than in samples taken elsewhere in North America. He concluded that some evolution might have taken place in this species since its arrival in southern California. In the present study samples were analyzed from Berkeley, California, one of Lack's localities, and Pasadena, California. The latter sample takes in only a small part of the total geographic area included in Lack's southern California and Baja California sample, since this included birds taken as far north as Fresno County, and as far south as Baja California. The samples used in this study are much smaller than Lack's, because of geographic restriction, seasonal segregation, and the elimination of fall specimens. If summer samples from Pasadena are compared to winter samples from Berkeley, the average differences in bill length are significant in both sexes. If samples are compared on a seasonal basis, the Pasadena samples average longer, but not significantly so. Thus, the variation described by Lack should be checked in large series of seasonally comparable specimens before any conclusions are drawn.

In addition to seasonal change in bill length in the English Sparrow, there is also increased downgrowth of the tomia of the upper mandible in some birds in spring and summer. This growth results in the formation of prominent flanges on the central portions of the upper tomia which overlap the lower mandible by as much as one millimeter. In some birds these flanges are produced bilaterally, and in others there may be only one such flange, on either side. Of 52 individuals either breeding or coming into breeding condition, trapped near Pasadena between March 14 and July 15, 1953, six (11.5 per cent) bear such flanges on the bill. Of these, three are male and three are female. Of the males, two bear a single flange on the left side, and one bears a single flange on the right side. There may be some yearly variation in the frequency of occurrence of individuals with tomial downgrowth, since it appeared in none of 25 breeding adults trapped near Pasadena between June 3 and July 31, 1952. Three juveniles, one male and two unsexed, with bilateral flanges, were trapped in May and July, 1953. One juvenal male with bilateral flanges was trapped on June 21, 1952. Many other juveniles were trapped in 1952 but were not examined for this character, so that no conclusions may be drawn as to the relative frequency of occurrence of tomial downgrowth in juveniles in 1952 and 1953.

It was thought advisable to check the validity of a recently named subspecies of the White-throated Towhee, *Pipilo rutilus parvirostris* Davis (1951:84). This race was differentiated from *P. r. rutilus* mainly on the basis of shorter bill length. Although nothing is known of the food habits of *Pipilo rutilus*, it is closely related to *Pipilo fuscus*, a species which, at least in California, has a definite seasonal change in diet. The bulk of the material on which *parvirostris* was based was taken between September and December, whereas the bulk of the series of the nominate race with which it was compared was taken between May and July. The average bill length of 12 male *parvirostris* taken in October, November, and December is 10.35 mm., of three taken in April 10.50 mm., and a single male taken in July has a bill 10.8 mm. long. The average bill length of seven females taken in October, November, and December is 10.26 mm., and of the two taken in July 10.70 mm. Nineteen male *rutilus* taken in May, June, and July have an average bill length of 11.15 mm., and a single male taken in December has a bill 10.2 mm. long. Twelve summer females average 10.62 mm., nine February females average 10.82 mm., and a single December female has a bill 10.4 mm. long. Unfortunately, summer samples of *parvirostris* and winter samples of *rutilus* are too small to indicate definitely seasonal changes in bill length within each race. The material at hand does indicate the possibility of such change. It is hoped that further collecting will provide sufficient material to settle this matter.

Another type of variation affected by seasonal change in bill length is the degree of sexual dimorphism. This is well exemplified by the four races of *Passerella melodia* (table 1). In each race, the bill of summer females averages longer than the bill of winter males. When the samples are compared on a seasonal basis it is seen that in all cases except one, winter *gouldii*, the male samples average longer than the female samples.

Thus, it is apparent that when critical analyses of variation in bill length are undertaken, the possibility of seasonal change must be considered. Even if there is no information on the diet of the particular species concerned, the largest available sample should be checked for evidence of seasonal bill changes.

SUMMARY

1. Summer increase in bill length is demonstrable in certain passerine species which eat significant amounts of insects in summer, but are almost entirely vegetarian in winter.

2. The most likely cause of increase in bill length in summer is the reduced amount of wear put on the constantly growing bill tip by a diet rich in insects.

3. Seasonal changes must be taken into consideration when analyses are made of geographic variation in bill length of species which have a seasonal change in diet.

LITERATURE CITED

Barrows, W. B.
1889. The English sparrow (*Passer domesticus*) in North America. U. S. Dept. Agric., Div. Econ. Ornith. and Mammal., Bull. No. 1:1-405 + map.

Beal, F. E. L.
1907. Birds of California in relation to the fruit industry. Part I. U. S. Dept. Agric., Biol. Surv. Bull., 30:1-100.
1910. Birds of California in relation to the fruit industry. Part II. U. S. Dept. Agric., Biol. Surv. Bull., 34:1-96.

Clancey, P. A.
1948. Seasonal bill variation in tree-sparrow. Brit. Birds, 41:115-116.

Davis, J.
1951. Distribution and variation of the brown towhees. Univ. Calif. Publ. Zool., 52:1-120.
Kalmbach, E. R.
1940. Economic status of the English sparrow in the United States. U. S. Dept. Agric., Tech. Bull. No. 711:1-66.
Keck, W. N.
1932. Control of the sex characters in the English sparrow, *Passer domesticus* (Linnaeus). Proc. Soc. Exp. Biol. and Med., 30:158-159.
Lack, D.
1940. Variation in the introduced English sparrow. Condor, 42:239-241.
Marshall, J. T., Jr.
1948. Ecologic races of song sparrows in the San Francisco Bay region. Condor, 50:233-256.
Miller, A. H.
1941. Speciation in the avian genus *Junco*. Univ. Calif. Publ. Zool., 44:173-434.
Pitelka, F. A.
1951. Speciation and ecologic distribution in American jays of the genus *Aphelocoma*. Univ. Calif. Publ. Zool., 50:195-464.
Soriano, P. S.
1931. Food habits and economic status of the Brewer and red-winged blackbirds. Calif. Fish and Game, 17:361-395.

Hastings Natural History Reservation, Carmel Valley, California, January 4, 1954.