THE BIOLOGY OF IMMATURE MOUNTAIN WHITE-CROWNED SPARROWS (*ZONOTRICHIA LEUCOPHRYS ORIANTHA*) ON THE BREEDING GROUND

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Because of the relatively rich food supply, minimal competition, and low predation, the breeding grounds of migratory species are well suited for the growth and development of young birds. These same environments, however, especially at high latitude or high altitude, are often characterized by abrupt seasonal climatic changes at the end of summer and conditions may become unfavorable to the immature birds in a very short time. Before this happens, they must have attained the size and energy reserves necessary for a successful migration from the breeding area. To see how this is accomplished we studied the development of young Mountain White-crowned Sparrows (*Zonotrichia leucophrys oriantha*) for three summers. This is a little-studied migrant that breeds in high mountain meadows of the western United States and winters in the lowlands of the southwestern United States and northern México.

MATERIALS AND METHODS

The study was conducted during the summers of 1968–70 near Tioga Pass, Mono County, California. The subalpine meadows in this area at an altitude of 9500 to 10,300 ft were utilized as breeding habitat by *Z. l. oriantha*. More details on the study area were provided in a previous paper (Morton et al. 1972).

We were on the study area from June through September of all three summers. Most of our observations on behavior were done with the aid of binoculars and some activities, such as the feeding of young, were observed from the concealment of shrubbery or a blind.

The sex of adults was identified by laparotomy or by the presence of a brood patch or cloacal protuberance. Sex in immatures was determined by laparotomy. Females were marked with a red plastic leg band and males with a blue band above their Fish and Wildlife Service band.

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In 1969 and 1970, immature birds were held at our camp near the study area and exposed to natural oscillations in temperature and photoperiod. They were placed in $30 \times 21 \times 20$-cm cages, fed mixed seed and commercial game bird mix, and given water in dropper bottles. Body weights of captive and wild birds were measured to the nearest 0.1 g on a pan balance. Total body lipids were extracted with petroleum ether in a soxhlet apparatus.

RESULTS AND DISCUSSION

EVENTS INSIDE THE NEST

Hatching. Young *Z. l. oriantha* hatch between 9 and 15 days after the beginning of incubation, the average in 55 cases being 11.8 days (Morton et al. 1972). By examining nests and watching incubating females, we could often determine hatching times with an error of a few minutes. Hatching times of still damp nestlings were arbitrarily set at 15 min before discovery; hatching times of dry nestlings were not estimated. Almost all of the chicks hatched in the morning hours and during midafternoon (fig. 1). We suspect that a much greater proportion hatched in the early morning or during the previous night than is indicated because many newly hatched young found in the morning had dry plumage.

Six times we were watching incubating females from a blind about 2 m distant when young hatched. During the hatching process, the females frequently turned the eggs with their feet or beaks and made shaking or settling movements with their bodies. Once a female picked up in her beak a chick still encased by more than half of a shell. She removed the shell from the chick, dropped both into the nest, and then ate the shell. Females always consumed shell fragments at the nest. Chicks that died during the hatching process were carried from the nest by the head and probably discarded some distance away.

The average size of the 143 complete clutches that we observed was 3.93 eggs
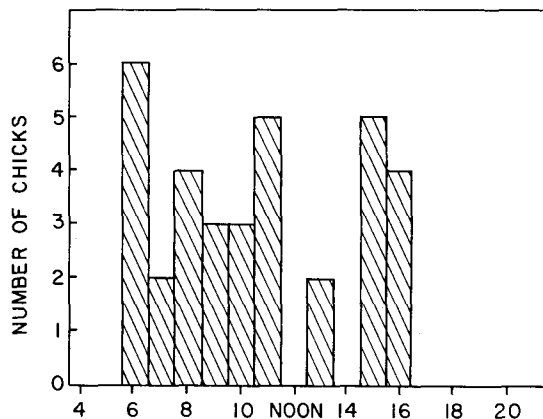
FIGURE 1. Hatching times of *Zonotrichia leucophrys oriantha*.

(Morton et al. 1972). Incubation began at the time the clutch was completed or with the laying of the penultimate egg.

The synchrony of hatching for 77 clutches that contained a total of 279 eggs that hatched is illustrated in table 1 (Day 0 refers to the first day that any or all of the chicks hatched in a given nest). Clearly, in terms of the age relationships among nestlings, there is an excellent hatching synchrony, since the chicks in a given nest were usually separated by one day of age or less.

Development of Nestlings. The appearance and behavior of *Z. l. oriantha* nestlings are very similar to those of *Z. l. pugetensis* and *Z. l. nuttalli* as described in detail by Blanchard (1941) and Banks (1959). Below are supplementary observations on *Z. l. oriantha*.

Day 0: Bodily movements are feeble and poorly coordinated except for the gaping response. Nestlings can gape 10 min after hatching and are usually fed within an hour after hatching. In one case, we observed one being fed successfully 14 min after hatching. Gaping occurs when the female leaves the nest, sometimes while she is gone, and again when she or the male hop onto the nest rim.

Day 1: Wings and legs are moved vigorously when the nestling is handled. Gaping occurs when the female leaves the nest and intermittently thereafter until her return. Vibration of the nest is a strong stimulus for gaping.

Day 2: Motor coordination is improved. Some nestlings can right themselves when placed on their backs. Gaping occurs as on Day 1, and a "cheep" vocalization may occur upon handling. The primaries have erupted by midday.

Day 3: Nestlings can locomote slightly through scrambling efforts when removed from the nest. Gaping occurs as before except now there appears to be a functional aural response in that gaping may occur well before the adult hops onto the nest. The eyes are still closed. Feather sheaths protrude slightly from the ventral and spinal tracts. The first noticeable increase in metabolic rate occurs (Morton and Carey 1971).

Day 4: Righting is now easily accomplished by most nestlings. Gaping tends to occur only when adults approach the nest. The eyes are starting to open. Feathers in all major tracts except the caudal tract have erupted. The nestlings may "cheep" in alarm and defecate when handled.

Day 5: Some nestlings gape when handled and some crouch in an apparent fear reaction. The eyes are open in almost all individuals. The mean age at which eyes open in 87 nestlings was 4.6 days (range 4–6 days). The rectrices have now erupted and barbs have broken through at sheath tips in the major body tracts. In terms of feather development, *Z. l. oriantha* seem to be about a day ahead of *Z. l. nuttalli*, as described by Banks (1959).

Day 6: Nestlings are alert and their movements are fairly well coordinated. They gape if the nest is vibrated. They can sit erect and balance on their feet with wings held to the sides. When placed on a perch they maintain themselves, but awkwardly. Barbs have erupted from tips of sheaths in all the flight feather and contour feather tracts. All nestlings show a well developed shivering response when exposed to cold air (Morton and Carey 1971). Nestlings can cue visually on adults and may gape when an adult is still a meter or so away while approaching the nest.

Day 7: Nestlings may sit up in the nest and exercise their wings. Many now defecate, give an open-mouth threat display, or a loud fright note when handled. This note will

TABLE 1. Synchrony of hatching in *Zonotrichia leucophrys oriantha*.

	Day 0	(%)	Day 1	(%)	Day 2	(%)
Number of clutches wherein all hatching was complete	37	(48.0)	34	(44.2)	6	(7.8)
Number of eggs hatched	222	(76.8)	61	(21.1)	6	(2.1)

TABLE 2.   Age of fledging in various races of *Zonotrichia leucophrys*.

Race	Migratory or nonmigratory	Latitude	N	Mean age at fledging (days)	Reference
Z. l. nuttalli	NM	37°48′N	23	10.1	Oakeson (1954)
Z. l. oriantha	M	37°55′N	221	9.5	Present study
Z. l. pugetensis	M	48°30′N	26	9.6	Oakeson (1954)
Z. l. gambelii	M	62°07′N	13	9.0	Oakeson (1954)

cause siblings in the nest to hop out immediately and hide in nearby vegetation. They can survive overnight at this age out of the nest. Oakeson (1954) has noted one case wherein disturbed *Z. l. gambelii* left the nest on Day 7. Perching is easily accomplished and the insulative feather layer and control of metabolism are sufficient for maintaining a high body temperature.

Day 8: The responses to handling are the same as on Day 7. When placed on the ground, they run with good coordination.

Day 9: Nestlings are very alert. When the nest is approached they may jump out and run into cover. If tossed into the air, they flap but generally do not make horizontal progress. However, one chick flew about 10 m in a low ground-skimming flight when we frightened it from the nest. Many leave the nest on this day even when undisturbed.

Day 10: Usually the remainder fledge on this day when undisturbed. Some can fly only a few meters and others apparently not at all at this stage. It is now possible to state the time of fledging in all but the nominate race of *Zonotrichia leucophrys* (table 2). The three migratory races all fledge at an earlier age than the nonmigratory race (*Z. l. nuttalli*). Disregarding *Z. l. oriantha*, there is an inverse relationship between latitude and age at fledging. The relatively early fledging age in *Z. l. oriantha* could be related to its migratory habit or to breeding at high altitude, if high altitude imposes many of the same selective pressures on breeding birds as high latitude.

Body Weight. Body weight increased rapidly in nestlings during the first 5 days of life (table 3). Thereafter, the rate of growth decreased considerably, apparently due to the metabolic cost of thermoregulation and feather growth. The rate of growth in broods of two, three, four, or five nestlings were not significantly different.

Parental Attentiveness. After hatching, nestlings always received their first food from the female parent. The male began bringing food some time during the day of hatching, from minutes to hours after feeding was initiated by the female. We did observe one

case where the male approached with food within a few minutes after two chicks had hatched. In this case the female remained on the nest and gave an open-mouth threat. The male hesitatingly gave her the food and she swallowed it. This was repeated twice more during the next 54 min, then the female for the first time left to gather food for the nestlings. This is in contrast to DeWolfe's (*in* Bent, 1968) observation that in *Z. l. nuttalli* the male does not visit the nest until the young are 2 to 3 days old.

After both parents had begun to feed, a routine was often established wherein the female would feed and begin brooding. As the male approached with food, the female became very alert and usually left the nest just before the male arrived, giving a muted note as she left. If the female did not leave when the male approached, the male gave the food to her, whereupon she stood up and fed the nestlings, and resumed brooding. This behavior was observed when the nestlings were Day 3 or younger or during the cold hours of early morning. Before the nestlings begin to thermoregulate, the female must juggle the dual responsibilities of brooding and feeding. Clearly, priorities between these responsibilities change constantly during this time.

TABLE 3.   Body weight and rate of growth in nestling *Zonotrichia leucophrys oriantha*.

Age (days)	N	Mean body weight (g) ± S.D.	Growth rate constant (days⁻¹)[a]
0	56	2.70 ± 0.44	—
1	95	4.28 ± 0.85	0.461
2	96	6.56 ± 0.92	0.428
3	93	9.24 ± 1.25	0.343
4	96	12.39 ± 1.68	0.295
5	95	16.12 ± 1.85	0.263
6	65	17.62 ± 1.50	0.090
7	56	19.44 ± 1.46	0.096
8	45	20.14 ± 1.61	0.037
9	17	20.36 ± 1.35	0.012
10	6	20.78 ± 1.37	0.020

[a] Calculated as $\ln$ body weight on day $n + 1 - \ln$ body weight on day n.

TABLE 4. Rate at which broods of *Zonotrichia leucophrys oriantha* are fed. Brood size is three or four in all cases.

	Age (days)	Number of broods observed	Time observed (hr)	Number of feedings				
				by female	(%)	by male	(%)	Feedings per hour
In nest	0	5	15.3	40	(80.0)	10	(20.0)	3.3
	1	5	13.7	41	(67.2)	20	(32.8)	4.5
	2	3	7.1	22	(61.1)	14	(38.9)	5.1
	3	5	14.1	47	(51.1)	45	(48.9)	6.5
	4	4	12.4	59	(54.6)	49	(45.4)	8.7
	5	6	19.7	109	(44.9)	134	(55.1)	12.3
	6	5	11.8	81	(56.6)	62	(43.4)	12.2
	7	5	23.0	174	(56.3)	135	(43.7)	13.4
	8	2	4.0	23	(50.0)	23	(50.0)	11.6
	9	4	8.1	86	(65.2)	46	(34.8)	16.4
	10	2	7.0	56	(67.5)	27	(32.5)	11.9
Fledged	10	1 (#7)	4.1	24	(57.1)	18	(42.9)	10.2
	11	1 (#7)	5.5	26	(100.0)	0	(0.0)	4.7
	13	1 (#K)	3.2	38	(67.9)	18	(32.1)	17.5
	14	1 (#7)	4.0	38	(100.0)	0	(0.0)	9.5
	15	1 (#K)	2.4	8	(66.7)	4	(33.3)	5.0
	17	1 (#7)	3.8	12	(100.0)	0	(0.0)	3.2

The rate at which nestlings were fed was lowest on Day 0, increased through Day 5, and remained about the same thereafter (table 4). The average size of the broods observed was 3.6 nestlings and we estimate that two nestlings were fed at each visit. This means that each nestling was fed about twice per hour on Day 0 and about seven times per hour on Day 5. The relative contributions of the adults to feeding nestlings changed with time (fig. 2). On the day of hatching the females made 80% of the observed feedings and the males 20%. The efforts of the males increased steadily and from Day 3 through Day 8 they performed about half of the feedings. Thereafter their efforts decreased in relation to those of the females.

An interesting point can be made here about fecal sacs. In our observations, the adults always ate the sacs, either at the nest or after flying with them to a nearby perch. Watching the routine at a nest, one has to be impressed by the quantity of sacs consumed in a day of feeding nestlings of advanced age. For example, we estimate that a brood of four nestlings produces about 70 fecal sacs on Day 5. Nine sacs that we collected from Day 5 nestlings had a mean weight of 0.61 g (S.D. = 0.27). If the adults eat equal numbers of sacs, then each one consumes 21.4 g of fecal material during that day! We do not know the nutritional value of these sacs, but they must have a significant effect on the water and energy balance of the adults. This is a particularly interesting aspect of the energetics of breeding birds that should be investigated.

The rate at which nestlings were fed varied with time of day as well as with age. In one case we observed a nest with three Day 7 nestlings from before daylight until after dark (fig. 3). The female first left the nest at 05:20. At 05:27 the male appeared and fed the nestlings. The female fed 2 min later. Both adults then fed about every 6 min for the next 2 hr. Their rate of feeding decreased gradually until early afternoon when a low of
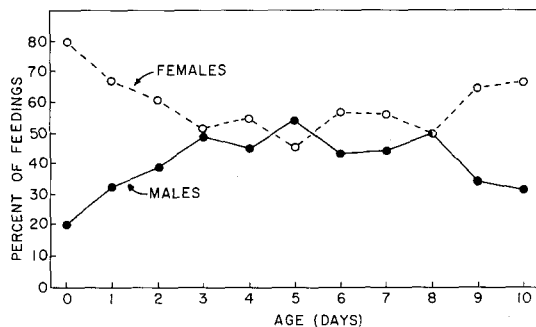

FIGURE 2. Relative contributions of male and female *Zonotrichia leucophrys oriantha* to feeding their nestlings.
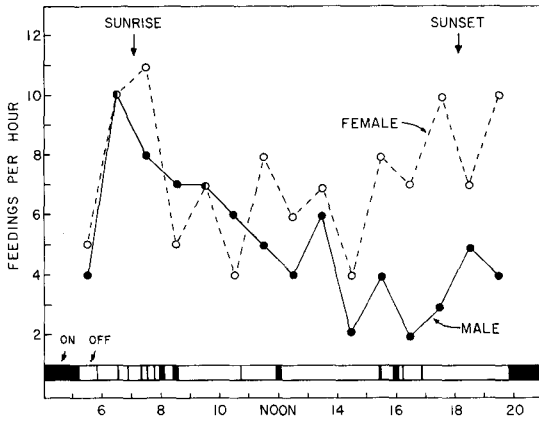
FIGURE 3. Diurnal pattern of feeding of Day 7 *Zonotrichia leucophrys oriantha* nestlings by adults. Brood size is three. Horizontal bar shows brooding time of female.

only six feedings occurred between 14:00 and 14:59. Thereafter the female fed every 6 to 9 min, but the male fed only every 12 to 30 min.

The decline in feeding by the male corresponded to an increase in his propensity to patrol the territory and assume singing perches. Between the time the female terminated nighttime brooding at 05:20 and resumed it at 19:52, she brooded a total of 71 min in 14 bouts. This is an indication, of course, of the good thermoregularity abilities of Day 7 nestlings.

It appears that the greater total daily amount of feeding performed by females compared with that of males, at least in older nestlings, occurs because of their greater activity late in the day. It is our impression that the greater contribution to feeding by females early in nestling life (Day 0–2) occurs not only because they feed more in late afternoon but also because the males have not yet established a regular pattern of feeding.

We have not made a systematic inventory of what nestlings are fed, but from direct observations and from a few samples retrieved from the gullets of nestlings, it appears that a large variety of items are fed: insects, spiders, earthworms, seeds, tiny flowers, willow leaves, and catkins. In terms of utilizable energy, insects are undoubtedly the most important food.

EVENTS OUTSIDE THE NEST

Parental Attentiveness. Fledging may be stimulated by stress to nestlings or by the adult's refusal to feed them unless they come out of the nest (Morton and Carey 1971). At this time, the chicks hop out of the nest and

scramble into nearby vegetation where they perch and are fed by the adults. It is very difficult to obtain information about parental attentiveness after the brood has fledged, and only a few quantitative data on this aspect of the life of young passerines have been collected (cf. Blanchard 1941; Morehouse and Brewer 1968; Tyrväinen 1969). We did make many observations of recently fledged young, and two nests (#7 and #K) were located below road banks which gave us good vantage points for observing. Our data on these broods are instructive (table 4, lower portion). In the case of nest #7, a brood of three that fledged on Day 9, the male did a considerable amount of feeding (42.9%) on Day 10, but none at all during our observations on Days 11, 14, and 17. At #K, another brood of three that also fledged on Day 9, the male did 32.1% of the feeding during Day 13, and 33.3% during Day 15 observations. These data support our impression, gained from many short periods of observations on other broods, that the decreased role of feeding by males seen in older nestlings continues after fledging. Many males feed little, if at all, after fledging has occurred. This change in the time and energy budget of adults has a noticeable effect on their seasonal changes in body weight. The male population begins to gain weight at the time of fledging and females lose weight.

Fledgling Development. The following chronology of events with regard to age has been compiled from field notes on banded birds with known histories.

Days 10–15: Fledglings of this age remain perched in bushes near the nest and are usually within a few meters of one another. When an adult appears with food they beg loudly and often flutter their wings and scramble forward. The adult may use this behavior to lead them to another location. The young can make awkward 5–20-m flights, but they are very reluctant to do so. A few fecal sacs are still being produced and eaten by adults at this stage.

Days 16–20: During this time, the young are usually on or near the parents' territory and are being fed by them. They are, however, beginning to forage for themselves. We have captured four that were Day 19 in traps baited with seed. Two of these were held in captivity. One "cheeped" constantly and did not feed. It survived about 18 hr. The other did not vocalize, began feeding the first day in captivity, and survived.
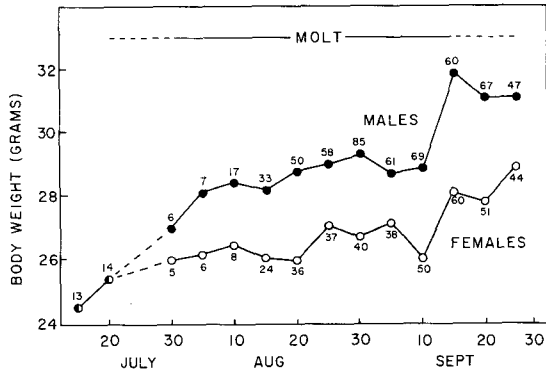
In three cases we knew the age of young

FIGURE 4. Seasonal changes of mean body weight in wild immature *Zonotrichia leucophrys oriantha.* Numbers indicate sample size.

FIGURE 5. Seasonal changes of mean body weight in captive immature *Zonotrichia leucophrys oriantha.*

when the female laid the first egg of a second brood. In one case they were Day 16, and in two others they were Day 17. At least some of these young survived because two of them were later captured on Day 28 when they weighed 22.5 g and 26.5 g. This means that the interval between fledging and the beginning of incubation of the second clutch is about 11 days; the same interval was found for *Z. l. pugetensis* by Blanchard (1941). We suspect that the male may adjust his usual behavior and take over the feeding of fledglings in the few cases wherein the female begins incubating a second clutch, as in *Z. l. pugentensis* and *Z. l. nuttali* (Blanchard 1941).

Days 21–25: The young may now have moved substantial distances from the original territory. For example, we netted a Day 22 individual 0.5 km from its nest. They can make flights of at least 100 m, but prefer to skulk in thick cover and run when chased. At least one adult, usually the female, is still with them and feeding.

Days 26–30: The female may still travel with the young and feed them irregularly. Twice we captured an adult female and two of her Day 26 young at the same time, once with a net and another time with a trap. In one case, the young weighed 24.5 g and 27.8 g and, in the other, 27.6 g and 31.7 g. These young were strong flyers and of adult body size. During this age period, the young may form into small flocks. In all 3 years in early August, we noticed flocks of five to eight immature birds traveling together. Once we captured four from a group like this. They were from two different broods and all were Day 28.

Beyond this time the young seem to be totally independent and may disperse to other locations. For example, we captured one Day 34 male 2.9 km from his place of hatching.
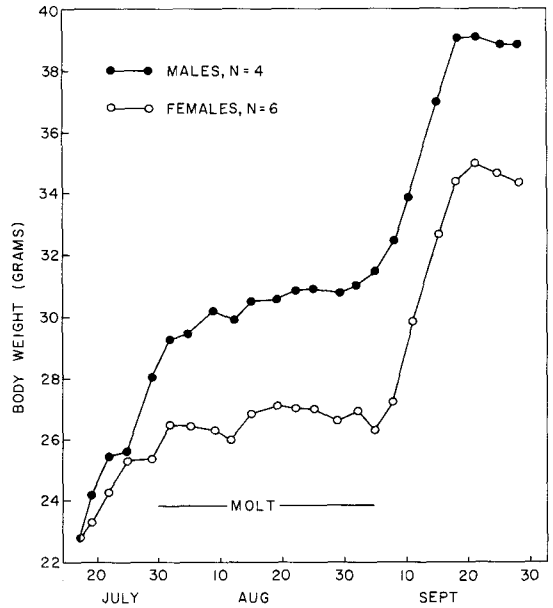
Body Weight. In mid-July each year we began obtaining body weights of immature birds. These individuals were about 2 to 4 weeks of age and sex was not determined in most of them (fig. 4). From the first of August onward, however, laparotomies were performed on many immatures to determine sex, and mean body weights for males and females can be shown. Males were significantly heavier than females in all samples ($P < 0.05$). In both sexes, adult body size was attained during early August and weights were fairly stable during the period of postjuvenal molt. This is similar to the findings of Newton (1968) on Bullfinches (*Pyrrhula pyrrhula*) and of Myrcha and Pinowski (1970) on European Tree Sparrows (*Passer m. montanus*).

An increase in body weight due to premigratory fattening occurred in mid-September. During one 5-day interval, this increase averaged 2.1 g in females and 3.0 g in males. Gain in individuals was much greater than this, but the curve for the population is damped due to a disparity in age of about 6 weeks and the migration of individuals once they fatten. There is no doubt that extensive fat reserves were accumulated by individuals. We captured many immatures in September with visibly bulging fat deposits. Females with this appearance often weighed 32–35 g, and males weighed 36–40 g. A sample of six fat females taken in September 1968 and 1970 had ether-extractable lipid reserves amounting to 13.5 ± 3.7% of total body weight. This is

similar in quantity to the reserves of fattened adults in this population just prior to migration.

A more precise indication of seasonal changes in body weight was obtained from a group of captive immatures (fig. 5). The weights of these individuals have been shifted to a common point in their cycle, namely, the first day of postjuvenal molt, in order to show more realistically the magnitude of the fattening response and its relationship to molt. The end of growth and stabilizing of body weight in the captives was in synchrony with wild birds. Weight in females during molt was about the same as in wild birds (26–27 g), but captive males were about 2 g heavier than their wild counterparts (30–31 g vs. 28–29 g). We do not have an explanation for this difference.

Following completion of molt, the captives showed a marked fattening response. The weight increase was about 28% in females and 21% in males. This difference suggests that the extra weight carried by males during the molt was due to fat storage.

The rate and magnitude of the fattening response indicate that it is due to a regulated hyperphagia. This has been suggested to occur also during autumnal fattening in adult Z. l. gambelii (King 1963; King et al. 1965).

Molt. At about 12–14 days of age, the last traces of natal down disappear and the juvenal plumage is assumed. There is never a complete, separate juvenal plumage since flight feathers, especially the rectrices, are not full length when the postjuvenal molt of body plumage begins. This was true also in 11 species of finches studied by Sutton (1935).

The age at which postjuvenal molt begins and its duration in wild individuals are extremely difficult to determine. Several times we captured young about 4 weeks of age in which molt had recently begun, and from data on retrapped individuals we estimate that it lasted 4 to 6 weeks. More precise data were obtained from seven captives (three males, four females) that we banded as nestlings and later trapped and placed in cages at 18–20 days of age. Their postjuvenal molt began at 34.3 ± 5.2 days of age, and lasted for 32.4 ± 4.6 days. This compares closely to the duration for postjuvenal molt in Z. l. gambelii of 33 days found by DeWolfe (1967) and of 34 days by Morton et al. (1969). The age at which postjuvenal molt begins in finches has been determined for very few species; it began at 6–7 weeks of age in the Song Sparrow (*Melospiza melodia*) (Nice 1943), at about 4

weeks of age in the Grasshopper Sparrow (*Ammodramus savannarum*) (Sutton 1941), and at about 8 weeks of age in the Andean Sparrow (*Zonotrichia capensis*) (Miller 1961).

The data in figure 5 suggest a precise relationship between the end of molt and fattening. In general, the two events seemed to be related in the wild population in the manner portrayed in that fattening began as molt ended. There were exceptions to this, however. We captured many immatures nearing the end of molt that had already begun to fatten, and conversely, but less often, we saw lean birds with fresh plumage. In one captive male (not included in fig. 5), fattening began 14 days after the end of postjuvenal molt. We suggest, therefore, that autumnal fattening in immature Z. l. oriantha is controlled independently of postjuvenal molt.

It may be that one or both of these functions are controlled in a manner completely different from that in adults. In the latter we found (Morton, Horstmann, and Carey, unpubl.) that fat tended to be gradually accumulated during molt and that about half of the total autumnal premigratory reserves had been deposited by the time molt was completed. Considering their immediately preceding different life histories, it is not too surprising that separate mechanisms with respect to molt and fat accumulation could be operating in adults and immatures on the breeding grounds.

The question of how metabolic preparation for autumnal migration is controlled in immature migratory birds is only one of a host of intriguing questions that remain unanswered about migrants of all ages.

ACKNOWLEDGMENTS

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