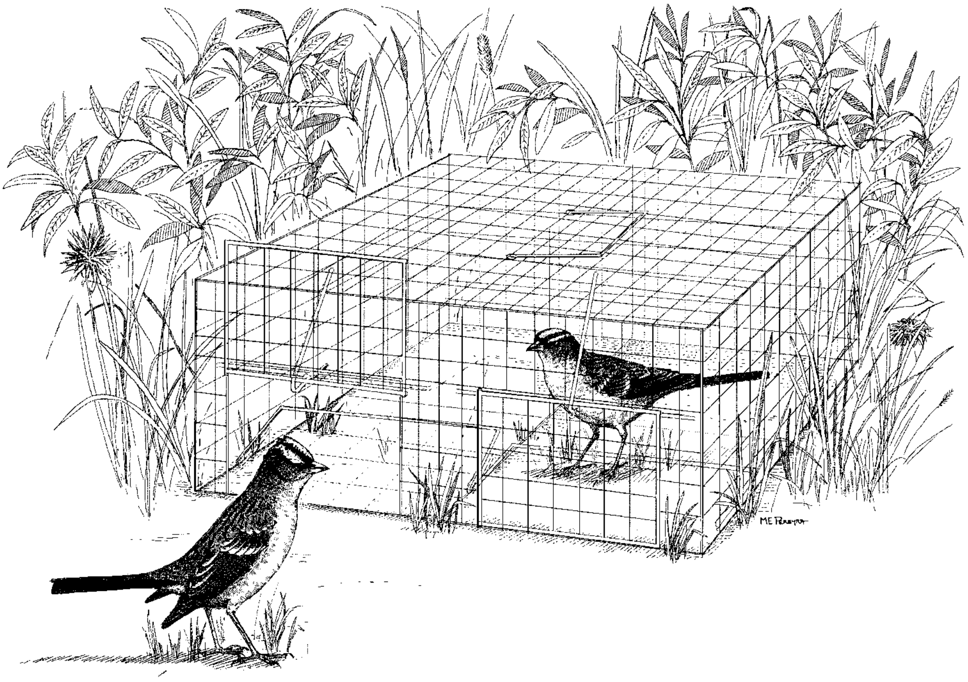

CHAPTER 4: Demography

One of the most interesting questions about members of any study population is, "How long do they live?" For avian populations, despite a few drawbacks and assumptions, this question has been profitably addressed by affixing individuals with uniquely numbered bands (Farner 1955b). From banding returns it is then possible to accumulate demographic statistics that can be used for obtaining basic information on such parameters as age-specific survival and population growth rates and, eventually, to comparisons that can illuminate the relative hazardousness of events such as those involving migration flights and occupancy of different types of breeding habitat. A traditional method for consolidating demography data into a concise and standard format is the life table (Deevey 1947).

LIFE TABLE

A dynamic-composite life table was constructed for Tioga Pass *oriantha* by using data obtained from philopatric juveniles. That is, a cohort was assembled from juveniles, banded during the years 1978 to 1986, that returned as adults to nest on the study area. This method does not yield reliable information on survival during the first year of life (which is thought to be less than 30% in passerines; Newton 1989b), because there were probably many surviving one-year-olds that did not settle on the study area. Those that did settle there, however, were site-faithful with regard to their subsequent annual selection of breeding territories, so their survival statistics can provide a useful life table for individuals that lived for more than one year (Table 4.1). The sample size of males in this table was higher initially than that of females because females tended to be less philopatric than males (Morton 1992b, 1997). Median survival time for the individuals represented in Table 4.1 was 1.94 yr for males and 1.91 yr for females, and this was not different (Wilcoxon test: W = 0.102, df = 1, P = 0.750).

About half of the adult population, both males and females, survived each year (Table 4.1). This is similar to the rate obtained by Baker et al. (1981) for *nuttalli*, the sedentary subspecies, and is an interesting result because it suggests that migration may not be particularly hazardous for *oriantha*. Note that survival in *oriantha* has been computed in increments of one year, from one summer to the next, so the average bird is probably living about 0.5 yr longer than one might gather from looking at Table 4.1.

These data tend to support the hypothesis that passerines show a constant age-

TABLE 4.1. AGE-SPECIFIC LIFE TABLES FOR MALE AND FEMALE *Oriantha* BANDED AS JUVENILES AT TIOGA PASS

Age	Males				Females			
(yr)	n_x	d_x	l_x	e_x	n_x	d_x	l_x	e_x
1–2	134	71	1.000	1.49	80	44	1.000	1.40
2–3	63	28	0.470	1.60	36	16	0.450	1.50
3–4	35	17	0.261	1.49	20	10	0.250	1.30
4–5	18	10	0.134	1.42	10	7	0.125	1.10
5–6	8	3	0.060	1.55	3	2	0.038	1.45
6–7	5	2	0.037	1.19	1	0	0.012	2.50
7–8	3	2	0.022	0.64	1	0	0.012	1.50
8–9	1	1	0.007	0.43	1	1	0.012	0.50

Notes: n_x = cohort size, d_x = number of disappearances, l_x = the fraction of the initial cohort returning at each subsequent age class, e_x = the future life expectancy (see Deevey 1947, Stearns 1992).

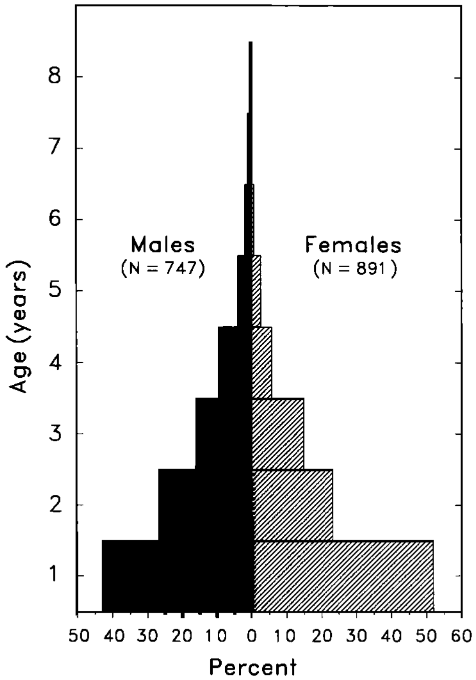

FIGURE 4.1. Age distribution of *oriantha* males and females known to be engaged in reproduction at Tioga Pass.

specific mortality rate once they reach adulthood (Deevey 1947, Bulmer and Perrins 1973). This evident lack of senility may be an artifact due to small sample sizes for older individuals found in most studies, or it may simply be that physiological time is scaled to body size (Lindstedt and Calder 1976). No generalization about survival chances seem possible, however, because significant declines have been demonstrated in several species, both short- and long-lived (Newton 1989b).

The maximum life span obtained for *oriantha* from the life table was eight years. This is not quite within the range of maximum longevities for four species of *Zonotrichia,* 9 to 13 yr, gleaned from banding records deposited with the Bird Banding Laboratory (Klimkiewicz and Futcher 1987). Interestingly, the oldest age reported, 13.3 yr, was for a *gambelii,* the subspecies of White-crowned Sparrow that migrates the greatest distances (Fig. 1.1).

AGE STRUCTURE OF BREEDING POPULATION

As would be expected in a small passerine, more one-year-old *oriantha* were engaged in reproduction in any given year than members of any other age class. The pyramid depicting the proportions of known-age breeders for each sex for all years of the study shows that 42.8% of the males and 52.0% of the females known to have nests were one-year-olds (Fig. 4.1). The maximum age attained by *oriantha* during this study was eight years (one male and one female), but it is worth noting that at the end of the study in 1997 there were three eight-year-old *oriantha* at Tioga Pass, two males and one female, and that one male and the

TABLE 4.2. AGES AND RETURN RATES OF *Oriantha* KNOWN TO HAVE NESTS

Age (yr)	Males		Females	
	N	% return	N	% return
1	320	—	463	—
2	199	62.2	208	44.9
3	117	58.8	134	64.4
4	68	58.1	52	38.8
5	26	38.2	24	46.2
6	11	42.3	7	29.2
7	5	45.5	2	28.6
8	1	20.0	1	50.0

female, then age nine, returned again in 1998 but not in 1999 (E. MacDougall-Shackleton, pers. comm.). Mean age of breeding individuals was 1.88 yr for females and 2.12 yr for males, a significant difference (Kolmogorov-Smirnov test: $N_1 = 891$, $N_2 = 747$, $D = 0.091$, $P = 0.002$). Sample sizes for the sexes were skewed somewhat by identification techniques because it was easier to prove that females were associated with nests than it was for males; females could be identified by their color bands when flushed from a nest (while incubating or brooding) or when bringing food to the nestlings, males only when bringing food. In addition, sitting females were sometimes driven off the nest into a mist net to obtain positive identification. About half of each age cohort depicted in Fig. 4.1 returned to the study area each year (Table 4.2).

These data are puzzling. The life table (Table 4.1) shows no difference in survival time for the sexes, yet among the breeders males were older. There could be at least two different reasons for this and they could be acting simultaneously. One is that mortality rates were actually higher in females than in males, although this was not shown in the life table because of small sample sizes. In fact, adult female passerines often die at a higher rate than males of the same age (Lack 1954), and this can happen both in early (Smith 1995) and late adulthood (McGillivray and Murphy 1984). Another reason is that a disproportionate number of the younger adult males, especially one-year-olds, did not gain territories and mates.

The age class with the lowest percentage of known nesters for both sexes was the one-year-olds (Table 4.3). Only 45.2% of the males and 63.3% of the females of that age were known to have nests. For reasons stated above, these numbers are underestimates (probably close to 100% of the older birds, especially the

TABLE 4.3. PERCENTAGE OF ADULT *Oriantha* OF VARIOUS AGES CAPTURED ON THE STUDY AREA THAT WERE KNOWN TO HAVE NESTS ON THE STUDY AREA

Age (yr)	Known to have nests (%)			
	Males	N	Females	N
1	45.2	520	63.3	474
2	50.5	223	74.3	187
3	60.7	107	80.5	82
4	66.0	50	75.5	49
5	68.2	22	73.3	15
6+	70.6	17	88.9	9

females, actually had nests), yet they undoubtedly reflect some biological realities. For example, unmated males were usually one-year-olds, and non-breeding adult males outnumbered females not only because males tended to outlive females, but also because some mated males were polygynous (Chapter 3). In a study of mortality in the Great Tit, Bulmer and Perrins (1973) also found that breeding males were older than breeding females. As in the case of *oriantha,* this was attributed to an excess of males caused by their lower mortality and to lower competitive abilities of younger males. Higher mortality rates in females are frequently associated with the energetic demands accompanying reproduction, and Sealy et al. (1986) have shown that female passerines are taken off their nests by predators, and that they sometimes die of exposure or starvation while trying to defend their nests during storms. No cases of death from starvation were known in *oriantha* females, but in a number of instances (three times in 1984 alone) feathers were found in and around disrupted nests, indicating that a predator had taken the tending female. Furthermore, females that nested late in the season were very lean and probably highly stressed. They were sometimes the sole providers of parental care, and often while undergoing molt (Chapter 11).

Table 4.2 does not have the legitimacy of a regular life table because the majority of the birds represented in it were handled for the first time on the study area as adults and were assumed at that time to be one-year-olds. And, like Table 4.1, its usefulness depends upon the adults being site-faithful. These caveats aside, among the birds known to be engaged in nesting, one-year-old females returned less often as two-year-olds than did males (Chi-square = 6.79, df = 1, P = 0.009). None of the other multiple contrasts of annual return rates of the sexes from age two to age six were significantly different (beyond that age sample sizes were too small to do valid Chi-squares). This is an interesting result because it mirrors what Smith (1995) found in Black-capped Chickadees. She discovered that males lived longer than females due to differential mortality during and immediately after the first breeding season. Females mated to young males were vulnerable because they were poorly provisioned by their inexperienced mates. Male *oriantha* are known to provision their mates, but only rarely (Zerba and Baptista 1980), and one-year-old *oriantha* females did have a higher percentage of one-year-old mates than females of any other age class (Chapter 3).