

AUTUMNAL MIGRATION DEPARTURE SCHEDULES IN MOUNTAIN WHITE-CROWNED SPARROWS¹

MARTIN L. MORTON AND MARIA E. PEREYRA

Department of Biology, Occidental College, Los Angeles, CA 90041-3392

Abstract. During seven autumn seasons, Mountain White-crowned Sparrows (*Zonotrichia leucophrys oriantha*) departed on migration from a subalpine meadow in September and October. On average, juveniles migrated 3.2 days earlier than adults and there was no difference in schedules of males and females within these two classes. Data from frequently trapped individuals showed that they departed as soon as they became fat. Peaks in departure dates did occur but only once did one occur just before a storm. Mean departure dates among years varied by 14 days in juveniles and eight days in adults. This interannual variation was related to reproductive schedule; departure of the population being delayed by about one day for every two days of delay in nesting (the latter being caused by late-lying snows). Reasons for a decrease in the fledging-migration interlude in juveniles in heavy snow years could have involved an overlapping of postjuvencal molt with premigratory fattening and/or telescoping of molt. Late-born young did not migrate later than those born earlier nor were they leaner at the time of departure. Temporal compensation in adults during heavy snow years was accomplished primarily by overlapping postnuptial molt with parental care and sometimes with premigratory fattening because molt duration did not decrease with season. Premigratory fattening occurred in about nine days in all birds with the average gain per day being 2.3 to 2.6% of initial body mass for the four sex-age groups. Propensity to return to the study area was not related to the body mass at departure in the previous autumn or to its date. It was hypothesized that the attainment of peak fat stores usually served as the proximate stimulus for migration.

Key words: *Migration; autumnal migration; migration departure; White-crowned Sparrow; Zonotrichia; premigratory fattening.*

INTRODUCTION

It is generally agreed that the autumnal migration of birds away from their summer breeding grounds or place of birth enhances their survival by allowing them to avoid exposure to the severe weather conditions and low food supplies that prevail in these areas during winter (Lack 1968, Gauthreaux 1982). In the ultimate sense, this is the reason for the migration. But what are the environmental or proximate factors that directly cue or stimulate migration behavior itself? More than 60 years ago, Rowan (1931) hypothesized that autumnal migration was controlled physiologically by gonadal involution which was itself linked causally to decreasing photoperiods. Other environmental factors, such as food availability, ambient temperature, barometric pressure, and changes in leaf color, did not correlate. A more recent view, based on field observations of migrants in passage and on extensive recordings of migration behavior in captives (Zugun-

ruhe), is that the urge to migrate in autumn is the expression of a circannual rhythm that is kept in synchrony or phased by the photoperiod (Gwinner 1971, 1977, 1986, 1990; King and Farnner 1974; Berthold 1975, 1988). This hypothesis, unlike Rowan's, can also be applied to the biology of juvenile migrants. Despite this apparent improvement in our understanding of how proximate controls are exerted, more information on migration departure dates of individuals is badly needed in order for migration theory to advance. Such information is exceedingly rare, especially in passerines that are too small to carry the currently available types of long-distance transmitters. Herein we provide data on departures of the Mountain White-crowned Sparrow (*Zonotrichia leucophrys oriantha*) from a breeding location at Tioga Pass in the Sierra Nevada range of California. Like most migrants that have been carefully studied, *Z. l. oriantha* exhibit hyperlipogenesis and fat deposition prior to migration departure (Morton et al. 1973). An interesting feature of this response in *Z. l. oriantha* is that upon its completion the birds migrate; they sel-

¹ Received 24 January 1994. Accepted 8 June 1994.

dom linger on the summer area, even for a day, once they have reached their peak premigration body mass (see fig. 4 in Morton 1992a). One can assume, therefore, that if an individual *Z. l. oriantha* was regularly trapped during its period of premigratory fattening, especially during the final days of that period, the date of its last capture can be taken as the time of migration departure, providing that regular trapping sessions were conducted beyond the date of last capture.

Data of this type are presented here on birds of known age and sex over a seven-year period with the hope that they will further our understanding of both the proximate and ultimate controls of autumnal migration schedules.

METHODS

The principal part of the study area was a 50 ha subalpine meadow, elevation 3,000 m, that borders on Yosemite National Park at Tioga Pass, Mono County, California. On this Tioga Pass meadow (TPM) from 1979 to 1985 a trapline with 24 stations, each with one to three seed-baited livetraps was tended, three to five days a week, from the summer months on through the time in October when all *Z. l. oriantha* had disappeared. Focal trapping of adults on their territories was also conducted, usually in June or July, using seed or a conspecific decoy to lure the desired individuals. All trapping was conducted in the morning hours and traps were baited lightly so that the seeds were quickly consumed each day by either birds or rodents. Body masses were measured to the nearest 0.1 g with a Pesola spring scale. All birds were banded with U.S. Fish and Wildlife Service bands and breeding adults were marked additionally with three plastic color bands in unique combinations. Juveniles were banded at the first opportunity, either as nestlings (exact age known) or subsequently as self-sufficient fledglings (exact age unknown) that had entered traps.

The majority of trapping was conducted on TPM but we frequently visited, and sometimes trapped, other nearby patches of *Z. l. oriantha* habitat in September and October in order to verify that fattened birds that had disappeared from the vicinity of the TPM trapline had migrated rather than simply shifted to another meadow. A map of the area that was under surveillance can be found in Morton (1992a, fig. 1).

Data on annual departure dates of individual

adults trapped on TPM for more than one year were treated independently for statistical purposes because the variances they displayed were similar to those observed for the cohort of adults trapped only one year and because we wanted to avoid selecting departure dates that were unnecessarily biased toward younger birds (presuming that only the first year we obtained a departure date for a bird could be used and that data from subsequent years would have to be discarded). There were 73 males that had data from one year, 16 from two years, three from three years, one from four years, and one from five years. Among adult females, there were 58 on which we had one year of data, six with two years, and two with three years.

RESULTS

Multiple records of body mass obtained on the same individuals during late summer and autumn were used in this study to determine, as closely as possible, the time when migration occurred. For purposes of accuracy, this requires that the analysis be restricted to frequently recaptured individuals. The records from one such individual, an adult male that was on the study area for six consecutive years, are shown in Figure 1 in order to illustrate these principles. The last date he was captured each year, except in 1982, was taken as his time of departure because the data fulfilled our basic requirements, namely that the bird must be trapped regularly through its full period of premigratory fattening, and that trapping sessions must be conducted beyond the time that the bird was last captured.

Premigratory fattening occurred in this male from about Julian day 260 (17 September) onward. From about day 200 to day 250 he was usually engaged in postnuptial molt and before that in reproductive activities. Only a fraction of the birds on the study area, those that we were able to recapture frequently, qualified in a given year for this analysis. Long-lived individuals, such as the subject in Figure 1, could be entered in the data base more than once as adults (juvenile individuals, of course, could only be included for one year as members of that particular age class). Figure 1 also illustrates some of the variation that occurred in individuals from year to year. For example, date of departure in this particular adult male varied from day 263 in both 1981 and 1985 to day 274 in 1983, and body mass at departure from 34.2 g in 1984 to 35.8 g in 1985.

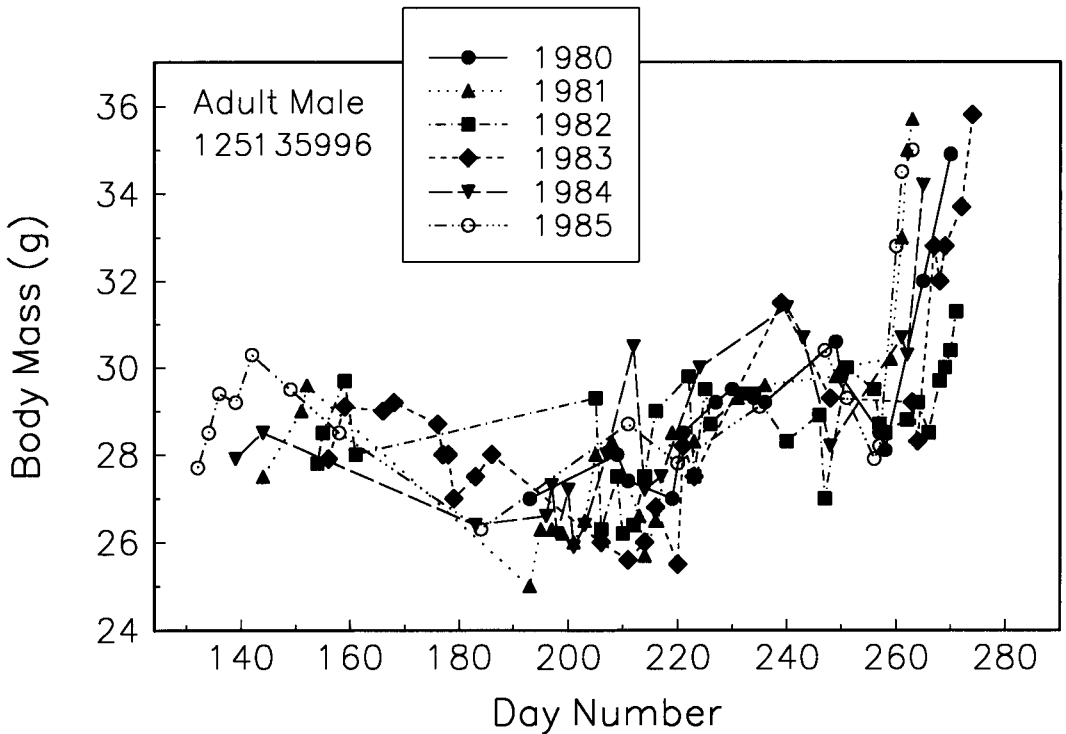


FIGURE 1. Seasonal changes in body mass of an adult male *Z. l. oriantha* (band number 125135996) captured repeatedly at Tioga Pass for six consecutive years.

Based on his performance in other years, this male probably did not actually migrate on day 271 in 1982, the last day of capture for that season when he weighed 31.3 g, but a few days later when he had added additional fat. Therefore, no departure date for this bird was entered in the 1982 data base. Data from other birds were evaluated similarly.

TABLE 1. Day of year of departure on autumnal migration in *Z. l. oriantha* by age class and sex, 1979-1985.

	\bar{x}	SD	Range	Number of departures	Number of individuals
Juveniles					
Male	266.8	7.4	251-284	140	140
Female	267.7	7.7	254-296	101	101
All	267.1	7.6	251-296	241	241
Adults					
Male	270.2	6.2	256-284	123	94
Female	270.3	6.5	254-291	76	66
All	270.3	6.3	254-291	199	160

During the seven years of this study we were able to assign migration departure dates 241 times to juveniles and 199 times to adults, the information on the latter being gathered from a total of 160 individuals (Table 1). The frequency of departures according to calendar date for all years combined occurred in approximately a normal distribution for both age classes, especially in juveniles (Fig. 2). The sexes within each of the two age classes did not have different schedules, but juveniles as a group did depart 3.2 days earlier than adults (Table 1), a significant difference (t -test, $P < 0.001$).

Mean departure date varied by about 14 days in juveniles and eight days in adults (Fig. 3), which helps to account for the large range in departure dates contained in Table 1, 45 days for juveniles and 37 days for adults. In six of the seven study years, the mean departure date of juveniles was earlier than that of adults but in one year (1983) it was not.

The interannual variation in departures of *Z. l. oriantha* from Tioga Pass appears to have been related to their reproductive schedule. A plot of

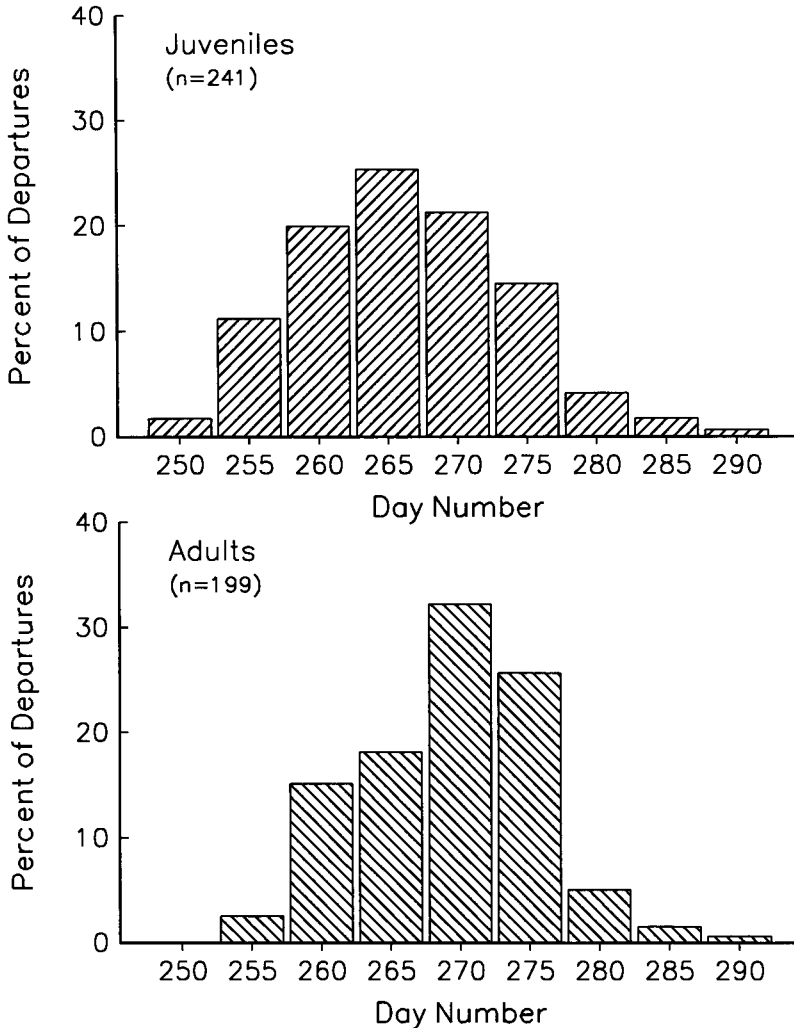


FIGURE 2. Migration departure schedules of juvenile and adult *Z. l. oriantha* from Tioga Pass. All years combined.

mean annual departure dates by the population (all ages and sexes combined) against the corresponding mean annual dates of clutch initiations (Fig. 4) shows a significant correlation (Spearman's correlation coefficient = 0.873, $P < 0.05$); departure was delayed by about one day for every two days of delay in reproduction.

Data from individual years indicate that departures did not follow annually a predictable, repetitive pattern (Fig. 5). Sometimes the frequencies of departures, according to calendar date, resembled a normal distribution (for example, 1979), but they could also be bimodal (1984) or multimodal (1981). The most departures

on one day recorded in the study (29 birds) occurred on 21 September 1981 (day number 264, Fig. 5). This date immediately preceded a two-day snowstorm that was accompanied by high winds and low ambient temperatures. Other peak departure dates, those involving 10–15 birds, did not occur just prior to storms on any other occasion, however. Deficiencies in the data on departure dates sometimes occurred because of unavoidably low sample sizes and because we skipped trapping days to avoid distortion of behaviors due to dependence upon bait.

The exact age in days at time of departure was known for 43 juveniles, 17 females and 26 males.

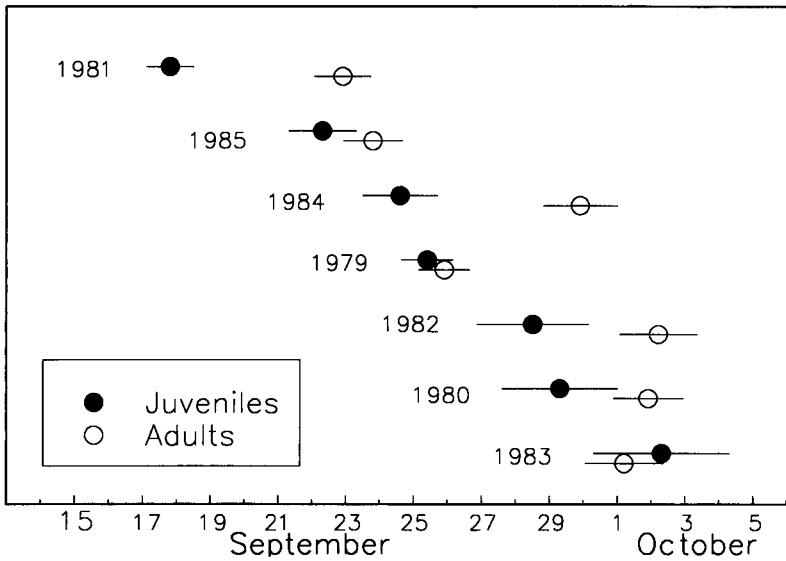


FIGURE 3. Mean migration departure dates (± 1 SE) of *Z. l. oriantha* from Tioga Pass for seven years, with years arranged from earliest schedule (1981) to latest (1983).

These were individuals that had been banded as nestlings and that subsequently went through postjuvencal molt and premigratory fattening without leaving the study area. The mean age at

departure for all of these juveniles combined was 76.7 days (SD = 7.2) and it was not different for the sexes (*t*-test, $P > 0.1$). The range in ages of juveniles at departure time was surprisingly large, being 64 to 98 days, and there was no apparent central tendency for departure within this span of ages (Fig. 6). Regressions of departure date on age and of body mass on age gave slope values that did not deviate significantly from 0 (departure date on age: slope = 0.00, $P = 0.49$, $n = 43$; body mass on age: slope 0.38, $P = 0.22$, $n = 43$). An overview of migration departure dates and body mass at the time of departure for the various age classes found in the study population (Table 2) indicates that juveniles (age 0 years) tended to migrate earlier than adults (as was shown earlier) but that age was not a determining factor in departure schedules of adults (ANOVA, $F = 1.28$, $P = 0.27$ for males and $F = 0.74$, $P = 0.57$ for females). Body mass at departure also did not vary with adult age (ANOVA, $F = 1.08$, $P = 0.38$ for males and $F = 0.13$, $P = 0.97$ for females). Males were consistently heavier than females at departure but this was expected because *Z. l. oriantha* males have larger bodies than females.

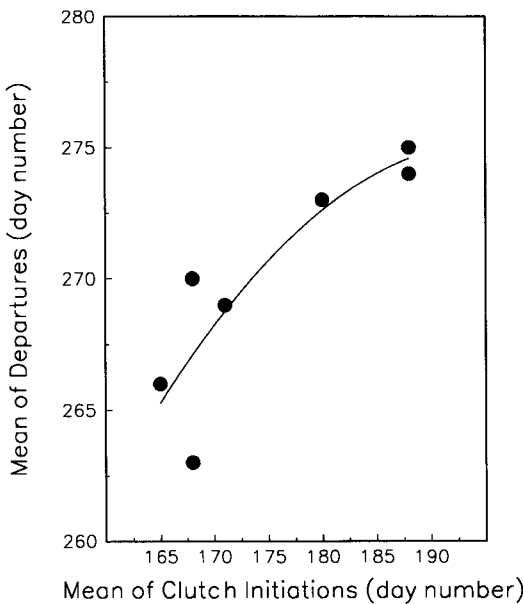


FIGURE 4. Relationship of all *Z. l. oriantha* migration departures from Tioga Pass to reproductive schedules (measured by egg-laying dates). Seven years of data 1979-1985. Curve fitted to the data points by a non-linear least squares regression.

The dynamics of fat deposition were remarkably alike for the age classes and sexes and no significant differences were found in the dura-

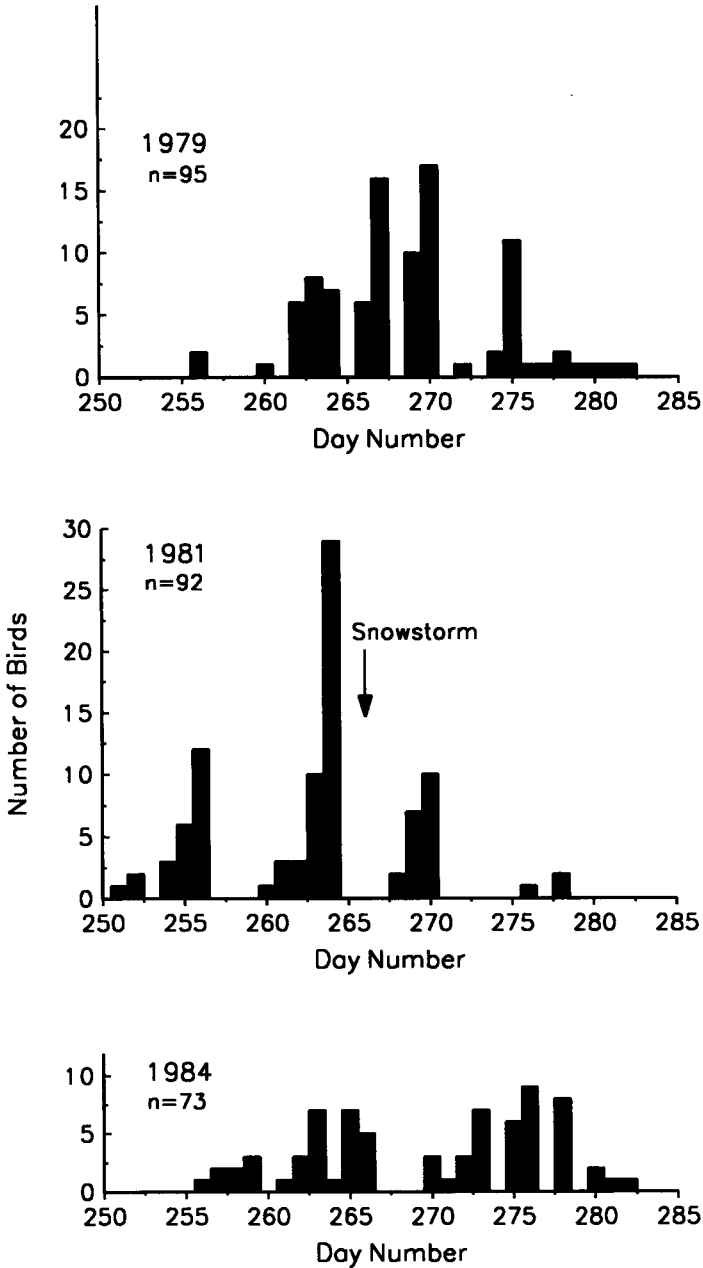


FIGURE 5. Frequency of daily migration departures of *Z. l. oriantha* from Tioga Pass by calendar date. Three years of data, selected for their variability in pattern, are shown.

tions of the fattening response or in the relative rates of increase in mass per day (Table 3). Maximum rates of fattening in individuals were occasionally measured at about 5% per day but the average was only about half of this (Table 3). Since *Z. l. oriantha* are philopatric, an analysis

was made to see if return rates from the wintering area to Tioga Pass varied with either the migration departure date or body mass at the time of the departure in the previous autumn. No statistical differences were found between those that returned and those that did not (Table 4).

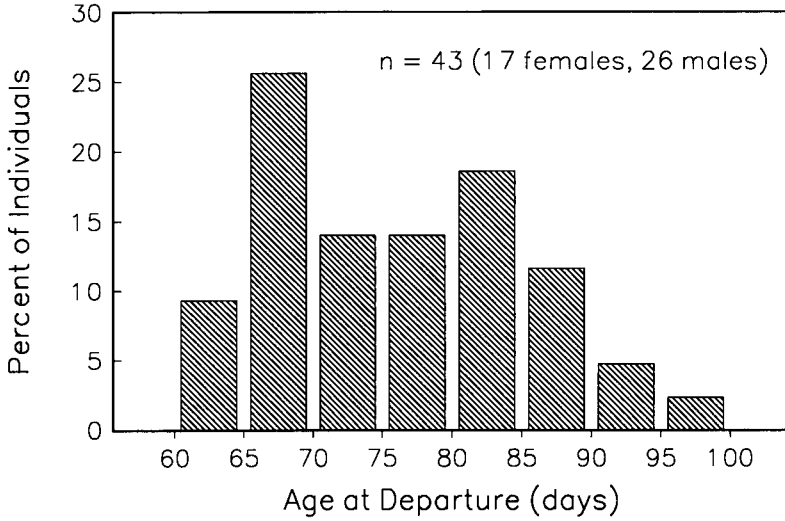


FIGURE 6. Age at time of migration departure of juvenile *Z. l. oriantha* at Tioga Pass.

DISCUSSION

The consolidated data for all years of the study suggest that autumnal migration occurs in *Z. l. oriantha* in an approximately normal distribution over a range of about six weeks in juveniles and five weeks in adults with the mean departure date of adults, day 270 (27 September), occurring three days later than that of juveniles (Fig. 2, Table 1). Juvenile passerines have often been observed while in passage to be ahead of their adult conspecifics (Gauthreaux 1982), but this could be due to many variables such as differences in travel speeds, in points of origin, and in departure dates. The present data show that mean differences in departure dates definitely occurred and that this age-related asymmetry held true over a number of consecutive annual cycles, al-

though there was one exception: in 1983 mean departure date for juveniles occurred slightly later than that of adults (Fig. 3). These results emphasize an important principle; studies of migration dynamics in wild populations should be performed through many annual cycles.

At Tioga Pass the schedule of reproduction in *Z. l. oriantha* can vary interannually by about a month, depending upon when the residual snow-pack melts away and frees-up nesting sites (Morton 1978, Morton and Allan 1990). It appears that when reproduction is delayed migration is also; the two being positively correlated, although in curvilinear fashion (Fig. 4). This suggests that migration can be pushed back somewhat in late years to allow the birds to cycle through a full period of reproduction. Time compensation must occur somewhere in the chain of

TABLE 2. Dates (day of year) for migration departure and body mass at departure in *Z. l. oriantha* according to age, 1979-1985. Age 0 years refers to juveniles.

Age (yrs)	Males					Females				
	Departure date		Body mass (g)		(n)	Departure date		Body mass (g)		(n)
	\bar{x}	SD	\bar{x}	SD		\bar{x}	SD	\bar{x}	SD	
0	266.8	7.4	34.4	2.4	(140)	267.7	7.7	31.6	2.1	(101)
1	270.2	6.7	35.1	1.8	(60)	269.7	6.7	31.7	1.9	(48)
2	269.1	5.6	35.0	2.0	(37)	271.7	5.2	31.8	1.8	(21)
3	273.8	6.2	35.5	2.8	(13)	263.0	0.0	32.4	0.0	(1)
4	271.3	5.3	34.4	1.9	(9)	270.6	9.2	32.0	1.7	(5)
5	268.0	4.2	32.4	2.6	(2)	274.0	0.0	30.7	0.0	(1)
6	267.5	6.4	35.9	1.3	(2)					

TABLE 3. Duration of autumnal premigratory fattening period in *Z. l. oriantha* at Tioga Pass, along with average gain in body mass per day both in g and as % of initial body mass.

	Duration of fattening period (days)			Gain in body mass per day (g)	Gain per day as % of initial body mass
	\bar{x}	SD	<i>n</i>		
Juveniles					
Males	9.29	2.84	103	0.66	2.3
Females	8.59	3.25	73	0.68	2.6
Adults					
Males	9.05	3.31	74	0.69	2.4
Females	8.22	2.88	46	0.61	2.3

events between breeding and migration, however. The reproductive cycle of *Z. l. oriantha* in late years appears not to be truncated (see fig. 4, Morton and Allan 1990) and premigratory fattening always seems to take about nine days. Thus, the pace and/or scheduling of molt must be where time can be saved. It is known that postjuvinal molt can be telescoped late in the season in some species (Berthold et al. 1970), but this has not yet been investigated in *Z. l. oriantha*. It has been shown, however, that their postjuvinal molt and premigratory fattening periods can sometimes overlap (Morton et al. 1972). Whatever the mechanism may be for time compensation among juveniles, strong selective forces are undoubtedly acting on them because their survival until return to natal areas as adults is greatly reduced as their hatching date increases (Morton 1992a). Postnuptial molt has been carefully studied in *Z. l. oriantha* and its duration did not decrease late in the season; it may have even increased slightly (Morton and Morton 1990). This means that postnuptial molt must

overlap at times with reproductive activities and perhaps even with premigratory fattening if substantial time savings are to occur in the breeding-migration interlude. It has been shown, in fact, that postnuptial molt can begin when *Z. l. oriantha* still have eggs and that at least a portion of the postnuptial molt co-occurs with parental care in about 75% of the adults known to be rearing young (Morton and Morton 1990, Morton 1992b). Thus, the ability to meet the energetic demands imposed when reproduction and molt overlap may be the key adaptation for minimizing the lateness of migration in heavy snow years. Interestingly, neither departure date nor body mass at departure were different in either juveniles or adults that did or did not return to Tioga Pass on the year after we had logged their time of migration (Table 4).

Apparently the autumnal migration departure schedule of *Z. l. oriantha* has evolved to be independent of immediately experienced environmental conditions. To be sure, weather-stimulated migration can occur as when it stormed in September of 1981 (Fig. 5), but usually the birds simply fattened and left; a reasonable response because heavy fat reserves are costly to maintain (Hurly 1992). These data suggest to us that attainment of a particular state of energy balance, adequate for meeting the metabolic cost of migration, can in itself be a stimulus for migration. The idea that a favorable migratory condition or disposition could cause the release of migration behavior was broached by Farner (1955) and later discussed at length by Berthold (1975). Both authors pointed out that an environmental stimulus, such as a sudden drop in ambient temperature, might also trigger migration once a favorable disposition had been attained (perhaps as we saw before the 1981 storm).

These notions seem to disagree with data ob-

TABLE 4. Departure dates (day of year) and body mass at departure in *Z. l. oriantha* that did or did not return to Tioga Pass the following year.

	Juveniles						Adults					
	Males			Females			Males			Females		
	\bar{x}	SD	(<i>n</i>)	\bar{x}	SD	(<i>n</i>)	\bar{x}	SD	(<i>n</i>)	\bar{x}	SD	(<i>n</i>)
Departure Dates												
Did return	268.9	8.3	(26)	264.8	5.0	(8)	271.1	6.8	(63)	271.2	6.2	(37)
Did not return	266.3	7.2	(114)	267.9	7.9	(93)	269.3	5.5	(60)	269.5	6.7	(39)
Body Mass at Departure												
Did return	34.4	2.3	(26)	32.0	1.2	(8)	34.8	2.1	(63)	31.6	2.0	(37)
Did not return	34.4	2.4	(114)	31.6	2.1	(93)	35.2	1.9	(60)	32.0	1.6	(39)

tained on captives which show that fattening is not a necessary prerequisite for expression of migratory restlessness (King and Farner 1963, Lofts et al. 1963, Gwinner 1968, Berthold 1977). Note well a point of possible confusion here. These experimenters were usually reporting on how intensity of nocturnal locomotor activity (Zugunruhe) varied in migratory species kept lean by forced semi-starvation. They were not investigating the actual onset of Zugunruhe (the analog of our studies on *Z. l. oriantha*) although records for individual *Zonotrichia* from three species suggests that Zugunruhe sometimes occurred full-blown on its first night and usually after the birds were already fat (King and Farner 1963). Certainly these two functions seem strongly coupled in wild *Z. l. oriantha*. Once they had attained adequate lipid stores (amounting to 15 to 20% of body mass, or sometimes more, Morton et al. 1973), they departed on migration.

Optimally, migration should be scheduled well ahead of impending persistent winter weather. This does not usually strike at Tioga Pass until about mid-October, at which time the long-term average of ambient temperatures plunges to near-freezing and the likelihood of precipitation, usually in the form of snow, increases greatly (Morton 1992b). Food is abundant on TPM in October because Gambel's White-crowned Sparrows (*Z. l. gambelii*) often use it then as a stop-over site to rest and fatten before resuming migration (Morton and Pereyra 1987). Thus, although southward migration can be delayed in years when reproduction has been delayed, *Z. l. oriantha* invariably leave well before the food is gone and before the weather turns bad. In other words, before ultimate factors are expressed. To understand where selection has operated to achieve this schedule, it now appears that we might profitably shift our attention onto the mechanism that controls premigratory fattening and other autumnal functions to which it is linked (Moore et al. 1982), because, indirectly, it or they may also control migration departure.

LITERATURE CITED

- BERTHOLD, P. 1975. Migration: control and metabolic physiology, p. 77-128. In D. S. Farner and J. R. King [eds.], *Avian biology*, vol. 5. Academic Press, New York.
- BERTHOLD, P. 1977. Über die Entwicklung von Zugunruhe bei der Gartengrasmücke (*Sylvia borin*) bei verhinderteter Fettdeposition. *Vogelwarte* 29: 113-116.
- BERTHOLD, P. 1988. The control of migration in European warblers, p. 215-249. In H. Ouellet [ed.], *Acta XIX Congr. Intern. Ornithol.*, vol. I. Univ. of Ottawa Press, Ottawa.
- BERTHOLD, P., E. GWINNER, AND H. KLEIN. 1970. Vergleichende Untersuchungen der Jugendentwicklung eines ausgeprägten Zugvogels, *Sylvia borin*, und eines weniger ausgeprägten Zugvogels, *S. atricapilla*. *Vogelwarte* 25:297-331.
- FARNER, D. S. 1955. The annual stimulus for migration: experimental and physiologic aspects, p. 198-237. In A. Wolfson [ed.], *Recent studies in avian biology*. Univ. Illinois Press.
- GAUTHREAUX, S. A., JR. 1982. The ecology and evolution of avian migration systems, p. 93-168. In D. S. Farner, J. R. King, and K. C. Parkes [eds.], *Avian biology*, Vol. VI. Academic Press, New York.
- GWINNER, E. 1968. Circannuale Periodik als Grundlage des jahreszeitlichen Funktionswandels bei Zugvögeln. Untersuchungen am Fitis (*Phylloscopus trochilus*) und am Waldlaubsänger (*P. sibilatrix*). *J. Ornithol.* 109:70-95.
- GWINNER, E. 1971. A comparative study of circannual rhythms in warblers, p. 405-427. In M. Menaker [ed.], *Biochronometry*. Natl. Acad. Sci., Washington, DC.
- GWINNER, E. 1977. Photoperiodic synchronization of circannual rhythms in the European Starling (*Sturnus vulgaris*). *Naturwissenschaften* 64:44.
- GWINNER, E. 1986. *Circannual rhythms*. Springer-Verlag, Berlin, Heidelberg, New York.
- GWINNER, E. 1990. Circannual rhythms in bird migration: control of temporal patterns and interactions with photoperiod, p. 257-268. In E. Gwinner [ed.], *Bird migration*. Springer-Verlag, Berlin, Heidelberg, New York.
- HURLY, T. A. 1992. Energetic reserves of Marsh Tits (*Parus palustris*): food and fat storage in response to variable food supply. *Behav. Ecol.* 3:181-188.
- KING, J. R., AND D. S. FARNER. 1963. The relationship of fat deposition to Zugunruhe and migration. *Condor* 65:200-223.
- KING, J. R., AND D. S. FARNER. 1974. Biochronometry and bird migration: general perspective, p. 625-629. In L. E. Scheving, F. Halberg, and J. E. Pauly [eds.], *Chronobiology*. Igaku Shoin Ltd., Tokyo.
- LACK, D. 1968. Bird migration and natural selection. *Oikos* 19:1-9.
- LOFTS, B., A. J. MARSHALL, AND A. WOLFSON. 1963. The experimental demonstration of pre-migration activity in the absence of fat deposition in birds. *Ibis* 105:99-105.
- MOORE, M. C., R. S. DONHAM, AND D. S. FARNER. 1982. Physiological preparation for autumnal migration in White-crowned Sparrows. *Condor* 84: 410-419.
- MORTON, G. A., AND M. L. MORTON. 1990. Dynamics of postnuptial molt in free-living Mountain White-crowned Sparrows. *Condor* 92:813-828.
- MORTON, M. L. 1978. Snow conditions and the onset of breeding in the Mountain White-crowned Sparrow. *Condor* 80:285-289.
- MORTON, M. L. 1992a. Effects of sex and birth date on premigration biology, migration schedules, re-

- turn rates and natal dispersal in the Mountain White-crowned Sparrow. *Condor* 94:117-133.
- MORTON, M. L. 1992b. Control of postnuptial molt in the Mountain White-crowned Sparrow: a perspective from field data. *Ornis Scand.* 23:322-327.
- MORTON, M. L., AND N. ALLAN. 1990. Effects of snowpack and age on reproductive schedules and testosterone levels in male White-crowned Sparrows in a montane environment, p. 235-249. *In* M. Wada, S. Ishii, and C. G. Scanes [eds.], *Endocrinology of birds: molecular to behavioral*. Japan Sci. Soc. Press, Springer-Verlag, Tokyo.
- MORTON, M. L., AND M. E. PEREYRA. 1987. Autumn migration of Gambel's White-crowned Sparrow through Tioga Pass, California. *J. Field Ornithol.* 58:6-21.
- MORTON, M. L., J. L. HORSTMANN, AND C. CAREY. 1973. Body weights and lipids of summering Mountain White-crowned Sparrows in California. *Auk* 90:83-93.
- MORTON, M. L., J. OREJUELA, AND S. BUDD. 1972. The biology of immature Mountain White-crowned Sparrows (*Zonotrichia leucophrys oriantha*) on the breeding ground. *Condor* 74:423-430.
- ROWAN, W. 1931. *The riddle of migration*. Williams & Wilkins, Baltimore, MD.