CHAPTER 10: Reproductive Success

Reproductive success, whether over the short term (cross-sectional), or the long term (longitudinal or lifetime), is the most essential of all measurements needed for evaluating individual fitness and for how extensively life history traits are bound together in various trade-offs, including those between the following: number, size, and sex of offspring; reproduction and survival; and current and future reproduction (Stearns 1992). Although the accurate determination of reproductive success is a central goal in studies of avian biology, it is a difficult one to accomplish. Ideally, the investigator would be dealing with a closed, tractable system, one that would favor the enumeration of offspring that not only survive to independence, but that eventually enter the population as breeders themselves. In practice this is often impossible, especially in passerine migrants, because dispersal by juveniles both before and after migration often causes them to settle as adults well beyond the boundaries of even the most ambitious study area. The pragmatic, and frequently employed, solution is simply to count the number of offspring reared to fledging, and a nesting effort is said to be successful if one or more of the young are known to have fledged.

ANNUAL REPRODUCTIVE SUCCESS OF NESTS

If only nests that had been laid in (one egg or more) were counted, the percentage of *oriantha* nests fledging young each year ranged from a low of 29.0% in 1992 to a high of 66.7% in 1989 (Table 10.1). The summer of 1992 was marked by bad weather and by considerable investigator impact. Four storms caused mortality and 18 nests were deserted, the most ever in one year. This happened because nests were visited frequently in the early morning hours to obtain data on laying times. As mentioned earlier, females flushed from the nest while building

TABLE 10.1. PERCENTAGE OF *ORIANTHA* NESTS THAT FLEDGED AT LEAST ONE CHICK

Yr	Number of nests	Percent fledging young
1968	42	50.0
1969	51	43.1
1970	63	41.3
1973	27	55.6
1976	55	56.4
1978	59	52.5
1979	78	43.6
1980	83	48.2
1981	76	57.9
1982	89	37.1
1983	59	38.2
1984	77	39.0
1985	51	56.9
1986	60	40.0
1987	50	54.0
1988	24	41.7
1989	36	66.7
1990	62	54.8
1991	96	52.1
1992	100	29.0
1993	57	40.2
1994	36	44.4

TABLE 10.2. NUMBER OF FLEDGLINGS PRODUCED PER NEST IN *Oriantha* NESTS THAT SURVIVED UNTIL FLEDGING OCCURRED

Chicks fledged per nest	Number of nests	Percent
1	14	3.4
2	70	16.8
3	135	32.5
4	181	43.5
5	16	3.8

or before clutch completion were prone to abandon. In contrast, there were no severe storms in 1989 and investigator interference at nests was low.

There was significant interannual variation in fledging success (Chi-square = 43.02, df = 1, P = 0.004), but in 17 of 22 years it was between 40 and 60%. Overall success was 47.0% (626 of 1,331 nests), and mean annual success was 47.3% (SD = 9.0%).

The mean number of chicks produced per nest, in those nests that survived until fledging occurred, was 3.28 (SD = 0.85, N = 416). Fewer than 4% of these nests fledged one (the fewest) or five (the most) chicks; in 76.0% of the cases, the number of fledglings was either three or four (Table 10.2).

ANNUAL REPRODUCTIVE SUCCESS OF INDIVIDUALS

The number of fledglings produced per season by an adult can be described as its annual reproductive success. This was 3.34 (SD = 1.69) for males and 3.16 (SD = 1.57) for females. Although polygyny sometimes occurred in the study population, these means were not different (t = 1.32, P = 0.188), nor were the medians (Mann Whitney U = 37,928, Z = −0.791, P = 0.429). The modal number of fledglings produced, per fledging event (Table 10.2) and per season, was four (Fig. 10.1). This was expected since four was the most common clutch size and most pairs were single-brooded. Recall, however, that, on average, more fledglings were produced when clutch size was five rather than four (Table 7.13).

About 10% of males and females had no success. This could be an over-

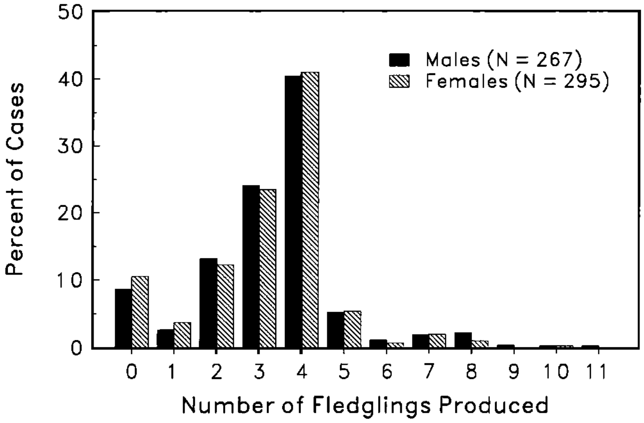

FIGURE 10.1. Frequency distribution of annual reproductive success of adult male and female *oriantha* at Tioga Pass.

statement because it is possible that a few birds counted in this category actually had successful nests very late in the season that eluded detection. Nonetheless, some birds did not bring off young. They were thwarted by predation, bad weather, and investigator activities. Reproductive failure was also known to occur in individuals that were in the crisis phase of infection by hematozoans (Richardson 1997).

Because of second nestings, a few birds were able to produce more than five fledglings in a season, with the maximum being 10 in a case wherein two successive broods of five were fledged. One male had 11 fledglings (Fig. 10.1). He was bigamous and one brood was fledged from one pairing and two broods from the other. Polygyny can greatly increase male reproductive success (Dhondt 1989a, Sternberg 1989), but it was uncommon at Tioga Pass (Chapter 3).

Effects of adult age

To determine if reproductive success varied with adult age, the following questions were asked: Did the number of young fledged per nest differ with age? Was success different among age classes if mortality of eggs during the laying period was excluded? Did the number of fledglings produced from successful nests differ with age? In all three analyses there was no difference with adult age for either sex. For example, data on the first question, which was aimed at finding out if parenting experience made a difference, showed that mean number of fledglings produced from successful nests did not vary significantly. It hovered between 3.0 and 3.3 for all ages (females: ANOVA $F_{6,325} = 1.14$, $P = 0.339$; males: ANOVA $F_{7,285} = 0.76$, $P = 0.618$).

In several studies of passerines the number of fledglings produced was slightly greater in older birds than in yearlings (Middleton 1979, Ross 1980, Yamagishi 1981), but in other cases no age effect was observed (Bédard and LaPointe 1985, Dhondt 1989b, Saether 1990). Obviously local environmental conditions, as well as social interactions, could be affecting populations in this regard (Crawford 1977). As pointed out by Clutton-Brock (1984), reproductive performance in birds and mammals, as opposed to other vertebrate classes, tends to remain constant with age although it may decline eventually. With some exceptions, birds do not show an increase in reproductive effort with age.

LIFETIME REPRODUCTIVE SUCCESS

At times it was possible to measure the total number of fledglings produced by an adult during every season that it was present on the study area, the lifetime reproductive success (LRS). LRS values are generally under-estimated because birds that leave the study area are assumed to be dead (Newton 1989a). *Oriantha* were site faithful and the analysis of their LRS was restricted to individuals known to be engaged in reproduction every year. Thus, floaters, which were usually yearling males that did not gain territories, were not included. Such males are known to have lower lifetime success (Smith and Arcese 1989). Another caveat is that the genetic LRS of males undoubtedly varied from the picture presented here due to the prevalence of extra-pair fertilizations in *oriantha* (Sherman and Morton 1988, MacDougall-Shackelton 2001).

Despite the restriction that an individual's complete reproductive history had to be known, LRS was determined for 95 males and 134 females (sample sizes

TABLE 10.3. PRODUCTION OF FLEDGLINGS BY *Oriantha* PARENTS OF VARIOUS LIFESPANS

Parents			Number of fledglings produced			
Sex	Lifespan (yr)	N	Min	Max	Mean	SD
Male	1	38	0	8	3.39	1.64
	2	16	2	8	5.56	2.16
	3	18	4	14	9.89	2.81
	4	12	8	18	12.58	3.00
	5	3	13	18	16.00	2.65
	6	6	16	26	21.17	3.92
	7	2	25	26	25.50	0.71
	All	95	0	26	8.14	6.15
Female	1	63	0	5	3.06	1.31
	2	25	0	12	6.68	2.79
	3	19	4	15	10.05	2.80
	4	15	5	19	12.73	3.37
	5	7	8	22	15.86	5.11
	6	4	17	23	19.75	2.50
	7	1	19	19	19.00	—
	All	134	0	23	7.10	5.32

were larger for females because it was easier to associate them with a nest). Mean LRS was 8.14 (SD = 6.15) for males and 7.10 (SD = 5.32) for females. Males appeared to produce about one more fledgling per lifetime than females, but, as is true for most of the data on passerines, the coefficient of variation was high and the means were not different (t = 1.37, P = 0.296). Mean LRS increased steadily with lifespan in both sexes (Table 10.3), and a regression of LRS on age showed that the two were highly correlated. For females r^2 was 0.790 ($P < 0.001$) and for males it was 0.850 ($P < 0.001$). Visual inspection of a scatterplot revealed no evidence of senescence, in other words, no tendency for the rate of success to decline with age.

For purposes of comparison with other studies, the distribution of fledglings produced per lifetime was determined for both males and females (Fig. 10.2). These distributions were highly skewed, but did not differ for the sexes (Kolmogorov-Smirnov Z = 0.631, difference = 0.085, P = 0.820). The modal number of young was four for both sexes. This is anticipated because the mode for brood size was four and the mode for number of breeding seasons per lifetime was one. Total young produced ranged from 0 to 26 by males and 0 to 23 by females. Twenty-six offspring were produced by two different males, one of which lived for six years and the other for seven. The most successful female was one that lived for six years (Table 10.3).

The mean LRS of seven to eight found in *oriantha* is high in comparison to other short-lived open-nesting passerines. It was about six in Meadow Pipits (Hötker 1989), for example, and only three to four in Indigo Buntings (Payne 1989). As pointed out by Newton (1989b), enormous individual variations in LRS occur in natural populations and, typically, large numbers of offspring, far more than are needed for replacement, are produced by a relatively small fraction of the breeding population. For many avian populations, the LRS can provide gene frequency changes and a good approximation of fitness (Partridge 1989). Murray

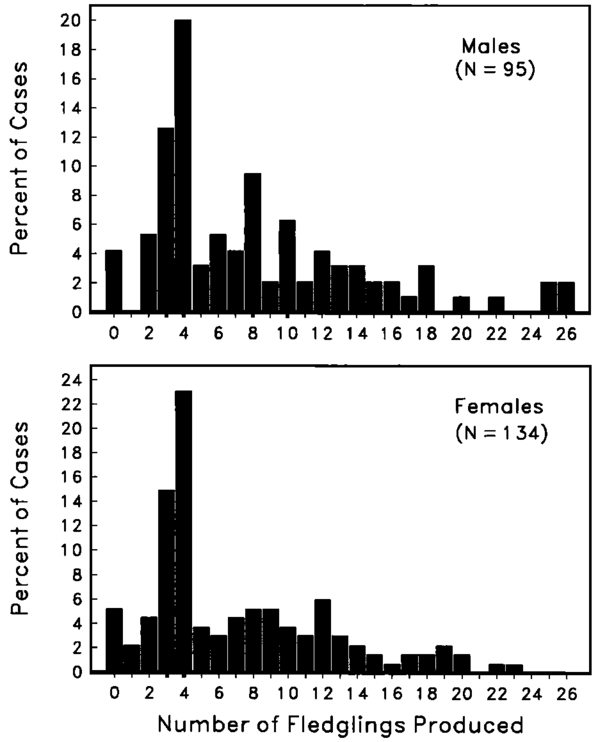

FIGURE 10.2. Frequency distribution of lifetime reproduction in male and female *oriantha* at Tioga Pass.

(1992) agrees, but cautions that differences between individuals in this regard does not necessarily have evolutionary significance.

SNOW CONDITIONS

Snow has a key role in circumpolar and high-altitude ecosystems. It stores and releases energy, and acts as a radiation shield and as an insulator. It is a reservoir for water; a transport medium, moving as a vapor flux because of sublimation; and host for a food web that occurs both within the snow and at its upper and lower boundaries. These functions occur over time scales that are diurnal, seasonal, and decadal (Jones et al. 1994). In addition, snow can be an overburden on low-lying vegetation that is sometimes utilized by birds as nesting habitat. By controlling access to these nesting sites, it can greatly influence nesting phenology and breeding productivity. Furthermore, there is great interannual variation in snow depth and water content (see Table 1.2), and this, along with the vagaries of spring weather that affect melting rates, can generate large variations in the timing of habitat availability. Thus, in a long-term study natural experiments occur that offer unusual opportunities for learning about environmental adaptation in breeding birds.

In the beginning we thought that sub-freezing temperatures, or perhaps summer storms, might be the environmental factors that most strongly affected reproduction of migrants in the subalpine. Our attention was soon drawn to the snowpack,

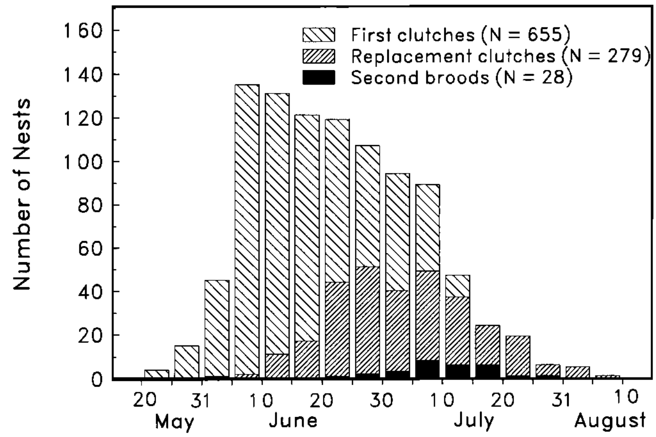

FIGURE 10.3. Distribution of clutch starts in *oriantha* during 20 nesting seasons at Tioga Pass according to nest status: first clutch, replacement clutch, or double brood.

however, because of the way it affected nesting schedules and nest locations (Morton et al. 1972a; Morton 1977, 1978, 1994a; Morton and Allan 1990). As pointed out previously, the attempts of *oriantha* pairs to settle and begin nesting could be delayed by a heavy snowpack (see Fig. 5.4). Next, interannual variations in reproductive schedules will be discussed in more detail, and how they, as well as productivity, were affected by snow conditions.

Effects on reproductive schedule

There were 20 seasons wherein an attempt was made to find every nest that was laid in and to determine, if possible, first egg dates. These were obtained by direct observation of the laying sequence and by back-dating from known hatching times in cases wherein the nest was found after clutch completion. In all, first egg dates or clutch starts were determined for 962 clutches. The earliest of these was on 23 May and the latest on 7 August, a span of 76 days. The greatest share of clutch initiations, 97.4%, were in June and July. Their frequency increased until early June, then decreased steadily thereafter (Fig. 10.3).

For much of the summer, if a nest was lost with either eggs or nestlings the female soon produced a replacement clutch. Some replacements were already present in early June and they were the last type of clutch produced during the nesting season. A few second broods were also produced, mostly in July. Eventually, in late July and early August, the birds became refractory and lost their ability to renest. Because the vegetation was so well developed, the last of these renests were difficult to find and their frequency toward the end of the nesting season must have been greater than that shown in Fig. 10.3. The 962 nests represented in Fig. 10.3 were restricted to those in which both starting date and status (first clutch, replacement clutch, or second brood) were known and they give a good view of the average seasonal pattern of clutch initiations by *oriantha* at Tioga Pass. Another representation of this pattern, one that was unrestricted as to nest status, can be found in Morton and Allan (1990). Note that Fig. 10.3 is a composite drawn from 20 different nesting seasons, and it does not inform us about among-year variation in clutch initiations.

TABLE 10.4. INTERANNUAL VARIATION IN THE ONSET OF NESTING (MEAN OF FIRST 10 CLUTCH STARTS) BY *Oriantha* ON TIOGA PASS MEADOW

Date	Number of yr	Percent of yr
26–31 May	1	4.0
1–5 June	4	16.0
6–10 June	10	40.0
11–15 June	2	8.0
16–20 June	3	12.0
21–25 June	1	4.0
26–30 June	3	12.0
1–5 July	0	0.0
6–10 July	1	4.0

As it turns out, this variation, especially in nesting onset, was quite large. This can be shown from 25 years of data wherein the seasonal onset of laying by TPM-nesters was known, onset being defined as the mean date of the first 10 clutch starts of the season. The earliest of these mean dates was 27 May (in 1992) and the latest was 7 July (in 1995), a range of 41 days. In all of the remaining 23 years, nesting began in June and in 10 of these years within the interval of 5–10 June (Table 10.4). For all years combined, mean date for the seasonal onset of nesting was 12 June (SD = 9.5 d). In a study of *oriantha* in Colorado, Hubbard (1978) saw an interannual variation of about 14 days in nesting onset. He sampled for fewer years (4 vs. 25), however, so a smaller range in onset dates is not surprising. Also, on his study area at Niwot Ridge, *oriantha* were reliant upon thick, shrubby tree islands (krummholz) for nesting locations. Such sites are highly sheltered, and they were probably less affected by variations in environmental conditions, especially snowpack, than the krummholz-devoid subalpine vegetation at TPM.

Given the year-to-year variation in the beginning of egg laying, one might expect the complete schedules for first clutches of the season also to be quite different and for them to occur under largely differing ecological conditions. This, indeed, was the case. For example, in 1976, a drought year, nesting began on 29 May and all females had begun their first clutches by 16 June (Fig. 10.4). There was some renesting beyond that date, but the key point is that the meadows dried out very early in 1976 and nesting took place under snow-free conditions. In contrast, in 1983, because of an El Niño winter, snow did not completely disappear until August and all females started their first nests of the season while a considerable portion of the habitat was still covered (Fig. 10.4).

Clutches were initiated from one year to the next, therefore, under very different moisture and cover conditions (willows did not leaf out, for example, until they were snow-free), to say nothing of variation in other factors such as microclimate and food abundance. At times the temporal disparities were so great that the schedules of first clutches did not overlap at all when certain years, such as 1976 and 1983, were compared. This has important implications because this variation in the alignment of clutch start frequencies to photoperiod can have effects that extend both to clutch size (Chapter 7) and to fledgling survival (Chapter 11).

But did this wide range in snow conditions influence the nesting schedule in a regular, predictable pattern? The answer is, yes. Nesting onset dates were highly correlated with maximum snow depth ($r^2 = 0.70$, $P < 0.001$; Fig. 10.5). This

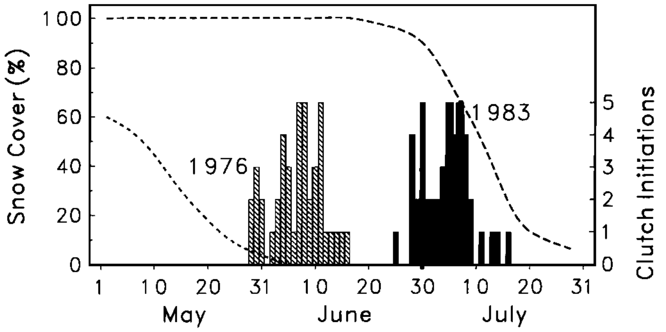

FIGURE 10.4. Temporal distribution of first clutches only in 1976 and 1983 on Tioga Pass Meadow.

happened because the birds had to wait until snow cover had decreased to 90% or less before there were adequate places for them to build and hide their nests; females would not build on the ground, or a site above it, unless that particular spot was snow-free.

A natural experiment in 1986, along with the deliberate manipulations recounted in Chapter 5, provides strong support for the hypothesis that nest site availability could operate as a proximate factor in the control of reproduction. In February of that year about 10 cm of rain fell within seven hr onto a previously accumulated snowpack. This added weight induced numerous avalanches in the central Sierra Nevada, including the Tioga Pass area. One major slide came off the west slope of TPM and several others from both north and south slopes above Lee Vining Creek. Lodgepole pines were snapped off by these moving masses of heavy, wet snow, incorporated into them, then deposited with the snow in runout areas. In mid-May these pines, still fresh and green in appearance, lay scattered across the snow surface. Snow cover remained above 90% until early June at which time *oriantha* females began building nests in some of the avalanche pines. In fact, 14 of 35 first clutches and 3 of 25 replacement clutches were built in these pines during the 1986 season. The fallen trees were more than just places

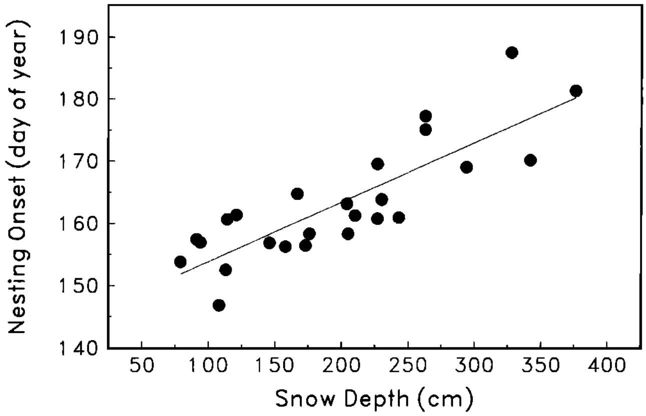

FIGURE 10.5. Onset of nesting (mean date of first 10 clutch starts) by *oriantha* on Tioga Pass Meadow in relation to 1 April snow depth (the date when snow was at or close to maximum depth). Data are for 25 yr.

to hide nests, they were the first places selected, and females using them tended to begin laying significantly earlier than their nearest neighbors which nested in more traditional sites (mean difference = 6.9 d; Wilcoxon Signed Rank Test, Wilcoxon statistic = 89.5, P = 0.002). One female that built in the base of a large unleafed willow laid four days before the neighboring avalanche-pine bird, another comparison pair started laying on the same day, and in all 12 of the other situations, neighbors started later (by as much as 15 days) than the avalanche-pine nesters. Interestingly, other species also utilized avalanche pines as nesting sites. These included American Robins, Hermit Thrushes (*Catharus guttatus*), Dark-eyed Juncos, and Dusky Flycatchers. Of these, only the junco habitually nests on or near the ground so the dense masses of branches and needles of these recumbent pines must have been, in general, a highly attractive location for building nests.

Effects on breeding productivity

During eight years of the study, 1979–1986, TPM was trapped three to five days per week from the time that fledglings first appeared until migration departures were completed. The goal was to band every *oriantha* on the study area. Aside from assuring an accurate population age structure, this extensive trapping effort provided an estimate of breeding productivity because it censused the independent juveniles.

A total of 1,467 juveniles was captured and banded in those eight seasons and their numbers varied between 88 (in 1982) and 290 (in 1985), a 3.3-fold difference. A regression of juvenile numbers on the date that nesting began gave a significant negative result ($r^2 = 0.62$, $P = 0.020$). An even stronger negative relationship existed between juvenile numbers, or productivity, and maximum snowpack ($r^2 = 0.80$, $P < 0.001$; Fig. 10.6). Compared to other years, 1983 had higher than expected productivity. This was the year with the deepest snowpack (376 cm) and 116 juveniles were captured. This was considerably more than in 1982, the year with the second-deepest snowpack (294 cm), when only 88 were captured. Productivity was relatively high in 1983 because the spring weather was unusually warm, and although the snow was deep on 1 April, it melted very quickly (see Fig. 10.4). This meant that nesting was not delayed as much as predicted. If 1983 is omitted from the data set, the regression of number of juveniles captured on maximum snowpack depth shows a very high negative correlation ($r^2 = 0.98$, $P < 0.001$).

As implied above, reproductive success was probably greater in light snow years because nesting began sooner. This allowed more opportunities for renesting and double brooding before refractoriness set in, the latter being a physiological condition that caused reproduction to be terminated at about the same date every year (Chapter 11). Deep snows decreased the time available for nesting by the population and, by delaying breeding, they also caused clutches to be started when the photoperiod was decreasing, a situation that may have caused smaller clutches to be produced (Chapter 7). Both of these effects, along with others that we did not detect, could have contributed to the variation in productivity displayed in Figure 10.6.

The snows of winter often endure into spring and summer in arctic and alpine regions. In so doing they influence both the timing and outcome of breeding

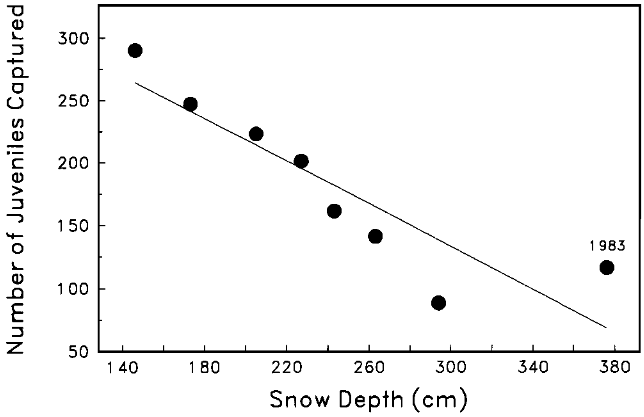

FIGURE 10.6. Number of juvenile *oriantha* captured per season on Tioga Pass Meadow in relation to maximum snowpack depth (as measured on 1 April). N = 8 yr.

efforts of avian populations that occupy those regions. In alcids and shorebirds, for example, egg-laying schedules can be delayed by several weeks as the birds wait for snow to clear away from the tundra (Sealy 1975, Green et al. 1977). Furthermore, snow-free patches must be large, otherwise there is high vulnerability to predation (Byrkjedal 1980). Snow cover also affected egg-laying dates in arctic-nesting passerines such as Snow Buntings (Hussell 1972, Pattie 1977) and Lapland Longspurs (*Calcarius lapponicus*; Hussell 1972, Custer and Pitelka 1977, Fox et al. 1987). Like *oriantha,* breeding productivity was reduced in both of these species when there was a late thaw (Pattie 1977, Fox et al. 1987). As pointed out by Green et al. (1977), snow cover, not adaptations to seasonality of food supply, determines breeding dates in these wintery habitats.

Nesting success in White-tailed Ptarmigan (*Lagopus leucurus*) was negatively correlated with springtime snow depths (Clarke and Johnson 1992). Furthermore, Smith and Andersen (1985) found that Dark-eyed Juncos had longer breeding

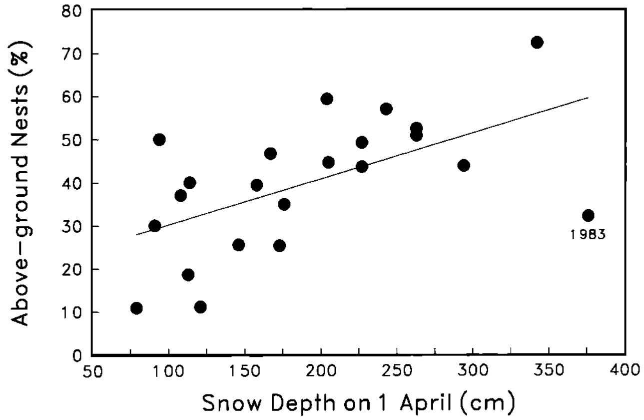

FIGURE 10.7. Percentage of *oriantha* nests built in above-ground or elevated sites in relation to maximum snowpack depth (measured on 1 April, N = 22 yr, $r^2 = 0.32$, $P = 0.010$; if 1983 was excluded, a year when warm spring weather caused early melting of the snowpack, $r^2 = 0.52$, $P < 0.001$).

seasons when snowmelt was early; there was time for only one nesting attempt when it was late. What can birds do to ameliorate the negative effects of heavy snowpack on reproductive success? In Dark-eyed Juncos clutch size increased when nesting was delayed and Smith and Andersen (1985) suggested that females produced larger clutches because they were unstressed and had more time to accumulate energy reserves before the onset of laying. Clutch size did not increase in *oriantha* but they were able to adjust partially to the inhibitory effects of late-lying snow by altering nest-site preferences. This was untrue in other species. For example, no matter the ecological conditions at Tioga Pass, Hermit Thrushes always constructed their nests in elevated sites and Dark-eyed Juncos (a close relative of *oriantha*) built on the ground, but *oriantha* were more flexible. Although the junco pattern seemed to be preferred in most years, those propensities were modulated in response to snowpack persistence; the more snow there was in any given year, the higher the proportion of their nests built in elevated sites (Fig. 10.7). This plasticity in what is often a stereotyped response in avian species is a key adaptation of *oriantha* to the variation in snow conditions that occurs at high altitude.