DEVELOPMENT OF NESTLING WHITE-CROWNED SPARROWS IN CENTRAL COASTAL CALIFORNIA

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The White-crowned Sparrow (*Zonotrichia leucophrys*) is an abundant bird along the Pacific Coast. Although a survey of literature reveals many references to the White-crown, few major studies of the species have been made. Blanchard has been the chief worker and has described the general life history and breeding physiology (1941), behavior (1936, 1941), and migration (1942) of the western races of the species. Most work on the White-crowned Sparrow has dealt with adult birds. Blanchard (1941: 30–34) gives a brief description of the development of the young, but so far as I know there has been no other work done on nestling White-crowned Sparrows.

In this report, the nestling life of *Zonotrichia leucophrys nuttalli* will be described from the time of hatching to the time of fledging. The local race of the Song Sparrow (*Melospiza melodia gouldii*) was studied concurrently, but much less successfully; however, some comparative data are presented. Preliminary work was begun in 1956, but the report covers only the nesting season of 1957. All field work was done on and around the campus of the University of California, Berkeley.

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METHODS

The techniques of this study were fairly simple. Early in the nesting season birds were observed and territories of nesting pairs were noted. An effort was made to locate as many territories and to find as many nests as possible. Once a nest was found, a close watch was maintained through the incubation period, and the time of hatching of the eggs was determined. Twenty nests were observed during the breeding season of 1957.

When the young had hatched, they were observed twice daily. The birds were toe clipped for individual recognition at early ages. At every visit to the nest, each bird was weighed, general appearance and behavior were recorded, and the eighth primary was measured. Usually the young were color-banded before they left the nest.

The usual nest site was in a clump of shrubs or vines in an extensive area of shrubs. Occasionally an isolated bush was used. Shrubby areas along walls, fences, or buildings were preferred to equally dense areas away from such structures. The nest was normally quite close to the structure, often within a foot, even though suitable shrubbery extended over a larger area. A bank of higher bushes or trees seemed to be a good substitute for a wall. The selection of such nest sites may have been based only on availability; in a highly landscaped area, such as a university campus, most heavy shrubbery is near walls

or buildings. However, many hedges and shrubby areas away from these artifacts fulfilled, to my eyes, the needs of nesting White-crowned Sparrows, but they were not utilized. Blanchard (1941) notes that nests in isolated bushes were always near more extensive shrubbery, but she does not mention proximity to a wall as a factor in nest site location.

The male White-crown uses as many as three singing perches during nesting activities. It was noted that usually one of the perches was in high shrubbery, or atop a wall, almost directly over the nest. This circumstance aided substantially in locating nests in known territories.

APPEARANCE OF YOUNG

The following descriptions of young White-crowned Sparrows represent composite pictures. Individual variation occurs in the timing of the appearance of certain features. These descriptions are compiled from daily field notes and from young of known age collected and preserved in alcohol.

The ages are given in days. Despite the nightly fast, the rate of development in all respects except weight seemed to be fairly constant over a 24-hour period. The first number in parentheses indicates the number of field observations on birds of a given age; the second number refers to collected specimens of that age. More specimens were collected than are indicated later. Most were collected at the midpoint of the 24-hour interval used in calculating age. An attempt was made to collect at least one bird at each age considered. The actual number collected fell somewhat short of this goal, but a series without serious gaps was secured. All birds found dead in nests were preserved. In most instances the birds died at night, and their ages were recorded as that of the time of my last visit to that nest.

Age 0 days (18–1).—The transparent pink skin soon turns yellowish, and the mouth lining, originally a deep pink, turns bright red. Down is usually found on the coronal, occipital, dorsal, humeral, alar, and femoral tracts (terminology after Saunders, 1956:122). The amount and length of down on each tract varies from one individual to another. Faintly dark spots, indicating feather papillae, may be seen beneath the surface of the skin of most newly hatched young, on the alar (primaries), humeral, dorsal, and coronal areas. Spots in the primary region are often coalesced, appearing as a dark streak. Other feather tracts, especially the ventral tract, may be discernible in some individuals, but they are not dark.

Many other species at hatching show juvenal feather papillae marked by pigment. The robin, *Turdus migratorius* (Howell, 1942:571), Traill Flycatcher, *Empidonax traillii* (King, 1955:161), and House Sparrow, *Passer domesticus* (Weaver, 1942:183) are in this group. Conversely, the Tree Sparrow, *Spizella arborea* (Baumgartner, 1938:70) and the Black-capped Chickadee, *Parus atricapillus* (Odum, 1941:529) show little or no sign of developing feathers. Variation in respect to the degree of development of these feather papillae occurs in White-crowns, and presumably in other species.

Age 1 day (25–1).—After one day the spots representing the papillae of future primaries have, in all birds, become darker and have merged, giving the appearance of a dark streak along the forearm. On other tracts the previously noted spots are darker, and additional spots show. In some birds, also, darkening of the crural tract, usually as two rows of spots, becomes evident. The ventral tract is normally well evident but shows no darkening.

Age 2 days (25–0).—This stage is marked by the closer approach of the primary papillae to the surface of the skin, so that the skin shows a series of bumps. On a few two-day old birds the outer primaries have actually broken through the skin. Blanchard (1941:30) first noted this on the third day, but I found that in most birds the feathers protruded by 2½ days.

All previously mentioned tracts are now well marked with dark spots. In addition, the ventral tract is beginning to darken anteriorly, especially on the throat, where the parts of this tract join.

Age 3 days (23–0).—The inner primaries, secondaries, and alula soon follow the outer primaries in emerging from the skin; they are all out at three days, but of course still sheathed. Some of the greater primary coverts may also be out.

Interspecific variation may be seen in the order and time of appearance of feather sheaths. In the Traill Flycatcher, King (1955:161–162) recorded the secondaries as the first to break through the skin, with the pectoral (= ventral), spinal (= dorsal), and humeral tracts showing exposed sheaths before the primaries emerge. The Ovenbird (*Seiurus aurocapillus*) at this age shows feather sheaths on all tracts but the caudal (Hann, 1937:177). Three-day old robins have no feathers through the skin (Howell, 1942). An extremely rapid development occurs in the Summer Tanager, *Piranga rubra* (Fitch and Fitch, 1955) where by the third day the quills of the remiges measured 11.5 mm.

Age 4 days (14–2).—All greater coverts are out and a few lesser coverts are through the skin. The inner rows of sheaths along the anterior edge of the wing have emerged, as have some of those of the humeral tract. Some sheaths on the thigh (femoral tract) have erupted. At least part of the ventral tract shows sheaths through the skin. This tract erupts first anteriorly, at the junction on the throat, and develops posteriorly. However, the upper throat and chin lag behind the rest of the ventral tract. The crown feather sheaths are barely out of the skin; those at the base of the culmen are clearly evident, but they are not quite through. Supercilliary, auricular, and other minor facial tracts are not yet emergent, but they are clearly defined. The occipital region and the entire back have sheaths showing. Normally the middorsal saddle is ahead of the upper and lower parts of the back, both in time of sheath appearance and in length of the sheaths. Light-colored sheaths are out along the front (anterior) of the crural tract; dark spots still show at the sides of this tract.

Age 5 days (20–2).—At this age many of the birds have their eyes open, at least part of the time. All the major pterylae have most or all their sheaths out, and some sheaths of the minor facial tracts are through the skin. Rectrices and upper tail coverts have not yet emerged, but show as dark areas beneath the surface of the skin. The feathers of the anal circlet are not yet through the skin.

In White-crowns at age five days, no feathers have yet burst the sheaths. This seems also to be so in many other birds of similar size. The robin, however, in which the sheaths were relatively late in coming through the skin, shows broken sheaths in several tracts at this age (Howell, 1942:574–575).

Age 6 days (17–0).—As early as 5½ days some feathers of the dorsal and ventral tracts have broken their sheaths. Many other sheaths, including some on all tracts, show light-colored tips, indicating that they are ready to burst. It is to be noted that the alar feathers, although first to emerge from the skin, are not the first to rupture their sheaths. The first sheaths to be broken are those of the ventral tract, particularly light-colored ones in the posterior region of this tract. Feathers of the humeral tract also rupture very early, at about the same time as the ventral feathers. Sheaths of the mid-back are also broken at about 5½ or 6 days of age. In fact, during the half-day between visits at this stage, all the previously mentioned tracts may show sheath rupture. On some birds a few of the femoral tract feathers may also show. This may likewise be true of a few secondary coverts; the outer ones are the first to appear.

In feathers about to break through, the sheath tip first lightens in color. Some sheaths, notably of the remiges, split along the side instead of breaking at the tip. As a feather continues to grow, the sheath remains about its base for many days; young birds leaving the nest still have sheaths on most feathers, indicating that the feather growth is incomplete.

At six days of age, also, the rectrices and tail coverts have broken through the skin as sheaths. Indeed, all tracts except the anal circlet and underwing coverts have normally produced their full complements of exposed sheaths.

Feather development is not always symmetrical. On one six-day old bird the main alular feather on each wing was extruding from its sheath. On another of the same age only the right wing showed an alular sheath broken. One individual had two greater secondary coverts out on the right wing, but only one on the left wing. Other examples could be cited. Usually the lag involved is not great, but it is most pronounced in the primaries.

Age 7 days (14–0).—The major change that takes place at this age is the bursting of the distal parts of the sheaths of some of the primaries. There appears to be no definite order in which the primaries break through, and no definite span of time over which the rupture of all primary sheaths takes place. The two wings act independently in this respect. Almost any combination of unsheathed primaries may be seen. It is likely that the breaking of the primary (or other) sheaths may be partly independent of the stage of feather growth and that the sheath may break as much as a result of external pressure or friction—brushing against the nest or nestmates—as of internal pressure of the

growing feather. This explanation may apply also to the greater primary coverts, which are becoming free at this age, too, and which show as much variability as do the primaries.

The secondaries and their coverts, on the other hand, normally are constant in the order of rupture. The outer secondary sheaths break first; this occurs at seven days. The others follow shortly. Some of the feathers of the occipital region are also free by this age, and a few crown feathers may have broken their sheaths. Most feathers of the dorsal tract are out, with those of the mid-back farthest beyond the sheath tip. On femoral, crural, and humeral tracts, most feathers are freed terminally. Almost all ventral feathers are out, except for those on the throat. On some individuals, the rectrices and upper tail coverts are breaking their sheaths; the order here is usually from outer toward inner. Probably feathers of these tracts, with the exception of the tail, are less subject to abrasion than are the primaries and primary coverts, and a natural breaking of the sheath by internal pressure occurs. The outer tail sheaths are longer than the inner ones, and probably suffer more from abrasion.

The seventh day is the time of primary sheath rupture in some other species that have been studied. The Black-throated Green Warbler, *Dendroica virens* (Pitelka, 1940:7) and Traill Flycatcher (King, 1955:162) reach this stage at age seven days, but the Prothonotary Warbler, *Protonotaria citrea* (Walkinshaw, 1938:42) and House Sparrow (Weaver, 1942:184) are a day earlier. The Barn Swallow (*Hirundo rustica*), Cliff Swallow (*Petrochelidon pyrrhonota*), and Eastern Phoebe, *Sayornis phoebe* (Stoner, 1935, 1945, 1939) first break primary sheaths on the ninth day, and the Black-capped Chickadee (Odum, 1941:529) is even later.

Age 8 days (13–0).—At this age all remiges and their coverts are usually broken through their sheaths. The area of greatest change is the crown. By eight days most coronal feathers are out, only those closest to the base of the bill remaining ensheathed. Toward the nape the light central stripe is beginning to appear. On most other tracts, virtually all feathers have emerged but are still growing.

Age 9 days (9–2).—Feather covering is adequate for its role in temperature regulation at this time. The young birds could leave the nest, but normally they remain another day or so. The free part of the greater primary coverts is long enough to hide the basal sheaths of the primaries. The crown stripe is plainly evident, with even the feathers at the base of the bill free from their sheaths. Over the entire body few sheaths can be seen. The ventral feathers are nearly long enough to cover the large ventral apterium. Feathers of the throat and chin, and of the minor tracts of the head, have mostly broken their sheaths, but they are barely out of the sheath tips.

Howell (1942:575) mentions that feathers of the crural tract and anal circlet of the robin appear without external sheaths. This is also noted by Weaver (1942:184) for some alar feathers of the House Sparrow. This seems to be true in the anal circlet of the White-crowned Sparrow as well.

Age 10 days (0–1).—One nest was found in which the young were better developed than fledging birds in all other nests observed. Blanchard (1941:31) gives the usual fledging age as 10 days. From these two considerations, the age of the one bird removed from this nest was estimated as close to 10 days.

There were few differences between this bird and those observed at nine days except that most greater primary covert sheaths had completely disappeared, giving an appearance of nearly complete feathering of the wing. Under these coverts the primary sheaths remained on the basal third of the feathers. No sheaths were seen on the crural tracts.

The validity of some of the comparisons with previously published material dealing with other species may be open to question at the present time. Correlation between development and length of nestling life, on an interspecific level, awaits a proper summary of the wealth of published material. Comparative material used here deals entirely with other passerine species. Developmental data on gallinaceous birds (Sumner, 1935), birds of prey (Sumner, 1933), a duck (Weller, 1957), and various domestic fowl (Milby and Henderson, 1937) are available, but it is felt that attempted comparison would be meaningless at this time because of the many differences between these birds and the passerines mentioned here.

BEHAVIOR

The following descriptions of behavioral traits of nestling White-crowned Sparrows are compiled from field notes made concurrently with those on growth.

In species with highly concealed nests, behavior of the young can be observed only by disturbing them, and many of the behavioral traits recorded are, therefore, in relation to an unnatural situation. Some traits, however, are probably invariable, particularly in very young birds. In older nestlings certain traits may be modified by handling, and certain others, inherent but not normally manifest without disturbance, may be revealed. Nevertheless, since these reactions would probably be similar whatever the nature of the disturbing influence, and since disturbance *per se* is not necessarily abnormal, these descriptions may indicate usefully the main events in behavioral development.

Age 0 days.—The position maintained at hatching is what Blanchard (1941:30) refers to as the "egg position." The head is bent under the fore part of the body and the legs are stretched forward; the bird rests on its abdomen. A similar posture was noted in the Traill Flycatcher by King (1955: 161) and in the Prothonotary Warbler by Walkinshaw (1938:41). It was also seen in Song Sparrows that I observed, and it is probably common to all altricial birds.

A very strong gaping reaction was present. The neck was outstretched, mouth wide open, for a short time; then the resting position was resumed.

Age 1 day.—There is very little change during the first day. In gaping, some birds stretched to a nearly erect position and seemed almost to balance on their tails; others did not rise to an erect position to gape, the weight remaining on abdomen and toes. Gaping in the nest is not hazardous, but when held in my hand some birds stretched up so far that they fell backward. One bird even gaped from this awkward position. They could not right themselves.

In the Ovenbird (Hann, 1937:176) and Prothonotary Warbler (Walkinshaw, 1938:41), gaping occurs as a response to noise. In White-crowned and Song sparrows this action was apparently stimulated only by movement, such as jarring of the nest (Blanchard, 1941:30). Merely waving a hand over a nest without touching the nest or the supporting shrubbery did not elicit a response. No sounds made by me or by the excited parent birds appeared to act as a stimulus for gaping. It appears that the gaping response is dependent on a much simpler stimulus at early ages than the tripartite stimulus described by Tinbergen (1951:41) for 10-day old thrushes.

Age 2 days.—There was evident at this age a slight difference in the posture of the young birds. The head was held more erect than earlier. In one nest the three young rested their heads on the remaining unhatched egg. Two birds at this age lay on their sides. At this time the first effective righting movement was noted, by which a bird lying on its side or back could move to the normal position of rest on its ventral surface.

Interspecific variation occurs in the age at which the righting response becomes evident. The Long-billed Marsh Wren (*Telmatodytes palustris*) can right itself shortly after hatching (Welter, 1935:26); this ability in Ovenbirds was noted by Hann (1937:161) on the day of hatching.

Age 3 days.—Most birds cannot yet hold themselves erect, although at 2½ days one bird held its head up between gapes. The eyes are beginning to open at this time. One bird uttered a faint squeak while gaping; this is the youngest age at which I heard sounds from any White-crown. The Ovenbird (Hann, *loc. cit.*), Robin (Howell, 1942:571), and Eastern Phoebe (Stoner, 1939:34) all give audible sounds shortly after hatching. On the other hand, the first sounds from young Tree Sparrows were noted at five days of age (Baumgartner, 1938:74).

Age 4 days.—At this age some young birds clung to the nest lining when I tried to remove them. One bird exhibited this reaction at 3½ days. Blanchard (1941:30) states that this action began at about 4 days in the White-crowns that she studied. This character is probably related to the working of the toes mentioned by Hann (1937:176), which action appeared much earlier in Ovenbirds.

Age 5 days.—The positions maintained by the young birds until now all included a hanging of the head or an extension of the neck. At five days a new posture, crouching, was seen. In this position the head was retracted, and the birds sat more erect. In the nest this position replaced gaping when the birds were disturbed by my visit. Not all birds assumed this position this early; when removed from the nest, some still lay in my palm with head and neck extended, and nearly the entire ventral surface was in contact with my hand.

This crouching position may indicate the beginning of a fear response. It appears to be correlated with the complete opening of the eyes. Correlation of the development of fear and the opening of the

eyes was noted by Odum (1941:530) in Black-capped Chickadees. Baumgartner (1938:74–75), although mentioning that responses in young Tree Sparrows were more discriminate after the opening of the eyes (at five days), correlates the fear reaction "with the development of physical independence" at 7½ to 8 days of age.

At five days the first sounds other than begging notes were heard. One bird gave what seemed to be a protest note when replaced in the nest.

Age 6 days.—By this time most of the nestlings would crouch quietly in the nest rather than gape. Gaping did occur, when the nest was jarred rather sharply, but in general it was less noticeable than on previous visits. The birds were extremely active, and often their movements on the balance pan made weighing difficult.

Age 7 days.—A large number of the birds now gave protest notes when handled. A slightly different note, seemingly a fright note, was heard from one bird at 6½ days. The usual resting position now is an erect one in which the weight rests on the abdomen, tarsi, and toes. Crouching has almost entirely replaced gaping when the birds are disturbed. However, the gaping reaction to my presence never completely disappeared.

Age 8 days.—No new development was noted at this age. Birds were generally more active on the balance pan than in my hand. Possibly that activity was a result of the coolness of the pan.

Age 8½ days.—The first concerted escape attempt occurred at this age. Although most birds still sat on tarsi and toes, two birds stood erect on their toes.

Blanchard (1941:32) gives two instances of birds returning to the nest on the day they left it. Ages of these birds are not given, but presumably they had left the nest under natural conditions. In the many nests which I observed in 1957 I did not note this, but it did occur once in May, 1956. A bird of uncertain age, probably 8 to 8½ days old, jumped from my hand and disappeared into the viney tangle of brush around the nest. Its three siblings remained in the nest despite the commotion raised by the escaped bird and the adults. About one hour later I revisited the nest and found all four young birds present.

Age 9 days.—Most activity in birds of this age was directed toward escape. Usually their attempts failed, and when they were replaced in the nest they would become calm and would remain. One individual at nine days performed what may have been a threat display. While sitting quietly in my hand, facing away from me, it turned its head toward me and opened its mouth widely. This was not considered to be a begging action; the head was not raised and no sound was heard. An eight-day-old Song Sparrow gave a similar display. This bird also looked directly at me and opened its mouth widely. This was repeated after a few moments, and the second display was accompanied by notes that seemed different from either begging, protest, or fright notes heard earlier.

Visits to the nest were usually stopped when the birds reached the age of nine days in order to prevent premature departures from the nest. Considering the numerous escape attempts and the finding of a nest containing young birds obviously older than the oldest birds in nests which I followed, it seems certain that my visits did cause premature departures. This belief is strengthened by Blanchard's (1941:31) statements that the birds she observed left the nest when touched after the eighth or ninth day, and that the usual age for leaving the nest is 10 days. My observations on Song Sparrows were similar to those on White-crowned Sparrows and are in accord with Nice's (1937) comments. These findings are at variance with Lack and Silva (1949:64–65) and King (1955:160–161) who indicate that repeated visits to the nest, beginning at the time of hatching, inhibit the natural fledging reaction of disturbed young in the English Robin (*Erithacus rubecula*) and Traill Flycatcher, respectively.

Table 1 summarizes the material on first appearance of certain behavioral traits in White-Crowned Sparrows in relation to age.

GROWTH

In the following discussion, all birds are considered to have hatched at dawn or at dusk, corresponding roughly to the times of my visits to the nests. This age determination is believed to be accurate within limits of about two hours. It is possible to determine fairly accurately, mainly by the dryness of the natal down and by skin color,

Table 1

Appearance of Behavioral Traits in Nestling White-crowned Sparrows in Relation to Age

Age in days	Gaping	Righting	Begging notes	Clinging	Protest notes	Crouching	Fright notes	Escape attempt	Leave nest	Threat display
0	X									
1										
2		X								
3			X							
4				X						
5					X	X				
6										
7							X			
8										
8½								X	X	
9										X

whether a bird had been hatched for longer than a few hours. Those birds known or believed to have hatched toward the middle of the day were disregarded in the calculations.

The actual time of my visits to the nests varied throughout the season, as day length increased. Birds were weighed as near dawn and dusk as possible. Weighing the birds before the first morning feeding and after the last evening feeding was considered preferable to maintaining a strict 12-hour interval. Although the attempt to weigh at these times was not completely realized, discrepancies introduced by daylight and activity before and after weighing were minimized.

Birds were weighed in the field to a tenth of a gram. No effort was made to remove detectable fecal sacs, as was done by Mewaldt (1956), and no correction was made for defecation by some birds prior to weighing. Any error introduced by the presence or absence of fecal material is considered slight.

A full day was considered to extend from dusk to dusk, and for purposes of growth rate calculation and comparison morning weights were disregarded. A bird hatched in the evening was considered to have lived for one day at the following dusk. Likewise, a bird which hatched at dawn was considered to have lived for one day by the evening of the day it hatched, when it was in reality only one-half day old. This technique is permissible for several reasons. All food utilized in posthatching growth is delivered to the young birds during daylight hours. Blanchard (1941:29) saw a female White-crown begin "to gather insects within two hours after the young hatched." A two-hour lag in feeding would be enough to prevent a bird hatched late one day from receiving such food sooner than another hatched the following morning.

For the first few days of nestling life, morning weights of birds are very close to weights of the same birds on the preceding evening. Later in life the nestlings lost weight over night.

It must be emphasized that calculations of average growth rates are based on dusk-

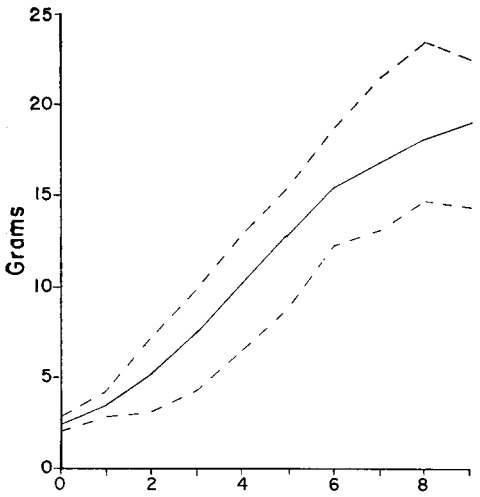

Fig. 1. Mean daily weights of nestling White-crowned Sparrows with range of variation, arithmetic scale.

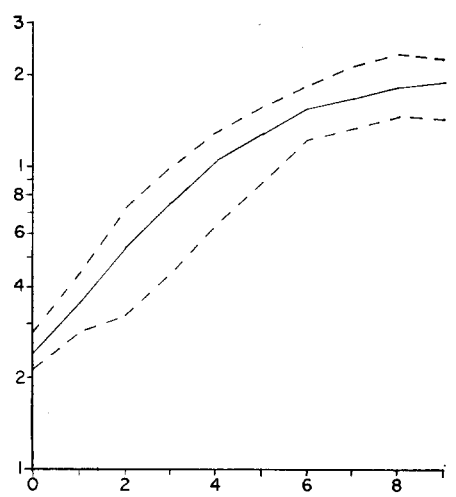

Fig. 2. Mean daily weights of nestling White-crowned Sparrows with range of variation, logarithmic scale.

to-dusk days lived by the birds, not on age *per se*. Plots of daily weights of individual birds were made on semilogarithmic graph paper. It was apparent that the growth of these nestling White-crowned Sparrows is not logarithmic, that is, the line connecting the plotted points cannot be approximated by a straight line. Instead, there is a gradual curve to the right, indicating a progressive decrease in relative growth rate (see fig. 2).

The data, therefore, were treated in two ways. The first and simplest method was the calculation of the daily increment or gain, expressed in grams per day. The formula used was $G = \frac{W_2 - W_1}{t_2 - t_1}$, where W_1 is the weight at time t_1, and W_2 is the weight at a later time, t_2. Since calculations were for daily periods, $t_2 - t_1$ always was equal to 1, and the expression became simply $G = W_2 - W_1$. This method shows differences in absolute gain on a day-to-day basis.

A more effective method of analyzing growth data is to consider the gain relative to the weight of the bird at the time of gain. Brody's formula (1945:508) for this instantaneous relative growth rate is inapplicable to non-logarithmic growth such as is found in the White-crown. However, if the constant K is replaced, this formula can be modified to $R = 2.3 \frac{\log W_2 - \log W_1}{t_2 - t_1}$ (2.3 being a factor to convert logarithms to the base 10 to natural logarithms) and used on a daily basis to give a figure, R, for the average of the growth rates manifest during each day. This figure is valid for comparisons between individuals and between days if it is assumed that growth during any one day is logarithmic, even though over the entire nestling period it is not. This method was also used by Dawson and Evans (1957).

Individual variation.—Although the averages of the daily weights for all birds show an increase which compares favorably to the daily increase for any individual bird (figs. 1, 2), there is a large amount of variation in the weights of birds in any age group. This variation is summarized in table 2. The range of weights for every age overlaps the

range for younger and older birds; in many instances this overlap spans more than one day. For example, a bird weighing five grams might be either two or three days old; a

Table 2

Mean Daily Weights of Nestlings of *Zonotrichia leucophrys* in Grams

Age	Sample size	Mean with standard error	Range
0	19	2.4±.04	2.1– 2.8
1	26	3.5±.09	2.8– 4.4
2	22	5.4±.17	3.2– 7.3
3	19	7.6±.27	4.4– 9.9
4	19	10.3±.32	6.5–13.0
5	19	12.8±.40	8.8–15.6
6	16	15.5±.47	12.3–18.8
7	16	16.9±.49	13.2–21.6
8	16	18.1±.55	14.8–23.5
9	14	19.0±.62	14.5–22.7

bird weighing 15 grams could be from five to nine days of age. It is evident that weight alone is not a good criterion for ageing nestling White-crowned Sparrows.

A certain amount of individual variation in daily weight, as in any other character, is to be expected. However, the magnitude of variation observed in these White-crowns is beyond that expected. Investigation of several factors may explain this diversity.

Differential food-gathering activity of various pairs of parent birds would lead to a larger food supply, greater gains, and higher daily body weights in birds of one nest compared to birds of another brood. Food available in the various territories may vary in quality or quantity; this could be reflected in the weights of the young birds. Differences in individual growth patterns, possibly genetically controlled through metabolic activity, might also be responsible for some variation in daily weights. There is no direct evidence from this study to support any of these suppositions. It is felt, however, that all three possibilities are extremely likely, if only because of the normal variations found in all wild populations. But unless, by chance, the above three factors occur in a definite relationship to one another, that is, with less active parents giving lower quality food to genetically slower growing young, their effects would tend to cancel one another.

One factor, however, may offer an explanation for much of the observed variation. More rapid growth of nestlings later in the season would tend to increase the spread, especially in the last few days of nestling life. The range of variation in birds seven, eight, and nine days old is noticeably greater than in birds six days of age or younger, and the range increases throughout the period of nestling life, as expected. As is shown beyond, a slight increase of average growth rates did occur during the season. Although the sample of April birds is far too small to permit one to draw definite conclusions, a comparison of the range of variation in daily weight of April birds to that of May birds indicates both more spread and higher average values for the May birds.

Variation with age.—The daily values of the average growth rate, R, and increment, G, are given in table 3; the relationship of one to the other may be seen in figure 3. The values shown are derived by averaging the daily values of R and G for all birds.

The average growth rate is greatest on the second day of life. There is a gradual decrease in R through the sixth day, and on day seven the value drops sharply. The average growth rate then decreases more slowly during the remaining days of the nestling period. The daily increment, on the other hand, increases slowly during the first six

Table 3

Mean Growth Rates and Weight Increases in Nestlings of *Zonotrichia leucophrys*

Day of life	Sample size	Mean growth rate (R)	Mean increment (G)
1	22	.411±.022	1.2±.09 grams
2	24	.421±.013	1.8±.02
3	21	.354±.012	2.3±.13
4	18	.283±.017	2.5±.15
5	19	.233±.012	2.6±.15
6	19	.212±.019	2.9±.17
7	19	.104±.012	1.1±.20
8	19	.064±.016	1.3±.20
9	17	.040±.056	0.7±.27

days of life, then decreases sharply to a lower value for the seventh and eighth days. The lowest value for G is on the last day of nestling life. Although the data from Song Sparrow observations are not numerous enough to warrant mathematical treatment, a similar trend is apparent.

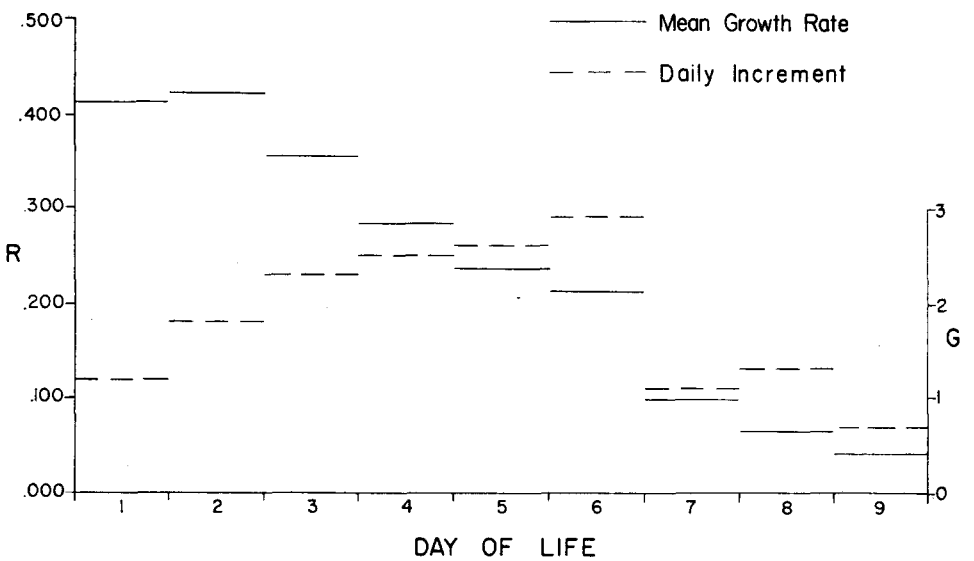

Fig. 3. Mean growth rates (R) and weight increments (G) in *Zonotrichia leucophrys* in 1957.

The decrease in daily gain during the later stages of nestling life is difficult to understand at first, even though it occurs in many other species as well. About four days after the hatching of the eggs, the male White-crown begins to assist the female regularly in feeding the young (Blanchard, 1941:29). Baumgartner (1938:76), Hann (1937:182), and Nice (1937:130) all report increases in feeding activity as the young birds they studied grew older. Presumably this is true also in White-crowns, and very likely it is so in all passerine species.

Why, then, if the young birds are getting more food each day during the later stages of the nestling period, do they gain less weight? Part of the answer must lie in the fact that this period, from the seventh day on, is one of very rapid feather growth and devel-

opment as well as one of increased physical activity. A similar conclusion was reached by Paynter (1954:107). Presumably food brought to the young at earlier ages supports growth of body tissue, but at later ages it also supports feather growth and maintenance of body temperature. Certainly the amount of heat produced metabolically is greater than previously (Kendeigh and Baldwin, 1928:276–277). The fact that over-night weight decreases are greatest in later phases of nestling life indicates that energy sources are being more fully utilized. Edson (1930) postulated a relationship between weight recession and feather development in the Violet-green Swallow (*Tachycineta thalassina*).

Variation during the season.—The usual progression of the avian breeding season in California involves an increase in air temperature and a decrease in rainfall. These changes favor insect life as the season progresses, and a better food supply for young birds is presumably available later in the spring. Also, the longer daily period of light increases the amount of time spent by the adults in gathering food for their young. Presumably, too, lower night temperatures in April would affect adversely the growth of nestlings more than would May night temperatures. Under these circumstances, a higher value for R, the daily average growth rate, would be expected later in the season.

By taking averages of the daily individual R values over the nine-day nestling period, we can obtain figures which will serve as indices of growth rates for a number of birds in particular intervals of the nesting season. Data treated in this way for the two months, April and May, are summarized in table 4.

Table 4

Growth-rate Indices for Nestling White-crowned Sparrows at Berkeley, California

Month	Time of weighing	Surviving nestlings only		All nestlings	
		Number of rates	Index	Number of rates	Index
April	a.m.	51	0.194	67	0.195
	p.m.	48	0.217	58	0.222
May	a.m.	49	0.252	58	0.249
	p.m.	85	0.243	117	0.225

Examination of pairs of corresponding indices for the two months (for example, April a.m. versus May a.m.) reveals considerable differences between members of all pairs except the one based on afternoon weights of all nestlings. The fact that these differences occur seems to indicate seasonal variation in growth rate. The highest indices, it should be noted, are obtained from data based on weights of birds hatched in May.

The fact that a difference in growth exists between birds in April and in May is further indicated by a comparison of weights of survivors at ages 8½ or 9 days. Although the number of weights available is small, the difference between the months is striking, as the following summary shows:

Month	April	May
N	6	9
Mean with standard error	17.6±1.08 gms.	20.2±0.90 gms.
Range	14.5–21.7 gms.	18.2–22.7 gms.

Only one bird in April weighed more than the average for May, and no bird in May was as light as the average for April. A t-test shows that the difference between the means is highly significant at the 95 per cent level ($t = 2.52$).

Thus, the growth rate of nestling White-crowns appears to be higher in May than in April. Although nestlings were found in March and June, also, data obtained from these birds are too few to permit examination of growth rate over the entire breeding season.

Correlation with clutch size.—Of the six observed clutches in which young birds of known age attained fledging age, four contained three young each and two held four young each. If, as in the preceding section, average values for all daily growth rates are taken as an index of growth over the period of nestling life, there is no suggestion that birds from clutches of three (index value 0.228) and from clutches of four (index value 0.231) differ in rate of growth.

Lack and Silva (1949:71–72) also concluded, in their study of the robin (*Erithacus rubecula*), that brood size does not influence growth. They considered weight, however, rather than rates. In explanation, they postulated that the lack of difference might be due to unusually good conditions for insects during the years of their study. Although no observations on the quantity of food available for young White-crowns were made in my study, I feel that the unusually wet spring of 1957 offered somewhat poorer than average conditions.

Growth of flight feathers.—The sheaths of primaries of most of the nestling White-crowned Sparrows which I observed extended a measurable distance beyond the skin for the first time on the fourth day of life; on one individual, these sheaths were out on the third day, and on a few others, emergence was delayed to the fifth day. The eighth primary of each bird was measured each time a nest was visited. Measurements were to the nearest millimeter, with half-millimeter intervals being estimated. The data are summarized in table 5.

Table 5

Growth Rate of Eighth Primary in *Zonotrichia leucophrys*

Day of primary growth	Sample size	Mean with standard error	Range
1	24	2.4±.15 mm. per day	1.5–3.5
2	21	3.4±.24	2.0–5.0
3	21	3.8±.11	2.0–4.5
4	21	3.8±.11	3.0–5.0
5	15	3.9±.11	3.0–5.0
6	7	3.4±.19	3.0–4.0

After an initial period of 1 to 1½ days, primary growth was rapid and fairly constant. Often by the time the young birds were 8½ to 9 days old, and ready to leave the nest, the eighth primary had reached a length of 20 mm. or more. The impression in the field was that the primaries grew about 4 mm. in any 24-hour period. Later analysis showed that this estimate was high, but only slightly so. Primary growth, as feather growth in general, seemed to be continuous and not restricted to daylight hours.

Primaries grew most rapidly on the fifth day of their growth, increasing, on the average, 3.9 mm. The third and fourth days were also periods of rapid increases in length, with mean increments of 3.8 mm. The low value for the sixth day may indicate a trend toward slowing of feather growth at fledging time, or it may be an artifact due to the inadequate sample.

The outer rectrices of only a few birds were measured. These feathers normally extended a measurable distance beyond the skin at six days of age. By the time of my last visit, at nine days, the outer rectrices of one bird had attained a length of 9 mm.

SUMMARY AND CONCLUSIONS

Young from 20 nests of the White-crowned Sparrow (*Zonotrichia leucophrys nuttalli*), found during the 1957 breeding season in Berkeley, California, were weighed and observed daily. From records of these observations, day-by-day accounts of development of external morphology and behavior have been prepared.

At hatching, dark spots representing feather papillae are visible beneath the skin surface on the alar, humeral, dorsal, and coronal tracts of White-crowns. External feather sheaths first appear when the birds are 2½ to 3 days of age. The first rupture of these sheaths occurs at age 5½ or 6 days. At 7 days of age, the tips of the primary sheaths begin to break. Feathers of the anal circlet appear without visible external sheaths.

Gaping is replaced by a crouching posture at 5 or 6 days of age. A threat display was given at age 9 days. Young White-crowns may leave the nest at the age of 8½ days, if disturbed, but under normal conditions do not fledge until about 10 days old.

Growth rates were calculated in terms of actual increase, in grams per day, and on a relative basis. Evidence is given showing that there is a slight increase in growth rate as the season progresses. The wide range of variation seen in daily weights may be at least partly explained by this.

The largest relative gain occurs during the second day of nestling life. A gradual decrease in relative gain occurs throughout the remaining nestling period. The actual weight gain, however, gradually increases until the greatest gain occurs on the sixth day. The decrease in both actual and relative gain on the final three days of nestling life is probably due to a shift in the energy budget, as more food is utilized in the production of feathers and heat than is converted to flesh.

No correlation of growth rate with clutch size was found.

After an initial slow start, feather growth is rapid and constant. Primaries grew at a maximum rate of 3.9 mm. per day; rectrices grew as much as 9 mm. in three days. Although weight increases occured only during daylight hours, feather growth continued throughout the day.

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