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CHAPTER 7: Nests and Eggs

NESTS

Ancestral birds are thought to have first nested on the ground using an open cup that was molded to body size. This open-style nest may have evolved from a small pit wherein eggs were covered with debris and left for solar incubation. Once birds were able to maintain high nocturnal body temperatures, selection favored direct parental incubation because this served to shorten the period of development, a time when young are highly vulnerable. The acquisition of endothermy must also have facilitated radiation of birds into colder regions free from reptilian predators (Collias and Collias 1984). In species with precocial young, the nest is vacated soon after hatching—they are nidifugous. In other species, and this includes all of the passerines, the young are altricial and are heavily reliant upon parental care until they develop enough to fledge—they are nidicolous. Nidicolous species build the most well-formed nests of all birds (Collias and Collias 1984). Their nests must provide a microhabitat that is favorable for incubation of eggs, and also for the brooding and protection of nestlings. They must be hidden away from predators and still have properties of insulation and durability that are sufficient for prolonged occupation. Not surprisingly, environment plays a strong role in nest composition and location, and the type of nest is often species-specific and an indicator of evolutionary history. Well over one thousand nests were located in the present study, and their histories contribute to high altitude biology by providing reliable information on physiological and behavioral responses of breeding birds to environmental variation.

Construction

Early in the season the first behaviors associated with nest building were sometimes observed. Typically, these occurred when a foraging female interrupted her food gathering by grasping, manipulating, then dropping pieces of grass or other plant material. Handling of potential nest-building materials continued to be interspersed with feeding behavior at irregular intervals for a day or two. The female then began carrying these materials to the site chosen for nest construction. It was difficult to observe the process of nest-site selection, but in the days immediately preceding nest building, a female often spent considerable time hopping in and around the vegetation where the nest was eventually built. The male was usually close by at these times, exhibiting guarding behavior.

The method of nest construction varied somewhat, depending upon the site chosen. For nests built on the ground, females often first scratched out a hole in the usually damp soil or litter, then began adding twigs or coarse, wet stalks of grass. The nest was usually built from the top down with the first material being formed into a ring or rim around the hole, followed by the lining of the cavity walls and then the bottom. Lastly, finely-divided inner lining material was added. A few ground nests were built directly onto the undisturbed soil, rather than into an excavation, a position that may increase vulnerability to predation (Collias 1997). Their construction sequence was much the same: walls first, then bottom, followed by the lining.

In contrast, nests in elevated sites were constructed from the bottom up, especially those placed in pines and on large willow branches. First, a platform of cris-crossing twigs and/or grass stalks was placed to form the bottom of the nest.

TABLE 7.1. COMPOSITION OF *Oriantha* NESTS ACCORDING TO LOCATION

| | Nest location | |
| | Ground[a] (% of total mass) | Elevated[b] (% of total mass) |
Nest components		
Fine grass	18.9	15.7
Medium grass	50.9	23.1
Coarse grass	8.4	25.3
Twigs	4.8	16.1
Bark	1.5	2.8
Duff	10.4	5.5
Other	5.1	11.5

Note: Nests collected at Tioga Pass during laying or incubation (Kern 1984).
[a] Mean mass = 18.2 g, N = 5.
[b] Mean mass = 38.9 g, N = 17.

Walls were then built to their final height, and the inner lining was added as a last step. In some of the more densely leafed-out willows, walls were often built ahead of the bottom, as in ground nests, perhaps because they were held in place and supported more by the surrounding branches. In all types of constructions, females relied heavily on wet materials for the bottom and walls. After being put into position, these were molded and shaped by her body as she sat inside, scratching and moving from side to side. As the material dried it tended to hold to the shaped configuration. The innermost lining material was added dry, and the interior would take on a frayed, rather than smooth, appearance in a day or so unless the female revisited periodically and sat within. The total time spent by females constructing their nests was difficult to determine accurately, particularly since they tended to abort the effort if disturbed by an observer. Nonetheless, some crude data were accumulated (total building time determined to the nearest half-day).

Despite the lower volume of materials placed into ground nests as opposed to elevated nests, there was no difference in their construction times. What did vary, however, was the construction time for first nests of the season versus those built subsequently as replacements. First nests required a mean of 2.5 d (SD = 0.5 d, N = 23, min = 2 d, max = 3.5 d) whereas replacement nests required one d less (mean = 1.5 d, SD = 0.5 d, N = 14, min = 1 d, max = 2.5 d), a significant difference (t = 11.80, P < 0.001). Four first nests that were under construction at a time when snowstorms occurred were not included in these data. Usually snowed-upon, unfinished nests were abandoned, but in these four cases construction was resumed after a pause of three or four days, more than doubling the usual duration of construction. Direct observations of building females showed that effort devoted to first nests was discontinuous, and that when building bouts occurred, trips were usually three min or more apart. Renests, on the other hand, involved a more concerted effort. Trip frequency was sometimes one per min, even one per 10 sec, and in five of the 14 that were observed, the entire nest was built during one daylight period.

Nests built in elevated positions were much bulkier in appearance and weighed more than twice as much as ground nests (Table 7.1). From a thorough analysis of the composition, dimensions, and thermal properties of *oriantha* nests collected from our study area, Kern (1984) found that elevated nests had a greater propor-

TABLE 7.2. DIMENSIONS AND THERMAL PROPERTIES OF *Oriantha* NESTS ACCORDING TO LOCATION

	Nest location		
	Ground	Elevated	P
Nest dimensions (cm)			
Height	5.9	8.7	<0.01
Depth of nest cavity	3.8	3.8	NS
Wall thickness	3.8	3.8	NS
Floor thickness	2.1	3.9	<0.05
Surface area of nest cavity (cm^2)	70.3	71.5	NS
Wind resistance (% of airstream penetrating)			
Walls	3.8	1.1	<0.05
Floor	1.8	0.6	NS
Thermal conductance (W · m^{-2} · °C^{-1})			
Walls	8.1	6.8	NS
Floor	4.1	3.0	<0.005

Note: Nests were collected during laying or incubation (Kern 1984). P-value from t-test of mean differences; sample size in Table 7.1.

tion of coarse grass and twigs than ground nests, thus accounting for their extra mass and bulk (Table 7.1). In both nest types the inner lining consisted mostly of very thin blades of bunchgrass (*Muhlenbergia* sp.).

Elevated nests had thicker floors, and thus had higher walls than ground nests, because the depth of the nest cup and its surface area were the same for the two types (Table 7.2). Uniformity in cup dimensions is to be expected because they were the product of female body size and not nest position. Nest cups were generally wider than deep, and their width increased in active nests due to the growth and movements of nestlings (Morton et al. 1972a, Kern 1984).

Thermal properties

Kern (1984) also found in the laboratory that elevated nests tended to be less penetrated by wind than ground nests and that their conductance (the reciprocal of insulation) was lower (Table 7.2). Porosity of walls, rather than their thickness, was a decisive factor here. Bear in mind that ground nests were usually located in highly sheltered positions and if thermal properties of nests had been measured *in situ* they might well have proven to be more effectively insulated than elevated nests. Indirectly, this is borne out by egg temperatures recorded from the two types of nests (Fig. 7.1). When ambient temperatures began to drop below 16 C, mean egg temperature began declining more rapidly in elevated than in ground nests. This trend was reversed when it was colder than 8 C, probably because females incubating in elevated nests began shivering in order to defend their body temperatures. Similar responses were observed in Dusky Flycatchers (*Empidonax oberholseri*) also nesting at Tioga Pass (Morton and Pereyra 1985).

These data suggest that the lower critical temperature of *oriantha,* the ambient temperature where shivering thermogenesis begins, is much lower in females sitting in their nests (about 8 C in elevated nests, and probably much lower in ground nests) than it is presumed to be in those perched outside the nest (about 23 C; Maxwell and King 1976).

Since the eggs and body of an incubating female form an integral thermal unit (Drent 1975), and since egg temperature is about three degrees cooler than core
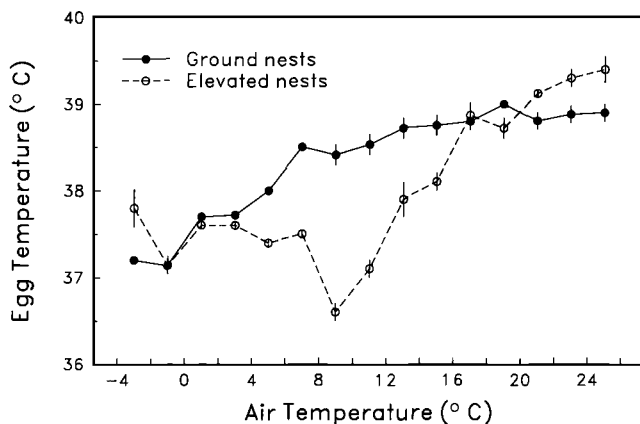
FIGURE 7.1.   Mean egg temperatures ($\pm$ 1 SE) recorded during constant attentiveness by incubating female *oriantha*. Modified from Zerba and Morton 1983a).

body temperature in *oriantha,* core temperature at onset of shivering in females that were incubating in elevated nests must have been about 39–40 C; in other words, about three degrees above that of the eggs when they were first boosted upward (Fig. 7.1). Note that incubation patch temperature was found to be less than one degree cooler than core temperature (see below).

The increase in metabolism by females incubating in elevated nests may not have been trivial because temperatures at Tioga Pass were often below 8 C in the daytime, and nearly always so at night. Recall that body mass of females with elevated nests was about 5% lower than in those with ground nests (Chapter 6), another indicator that their energy expenditure was higher. It seems that females adjusted to the thermal environment of elevated sites by building in those locations nests with less-porous, better-insulated walls. But the walls were not thicker than those of ground nests, and despite being in a more tightly woven nest, the eggs, and by inference, the female's body, were susceptible to cooling. To overcome this, females had to expend more energy. This could have been prevented, one assumes, if elevated nests were larger and bulkier, but this would undoubtedly have made them more visible to predators. Thus, a trade-off seems to be present between predation avoidance and energy cost to the incubating female when she chooses to build above the ground. In a review of metabolic rates taken under field conditions, Williams (1996) concluded that incubation is not a time of reduced energy expenditure for birds, a result that tends to be supported by our data on body mass and egg temperatures of *oriantha* females striving to keep themselves and their eggs warm during the cold mountain nights, particularly when their nests were in exposed locations.

An additional interesting outcome of Kern's (1984) study was that the thermal conductance of elevated nests varied with their distance from the ground; the higher the nest was placed, the more conductance (and the poorer the insulation). It remains to be shown, but perhaps the amount and types of materials used is correlated with nest height and/or predation frequency. In a comparison of insulative properties of nests of 11 North American passerines, Skowron and Kern (1980) found that heat flux was fourth-lowest in *oriantha.*
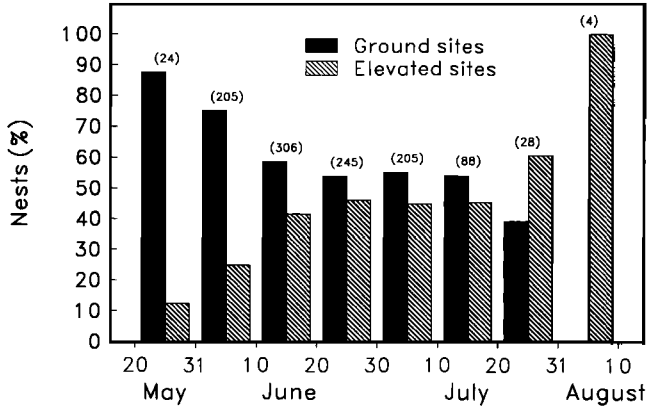
FIGURE 7.2.   Seasonal change in nest locations (on the ground or in elevated sites) for *oriantha* at Tioga Pass. Sample sizes in parentheses.

Nest sites

Nests are often in peril from predators and from fluctuations in microclimate and weather. As alluded to above, these forces seem to exert selection pressures on nest size that are in opposition to one another. A well-hidden nest, in a cavity under thick vegetation, for example, could be well protected from both of these factors. But when ground cover is sparse or when elevated locations are utilized, sites are less sheltered, and nests should be provided with more insulation. In other words, they should be larger and/or more densely constructed. However, predators would seem more likely to detect larger nests.

Nest sites utilized by *oriantha* ranged from those placed on the ground with little surrounding cover, other than short, dry grass, to elevated positions among thick pine boughs or crowns of willows. Data accumulated in every year of the study on nest positions indicate that both ground and elevated sites were used heavily but, overall, ground sites were preferred, 59.6% to 40.4% (N = 776 ground nests and 525 elevated nests, Chi-square = 48.4, df = 1, P < 0.001).

Because nest sites were tagged every year, and because many were highly familiar to us, such as those that might be in a particular grassy hummock or isolated pine, we were able to determine that some sites were used repeatedly by the same female and, over the years, by different females. Of 508 first nests of the season built on TPM, 29 or 5.7% were located under or within the same pine or willow as a previous nest. Eighteen of these 29, or 3.5% of the total, were thought to have been in precisely the same place as a nest from a previous year. We were certain of this because the spot had unique features or because the new nest was built on the remnants of an old one (most nests were destroyed every winter but sometimes material from an old nest did remain in place). One year an *oriantha* female built her nest inside a well-preserved American Robin nest from the year before.

Nests tended to be placed in different locations during the season. Ground sites were the most heavily utilized in May, but elevated sites were selected nearly half of the time in June and July, and in late July and August they were preferred (Fig 7.2). Nests in elevated sites were placed either in willows or pines. For the first

TABLE 7.3. Seasonal Change in Type of Vegetation Utilized by *Oriantha* Females for Nests Placed in Elevated Sites

Date	Vegetation utilized		N
	Pines (%)	Willows (%)	
20–31 May	66.7	33.3	3
1–10 June	56.9	43.1	51
11–20 June	51.6	48.4	126
21–30 June	50.0	50.0	114
1–10 July	34.8	65.2	92
11–20 July	25.6	74.4	39
21–31 July	12.5	87.5	16
1–10 August	0.0	100.0	4

month or so of the nest-building season, pines were utilized slightly more than willows. Thereafter, willow sites predominated (Table 7.3). The very last nests of the season were built almost exclusively in the crowns of fully leafed-out willows. The picture drawn here about nest locations is an average one, taken over many seasons. It does not convey accurately the extent of inter-seasonal variations that were linked to snow conditions and that illustrated environmental adaptation by nesting females (Chapter 10 and Fig. 10.7).

Through the use of transects, the heights of pines and willows on the TPM portion of the study area were sampled to characterize that aspect of vegetation structure (Table 7.4). These data show that *oriantha* tended to nest beneath plants that were shorter than the average for that type (i.e., pine or willow), and within plants that were taller than the average (Table 7.4). The functional significance of these propensities has not been pursued, but a study of nest-site microclimates through the whole season might be worthwhile.

Mean nest height for elevated nests was 59.6 cm (SD = 53.5 cm, N = 508), and height distribution of nests was quite different in pines and willows. Willows could provide hiding places even when quite small, and most willow nests were located below 50 cm (mean = 41.3 cm, SD = 24.0 cm, min = 4 cm, max = 180 cm, N = 279). Pine nests occurred over a wider range of heights, although most were built at or above 50 cm, and they often occurred at well over 100 cm (mean = 82.2 cm, SD = 68.9 cm, min = 12 cm, max = 650 cm, N = 229). The highest willow nests tended to be those built late in the season in the crown area whereas the highest pine nests occurred when deep snow was present and more traditionally used sites were scarce. When all elevated nests were compared, pine tree nests were significantly higher than willow nests (t = 8.58, P < 0.001).

The function of a bird's nest is to provide warmth and safety for the developing

TABLE 7.4. Height of Individual Pines and Willows (cm) on Tioga Pass Meadow as Sampled in Transects, and Nested Beneath (Ground Nests) or Nested Within (Elevated Nests) by *Oriantha*

	Plant height								
	Transects			Nested beneath			Nested within		
	Mean	SD	N	Mean	SD	N	Mean	SD	N
Pine	174.2	84.0	484	142.1	200.0	42	194.1	160.7	161
Willow	84.5	47.1	784	60.9	51.1	318	125.7	51.8	140

eggs and young (Collias and Collias 1984). Thus it should be built so as to counteract weather effects as well as those of predation, a supposition which is frequently borne out by field data (Lawton and Lawton 1980, McGillivray 1981, Martin and Roper 1988). Nest-site selection is a key behavior affecting reproductive success and it has presumably evolved in relation to a variety of factors. Among these are local availability of resources, including food and nesting materials, shelter or a favorable microclimate, and concealment from predators (Walsberg 1981, Collias and Collias 1984). Judged from the perspective of success, interaction of these factors would seem to have a similar outcome in ground and elevated *oriantha* nests: fledging success was 44.7% (335 of 750) in ground nests and 49.0% (245 of 500) in elevated nests, an insignificant difference (Chi-square = 2.26, df = 1, P = 0.132).

Although ground sites are thought to represent the primitive condition for birds, factors such as disturbance, predation, and competition probably led eventually to sites being selected off the ground, often in dense shrubbery (Preston and Norris 1947). A study of 233 nests of 26 open-cup nesters, utilizing 62 different plant species, showed that nest height varied directly with plant height (Gates 1979). As in the present study, first nests of the season were placed lower than later nests in response to growth and increased density of foliage as leaf emergence occurred. Presumably, this is an anti-predator response (Nice 1937, Walkinshaw 1939, Salt 1966). That view may be too simple, however, because microclimates can also change markedly with vegetation development. Horváth (1964) found, for example, that movement of hummingbird nests from low sites in spring to high ones in summer probably occurred because low sites were buffered from climate extremes and high sites were cooler because of evapo-transpiration from trees.

Concealment of nests from predators and protection from weather can both be accomplished if the nest is placed in the proper location, such as among thick boughs (Martin and Roper 1988). Still there are situations wherein elements of nest construction or orientation seem to be primarily in response to microclimatic factors. For example, the nest opening or entrance can be oriented toward the warming sun of early morning (Austin 1976), or away from the direction of prevailing winds and storms (McGillivray 1981, Böhm and Landmann 1995), especially in the alpine (Verbeek 1970, Norment 1993). In addition, nests may be situated beneath a plant canopy so as to create a favorable radiative environment, a situation found in Warbling Vireos (Walsberg 1981) and in *oriantha* (Walsberg and King 1978). *Oriantha* at Tioga Pass also tended to position their nests on the northeastern side of bushes, away from the southern winds that brought most of the cold air and storms onto the study area (Zerba and Morton 1983a).

EGG LAYING

Many passerines make over a thousand trips in constructing their nest, so this endeavor requires a great deal of time and energy (Collias and Collias 1984). And once the nest is built females must also accomplish another energetically-expensive function, egg laying. The nest-ready interval, the interval between building and laying, will be examined next to learn more about the relative importance of physiological preparation and of energetic constraints in determining the temporal phasing of these events.
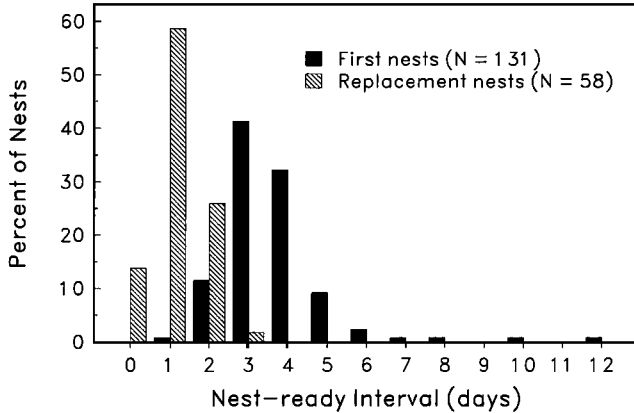
FIGURE 7.3.   Nest-ready interval (days between nest completion and laying of first egg) in *oriantha* at Tioga Pass.

Nest-ready interval

During the first three years of this study, the average of the time between the end of nest construction and laying of the first egg was found to be 2.5 d (Morton et al. 1972a). Many more data are now available, and it appears that the duration of the nest-ready interval depends upon the nest's history. For example, first nests of the season usually sat empty for several days before laying began (mean = 3.63 d, SD = 1.40 d, min = 1 d, max = 12 d). Replacement nests, on the other hand, were empty for a much shorter time (mean = 1.16 d, SD = 0.67 d, min = 0 d, max = 3 d; Fig. 7.3), a highly significant difference (t = 16.42, P < 0.001).

In two of the 12 first nests of the season with a nest-ready interval of five days, and in all of the remaining seven nests wherein the interval was six days or more, the delay in laying could be attributed to intervention by snowstorms. Usually nests that had been constructed, but not yet laid in, were abandoned when covered by snow. In a few cases, however, the female returned after the thaw to begin laying, thus extending the interval to as long as 12 days (Fig. 7.3).

The physiological condition of females building these two types of nests must have been quite different. Since ovulation precedes oviposition by approximately 24 hr, it is clear that many of the renesting females finished their nests at just about the time they ovulated; 34 of 58 (58.6%) of the nests were empty for only one day (Fig. 7.3). There were even eight cases (13.8%) wherein the nest was built in entirety on the day before laying, yielding a nest-ready interval of zero days. In three of these eight, females were observed adding more nest lining material on the morning of the first egg, after laying had already occurred; one of them was moving the lining from her old nest to the new one, rather than gathering fresh material. Obviously some renesting females accomplished all or nearly all of their nest building while heavily engaged in vitellogenesis and even while carrying an egg in the oviduct. For first nests this situation was quite different. Females built them at a more leisurely pace and then usually did not lay until several days had elapsed. Judging from concurrent changes in body mass (see Fig. 6.4), the nest-ready interval coincided closely to the time (3–4 d) re-

quired to prepare physiologically and metabolically for laying. In these situations, nest building and rapid ovarian development did not overlap.

This temporal flexibility in the nest-ready interval, as shown by the influence of environmental conditions and by the difference between first nests and renests, strongly indicates that nest building and ovarian preparation for oviposition are controlled by different mechanisms. Furthermore, their co-occurrence in renesting females shows that neither function by itself exerts maximal energetic stress.

Laying times

Egg laying occurred in the early morning hours in *oriantha,* at about sunrise or shortly thereafter. By watching laying females from concealment or by frequent visits to their nests, we were able to show that mean time of laying was 05:44 (SD = 0.7 hr, N = 32) and that the time did not vary with egg order (Oppenheimer et al. 1996). In 16 instances for which laying times between successive eggs were known, it averaged 24.1 hr (SD = 0.9 hr).

Laying occurred, with few exceptions, on successive days until the clutch was completed. There was no effect on the laying schedule by conditions such as subfreezing temperatures or storms unless the storm was severe enough to interrupt the nesting cycle altogether. In only four of many hundreds of nests monitored did it appear that the regular sequence of ovipositions was broken. In other words, a day of laying was skipped. In three cases the skip followed the first egg, in the other case the second egg. Our discovery of the nest could have disturbed the laying female and caused her to lay one egg somewhere away from the nest, but in these four nests we doubt this happened. More likely, the female failed to ovulate or the oviduct failed to capture the ovum.

DESCRIPTION OF EGGS

Oriantha eggs were pale blue with reddish brown spots. Spots were usually irregular in shape and ranged in size from tiny specks to 2 mm or more in greatest dimension. They could be distributed rather uniformly over the whole egg but usually they were concentrated toward the blunt end. Occasionally spots were condensed into a band or ring on the blunt end. In a long-term study of captive Village Weavers (*Ploceus cucullatus*), Collias (1984, 1993) found that the color and amount of spotting of eggs was constant throughout a female's lifetime. Eggs within *oriantha* clutches closely resembled one another in appearance and this resemblance carried over into consecutive clutches (a direct comparison of eggs could be made when a first clutch was deserted with eggs intact and the renest was found).

EGG DIMENSIONS

Eggs were numbered on their blunt ends throughout the breeding season according to laying order, if known, for 13 consecutive years, 1981 to 1993. Many were then measured with calipers to the nearest 0.01 mm to obtain maximum lengths and widths. A sample of 25 eggs from seven clutches was also weighed within two hr of laying in order to obtain the fresh egg mass. Maximum lengths and widths of these same 25 eggs were then entered into Hoyt's (1979) formula for determining egg volume: volume = 0.51 × length × width^2. The eggs had a mean mass of 3.20 g (SD = 0.12 g) and a mean volume of 3.20 cm^3 (SD = 0.13
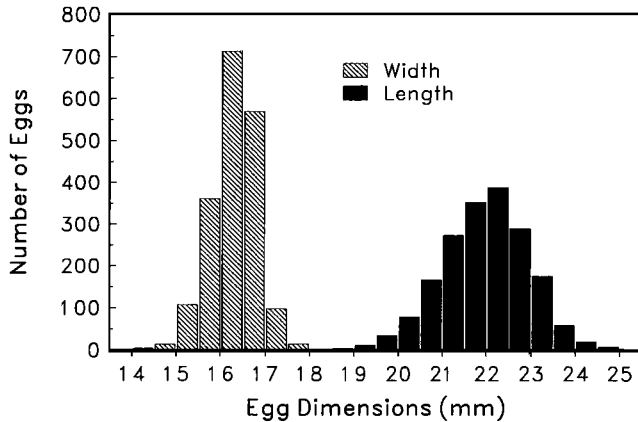
FIGURE 7.4. Frequency distribution of width and length measurements of 2,030 *oriantha* eggs.

cm^3). A regression of calculated volume on measured mass showed the two to be highly correlated (r^2 = 0.952, P < 0.001). It appears, therefore, that fresh egg mass can be reliably estimated from egg dimensions.

Length and width measurements were obtained on 2,030 eggs. Both measures were rather symmetrically distributed (Fig. 7.4). Mean width was 16.29 mm (SD = 0.51 mm) and mean length was 21.99 mm (SD = 1.00 mm), a length-to-width ratio of 1.35. Egg widths ranged from 14.05 to 17.88 mm and lengths from 18.46 to 27.50 mm, so, even at their extremes, these dimensions did not overlap. A single runt egg, 13.09 × 17.41 mm, that did not hatch was omitted from this analysis.

The fact that calculated volumes seemed to predict egg mass suggests that a regular relationship exists between egg length and width. To test this idea width was regressed on length for all 2,030 eggs in the sample. This gave the line, Y = 0.183X + 12.25, and an r value of 0.36, slightly below the one of 0.41 found for Hooded Crow (*Corvus corone*) eggs by Rofstad and Sandvik (1985). Egg volumes, as calculated from the linear measurements, were normally distributed in *oriantha* (Fig. 7.5). Mean volume was 2.98 cm^3 (SD = 0.26 cm^3) and, disregarding the lone runt egg, ranged from 1.95 to 3.83 cm^3, almost a two-fold difference.

Egg size has been shown to be a highly heritable trait in a diverse array of avian species (Moss and Watson 1982, Byrkjedal and Kålås 1985, Wiggins 1990), and the major share of variation in egg dimensions is genetic (Ojanen et al. 1979, Van Noordwijk et al. 1980). There is little unequivocal evidence, however, that a positive relationship exists between egg size and offspring fitness in birds (Williams 1994). Still, egg size is an important determinant of reproductive investment (Flint and Grand 1996), and volumes are known to vary among years and between nesting sites as, for example, in American Pipits (*Anthus rubescens*) breeding at high altitude in Montana (Hendricks 1991). At Tioga Pass, egg volume in *oriantha* also varied significantly among the 13 years (ANOVA $F_{12, 1986}$ = 4.17, P < 0.001). Eggs averaged the smallest in 1991, 2.92 cm^3 (N = 230), and the largest in 1984, 3.07 cm^3 (N = 175), a 5.1% difference.
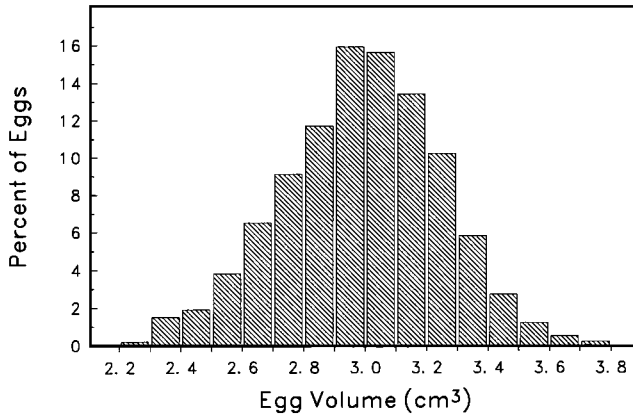
FIGURE 7.5.   Frequency distribution of volumes for 2,030 *oriantha* eggs. Volumes were determined from Hoyt's (1979) formula.

EGG VOLUME

The characteristics of eggs, especially their size and number, provide useful information for quantifying reproductive investment. In a long-term study, furthermore, it is possible to evaluate this investment within a context of environmental variability and also in relation to clutch size and to traits of individuals such as age, body size, and body condition. This sort of information can then be used to test models and hypotheses that address differential investment strategies (Slagsvold et al. 1984).

Collias (1984, 1993) has shown that individual Village Weavers in captivity (where environmental conditions can be expected to vary minimally) laid eggs of a consistent size and shape from one year to the next. In *oriantha*, however, significant interannual variation in egg volumes were found in three of six females whose eggs were measured over a span of four to seven consecutive years (Table 7.5).

Effect of clutch size

An inverse relationship commonly occurs between egg size and clutch size, suggesting that a trade-off exists between quality or size of young and their numbers (Blackburn 1991). This relationship was not found in *oriantha*, however (Table 7.6). Egg size did not vary significantly with clutch size (ANOVA $F_{5, 2024}$ = 2.26, P = 0.060).

TABLE 7.5.   INTERANNUAL VARIATIONS IN EGG VOLUME (%) IN SIX *Oriantha* FEMALES

Band number	Years of data	Number of clutches	Percent variation	ANOVA F	P
127169348	7	7	11.5	2.395	0.066
138116546	4	4	16.3	6.192	0.009
138116752	5	5	4.8	1.175	0.367
138116782	5	7	8.3	0.946	0.458
138116935	4	6	7.7	4.502	0.015
138116942	4	5	11.1	4.321	0.024

TABLE 7.6.   Egg Volume According to Clutch Size in *Oriantha* at Tioga Pass

Egg volume (cm³)	Clutch size				
	2	3	4	5	6
Mean	2.98	2.98	2.98	2.39	3.12
SD	0.28	0.27	0.26	0.29	0.18
No. of eggs	18	228	1,592	180	12

Effect of season

Egg volumes did vary with season, however. When plotted according to laying date, a distinctive pattern emerged (Fig. 7.6). Volumes were lowest in May and June and highest in July and August, and the difference was highly significant (Table 7.7). This seasonal difference could be related to the nesting history of females because, as one might suspect from examining Fig. 7.6, eggs in first nests of the season were not as large as those in subsequent nests (Table 7.7). Linear dimensions also varied significantly when segregated seasonally by laying date or nest type (Table 7.7).

Egg size decreased significantly in late June then increased (Fig. 7.6). Inspection of the data revealed that this effect could be attributed to four years of light snowpack (1987, 1988, 1990, and 1992) when nesting began early. In those four years, eggs had a mean volume of 3.00 cm³ (SD = 0.23 cm³, N = 219) when laid before 20 June and 2.87 cm³ (SD = 0.22 cm³, N = 75) when laid between 21 and 30 June, a highly significant difference (t = 4.33, P < 0.001).

Effect of female age

Egg size was essentially invariant with female age in Great Tits and Pied Flycatchers (*Ficedula hypoleuca*; Ojanen et al. 1979, Järvinen and Pryl 1989), but it seemed to increase in Tree Swallows (*Tachycineta bicolor*), at least for the first two years of life (Wiggins 1990). In *oriantha*, a regression of 1,729 egg volumes on the ages of the females that laid them indicated that there was no significant relationship between the two (r² = 0.032, P = 0.090), nor did clutch volume
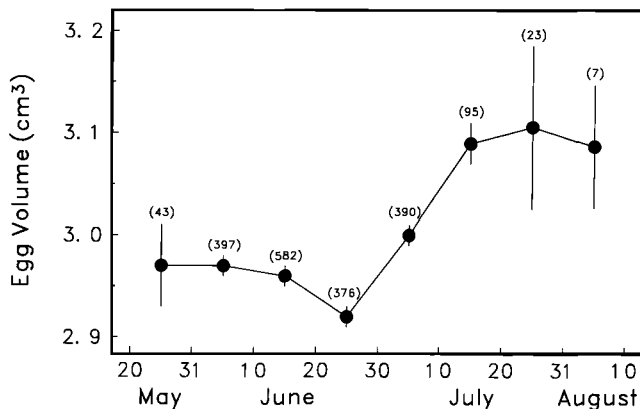

FIGURE 7.6.   Seasonal changes in egg volume (mean ± 1 SE) in *oriantha* at Tioga Pass in relation to laying date. Number of eggs in parentheses.

TABLE 7.7. VARIATION IN SIZE OF *Oriantha* EGGS IN RELATION TO LAYING DATE AND TO TYPE OF NEST

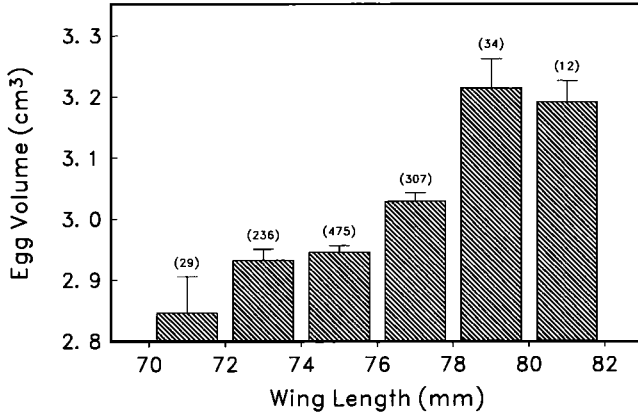| Egg dimension	Laying Date								Type of nest							
	May–June			July–August					First nest			Renest				
	Mean	SD	N	Mean	SD	N	t	P	Mean	SD	N	Mean	SD	N	t	P
Volume (cm³)	2.96	0.26	1,398	3.02	0.27	515	4.88	<0.001	2.95	0.26	1,005	3.01	0.26	502	4.62	<0.001
Width (cm)	16.25	0.49	1,398	16.42	0.87	515	4.09	<0.001	16.23	0.51	1,005	16.42	0.83	502	4.81	<0.001
Length (cm)	21.91	1.02	1,398	22.11	1.25	515	3.20	0.001	21.90	1.02	1,005	22.03	1.13	502	2.18	0.029

FIGURE 7.7. Relationship of mean egg volume (+ SE) to female body size, as measured by wing length, in *oriantha*. Number of eggs in parentheses.

differ with female age (r^2 = 0.060, P = 0.213, N = 438). The influence of nest type (first nest or renest) observed in Table 7.7 persisted with age; eggs in renests (which included replacement clutches and double broods) were significantly larger than those in first clutches at all ages.

Effect of female size

A positive relationship between egg size and female size has been demonstrated in a large number of avian species (Ojanen et al. 1979, Otto 1979, Byrkjedal and Kålås 1985, Järvinen and Ylimaunu 1986, Rohwer 1988, Järvinen and Pryl 1989, Järvinen 1991), and *oriantha* were no different, although the relationship was weak (r^2 = 0.048, P < 0.001, N = 1,093; Fig. 7.7). King and Hubbard (1981) suggested that most variation in egg mass in fringillids can be accounted for by female mass and that any remaining variation will be small and of questionable ecological significance. They make an interesting point, but they may have underestimated the difficulties involved in evaluating female mass. Murphy (1986), for example, found that egg mass and female mass were not correlated in Eastern Kingbirds (*Tyrannus tyrannus*). Egg mass was correlated, however, with a measure of body condition, the flight muscle weight.

Effect of nutrition

In wild, unmanipulated birds it is difficult to tie egg size to female condition because the latter can change so rapidly in the time immediately preceding egg synthesis. In general, the summed contributions from stored nutrients and concurrent foraging are usually sufficient for females to lay high-quality eggs. At Tioga Pass, however, there were years when the snow cover persisted for many weeks into the potential breeding season. Females (and males) were present on the study area, but nesting sites were covered with snow and unavailable. In these situations, food appeared to be scarce and individuals were known to move periodically to lower elevations, probably to obtain better foraging opportunities (Hahn and Morton 1995).

Were egg sizes affected in females exposed to these kinds of environmental conditions? To address this question, egg volumes obtained from the 10 earliest
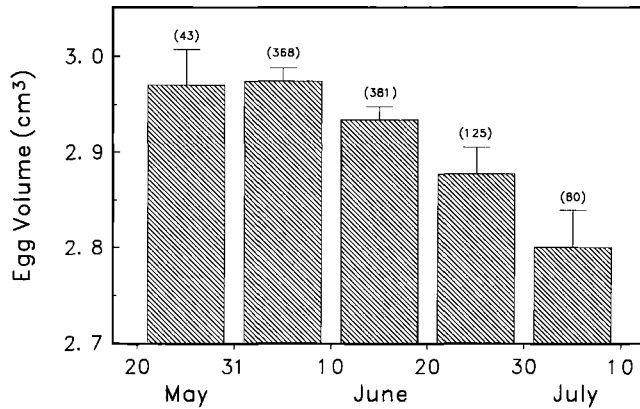
FIGURE 7.8.   Mean volume (+ SE) of eggs laid in the first 10 nests of the season by *oriantha* at Tioga Pass Meadow. Number of eggs in parentheses.

clutches produced in each season were separated out and plotted by laying date. These data show that females laid smaller eggs in the first week of the nesting season in years when onset of nesting was delayed until 20 June or later (Fig. 7.8, ANOVA $F_{4, 996} = 9.14$, $P < 0.001$). This could be evidence for a nutritional effect on egg size because delayed nesting was associated with deep snow, undeveloped vegetation, and trips to lower altitude, all indicators of suboptimal foraging conditions.

Effect of laying order

Egg volumes did not vary significantly with laying order, except in 5-egg clutches. The difference in volume between first- and last-laid eggs in a clutch was less than 2% for clutch sizes of 2, 3, and 4, although it did increase by more than 8% in 5-egg clutches (Table 7.8). Egg size was found to increase with laying order in 4-egg clutches, however, when sizes were standardized to account for intra-clutch variation (Mead and Morton 1985).

There is considerable interest in the way reserves are apportioned during the laying sequence because the most prevalent patterns may reflect differential in-

TABLE 7.8.   Egg Volume (cm^3) With Egg Number (= Laying Order) in *Oriantha*, According to Clutch Size

| | Clutch size | | | | | | | | | | | |
| | 2 | | | 3 | | | 4 | | | 5 | | |
Egg number	Mean	SD	N	Mean	SD	N	Mean	SD	N	Mean	SD	N
1	2.97	0.27	8	2.93	0.28	41	2.95	0.27	198	2.78	0.21	19
2	2.98	0.33	8	3.00	0.28	41	2.97	0.24	198	2.86	0.21	19
3				2.99	0.29	41	2.97	0.25	198	2.87	0.24	19
4							3.00	0.28	198	2.98	0.22	19
5										3.01	0.36	19
Percent change[a]	0.34			1.82			1.62			8.27		
ANOVA F	0.01			0.64			1.44			2.76		
P	0.948			0.529			0.229			0.032		

[a] Comparison of first and last eggs in the clutch.

TABLE 7.9. FREQUENCIES AT WHICH EGGS OF KNOWN LAYING ORDER IN 4-EGG CLUTCHES WERE SMALLEST OR LARGEST WITHIN THEIR RESPECTIVE CLUTCHES (N = 198 CLUTCHES)

	Laying order			
	1	2	3	4
Smallest (% of cases)	38.4	19.7	22.7	19.2
Largest (% of cases)	26.8	18.2	17.7	37.4

vestment strategies by females (Howe 1976, 1978). It is common among open-nesting passerines, for example, for the last-laid egg to be the largest in the clutch, and Slagsvold et al. (1984), in a highly influential paper, have argued that this is adaptive. [Larger eggs usually produce heavier but not dimensionally larger chicks; chicks are heavier because they have more nutrient (yolk) reserves (Williams 1994)].

Because passerines usually begin incubating before clutch completion, hatching asynchrony occurs and late-hatched young are competitively disadvantaged because they are behind their older siblings on the growth curve. Since egg size and hatching size of the chick are tightly coupled, and since increased body size confers competitive advantage, it is reasoned that last-laid eggs should be large to maximize survival of all members of the brood. This is the brood-survival strategy (Slagsvold et al. 1984). Alternatively, some species exhibit decreased egg size with laying order and the last egg or eggs are smallest. These species, many of which have large clutches, are said to be following a brood-reduction strategy (Slagsvold and Lifjeld 1989).

Is there evidence in our data, other than that already presented on small increases in volume with laying order, that *oriantha* might be following either one of these strategies? When we examined egg-size hierarchies in the modal clutch, 4-eggs, a surprising result emerged: egg 1 was indeed most often the smallest (38.4% of clutches) and egg 4 the largest (37.4% of clutches), but after egg 4, egg 1 was also most frequently the *largest* (26.8% of clutches, Table 7.9). Among the 198 4-egg clutches where all eggs were numbered on the day of laying and subsequently measured, two patterns prevailed in 91 (46.0%) of the clutches: in one, eggs 1 and 4 were both larger than eggs 2 and 3 (53 clutches), and in the other, egg 1 was the smallest in the clutch and egg 4 the largest (38 clutches). A close check of the data shows that the frequency of large first eggs decreased with season whereas the frequency of small first eggs increased. Since egg 4 remained fairly stable in hierarchical status throughout, a seasonal change in egg size pattern occurred (Fig. 7.9). Essentially, females laid eggs in decreasing size from 1 to 3 followed by a large number 4 during the first half of the summer. They then switched to a pattern of increasing size with laying order during the second half. Note that in both patterns the last egg tended to be large, as predicted by a brood-survival strategy. The seasonal switch in pattern of egg size with laying order supports Perrins' (1996) proposal that environmental cues, such as food supply, influence egg size. Perhaps both ecological (food availability) and evolutionary (brood survival) factors interact in laying *oriantha* to give these seasonal effects.

There are no consistent hierarchical patterns in egg size with laying sequence for passerines as a whole, although consistency can sometimes be found within
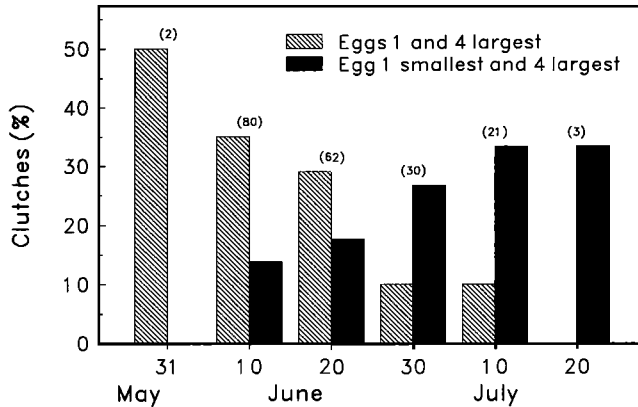
FIGURE 7.9.   Seasonal changes in hierarchy of egg size, according to date of clutch start, within 198 4-egg clutches laid by *oriantha* at Tioga Pass. Number of clutches in parentheses.

species. For example, egg size increased steadily with laying order in Goldcrests (*Regulus regulus*; Haftorn 1986), Least Flycatchers (*Empidonax minimus*; Briskie and Sealy 1990), Tree Swallows (Wiggins 1990), captive Bengalese Finches (*Lonchura striata*; Coleman and Whittall 1990), Eurasian Blackbirds (*Turdus merula*; Rydén 1978), and Common Grackles (*Quiscalus quiscula*; Howe 1976). On the other hand, the opposite pattern was observed in Hooded Crows (Rofstad and Sandvik 1985), no difference was detected in Black-eared Wheatears (*Oenanthe hispanica*; Suarez 1991) and, in the present study, *oriantha* switched patterns seasonally. Still the majority of passerines appear to increase provisioning in their last-laid eggs, thereby following a brood-survival strategy.

At this time there is no agreement, however, that intra-clutch variations in egg mass are adaptive. Several investigators are convinced that such variations are unselected and simply the result of prevailing energetic conditions. For example, four species of hole-nesting passerines in subarctic Finland showed egg volume variations that were unrelated to laying order, laying date, clutch size, or female age. Instead, female mass or condition, and thus egg size, was correlated with ambient temperatures, presumably because of the energy costs of thermoregulation. Eggs were smaller when cold weather occurred prior to laying times, and larger when there was warm weather. The authors concluded that these environmental effects were sufficient to explain intra-clutch variations in egg size (Ojanen et al. 1981, Järvinen and Väisänen 1983, Järvinen and Ylimaunu 1986; Järvinen 1991, 1994).

Bancroft (1984) found that Boat-tailed Grackle (*Quiscalus major*) eggs were smaller early in the season because females were in relatively poor body condition. Egg size has also been linked to food availability or female body condition in various other species such as Eastern Kingbirds (Murphy 1986), Fieldfares (*Turdus pilaris*; Otto 1979), and European Starlings (Greig-Smith et al. 1988). Magrath (1992) found that egg mass in Eurasian Blackbirds correlated directly with air temperatures that occurred during the period of rapid follicular growth. Thus, seasonal increases in egg mass appear to be related to ambient conditions and associated thermoregulatory costs to laying females.

Magrath (1992) also pointed out that the variation in size of last-laid eggs is

probably too small to have much effect on sibling competition in nestlings. Rather than endorse the ideas proposed about brood-survival strategies by Slagsvold et al. (1984), he suggests that last-laid eggs appear to be more vulnerable to environmental fluctuations, and since egg viability is tied to egg size, a tendency to lay larger eggs late in the clutch might be selected for to counter the increased risk. He calls this the environmental variance hypothesis. There are two corollaries: smaller species will be less-well buffered against environmental variance than larger ones and should, therefore, lay relatively larger last eggs, and open-nesting species should lay relatively larger last eggs than hole nesters because the latter have more sheltered nest sites. Both of these relationships have been documented by Slagsvold et al. (1984).

How can the *oriantha* data be interpreted in light of these hypotheses? The mid-summer decline in egg size (Fig. 7.6), which occurred in years of light snowpack, might have been related to deteriorating environmental conditions (a lowering of insect availability as the habitat dried up, for example), whereas the larger eggs in July and August (Table 7.7) might have been the result of decreased thermoregulatory costs to laying females because of warmer weather. The same could be said about the difference in egg size between first nests and renests. The decrease in egg size observed in the first eggs of the season in heavy snowpack years is evidence for an environmental effect on egg volume (Fig. 7.8); the later in the season females began laying, the smaller their eggs. We know that *oriantha* can subsist on a wide variety of foods, and that they readily move to lower altitude when exposed to storms or a persistent snow cover. This high degree of omnivory and mobility makes quantification of food availability an impossible task, but this might not be necessary if body mass of females is a reliable indicator of overall condition and readiness to lay.

This idea was evaluated by comparing body masses during the 21 days preceding the appearance of the first eggs on TPM in 1988 and 1995. Recall that, ecologically speaking, these were very different years, with commencement of first clutches being more than a month apart due to snow conditions (Fig. 5.4). Body mass during this 21-d interval was not different in females (1988: mean = 26.15 g, SD = 1.67 g, N = 60; 1995: mean = 25.80 g, SD = 1.72 g, N = 51; t = 1.08, P = 0.280), or in males (1988: mean = 27.96 g, SD = 1.60 g, N = 112; 1995: mean = 27.99 g, SD = 1.26 g, N = 88; t = 0.15, P = 0.880). This indicates that omnivory and altitudinal movements were effective strategies for maintaining energy balance under a wide range of environmental conditions. It is not known if the precise nutritional needs of these first 10 laying females were being met in late years, however, nor are there enough body mass data to see just how effectively they accumulated reserves during those few days when ovulations were occurring. Functionally speaking, that brief three- or four-day period could be the crucial window of time when body condition is translated to egg mass. Variable environmental conditions encountered by females during nesting attempts could also be the reason why some females exhibited significant differences in egg volumes among years and some did not (Table 7.5). Taken together, intra-clutch variations in egg size in *oriantha* provide support for both the environmental variance hypothesis and the brood-survival hypothesis.

Effect of sex

We discovered several years ago that the volume of male eggs in *oriantha* was slightly larger than that of female eggs. This difference was significant if one controlled for inter-clutch variation in egg size, but not if all male eggs were simply compared to all female eggs, regardless of their relative sizes within a particular clutch. In addition, males were larger at hatching than their female siblings (Mead et al. 1987). Since reproductive success of adult males is probably more variable than that of females, these results were interpreted as being an example of facultative manipulation of offspring sex according to parental investment abilities (Trivers and Willard 1973). At the time our paper was written the sample size was 102 male eggs and 86 female eggs. The data set now contains 283 males and 288 females but there is still no significant difference when the volumes are compared directly (female eggs: mean = 2.99 cm^3, SD = 0.26 cm^3; male eggs: mean = 3.02 cm^3, SD = 0.25 cm^3; t = 1.39, P = 0.166).

WEIGHT LOSS OF EGGS DURING INCUBATION

Bird eggs typically lose about 18% of their initial mass during incubation. Since the mass exchanged by O_2 and CO_2 through pores in the egg shell are equal during this time, all of this loss is due to the diffusion of water vapor from the egg's interior. The total amount of water transferred is a function of pore geometry and area, and of the water vapor gradient, the latter being about 35 torr (Rahn and Ar 1974). Since the diffusion coefficient for gases is inversely related to barometric pressure, water loss of eggs should increase when birds nest at high altitude. Carey et al. (1983) showed, however, that rates of daily water loss during incubation, and final water content of hatching embryos, were independent of altitude in both Red-winged Blackbirds and American Robins nesting at elevations ranging from sea level to above 3,000 m. They found that modifications in water vapor conductance in eggshells were responsible for this effect; it decreased as altitude increased. This relationship was also observed in Cliff Swallows (*Petrochelidon pyrrhonota*; Sotherland et al. 1980).

The daily rate of water loss of eggs can change markedly from time of laying onward, especially once incubation begins, because the eggs are then warmed regularly by the incubating parent. Changes in shell structure can also occur due to wearing away or fissuring of the egg's cuticle and/or to erosion of the inner shell as minerals are extracted for ossification of the embryonic skeleton. The erosion process can lead to an increase in the functional cross-sectional area of pores and an increase in shell permeability (Booth and Seymour 1987, Kern et al. 1992).

Between *nuttalli*, the coastal-dwelling subspecies, and *oriantha*, White-crowned Sparrows nest over substantial altitudinal gradients, but their eggshell properties have not been determined. Egg masses were obtained for nine 4-egg *oriantha* clutches, however, from laying until hatching. They indicate that mass loss occurred from first day to last throughout the incubation period in all eggs. Mean mass of these 36 eggs on the day of laying was 3.12 g and at pipping time it was 2.60 g, a 16.7% decrease.

Plots of individual eggs indicate that the rate of mass loss tended to increase slightly as incubation proceeded (Fig. 7.10, Table 7.10). Loss was slowest at the
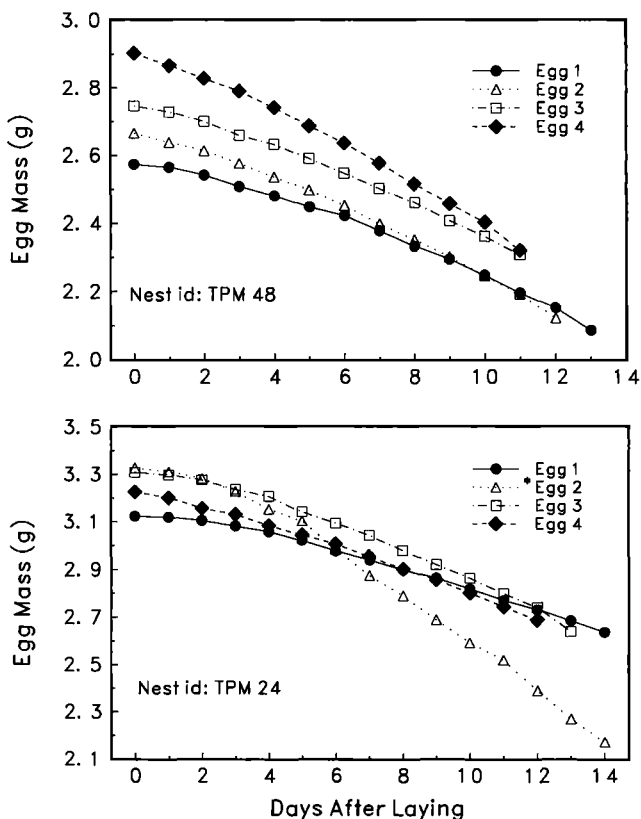
FIGURE 7.10. Changes in egg mass for two *oriantha* clutches from day of laying onward. Note that egg no. 2 in nest TPM 24 (lower panel) was infertile.

TABLE 7.10. PERCENT OF DAILY MASS LOSS IN *Oriantha* EGGS FROM DAY OF LAYING (DAY 0) ONWARD (VIABLE EGGS ONLY)

Age (days)	Mass loss from previous day (%)		
	Mean	SD	N
1	0.37	0.11	9
2	0.65	0.36	11
3	1.06	0.41	12
4	1.16	0.35	12
5	1.26	0.21	12
6	1.27	0.40	14
7	1.36	0.36	16
8	1.51	0.42	16
9	1.30	0.42	16
10	1.62	0.37	17
11	1.72	0.43	19
12	1.82	0.35	19
13	1.75	0.77	17
14	2.57	1.40	14

beginning, probably because females neglected their nests early in the laying period and first-laid eggs commonly became quite cold during the night (Zerba and Morton 1983b). The second egg in nest TPM 24 (bottom panel of Fig. 7.10) was infertile and it lost more mass than any of the other eggs. In contrast, a fertile egg in another nest (not shown) that suffered embryo death lost mass at a slower rate than other eggs in the clutch. The daily percentage of mass losses shown in Table 7.10 were obtained exclusively from eggs that hatched out live chicks.

CLUTCH SIZE

Clutch size is probably the most frequently assessed life history trait in studies of avian reproduction, and its variations have been correlated with a wide range of environmental and populational parameters as well as female condition. For example, it tends to decrease in passerines over the breeding season (Lack 1954, Klomp 1970, Middleton 1979, Bijlsma 1982, Ewald and Rohwer 1982, Daan et al. 1988, Perrins and McCleery 1989, Rowe et al. 1994, Brown and Brown 1999b), although this decline may be preceded by an early-season increase (Haukioja 1970, Smith and Andersen 1985, Askenmo and Unger 1986). It may also decrease when females are stressed energetically, as shown in handicapping experiments (Slagsvold and Lifjeld 1988, Winkler and Allen 1995). Clutch size has been observed to increase with population density (Slagsvold 1981), with age (Klomp 1970), with latitude (Morton 1976, Kulesza 1990), and with food availability (Hussell and Quinney 1987). Its variation also has a significant genetic component (Perrins and Jones 1975, von Brömssen and Jansson 1980, Gwinner et al. 1995).

The phenotypic plasticity of this trait has led some authors to conclude that it is optimized by individuals in response to environmental heterogeneity (Högstedt 1980, Tinbergen and Daan 1990). But clutch size can also covary with female survival rate (Nur 1988, Saether 1988, Lindén and Møller 1989), so a trade-off probably exists here between current and future reproduction (Charnov and Krebs 1974, Daan et al. 1990, Tinbergen and Daan 1990, Vander Werf 1992).

Interannual changes

Clutch size in 1,154 *oriantha* nests, observed during 23 years, ranged from two to six eggs, with the mode being four (878 or 76.1% of all nests) and the mean being 3.86 (Table 7.11). All two-egg clutches were laid after 15 July, near the end of the nesting season, whereas all 5- and 6-egg clutches were started before 15 July. Both of the 6-egg clutches that occurred in our study were deemed legitimate, and not the result of egg dumping, because eggs appeared in the nest at the rate of one per day, and because all the eggs in each clutch looked alike with regard to their background color and to the size and distribution of spots. Mean clutch size fluctuated among years by as much as 16.3% (1988 vs. 1992, Table 7.11), and this variation was significant (ANOVA $F_{22, 1153} = 3.36$, P < 0.001).

Seasonal changes

There was also a significant seasonal change in clutch size. This was expressed as a monotonic decrease that became noticeable about midway through the time period used for nesting (Table 7.12). The data in Table 7.11 represent a 23-yr

TABLE 7.11. CLUTCH SIZES IN *Oriantha* AT TIOGA PASS DURING 23 YR

Years	Clutch size					N	Mean	SD
	2	3	4	5	6			
1968	0	9	30	1	0	40	3.80	0.46
1969	0	5	41	1	0	47	3.92	0.35
1970	0	5	44	7	0	56	4.04	0.47
1973	0	3	23	0	0	26	3.88	0.33
1976	0	7	48	1	0	56	3.89	0.37
1978	0	16	36	0	0	52	3.69	0.47
1979	0	8	48	2	0	58	3.90	0.41
1980	1	14	50	4	0	69	3.83	0.54
1981	1	11	58	1	0	71	3.83	0.45
1982	0	14	58	9	0	81	3.94	0.54
1983	1	5	44	6	1	57	3.98	0.52
1984	0	13	40	5	0	58	3.86	0.54
1985	1	7	32	5	0	45	3.91	0.60
1986	0	3	46	3	0	52	4.00	0.34
1987	1	5	28	0	0	34	3.79	0.48
1988	0	0	16	2	1	19	4.21	0.53
1989	0	3	26	5	0	34	4.06	0.55
1990	0	6	37	3	0	46	3.93	0.44
1991	3	24	52	3	0	82	3.68	0.61
1992	4	23	52	1	0	80	3.64	0.62
1993	1	8	39	2	0	50	3.84	0.55
1994	1	5	23	1	0	30	3.80	0.55
1995	0	2	7	2	0	11	4.00	0.51
All	14	196	878	64	2	1,154	3.86	0.51

summary, but be reminded that in many years nesting did not begin until mid-June or later. This means that in early-nesting years many of the birds could be renesting during the same calendar period that those in late-nesting years were laying their first clutches. The question arises then, did clutch size vary seasonally in the same fashion in first nests as in renests? The answer is, yes. The seasonal pattern was, in fact, almost perfectly matched for the two types of nests, and means were not different in any of the five 10-day intervals wherein their schedules overlapped (Fig. 7.11).

Females gained considerable mass when preparing to lay and the brood patch was only partially defeathered when the season's first clutches were begun. Thereafter, until nesting was terminated, brood patches remained completely defeathered. From behavioral observations, body mass, and patch condition of known (banded) individuals, therefore, first nests could be distinguished from renests.

TABLE 7.12. SEASONAL CHANGES IN CLUTCH SIZE IN *Oriantha* ACCORDING TO FIRST-EGG DATE (= DATE OF CLUTCH INITIATION)

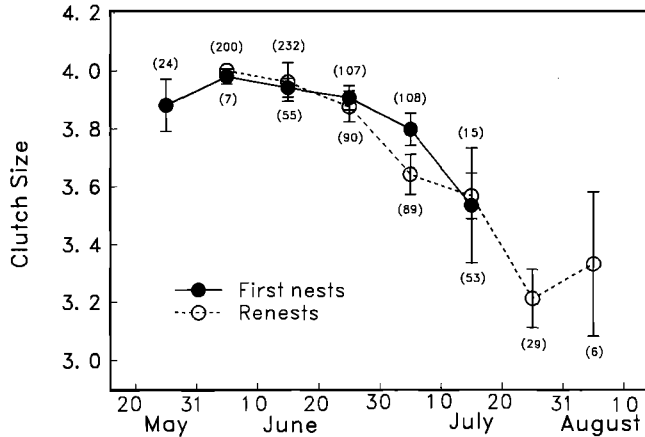| Date	Mean	SD	N
21–31 May	3.88	0.45	24
1–10 June	3.99	0.36	207
11–20 June	3.95	0.49	287
21–30 June	3.89	0.46	197
1–10 July	3.73	0.61	197
11–20 July	3.56	0.61	68
21–31 July	3.21	0.56	29
1–10 August	3.33	0.58	3

FIGURE 7.11.   Seasonal changes in clutch size in first nests and renests (replacement clutches and double broods) in *oriantha* at Tioga Pass. Symbols indicate means ± 1 SE. Sample sizes (in parentheses) are shown above the symbols for first nests and below the symbols for renests.

Note that interannual variation in ecological conditions could be quite large at the time when initial clutches and replacement clutches were laid. Many of the initial clutches in heavy snow years were started in July in small islands of vegetation that had only recently thawed out from under the covering snow. Willows were unleafed and low and herbaceous vegetation, such as grasses and forbs, were also undeveloped; full growth of the vegetation did not occur in these years until the nesting season was nearly completed. In contrast, in light or moderate snow years nesting began in late May or early June. By early July the vegetation was completely regrown and all new nests were replacements.

Although clutch sizes of first nests and renests were evenly matched in size at all calendar intervals where they co-occurred, first nests tended to occur in higher numbers earlier in the season. Therefore, given the seasonal trend shown in Table 7.12, it is no surprise that clutch size of first nests was greater than that of renests: 3.92 ± 0.48 (N = 770) vs. 3.74 ± 0.57 (N = 342), respectively (t = 5.40, P < 0.001).

Clutch size did not vary with the age of either parent (females: r^2 = 0.004, P = 0.073, N = 783; males: r^2 = 0.003, P = 0.189, N = 652), nor did it vary with age of paired birds. A contingency table of pair ages arranged from 1 to 4+ yr of age for both sexes gave the following: Chi-square = 21.88, df = 15, P = 0.111. Clutch size also did not vary with body size, as expressed in wing length (females: r^2 = 0.003, P = 0.344, N = 284; males: r^2 = 0.001, P = 0.704, N = 234).

Compared to some passerine groups, such as hole-nesting parids, clutch size did not vary appreciably in *oriantha*; 76.1% of all clutches had four eggs and together three- and four-egg clutches comprised 93.1% of the 1,154 clutches reported in Table 7.11. Still there was a significant seasonal decrease in clutch size of about 0.8 eggs. When this decrease was partitioned into first nests or replacement nests, the seasonal change was the same in both nest types; within-season reproductive history did not affect clutch size but calendar date did (Fig. 7.11). The tendency for clutch size to decline with season has been linked to a presumed

decrease in the quantity of food available to feed dependent young (Lack 1954, 1966), and with a decrease in offspring value (Rowe et al. 1994).

Laying dates are usually distributed on the upward slope of food supply, but fledging may occur before, during, or after the seasonal food peak (Daan et al. 1988). In *oriantha,* nesting often occurred under greatly different ecological conditions from year to year because of variation in the residual snowpack and in the frequency of early summer storms. As Lack (1947) pointed out long ago, confusion about the evolution of clutch size can occur because we fail to distinguish between the ultimate factors affecting survival value and the proximate factors affecting physiological control.

Because egg production is presumed to be energetically and nutritionally demanding for laying females, the development of theory about proximate control of clutch size has centered mostly on food availability in relation to energy requirements. But food supplementation studies of passerines in the wild have shown that while extra food tends to advance laying dates, clutch size usually remains unaffected (Ewald and Rohwer 1982, Davies and Lundberg 1985; Slagsvold and Lifjeld 1988, 1990). In other words, clutch size is largely independent of food supply (Daan et al. 1988, Rowe et al. 1994). The identical clutch sizes of *oriantha* in the same calendar period, despite greatly different environmental conditions wrought by snowpack variation, is consistent with this generalization. It has been hypothesized that a seasonal decrease in clutch size probably evolved because it is a strategic response to seasonally unfavorable conditions that might affect offspring survival (Rowe et al. 1994, Winkler and Allen 1996).

If not by food supply and its effects on female condition, how then might inhibition of ovarian function increase as the reproductive season progresses? It may be helpful, at this point, to take a more mechanistic or physiological view of clutch size regulation. Egg production is controlled through an axis of endocrine tissues contained in the hypothalamus, anterior pituitary, and ovary. Among many temperate zone passerines, this axis is widely understood to be stimulated by the vernal increase in photoperiod. Less appreciated, however, is that the endocrine pathway is inactivated toward summer's end by the inception of a photorefractory condition. Reproduction is terminated, while days are still long, through a shift to a new functional state. Gonadal involution is a key component of this altered physiological condition, and because the change in gonad size occurs rather quickly, onset of photorefractoriness was assumed to be abrupt. It is now evident, however, that refractoriness actually develops slowly, over weeks or months, possibly through a gradual depletion of hypothalamic gonadotropin releasing hormone (Nicholls et al. 1988).

The seasonal decrease in clutch size observed in *oriantha* began about when daylengths started to shorten (see Fig. 7.11 and Table 7.12). The stimulatory effects of daylength are directly related to their duration, but for present purposes this should not enter into consideration because the inception of refractoriness occurs spontaneously, as shown in captive *Zonotrichia,* males and females alike, held on long days (Harris and Turek 1982, Moore et al. 1983, Morton et al. 1985).

Meijer et al. (1992) have made a convincing argument, based on data from captive Eurasian Kestrels (*Falco tinnunculus*) breeding under controlled photoperiods, that seasonal decreases in clutch size are likely due to the development of photorefractoriness by a slow, spontaneous turning off of ovarian function, and

TABLE 7.13.   SUCCESS OF *Oriantha* NESTS IN RELATION TO CLUTCH SIZE

	Clutch Size			
	2	3	4	5
Number of nests	7	105	638	54
Nests fledging at least one chick (%)	28.6	42.9	50.6	46.3
Mean chicks produced per successful nest	1.50	2.67	3.31	4.08
Fledglings produced per nesting effort	0.43	1.15	1.67	1.89

that this inhibition of gonadal function might be related to prolactin secretion. Interestingly, prolactin both inhibits gonadal function and stimulates brooding behavior, and since several species, including Eurasian Kestrels, tend to incubate their first-laid eggs more attentively toward the end of the season, Meijer et al. (1992) suggest that the seasonal progression toward smaller clutch sizes could be a function of prolactin secretion rates. The data on *oriantha* are consistent with the hypothesis that a photoperiodically-controlled down-regulation of ovarian function is responsible for a seasonal decline in clutch size. In a thorough review of clutch size dynamics in nidicolous birds, including influences of abiotic factors, Murphy and Haukioja (1986) pointed out that because calendar date often seems to be the best predictor of seasonal changes in clutch size, photoperiod is probably the cue for these adjustments. Presumably such a response has evolved because ecological conditions at laying time do not predict trophic conditions weeks hence, when dependent young are present, as reliably as daylength.

Reproductive success in relation to clutch size

One oft-used measure of reproductive success is the frequency at which nests fledge at least one chick. In relation to clutch size, this varied from a low of 28.6% in 2-egg clutches to a high of 50.6% in 4-egg clutches (Table 7.13). Neither of the two 6-egg clutches produced fledglings and they have not been included in the table.

It is also instructive to compare the number of fledglings produced in relation to clutch size. As might be expected, these numbers increased steadily with clutch size, from 1.50 to 4.08 (Table 7.13). The product of two measures, the percentage of successful nests and the average number of chicks that fledge in those nests, yields the number of fledglings produced per nesting effort in cases wherein the clutch had been completed. This shows that 5-egg clutches were the most productive (Table 7.13).

The most productive clutch size is sometimes the modal one (Haukioja 1970, Dixon 1978, De Steven 1980, Boyce and Perrins 1987), but our results, like those of many other studies (Murphy 1978, Smith and Andersen 1982, Murphy and Haukioja 1986, Power et al. 1989, Møller 1991, Robinson and Rotenberry 1991), show that the modal clutch size (four) was smaller than the most productive one (five). Only 5.5% of all *oriantha* nests held five eggs, however, and their frequency per year ranged from none to as many as nine (see Table 7.11). Five-egg clutches could be either first nests or renests and although they could be preceded or succeeded by clutches of another size, usually one of four eggs, close inspection of nesting records revealed that within one season individual females sometimes laid two or even three 5-egg clutches in succession. These results suggest that

favorable conditions on individual territories can generate short-term environmental feedback that affects clutch size, a type of input that can have adaptive value (Högstedt 1980). In the long run, however, *oriantha* appear to produce smaller clutches than they can raise. Like many other species, they are following a risk-averse strategy (Brown and Brown 1999a).

Lack's (1954, 1966) suggestions that clutch size must be limited by the capacity of the parents to rear their young and that the modal clutch size within a population should be the most productive remain as useful concepts, but they need to be expanded to include new data and new hypotheses. For example, clutch size might be affecting mortality in adults and lifetime reproductive success (Charnov and Krebs 1974, Högstedt 1981) as well as postfledging survival of offspring and recruitment (Pettifor 1993). An inclusive view of reproduction energetics should also come to include consideration of the operative energy threshold for clutch production. As pointed out by King and Murphy (1985), the true threshold for energetically costly functions are seldom expressed under field conditions and often lie well below that which is presumed by investigators. For example, egg size in the earliest *oriantha* nests of the season did not vary unless snow conditions delayed laying until after 20 June (Fig. 7.8). Apparently an energy threshold was finally crossed at that time and females did not have enough reserves to produce eggs of the usual size.

Relevant too, to regulation of clutch size in colder climates, are the difficulties faced by incubating females in maintaining sufficient brood patch contact in large clutches so that embryo viability is unaffected. This could have been a problem for *oriantha* females with 5- and 6-egg clutches (Chapter 9). Also, a brood size of four is the most efficient one in terms of heat conservation (Sullivan and Weathers 1992).

INCUBATION

During incubation the female applies heat to the eggs from the naked skin of her incubation patch to stimulate and maintain embryo development. With her body she can also shield offspring from direct exposure to weather conditions such as sun, wind, rain, hail, and snow and, perhaps, from predation. At the same time she must maintain her own health and condition by leaving the nest periodically to eat and drink. By recording egg temperatures, it is possible to deduce the tending female's on-off pattern while accomplishing this balance and also to obtain a description of the thermal environment experienced by embryos. Both of these are rich sources of information on the physiology and behavior of nesting birds, especially when examined over the wide range of diurnal fluctuations in ambient conditions that are typical of high altitudes. Relatively large oscillations in egg temperature can occur in these environments and they can define the limits of embryo tolerance, both to the frequency of such excursions themselves and to their extremes.

Incubation period

The incubation period is defined as the interval between the laying of the last egg in a clutch and the hatching of that egg. This was measured in 256 *oriantha* nests where eggs were numbered on the day of laying and where the time when chicks hatched from the various eggs was known. Nearly all clutches (93.0%)

TABLE 7.14.   INCUBATION PERIODS AND THEIR FREQUENCIES IN 256 *Oriantha* NESTS AT TIOGA PASS

Incubation period (d)	Number of nests	Percent of nests
11	9	3.5
12	161	62.9
13	77	30.1
14	7	2.7
15	2	0.8

had an incubation period of either 12 or 13 d, 12 being the mode (Table 7.14). The mean was 12.34 d (SD = 0.63 d) and the range was four d (11 to 15).

The incubation period tended to decrease as the season wore on (Fig. 7.12), and a regression of its duration on the day of year that incubation began yielded a negative slope (r^2 = 0.04, P < 0.001). Some years ago we pointed out that the incubation period of all eggs in the clutch became shorter as the season progressed and that the last-laid egg was least affected (Mead and Morton 1985). This decrease was probably related to a seasonal increase in temperature; in warmer air eggs tended to cool less when females were off the nest, thereby enhancing embryo development and decreasing the incubation time.

Surprisingly, there was an effect of female age on incubation period (ANOVA $F_{4, 188}$ = 3.15, P = 0.015). It decreased after age two yr and was significantly shorter in the older females, age three yr or older, than in the young ones, age one or two yr (t = 3.30, P < 0.001; Table 7.15). This effect could not be related to season because nesting schedules did not vary with female age. Perhaps older females were somehow more attentive than younger ones. They might have spent more time incubating and less time on other activities, such as foraging, especially if they were more efficient foragers or occupied territories with better habitat. There are good indications that the latter does occur (Chapter 8). It seems remotely possible, too, that older females interfered with the nesting efforts of the younger ones.
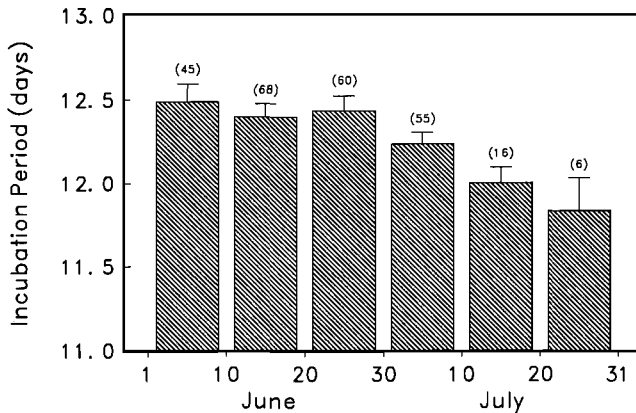

FIGURE 7.12.   Mean incubation period (+ SE) in *oriantha* according to date of incubation onset. Number of nests in parentheses.

Plate 1. The Tioga Pass area, as seen from Tioga Peak, looking south into Yosemite National Park. Tioga Lake is in the mid-foreground and directly above it, extending for 1 km, is Tioga Pass Meadow. The photos were taken in different years, but on the same day of year, July 4th, and they illustrate the large interannual variation in conditions encountered by *oriantha*.

Plate 2. Two views of Tioga Pass Meadow, the subalpine meadow that was an important part of the study area. The upper photo was taken in mid-June at a time when snow cover was about 10% and when *oriantha* nesting was in progress. The lower photo was taken in mid-September when nesting had ceased and when *oriantha* were fattening in preparation for migration.

Plate 3. Upper: An adult *oriantha* being fitted with a radio transmitter at Tioga Pass Meadow. Lower: Tom Hahn tracking a transmitter-bearing individual that had descended from the snow-covered meadows to more open ground near Mono Lake.

Plate 4. An *oriantha* nest built on the ground (upper) and another in a small lodgepole pine (lower). Eggs exposed directly to sun, such as those in the photos, were usually shielded by the incubating female.

Plate 5. An *oriantha* nest in a lodgepole pine. The female is brooding chicks (upper) and one of the adults is bringing food (lower).

Plate 6.   The major mammalian predator of *oriantha* nests at Tioga Pass, the Belding's ground squirrel (upper) and the major avian predator, the Clark's Nutcracker (lower).

Plate 7. Upper: An *oriantha* nest that was successfully defended by the tending female during a snowstorm. Lower: A nest that failed because it became buried in snow and inaccessible to the tending female (shown perched on a willow twig above the nest's location).

Plate 8. Upper: An adult *oriantha* with its wing spread to show an early stage of postnuptial molt, when the inner primaries are starting to be replaced. Lower: The author in 1978 (age 44).

TABLE 7.15. INCUBATION PERIOD IN *Oriantha*, ACCORDING TO FEMALE AGE

| | Incubation period (d) | | |
Age (yr)	Mean	SD	N
1	12.33	0.64	116
2	12.48	0.59	42
3	12.00	0.50	17
4+	12.00	0.57	18

Attentiveness patterns and egg temperatures

All parental care of eggs was performed by females and their activity or attentiveness patterns at the nest were obtained by direct observation and by changes in egg temperature measured from implanted thermocouples (Zerba and Morton 1983a,b). As can be seen from warming and cooling cycles in the eggs, females began to tend their eggs in daylight hours even from the first egg onward (Fig. 7.13). Most of their visits to the nest during the laying period were made at midday and they were observed standing over the eggs rather than sitting on them. Although there could be several functions for daytime attentiveness during laying, its primary purpose appeared to be protection from solar heating because the temperature of an egg left in an unshaded, untended nest soared quickly to lethal levels (Zerba and Morton 1983b). Untended nests can act as heat traps and, unless females intervene, eggs in unshaded nests would surely not survive the laying period, much less incubation. In fact, females clearly adjusted their daytime attentiveness throughout the incubation and nestling periods in response to solar heat loads, especially in poorly shaded nests. They were more attentive in nests fully exposed to the midday sun than in those that were shaded by a full or partial canopy of vegetation; females used their own bodies to shade the eggs and nestlings.

Daytime attentiveness varied in duration during the laying period, but tended to increase as eggs were added (Fig. 7.13). When clutch size was four, females
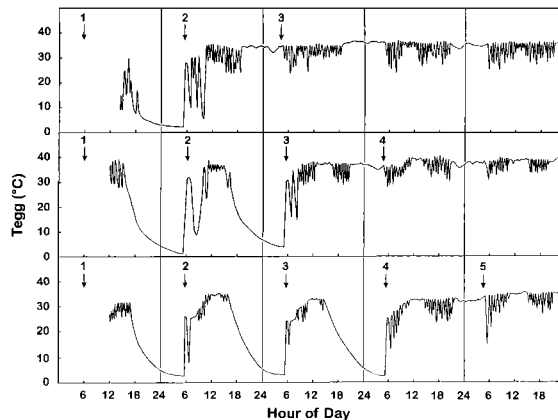

FIGURE 7.13. Five-day recordings of egg temperatures from three *oriantha* nests. Clutch sizes were three, four, and five eggs (top, middle, and bottom sequence of panels, respectively). Arrows with numbers show when each egg in the clutch was laid. A thermocouple was installed in the first egg of each clutch about 6 hr after it was laid.

were on the nest in daylight hours about 8% of the time the day the first egg was laid, about 16% the day of the second egg, 30% the day of the third egg, and about 75% of the time on the day of the last egg (Zerba and Morton 1983b). The transition to nighttime attentiveness was much more abrupt because females rarely visited the nest during the night prior to laying the penultimate egg. In the daytime, following that event, they became fully attentive and then transited to continuous occupation of the nest at night, with full application of the brood patch promoting high egg temperature on all nights thereafter. This pattern for the onset of full-time incubation was consistent no matter the clutch size (Fig. 7.13). Because of nocturnal neglect, some of the earliest-laid eggs dropped to near-freezing temperatures. This did not result in retarded growth or extension of the incubation period, as found in some species when prolonged periods of neglect occurred (Baerends 1959, Kashkin 1961, Hoyt et al. 1978, Boersma and Wheelwright 1979, Lill 1979, Prinzinger et al. 1979, Wheelwright and Boersma 1979, Vleck and Kenagy 1980, Vleck 1981b, Morton and Pereyra 1985). Still, there are indications that hypothermia caused mortality in *oriantha* embryos (Chapter 8).

Published around-the-clock records of attentiveness during the laying period in birds are scarce, but hole nesters commonly roost in their nest cavity at that time and so do some open-cup nesters, such as American Tree Sparrows (*Spizella arborea*; Weeden 1966). We have recorded egg temperatures from the first egg onward in several additional species of open-cup nesters at Tioga Pass, including Dusky Flycatchers, Hermit Thrushes, American Robins, and Song Sparrows. All roosted in their nests at night except Dusky Flycatchers; they neglected their eggs during laying, much like *oriantha* (Morton and Pereyra 1985). So some species appear to protect their eggs (and embryos) from excessive cooling at night during the laying period and some do not. Haftorn (1988) has suggested that low egg temperatures are associated with adaptive incubation rhythms. It would be interesting to know if parental behavior in these cases is related to abilities of incipient embryos to tolerate chilling. If so, it may mean that the nocturnal egg defenders at Tioga Pass, such as Hermit Thrushes, have cold-intolerant embryos because they are more recent and, therefore, less well adapted occupants of high altitude areas than the egg neglectors, such as Dusky Flycatchers and *oriantha*. Another possibility is that nocturnal egg temperatures reflect interspecific variation in antipredator behavior by laying females. It may be, for example, that small mammals could be deterred from eating eggs by the presence of the female in the nest.

During the laying period females undergo major adjustments in endocrine function as ovulatory cycling is first stimulated, then inhibited completely, once final clutch size is attained. Behavioral changes parallel those in physiology because females must make the transition from regular maintenance behaviors to those of full-time incubation. This transition occurs gradually in passerines (Kendeigh 1952, Davis 1955, El-Wailly 1966, Jehl and Hussell 1966, Weeden 1966; Haftorn 1978a, b, 1981; Morton and Pereyra 1985), and it, along with the subsequent maintenance of regular incubation behavior, has often been associated with elevated prolactin levels (Dawson and Goldsmith 1982, Goldsmith 1982, Hall and Goldsmith 1983, Silverin and Goldsmith 1984).

During incubation, *oriantha* embryos experienced brief excursions to low temperature (17 to 30 C) when females left the nest to forage (Zerba and Morton 1983a). It is doubtful that this retarded embryo growth or extension of the in-
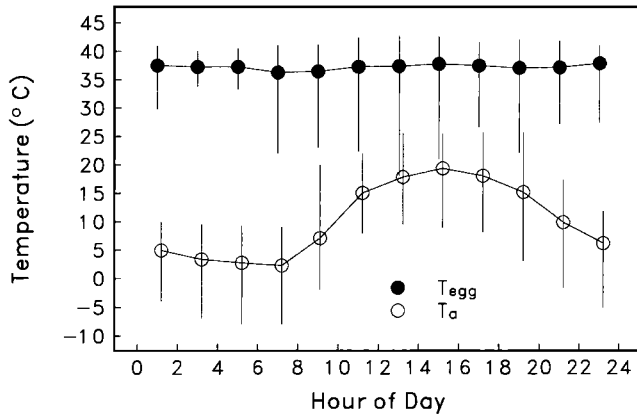
FIGURE 7.14. Mean egg temperatures recorded from eight *oriantha* nests at 3-min intervals, along with mean air temperatures measured near the nests, also recorded at 3-min intervals, between 13 June and 11 August 1980 at Tioga Pass. Vertical lines show ranges of temperatures that occurred above and below the means. Adapted from Zerba and Morton (1983a).

cubation period because their incubation period, about 12 days, was the same as that of conspecifics breeding at low altitude (Blanchard 1941, Morton 1976), where embryos are probably not exposed to such low temperatures.

Once laying had ceased and full-time incubation was underway, *oriantha* females managed to maintain mean egg temperatures, both day and night, between 36 and 38 C. This was accomplished even though there were frequent trips off the nest in daytime in order to forage, and in the face of air temperatures that were sometimes below freezing at night and in the early morning hours (Fig. 7.14). Egg temperature was between 36 and 40 C for more than 65% of the time during the female's active day and for more than 84% of the time during her period of night rest (Table 7.16). Mean egg temperature was 37.3 C (SD = 2.3 C) when taken at 3-min intervals in eight nests throughout the incubation period. This is quite similar to the average temperature of incubation reported for other

TABLE 7.16. OCCURRENCE OF EGG TEMPERATURES AS PERCENT OF TIME DURING ACTIVE DAY AND NIGHT REST PERIODS OF INCUBATING FEMALE *Oriantha* (ZERBA AND MORTON 1983A)

Temperature interval (C)	Percent occurrence	
	Active day	Night rest
16–18	0.01	0.00
18–20	0.02	0.00
20–22	0.03	0.00
22–24	0.10	0.00
24–26	0.19	0.00
26–28	0.26	0.01
28–30	0.72	0.04
30–32	2.27	0.04
32–34	6.59	1.06
34–36	16.13	8.63
36–38	32.50	46.11
38–40	33.11	38.83
40–42	7.90	5.28
42–44	0.09	0.00

passerines (Huggins 1941, Irving and Krog 1956, Kendeigh 1963, El-Wailly 1966; Drent 1972, 1975; Haftorn 1978a,b, 1979; Morton and Pereyra 1985, Weathers and Sullivan 1989).

Mean egg temperature was significantly higher in ground nests than in elevated nests (37.5 C vs. 36.8 C, P < 0.001). The absolute difference here was not great and hatchability was unaffected; in 140 ground nests (540 eggs) that were not manipulated by investigative techniques other than direct observations, hatchability was 92% and in 109 elevated nests (421 eggs) it was 91% (Zerba and Morton 1983a).

Mean egg temperature increased by 2–3 C during the first four days after clutch completion, then remained virtually steady thereafter (Zerba and Morton 1983a). This initial rise early in incubation has been noted in a variety of species and may be due to an increase in heat-transfer abilities of the developing brood patch (Bailey 1952, Farner 1958b, Jones 1971, Drent 1975, Afton 1979, Barrett 1980). Along these lines, Bailey (1952) showed that vascularization of the brood patch in White-crowned Sparrows began approximately two days before the first egg of the season was laid and reached completion on the third or fourth day of incubation. By that time the dermal tissue had become thickened and edematous, a condition that persisted throughout the remainder of incubation and during brooding of the young.

Mean brood patch temperature, obtained by application of a thermocouple to hand-held females, was 41.84 ± 0.81 C (N = 37). Mean core (cloacal) temperature of these same females was 42.48 ± 0.77 C, so patches were less than one degree cooler, on average, than core body temperature.

Despite evidence for energy costs associated with incubation alluded to earlier in this chapter, particularly at night and in elevated nests, females were able to maintain modest fat stores throughout incubation (Fig. 6.3B), a condition of positive energy balance that is likely facilitated by their spending so much time in the favorable microclimate of the nest (Walsberg and King 1978). In Zebra Finches (*Poephila guttata*), ameliorating effects of the nest microclimate approximately compensates for the energy cost of incubation (Vleck 1981a), and in European Starlings, heat from normal metabolism is sufficient to maintain egg homeostasis even in sub-freezing conditions (Biebach 1979).

The rhythm of incubation in *oriantha* was characterized by constant attentiveness or sitting at night followed by a regular pattern of alternating periods on and off the nest during the daylight hours. Periods on (incubation bouts) during the active day averaged 19.6 min (SD = 2.7 min). Periods off (foraging bouts) averaged 7.8 min (SD = 0.5 min). The proportion of time spent on the nest by females during the active day, the mean daytime attentiveness, was 74.5% (SD = 1.3%). Females did not depart on foraging trips until their eggs had reached a consistent temperature, or set-point value, of about 38 C (Zerba and Morton 1983b). This observation is in agreement with White and Kinney's (1974) suggestion that attentiveness ceases when eggs reach a "release" temperature. Likewise, Calder (1971) found that Calliope Hummingbird (*Stellula calliope*) females did not depart to forage until nest temperatures were restored to within a consistent range (34–37 C).

White and Kinney (1974) made the generalization that passerines tend to decrease their attentiveness as air temperature comes near to the optimum incubation
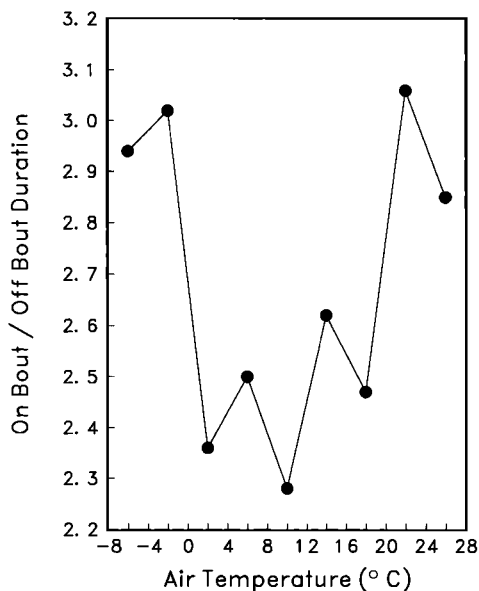
FIGURE 7.15.   Ratio of incubating (on) to foraging (off) bouts in incubating female *oriantha,* in relation to air temperature. Adapted from Zerba and Morton (1983b).

temperature. Essentially, egg and ambient temperatures approach an equilibrium condition and little input is required of the tending bird. This model does not incorporate actual operative temperature, however, so it does not extend smoothly to high elevation conditions. For example, total daytime attentiveness by *oriantha* females tended to *increase* slightly as ambient temperature began to exceed 20 C (Zerba and Morton 1983b). This pattern of increased attentiveness with increasing temperature was even more pronounced in Dusky Flycatchers nesting at Tioga Pass (Morton and Pereyra 1985). Neither incubation nor foraging bout durations were constant throughout, however, so it is instructive to evaluate daytime attentiveness during incubation by the ratio of on to off bout durations.

This ratio had a U-shaped pattern during the active day, being highest when ambient temperatures were either at their lowest or at their highest (Fig. 7.15). That females would sit longer at low temperatures, relative to the time taken off for foraging, is understandable in that eggs cool more quickly when the air is cold and it takes longer to rewarm them. The high ratio of on to off bouts when ambient values were at maximum is not to be expected from the White and Kinney model, however. This behavior does not make sense unless one returns to the theme recounted earlier, that open-nesting birds in high altitude environments must cope with potentially lethal overheating of eggs from solar radiation. Females protect their offspring from these conditions by spending relatively longer periods on the nest during the hotter portions of the day.

In contrast, at low altitude, particularly at the higher latitudes, exposure to solar heating appears to generate a more moderate microenvironment in nests. Lapland Longspurs in the Northwest Territories, for example, may actually benefit from solar warming of the nest because it allows incubating females to extend the duration of their foraging bouts (Lyon and Montgomerie 1987).