

CHAPTER 9: Nest Failure

The causes of nest failure and the responses to them are at the heart of reproductive success. Of 1,331 *oriantha* nests found and monitored during 22 summers, 626 managed to fledge at least one chick, a success rate of 47.0%. But what were the modifying factors that caused the other 53.0% to fail? The primary reason for interruption of the nesting cycle proved to be predation. It accounted for 57.0% of all nest failures. Beyond that, desertion of nests (22.3%), bad weather (16.2%), and other factors (4.5%) impacted nesting attempts. The latter, the other factors, included nests falling apart due to poor construction (N = 2), death of the tending female (N = 8), flooding caused by rising streams (N = 10), and additional cases that were unfathomable to us (N = 12). The top three causes of nesting failure, and ramifications thereof, will now be considered in more detail.

PREDATION

During the years that comprehensive data were obtained on nest fates, predation rates were remarkably constant (Fig. 9.1). The mean annual rate was 30.5% of all nests (SD = 4.7%). This constancy was attributed to the presence of a large and stable population of Belding's ground squirrels (*Spermophilus beldingi*) on the study area (Morton et al. 1993). These rodents are thought to be the principal predator on *oriantha* nests and they have been observed eating both eggs and

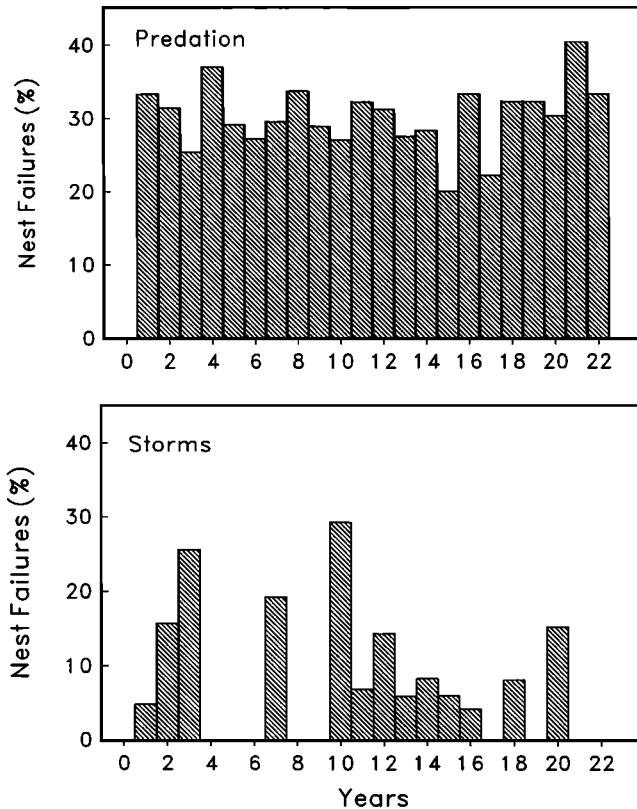


FIGURE 9.1. Percent of *oriantha* nests lost from predation (upper panel) and storms (lower panel) at Tioga Pass during 22 breeding seasons.

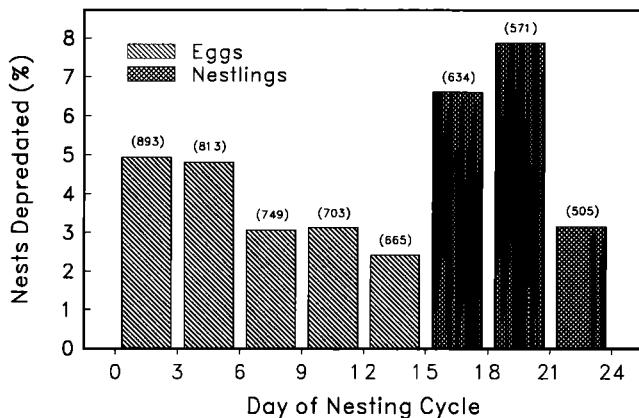


FIGURE 9.2. Percent of *oriantha* nests depredated per 3-d interval throughout the nesting cycle. The cycle begins with the laying of the first egg (day 0) and ends at fledging (day 24). Number of nests in parentheses.

nestlings. Other mammalian predators of import, across the study area as a whole, were long-tailed weasels (*Mustela frenata*) and coyotes (*Canis latrans*). Coyote predation was not observed directly but tracks in the snow showed that they sometimes followed our circuit of nests or traps, and their presence at nests was known from both tracks and tufts of hair snagged on bushes. And nests built off the ground were sometimes tipped down and indented as though by a coyote reaching up and pulling the nest down with its muzzle. Early in the season, patches of habitat that had recently emerged from beneath the snow were often used by *oriantha* as nesting areas. Coyotes habitually hunted through these patches, probably in pursuit of small mammals such as voles or ground squirrels, but they undoubtedly chanced upon nests at such times.

Among avian predators, Clark's Nutcrackers (*Nucifraga columbiana*) were probably the most important. They were observed eating eggs, nestlings, and fledglings of several species, including *oriantha* (Mulder et al. 1978), and Common Ravens (*Corvus corax*) did the same. Ravens were not observed on the area until 1979 but they had become regular residents by the end of the study. They can be expected to have an increasingly greater impact on the nesting birds of Tioga Pass in the years ahead.

Predation rate varied as nests passed through various stages of the cycle from laying to fledging, a process that lasted about 24 days (Fig. 9.2). About 5% of all nests were depredated per three-day period when eggs first appeared in the nest (laying and early incubation), and the rate then tailed off somewhat. This was probably because the most easily located nests were depredated early on. As the first hatchlings began to appear, at about day 15 in the nesting cycle, predation rates more than doubled. Doubtless, the added activity, noise, and odors at the nest provided cues that attracted predators at that time. This kind of effect has been verified experimentally in nestling passerines by Leech and Leonard (1997).

Because the number of viable nests decreased at about 2% per day, the total number of nests lost per three-day interval was not as variable as one might expect from Fig. 9.2. For example, 19.1% of all nest losses occurred during laying, days 0–3, and 18.2% when nestlings first appeared, days 15–18. Predation rates did

not vary with nest location (on the ground vs. above ground), nor with the age of either parent (Morton et al. 1993).

Both members of pairs tried to distract or drive away predators in the vicinity of the nest. Females on nests would sit tightly if one looked directly at them at close range. If the gaze was then averted, however, they would immediately slip quietly away. They sometimes displayed a distracting tail-wag maneuver when running from ground nests. If disturbed early in the nesting cycle by a real or perceived (human) predator, females sometimes deserted even though the eggs had not been touched.

DESERTION

Other than exposure to bad weather (treated separately below), the reasons why females deserted nests varied widely. For example, a clutch was sometimes reduced in size with the female alive but no longer in attendance. Hill and Sealy (1994) also found that clutch reduction caused desertion in Clay-colored Sparrows (*Spizella pallida*). Such episodes could have been due to partial predation (observed once when a juvenile Clark's Nutcracker removed one of four eggs from a nest then flew off to join siblings), to interference by nesting heterospecifics (in one case we thought the culprit was a Lincoln's Sparrow, *Melospiza lincolnii*), or to conspecifics; usually we could not tell. About one-third of all desertions could be attributed to these types of natural causes and the other two-thirds to investigator activities (Morton et al. 1993).

Once an adult *oriantha* (sex unknown) was observed at close range from a blind to kill and remove two hatchlings from a nest. Of 10 probable cases of infanticide, where chicks were pecked about the head and neck and left dead inside the nest or immediately outside it, this was the only time we actually saw it happen. Interestingly, five of these 10 cases occurred on the day after male songs were broadcasted on territories where there were nestlings. The males at those locations were unresponsive and seemed reluctant to counter-sing, thus allowing their dialects to be identified (the purpose of the experiment). As a result, the playback experiments were conducted for an hour or more at each location. Although males with dependent young usually have low levels of circulating testosterone, it can increase if they are exposed repeatedly to simulated intrusions (Wingfield and Wada 1989), thereby increasing the likelihood of aggression (Wingfield et al. 1987, 1990). It may be that prolonged periods of song playback induce high testosterone levels in either the parent or a neighbor thereby facilitating infanticidal behavior.

Investigator activities that involved spending considerable time at the nest, such as measuring eggs or implanting thermocouples, especially during laying or the first few days of incubation, were the ones most likely to cause desertion. Females flushed at close range while engaged in nest building or laying were also known to desert. As implied above, females were most prone to desert early in the nesting cycle. Once nestlings were present they did not desert even though we sometimes spent prolonged periods at the nest conducting procedures such as banding, weighing, laparotomies, feather measurements, or thermoregulation experiments. On the other hand, these activities undoubtedly caused increased predation rates on nestlings (Mead and Morton 1985). Desertion of offspring appears to be a part of normal reproductive behavior in many avian species, and it may be advantageous

TABLE 9.1. TYPES OF STORMS AND THEIR MEAN FREQUENCY OF OCCURRENCE FROM MAY TO OCTOBER AT TIOPA PASS, AS EXTRACTED FROM LOGBOOKS OF F. CASTILLO (N = 15 YR)

Month	Type of Storm			Total storms
	Snow	Hail	Rain	
May	4.6	1.1	2.6	8.3
June	2.2	1.9	4.5	8.6
July	0.1	1.9	6.3	8.3
August	0.8	2.3	6.1	9.2
September	1.1	1.3	3.2	5.6
October	6.2	1.2	3.3	10.7

if it provides the opportunity to abort a flawed breeding attempt and to renest (Székely et al. 1996).

STORMS

As is typical of montane climates (Ehrlich et al. 1972, Hendricks and Norment 1992), summer storms were a frequent occurrence at Tioga Pass. Usually these swept through in the afternoon or evening and seldom lasted for more than an hour or two. Often only trace amounts of moisture were deposited, but readable quantities of precipitation were sometimes left in our rain gauges. Mean depth recorded from 39 storms was 0.97 cm (SD = 0.90 cm) with the minimum measured being 0.19 cm and the maximum 3.94 cm. Nest mortality from these storms sometimes occurred and their effects varied immensely from year to year; during 22 seasons with complete data, mean annual rate of mortality from storms was 7.3% of all nests (SD = 8.8%).

A valuable source of information on weather at Tioga Pass was compiled by F. Castillo, a National Park Service employee who was in summer residence for many years at the southern end, and highest elevation, of the study area. Castillo recorded daily weather observations in logbooks from which we extracted 15 years of data (1968–1982). These show that storms occurred at their lowest frequency in September, when *oriantha* were completing molt, fattening, and leaving on migration (Table 9.1). During the key nesting season months of June and July there were 8+ storms per month. As one might expect from seasonal temperature changes, snowstorms and rainstorms tended to vary inversely in frequency, with the former being most common at the beginning and end of the summer season, and the latter during the middle. Hailstorm frequency also tended to peak during the middle months (Table 9.1).

How many of these storms caused mortality in nests and how lasting was their effect? In nine of 22 years none of the storms induced mortality; in the other 13 years a total of 22 storms occurred that caused death in *oriantha* offspring. If it is assumed that eggs and nestlings were present over about a two-month period between May and August in any particular breeding season, then in 22 years, according to the Castillo data, they must have been exposed to about 374 storms (17×22). Thus, about one storm in every 17 (6%) was a selective event.

As can be seen from Fig. 9.1 (bottom panel), nest failure due to storms varied from zero to nearly 30% of all nests in any one year. In eight of the 13 years during which mortality occurred there was one killer storm, in three years there were two, and in two years (1984 and 1992) four such storms occurred. These

TABLE 9.2. EFFECTS OF 22 STORMS ON EGGS AND NESTLINGS OF *Oriantha* AT TIOGA PASS (DATA OBTAINED FROM 13 YR)

Storms		Eggs			Nestlings			All individuals		
Type	Date	N	Killed	Mortality (%)	N	Killed	Mortality (%)	N	Killed	Mortality (%)
Rain	7-8 July 68	—	—	—	31	7	22.6	31	7	22.6
Rain	13 July 69	44	10	22.7	48	8	16.7	92	18	19.6
Rain/Hail	21 July 69	16	0	0.0	14	8	57.1	30	8	26.7
Snow	8-14 June 70	31	23	74.2	—	—	—	31	23	74.2
Snow	26-27 June 78	16	6	37.5	—	—	—	16	6	37.5
Snow	17 June 79	92	47	51.1	—	—	—	92	47	51.1
Rain/Hail	19 July 79	7	1	14.3	18	2	11.1	25	3	12.0
Snow	28-30 June 82	120	78	65.0	5	5	100.0	125	83	66.4
Hail	26 July 82	20	2	10.0	85	19	22.4	105	21	20.0
Rain	9 Aug 83	4	0	0.0	7	2	28.6	11	2	18.2
Snow	4 June 84	6	6	100.0	—	—	—	6	6	100.0
Snow	6 June 84	10	7	70.0	—	—	—	10	7	70.0
Snow	13-14 June 84	24	8	33.3	—	—	—	24	8	33.3
Rain/Hail	18 July 84	7	7	100.0	17	17	100.0	24	24	100.0
Rain/Hail	23 July 86	15	0	0.0	22	18	81.8	37	18	48.6
Rain/Hail	28 June 87	22	0	0.0	20	2	10.0	42	2	4.8
Snow	6 June 88	6	3	50.0	—	—	—	6	3	50.0
Snow	14-15 June 90	114	21	18.4	—	—	—	114	21	18.4
Snow	13-15 June 92	69	42	60.9	36	19	52.8	105	61	58.1
Snow	29 June 92	62	4	5.5	15	8	5.3	77	12	15.6
Rain	12 July 92	43	0	0.0	37	15	40.5	80	15	18.8
Rain	14 July 92	48	0	0.0	17	7	41.2	65	7	10.8
Totals		776	265	34.1	372	137	36.8	1,148	402	35.0

storms were evenly divided as to type; 11 involved snow and 11 rain and hail. All 11 of the snowstorms occurred in June and the other storms thereafter (Table 9.2). Together, the 22 killer storms affected 233 nests containing eggs and another 108 with nestlings.

The outcome of each of these storms is chronicled in Table 9.2. Of 776 eggs that were present during storms, 265 (34.1%) did not survive. Of 372 nestlings, 137 (36.8%) did not survive. These mortality rates were not different (Chi-square = 0.793, df = 1, P = 0.373). More than twice as many eggs as nestlings were exposed to storms, and looking within Table 9.2 it can be seen that eggs were present in 21 of 22 storms, but nestlings in only 14 of 22. In nine of the 22 storms total mortality was 20% or less. In two storms, however, mortality was 100%. One of these occurred at the very beginning of the season, 4 June 1984, and involved six eggs in five newly started nests. All were wiped out. The other occurred on 18 July in the same year and involved seven eggs in two nests and 17 nestlings in five nests. This was a particularly violent storm that included hail and torrential rains. It lasted for three hr in the late afternoon, and it was the only time that all eggs and nestlings under surveillance were lost. Despite these two storms, plus two others in 1984 (see Table 9.2), weather caused mortality in only 14.3% of all nests in 1984.

The most individuals killed at one time was 83, 78 of which were eggs, in a three-day snowstorm that began on 28 June 1982. At least 20 cm of snow accumulated in this storm, burying much of the low-lying vegetation and many nests. Some nests survived, however, because they were in naturally sheltered

TABLE 9.3. MORTALITY RATES AT TIOGA PASS OF *Oriantha* NESTS, AND INDIVIDUALS CONTAINED THEREIN, ACCORDING TO TYPE OF STORM

Storms		Nest mortality					Individual mortality		
Type	N	Nest status	None	Partial	Complete	% with mortality	Survived	Died	Mortality (%)
Snow	11	Eggs	82	9	73	50.0	305	245	44.5
	3	Nestlings	6	1	8	60.0	24	32	57.1
Rain/hail	10	Eggs	62	2	5	10.1	206	20	8.8
	11	Nestlings	55	11	27	40.9	211	105	33.2

locations and because some incubating females managed to defend their eggs even though their nests were covered by snow. They sat tightly and the falling snow completely covered them and the nest. Eventually they exited by tunneling out to the side leaving the covered nest in an igloo-like configuration. Nests were tended in this condition until the snow had melted away. By the morning of 2 July the storm had ended and females that had lost their nests were already building at new sites. Interestingly, Hendricks and Norment (1992) found that nestlings of the American Pipit that were old enough to thermoregulate could survive burial beneath the snow for at least 24 hr, even when unbrooded.

When a snowstorm causes many nests to fail simultaneously, the reproductive systems of the females involved are reset to the same physiological condition. Thus, when the storm ends they are synchronized and clutch starts of their renests tend to be clustered. Aside from *oriantha* at Tioga Pass (Morton and Allan 1990), this type of population-wide response has been documented in three species of thrushes (*Turdus*) in Finland (Pulliainen 1978).

Snowstorms usually occurred early in the nesting season and nestlings were present during only three of the 11 snowstorms that caused mortality. The total loss of nests containing nestlings and of individual nestlings was low, therefore, compared to that of eggs (Tables 9.2 and 9.3). Nestlings were more likely to be present later on when rainstorms occurred, and they proved to be more vulnerable than eggs to cold, drenching rains. One such storm occurred on 23 July 1986. Only 1.1 cm of rain fell, all in the first hour of the afternoon, but it was cold enough to include some hail and 18 of 22 nestlings died whereas all 15 eggs present survived (Table 9.2). In severe downpours females sometime had to leave the nest in self defense and could not prevent the nest-nestling unit from getting soaked. They would return immediately after the storm to brood, and even though the nestlings might already be dead they would stay on for several hours, apparently attempting to revive them. Eggs, of course, were only superficially wetted in such situations and often survived. Embryos appeared to be less susceptible to cooling than nestlings. Jehl and Hussell (1966) found much the same thing in young passerines exposed to chilling rains in Manitoba.

A summary of how the type of storm affected *oriantha* young shows that mortality was slightly higher in nestlings (57.1%) than in eggs (44.5%) during snowstorms, an insignificant difference (Chi-square = 3.25, df = 1, P = 0.072). Note, however, that only 56 nestlings from 15 nests were exposed to this type of storm as compared to 550 eggs from 164 nests. In rainstorms, overall mortality was again lower in eggs (Table 9.3), being only 8.8% (20 of 226) as compared to 33.2% in nestlings (105 of 316). So mortality from rain was nearly four times

TABLE 9.4. RATE OF STORM-INDUCED MORTALITY IN *Oriantha* NESTS ACCORDING TO DAY OF THE NESTING CYCLE (FIRST EGG BEING LAID ON DAY 0)

Day of nesting cycle	Type of offspring present	N ^a	Mortality (%)
0–3	Eggs	56	36.4
4–6	Eggs	129	31.5
7–9	Eggs	158	28.8
10–12	Eggs	92	32.4
13–15	Eggs	71	33.0
16–18	Nestlings	65	29.3
19–21	Nestlings	70	44.0
22–24	Nestlings	89	36.4

^a Number of offspring (eggs and nestlings) that were present when killer storms occurred.

higher in nestlings than in eggs, a highly significant difference (Chi-square = 44.13, $df = 1$, $P < 0.001$).

The rate of weather-related mortality was fairly constant across the nesting cycle (Table 9.4). Among eggs it was highest during the laying period (days 0–3) but the effect was not significant (Chi-square = 1.52, $df = 1$, $P = 0.218$). The data on egg temperatures (Chapter 7) show that eggs were neglected for much of the time during laying, so one might expect storm damage to be high for that period. We have noticed, however, that females, even those with just a first egg, will come back onto the nest during storms even if it already contains snow or ice. This behavior seemed to be effective, although there were exceptions. In one case, for example, a nest with an incomplete clutch of two eggs became snow-filled during a storm. Over the course of the next two days the presiding female laid her third egg nearby on the ground and then instead of deserting as expected, laid her fourth egg in the still-frozen nest and began to incubate. None of these eggs hatched and the female continued in attendance for 22 days, 10 days beyond the normal period of incubation, before deserting.

Although unpredicted by the brood reduction data (Table 8.4), storm-induced mortality in nestlings was lowest in the recently hatched, days 16–18 of the cycle (Table 9.4); compared to older nestlings, the difference was significant (Chi-square = 4.77, $df = 1$, $P = 0.029$). Apparently, broods of young, ectothermic chicks tolerate chilling better than older ones whose members are endothermic or transiting to that condition. Younger nestlings may also suffer less during storms because they require less food overall than older nestlings (Hays 1969).

There are numerous published notes about storms impacting birds at various times throughout the year, sometimes catastrophically (Gessaman and Worthen 1982), but these reports invariably focus on one storm and its potential long-term effects usually are not addressed. For example, if a massive storm strikes a breeding population, what is the effect on productivity for that year? The same sort of question could be asked about variations in predation pressure. Information relevant to these questions can be derived from the Tioga Pass study because during eight years (1979–1985) the total number of independent juveniles on the study area was known (Chapter 8). A regression of those data on predation losses showed no significant relationship ($r^2 = 0.053$, $P = 0.582$), nor was there one for weather-related losses ($r^2 = 0.177$, $P = 0.299$).

Wingfield et al. (1983) found that *pugetensis* exposed to storms while caring

for young were highly stressed, as assayed by depleted fat depots and high plasma concentrations of corticosterone. Despite the stress, however, circulating levels of gonadotropin and sex steroids remained normal, reproductive organs were maintained in a functional state, and renesting efforts proceeded immediately when environmental conditions improved (Wingfield 1984c). The fact that *oriantha* can respond in much the same manner and maintain productivity despite loss of nests shows high fitness for reproducing in an environment where stochastic events can interrupt or terminate reproductive efforts. Their ability to recover quickly from nesting losses would seem to hinge on energy availability, and on a mating system and reproductive physiology that are flexible enough to permit immediate renesting. As we will see next, they can renest and, if necessary, do it repetitively.

RENESTING

Predators regularly took about 30% of all *oriantha* nests, and weather effects, although unpredictable, could also cause substantial additional losses, to say nothing of investigator impacts. Reproductive success in the Tioga Pass population would seem to depend heavily, then, upon the birds' ability to recover quickly from disruption of the nesting phase (modifying information) and begin the nesting cycle anew. To accomplish this, pairs must re-initiate courtship and prepare physiologically. This is a larger task for females. Not only must they undergo reactivation of endocrine pathways involved in sexual behavior and ovarian development, they must also build a nest and re-acquire and mobilize nutrients sufficient for producing a new clutch. This same suite of responses can be used by pairs, environmental conditions permitting, to enhance their reproductive output by double brooding.

Renesting intervals

If a predator appeared near a nest with young, the parents would aggressively attempt to deter or distract it by close approaches, occasionally (in the case of ground squirrels) even by direct buffeting with their bodies and wings, and they always gave *chip* vocalizations. In one instance brood reduction occurred when a group of Clark Nutcracker's was near a nest for about three hr. The agitated *oriantha* adults did not bring food during this whole time and two of their four nestlings died from the neglect. If a predator removed all of the young and departed the parents continued *chipping* for several minutes. Eventually, they would cease and within one or two hr lose interest in the nest. Females then launched into sustained bouts of foraging and males appeared to increase their singing rates. Although these behaviors were not quantified, they are similar to Wasserman's (1980) observations, obtained under similar circumstances, on White-throated Sparrows.

Within the next few days the major elements of courtship reappeared in the *oriantha* pair, including mate guarding and copulations. If a nest was lost during egg laying, females sometime built a new nest as early as the third day after the depredation and laid the first egg of the replacement clutch on the next day. So the renesting interval, the time between the loss of a nest and clutch initiation in the next one, was as few as four d. As related in Chapter 7, nest building was speeded up in reests, building activity and vitellogenesis were concurrent, and completed nests sat empty for less time.

TABLE 9.5. TIME USED FOR REPLACEMENT OF NESTS BY *Oriantha* FEMALES (= RENESTING INTERVAL)

Renesting interval (d)	N	Percent of nests
4	8	12.5
5	26	40.6
6	13	20.3
7	6	9.4
8	5	7.8
9	2	3.1
10	2	3.1
11	2	3.1

Accurate data on 64 renesting intervals were obtained when nests were lost from the usual variety of factors: predation, desertion, storms, etc. The mean of these intervals was 6.0 d (SD = 1.7 d) with five d being the mode (Table 9.5). Thirty-nine of 64 nests (60.9%) were replaced in five or six days. This schedule was followed when nests contained full clutches or nestlings when they were lost. The extension of the renesting interval to seven days or more was always coincident with bad weather. In those situations, females were forced to wait because of constraints on energy or nest site availability before they could nest-build and ovulate again.

The temporal realities of such nest losses are illustrated in the seasonal histories of nesting sequences that involved the loss of one or more nests by six different pairs (Fig. 9.3). In nesting sequence number one, for example, the first nest of the season was depredated during incubation. Five days later a replacement clutch was begun and nestlings eventually fledged from the second nest. Pair number two lost their nest to a predator during the laying period and started a nest five days later that was successful. Much the same occurred in nesting sequence three except that the renesting interval was extended to nine days because of a storm.

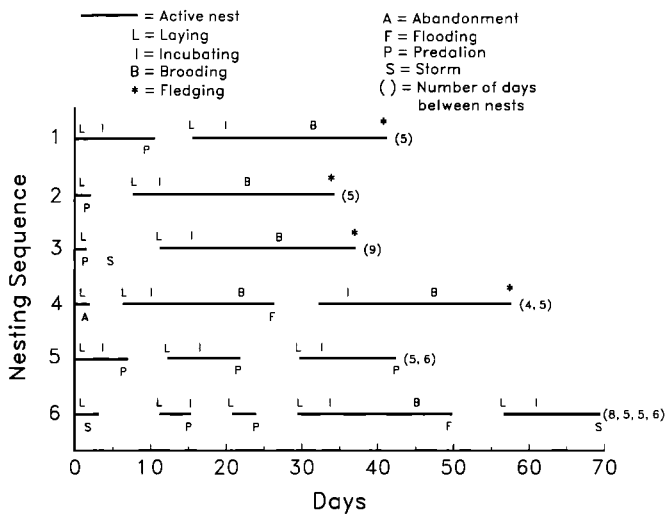


FIGURE 9.3. Six different seasonal nesting sequences exhibited by *oriantha* at Tioga Pass.

Number four was unusual in that the female abandoned her first nest because it was located within a Song Sparrow territory and both members of that pair attacked her relentlessly. Her next nest proceeded without interspecific conflict but was lost to a flood. Fledglings were eventually produced from the third nest.

Sometimes a pair never managed to fledge young because every one of their nests was lost. Examples of this are shown in sequences five and six. Note that in number six, five different nests were built and laid in. Two nests were lost to storms, two to predators, and one to a flood. Despite the tenacity of this pair and their ability to renest repeatedly, they fledged no young that year. An important component of this temporal efficiency in renesting efforts was the durability of the pair bond. As pointed out in Chapter 3, pairs nearly always stayed together and on the same territory when nesting failures occurred.

Double brooding

When fledglings were produced relatively early in the season, from the first or second nesting effort, *oriantha* females sometimes attempted to produce a second brood. The time between occurrence of fledging in the first nest and laying of the first egg in the next nest, the mean inter-clutch interval, (Verhulst and Hut 1996), was 9.1 d (SD = 4.3 d, N = 28). The minimum interval was three d and the maximum 18 d. This 15-d range between efforts suggests that some females extended parental care to fledglings for a much longer time than others before renesting. Since males shared these responsibilities, and since females did not care for fledglings after they began a new nest, it seems possible that the inter-clutch interval varied with the number of fledglings (which ranged from two to five). In other words, the fewer the number of fledglings, the sooner the male might take over their complete care. A regression analysis shows, however, that the inter-clutch interval was not related to the number of fledglings ($r^2 = 0.050$, $P = 0.251$).

Fledglings achieved independence about three weeks after fledging so females with some of the longer inter-clutch intervals may have been caring for first-brood fledglings almost to the time when those young could survive without further parental assistance. Mortality among the dependent fledglings, as well as parental efforts by the male, could also have affected the inter-clutch interval.

The incidence of double brooding was highly irregular. Examples were found in only 11 of 22 years. In those 11 years it occurred once in six of them, twice in two of them, four times in two of them, and 10 times in one year, 1985. Except for 1985 then, double brooding was seldom seen. What was special about that year? Snowpack was 145.8 cm on 1 April, slightly below average, but 1985 was not a drought year. The key may have been that the weather in April and May was unusually mild and by the end of May about 90% of the study area was snow-free. Most *oriantha* began nesting in late May and early June and many pairs that brought off their first broods then went ahead with second ones. Clutch manipulation experiments on Great Tits indicate that double brooding was promoted by early breeding, as opposed to other factors such as pair quality (Verboven and Verhulst 1996).

Double brooding would seem to be a highly desirable tactic because it can enhance the number of fledglings produced, but it may have drawbacks. It can cause postnuptial molt to be delayed or to overlap with the period of parental

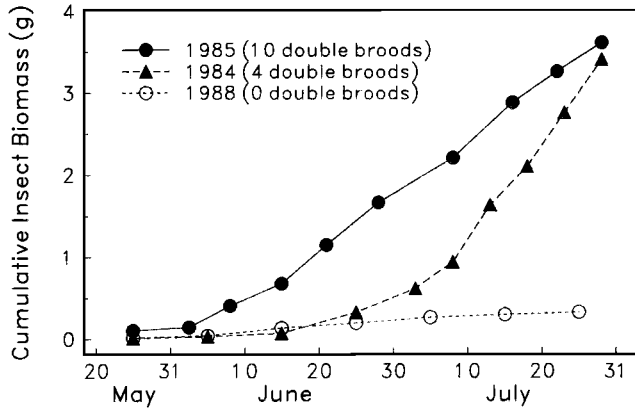


FIGURE 9.4. Cumulative insect biomass per collecting pan (dry mass), for three yr along with number of *oriantha* double broods that occurred in those years.

care, for example (Evans Ogden and Stutchbury 1996), and there may be an undesirable trade-off if it causes a reduction of the female's contribution to post-fledging care (Verhulst and Hut 1996).

The sporadic nature of double brooding at Tioga Pass tends to support the contention that this phenomenon may be inhibited in environments with relatively short breeding seasons because there is usually not enough time to raise two broods before a decline of invertebrate food occurs (Nilsson 1983). Another possibility is that a female's quality, determined by her fat stores or foraging skills, for example, could be limiting (Drent and Daan 1980, Rooneem and Robertson 1996). In view of the ability of *oriantha* females to readily produce replacement clutches in all years of the study, it seems unlikely that female quality was restrictive to double-brooding attempts. This leaves time available to produce two broods as a possible factor (but probably not a problem in many cases given the extension of re-nesting attempts into late summer), and another could be the quantity of food available for provisioning the young. The latter is difficult to measure, but during nine years (1984–1992) data were obtained on both the frequency of double brooding and on food availability (as indexed by the dry mass of insects collected in pan traps). All second nests were started by the end of July so the frequency of double brooding was compared to the cumulative insect biomass from 20 May to 31 July in these nine years. As it turns out, the two parameters were significantly related (Spearman's $\rho = 0.601$, $P = 0.043$). To illustrate: in 1985 invertebrates were abundant from the beginning of the season onward and 10 cases of double brooding occurred (Fig. 9.4). In 1984 the bloom of insects was heavy, but delayed somewhat (Pereyra 1998), and there were four cases of double brooding. In 1988, as in many other years, cumulative insect biomass was relatively low and no cases of double brooding were detected. This suggests that the decision about going ahead with second nests depends upon food abundance.

Within-year breeding dispersal

If a female loses a nest and begins another or is multiply brooded, the distance between her successive nests is a measure of within-year breeding dispersal. This was obtained in 164 cases wherein the first nest was lost from either predation,

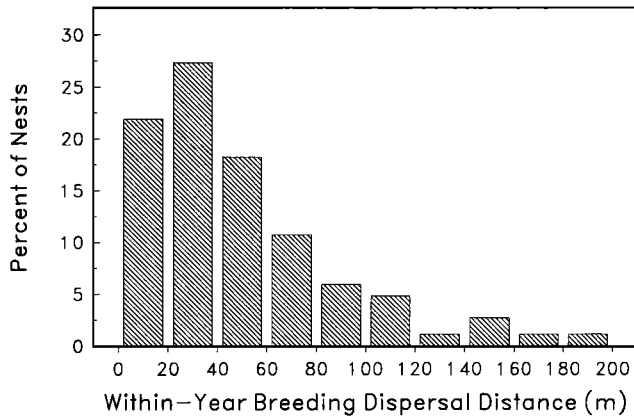


FIGURE 9.5. Distances between successive nests in the same year in *oriantha* nesting on TPM, N = 186 nests.

bad weather, or desertion, plus 22 additional cases wherein young had been fledged and the female went ahead with a second brood. The distance between successive nests did not differ for these four categories (Morton 1997).

Areas defended by pairs, their territories, varied greatly in size and shape, depending upon the terrain, but TPM was large enough to contain many that were contiguous. In that setting, territories were estimated to be about one hectare in size or 112 m in diameter (Morton 1992b). Replacement nests or second nests were seldom placed beyond that distance (Fig. 9.5). The median distance of dispersal for within-year nests on TPM was 39.7 m. It should be noted, however, that T. Hahn (pers. comm.) has recently discovered through radio tracking that renesting females will travel greater distances than we have indicated, and even change mates. One radioed female, for example, had two failed nests on the south end of TPM then moved about 1 km to the upper East Slope (Fig. 1.3) for another attempt with a new mate—also a failure.

Among open-nesting passerines, within-year breeding dispersal distances are generally shorter than those observed between years (Bédard and LaPointe 1984). They can be quite lengthy in some species, however, such as the Gray Catbird (*Dumetella carolinensis*). If a breeding pair of catbirds experiences a nesting failure, they may shift to an entirely different area up to 450 m away (Darley et al. 1971). Nest failures in *nuttalli* often resulted in dissolution of the pair bond and movement of the female to a new (but nearby) territory (Blanchard 1941). In *oriantha*, however, nearly all pairs remained together and renested as soon as possible. They also tended to remain on their territory. This response to nest failure has ultimate consequences. Annual productivity in *oriantha* has been shown to be directly related to time available for nesting (Morton 1992b), and high altitude breeding areas, such as Tioga Pass, can have truncated summer seasons due to prolongation of winter conditions in the spring and to early onset of harsh weather in autumn. Natural selection, therefore, should favor immediate renesting. This can probably best be accomplished by retaining existing mates and territories, especially for birds like *oriantha* that inhabit ecological islands where suitable habitat is limited in area and availability.

Finally, it should be mentioned that after the nesting season, in August and

September, many adults were captured on TPM that had not been handled there previously that season. These newcomers were in the final stages of postnuptial molt or had recently completed it. They comprised 14.8% of the one-year-old females and 20.1% of the one-year-old males captured on TPM during the entire season. For birds two years old or older, these proportions were 8.6% for females and 4.7% for males. Usually the breeding areas that these individuals originated from was a mystery, although we assumed that they were nearby. One banded male was known to be a territory holder on the slope north of Ellery Lake, about 3 km away (see Fig. 1.3) and a female was known to have nested on Lee Vining Creek, about 4 km away. The purpose of this post-breeding dispersal onto a large meadow such as TPM is unknown. It could be that it was a highly suitable location for preparing metabolically and/or socially (by joining flocks) for migration. It might also have provided more protection from predators, a factor found to be important in postbreeding movements of Wood Thrushes, *Hylocichla ustulata* (Vega Rivera et al. 1999).

