BIOLOGY OF WHITE-CROWNED SPARROWS IN LATE SUMMER AT COLLEGE, ALASKA

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This paper reports on the results of observing, banding, and collecting Gambel's White-crowned Sparrows (*Zonotrichia leucophrys gambelii*) at College, Alaska, near Fairbanks (lat 64°49′ N) in late summer of 1957. For ease of communication, this race will be called Gambel's Sparrow hereafter in this report. Its behavior and physiological concomitants have been studied extensively on the wintering grounds from September through April and on the breeding grounds from arrival of the males in early May through fledging of the young in mid-June (Michener and Michener, 1943; Blanchard and Erickson, 1949; Oakeson, 1954; Wilson and Farner, 1960; and King and Farner, 1963). Less is known of the behavior of *Z. l. gambelii* from late June through August. The work presented here concerns behavior and physiological concomitants in Gambel's Sparrows at College from late June through 30 August 1957. King, Farner, and Morton (1965) analyzed body weight and lipid reserves and King, Follett, Farner, and Morton (1966) studied gonad cycles in Gambel's Sparrows collected near Fairbanks in late summer of 1962 and in May and June of 1963. Although their aims and methods were different from mine, our data are complementary in several respects.

This work was undertaken in connection with analysis of seasonal changes in thyroid histology in this race (Oakeson and Lilley, 1960). I wanted to know whether specimens collected near Fairbanks in July and August represented only local breeding birds and their offspring or whether my samples included individuals that moved into the area after nesting was over. If my samples included transients, I wanted to find out how long they lingered, when local breeding birds stopped entering traps, and what was the date of the earliest sign of fall migration. Since individual birds may move about while the number of birds foraging in a given area stays approximately the same, the only way to discover whether I was sampling a stable or shifting population was to band large numbers of individuals in a restricted area and retrap there frequently.

From observations by T. T. McCabe, reported in Blanchard and Erickson (1949), we know that in British Columbia Gambel's Sparrows with young still begging for food may move at least 40 or 50 miles away from breeding grounds by early July. Early storms in the mountainous breeding grounds of British Columbia might provide the stimulus for such movement. In the lowland nesting grounds of central Alaska, on the contrary, the climate of late summer is reliably warm, and the forage is excellent at least until early September. Is there evidence of movements of Gambel's Sparrows in July there also?

I hoped to throw light on this question by concentrating banding operations in a cultivated field where I had watched Gambel's Sparrows during nesting. I knew the number of pairs whose territories included parts of this field, and the range of clutch sizes. I could, therefore, estimate the theoretical maximum number of local Gambel's Sparrows that might forage in this field before movement away from or into the area took place. This estimate constituted a basis of comparison for subsequent observations of numbers at this place.

METHODS

Three hundred and forty-six Gambel's Sparrows were examined between 26 June and 27 August 1957. Two hundred and fifty-four of these were live birds trapped, banded, and released; 92 were specimens, of which 50 were trapped at the same locations as the banded birds and 42 were shot a few miles from the trapping grounds. Thirty-two of the banded birds were recaptured a total of 45 times, and records were kept of their molt.

I trapped at the east and west edges and northwest corner of a cultivated field on the Agricultural Experiment Station of the University of Alaska. The west edge was bounded by a narrow dirt road and the north edge by railroad tracks and a wide road, to the north of which lay the Experiment Station headquarters and other cultivated fields. Open farm land extended to the south of the trapping field at least a quarter of a mile. To the east was uncultivated ground with weeds and scattered clumps of small trees.

Dense shrubbery grew along the west and north borders of the trapping area and provided roosting spots for Gambel's Sparrow flocks. In the field grew a variety of vegetable and seed crops attractive to sparrows. More Gambel's Sparrows foraged here in late summer than in uncultivated fields of similar area where this species had also nested. The Experiment Station headquarters to the north also provided attractive foraging places, and flocks of Gambel's Sparrows flew back and forth across the road between the Station and the trapping field.

On 23 mornings from 29 June through 27 August I trapped at two places about 0.3 mile apart, using nine two-cell Potter traps. The first place (Area A) included part of the west edge and the northwest corner of the field. Here I kept several sites prebaited. On a given trapping morning I put three traps each at the three places where the least bait remained. From 29 June through 22 July I confined the trapping to Area A. Then I prebaited three sites (Area B) 0.3 mile to the east, where in mid-July flocks of Gambel's Sparrows, consisting largely of young birds, had begun to gather. From 31 July to 25 August I alternated the trapping between Areas A and B. Since after the first week in August, the catch in Area B was greater than in Area A, I spent more trapping hours in Area B. Most of the banding was done between 0600 and 0900, although I made no effort to keep the periods identical on different days. As long as Gambel's Sparrows continued to enter the traps in appreciable numbers, I kept them open. When even in early morning I caught few birds and a search of the field revealed few Gambel's Sparrows, I closed the traps earlier. The short trapping period on such mornings is the result, rather than the cause, of the low catch for those dates.

Each trapped bird was examined for a brood patch, for presence of molt, and, from mid-August on, for subcutaneous fat. If the bird had a brood patch, it could be designated with certainty as a female. If it did not, it could with reasonable certainty be designated as a male until late July when new feathers began to obscure the brood patch. Birds designated in this report as males are all specimens sexed after dissection. Each bird, banded or collected, was assigned to one of five categories of molt: (1) "plumage, worn, no molt"; (2) "molt slight," where a few feathers, usually those of the rump, were in sheaths; (3) "molt general," where feathers in several tracts were in sheaths; (4) "molt finishing," where most of the feathers were freshly molted and only a few, usually those on the head, were still in sheaths; and (5) "plumage fresh, no molt." By mid-August I could feel the fat in the furcular fossa and could see fat on the abdomen of live birds. From then on, I estimated the approximate amount of subcutaneous fat and assigned each live bird to one of three categories: (1) "little or no fat," where the bird felt thin and I saw no fat on the abdomen; (2) "moderate fat" where I could feel fat in the furcular fossa and could see at least a little fat on the abdomen; and (3) "fat or very fat," where the contours of the bird's trunk were rounded owing to subcutaneous fat. I tested my estimates by using the same procedure on intact specimens which I later dissected. The estimates checked well.

All specimens were dissected, examined for molt, fat, and presence of brood patch, and assigned to one of the five categories of molt described above and to one of the five fat classes described by McCabe (1943). Longest and widest axes of the larger of the two testes were measured and the testis volume was calculated by use of the conventional equation for an ellipsoid. The diameters of

TABLE 1

RÉSUMÉ OF EVENTS OF THE BREEDING CYCLE, 1957

Event	Number of individuals observed	Date of earliest record	Date of latest record	Median date for all observations
1. Arrival of males destined to breed locally	19	5 May	19 May	7 May
2. Arrival of females	12	16 May	19 May	17 May
3. Copulation	3	20 May	21 May	20 May
4. Nest-building	7	20 May	27 May	22 May
5. First egg of clutch laid	13[a]	21 May	1 June	23 May
6. First egg of clutch hatched	11[a]	4 June	16 June	7 June
7. First nestling of brood fledged	8	12 June	25 June	15 June

[a] Either observed directly or calculated from the date of a subsequent, directly observed event.

the three largest ovarian follicles were recorded. When circumstances permitted, total body weight was recorded. This was not always feasible because it was necessary to get the thyroids into fixative with all possible speed.

On days when I did not band, I checked on the behavior and numbers of Gambel's Sparrows in three other areas where I had observed nesting pairs. I recorded the dates when I noticed a decline in strength of territorial behavior in the adults, when I first saw flocks, when the numbers of Gambel's Sparrows began to decrease, and finally, when I could find none on former breeding territories. Most of the graphs include data on dissected specimens and birds that were banded and released alive. Of the 92 specimens, 64 were males and 28 were females. It seemed inadvisable to fragment the information in the graphs by using separate symbols for male and female specimens, however, since the sex of most of the live birds could not be determined. Therefore, information in each figure is presented separately for adults and young, but that for the sexes is combined. Where the sex of individual specimens is pertinent to the discussion, however, it is given in the text.

RESULTS AND DISCUSSION

BACKGROUND: TIMING OF EVENTS IN THE 1957 BREEDING SEASON

Table 1 summarizes the events of the breeding season, based on my observation of 13 nesting pairs, and provides background for the data on events in late summer. As shown by the near-identity of the date an event was first observed and the median date for that event, the pairs I watched were closely synchronized with each other. This contrasts with the large individual variability in the stages of molt and of fat accumulation in Gambel's Sparrows at the same place in late summer.

It is remarkable that dates for events in the nesting cycle of 1957 are close to those for 1963, as given by King, Farner, and Morton (1965) for the Fairbanks area. In 1963 White-crowned Sparrows were first reported on 7 May, and there were no females present until "about 18 May." The first complete clutches of eggs were found on 26 May, and the first newly hatched chicks were found on 10 June.

Dates for these events in 1957 are 5 May, 16 May, 25 May, and 4 June, respectively.

A second point of agreement is that testicular size, as measured by weight in the 1963 specimens and by volume in the 1957 specimens, increased for at least a month after arrival of the Gambel's Sparrows in the Fairbanks area. King *et al.* (1966) found a significant increase in testicular weights between 13 May and 15 June 1963. (They did not collect the earliest males, which arrived about 7 May.)

On 6–8 May 1957, I collected 11 males known to be newly arrived. The volume of the larger testis in these birds ranged from 75.42 mm^3 to 182.35 mm^3, and averaged 118.37 mm^3. Four males collected 6 June had testis volumes ranging from 108.60 mm^3 to 251.11 mm^3 and averaged 180.89 mm^3. From these data we conclude that in both years copulation occurred at least two or three weeks before maximum testis size was reached.

Banding

Total Numbers Trapped

Three hundred and four Gambel's Sparrows were trapped in the Experiment Station field. This number far exceeded the theoretical maximum of local breeding birds and their offspring that could have been expected to forage there, had no other individuals moved in. During nesting, parts of the field had been incorporated into the territories of 10 pairs. Even if we assume that all these adults would later enter the traps, which is improbable, this could account for no more than 20, whereas I caught 43. Similar calculations for the young of the year show an even wider discrepancy. Assuming that the 10 breeding pairs fledged five young each, that all survived to trappable age and all entered the traps, the maximum expected catch would be 50. This theoretical figure is too high, for some females laid clutches of only four eggs, and several pairs lost their nestlings. Yet the number of young trapped was over five times the theoretical maximum. Between 11 July, when the first juvenal entered a trap, and 27 August, I caught 261 young Gambel's Sparrows. On the basis merely of total numbers caught, therefore, many individuals, both adult and young, must have moved into the trapping area. Table 2 shows the number of unbanded adults and young caught each trapping day, and the percentage of each day's total represented by unbanded birds.

The ratio of immatures to adults trapped, including recaptured individuals, remained above 80 per cent throughout the trapping period. Percentages of total catch represented by immatures for 10-day periods from 11 to 20 July through 21 to 30 August varied from 80.7 to 88.9. The grand total of 261 immatures trapped between 11 July, the first day any entered the traps, and 27 August, the last trapping day, represents 87 per cent of all Gambel's Sparrows I trapped at College during that period in 1957. In contrast to this, King, Farner, and Mewaldt (1965) report that the age composition of Gambel's Sparrows captured in mist nets in the Fairbanks area in July and August of 1962 varied from nearly 100 per cent immatures to less than 60 per cent immatures (their fig. 1). One possible difference in procedure may account for some of the discrepancy: King and his coworkers may have retained a greater proportion of the birds captured for specimens, whereas I banded and released most of those I trapped, so the same individuals had a chance to return and be included again in the totals. Many other considerations too complicated to discuss here also enter into the comparison.

Fluctuations in Numbers Trapped

Both the total number of birds caught each trapping day, and the average number of new (unbanded) birds caught per trapping hour on a given day, fluctuated markedly.

Figure 1 shows the total number of adult and young Gambel's Sparrows (54 and 297, respectively) caught in Areas A and B from 29 June through 27 August. These records include 254 unbanded birds which I banded and released, 50 unbanded

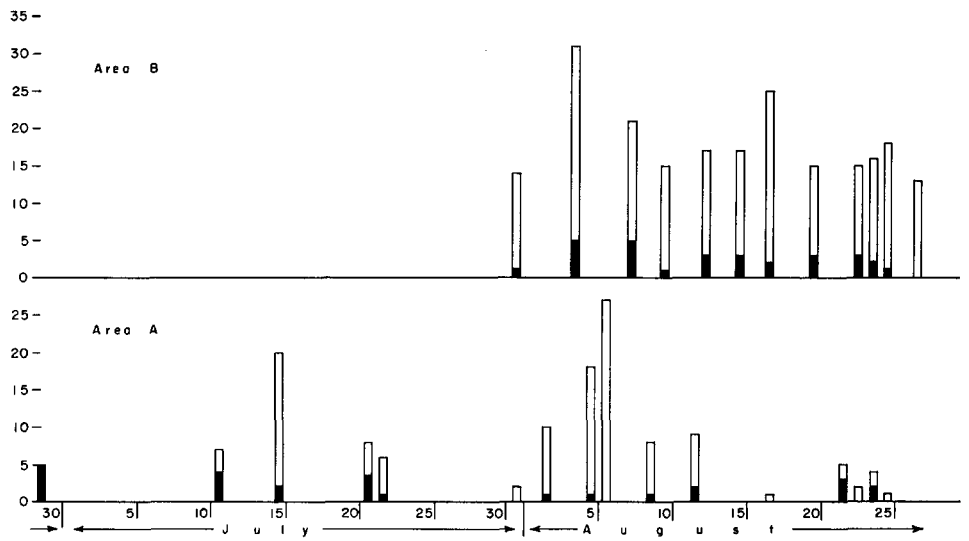

Figure 1. Fluctuations in total number of Gambel's Sparrows caught each trapping day (ordinate), including recaptures of banded birds. Solid bars = adults, hollow bars = young.

birds retained for specimens, and 47 records of recapture of 35 birds banded that season at the trapping grounds. The total number of birds caught each trapping day in Area A shows two cycles of increase and decrease, with the largest catches on 15 July and 6 August. Additional cycles may have occurred in Area A in early and late July when I did not trap there, but I am sure there was no substantial increase in numbers after mid-August. Considerable searching revealed only a few birds there after 12 August and none after 25 August. The total number of birds caught in Area B shows three cycles, with maxima on 4, 17, and 25 August. Dates for the largest numbers caught in one day are 6 August for Area A and 4 August for Area B.

The effect of retaining some trapped birds for specimens on the numbers subsequently caught cannot be assessed accurately, but I think it is probably negligible. Collecting extended through more than six weeks, from 11 July through 27 August. On the majority of the 17 collecting days three or fewer birds were kept for specimens. Furthermore, removal of these individuals would have affected the numbers subsequently trapped only if they had stayed in the area. This is unlikely, judging from the recapture records presented below. If, as the data indicate, the birds present in the area on a given day departed shortly thereafter and were soon replaced by others, my collecting would have had little effect on the numbers subsequently caught.

Figure 2 is based upon trapping records of the 304 unbanded birds caught between 29 June and 27 August. The graph shows fluctuations in the average number of unbanded birds caught per trapping hour on a given day. A trapping hour is defined as one hour when all nine traps were kept open continuously. Both Areas A and B show at least two cycles of increase and decrease. Area A shows an additional minor cycle between 22 and 25 August. There were no obvious differences in the weather for days when large and small catches were made. The greatest average

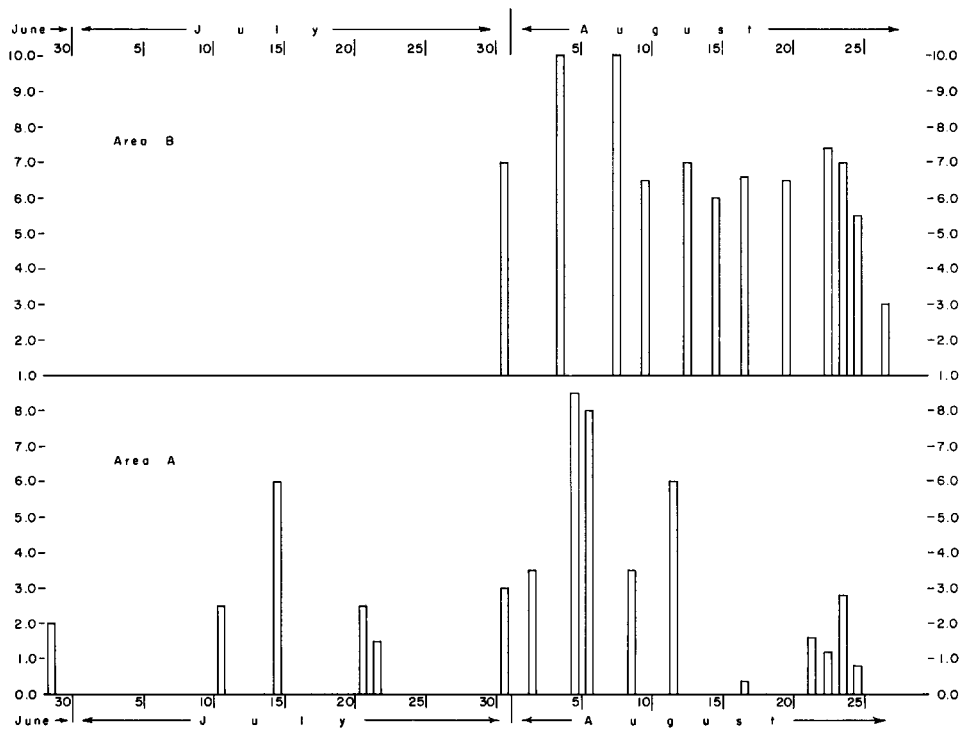

Figure 2. Fluctuations in average number of unbanded birds caught per trapping hour (ordinate).

number of birds trapped per trapping hour falls on 5 August for Area A and on 4 August and 8 August for Area B. These are close to the dates for the largest total catches for Area A and Area B (6 August and 4 August, respectively), and to the date when migration was first observed (7 August).

The data on total numbers captured and on average number of new birds caught per trapping hour, therefore, indicate that in 1957 waves of Gambel's Sparrows were moving into and out of the trapping area, at least from 15 July through 27 August. Additional evidence of the unstable nature of the population in the trapping area in late summer is given in the sections that follow.

Percentage of Catch Represented by Unbanded Birds

Even more impressive evidence for the instability of the Gambel's Sparrow population at the trapping area in late summer is provided by figures for the percentage of each day's catch consisting of unbanded birds (table 2). If banded and unbanded birds are equally likely to enter the traps, banding a stable or stationary population should yield progressively smaller ratios of unbanded to banded birds. (Actually, once a Gambel's Sparrow has found bait and entered a trap, it is more likely to re-enter the trap than a new bird is to enter it for the first time. Also, members of a local breeding population would tend to be dominant over birds passing through. Although we cannot translate these considerations into an expression of probability, we can at least say that the experience of being trapped

TABLE 2

PER CENT OF CATCH REPRESENTED BY UNBANDED BIRDS

Date	Number unbanded birds caught			Total number caught, including recaptures	Per cent of total catch represented by unbanded birds
	Ad.	Im.	Total		
29 June	4	0	4	5	80
11 July	2	3	5	7	71
15 July	1	17	18	20	90
21 July	1	4	5	8	63
22 July	0	3	3	6	50
31 July	1	16	17	17	100
2 August	1	6	7	10	70
4 August	5	25	30	31	97
5 August	1	16	17	18	94
6 August	0	24	24	27	89
8 August	3	17	20	21	95
9 August	1	6	7	8	88
10 August	1	12	13	15	87
12 August	2	7	9	9	100
13 August	3	11	14	17	82
15 August	2	10	12	17	71
17 August	2	22	24	26	92
20 August	3	10	13	15	87
22 August	2	2	4	5	80
23 August	3	12	15	17	88
24 August	4	14	18	20	90
25 August	1	15	16	19	84
27 August	0	9	9	13	69
Totals	43	261	304	351	

does not deter the bird from returning to the same trap but may, in fact, facilitate its recapture.) Starting with 100 per cent unbanded birds on the first trapping day, then, the percentage of unbanded individuals in a stable population should decrease until, if trapping is continued long enough, there are no unbanded birds left.

The banding results show nothing approaching this theoretical picture. On 15 July, for example, 18 out of 20 birds caught were unbanded. Three weeks and 23 trapping hours later, on 5 August, 17 out of 18 birds caught were unbanded. By 12 August, I had banded 157 birds in Areas A and B, yet none of the nine birds caught that day was banded. Similarly, in Area B on 31 July, the first trapping day in the area, I trapped 14 birds, all unbanded. Seventeen days and 39 trapping hours later, on 17 August, I caught 26 birds, 24 of which were unbanded. On August 20, 22, 23, 24, and 25, the percentage of unbanded birds stayed between 80 and 90 per cent. On the last trapping day, when a marked decrease in numbers of Gambel's Sparrows had occurred at the trap sites and elsewhere, the percentage of unbanded birds was still high (69 per cent). In figure 3 I have graphed the percentages of the total numbers caught represented by unbanded birds, for five-day periods from 29 June–3 July through 23–27 August. From the period 29 July–2 August on, the percentage of unbanded birds remained above 80 per cent. These results complement those of

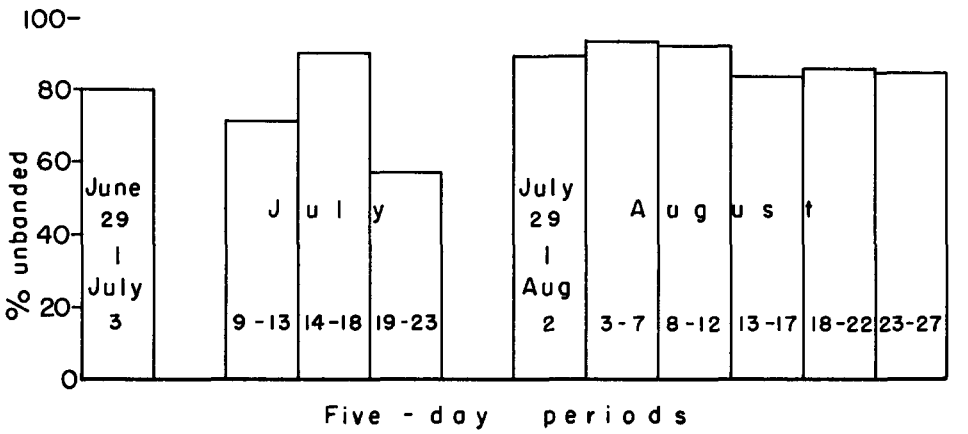

Figure 3. Percentage of total catch represented by unbanded birds, for five-day periods.

the preceding section by indicating a mobile population of Gambel's Sparrows at the trapping area.

Recaptures

Percentage and frequency. Figure 4 shows the dates of banding and recapture of 35 individuals that were retaken at least once. These shown at the top of the graph were banded during the nesting season. Four, shown at the bottom of the graph, were banded 24 August or later. These seven are excluded from the calculations below. Of the 206 Gambel's Sparrows banded between 29 June and 22 August, inclusive, six adults and 22 young, or 13.6 per cent, were recaptured one or more times by 27 August, the last day I trapped. Twenty-two came back once, two returned twice, and four returned to the traps three times.

Interval between first and last capture. The interval between first and last capture of the 28 recaptured birds varied from one to 26 days, with a median value of six days. For the six adults, the mean value for the interval between first and last capture was 9.8 days; for the 22 young birds, the mean was only 7.7 days. The commonest intervals are short: four days between banding and recapture for five birds; five days for four birds; and seven days for three birds.

If all the birds first caught had stayed, then as additional birds came into the trapping area, the frequency with which the first birds caught were retrapped might decrease but the interval between first and subsequent trappings would not be affected. The fact that intervals between first and last captures are short provides evidence that birds which started the season in Areas A and B did not stay there to the end. After mid-August I was not recapturing any of the birds I trapped in June or July.

Histories of banded adults. It is not unexpected that young of the year should move about in late summer, showing little attachment to any one locale. It is more surprising to discover from the indirect evidence provided by banded adults that Gambel's Sparrows breeding in central Alaska may leave their territories in July before they have completed the molt.

Of 21 adult Gambel's Sparrows banded in Areas A and B from 15 May through 20 August, eight were recaptured. Three of these, as explained below, were probably

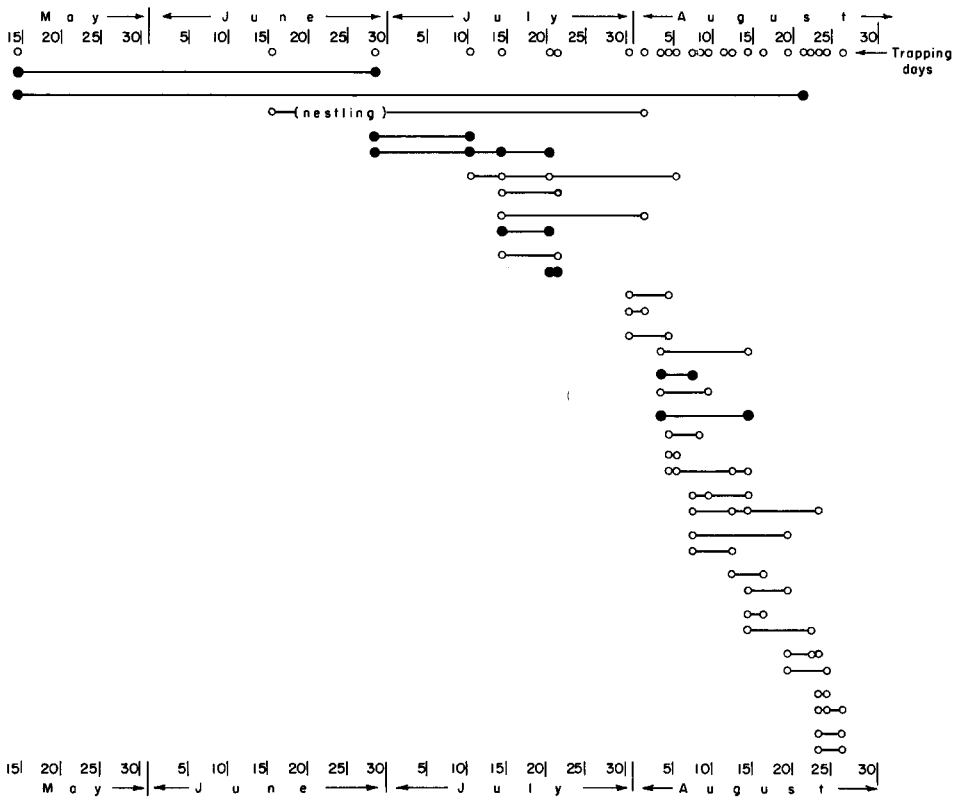

Figure 4. Banding and recapture dates for 35 Gambel's Sparrows banded at College in 1957. Solid dots = adults. Hollow dots = young.

members of the local breeding population, and one was probably a transient. The histories of the three local adults, all trapped in Area A, are as follows.

One male, band number 22-178932, was color-banded on 15 May. On 16, 17, 19, and 20 May I found it at the same place. It was unmated and singing. On 24 May it was accompained by another, presumably its mate. That day I saw it fight in midair with a neighboring male, also mated. On 29 June the color-banded male entered a trap at the same site where I had banded it. Its plumage was worn, with no sign of molt. This is the last date I trapped it. Although I subsequently trapped at the same place on 11 mornings, I neither saw or caught this male again. The second adult, band number 22-178964, was trapped on 29 June. Since it lacked a brood patch I assume it, too, was a male. I recaptured it once, on 11 July, when it was molting heavily. Like the color-banded male, it had many chances to re-enter the trap, but never did. The third local breeding adult, band number 22-178965, also banded on 29 June, was a female with brood patch. She may have been the mate of 22-178964, for the two were caught together twice at the same site. This female was captured three times—on 11 July, when she was accompained by 22-178964, and on 15 and 21 July. Her plumage was worn, and she had not begun to molt even by 21 July. Although I trapped at the same place on eight more mornings, I never caught her again. On 29 June I trapped two other females with brood patches, also in Area A. They, too, had probably bred locally. One had worn plumage, and the other was just starting to molt. Neither was ever recaptured. It is possible that these five adults stayed but avoided the traps, or that all five died. It is also a cogent

possibility, however, that they left the breeding grounds by mid-July, during the first cycle of fluctuation in numbers in Area A. If so, then they behaved in this respect like the adult Gambel's Sparrows observed by T. T. McCabe in July in British Columbia.

One adult was color-banded on 15 May 1957, in Area A, but did not nest there. I spent many hours near where I caught it, observing and trapping, but I did not see this bird again until over two months later. On 22 August it entered a trap at the same place where I had caught it in May. It is highly unlikely that this individual could have bred in the vicinity of the trapping area without being seen. Therefore I assume that it was a transient, passing through in May to more distant nesting grounds and returning in late August as it flew south. Since precise knowledge of migration routes for individual Gambel's Sparrows is almost entirely lacking, the recapture of this bird at the same place, over nine weeks after it was banded, is especially interesting. At least this individual touched down at the same locality on its northward and southward migrations.

The four remaining banded adults which returned were each recaptured once. One, banded 21 July, was retaken the next day. Another, banded 15 July, was retaken 21 July. The third was banded 4 August and retaken 8 August, and the fourth, also banded 4 August, was retrapped 15 August. On the dates of recapture three were assignable to the category "molt general." The fourth, recaptured 15 August, was classified as "molt finishing." If these four birds did not belong to the local breeding population, then they must have already been on the move while they were molting. If, as seems less likely, they did belong to the local population, then three of them disappeared before they finished the molt.

What was the stage of molt which had been achieved on the banding date by the 13 adults which were never recaptured? Two, as we have seen, were females with brood patches, one of which had worn plumage and the other of which had started to molt. Of the remaining 11, one had achieved the stage of "slight molt," seven were assigned to the category of "molt general," and only three, trapped on 15 August or later, had finished the molt. Again, it seems improbable either that all 13 birds stayed in the area but avoided getting caught or that all died. A more plausible explanation of their failure to re-enter the traps is that they did not stay. If so, the majority could have left before they finished molting.

The data for banded adults, then, furnish indirect evidence for movement away from the breeding grounds by mid-July, before the molt was finished. In this movement, they resemble the Gambel's Sparrows studied during prenuptial molt by Michener and Michener (1943) at Pasadena, California. These authors found that the prenuptial molt lasted about two months, beginning in late January. They concluded that some individuals departed before completing the molt; as late as 3 April some birds were trapped which had worn plumage and showed no hint of molt, yet most Gambel's Sparrows disappear from Pasadena by the first of May.

Capture of a banded nestling. During the nesting season I banded 28 nestlings. Only one of these was trapped later. It was a bird that hatched on 11 June, was banded on 16 June, and fledged either late on 19 June or early on 20 June. Forty-three days later, on 2 August, it entered a trap about 0.3 mile from where it had hatched. I never caught it again.

Observations on the Breeding Cycle

Independence of the Young

On 26 June I saw bob-tailed young which flew awkwardly and begged for food when their parents came near. On 29 June I saw a young bird with full-grown tail fly up from in front of one of the traps. Presumably it had been eating the bait. It still uttered food-begging notes when adults came near, but must have been at least partly independent. My notes for 9 July state "the young are definitely independent now." On 11 July, I trapped three juvenals—the first young to be caught. Also, for the first time that day I heard a young Gambel's Sparrow sing a fragment

of song. On 2 August I heard another young bird sing. The quality of its voice was that of a White-crowned Sparrow, but the pattern was not yet set.

Decline in Strength of Territorial Behavior

On 30 June I noticed a change in behavior of adult Gambel's Sparrows. My field notes state: "The pairs with young did not protest so vigorously this morning as on 25 June. The males sang infrequently and not with maximum force. It seemed harder to get a good shot; that is, the birds tended to put more shrubbery between them and me." On 10 July my notes mention that the adult males "still sing complete songs but sporadically. They are furtive, fly long distances, and do not stand their ground when pursued. The adult females tend to stay still and utter the 'ip' note, hence are now easier to collect than males." This is just the opposite of the situation during nesting, when the males are conspicuous and face an intruder as they sing, whereas the females are secretive.

Flocking

On 9 July I first saw Gambel's Sparrows in a flock. On 16 July I saw several small flocks. On 6 August Mr. Kallio, Superintendent of the Experiment Station, reported that Gambel's Sparrows were gathering in the strawberry patch at the Station.

Migratory Behavior

On 7 August at 2230 I heard Gambel's Sparrows a half-mile east of the trapping field uttering the "eep" location note. By this time it was nearly dark. My notes for 10 August state: "Gambel's Sparrows appear to be definitely in migration. They give location notes and occasionally sing weak, fragmentary songs." On 13 August I hunted along roadsides where breeding birds had been common two months before. My notes say: "The birds behave as a winter flock. They appear to be migrating. Two adults were seen in a flock of about ten. All were furtive, shy, keeping foliage between me and them."

The behavior of trapped birds had changed also. After 7 August they uttered call notes when I held them in a darkened cage. They fought to escape, and squirmed more vigorously in my hand than they had before.

Marked Decrease in Numbers

On 15 August Mr. Kallio reported that the numbers of Gambel's Sparrows he saw at the Experiment Station were "markedly fewer." On 18 August I spent seven hours in a boat on the Chena and Tanana rivers, and was impressed by the absence of small birds on shore. I heard only a few Gambel's Sparrows. On 26 August my notes say: "At meadow between 8- and 9-mile, found only three immatures." (On 19 August I had seen a flock of 18 Gambel's Sparrows there.) "Heard no song. Saw no adults. I listened and looked at spots where found Gambel's Sparrows last week. None there. Did not see any large migrating flocks anywhere this AM." The next day I returned to the same places and found only one immature Gambel's Sparrow and no adults. By 30 August I could find no Gambel's Sparrows in any of the places I had kept under surveillance. I checked the trapping field thoroughly but found none there.

Other observers have records indicating that by late August or early September most of the Gambel's Sparrows have left the vicinity of Fairbanks, but that small numbers of sparrows are there much later. Brina Kessel (personal communication)

TABLE 3

CHRONOLOGY OF GAMBEL'S SPARROW BEHAVIOR, LATE SUMMER, 1957

Event	Earliest record	Subsequent records	Evidence from which dates of events are inferred
1. Young becoming independent	29 June		Young bird foraging at trap, yet begs for food as adults come near.
		9 July	First flock seen. Young observed without parents.
		11 July	Three juvenals enter traps.
2. Decline in territorial behavior	30 June		Males shy, song weak. Parents protest less vigorously when intruder comes near young.
		10 July	Males sing only sporadically. No longer stay in territory when pursued.
3. Adults disappear from breeding territories	30 June		June 29 = last date color-banded male seen or trapped. Three adults, banded on 29 June, never re-enter traps.
		22 July	July 21 = last date any local breeding bird trapped.
4. Influx of birds into trapping areas	15 July		First increase in numbers trapped, Area A.
		15 July, 5, 24 August	Peaks in average number birds trapped per trapping hour, Area A.
		4, 23 August	Peaks in average number birds trapped per trapping hour, Area B.
5. First sign of birds behaving as if migrating	7 August		Flock heard at night uttering location notes.
		10, 13 August	Migrating flocks seen.
		22 August	Adult, color-banded 15 May and not seen during nesting season, returns to same trap.
6. Decrease in numbers	9 August (Area A) 10 August (Area B)		Average number birds caught per trapping hour declines, never returns to maximum level.
		15 August	Decrease noted at Experiment Station Headquarters.
		18 August	Lack of small birds noted on shores of Chena and Tanana.
7. White-crowned Sparrow country vacant	30 August		Numerous observations at places where in July and August Gambel's Sparrows had been common.

contributes the following report: "Heinrich Springer, banding at Forth Wainwright, stated that a big part of the population had left by August 31, 1960. On September 5, 1960, he saw two adults and a group of 25 immatures. His next observation, of one immature white-crown, is for October 11. John Weske banded at the same place throughout fall of 1959. He reported that white-crowns were common until Septem-

ber 5, and that he last saw one, caught in a net, September 20." Kessel provides an exceptional record for 18 December 1960. "Two immature white-crowned sparrows still surviving at a feeding station in Fairbanks! . . . The winter has been mild, though not overly so." Irving (1960) gives his latest record for Gambel's Sparrows at Anaktuvuk Pass as 12 September 1960, when he saw two birds, one a young of the year, at Contact Creek (lat 67° 40′ N).

Correlation of Data from Observation and Trapping

Table 3 summarizes the chronology of events of Gambel's Sparrows' behavior in late summer of 1957. Data from observation and trapping agree closely as to the dates when young became independent (9 and 11 July) and as to dates for first signs of migration (7 and 10 August for first observed migratory behavior and 9 and 10 August for the start of decline from the maximum in average numbers caught per trapping hour). In addition, banding revealed movements that I would have overlooked had I relied on observation alone. At least by mid-July, membership of Gambel's Sparrow flocks foraging in the trapping area, as revealed by banding records, was in a state of flux, but it was not until 7 August that I noticed a migrating flock. Without the banding records, I might have made the erroneous assumption that specimens collected in July and early August belonged to a single population which had bred there or been hatched there.

Whether or not my dates for the start of migration in 1957 agree closely with those of King, Farner, and Morton (1965) for 1962 depends on what event is used as an index.

These authors state: "By August 17–20 in 1962 flocks began to disappear from areas formerly occupied. We assume that this indicated the onset of migration." If I make the same assumption, I would set 15–18 August as the time migration began in 1957, and the difference between the two years would be negligible. As stated above, however, I assume that the first signs of migration are either flocks observed moving at night (7 August) or the start of a decline from the maximum in numbers trapped (9 and 10 August in Areas A and B, respectively). Thus I would date the start of migration in 1957 as between 7 and 10 August, 10 days earlier than King and colleagues assume that it began in 1962. Also, if these authors confine "migration" to the disappearance of the local breeding population, their data and mine are not comparable, for I was probably recording movement of transients through the area as well as the disappearance of local breeding birds and their offspring. Any index for the start of migration is, in any case, only one point in a mesh of behavioral and physiological changes. What is important is not the date of the single event but the time curve of each process contributing to the culminating act of departure for the south—an event which varies as to date even for members of the same breeding population.

This brings us to the question of whether the picture of the constantly changing population at the trapping area in late summer of 1957 resulted from the temporary co-existence of transient migrants with the local breeding population. The fluctuation in numbers of birds trapped each morning, and in average number caught per trapping hour, does not rule out the possibility that influxes and departures of transients were superimposed on a stable core of summer residents. However, the short intervals between first capture and last recapture described above do not support such an hypothesis. Also, the limited data on adults banded in May and June indicate that local breeding birds may have left their nesting grounds in the trapping area by at

least mid-July. Hence the picture is one of a series of arrivals and departures, with no substantial core of local breeding birds remaining in the trapping area after mid-July.

A separate question is whether the influxes of Gambel's Sparrows into the trapping area at College in 1957 comprised birds from adjacent breeding grounds of approximately the same latitude, or birds already in migration from farther north, or a combination of the two. We cannot decide this question from the data presented here. All that can be said is that the third possibility seems the most likely: birds and their offspring from nearby territories may have accounted for the influx in July; migrants from farther away, presumably from the north, may have accounted for some or all of the influxes in August. We know from the observations of T. T. McCabe in British Columbia that Gambel's Sparrows can move away from breeding grounds as early as the first week in July. Whether such movements, and those recorded in July and early August at College in 1957, should be included under the term "migration" is debatable. Preferably a different designation should be given to movements, within or on the fringes of the breeding grounds, which occur prior to the sustained, directional movements to which the term migration is traditionally applied.

Physiological Concomitants

In this section are presented the changes recorded in body weight, gonad dimensions, molt, and subcutaneous fat. Sizes of the samples vary, depending upon the characteristic being analyzed. The total number of individuals involved is therefore stated separately for each graph.

Body Weight

The data presented here are those for 37 males collected in late July and August. As stated previously, body weights could not be recorded for all specimens. Data for females and for males taken in June and most of July are too few to be significant.

Body weights of eight adult males taken in the 10-day period from 8 to 17 August range from 24.0 g to 29.9 g. The mean ($\pm$ SE) is 26.4 $\pm$ 0.62 g. Eight adults collected in the next 10-day period, from 18 to 27 August, range from 24.4 g to 29.9 g, and the mean is 27.4 $\pm$ 0.57 g. In contrast to this small difference, the two samples varied markedly as to the amount of subcutaneous fat. Of nine adults taken 8–17 August, only one had more than a little fat, whereas seven out of eight of the adults taken 18–27 August had more than a little fat; four were classified as "moderately fat," two were "fat," and one was "very fat."

Body weights for immatures present a similar picture. Six young taken within the 10-day period 29 July–7 August range from 24.6 to 28.1 g, with a mean of 26.2 $\pm$ 0.49 g. Nine young taken 8–17 August range from 25.0 to 27.7 g, with a mean value of 26.5 $\pm$ 0.29 g. Six young taken within the period 18–27 August range from 26.1 to 29.8 g, with a mean value of 27.2 $\pm$ 0.53 g. In the period 29 July–7 August, only one young male had more than a little fat, whereas seven out of nine taken 8–17 August were "moderately fat" or fatter. Yet the mean body weight was slightly lower for this period than for the preceding one. All six of the young males taken 18–27 August had more than a little fat; one was classified as "moderately fat," four as "fat," and one as "very fat."

Thus our data indicate that body weight is not a reliable criterion of the amount of subcutaneous fat. It is of interest that King, Farner, and Morton (1965) found

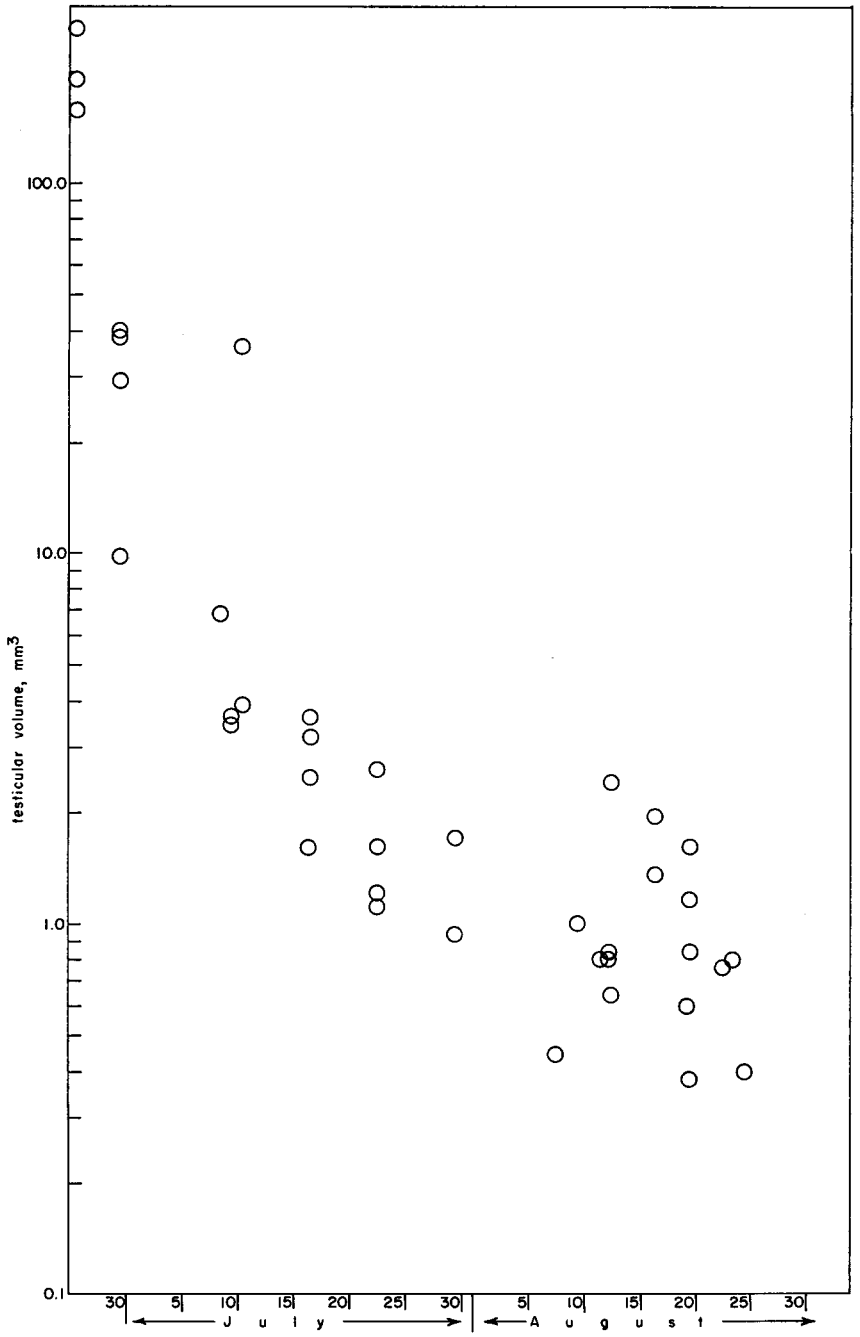

Figure 5. Volume of the larger testis in adult Gambel's Sparrows collected in late summer of 1957.

that variation in total body weight is not a reliable index of variation in lipid reserves of White-crowned Sparrows in summer and autumn.

Testis Volume

Figure 5 shows testis volume for 39 adult Gambel's Sparrows collected between 26 June and 25 August. Since volume is a rough indicator of histologic stage, we can say that the three males taken 26 June were still in breeding condition. None showed signs of molt. The four adults collected 30 June had testes averaging 29.0 mm^3, which must have already reached the "reorganization phase" as defined by Marshall (1959). Two of these had started to molt and two had not. These data complement those of King *et al.* (1966) who found that postnuptial molt in Gambel's Sparrows did not begin until testicular weight had markedly decreased.

It will be remembered that on 30 June I observed the first signs of decline in territorial behavior (table 2). One specimen with a testis volume of only 0.44 mm^3, close to the winter minimum, was collected 8 August. The mean testis volume for eight adults taken in the 10-day period 18–27 August was 0.81 mm^3. This is close to the mean value (0.62 mm^3) for testes of Gambel's Sparrows taken in December and January on the wintering grounds in California (Blanchard and Erickson, 1949).

Testis volumes of 22 young birds taken at College in July and August ranged from 0.17 mm^3 to 0.54 mm^3, with a mean of 0.28 mm^3.

Diameters of Ovarian Follicles

The means for diameters of the three largest follicles in the ovary of each adult specimen ranged from 1.67 mm for a female taken on 26 June to less than 0.5 mm for a female collected on 23 August. Eighteen other adults collected between these dates showed a continuous decline in mean diameter of ovarian follicles from the maximum given above to the winter level. The ovarian follicles of eight young females measured less than 0.5 mm in diameter.

Molt

Figure 6 shows the number of birds in successive molt stages on each collecting or trapping day for 346 individuals examined 391 times (recaptured individuals were examined for molt and were graphed the day they were caught). Eighty-five of the individuals were adults, 261 were young of the year, either juvenals molting to immature plumage or young which had already acquired the immature plumage.

It is obvious from figure 6 that there is a wide overlap in range of dates for each molt stage, especially in the young birds. Second, the period during which individuals in some stage of molt were captured lasted a long time, at least 57 days for adults and 47 days for young. These periods for the population are considerably longer than the estimates for duration of molt in individuals discussed below. Large numbers of young birds still molting were captured after 10 August, when observations indicated that migration was already under way. This is indirect evidence that young Gambel's Sparrows may leave the breeding grounds before they have finished the molt.

The wide variation in molt stage of young birds trapped on the same date contrasts with the narrow range of dates for hatching and fledging of the young in the same locality that year (table 1). On 15 July I trapped a young bird that had already acquired the head stripes characteristic of immature Gambel's Sparrows in their first winter. Yet I continued to trap birds with the juvenal head patterns until 20 August. This wide variation in timing of the molt in the young is additional evidence that I may have been trapping members of more than one breeding population, al-

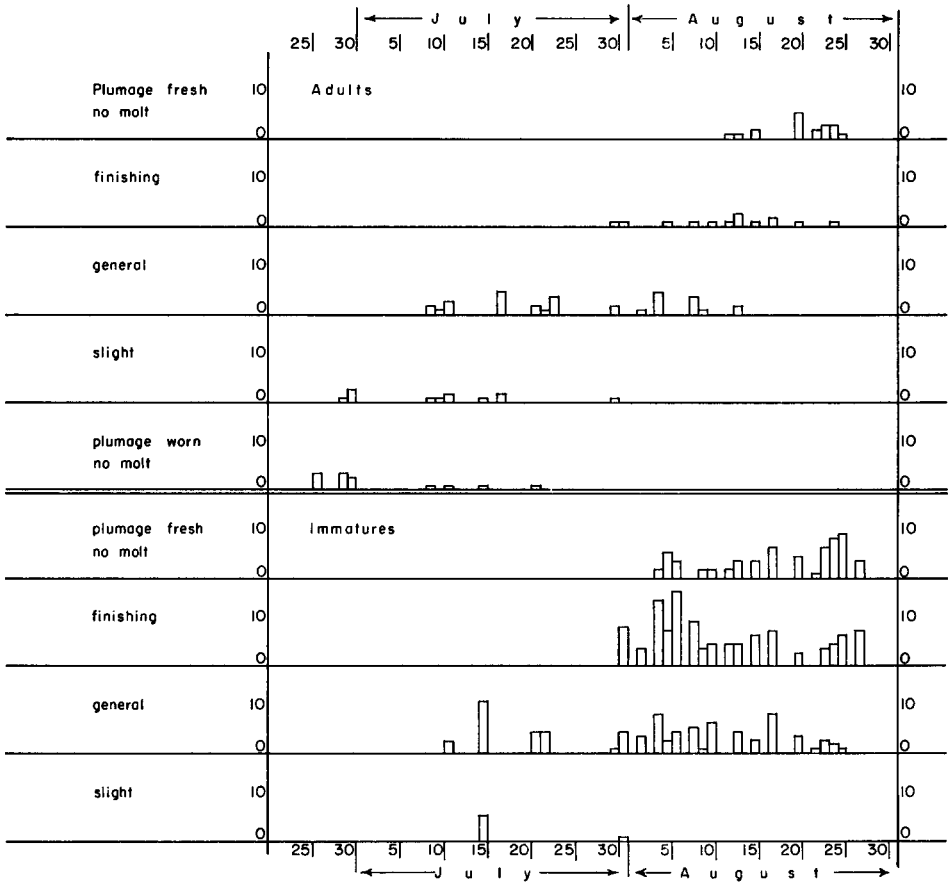

Figure 6. Number (on ordinate) of Gambel's Sparrows in each stage of late-summer molt. Includes all specimens and live birds banded and recaptured.

though we must recognize another possibility—that some of the late molters were offspring from pairs that lost their first clutches or broods. The pairs that nested in the immediate vicinity of the trapping grounds did not contribute many young in this category, but pairs a few miles away, where I did not keep a census of broods attempted, may have.

King, Farner, and Morton (1965) present data on molt in Gambel's Sparrows in the Fairbanks area in 1962. The authors assign index numbers to the stages of molt and compute the average for each 10-day sample (their tables 3 and 4). Although my categories of molt do not coincide exactly with theirs, and I cannot separate the sexes, I can render my data more closely comparable by assigning index numbers as follows: 0 = "plumage worn, no molt" and "plumage fresh, no molt"; 1 = "slight molt" and "molt finishing"; 2.5 = "molt general" (this category includes the classes "medium" and "heavy" to which King and coworkers assigned index numbers 2 and 3, respectively). Table 4 gives the average molt indices for 10-day periods. The period in 1957 with highest molt index for both adults and immatures is 19–28 July.

TABLE 4

AVERAGE MOLT INDEX IN GAMBEL'S SPARROWS FOR 10-DAY PERIODS, SUMMER OF 1957

Period	Adults		Immatures	
	N	Average molt index	N	Average molt index
19 June–28 June	4	0	–	—
29 June–8 July	11	0.1	–	—
9 July–18 July	21	1.8	21	2.1
19 July–28 July	8	2.1	10	2.5
29 July–7 August	13	1.7	94	1.3
8 August–17 August	19	1.3	96	1.3
18 August–27 August	17	0.1	74	0.7

This falls within the period found by King and coworkers in 1962 to encompass the highest molt indices for adults, young, males and females (11 July–10 August).

Dates for the start of molt in 1957, and in 1962 as described by King, Farner, and Morton (1965), are not close. These authors state that "Molt began in both adults and juvenals in the second week of July and was completed by mid-August." In 1957 molt began in adults by 29 June. On that date I trapped an adult female which showed slight molt. On 30 June I collected three adults, two males and a female, all of which showed slight molt. On 9, 10, and 11 July 12 adults were captured, three of which were molting slightly and six of which were molting heavily. The latter must have started molting before the second week of July. On 11 July, the first day juvenals entered the traps, I caught three young which were already molting heavily. They must have begun to molt at least in the first week of July. Immature birds still molting continued to enter the traps until 27 August, the last day I trapped. In 1957, therefore, molting birds were caught during a period of more than eight weeks.

Records for banded birds can be used to estimate the approximate duration of the fall molt in an individual. The picture is necessarily composite, since no one bird was trapped and recaptured over a sufficiently long period to include both start and finish of the molt. The data for young birds are as follows. One was trapped twice seven days apart and had progressed from "slight molt" to "molt general." Eleven birds were trapped twice while they were in the stage "molt general." The intervals ranged from four to 12 days. Three others were trapped 11, 16, and 18 days apart, and during these intervals had progressed from "molt general" to "molt finishing." Four birds were trapped twice while in the "molt finishing" stage. The intervals between trappings ranged from two to six days. If we choose the maximum known intervals for the duration of a given molt stage, and the minimum known interval for the time necessary to progress from one stage to the next, we obtain the figure of 34 days for the period from "slight molt" to "molt finishing" (seven days to progress from "slight molt" to "molt general," 10 days for duration of the "molt general" stage, 11 days to progress from "molt general" to "molt finishing," and six days for the duration of the "molt finishing" stage). This can be only a rough estimate, for I probably did not catch the birds classified as having "slight molt" the day they started, and the birds classified as "molt finishing" may have taken a few more days

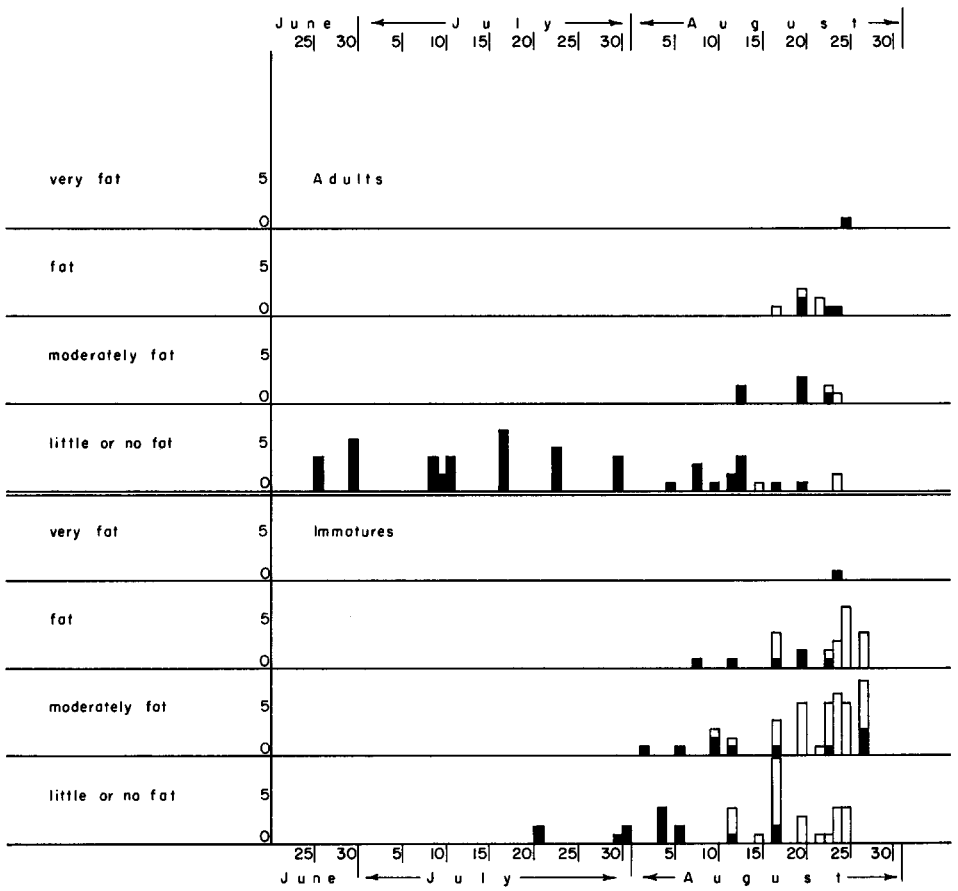

Figure 7. Number (on ordinate) of Gambel's Sparrows in each stage of fat accumulation. Solid bars = dissected specimens. Hollow bars = estimates of fat on live birds.

to finish. Also, since molt is a continuous process, it is unrealistic to try to set an accurate figure for the transition from one arbitrarily defined stage to the next.

Data for banded molting adults which were recaptured, when manipulated the same way, indicate that about 27 days elapsed between the start of the molt and the achievement of the "molt finishing" stage. We have no data on how long adults stayed in the "molt finishing" stage; but if we assume they stayed at least as long as did the young, then we should add six days to the above figure, making 33 days for duration of fall molt in an adult. Again, this is probably a minimum figure.

That these estimates for the individual are much shorter than those for all the birds trapped is to be expected, since I was catching members of a heterogeneous, unstable population.

Subcutaneous Fat

Figure 7 shows the distribution of successive stages of fat accumulation as revealed by examination of 166 individuals, 92 of which were dissected specimens and 74 of which were live birds caught 10 August or later. Estimates of the amount of fat on

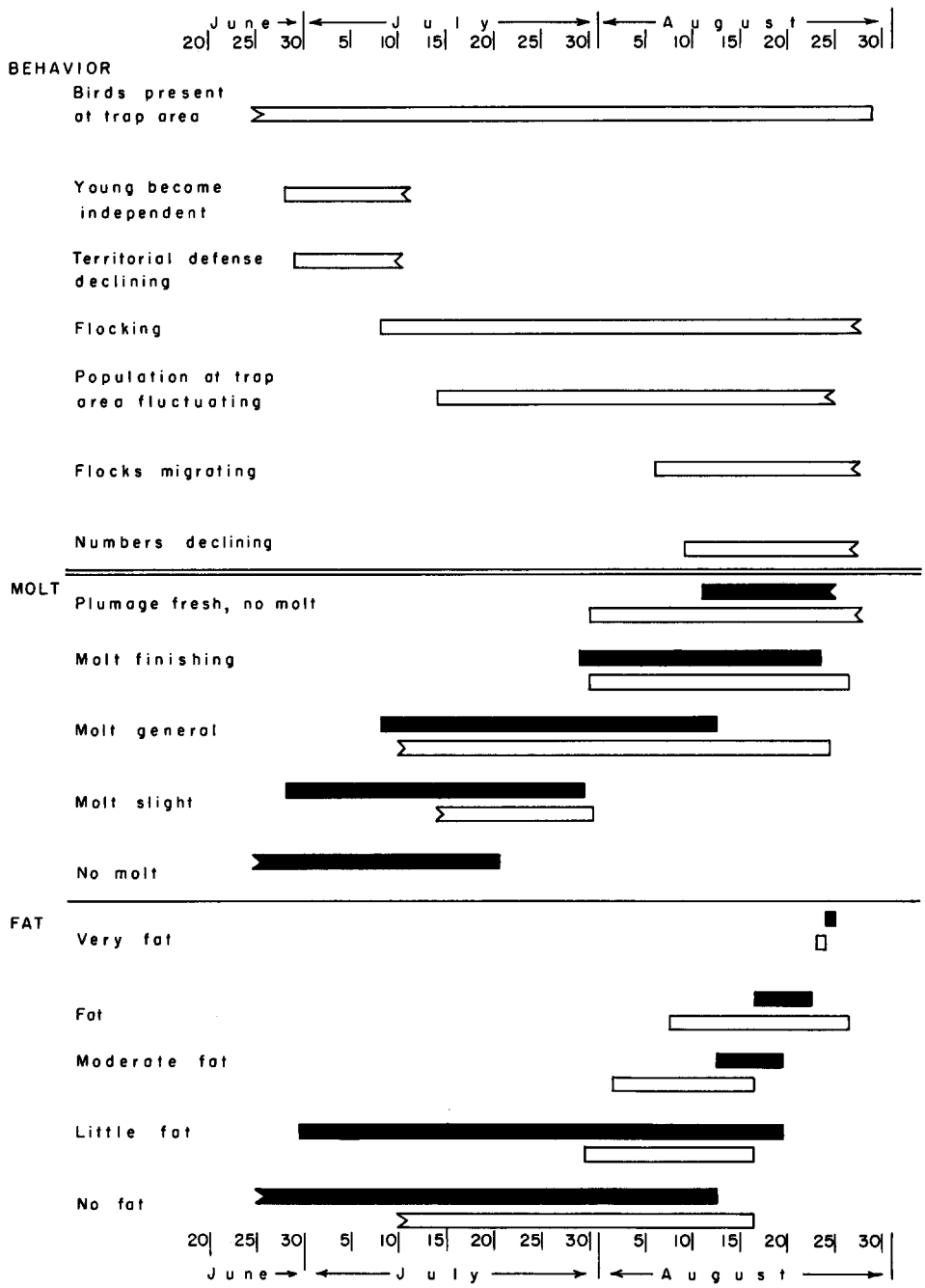

Figure 8. Duration of stages in postbreeding behavior, molt, and fat accumulation, summer of 1957. Solid bars = adults. Hollow bars = young (see text).

the live birds were made as described in the section on Methods. Before 10 August no live birds had enough fat for it to be obvious either from visual examination of the abdomen or from palpation of the subcutaneous fat pads.

The first specimen with more than "little fat" was an immature male taken on 2 August, the first classified as "fat" was an immature male taken on 8 August. Only two specimens were classified as "very fat": an immature male taken on 24 August and an adult male taken on 25 August. Figure 7 shows that, as in the molt, there is overlap in range of dates for the successive fat stages. Also, large numbers of birds either with little or no fat or only moderately fat were captured after 10 August, by which date migration was under way. This is indirect evidence that birds may begin migration before the maximum amount of fat is accumulated, and complements the evidence presented in the preceding section that birds may leave the breeding grounds before they have finished molting. Even as late as 24 August, 14 of the 19 birds examined were judged to be no more than moderately fat. In this connection, King and Farner (1963) conclude that "mechanisms of development of *Zugunruhe* and fat deposition [in Gambel's Sparrows] are essentially independent. . . ." Furthermore, King, Barker, and Farner (1963) found that the mean total energy reserve of Gambel's Sparrow migrants at Pullman, Washington, in autumn "is approximately equal to that of the overwintering birds in December; and is only about one-third of that of vernal migrants."

Chronology of Behavior and Physiological Concomitants

The chronology of events of postbreeding behavior and of the stages of molt and fat accumulation is graphed in figure 8. Both live birds and specimens are included in the graph of molt stages, whereas only dissected specimens are included in the graph of stages of fat accumulation. Smooth ends of the bars indicate specific dates for first or last observations; jagged ends indicate that the process in question had been in progress before the first observation or was to be continued after the last observation made at College. Figure 8 shows that the early fluctuations in population at the trapping area began before or during the first stages of molt and fat accumulation, and that the first migrating flock and the start of decline in numbers were recorded while birds still molting and laying on fat were being trapped. This graph also shows the long periods when birds still thin and with no or slight molt were trapped or collected nearby.

The long duration of periods for identical stages of molt and of fat contrast with the much shorter span of periods for identical stages of nesting (table 1, columns 3 and 4). This could be interpreted as further indirect evidence of the greater heterogeneity of the flocks sampled in late summer, compared with the breeding population of the same locality. An equally cogent interpretation would be that the same population differs as to the degree of synchronization for specific events in its cycle in spring and fall. King (1963) found that autumnal fat deposition in captive Gambel's Sparrows develops relatively slowly and lacks temporal precision.

CONCLUSIONS

The most important fact emerging from this study is that of the constantly changing population of Gambel's Sparrows at a locality on the breeding grounds in late summer. If our inferences from the banding data are valid, Gambel's Sparrows moved away from and into the trapping area in July and early August, before any dramatic change in behavior or any drastic or continuous decrease in numbers occurred. To detect the earliest movements away from this locality we could not have relied on

decrease in numbers, detection of migratory behavior, or the completion of molt or accumulation of fat. None of these events occurred until much later. Because departures go unnoticed if those leaving are replaced by others so that the net number of birds does not change, the only way to know that birds have moved away from a given area is by banding, and even this evidence is at best indirect. Obviously, more banding data for late June and the month of July are needed from several localities in the breeding range of this species before we can say that the situation as interpreted here, for one Gambel's Sparrow microcosm for one season, is a general phenomenon.

Because *Zonotrichia leucophrys* has become the favorite subject for a host of physiological and endocrinological studies, it is especially important not to lose sight of the fact that specimens collected in late summer, prior to the obvious diminution in numbers, are not necessarily birds which bred, or were hatched, at the collecting site. Part of the variation in such samples may be due to the individual variation within a single population, but part of it may be due to the fact that different samples are unwittingly taken from different breeding populations. Analysis of the physiology of native vertebrate populations is still in its infancy. A clear concept of the sources of variation within the populations sampled is necessary before the significance of such variation can be judged.

SUMMARY

This paper presents data on banding, behavior, body weight, gonad dimensions, molt, and fat in the postbreeding period for *Zonotrichia leucophrys gambelii* at College, Alaska (lat 64° 49′ N) in 1957. Between 26 June and 27 August, 346 birds were examined. Of these, 254 were banded and released, and 92 were kept for specimens. Thirty-two of the banded birds returned to the traps at least once.

Defense of territory began to decline by 30 June, flocks started to form by 9 July, migratory behavior was first seen 7 August, and decline in numbers began 9 August. By 30 August all the observation areas in which Gambel's Sparrows had been followed were vacant.

A number of facts indicate that Gambel's Sparrows taken on the breeding grounds in late summer, before any migratory behavior can be detected, are not necessarily birds which bred at the collection site. First, the number of Gambel's Sparrows caught in the trapping area (43 adults and 261 young) far exceeded the theoretical maximum of breeding pairs and their offspring (20 adults and 50 young) which would have been expected to forage there, based on counts of nesting pairs and clutches in May and June. Second, the percentage of each day's catch consisting of unbanded birds remained high throughout the trapping period. During the last 10 trapping days (12 August and later) unbanded birds constituted from 69 to 100 per cent of the total catch, with a mean of 84.3 per cent. Third, the total numbers caught, and the average number of unbanded birds caught per trapping hour, fluctuated markedly, beginning in mid-July, more than three weeks before migrating flocks were seen or a steady decline in numbers, not subsequently replenished, set in. Fourth, intervals between dates of first and last capture of banded birds were short: they average 9.8 days for six adults and 7.7 days for 22 young. The median value for the interval for 28 individuals is six days. Fifth, banding records of adults trapped in May and June provide indirect evidence that breeding birds may have moved away from their nesting grounds within the trapping area by early or mid-July.

The data reported here complement those reported for *Z. l. gambelii* at the same latitude in 1962 and 1963 by King, Farner, and Morton (1965). The timing of the

events of the nesting cycle, the lack of correlation between changes in body weight and amount of fat, and the lack of precision in timing of autumnal fat deposition are points of agreement. Chief differences between the two sets of observations involve the date molting birds were first collected, the duration of the period from earliest sign of molt to the date the last molting bird was taken, and the behavioral events used as an index for the start of migration.

Zonotrichia leucophrys has become a favorite subject for physiological studies. It is important to realize that samples taken from the same place on the breeding grounds in late summer may include individuals from several different breeding populations. Hence the variation within such samples may be due not only to individual differences but to intrapopulational differences as well.

ACKNOWLEDGMENTS

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