AUTUMN MIGRATION OF GAMBEL'S WHITE-CROWNED SPARROW THROUGH TIOGA PASS, CALIFORNIA

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Abstract.—Over a seven-year period, we found that 56.6% of 1476 Z. l. gambelii captured during autumn migration in a subalpine meadow were males and 67.4% were adults. The sex ratio, but not the age ratio, matched that of a nearby wintering population, so no conclusion could be reached about the destination of the study population. There were large interannual variations in numbers of migrants and in their sex and age ratios, indicating that several years of data acquisition are required for studies of this kind. The population showed a normal distribution in its time of arrival suggesting that it was derived from a single area of origin rather than from several merged subpopulations.

Males tended to arrive later in the season than females, but stop-over durations of the sexes were not different. Mean weight gain in both sexes during stop-over was about 0.4 g per day for a total of 1.8 g. Nearly 30% of the birds lost or failed to gain weight between their first and last capture, although most often this occurred when the recapture interval was one or two days. Birds known to be stopping over for a longer time than this usually showed a weight increase.

Many birds were sexed by the surgical procedure of laparotomy. The operation did not significantly affect any parameter except stop-over duration, which increased among laparotomized sparrows.

MIGRACIÓN OTOÑAL DE *ZONOTRICHIA LEUCOPHRYS GAMBELII* A TRAVÉS DEL PASO TIOGA, CALIFORNIA

Sinopsis.—Durante siete años se estudió la migración otoñal de Zonotrichia leucophrys gambelii en una pradera subalpina de California. De 1476 aves el 56.6% resultaron ser machos y el 67.4% adultos. La proporción de sexos, pero no la de edad, armonizó, con la de una población invernal de estas aves en un lugar aledaño, por lo que no se determinó nada referente al destino de la población estudiada. Hubo una gran variación interanual en el número de migrantes, su sexo y proporción de edades; indicativo de que se necesita recopilar datos por varios años para este tipo de estudios. La población mostró una distribución normal en su tiempo de llegada, lo que sugiere que las aves se originaron de una misma área y no de varias subpoblaciones.

Los machos tendieron a llegar después de la hembras, sin embargo la estadía de las aves fue similar para ambos sexos. La ganancia promedio en peso obtenida por hembras y machos durante su corto periodo de estadía resultó ser aproximadamente 0.4 g por dia, para un total de 1.8 g Cerca del 30% de las aves no ganaron o perdieron peso entre la primera y última captura, aunque esto ocurrió principalmente cuando el intérvalo de recaptura fue de uno o dos dias. Las aves que permanecieron mas tiempo que lo usual, mostraron una ganacia en peso.

El proceso quirúrgico conocido como laparotomía, se utilizó para determinar el sexo de las aves. La laparotomía no afectó ningun parámetro, excepto que aquellas aves operadas permanecieron más tiempo en el área, que aquellas que no fueron expuestas al proceso.

Gambel's White-crowned Sparrow (Zonotrichia leucophrys gambelii) is a nocturnal migrant that breeds in Canada and Alaska and winters in the western half of the United States and northern Mexico. Spring migration to the breeding grounds occurs in April and May; autumn migration to wintering areas in September and October (Cortopassi and

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Mewaldt 1965, Farner and Lewis 1973). In western populations the southward migration route is parallel to the Pacific Coast in California and is east of the Cascade Mountains in Oregon and Washington (Cortopassi and Mewaldt 1965). Although this bird has been investigated extensively in the field and laboratory, it has seldom been studied during migratory passage. Certainly this is a key time for migratory species and one that needs attention if we are to understand fully their ecology (Bairlein 1983). King et al. (1965a) reported on sex and age ratios of Z. l. gambelii during spring and fall migrations through southeastern Washington and Stewart et al. (1974) on age ratios during fall migration at California coastal sites. DeWolfe et al. (1973) and King and Mewaldt (1981) also obtained observations on Z. l. gambelii marked and recaptured in spring passage in the southern Yukon Territory and at Hart Mountain, Oregon, respectively. Here we report seven years of data obtained on Z. l. gambelii stopping-over in autumn at Tioga Pass in the Sierra Nevada of California. These are the first mark-release data obtained for this race during fall migration.

METHODS

This study was conducted at Tioga Pass, Mono County, California. Birds were captured in four-cell live traps placed at 24 traditional sites on 10.4 ha of subalpine meadow. Traps were baited each trapping day with 15–20 g of mixed bird seed. Trapping operations were begun each year in August as part of another study on Z. l. oriantha, well ahead of the first Z. l. gambelii arrival times. For the first two or three weeks of the migration, the study area was occupied simultaneously by Z. l. gambelii and Z. l. oriantha. The latter breed at this location and depart by the end of September (Morton et al. 1972, 1973). The trapline was operated, morning hours only, for an average of 4.2 d/wk during the time that Z. l. gambelii were present on the study area.

In 1968–1970 trapping was stopped in late September before the migration ended. The only information used in this report from those three years is the date in September when the first Z. l. gambelii was captured (see Table 1). In 1979–1985, trapping was conducted for the full duration of the migration period. All other data reported herein are derived from this seven-year period.

Following capture, birds were banded, weighed to the nearest 0.1 g with a Pesola scale, and aged from crown color as either immatures or adults. Fat classes of 0–5, 5 being fattest, were assigned from visual inspection of subcutaneous depots according to the criteria of Morton et al. (1973). Wing lengths (relaxed chord) were measured to the nearest mm with a ruler. Sex was determined by laparotomy or assigned from body weight and wing length values because males were found to be significantly larger than females. Mean wing length in 351 laparotomized males was 78.32 mm (SD = 1.59), whereas it was 73.66 mm (SD = 1.53) in 275 laparotomized females (P < 0.001, t-test). Body weights of males were also consistently larger than those of females. We

	Ad	ults	Imm	Total birds	
Year	Males	Females	Males	Females	per season
1979	104	54	39	31	228
1980	50	26	20	19	115
1981	86	87	25	22	220
1982	13	19	15	19	66
1983	38	18	88	48	192
1984	242	165	43	57	507
1985	48	45	25	30	148
Sum	581	414	255	226	1476

TABLE 1. Number of *Zonotrichia leucophrys gambelii* captured during autumn migration at Tioga Pass and their composition by age and sex.

define "arrival" of an individual as being the time of its first capture and banding. "Departure" is the time of its last capture on a subsequent day.

RESULTS

Number and composition of migrants.—A total of 1476 Z. l. gambelii was captured during the autumn migrations of 1979–1985 at Tioga Pass (Table 1). The sex ratio favored males in both age classes, being 58.4% in adults and 53.0% in immatures or 56.6% overall, a significant deviation from a 1:1 ratio ($\chi^2 = 26.0$, P < 0.001). Adults outnumbered immatures in five of seven years and in total, 67.4% vs. 32.6%.

The total number of birds captured per season varied nearly eightfold, from a low of 66 in 1982 to a high of 507 in 1984. Although adults outnumbered immatures by about two to one, the 1982 and 1983 data taken together show a reversed ratio. Immature males comprised only 17.3% (255/1476) of all birds captured in the study, but, in 1983, 45.8% (88/192) of the individuals trapped were of this cohort.

The percentage of males (56.6%) is identical to that of a population overwintering in the Owens Valley about 100 km southeast of Tioga Pass, but the proportion of adults (67.4%) in the Tioga Pass sample of migrants is considerably greater than that found in Z. l. gambelii wintering to the south or in fall passage (Fig. 1).

We had one recovery and one return. The recovery was of an adult male (band number 127169889) banded at Tioga Pass on 25 September 1981, and found dead in LaGrande, Oregon, on 28 April 1982. At that time it was undoubtedly in passage to its breeding area. The return was of an adult female (band number 132133081) banded at Tioga Pass on 15 September 1984 and captured again at Tioga on 24 September 1985.

Arrival and departure schedules.—The first Z. l. gambelii usually appeared on our study area each year during the second week of September, the mean and median date of first arrival for 10 yr being 11 September (Table 2). The largest deviation from this date occurred in 1985 when the first birds did not appear until 17 September. This delay coincided



FIGURE 1. Sex and age ratios of Zonotrichia leucophrys gambelii in passage at Pullman, Washington (King et al. 1965a), California at Tioga Pass (present study), and coastal sites (Stewart et al. 1974) or wintering in California at Bakersfield (Hardy et al. 1965), the Owens Valley, and Thousand Oaks (Morton 1984).

with a series of severe storms bearing rain, hail, and snow which originated in the Gulf of Alaska and then swept down the Sierra Nevada and through Tioga Pass from 3 to 11 September. During this period we checked lower elevation areas along the western edge of the Great Basin known from previous years to harbor migrants of several species, including Z. l. gambelii, but none were present. We assume that movements of many avian migratory species through the northwestern United States were suspended during this period of bad weather.

The final captures of Z. l. gambelii usually occurred during the second or third week in October, and the number of days they were known to

Year	First capture (September)	Last capture (October)	Migrants present (days)
1968	12	_	_
1969	12	_	_
1970	11	_	
1979	11	9	28
1980	10	18	38
1981	7	9	32
1982	14	15	31
1983	11	23	42
1984	9	15	36
1985	17	5	18
Mean	11 September	11 October	32.1 days
SD	2.7 days	6.2 days	7.8 days

TABLE 2. Dates of first and last captures of *Zonotrichia leucophrys gambelii* at Tioga Pass and number of days migrants were known to be on the study area.

be at Tioga Pass averaged 32.1 per season (Table 2). The end of migration was usually marked by snow storms and persistent cold. Such conditions occurred between 5 October (1985) and 23 October (1983). Thus, in 1985, storms caused the birds to arrive late and leave early, and migration through Tioga Pass lasted only 18 d.

The number of migrants arriving at Tioga Pass increased through the first four weeks of migration then decreased (Fig. 2). This pattern was followed by each sex and age group except the immature males. According to a Kruskal-Wallis one-way ANOVA, significant variation in mean arrival schedule and in mean departure schedule occurred among the four age-sex groups, P < 0.001 for both cases. Immature males consistently arrived and departed later each year than any other group. The mean date of their arrival was 6 October, seven days later than that of adult females, the earliest group (Table 3). The mean date of departure for immature males was 11 October, nine days later than that of adult females (Table 3). Both immature and adult males arrived and departed later than their female counterparts (P < 0.001, t-test, both schedules).

If large numbers of birds are captured at one location on the migration route with a uniform distribution of trapping effort throughout the migration period, then temporal dynamics of the migration can be assessed graphically. A plot of the cumulative percentages on probability paper against number of calendar days yields a straight line if the temporal distribution of migrant arrival times conforms to a normal distribution (Preston 1966). Our data fit such a distribution (Fig. 3). Also shown in Figure 3 is a line representing the course of spring migration in Z. l. gambelii.

Capture frequency.—Of 1476 individual Z. l. gambelii captured, 809 were never recaptured; 667 (45.2%) were repeats, that is, were captured again on a subsequent day before they left the study area. The propensity



FIGURE 2. Numbers of Zonotrichia leucophrys gambelii arriving at Tioga Pass by weekly intervals beginning on 7 September 1979-1985.

for repeating ranged between 38.0% and 65.6% over the six-plus weeks of the migration period with no seasonal trends (Table 4). Of those individuals repeating, 653 (97.9%) were captured 2–6 times. The remaining 14 birds were captured 7–9 times each (Table 4).

Stop-over duration.—From the data on birds repeating (captured 2-9) times each, Table 4), we have computed information on minimum stopover times at Tioga Pass. Throughout our analysis of data for this paper, we have checked to see if birds sexed by laparotomy differed statistically from those sexed by wing length and body weight. The only place that a significant difference was found was in amount of time these groups were known to be on the study area (=the minimum stop-over time; Table 5). For laparotomized birds the mean of this period was 5.9 d and for the others, 3.6 d, a significant difference according to a Mann-Whitney U-test (P < 0.001). In Table 5, therefore, only stop-over times of unlaparotomized birds should be considered to be representative of Z. l. gambelii in fall passage. There were no obvious changes in stop-over times as the migration progressed except that the first few birds to arrive in September stayed the longest period of time (mean = 7.6 d), and those arriving toward the end of migration stayed the shortest period (mean = 2.5 d). Stop-over times were not different among the four age-sex groups (Kruskal-Ŵallis one-way ANOVA, P > 0.05). The longest stop-over recorded for a male was 21 d and for a female, 23 d.

Body weights and fat classes.-Mean body weights and fat classes of

	Arı	rival1	Departure ²			
	Mean date	SD (days)	Ν	Mean date	SD (days)	Ν
Adult males	1 October	6.31	581	5 October	6.35	277
Adult females	29 September	8.11	414	2 October	8.65	160
Immature males	6 October	9.29	255	11 October	9.00	135
Immature females	1 October	10.10	226	7 October	10.53	95
All males	2 October	7.74	836	7 October	7.99	412
All females	29 September	8.93	640	4 October	9.62	255
All birds	1 October	8.38	1476	6 October	8.76	667

TABLE 3. Schedules of arrival and departure of Zonotrichia leucophrys gambelii at Tioga Pass (1979-1985).

¹ Determined as the day a bird was first captured and banded.

² Determined as the interval between banding and final capture on a subsequent day.

each of four age and sex groups were significantly higher upon departure than at arrival (Table 6; P < 0.001 for every comparison, *t*-test). Comparisons of body weights by sex and age indicate that males were heavier than females at both arrival and departure (P < 0.001 all cases, *t*-test). Adult males were only about 2% heavier than their immature counterparts, but this difference was significant at both arrival and departure (P < 0.025 both cases). Adult females, on the other hand, were heavier than immature females at arrival (P < 0.005) but not at departure. The young females were, in fact, heavier during the latter period, although not significantly so (P > 0.05).

We anticipated that body weights would increase during the stop-over period as birds refattened in preparation for another migratory flight. Furthermore, we expected the increase to be greatest in those birds that stayed the longest. These expectations were met somewhat when we compared body weights at arrival with those at departure according to stop-over duration (Table 7). For the sake of simplicity, we have pooled males and females of both age groups. Mean body weight of males was 26.57 g at arrival and 29.53 g in those that departed 10+ d later. In females, comparable data were 24.12 g and 27.06 g. Total gain was 2.96 g for males and 2.94 g for females. Gain in weight was steady for only the first four or five days after arrival, thereafter mean weights at departure remained well above those measured at arrival but fluctuated irregularly (Table 7). Weight gain for all males, regardless of stop-over duration, was 1.76 g and for all females, 1.83 g.

The average gain in body weight per day was 0.39 g (SD = 0.79, n = 411) for males and 0.36 g (SD = 0.73, n = 255) for females. These means were not different (P > 0.05, *t*-test). The gain per day did not vary significantly with time of season.

A few individual birds of either sex showed increases in body weight of 25-35% at a daily rate that was three to four times that of the averages



FIGURE 3. Cumulative percentage of Zonotrichia leucophrys gambelii arriving at Tioga Pass, 1979-1985. Day 0 equals 7 September. Line depicting spring migration taken from King and Mewaldt (1981).

given above. Some birds gained very little, however, and quite a few even lost weight. A frequency distribution of weight changes in Z. l. gambelii during stop-overs at Tioga Pass shows that these changes ranged from a loss of 4 g to a gain of 9 g in both sexes (Fig. 4). Of 411 males, 121 (29.4%) did not gain (-4 to 0 g change). Of 255 females, 72 (28.2%) did not gain (Table 7). Failure to gain occurred in about half of the birds during their first two stop-over days but this percentage declined



FIGURE 4. Frequency of weight changes exhibited by Zonotrichia leucophrys gambelii during stop-overs at Tioga Pass, 1979-1985.

sharply thereafter (Table 7). Laparotomy did not inhibit fattening. Failure to gain weight occurred in 26.6% of the laparotomized birds (n = 284) and in 30.8% of those not undergoing the operation (n = 384).

DISCUSSION

Routes and schedules of migration, sex and age ratios of migrants, their energy status as determined by body weights and fat class scores, and the slope of the curve representing the migration pattern, are primary

	Arrival periods								
No. of	7–13	14–20	21–27	28 Sept.	5–11	12–23	Total		
captures	Sept.	Sept.	Sept.	4 Oct.	Oct.	Oct.			
1 2 3	11	73	136	309	215	65	809		
	3	31	64	122	54	50	324		
	12	20	21	49	48	28	178		
4	3	9	12	35	15	8	82		
5	2	14	3	16	9	2	46		
6	1	5	1	8	5	3	23		
7	0	3	1	5	1	0	10		
8	0	1	0	2	0	0	3		
9 Total	0	1	0	0	0	0	1		
individuals	32	157	238	546	347	156	1476		
Repeats (%)	65.6	54.0	42.9	43.4	38.0	58.3	45.2		

TABLE 4. Number of times individual Zonotrichia leucophrys gambelii were captured according to period of arrival at Tioga Pass, 1979-1985.

areas of concern to investigations of autumnal migration in passerines (Hall 1981) and we shall discuss them in turn.

Precise routes being followed by Z. l. gambelii that appear at Tioga Pass are unknown. An adult male recovered during a subsequent spring migration was found in eastern Oregon about 860 km due north of Tioga Pass. Birds traveling southward through eastern Oregon on the reverse journey could easily encounter the Sierra Nevada and be deflected along their eastern side. It is only about 12 km from the eastern base of the mountains to the meadows at Tioga Pass. These meadows are not grazed by livestock and in the fall have a rich supply of standing grasses and sedges with mature seed heads that are fed upon heavily by Z. l. gambelii. It is possible also that the birds travel along the Sierran crest itself, moving from meadow to meadow. These areas are snow covered until May or June and are not utilized by overwintering birds nor by spring migrants.

	Un	laparotomi	zed	L	ed	
	Mean	SD	N	Mean	SD	N
7-13 Sept.	7.6	5.5	7	9.4	2.8	14
14-20 Sept.	3.9	3.2	25	7.7	4.9	59
21-27 Sept.	3.1	2.7	59	6.2	3.9	42
28 Sept4 Oct.	4.0	2.9	153	5.0	3.3	84
5–11 Oct.	3.5	2.8	92	6.0	4.3	40
12-23 Oct.	2.5	2.1	46	3.6	3.1	45
All birds	3.6	2.9	382	5.9	4.1	284

TABLE 5. Minimum stop-over times in days of *Zonotrichia leucophrys gambelii* at Tioga Pass according to period of arrival and sexing technique.

	Arrival					Departure				
	Body weight			Fat class		Body weight			Fat class	
Cohort	Mean	SD	Ν	Mean	SD	Mean	SD	N	Mean	SD
Adult males	26.74	2.10	581	1.52	1.08	28.51	2.41	277	2.64	1.22
Immature males	26.18	2.46	255	1.40	1.08	27.98	2.13	135	2.34	1.19
Immature females	23.73	2.08	226	1.49	1.07	26.19	2.30	95	2.76	1.23

TABLE 6. Body weights and fat classes of Zonotrichia leucophrys gambelii at first capture (arrival) and last capture (departure) at Tioga Pass, 1979-1985.

Individuals seldom revisit successfully utilized stop-over sites. Only one bird banded in a previous year was known to return to Tioga Pass. This supports the conclusion reached by Cortopassi and Mewaldt (1965) and DeWolfe et al. (1973) that White-crowned Sparrows migrate across broad fronts, probably using celestial rather than terrestrial landmarks to orient their nocturnal flights. Appropriate habitat for stop-overs must be sought wherever a particular migratory flight happens to end.

Sex and age ratios.—A latitudinal cline in sex ratio in wintering Z. l. gambelii is well-documented. Males comprise about 80% of populations in Washington, but only 25% or less near the California-Mexico border (King et al. 1965a, Morton 1984). Since Z. l. gambelii are highly philopatric (Mewaldt 1976), this cline is surely generated by a propensity for females to migrate further south than males. In the Owens Valley, only 100 km southeast of Tioga Pass (Fig. 1), a wintering population was 56.6% males (Morton 1984), precisely the same percentage found at Tioga. This could mean that birds stopping over at Tioga were near the end of migration. Age ratio data contradict this notion, however. Sixty-seven percent of the Tioga birds were adults whereas wintering populations to the south, including the Owens Valley, contain about 51 to 53% adults (Fig. 1). In contrast, adults comprised only 22% of the birds sampled during fall migration in southeastern Washington, approximately 1000 km north of Tioga Pass (King et al. 1965a). And 11 to 22% of fall migrants at insular, coastal, or near-coastal sites about 300 km west of Tioga Pass were adults (Stewart et al. 1974). Clearly fewer immatures pass through Tioga than would be expected from a source of birds to the north (the Washington sample) or from their proportions settling on wintering areas to the south. There could be differential mortality of immatures utilizing high altitude routes or perhaps they do not use these routes as readily as adults. Alternatively, many of the inexperienced birds may be responding to genetically-based navigational tendencies that cause them to be concentrated along coastlines (Ralph 1971) before winter settling occurs. A similar pattern exists in Blackpoll Warblers (Dendroica striata) near the Atlantic coast where adults comprise about 60% of fall migrants at inland sites but only 10-20% at coastal sites (Murray 1966, Nisbet et al. 1963).

		Ma	les		Females			
Stop-over duration (days)	Body v Mean	veight SD	- N	% failing to gain	Body v Mean	veight SD		% failing to gain
0	26.57	2.23	835	_	24.12	2.02	639	_
1	27.23	2.24	99	53.5	24.30	1.47	52	55.8
2	27.80	2.33	85	47.1	25.37	1.85	46	43.5
3	29.01	2.90	35	28.6	25.67	2.23	22	18.2
4	29.44	2.20	29	5.9	25.64	2.33	14	50.0
5	28.16	2.21	34	17.6	26.98	2.73	13	15.4
6	28.95	2.03	27	3.7	25.95	2.46	15	26.7
7	29.43	2.11	43	4.7	26.85	1.79	24	4.2
8	28.66	1.91	27	14.8	27.72	1.78	19	0.0
9	29.39	2.56	9	11.1	27.02	1.82	14	7.1
10+	29.53	2.22	23	7.7	27.06	2.02	36	13.9
All departures	28.33	2.42	411	29.4	25.95	2.21	255	28.2

TABLE 7. Body weight changes in Zonotrichia leucophrys gambelii at Tioga Pass as a function of stop-over duration. Day 0 is the day of initial capture (=arrival). Days 1 to 10+ are the days of last capture (=departure).

Arrival and departure schedules.—The first arrival of Z. l. gambelii at Tioga Pass each season was remarkably predictable. Only in 1985, when storms occurred, did arrival of the first birds deviate by more than four days from the mean date (Table 2). The date of their final disappearance, as well as total days they were present each season, were much more variable, both factors being related to migration-ending snowstorms. Spring passage is highly regular in Z. l. gambelii (King et al. 1965a, King and Mewaldt 1981) and thought to be controlled by daylength (Farner 1964, 1966). The proximate control of fall migration is not understood, although endogenous factors likely have a prominent role (Berthold 1975, 1984), and remains an intriguing question given the greatly different environmental experiences of adults and immatures prior to departure from summering areas.

Males tended to arrive at a later date than females, a result obtained also in fall migrants in southeastern Washington (King et al. 1965a), with immature males having the latest schedule of any cohort (Table 3). The reverse situation occurs in spring when males tend to travel ahead of females (DeWolfe et al. 1973) and to arrive earlier on the breeding grounds by a week or so (Oakeson 1954).

Despite the potential of storms to disrupt migratory movements through high altitude stop-over sites, the arrival schedule of the Z. l. gambelii population followed closely a normal distribution (Figs. 2 and 3), and without evidence of stragglers as observed in migrations at two other sites in spring (King and Mewaldt 1981). The rectilinear fit of the data found by us would be predicted if we were dealing only with passage migrants at Tioga Pass from one distinct subpopulation (Preston 1966). A comparison of our data with those of King and Mewaldt (1981) shows that spring migration is more synchronized than autumn migration in Z. l. gambelii (Fig. 3). Much the same situation has been found in other nocturnally migrating passerines (Preston 1966), including the Whitethroated Sparrow (Z. albicollis). Preston (1966) pointed out that the standard deviation of time of migration (=arrival at study area) is about 5 d in spring and 10 d in fall. At Tioga Pass this statistic for 1476 Z. l. gambelii was 8.4 d (Table 3). No comparable data are available for spring migration.

Stop-over duration.—In any mark-recapture study one must deal with artifacts caused by capture techniques. Birds may learn to avoid nets or traps. There is also a concern that traps can become feeding stations, thereby causing recapture frequency and stop-over duration to increase (Mueller and Berger 1966, Stack and Harned 1944). To minimize such effects we baited lightly and skipped trapping days.

Using nets and traps, DeWolfe et al. (1973) found 25.6% (51/199) of Z. l. gambelii on spring passage to repeat. Using nets and traps, and also in spring, King and Mewaldt (1981) obtained 28.4% (85/299) repeats. Our higher percentage of repeats (45.2%) could be due to differences in sample size, capture technique, collecting effort, or terrain. It could also be due to intrinsic differences in migration schedule. Migration is more rapid in spring than in fall (Fig. 3) and stop-over times reflect this. Mean minimum stop-over times in fall were 3.6 d (Table 5). In spring, when calculated by our method, wherein the date of banding is Day 0 and the next day is Day 1, etc., mean minimum stop-over times for Z. l. gambelii were 1.6 days (DeWolfe et al. 1973) and 3.1 days (King and Mewaldt 1981). These results are paralleled somewhat by the results of Stack and Harned (1944). In a 17-yr study at one site in Michigan, they captured with traps and nets 2712 Z. albicollis on spring migration and 1462 on fall migration. They found mean stop-over times to be 4.5 d in spring and 10.7 d in fall, with 24.6% of the birds repeating in spring and 63.3% in fall. Concurrent data were obtained on 2236 Slate-colored Juncos (Junco hyemalis) in spring and 3133 in fall. Mean stop-over times were 9.7 d in spring and 13.6 d in fall. Repeats were 29.6% in spring and 42.6% in fall. Borror (1948) also found stop-over duration in Z. albicollis to be shorter in spring than fall (5.2 vs. 8.7 days). Cherry (1982) found no difference between spring and fall stop-over durations in Z. l. *leucophrys*, but his sample sizes were relatively small. We conclude that lower percentages of repeats obtained on spring migrants could be due to lessened capture opportunities associated with shorter stop-over times.

Body weights and fat classes.—Numerous studies of migratory passerines enroute to wintering or summering areas show that stop-overs are used to rest and to replenish energy stores (Berthold 1975, King 1972). The usual assays of the latter are body weight and fat score changes, although total body fat has also been measured in Z. l. gambelii during both spring and fall passage. It was not as high in fall as in spring (King 1963, King et al. 1963). In our study, Z. l. gambelii males of both age

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classes showed an increase in mean body weight of 1.8 g during stopover. Adult females gained 1.5 g and immature females 2.5 g. Visible fat stores increased in all cohorts; the most in immature females (Table 6). Just before departing southward from summering areas in Alaska, immature Z. l. gambelii males weighed an average of 28.0 g (n = 12) and females 25.7 g (n = 9) (no weights reported for adults, King et al. 1965b). These weights closely resemble those obtained on the same two cohorts upon departure from Tioga Pass, 27.98 g and 26.19 g, respectively. This suggests that energetic preparation for departure following stop-over is the same as that of the initial migratory flight.

Although body weights varied widely, increases averaged about 0.4 g/d during the stop-over period, being most obvious during the first four or five stop-over days (Table 7). Extreme weight fluctuations varied from -4 to +9 g (Fig. 4). Some males (29.4%) and females (28.2%) failed to gain weight between first and last captures. The proportion of those losing weight decreased sharply after the second day (Table 7). Many investigators have reported weight loss in passage migrants during the first few days following arrival (DeWolfe et al. 1973, Dolnik and Blyumental 1967, Mascher 1966, Mueller and Berger 1966, Nisbet et al. 1963, Page and Middleton 1972, but see Cherry 1982). This has been attributed to trauma induced by handling (Mueller and Berger 1966) or to differences in appetite and "migratory mood" (Mascher 1966, Rappole and Warner 1976). We do not know if Z. l. gambelii failing to gain were near the end of migration or if they simply moved away from our trapline before fattening. We suspect that many moved some distance from the study area, perhaps even on a migratory flight, while still quite lean, a suspicion shared by Page and Middleton (1972) about Semipalmated Sandpipers (Calidris pusilla), also in autumn passage.

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