

CHAPTER 2: Migration Arrival

When migrants travel from wintering to summering areas they accomplish a journey that can take them through unfamiliar and inhospitable terrain and sometimes into the path of dangerous storms. Clearly the successful navigation of such hazardous passages requires substantial direction-finding and energy-managing abilities (Alerstam 1990). In addition, they must recognize and stop at the correct final destinations and arrive there near the optimum time for beginning their seasonally-restricted reproductive efforts. These problems can only be magnified when the final destination is a small mountain meadow that may still be buried under snow. This key part of vernal migration biology, its termination at the breeding area, will now be considered.

ARRIVAL SCHEDULE

To determine when *oriantha* were first arriving, an attempt was made to reach the study area before them. Daily searches of the area were then performed and seed-baited live traps were set next to emergent vegetation and to lodgepole pines at meadow borders. Most birds seemed willing to enter traps and the dates of first captures of individuals were taken to be the equivalent of their arrival times. Early season access to the study area was impossible in many years because of road closures, but in 1988, 1995, 1996, and 1997 Tioga Pass was reached ahead of the birds and their arrival times were recorded. The arrival period for the study population during these four years was arbitrarily defined as beginning with the first capture of the season and ending when the first clutches were started.

The first individuals trapped were males and their mean dates of arrival were from 8 to 12 d earlier than those of females (Table 2.1). For all birds combined, mean arrival time was 9.7 d earlier in males (N = 144) than in females (N = 94, $t = 8.28$, $P < 0.001$). Note that the number of males in the sample exceeded that of females by 53%. This can be attributed to males being more numerous in the population, to females being more difficult to capture, and also to the fact that some of the early-arriving males that eventually settled near the study area, such as the East Slope (see Fig. 1.3), tended at first to remain on TPM, where the traps were located, and where more open terrain, suitable for foraging, was available. By the time females arrived the slopes were thawed somewhat and they could go directly to them, bypassing the TPM trapline altogether.

The dynamics of arrival varied greatly from year to year, depending upon the extent of the residual snowpack and the frequency of spring storms. For example, in 1995 the snowpack was deep and persistent and four storms occurred during the arrival period, three in May and one in June (Fig. 2.1, upper). These storms

TABLE 2.1. TIME OF ARRIVAL (=FIRST CAPTURE OF THE SEASON) OF *Oriantha* AT TIOGA PASS MEADOW DURING FOUR YR

Year	Date of first individual's arrival		Mean difference for whole arrival period		N		First eggs
	Male	Female	Days	P ^a	Males	Females	
1988	3 May	13 May	7.8	0.004	34	21	5 June
1995	17 May	26 May	12.0	<0.001	32	27	7 July
1996	5 May	11 May	11.1	<0.001	42	23	10 June
1997	5 May	6 May	8.0	<0.001	36	23	1 June

^a P-values for t-test of mean differences in arrival times between males and females.

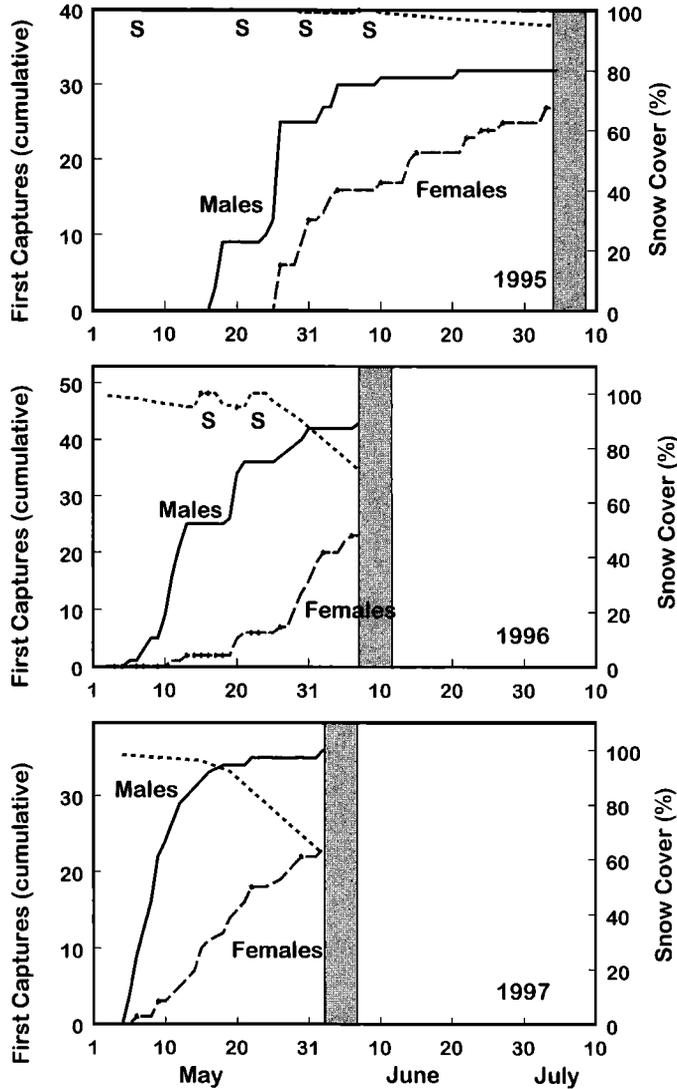


FIGURE 2.1. Arrival schedules of *oriantha* at Tioga Pass Meadow for three yr. Dashed line indicates percentage of ground covered by snow and S the occurrence of a storm. Gray bars show when the first clutches were started.

tended to inhibit the influx of new birds to the study area, and plateaus in the incidence of arrival occurred when storms were in progress. There was no open ground in May of 1995, only a little in June, and females did not begin laying until 7 July at which time snow cover (the percent of ground covered by snow) was still about 95%. The first females were captured on 26 May so the interval between their arrival and the appearance of eggs was 42 days.

There was less snow in 1996 than in the previous spring and birds began to show up earlier on TPM; males first appeared on 5 May and females on 11 May (Fig. 2.1, middle). Once again storms occurred (two in May) that briefly inter-

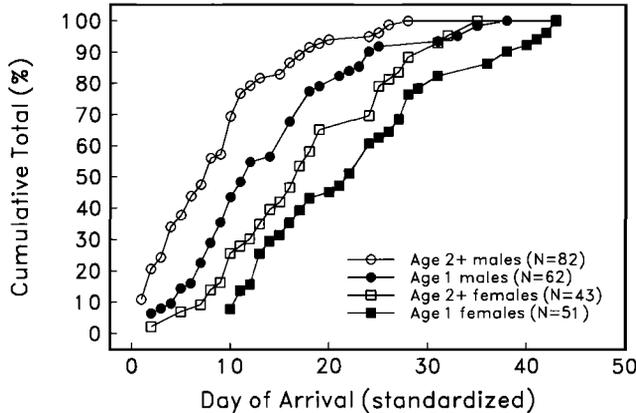


FIGURE 2.2. Arrival schedules of *oriantha* at Tioga Pass Meadow by sex and age class. Data are for four yr (1988, 1995, 1996, 1997), and are standardized such that the date the first bird was captured each year was called day 1 of arrival for that specific year.

rupted the appearance of new birds. The first eggs were laid on 10 June, 30 days after the first females were present and when snow cover was about 70%.

Spring conditions were unusually mild in 1997 and there were no storms to impede the arrival schedule (Fig. 2.1, lower). Laying began on 1 June, 26 days after the first female was captured. Warm weather and absence of storms caused the snow to melt rapidly and snow cover had already decreased to about 60% when the first clutches were started. Aside from highlighting the variation that occurred in arrival schedules, the above data indicate that environmental conditions, storms and snowpack in particular, strongly influenced the reproductive schedules of *oriantha*. How they adapted to these conditions will be described more fully in later chapters. Note that Fig. 2.1 shows cumulative first captures only; it does not accurately represent how many birds were present at any particular moment during the arrival period because, as will be explained below, following their initial arrival individuals were sometimes absent from the breeding habitat for hours or days at a time.

Arrival varied with age as well as sex. As a group, older males (age 2+ yr) tended to arrive earliest, followed in order by one-year-old males, older females, and one-year-old females (Fig. 2.2). It seems that previous experience as an adult on TPM facilitated early arrival in both sexes. The standardized data displayed in Fig. 2.2 show that older males ($N = 82$) had a mean arrival time that was 5.4 d earlier than that of one-year-old males ($N = 62$, $t = 4.20$, $P < 0.001$), and that older females ($N = 43$) arrived 5.0 d earlier than one-year-old females ($N = 51$, $t = 2.51$, $P = 0.014$). No cohort arrived within a time period exclusive of the others, however, and by about 10 d after the first individuals had been trapped, members of both sexes and of all age groups were likely to be present (Fig. 2.2).

There have been no studies of *oriantha* in transit, but data from *gambelii* during both vernal (DeWolfe et al. 1973) and autumnal (Morton and Pereyra 1987) migrations suggest that each bird more or less follows its own schedule (as opposed to being obligately attached to a particular flock). They tend to dribble into stop-over sites a few at a time then aggregate into small flocks while preparing for their next flight. The fact that only a few *oriantha* arrived at Tioga Pass on any

given day also supports the idea that individuals were traveling alone or in small groups. Another similarity in migration biology shared by the various subspecies is that males tended to arrive ahead of females in both *gambelii* (Oakeson 1954, Norment 1992) and *pugetensis* (Lewis 1975b). Many other species, for example, Snow Buntings (*Plectrophenax nivalis*; Meltofte 1983), Savannah Sparrows (*Paserculus sandwichensis*; Bédard and LaPointe 1984), and American Redstarts (*Setophaga ruticilla*; Lozano et al. 1996) also exhibit the males-first pattern. And old males tended to show up earlier than young ones in all of these studies. On the other hand, male and female Harris's Sparrows arrived at about the same time at breeding areas in northern Canada (Norment 1992). Interestingly, this species does not seem to be highly philopatric, and site fidelity in adults decreased greatly in years following reproductive failure (Norment 1994). Sexual differences in wintering ground latitude have been linked to arrival patterns because males often winter farther north than females (Ketterson and Nolan 1976, Morton 1984); thus, a shorter migration distance may facilitate earlier arrival by males.

As far as timing goes, there should be selection for all migrants to arrive early enough to utilize fully the season favorable for reproductive activities, particularly at high latitudes and high altitudes where summer seasons are briefest. Beyond this, however, additional pressure may be exerted on males in areas where competition for optimal territories is intense (presuming that initial territory holders have an advantage over would-be usurpers).

Analyses of costs and benefits associated with arrival schedules show that early arrival enhances production of more and higher quality offspring (Barba et al. 1995, Aebischer et al. 1996, Lozano et al. 1996). But there is a cruel bind for early birds because they are also more likely to encounter a lack of food and shelter and thereby incur an increased risk of death due to starvation, exposure, and, possibly, predation. A good example is provided by Snow Buntings in arctic Greenland where high-quality breeding habitat is scarce. Males arrive in early April, six to eight weeks before nesting, and two to four weeks ahead of females. During this lengthy pre-nesting period they commonly experience severe storms and temperatures down to -30°C , and considerable mortality can occur. Yet year after year, males continue to arrive well ahead of the breeding season (Meltofte 1983).

In situations where selection is relaxed somewhat because the breeding habitat is uniform in quality or relatively abundant, one might expect males to arrive at about the same time as females. Judging from Norment's data on Harris's Sparrows, these same conditions may also promote a decrease in breeding site fidelity after reproductive failures. All of this indicates that the arrival schedule is the product of opposing selective forces that vary with breeding site characteristics, and that once its pattern is understood certain features of the breeding habitat, such as its degree of patchiness and/or saturation, might also be predicted.

Why do one-year-old *oriantha* tend to arrive later than the older birds? An obvious explanation is that the more experienced birds knew the migration route and they recognized the breeding ground area once they had reached it. Knowing where to fly must be of major importance to migrants, but knowing when to terminate the journey is not a trivial matter either. In many years at Tioga Pass, for example, the breeding habitat was still inundated by snow in May and large subalpine meadows, such as TPM, appeared to be nothing more than great, almost

featureless, snowfields surrounded by forest. The older birds had been there before, however, and although winter-like conditions still prevailed, they settled, usually in and around the pines at the border of a meadow nearest their previous years' territory. One-year-olds did not have the benefit of this experience although they may have picked up some useful information on habitat quality prior to migration in the previous autumn. They were highly philopatric, however, so somehow they were able to find their natal areas. Given the difference in habitat appearance in spring from that of the previous autumn, it may be that young birds require some homing cues, other than landmarks, in order to settle accurately. Perhaps these are provided by older birds, already in place, that the young birds can see and hear. If this is the case, it might explain why one-year-olds tend to lag behind older birds. Note that in the previous autumn, when they were juveniles, these same young birds often left on migration toward the wintering areas *before* the older ones (Chapter 9).

The vernal migration period and its immediate aftermath can be a dangerous time for migrants, and storms, such as those experienced by *oriantha* and Snow Buntings, can be selective events. There are many observations of weather-related mortality occurring during migration (Gessaman and Worthen 1982). For example, Whitmore et al. (1977) found 569 individuals from 32 species dead after a violent spring storm in Utah. Those not killed outright were so hungry that they engaged in cannibalism and in scavenging the carcasses of others. Interestingly, these badly starved birds were found to be catabolizing their flight muscles for energy but not their gonadal tissues. Swanson (1995) discovered that Warbling Vireos (*Vireo gilvus*) had an elevated thermogenic capacity in spring and tolerated colder ambient temperatures than they could in summer or fall. This increased ability to generate heat by shivering, using fat to fuel the rapidly twitching skeletal muscles (Marsh and Dawson 1982, 1989), may be an important adaptation in vernal migrants and it would be interesting to see how ubiquitous it is. Relevant to this characterization of physiological state is that hematocrits were at their seasonal highs in arriving *oriantha* (Morton 1994b).

ALTITUDINAL MOVEMENTS

Birds that inhabit open highlands in the Peruvian Andes are known to fly down the mountains when snowstorms occur (O'Neill and Parker 1978, Fjeldså 1991). It seems reasonable, then, that North American migrants living in montane habitat, particularly in locations where the elevational gradients are steep, have this same option available to them; rather than confronting bad weather they could simply avoid it by retreating to lower elevations. Although it was suspected that *oriantha* were behaving in this way, proof did not come until a large storm moved into Tioga Pass on the night of 19 May 1987. A heavy downpour of rain was followed by snow that eventually accumulated to a depth of 15 cm. This storm continued through the evening of the 20th. On that day, at 15:30, a flock of 12 *oriantha* was observed in the lower end of Lee Vining Canyon, 10 km east of the study area and about 1 km lower in elevation. Although they were foraging together, members of this flock were expressing considerable hostility toward one another in the form of loud singing, physical displacements, and fighting. Nine members of the flock were trapped. They proved to be of both sexes, and five were banded individuals that had been

handled up on the study area within the previous 12 days. Two other *oriantha* flocks containing four and five birds (all unbanded) were located nearby and another three unbanded individuals were mixed in with a flock of about 25 Dark-eyed Juncos (*Junco hyemalis*). At 11:30 on 21 May two males were heard singing on the West Slope above TPM and by the next morning most individuals were back on their previously occupied territories.

A female captured on the morning of 22 May 1987 on TPM weighed 26.4 g and her ovary had large (4–8 mm) atretic follicles that were being reabsorbed. On 19 May, just before the storm, this same individual had a fully constructed nest and weighed 29.2 g. Judging from that body mass, she would probably have ovulated on 20 May and laid her first egg on 21 May if the storm had not occurred. Eventually, this female recovered, built a new nest, and started her first clutch on 3 June. So the storm was responsible for setting back her nesting schedule by 13 days (21 May to 3 June).

Ojanen (1979) reported that more than 3,000 birds of 42 species died in a May storm in northern Finland. Because of the terrain, no downhill movements were possible in these heavily stressed populations but, interestingly, individuals that had been spaced out onto territories formed again into flocks during the cold period. Much the same type of response also occurs in Snow Buntings (Meltofte 1983), and flock formation after movement to lower elevations during May snowstorms has been observed several times in the present study in American Robins (*Turdus migratorius*) and Dark-eyed Juncos, as well as in *oriantha*.

Based on information obtained from transmitter-carrying individuals, however, many downslope movements of *oriantha* were completely solo and did not result in flocks being formed at lower elevations. Radiotelemetry studies were begun in 1995, a year when there was a deep, persistent snowpack and many spring storms (see Fig. 2.1, upper). It was quickly apparent that repeated altitudinal movements of individuals occurred in the pre-nesting period, even during good weather, between the study area and sites that were at least 1 km lower and 6 to 16 km east in the bottom of Lee Vining Canyon and beyond into the Mono Basin (Hahn and Morton 1995). Males tended to spend more time on the breeding area than females, but both sexes showed fidelity to just two sites, one at each of the two elevations. In 1996 a second group was fitted with transmitters and temporary downslope movements, similar to those of the year before, occurred during both of the May storms (see Fig. 2.1, middle). There were no flocks formed in either year. These data show that *oriantha* readily flew to lower elevations when storms occurred and when open ground, suitable for foraging, was in short supply. Descent to lower altitude during the pre-nesting period for protection and for maintenance of energy balance was not a rare event, but a regularly-expressed component of their behavioral repertoire.

These vertical migrations of transmitter-bearing *oriantha* and observations from other studies also provide a clue as to the whereabouts of individuals in years, such as 1995, when arrival at the breeding habitat is delayed. Taylor (1912), for example, noted the presence of *oriantha* in mid-May at low elevations in Nevada, prior to their movement up to breeding areas, and Hubbard (1978) found that they arrived in foothill areas in Colorado and loitered there for nearly a month before moving up slope to their breeding habitat. It seems likely that the migration route of the Tioga Pass population includes the low-altitude shrub-steppe of the

Great Basin where it abuts the eastern side of the Sierra Nevada, and a few lone individuals have indeed been observed there in May. Once the proper latitude is reached they may remain there until conditions favor ascension to the high meadows. If storms subsequently push them back down they gravitate for a time to familiar locations at the base of the range.

Similar movements occur in Yellow-eyed Juncos (*Junco phaeonotus*) in the Chiricahua Mountains of Arizona. These birds summer at about 2,500 m, approximately 1,000 m higher than and 15 km away from wintering areas. They usually move to breeding areas several weeks before nesting begins, but if bad weather occurs they return to their usual wintering sites until it subsides (Horvath and Sullivan 1988). The regulation of facultative responses to stressful conditions such as these may be mediated via secretion of hormones of the hypothalamus-anterior pituitary-adrenal cascade. These hormones, most notable corticosterone, are thought to be released in greater quantities in emergency situations and to orchestrate physiological and behavioral responses, such as gluconeogenesis and irruptive movements. These same hormones also promote recovery once the environmental stressor disappears (Wingfield and Ramenofsky 1997, Wingfield et al. 1998).

FORAGING

Zonotrichia are well known for the breadth of both their dietary choices and foraging modes, and they ingest a wide array of plant and animal materials (Morton 1967, Norment and Fuller 1997). These eclectic feeding habits served *oriantha* well during the pre-nesting period, especially in heavy snow years. They foraged on any kind of available open ground, such as talus slopes and knolls that were swept free of snow by the wind, and they satisfied their need for water by eating snow. Other preferred locations, which were among the first to come open early in the season, included the thawed edges of stream banks and wet patches of ground that appeared where streamlets flowed under the snowpack and melted it away. They sometimes appeared to be indiscriminately eating surface material, or "organic ooze," in these wet areas. They also foraged on small patches of ground that occurred next to heat absorbers and reflectors such as large rocks and tree trunks. Holes in the snow, 2 m or more in depth, sometimes formed next to trees due to reflected solar radiation (see Marchand 1987). Once these holes extended down to bare ground *oriantha* would drop into them to forage. They, along with other species on the study area such as Dark-eyed Juncos, Gray-crowned Rosy-Finches (*Leucosticte tephrocotis*), American Robins, and Mountain Bluebirds (*Sialia currucoides*), were also reliant at times on arthropods immobilized on the snow surface. Usually these were thinly scattered but they were observed at times in densities of about 15 per m². Arthropod fallout onto snow has been identified as an important source of food for birds in central Alaska (Edwards 1972, Edwards and Banko 1976), the Sierra Nevada of Spain (Zamora 1990), and a variety of other mountain ranges around the world (Edwards 1987).

At a site near Tioga Pass, Papp (1978) found that the fallout consisted mostly of Diptera, Hemiptera, and Homoptera, and because of the species involved, concluded that many had originated from cultivated fields lying at low altitude to the west in the Central Valley. In support of Papp's hypothesis concerning effects of

prevailing winds, balloons bearing notes from schoolchildren in towns of the Central Valley were found several times by us on the study area. One balloon carrying an automobile advertisement came from Oakland, California, which is even further west.

