

EFFECTS OF SEX AND BIRTH DATE ON PREMIGRATION BIOLOGY, MIGRATION SCHEDULES, RETURN RATES AND NATAL DISPERSAL IN THE MOUNTAIN WHITE-CROWNED SPARROW¹

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Abstract. A long term mark-recapture study was conducted on a montane population of migratory sparrows to determine interannual variations in numbers of young produced, the behavior and physiology of young birds once independent from parental care, and their return in subsequent years as a function of sex, calendar date, birth date, and birth location. Measures of natal dispersal distance and subsequent involvement in breeding were also obtained.

Sex ratio of nestlings was 1:1 but 28% more independent juvenile males than females were trapped. Return rates were 6.8% for nestlings and 12.2% for independent juveniles and were higher in males than in females in both groups. Numbers of young trapped on the study area showed a three-fold interannual variation which was attributed to the impact of snowpack on reproductive success. Following completion of molt juveniles fattened quickly and departed on migration in late September but not before most had traveled some distance from their birth site.

Date of arrival on the breeding grounds from wintering quarters was not appreciably affected by age (1-year olds vs. 2-year olds +) and although males tended to arrive ahead of females, the sexes overlapped greatly in their schedules. Return rates of yearlings, among those handled as independent juveniles, were about 8 to 15%; no matter the sex or the duration they were known to linger as juveniles on a study area meadow, except for a group of males that stayed for more than four weeks. Members of this group were highly philopatric, having a return rates of 28.5%. Time spent on the same meadow as a juvenile did not affect the ability of either sex subsequently to attain breeding status although more yearling females than males were known breeders, 62.1% vs. 43.6%. The majority of yearlings (recruits) appearing on the study area each year were captured for the first time as adults. This group, called adult recruits, comprised 68.7% of the yearling males and 82.5% of the yearling females. In females, adult recruits were as successful at attaining breeding status as were juvenile recruits (birds captured and banded on the study area previously as juveniles). In males, however, previous familiarity with the area may have enhanced success because the number of known breeders was 10% higher in juvenile recruits than in adult recruits.

Return rates peaked at about 10% in both sexes born 10-20 July and decreased thereafter. This was attributed to increased mortality in late-born young due to inadequate preparation time for migration. Returns of females, but not males, also decreased in those born before 10 July. This was attributed to a propensity for postfledging dispersal distances of females to increase with available time. Natal dispersal (distance from birth nest to first nest as a yearling) was greater in females than in males but sample sizes were small and the difference was not significant. Close inbreeding was rare. It occurred once in 473 pairings.

Finally, the data are incorporated into a descriptive model of natal dispersal which suggests that natal dispersal is temporally divided, one part occurring in juveniles during the post-fledging period and the other in yearlings soon after arrival at potential breeding areas. Natal dispersal distances tend to be greater and apparent philopatry lower in females than in males because females are more vagile as juveniles and they establish larger home ranges which they may enlarge even further as yearlings while in the process of choosing breeding sites. Current hypotheses concerning sexual asymmetries in dispersal are considered and expanded upon, a key addition being the proposal that intrasexual competition in females may contribute importantly to dispersal patterns in migratory passerines.

Key words: Natal dispersal; dispersal; sex ratio; migration schedule; philopatry; recruitment; inbreeding; intrasexual competition; birth date; *Zonotrichia leucophrys*.

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INTRODUCTION

Natal dispersal, as described by Howard (1960) and later clarified by Greenwood (1980), and Greenwood and Harvey (1982) refers to a permanent movement made by juveniles from birth site to first breeding or potential breeding site. This behavior can be first discerned in young passerines at about two or three weeks after fledging as they gain freedom from parental care. At that age juveniles are often highly vagile (Goodbody 1952, Weise and Meyer 1979) and are known to travel several kilometers or more from the natal area in the first days or weeks of independence (Van Balen 1979, Morton et al. 1991). Understandably, these young wandering birds may experience considerable mortality (Nilsson and Smith 1985). In sedentary species there appears to be selection for natal dispersal to occur early and it is usually completed before the onset of winter. By then juveniles have settled individually or with a permanent flock on or near their future breeding site although final occupancy of a territory may not occur until spring (Tompa 1962, Nilsson and Smith 1988, Nilsson 1990). In migratory species, the temporal discontinuity between attainment of juvenile independence and territorial occupancy imposed by migration to distant wintering areas alters the dynamics of natal dispersal considerably from those of sedentary species. This makes the response more difficult to observe and to understand in migrants not only because dispersal may occur in divided periods and take longer from inception to termination, but also because most of the data, and associated useful hypotheses, have come from studies of sedentary species, particularly those that are hole nesters. There are important data now available, however, on a diversity of migrants, some of which are hole nesters (House Wrens *Troglodytes aedon*, Drilling and Thompson 1988; Pied Flycatchers *Ficedula hypoleuca*, Van Balen 1979, Sokolov et al. 1987) and some of which are not (Reed Warblers *Acrocephalus scirpaceus* and Sedge Warblers *A. schoenobaenus*, Catchpole 1972; Semipalmated Sandpipers *Calidris pusilla*, Gratto et al. 1985, Gratto 1988; White-crowned Sparrows *Zonotrichia leucophrys*, Morton et al. 1991).

It has sometimes been assumed that the major portion of natal dispersal must occur in yearling migrants soon after their arrival at suitable breeding terrain. This assumption stems in part

from the fact that return rates of migratory passerines to the natal site are low, often 3% or less (Farner 1945, Gauthreaux 1982), so young, first-time breeders are assumed to be scattering widely to unfamiliar areas (Farner 1945). Other information suggests, however, that significant portions of natal dispersal occur in independent juveniles prior to their first migration because during that period, sometimes called the period of postfledging dispersal, they wander extensively and may depart on migration from sites that are 5 km or more from their birth site (Van Balen 1979). One function of postfledging dispersal activity could be to acquaint juveniles with local physiographic features thereby enhancing their ability to home to breeding areas from winter quarters. This is termed a site fixation response and it is thought to be similar to imprinting in that it includes a critical or sensitive period (Hildén 1965, Able and Bingman 1987). If juveniles are held captive and not allowed freedom of movement during the postfledging period they do not return later as adults (Löhr 1959). Learning may ordinarily be occurring during this time as well. That is, juveniles may also be selecting their future potential breeding territories, if not actual nest sites (Hildén 1965, Catchpole 1972, Berndt and Winkel 1979). This could be highly advantageous in migrants because neither time constraints nor energy stresses are likely to be so great in late summer as in the following spring and habitat features can often be more accurately assessed in summer as well (Brewer and Harrison 1975). The latter certainly applies to high altitude regions where vegetation is undeveloped in spring and may even be covered completely by a residual snowpack until well after the birds arrive and begin to take up territories (Morton 1978). Postfledging dispersal may also function to improve trophic conditions for juveniles during the energetically demanding period prior to migration when they molt and fatten, and this does not necessarily occur in habitat suitable for breeding (Morton 1991).

A notable feature of natal dispersal is its sexual asymmetry. In most passerines, sedentary and migratory species alike, females disperse farther than males. The evolutionary explanations for this sex-biased pattern has been a subject of persistent debate (Pusey 1987) and two major hypotheses have emerged. One suggests that it is a mechanism for avoiding the detrimental effects of inbreeding and bias in dispersal distance is

thought to occur because males defend a resource or territory, rather than a mate, and their ability to do so is greatest in familiar surroundings. Thus males should be highly philopatric and establish themselves as potential breeders as close to the natal area as possible. Females choose among available males with territories but the burden of avoiding close inbreeding is now placed upon them so they should be less philopatric and disperse farther than males (Greenwood 1980). The other hypothesis argues that sex differences in dispersal are unselected consequences of sex differences in competition. Males should be highly philopatric for the same reasons stated in the previous hypothesis—they can obtain and defend a territory more easily, i.e., compete better, near their birthplace than away from it. Females then search for a high quality territory, which includes the attendant male, and in the process wind up farther from their natal area than males. According to this hypothesis there is no need to invoke inbreeding avoidance as a driving selective force because intrasexual competition sufficiently explains the observed asymmetries (Moores and Ali 1984). As a third alternative, the case has also been made that dispersal patterns are not shaped by a single factor alone but are likely to be the outcome of multiple factors operating simultaneously (Dobson and Jones 1985).

Herein data are presented from a long-term study of the biology of nestling and independent juvenile Mountain White-crowned Sparrows (*Zonotrichia leucophrys oriantha*), including their numbers, movements, and return rates as yearlings as functions of sex, birth date, and of trapping history. On yearlings there is also information on schedule of arrival at the breeding area, natal dispersal distance, and reproductive success. This information is then synthesized in order to apply it to existing hypotheses and to extend it to new ideas that can be helpful to our understanding of how and why sexual biases in natal dispersal occur in migratory passerines.

METHODS

The present study was conducted in Lee Vining Canyon near Tioga Pass at about 37.5°N latitude in the Sierra Nevada Mountains of California. This canyon was carved by a series of glaciers in the Pleistocene and it now contains subalpine meadows in its complexly branched upper ends. These meadows, kept green during the summer

by melting snows, are bounded and sometimes separated by stands of lodgepole pines (*Pinus contorta*), and are used for breeding purposes by a variety of avian species. The study area itself is irregularly shaped and winds along the canyon bottom for about 7 km between elevations of 2,900 m at Ellery Lake to 3,000 m at Tioga Pass (Fig. 1). Within the confines of its 280 ha, there were usually 35 to 40 breeding pairs of *Z. l. oriantha*. This is a migratory race whose members arrive on the breeding meadows in May and early June from wintering areas, principally to the south in Mexico, and depart for the wintering grounds in late September and early October (Morton and Allan 1990). From 1978 to 1990 my students and I have attempted to locate all nests, band all nestlings, and trap and band all previously unbanded adults (adults were also color banded) and independent juveniles on this study area. Trapping was done with two- or four-cell live traps baited with small quantities of seed. Breeding individuals of both sexes ranged from one to a maximum of about eight years of age.

Determinations of body mass, molt status, fat class, age and sex (by laparotomy if necessary) and exact location of capture on the study area using an accurate, gridded map were made routinely at each capture. Nestlings were banded, and sometimes laparotomized, between five and nine days of age, the latter being the usual age at fledging. Number of days spent on the study area by independent juveniles was determined as the time interval between their first and last captures of the season. Individuals captured only once were assumed to have been on the study area for one day.

Trapping and nest-searching efforts were not uniform across the study area because many of the meadows were small and not always utilized for nesting. Instead, we paid most attention to the larger meadows which were occupied by the most pairs and which often seemed to attract juveniles and nonbreeding or postbreeding adults as well. In this report data taken from one such meadow, Tioga Pass Meadow (TPM), which is located at the southern end of the study area, are frequently emphasized. Additional habitat often occupied by a few breeding pairs, was located at Gardisky Lake, on Mine Creek, and in Glacier Canyon (Fig. 1). We visited these areas only occasionally during the breeding season, mainly to locate nests and to check adults for bands. A trapline with 24 stations was maintained every

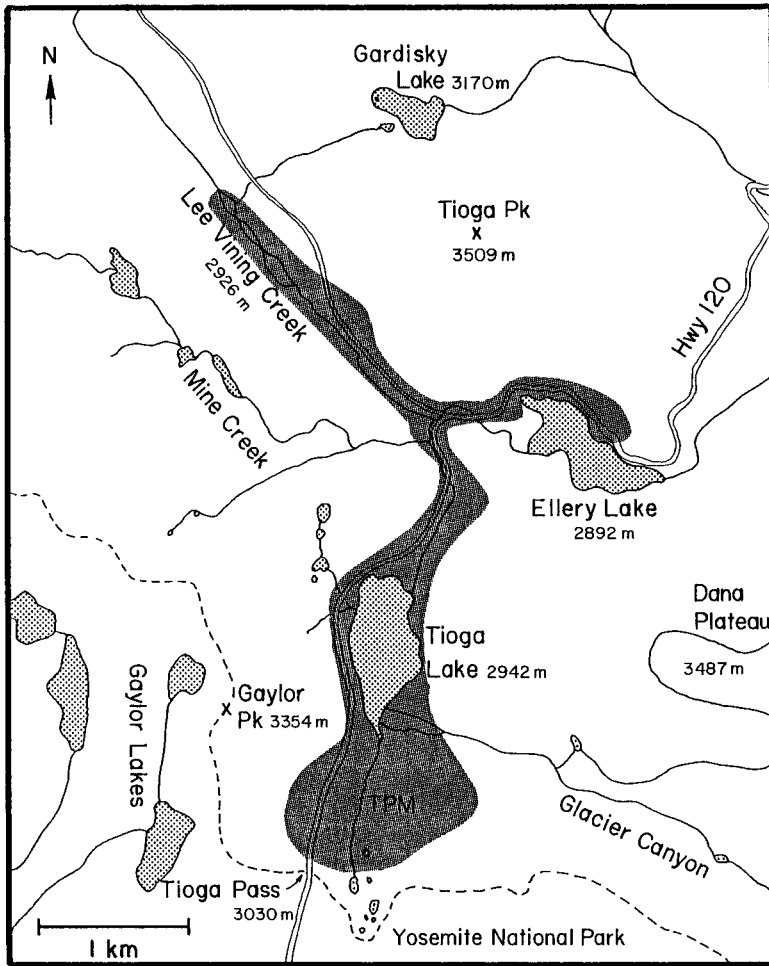


FIGURE 1. Map of the study area (shaded region).

summer on TPM enabling us to compile data on frequently recaptured individuals and to monitor movements, especially of juveniles, onto and through the area.

Territorial boundaries were difficult to determine in *Z. l. oriantha* because they varied so much with habitat characters (Morton et al. 1972a). In addition, breeding individuals usually defended no further than about 50 m from their nests yet they often flew sorties across other territories in the course of daily activities. Territory size was determined, therefore, by taking one 25 ha continuous patch of habitat on TPM and then dividing by the number of pairs utilizing it. This yielded an average territory size of about 1 ha or a circle with a diameter of 112 m. Thus,

territory width, as used in this report, is considered to be 112 m.

Snow depths were obtained from State of California snow survey measurements (Bulletin 120) taken on or about 1 April each year on TPM. Snowpack at that time is presumed by State hydrologists to be at or near the seasonal maximum and to be a good predictor of water runoff.

RESULTS

NESTLINGS AND INDEPENDENT JUVENILES

In the course of this study, 958 nestlings from 310 broods were banded. In 163 of these broods all nestlings (503) were sexed by laparotomy. There were 248 males and 255 females, a ratio

TABLE 1. Rates of return of yearling *Zonotrichia leucophrys oriantha* to the study area according to whether they were handled as nestlings and/or as independent juveniles.

	Males	Females	Total
Number of nestlings	479*	479*	958
Number that returned	42	23	65
% returned	8.8	4.8	6.8
Number of independent juveniles	894	700	1,594
Number that returned	124	70	194
% returned	13.9	10.0	12.2

* Sex ratio in nestlings assumed to be 1:1 (see text).

that did not differ from 1:1 ($\chi^2 = 0.097$, $P > 0.70$). Mean brood size in both the main sample and the laparotomized subsample was 3.09. Sex ratio in the main sample was considered, therefore, to be 1:1. Of the 958 nestlings, 272 (from 156 broods) were captured later in the summer as independent juveniles and 65 (from 54 broods) were captured in a later year as yearlings, a return rate of 6.8% (Table 1). The return rate of males was higher than that of females, 8.8% vs. 4.8% ($\chi^2 = 5.96$, $P < 0.02$). Of the 65 nestlings known to have returned as yearlings, 43 were the only ones to return from their brood whereas the other 22 were made up of 11 pairs of siblings from 11 broods. This pattern did not deviate significantly from the Poisson distribution for rare events ($G = 5.44$, $P > 0.10$, Sokal and Rohlf 1981) so there was no effect of the brood on likelihood of returning.

A second data base generated in this study was obtained from captures of independent juveniles on TPM. Some, but not all, of these birds had been previously handled and banded as nestlings. There were 1,594 individuals in this group, 894 males and 700 females. This sex ratio of 1.28:1 deviated significantly from 1:1 ($\chi^2 = 23.6$, $P < 0.001$). Data on return rates as yearlings of these independent juveniles are presented in a later section.

Fledgling *Z. l. oriantha* banded as nestlings on the TPM portion of the study area ("locals") began to make the transition to independence and to enter our traps when they were about 25 days of age. This corresponded to about 40 days after laying had started in the first nests of the season on TPM (Fig. 2). The data were standardized in this way because nesting schedule varied inter-annually by a month or more on TPM, depending upon how nest site availability was affected by the residual snowpack (Morton 1978, Morton

and Allan 1990). Each year we also trapped a second cohort of juvenile birds on TPM. These "nonlocals" began to show up in our traps about a month after the first of the locals (Fig. 2). Some nonlocals were known to have been born on other meadows of the study area because they were banded there as nestlings (see Morton et al. 1991) but most were unbanded upon arrival at TPM and could have dispersed from birth sites located several km or more from the study area. New members of both cohorts continued to appear in our traps for a month or so with locals being invariably outnumbered by nonlocals in any given year.

The data in Figure 2 also indicate that the number of juveniles captured varied considerably between years. For example, 290 juveniles (208 nonlocals and 82 locals) were captured in 1985 compared to only 88 (63 nonlocals and 25 locals) in 1982; the ratio of nonlocals to locals in both of these seasons being 2.5 to 1 and the interannual variation in total numbers for both cohorts varying by 3.3 to 1. This greater than three-fold range in total numbers captured appeared to be related to ambient conditions because it decreased in a regular way with maximum snow depth (Fig. 3). The fewest juveniles were captured in 1982, which had a summer preceded by a winter of heavy snows and also a summer wherein fledging success was diminished because of storm-induced nestling mortality.

Juveniles began molting at 34.3 ± 5.2 days of age with molt duration being 32.4 ± 4.6 days (Morton et al. 1972b). At about the time the postjuvinal molt was completed, usually in early September, individuals exhibited their seasonal minima in body mass. They then became hyperphagic and sometimes showed increases in body mass of 40–50% over a 10-day period (Fig.

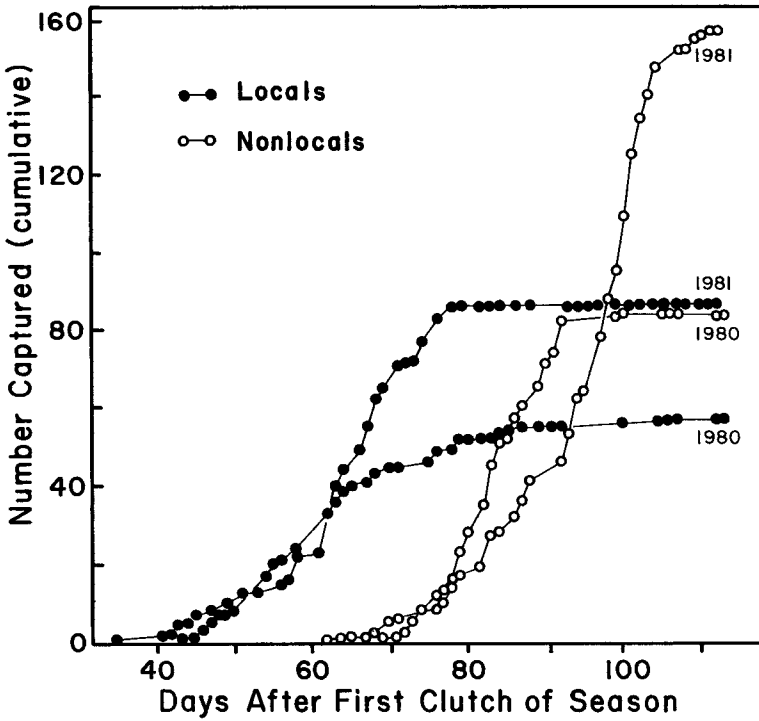


FIGURE 2. Cumulative numbers of independent juvenile *Zonotrichia leucophrys oriantha* captured on Tioga Pass Meadow in 1980 and 1981.

4). Direct observations of subcutaneous fat depots indicated that these increases were due to fat deposition. Maximally obese individuals were seldom retrapped suggesting that they had departed on migration to their wintering area. Clear records of body mass changes in individuals from about 30–70 days of age were difficult to obtain because they were obviously highly mobile during this period and infrequently retrapped. There was, for example, an influx of nonlocals to TPM and the disappearance of many locals from it during this age period. Nonetheless, individuals of both cohorts were known from trapping records to be on or near TPM for several weeks and many probably lived there right up to the moment of their departure on migration in late September (see below).

YEARLINGS AND OLDER ADULTS

Members of the breeding population arrived on the study area each year in May and June. An estimation of arrival schedule can be obtained from the dates that individuals were captured for the first time each season. A perfectly informative record of this type could be compiled

only if every bird was trapped on its actual day of arrival. This, of course, was not the case. Some birds probably did not enter traps until they had been on the area for at least several days, plus our trapping efforts were inconstant because the road to the study area was often closed to travel

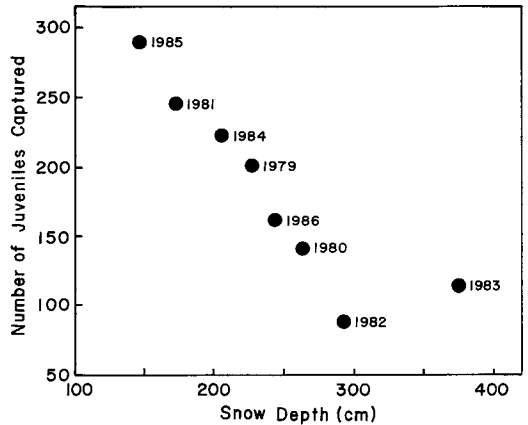


FIGURE 3. Interannual variation in total number of independent juvenile *Zonotrichia leucophrys oriantha* captured on Tioga Pass Meadow.

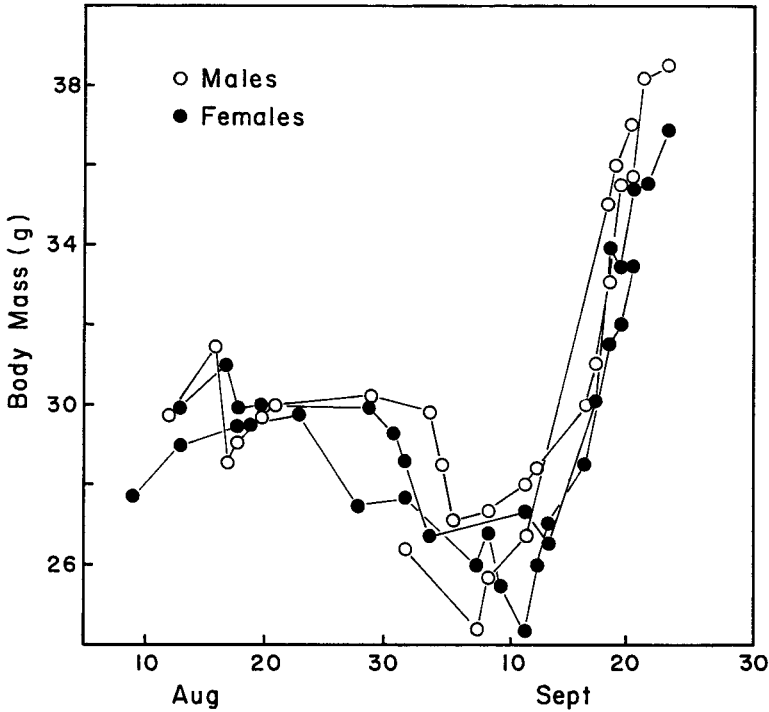


FIGURE 4. Seasonal changes in body mass in four juvenile *Zonotrichia leucophrys oriantha* (two males and two females).

at that time of the year. The data are useful, however, for age and sex comparisons. They show that yearlings (which were in adult plumage and sexually competent) arrived on about the same schedule as adults that were age two years or older (Table 2). For both age groups, males tended to be more numerous than females in the earliest sampling intervals showing that they were arriving earlier than females. The difference was only one of degree, however. As can be observed in the visual summary of these data, the ratio of males to females was about 4:1 in early May, became 1:1 by early June and favored females thereafter (Fig. 5). Arrival data for May alone are perhaps the most trustworthy indicator of sex differences in schedule. During May, 258 of the 585 males (44.1%) arrived and 142 of the 522 females (27.2%) arrived. These ratios were significantly different ($\chi^2 = 34.1, P < 0.001$).

When May and June data were combined and arrival schedules calculated according to Julian dates, yearling males arrived an average of 5.3 days earlier than yearling females. In older birds, the difference was 5.8 days. These differences were significant for both comparisons (Table 3).

Mean arrival dates averaged 1.6 days earlier in older females than in yearling females, an insignificant difference ($t = 1.63, P > 0.05$). In males, however, the 2.2 days difference in mean arrival

TABLE 2. Schedule of arrival of *Zonotrichia leucophrys oriantha* of known age and sex to the study area, as determined by number of individuals captured for the first time in the season (by 5-day intervals). Twelve years of data shown. Julian date 121 = 1 May.

Julian date	Age 1 year		Age 2+ years	
	Males	Females	Males	Females
121-125	1	0	1	0
126-130	10	2	11	4
131-135	12	3	23	5
136-140	30	14	31	15
141-145	28	19	34	24
146-150	24	24	41	26
151-155	30	26	41	20
156-160	35	52	59	48
161-165	26	35	30	27
166-170	26	41	22	30
171-175	28	36	19	31
176-181	15	22	8	18
Total number captured	265	274	320	248

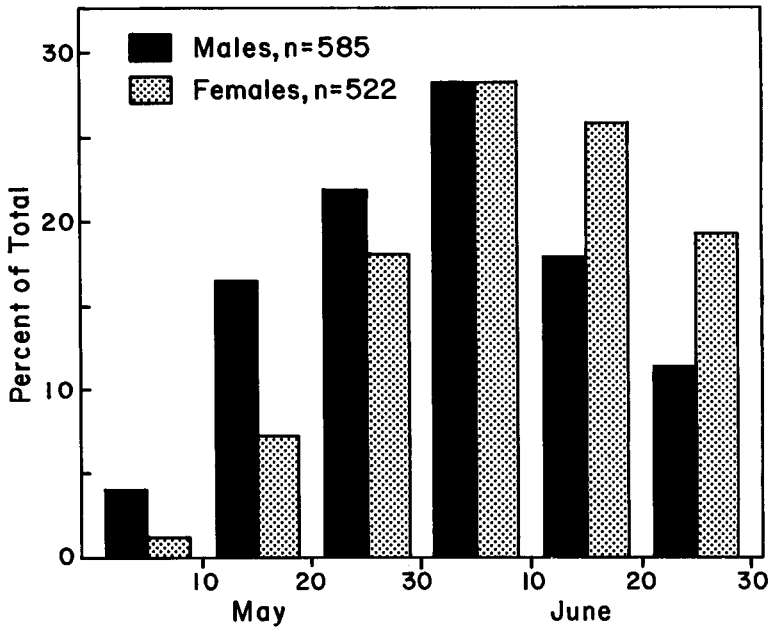


FIGURE 5. Schedules of arrival of *Zonotrichia leucophrys oriantha* to the study area over a 12-year period (1979–1990), as determined by first captures of the season. Data for the sexes were calculated separately.

dates was significant ($t = 2.02$, $P < 0.05$). Note that these were dates of first captures, not of actual settling times. Note also that all newly arrived unbanded adults were considered to be yearlings. This assumption seemed justified because breeding *Z. l. oriantha* are fairly site tenacious (Morton, unpubl. data) and we made a great effort each year to capture and band all unbanded adults. New adults, therefore, were considered to be only one year of age and to be visiting the study area for the first time. Furthermore, careful examination of these unbanded adults showed that many had one or more brown feathers, typical of juveniles, among the normal black feathers, typical of adults, at the bases of their bills and in males their wing lengths corresponded to the shorter lengths found among yearlings as compared to older individuals (Morton et al. 1990).

Among the yearlings captured were 65 individuals (42 males and 23 females) that had been banded as nestlings. Since birth dates of these individuals were known, propensity to return according to date of birth could be calculated. These data show that young of both sexes that hatched in mid-July were more likely to return than those born on earlier or later dates (Fig. 6). The later young hatched thereafter, the less likely they were

to return and the sexes were not different in this regard ($\chi^2 = 0.54$, $P > 0.30$). The pattern was different in individuals hatched prior to mid-July, however, with females being less likely to return than males ($\chi^2 = 8.85$, $P < 0.01$). Juvenile *Z. l. oriantha* complete their molt at about 66 days of age and pre-migratory fattening about 10 days later. The data in Figure 4, and others not illustrated, suggest that migration of juveniles often occurs on or near 25 September. Thus individuals born 76 days before 25 September, i.e., on 10 July, would have just enough time to be ready for departure. This raises questions about how date of birth might affect the duration of

TABLE 3. Mean time of arrival by Julian date of *Zonotrichia leucophrys oriantha* of known age and sex to the study area. Probability values determined by t -tests.

Age	Sex	\bar{x}	SD (days)	(n)	P
1	Male	154.56	13.86	(265)	
1	Female	159.88	11.63	(274)	<0.001
2+	Male	152.34	12.37	(320)	
2+	Female	158.14	12.68	(248)	<0.001
All	males	153.35	13.10	(585)	
All	females	159.05	12.16	(522)	<0.001

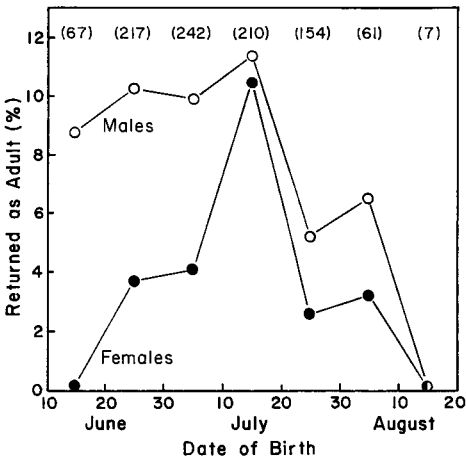


FIGURE 6. Return rates of nestling *Zonotrichia leucophrys oriantha* to the study area as adults versus date of birth. Numbers of nestlings banded per 10-day interval are shown in parentheses at the top of the figure. Sex ratio of nestlings assumed to be 1:1.

time spent on the study area. For example, if juveniles simply stay near their place of birth until migration, those born earliest would be present for more days than those born latest. The data show that this pattern is followed somewhat in males but not in females (Fig. 7). A least squares regression of the data in Figure 7 yields a slope of -0.35 for males ($r = 0.23$, $P = 0.003$, $n = 142$), and of -0.02 for females ($r = -0.02$, $P = 0.41$, $n = 133$).

There were 894 males in this study that were known to be alive as independent juveniles. Of these, 124 were captured again in subsequent years on the study area as yearlings, a return rate of 13.9% (Table 1). By comparison, 70 of 700 females or 10.0% returned. These return rates were different ($\chi^2 = 5.50$, $P < 0.02$). A breakdown of the return data by known duration of time spent on the study area as an independent juvenile reveals distinctly different patterns for the sexes (Table 4). Return rates were between 8.1 and 16.7% for both sexes when they were on the study area for four weeks or less (Group 1 birds). For those that stayed for more than four weeks (Group 2 birds), however, return rates of males increased markedly whereas those of females tended to decrease. Statistical comparisons (Table 5) show that the 10.5% return rate of Group 1 males was significantly lower than the 28.5% rate of Group 2 males. Return rates for this same comparison in females were not

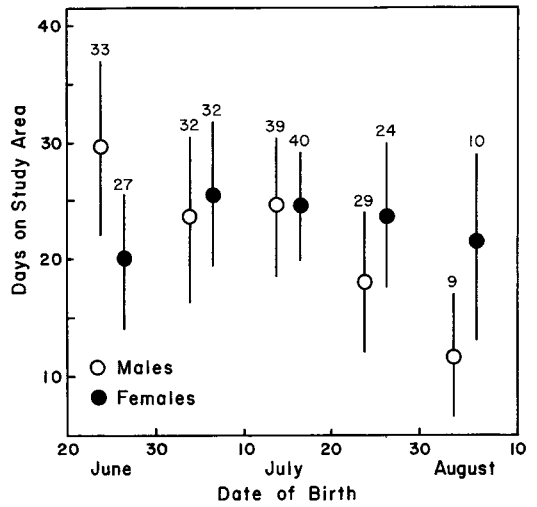


FIGURE 7. Number of days that juvenile *Zonotrichia leucophrys oriantha* were known to be on the study area versus date of birth. Means are indicated by circles and ± 2 SE by bars. Sample sizes given by numerals at tops of bars.

different nor did Group 1 males differ in return rate from Group 1 females. Group 2 males had a significantly higher return rate than Group 2 females (Table). A slightly higher fraction of Group 2 birds of both sexes was known to attain breeding status than Group 1 birds, but the difference was insignificant (Table 5).

Yearlings captured on the study area consisted of individuals that we had banded either as nestlings or as independent juveniles the previous summer plus individuals that had never been handled by us until they arrived on spring mi-

TABLE 4. Rates of return of yearling *Zonotrichia leucophrys oriantha* to the study area according to the number of weeks they were known to be present on the study area as independent juveniles.

Weeks	Males			Females		
	Returned?		% return	Returned?		% return
	Yes	No		Yes	No	
1	42	366	10.3	27	291	8.5
2	20	154	11.5	10	113	8.1
3	9	87	9.4	15	80	15.8
4	12	60	16.7	9	48	15.8
5	16	45	26.2	5	43	10.4
6	13	23	36.1	3	29	9.4
7	7	19	26.9	1	17	5.6
8	4	13	23.5	0	6	0.0
9+	1	3	25.0	0	3	0.0
Totals	124	770	13.9	70	630	10.0

TABLE 5. Rates of return and attainment of breeding status in *Zonotrichia leucophrys oriantha* according to period of time spent on the study area as independent juveniles. Members of Group 1 were on the area for four weeks or less as juveniles, those of Group 2 for five weeks or more (see Table 3). *P* values obtained from Chi squares.

	%	(n)	vs.	%	(n)	<i>P</i>
Returned as adults						
Group 1 males vs. Group 2 males	10.5	(750)		28.5	(144)	<0.001
Group 1 females vs. Group 2 females	10.3	(593)		8.4	(107)	0.552
Group 1 males vs. Group 1 females	10.5	(750)		10.3	(593)	0.940
Group 2 males vs. Group 2 females	28.5	(144)		8.4	(107)	<0.001
Attained breeding status						
Group 1 males vs. Group 2 males	43.4	(83)		48.8	(41)	0.569
Group 1 females vs. Group 2 females	62.9	(70)		66.7	(9)	0.823

gration. I will designate the former as "juvenile recruits" and the latter as "adult recruits." The number of adult recruits was large and they invariably outnumbered juvenile recruits in both sexes, the proportion being greater in females than in males (340 vs. 72 and 296 vs. 135, $\chi^2 = 21.80$, $P < 0.001$). Because our nest finding and trapping efforts were unremitting every season, I assume that the majority of these adult recruits were born off the study area and had never visited it as a juvenile.

Was time of arrival on the study area the same for both types of recruits? Again, the best available measure of this is the date of first capture on the study area. The data derived from the 265 males and 274 females previously identified in Table 3 indicate that in both sexes yearlings that were known to be on the study area as juveniles returned to the study area more than two days earlier than those not known as juveniles (Table 6). In neither case, however, was the difference significant.

TABLE 6. Arrival schedules (Julian date) of yearling *Zonotrichia leucophrys oriantha* to the study area according to banding histories. Juvenile recruits were banded on the study area as juveniles whereas adult recruits were already one-year old when first captured and banded. Probability values determined by *t*-tests.

	\bar{x}	SD	(n)	<i>P</i>
Males				
Juvenile recruits	153.06	13.52	(97)	0.181
Adult recruits	155.43	14.01	(168)	
Females				
Juveniles recruits	157.55	12.60	(47)	0.133
Adult recruits	160.36	11.39	(227)	

A next logical question is, was ability to obtain territories and mates affected by exposure to breeding area locations as juveniles, no matter how brief its duration? Perhaps it did in males because among them, about 10% or more of the juvenile recruits than the adult recruits were known breeders (Table 7). This difference was not quite statistically significant at the 0.05 level. Among females, the percentages of known breeders were almost identical in the two groups (Table 7). Significantly more yearling females than yearling males were known breeders, 62.1% versus 43.6% (Table 7). Note that sample sizes for yearlings that were juvenile recruits are now larger than in previous tables dealing with arrival schedules because the latter were generated from capture dates of individuals trapped as yearlings for the first time in a season in May or June. The data in Table 7 include those captured on later dates as well. These data also include an important piece of information on sexual differences

TABLE 7. Percentage of yearling *Zonotrichia leucophrys oriantha* recruits of differing banding histories that were known breeders. Terminology as in Table 5. Probability values determined from Chi-squares.

	%	(n)	<i>P</i>
Males			
Juvenile recruits	50.4	(135)	0.056
Adult recruits	40.5	(296)	
Females			
Juvenile recruits	62.5	(72)	0.944
Adult recruits	62.1	(340)	
All males combined	43.6	(431)	<0.001
All females combined	62.1	(412)	

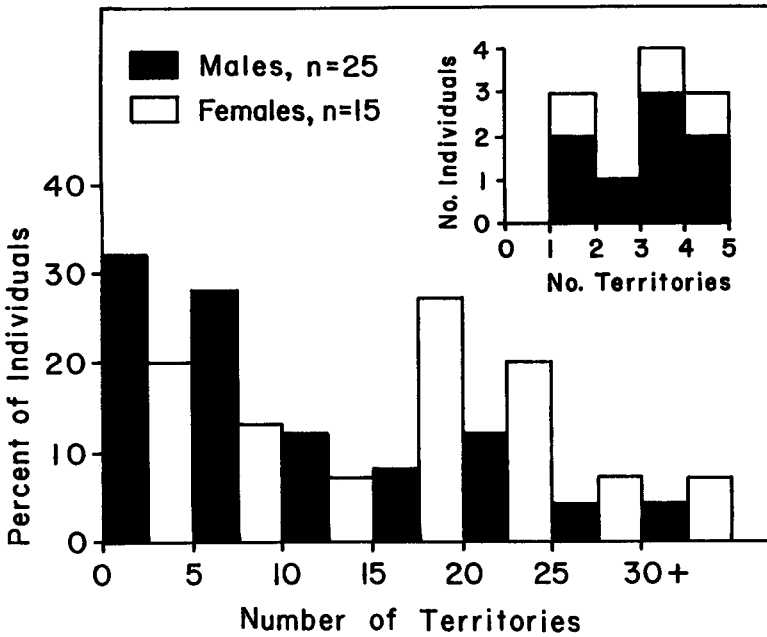


FIGURE 8. Natal dispersal distances in *Zonotrichia leucophrys oriantha* plotted by number of territories between the natal site and the first nest site as a yearling. Note in the inset figure that no individual was known to return and settle on its natal territory although two males and one female did settle on territories that were immediately adjacent.

in the relationship between philopatric tendencies and attainment of breeding status. They show that of 431 yearling males trapped on the study area, 135 (31.3%) were known previously as juveniles. In contrast, of 412 yearling females, only 72 (17.5%) were known as juveniles, a highly significant difference ($P < 0.001$). A note of caution, the percentages of known breeders in Table 7 represent the minimum and are undoubtedly well below the real numbers. Over the years we have often identified unmated yearling male floaters (Morton and Morton 1990), but thus far not even one female has ever been so categorized. This is true even though the percentage of known breeders increased with age for both sexes. For example, 219 of 366 males (59.8%) age two years or older were known breeders and 232 of 308 females (75.3%) were known breeders. According to a Chi-square analysis, these percentages were significantly higher than those in yearlings ($P < 0.001$ for both sexes).

It is apparent that a sizeable number of young *Z. l. oriantha* must have returned to the area of their birth in search of breeding habitat. On occasion the exact location of an individual's birth nest as well as that of its first nest as a yearling

were known, allowing us to calculate the distance of natal dispersal. In males the mean distance of dispersal was 1,172 m (SD = 972 m, range = 150–3,430 m, $n = 25$). In females it was 1,719 m (SD = 1,134 m, range = 189–4,340 m, $n = 15$). Median distance was 755 m in males and 1,721 m in females. Although natal dispersal distances were greater in females than in males, the difference was not significant (Mann-Whitney U , $P = 0.167$). A plot of the dispersal data by territory diameter intervals (112 m) shows that males tended to settle and breed closer to their birth site than females although no individual, male or female, was found to breed on its natal territory (Fig. 8, inset). Obviously, many young birds must have settled at locations that were beyond the boundaries of our study area. Even so, the possibility of incestuous matings exists. A check of 13 years of data on 473 pairs revealed no cases of parent-offspring matings and one case of siblings being mated. This pair, born on Lee Vining Creek in 1985, settled as yearlings about 0.7 km apart near the north end of Tioga Lake (see Fig. 1) but did not become mates until 1987 when the male moved to the female's area. That year, as two-year olds, they successfully fledged four

chicks. The female nested in the same location again in 1988 but with a different male. Her brother did not return.

DISCUSSION

MOVEMENTS, NUMBERS, RETURN RATES, AND RETURN SCHEDULES

Dispersion begins in juvenile *Z. l. oriantha* soon after fledging and may continue in some individuals right up to the time of fall migration. From direct visual observations of adults and their dependent fledglings, we found that young birds at one month of age and learning to feed themselves were already located, on average, about 200 m from their birth sites (Morton et al. 1991). From that point onward movement patterns of independent juveniles must be deciphered from trapping records. These indicate that juveniles born off the study area (nonlocals) often moved onto it between 30 and 70 days of age, with peak movement occurring at 50–55 days of age and that those born on the study area (locals) were also vagile during this period with many disappearing from the area being trapped (Fig. 2 and Morton et al. 1991).

There was considerable interannual variation in the total number of juveniles captured, ranging from a high of 290 in 1985 to a low of 88 in 1982, more than a three-fold difference. The variation in numbers was inversely related to snow depth (Fig. 3) because this is an environmental variable that powerfully affects the schedule of reproduction and the number of breeding pairs in *Z. l. oriantha*. Habitat suitable for nesting only becomes available as snow melts off the meadows so the deeper the snow the fewer the pairs breeding, the later their nesting begins and the fewer young they produce because re-nesting and double brooding opportunities diminish with the decrease in duration of reproductive season. Onset of egg laying in the Tioga population can vary interannually by at least a month and 75% of the variability observed in this schedule can be predicted by the 1 April snowpack data (Morton 1978, Morton and Allan 1990).

At about 34 days of age and concurrent with their attaining independence from parental care, juveniles begin the postjuvinal molt. This lasts until they are about 66 days of age (Morton et al. 1972b) with premigratory fattening being completed about 10 days thereafter (Fig. 4). The data in Figure 4, and others not illustrated, suggest that migration of juveniles often occurs on

or near 25 September. Those individuals born 76 days before that date, i.e., on 10 July, would have just enough time to be ready for departure. Presumably those born before 10 July would have extra time before migration (unless they migrated early) and these born after would incur an increased risk of being exposed to deteriorating weather conditions associated with the onset of winter. The data are in accord with this since individuals born 10–20 July had relatively high return rates which then decreased as birth dates occurred later in the season (Fig. 6). This pattern of increased mortality with later birth dates has been observed in other species as well (Perrins 1965, Drilling and Thompson 1988).

Return rates were also low in *Z. l. oriantha* females, but not in males, born prior to 10 July (Fig. 6). I propose that this pattern occurs because the more time juvenile females (but not males) spend on the summering area the greater the distance they will tend to wander before migration. In so doing, they establish home areas, to which they will return later as adults, that will be largest in those born earliest in the season and thus more likely to extend beyond the boundaries of the study area. This would lead to the observed pattern of return rates. A regression of time spent on the study area versus birth date lends some support to this hypothesis in that the number of days spent on the study area as a juvenile tended to remain the same in females and to decrease in males the later they were born (Fig. 7). The effects of birth date and body mass at fledging on postfledging survival are of considerable interest (Perrins 1965, Dhondt 1971, Krementz et al. 1989), but survival probability calculations can be plagued by an inability to separate effects of dispersal from those due to mortality (Dhondt 1979, Dhondt and Olaerts 1981). The data above indicate that the relative effects of these two factors can likely change with birth date and sex.

When adult *Z. l. oriantha* began arriving at Tioga Pass from their wintering areas, males tended to precede females, the mean difference being almost 6 days in yearlings as well as in older birds (Tables 2, 3). Still, there was not a temporally exclusive period during which males arrived because at least a few females were known to be present right from the beginning.

Of particular interest in this study are the dynamics of arrival and return rates of one-year-old or yearling birds and how these might relate to their abilities to obtain their first territory and

mate. These factors can be examined with respect to birth sites (origin), time spent on the study area as juveniles, if any, and sex in order to clarify how experiences of juveniles, particularly their dispersal tendencies, might be related subsequently to their reproductive success. For example, arrival schedules of yearlings were only about two days behind those of older birds of the same sex (Tables 2, 3) so age and its attendant experience had little effect on the birds' abilities to perform a timely migration and to locate suitable breeding habitat at its termination. Also, return rates of yearlings to the study area that were known to have been present on the study area as juveniles were quite different in the sexes. The overall return rate of 10.0% in females was significantly lower than the 13.9% observed in males. The duration of time females were known to have lived on the study area as juveniles did not strongly affect their propensity to return as adults but in males there was a positive effect of residency (Tables 4, 5). Males known to have been on the study area for more than four weeks as juveniles (Group 2) had an average return rate of 28.5%. This is exceedingly high for young migratory birds (Farner 1945) and it may represent nearly all members of Group 2 that were still alive as yearlings. An obvious conclusion is that Group 2 males were not only highly philopatric but that they and many other members of the population had identified future potential territories as juveniles. I hesitate to attribute these higher than usual rates of return to interspecific variation. It seems likely instead that the Tioga study area functions somewhat like an island because it encompasses most of the prime habitat in that part of Lee Vining Canyon. This could lead to higher natal return rates and lower natal dispersal distances from those observed in other migrant species (see Nyholm 1986).

Selection of breeding habitat by juveniles while still on their natal area may occur in a wide array of avian species (Löhr 1959, Hildén 1965, Haukioja 1971, Catchpole 1972, Berndt and Winkel 1979, Seastedt and MacLean 1979, Adams and Brewer 1981, Able and Bingman 1987, Morton et al. 1991). This behavior is thought to be adaptive because habitat conditions can be more accurately evaluated during the postfledging period by juveniles than upon their arrival the next spring when the vegetation is undeveloped (Brewer and Harrison 1975) or even completely covered by a residual snowpack as often occurs at high lat-

itude or altitude (Seastedt and MacLean 1979, Morton et al. 1991). Thus, yearlings might be able to locate suitable habitat and commence breeding as quickly as older, more experienced birds. This would be important in *Z. l. oriantha* because their annual productivity appears to be closely tied to breeding period duration (Fig. 3 and Morton and Allan 1990) and because yearlings comprise 40–45% of known age breeders on the Tioga study area (Morton, unpubl. data). The ability of yearlings to locate their natal areas upon migrating in from wintering areas depends upon how familiar they were as juveniles with local landmarks and how well they developed an internal "mosaic map" of the area that could be used for homing purposes (Wiltschko and Wiltschko 1978).

In summary, juveniles varied widely in their inclinations to remain within the confines of the study area. Among females this variation in experience did not substantially affect their propensity to return as adults or their ability to attain breeding status. Homing ability and philopatry increased greatly in males, however, if they spent at least four weeks on the area (Group 2 birds) although breeding status was unaffected (Table 5). There is another comparison not yet discussed, one that is not so fine-grained as that above, and it is of yearlings previously known on the study area as juveniles (Group 1 plus Group 2 birds) versus those never captured and banded until they were adults. The former have been called juvenile recruits and the latter adult recruits. Juvenile recruits tended to appear at Tioga two or three days earlier than adult recruits but the mean dates of arrival were not significantly different (Table 6). The birth location of females did not affect their subsequent abilities to achieve reproductive status on the study area. Those born on it or nearby (juvenile recruits) had the same percentage of known breeders as those born at a more remote location (adult recruits). In males, however, 50.4% of the juvenile recruits were known breeders as yearlings whereas only 40.5% of the adult recruits obtained that status. This difference was very nearly significant at the 0.05 level (Table 7). Thus, in males it appears that familiarity with the breeding area as a juvenile may increase the probability of attaining a territory and mate during the first reproductive cycle. Philopatry may be favored in males because information gathered when they are juveniles helps them to locate and defend

their first breeding territory and settling on or near their natal area may also reduce intrasexual aggression. For example, there are many distinctive dialects sung by *Z. l. oriantha* in the Sierra Nevada (Orejuela and Morton 1975, Baptista and King 1980) and it seems possible that juvenile males learn the dialect of local breeding males and later use it themselves as adults thereby reducing conflicts with the older males and enhancing their own ability to hold a territory (see Payne 1982, Payne et al. 1988, Thielcke and Krome 1989). Another indication that philopatry was greater in males than in females was that 83% of the female recruits were of the adult type and, therefore, strangers to the area whereas the proportion was only 69% in males, a highly significant difference (Table 7).

A DESCRIPTIVE MODEL OF NATAL DISPERSAL IN *Z. L. ORIANTHA*

The process whereby a migratory passerine locates and finally settles on its breeding territory is not well understood (Pärt 1990) but intense selection must be operating on the series of physiological and behavioral responses involved because their execution must be precise in timing and sequence in order to maximize the birds' survival and opportunities for reproduction. The data presented herein on *Z. l. oriantha* provide clues about this process, not definitive answers. Nonetheless, it may be useful to incorporate them into a descriptive model that can be used for comparative purposes and perhaps for stimulating additional studies. I envision the process, and some of its implications as follows:

The familiar world of *Z. l. oriantha* juveniles begins to expand soon after fledging at which time broods are usually divided between the parents. These family subunits tend to drift away from the nest site so that by the time juveniles are one month of age and separating from parental care they are already well away from their natal territory. Once independent, they continue to move and explore the meadow of their birth and those nearby, developing a mental map of these areas and assessing their suitability for settling as yearlings as they do so. By two months of age, many are located at least several km from the natal area (Morton et al. 1972b, 1991). Sexual differences are apparent by this time with females covering larger areas than males; those born earliest in the season travel the greatest distances, perhaps even into other watersheds and dialect

areas. Throughout this period the postjuvinal molt is in progress, but it involves only contour feathers, not flight feathers, so mobility is not severely affected. Eventually molt is completed, traveling subsides, the juveniles became hyperphagic, fatten, and depart on migration to wintering areas, often before the adults. An important effect of these dispersal movements is that a summer home range is established which is substantial in size, well known by the bird, and which includes terrain suitable for breeding purposes. The home range area of males is smaller than that of females and less likely to extend beyond the boundaries of the Tioga study area. An empirical result of this asymmetry is that upon their return the next spring as yearlings, more males than females are captured because the target home area in males is smaller and more closely approximates the study area in size. Many of the yearling males wander over meadows familiar to them looking for a place to settle but members of a subset that was highly sedentary the previous summer do not wander. They are site tenacious and return to the same meadow previously inhabited and remain there. Yearling females also wander over their previously established summer range looking for places to settle. Their movements may be greater in distance than those of males and the area settled in is unrelated to the duration of their occupancy in it the previous summer.

Quite a few predictions about the biology of yearlings can be made based upon this model and many are supported by data. For instance, females are not less philopatric than males; they just appear to be to the investigator because they are distributed over a wider area first as juveniles and later as adults. Thus their return rates to a particular study area are lower and natal dispersal distances greater than those of males. Another prediction would be that both sexes are exposed to a diverse array of dialects as juveniles. This might help to explain why females do not discriminate among dialects when choosing a mate (Baptista and Morton 1982) and why males are known to learn dialects other than the one of the father (Baptista and Morton 1988).

Other implications stem from this model. One is that natal dispersal begins in juveniles and for some, such as Group 2 males, may even be essentially completed before they leave on fall migration. Another is that philopatry is high (and desirable) for both sexes. It could, for example,

facilitate successful navigation in spring to suitable breeding habitat and lead the bird to an ancestral area for which it possesses highly adapted gene complexes (Shields 1982, 1983). The model also behooves us to think about why juveniles exhibit dispersal behaviors which probably increase their exposure to mortality-inducing situations. And why, in an ultimate sense, should females disperse farther than males? One possibility is that females need a larger summering area to successfully home to from wintering areas because they might not be as adept at navigating as males. A priori, this is unexpected because gonadotropins and gonadal hormones are not known to play a primary regulatory role in migratory behavior (Emlen 1975, Rankin 1991). However, male passerines do commonly winter closer to breeding areas than females (see review by Gauthreaux 1982) so given no sexual difference in propensity for or degree of navigational errors, females might still benefit from having a larger summering area target than males because they are trying to hit it from a greater distance.

Usually dispersal patterns and their sexual asymmetries are considered to be shaped by the need to minimize hazards or costs associated with moving into new areas (Eden 1987), to avoid close inbreeding (Packer 1985) or to avoid intrasexual competition for mates or resources such as high quality territories (Moore and Ali 1984, Waser 1985, Wrangham and Rubenstein 1986, Arcese 1987). Several of these factors could also be acting simultaneously to drive dispersal behavior (Dobson and Jones 1985). Apparently close inbreeding rarely occurs in *Z. l. oriantha* so if this is the reason for sexual differences in dispersal, the response is effective. Parent-offspring matings would be unexpected because yearlings did not settle on their natal territories but settling locations of the sexes did overlap substantially (Fig. 8). This leaves open the possibility that inbreeding avoidance occurs not by spatial segregation—a demographic consequence of dispersal—but by some other mechanism known to occur in birds, such as kin recognition (Bateson 1978, 1982; Koenig and Pitelka 1979; Nilsson 1989). If that were the entire mechanism in *Z. l. oriantha*, however, no sexual asymmetry in dispersal distance would be predicted. While not entirely decisive, the data on their natal dispersal distances, return rates, and composition of recruits suggest otherwise. This leaves us to

ponder the possible effects of intrasexual competition.

It is usually assumed that young males in sedentary avian species face stiff competition for breeding territories. In response to this, they disperse from their natal areas but only until an unoccupied territory is encountered. They then settle in that area and defend it (Murray 1967). This pattern of resource defense by males as opposed to mate defense, leads to monogamy and it is left to females to disperse greater distances in order to avoid overlapping with their close male kin and incurring the deleterious effects presumed to be caused by close inbreeding. Thus the sexual asymmetry in dispersal distance is established and it can be predicted from the characteristics of the mating system (Greenwood 1980). These ideas are not easily applied to the biology of migrants, however, nor do they comfortably fit the data reported herein. It strikes me that more consideration might be given to intrasexual competition among females. Such competition has been observed in European Nuthatches *Sitta europaea* (Matthysen 1986, 1987) and Song Sparrows *Melospiza melodia* (Arcese 1989a, 1989b, 1989c), but, on balance, it is a neglected area of avian behavior that could be important to understanding dispersal dynamics. We possess considerable unpublished data which suggest that female *Z. l. oriantha* can be quite aggressive. For example, they sometimes arrive in spring before their mate and take up territorial residence even before he does. Once on territory they will fly at and displace conspecifics other than their mate, and if a multiple-cell live trap is put out on the territory with a conspecific decoy in one of the cells, the female is captured more frequently than the male. About the time nesting begins females exhibit transiently elevated plasma testosterone levels and sing from elevated perches much in the manner of males (Morton et al. 1985). Furthermore, newly arrived yearling females, but not males, are often trapped on successive days at widely separated locations on our study area indicating that they are moving considerable distances in search of a place to settle. Older females do not do this, they tend to return to the previous year's territory and stay there even if a different male is present. My interpretation of this information is that female-female competition may be an important factor in their dispersion on the summering grounds, affecting the spacing of both experienced females

because of preferences they developed during prior occupancy and of naive, yearling females in search of their first nesting site.

LITERATURE CITED

- ABLE, K. P., AND V. P. BINGMAN. 1987. The development of orientation and navigation behavior in birds. *Quart. Rev. Biol.* 62:1-29.
- ADAMS, R. J., JR., AND R. BREWER. 1981. Autumn selection of breeding location by Field Sparrows. *Auk* 98:629-631.
- ARCESE, P. 1987. Age, intrusion pressure and territory defence against floaters by male song sparrows. *Anim. Behav.* 35:773-784.
- ARCESE, P. 1989a. Territory acquisition and loss in male song sparrows. *Anim. Behav.* 37:45-55.
- ARCESE, P. 1989b. Intrasexual competition and the mating system in primarily monogamous birds: the case of the song sparrow. *Anim. Behav.* 38:96-111.
- ARCESE, P. 1989c. Intrasexual competition, mating system and natal dispersal in song sparrows. *Anim. Behav.* 38:958-979.
- BAPTISTA, L. F., AND J. R. KING. 1980. Geographical variation in song and song dialects of montane White-crowned Sparrows. *Condor* 82:267-284.
- BAPTISTA, L. F., AND M. L. MORTON. 1982. Song dialects and mate selection in montane White-crowned Sparrows. *Auk* 99:537-547.
- BAPTISTA, L. F., AND M. L. MORTON. 1988. Song learning in montane white-crowned sparrows: from whom and when. *Anim. Behav.* 36:1753-1764.
- BATESON, P. 1978. Sexual imprinting and optimal outbreeding. *Nature* 273:659-660.
- BATESON, P. 1982. Preferences for cousins in Japanese quail. *Nature* 295:236-237.
- BERNDT, R., AND W. WINKEL. 1979. Verfrachtungsexperimente zur Frage der Geburtsortsprägung beim Trauerschnäpper (*Ficedula hypoleuca*). *J. Orn.* 120:41-53.
- BREWER, R., AND K. G. HARRISON. 1975. The time of habitat selection by birds. *Ibis* 117:521-522.
- BROWN, J. L. 1975. The evolution of behavior. Norton Publ., New York.
- CATCHPOLE, C. K. 1972. A comparative study of territory in the Reed warbler (*Acrocephalus scirpaceus*) and Sedge warbler (*A. schoenobaenus*). *J. Zool., Lond.* 166:213-231.
- DHONDT, A. A. 1979. Summer dispersal and survival of juvenile Great Tits in southern Sweden. *Oecologia* 42:139-157.
- DHONDT, A. A., AND G. OLAERTS. 1981. Variations in survival and dispersal with ringing date as shown by recoveries of Belgian Great Tit *Parus major*. *Ibis* 123:96-98.
- DOBSON, F. S., AND W. T. JONES. 1985. Multiple causes of dispersal. *Am. Nat.* 126:855-858.
- DRILLING, N. E., AND C. F. THOMPSON. 1988. Natal and breeding dispersal in House Wrens (*Troglodytes aedon*). *Auk* 105:480-491.
- EDEN, S. F. 1987. Natal philopatry of the Magpie *Pica pica*. *Ibis* 129:477-490.
- EMLEN, S. T. 1975. Migration: orientation and navigation, p. 129-219. *In* D. S. Farner and J. R. King [eds.], *Avian biology*, vol. V. Academic Press, New York.
- FARNER, D. S. 1945. The return of Robins to their birthplaces. *Bird-Banding* 16:81-99.
- 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.
- GOODBODY, I. M. 1952. The post-fledging dispersal of juvenile titmice. *British Birds* 45:279-285.
- GRATTO, C. L. 1988. Natal philopatry, site tenacity, and age of first breeding of the Semipalmated Sandpiper. *Wilson Bull.* 100:660-663.
- GRATTO, C. L., R. I. G. MORRISON, AND F. COOKE. 1985. Philopatry, site tenacity, and mate fidelity in the Semipalmated Sandpiper. *Auk* 102:16-24.
- GREENWOOD, P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. *Anim. Behav.* 28:1140-1162.
- GREENWOOD, P. J., AND P. H. HARVEY. 1982. The natal and breeding dispersal of birds. *Ann. Rev. Ecol. Syst.* 13:1-21.
- HAUKIOJA, E. 1971. Short-distance dispersal in the Reed Bunting *Emberiza schoeniclus*. *Ornis Fenn.* 48:45-67.
- HILDÉN, O. 1965. Habitat selection in birds. *Ann. Zool. Fenn.* 2:53-75.
- HOWARD, W. E. 1960. Innate and environmental dispersal of individual vertebrates. *Am. Midl. Nat.* 63:152-161.
- KOENIG, W. D., AND F. A. PITELKA. 1979. Relatedness and inbreeding avoidance: counterplays in the communally nesting acorn woodpecker. *Science* 206:1103-1105.
- KREMENTZ, D. G., J. D. NICHOLS, AND J. E. HINES. 1989. Postfledging survival of European Starlings. *Ecology* 70:646-655.
- LÖHRL, H. 1959. Zur Frage des Zeitpunktes einer Prägung auf die Heimatregion beim Halsbandschnäpper (*Ficedula albicollis*). *J. Orn.* 100:132-140.
- MATTHYSEN, E. 1986. Some observations on sex-specific territoriality in the Nuthatch. *Ardea* 74:177-183.
- MATTHYSEN, E. 1987. Natal dispersal in the Nuthatch. *Ornis Scand.* 18:313-316.
- MOORE, J., AND R. ALI. 1984. Are dispersal and inbreeding avoidance related? *Anim. Behav.* 32:94-112.
- MORTON, M. L. 1978. Snow conditions and the onset of breeding in the Mountain White-crowned Sparrow. *Condor* 80:285-289.
- MORTON, M. L. 1991. Postfledging dispersal of Green-tailed Towhees to a subalpine meadow. *Condor* 93:466-468.
- 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*. Japan Sci. Soc. Press, Tokyo. Springer-Verlag, Berlin.
- MORTON, M. L., J. L. HORSTMANN, AND J. M. OSBORN.

- 1972a. Reproductive cycle and nesting success of the Mountain White-crowned Sparrows (*Zonotrichia leucophrys oriantha*) in the central Sierra Nevada. *Condor* 74:152-163.
- 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., J. E. OREJUELA, AND S. M. BUDD. 1972b. The biology of immature Mountain White-crowned Sparrows (*Zonotrichia leucophrys oriantha*) on the breeding ground. *Condor* 74:423-430.
- MORTON, M. L., M. E. PEREYRA, AND L. F. BAPTISTA. 1985. Photoperiodically induced ovarian growth in the White-crowned Sparrow (*Zonotrichia leucophrys gambelii*) and its augmentation by song. *Comp. Biochem. Physiol.* 80A:93-97.
- MORTON, M. L., L. E. PETERSON, D. M. BURNS, AND N. ALLAN. 1990. Seasonal and age-related changes in plasma testosterone levels in Mountain White-crowned Sparrows. *Condor* 92:166-173.
- MORTON, M. L., M. W. WAKAMATSU, M. E. PEREYRA, AND G. A. MORTON. 1991. Postfledging dispersal, habitat imprinting, and philopatry in a montane, migratory sparrow. *Ornis Scand.* 22:98-106.
- MURRAY, B. G., JR. 1967. Dispersal in vertebrates. *Ecology* 48:975-978.
- NILSSON, J.-Å. 1989. Causes and consequences of natal dispersal in the marsh tit, *Parus palustris*. *J. Anim. Ecol.* 58:619-636.
- NILSSON, J.-Å., AND H. G. SMITH. 1985. Early fledging mortality and the timing of juvenile dispersal in the marsh tit *Parus palustris*. *Ornis Scand.* 16:293-298.
- NILSSON, J.-Å., AND H. G. SMITH. 1988. Effects of dispersal date on winter flock establishment and social dominance in marsh tits *Parus palustris*. *J. Anim. Ecol.* 57:917-928.
- OREJUELA, J. E., AND M. L. MORTON. 1975. Song dialects in several populations of Mountain White-crowned Sparrows (*Zonotrichia leucophrys oriantha*) in the Sierra Nevada. *Condor* 77:145-153.
- NYHOLM, N.E.I. 1986. Birth area fidelity and age at first breeding in a northern population of Pied Flycatcher *Ficedula hypoleuca*. *Ornis Scand.* 17:249-252.
- PACKER, C. 1985. Dispersal and inbreeding avoidance. *Anim. Behav.* 33:676-678.
- PÄRT, T. 1990. Natal dispersal in the Collared Flycatcher: possible causes and reproductive consequences. *Ornis Scand.* 21:83-88.
- PAYNE, R. B. 1982. Ecological consequences of song matching: breeding success and intraspecific song mimicry in Indigo Buntings. *Ecology* 63:401-411.
- PAYNE, R. B., L. L. PAYNE, AND S. M. DOEHLERT. 1988. Biological and cultural success of song memes in Indigo Buntings. *Ecology* 69:104-117.
- PERRINS, C. M. 1965. Population fluctuations and clutch-size in the Great Tit, *Parus major*. *J. Anim. Ecol.* 34:601-647.
- PUSEY, A. E. 1987. Sex-biased dispersal and inbreeding avoidance in birds and mammals. *Trends Ecol. Evol.* 2:295-299.
- RANKIN, M. A. 1991. Endocrine effects on migration. *Am. Zool.* 31:217-230.
- SEASTEDT, T. R., AND S. F. MACLEAN. 1979. Territory size and composition in relation to resource abundance in Lapland Longspurs breeding in arctic Alaska. *Auk* 96:131-142.
- SHIELDS, W. M. 1982. Philopatry, inbreeding and the evolution of sex. State Univ. of New York Press, Albany, NY.
- SHIELDS, W. M. 1983. Optimal inbreeding and the evolution of philopatry, p. 132-159. *In* I. R. Swingland and P. J. Greenwood [eds.], *The ecology of animal movement*. Clarendon Press, Oxford, England.
- SOKAL, R. R., AND F. J. ROHLF. 1981. *Biometry*. Second Ed. W. H. Freeman, San Francisco.
- SOKOLOV, L. V., V. G. VYSOTSKY, AND A. V. BARDIN. 1987. Post-fledging dispersal of the Pied Flycatcher, *Ficedula hypoleuca*, at the Kurische Nehrung. *USSR Acad. Sci., Proc. Zool. Institut.* 163:126-135.
- THIELCKE, G., AND M. KROME. 1989. Experimente über sensible Phasen und Gesangsvariabilität beim Buchfinken (*Fringilla coelebs*). *J. Ornithol.* 130:435-453.
- TOMPA, F. S. 1962. Territorial behavior: the main controlling factor of a local Song Sparrow population. *Auk* 79:687-697.
- VAN BALEN, J. H. 1979. Observations on the post-fledging dispersal of the Pied Flycatcher, *Ficedula hypoleuca*. *Ardea* 67:134-137.
- WASER, P. M. 1985. Does competition drive dispersal? *Ecology* 66:1170-1175.
- WEISE, C. M., AND J. R. MEYER. 1979. Juvenile dispersal and development of site-fidelity in the Black-capped Chickadee. *Auk* 96:40-55.
- WILTSCHKO, W., AND R. WILTSCHKO. 1978. A theoretical model for migratory orientation and homing in birds. *Oikos* 30:177-187.
- WRANGHAM, R. W., AND D. I. RUBENSTEIN. 1986. Social evolution in birds and mammals, p. 452-470. *In* D. I. Rubenstein and R. W. Wrangham [eds.], *Ecological aspects of social evolution*. Princeton Univ. Press, NJ.