

CHAPTER 8: Nestlings and Fledglings

HATCHING

If all has gone well during incubation, the day arrives when chicks begin to cut through the eggshell. Eventually they hatch and, in the case of *oriantha*, begin a nine-day period as nestlings that is terminated when they fledge. The proportion that succeed in hatching out provides a measure of egg viability or hatchability. Because eggs are laid at 24-hour intervals, each one in the succession is a day younger than its predecessor. If the eggs remain cold and below the threshold for development until the end of clutch completion, conceivably they might hatch in unison with perhaps only a few minutes or hours separating them. This does not happen because females sit in the nest during the laying period for varying amounts of time, and this causes asymmetries in development and hatching schedules (Chapter 7). This female-promoted hatching spread can cause substantial differences in nestling age (a day or more) and competitive abilities—a condition that appears to facilitate mortality, especially in the last-hatched, when food shortages occur. Reduction of the brood in this way is a widespread phenomenon that has spawned a plethora of hypotheses to explain its reason for being. Seasonal changes in the relative contributions of male and female parents to rearing the young make this aspect of passerine biology even more difficult to understand.

Hatching mechanics

Pipping of eggs by incipient hatchlings usually began on the day before hatching, but sometimes on the same day if started in the early morning. Eventually, the shell was cut completely around about mid-way of the egg and the chick emerged. At six nests we watched from nearby blinds while chicks were hatching out. During that time the females turned the eggs with their feet or beaks and made shaking and settling movements with their bodies. One female assisted the hatching process by removing a half-shell that was still adhering to the chick. Shell fragments, large and small, were always consumed by females at the nest. Chicks that died during hatching, or at any other time, were carried from the nest and discarded some distance away.

Hatching times

The temporal distribution of hatching times in alpine and subalpine populations of *oriantha* has been described as being primarily an early-morning phenomenon (Morton et al. 1972b, King and Hubbard 1981). But those data were gathered more-or-less during regular daytime working hours. During two breeding seasons, Mead (1983) checked *oriantha* nests at Tioga Pass around-the-clock. He found that hatching peaked at dawn and that 110 of 198 hatching times (55.6%) occurred between 04:00 and 12:00. Another 68 hatchings (34.3%) occurred between noon and 20:00, and the final 20 (10.1%) during the following eight hr of darkness. Skutch (1976) pointed out that hatching may occur at any hour of the day or night, but that it tends to be a rhythmic process wherein most of the hatching effort by chicks occurs toward the end of the night and in the early morning, coincident with maximum warmth derived from brooding. Mead's data are in agreement with this generalization.

TABLE 8.1. HATCHABILITY OF *Oriantha* EGGS IN RELATION TO LAYING DATE

Interval	Hatchability (%)	N ^a
20–31 May	62.7	67
1–10 June	70.0	470
11–20 June	67.7	668
21–30 June	76.9	532
1–10 July	75.4	532
11–20 July	74.0	231
21–31 July	83.3	66
1–10 August	100.0	3

^aTotal number of eggs in each time interval.

Hatchability

Hatchability, the percentage of eggs surviving to the time of hatching that produce a chick, increases with latitude, but not with altitude (Koenig 1982). It is generally greater than 90% in passerines, although it has been found to be as low as 70 to 80% in some species (Ricklefs 1969, Koenig 1982).

In *oriantha*, hatchability for the whole study was 72.6% (1,962 of 2,701 eggs). This is low, and was unexpected since an earlier sample of unmanipulated eggs had shown viability to be 91.6% (Zerba and Morton 1983a). It seems probable that the examination, marking, and measuring of eggs caused damage and subsequent mortality in some of them. Our field notes are inadequate for quantifying the amount that each egg was handled, but those that were measured with calipers can be compared to those that were not. Of 1,390 measured eggs, 970 (69.8%) hatched, whereas 992 of 1,311 unmeasured eggs (75.7%) hatched. This difference was significant (Chi-square = 11.75, df = 1, $P < 0.001$), so handling of this type reduced hatchability by at least 5.9%, and it follows that other procedures such as numbering eggs and checking them for hatching pips could also have contributed to mortality. Beyond these manipulations, however, could environmental factors have also impacted hatchability?

Several lines of evidence can be explored. For example, there was a nest in 1985 and another in 1988 wherein sub-freezing weather conditions prevailed while the females were laying. In both nests the first two eggs froze and cracked slightly whereas the second two eggs survived and later hatched, probably because they were protected by the onset of nocturnal attentiveness by the females. Usually females abandoned the nest when part or all of the clutch was frozen, or at least they removed eggs that were cracked or broken, but in these two nests this did not happen.

A seasonal variation in hatchability provided additional evidence for a temperature effect. Eggs laid early in the season (before 21 June), when sub-freezing temperatures were most prevalent, were less likely to hatch than those laid later on (Chi-square = 21.85, df = 6, $P < 0.001$; Table 8.1). Eggs were particularly vulnerable during the laying period because they were not tended during the first few nights. Harmeson (1974) also observed a seasonal increase in hatchability in Dickcissels (*Spiza americana*), from 72% to 88%, but attributed it to an increase in food availability (which allowed females to spend less time foraging and more time tending their eggs). Hendricks and Norment (1994) found that hatchability decreased in American Pipits (*Anthus rubescens*) nesting in the alpine when laying

TABLE 8.2. HATCHABILITY OF *Oriantha* EGGS IN RELATION TO CLUTCH SIZE

Clutch size	Hatchability (%)	N ^a
2	78.6	14
3	77.3	132
4	73.0	529
5	58.1	31
6	00.0	1

^a Number of nests.

was delayed because of a late spring. They hypothesized that the lower egg viability could have been due to poor nutrition in females or to increased exposure of eggs to cold; they could not distinguish.

Nesting experience did not affect hatchability because it was the same in one-year-old females as in older females (Chi-square = 2.68, $df = 1$, $P = 0.102$). On the other hand, there was an effect related to clutch size, primarily because hatchability decreased substantially in 5-egg clutches (Chi-square = 21.50, $df = 3$, $P < 0.001$; Table 8.2). It may be that females could not adequately protect and incubate clutches of that size or larger from freezing temperatures because the area occupied by the eggs exceeded the boundaries of the incubation patch. Thus, high altitude conditions could be selecting against 5-egg clutches even though, compared to other clutch sizes, they tended to fledge the most chicks (Chapter 7). Snow (1958) obtained results in Eurasian Blackbirds that were the opposite of these. Hatchability was lower in one-year-olds than in older females (92.2% of hatching failure being due to infertility), and hatchability was unaffected by clutch size. Of course, a low-temperature effect on embryo survival was unlikely in Snow's study, the climate undoubtedly being milder in the Botanic Garden at Oxford than at Tioga Pass!

Eggs fail to hatch because they are infertile or the embryo dies. In order to see if the number of hatching failures due to embryo death was unusually high, and possibly induced by environmental conditions such as chilling, it is useful to compare the *oriantha* data to those gathered by Rothstein (1973) on Cedar Waxwings (*Bombycilla cedrorum*). He found that 58 of 73 unhatched eggs (79.5%) were infertile and that 15 were fertile but contained dead embryos (20.5%). In a sample of 78 unhatched, unmanipulated *oriantha* eggs 42 were infertile (53.8%) and 36 had dead embryos (46.2%). These ratios are different from Rothstein's (Chi-square = 11.05, $df = 1$, $P < 0.001$), suggesting that embryo deaths were disproportionately high in *oriantha*, a result that is consistent with the hypothesis that egg survival at Tioga Pass was reduced by low temperatures. Finally, although hatchability did vary substantially among years (for example, 64.9% in 1984 and 87.1% in 1970), this variation was not significant (Chi-square = 25.22, $df = 21$, $P = 0.241$).

Hatching sequence

In general, *oriantha* eggs hatched in the order laid (Chi-square = 69.05, $df = 3$, $P < 0.001$; Table 8.3), but there were some interesting exceptions. For example, there were three 4-egg clutches wherein the last-laid egg was the first to hatch. In two of these cases storms with sub-freezing temperatures occurred during lay-

TABLE 8.3. HATCHING ORDER IN 45 4-EGG *Oriantha* CLUTCHES WHEREIN BOTH LAYING ORDER AND HATCHING ORDER WERE KNOWN FOR EVERY EGG IN THE CLUTCH

Hatching order	Laying order			
	1	2	3	4
1	35	6	2	3
2	6	31	8	0
3	3	6	32	3
4	1	2	3	39

ing, but ended about the time the last egg was laid. It appears that cold-shock caused development to be delayed in untended eggs and that this phenomenon explains much of the out-of-sequence hatching events shown in Table 8.3.

When hatching times of all eggs in the clutch were plotted in relation to hatching time of the first-laid egg, considerable asynchrony was apparent (Fig. 8.1). No matter the clutch size, the last-laid egg tended to hatch considerably later than the first one. This pattern was undoubtedly due to the schedule early in incubation (see Fig. 7.13), specifically the tendency of females to begin full-time incubation when the penultimate egg was laid.

Hatching asynchrony increased between early June and mid-July. Presumably, this was a warm-weather effect. Eggs did not cool down as much when females were inattentive during the laying period and some additional development of embryos occurred (Mead and Morton 1985).

BROOD REDUCTION

Because of hatching asynchrony, siblings were often of different ages and at very different places on their growth curves. This caused hierarchies in both body size and competitiveness to be established in the nest. Such hierarchies occur in many avian species and Lack (1954) suggested that they are adaptive because when food shortages occur the smallest and least competitive nestlings would be fed the least, and if mortality occurred they would die first. This orderly reduction

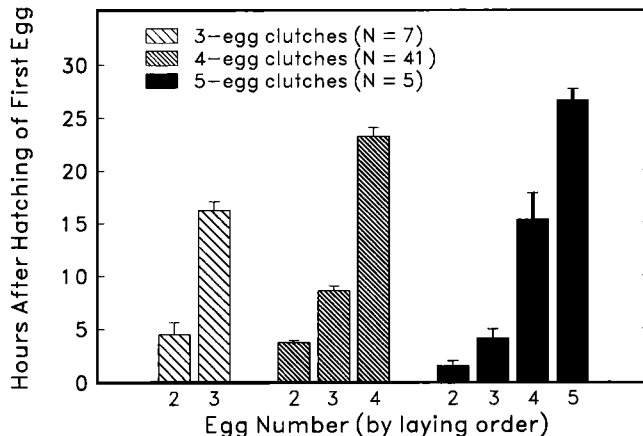


FIGURE 8.1. Hatching times of *oriantha* eggs with laying order, in relation to hatching of the first-laid egg. Lines show 1 SE. Adapted from Mead and Morton (1985).

TABLE 8.4. AGES OF *Oriantha* NESTLINGS WHEN THEY DISAPPEARED FROM BROODS

Nestling Age (d)	Percent of All Brood Reductions	N
0	5.2	4
1	13.0	10
2	18.2	14
3	20.8	16
4	22.1	17
5	7.8	6
6	9.1	7
7	2.6	2
8	1.3	1
9	0.0	0

of the brood might allow some of the older, larger nestlings to be spared long enough to survive periods of food deprivation, such as might occur during a storm. In other words, hatching asynchrony has been selected for because, under certain conditions, it can enhance reproductive success.

A partial loss of nestlings occurred in 14% of otherwise successful *oriantha* nests. Since the smallest chicks received the fewest feeding offers, even during moderate weather, it was assumed that these losses were due to starvation. And, true to Lackian expectations, two-thirds of the mortality could be traced to the smallest nestling. Aside from these instances of naturally-occurring brood reduction, it was also induced experimentally by trapping and holding the male parent. Without his contribution toward feeding of nestlings the whole brood sometimes died, but, again, the smallest and youngest died first (Mead and Morton 1985). In subsequent experiments it was discovered that brood reduction occurred when both parents were trapped and held for only two hours, even in good weather. Once rewarmed by the female, these briefly-deprived nestlings appeared to be ravenous and the oldest and largest aggressively competed for feedings. The smallest nestling(s) obtained little or no food and died within a few hours. These experiments mimicked events that sometimes unfolded after one of the brief-but-violent summer storms that occurred on the study area, and they suggest that brood reduction can be avoided if the parents bring food as soon as the storm is over, but they must provide it to *every* nestling (nestlings can survive for several days at reduced growth rates if given only relatively small amounts of food). These observations, and others, have often caused us to question the general applicability of hypotheses which suggest that brood reduction is adaptive.

There were 77 cases of naturally occurring brood reduction so it was possible to examine when it occurred with regard to both nestling age and time of season. First, it increased with nestling age through Day 4 then decreased sharply (Table 8.4). This result shifts attention to nestling growth and thermoregulatory abilities. Clearly, the period of exponential growth in nestlings (Fig. 8.5) and that of maximum brood reduction tended to occur together. At that time (Day 4 of age and earlier) disparities in body size, and probably competitive abilities, were largest and energy was being heavily partitioned into biomass rather than into thermoregulation. Once nestlings became more equal in body size and began to develop thermogenic capacities (about Day 5), to shiver and defend their own body temperature without dependence upon maternal brooding, their vulnerability to epi-

TABLE 8.5. SEASONAL CHANGES IN PROPENSITY FOR BROOD REDUCTION TO OCCUR IN *Oriantha*

Interval	Number of nests with nestlings	Percent of nests showing brood reduction
10–20 June	153	5.2
21–30 June	193	6.7
1–10 July	153	12.4
11–20 July	158	5.1
21–31 July	67	31.3
1 August +	26	30.8

sodes of bad weather decreased. Very little brood reduction occurred from Day 7 on, when they were fully functional endotherms (Table 8.4). Second, brood reduction had a strong seasonal component. It was about 5–12% in nests with young through mid-July, but rose sharply in the following weeks to around 30% (Table 8.5).

Brood reduction at Tioga Pass was often associated with foul weather. During storms, nestlings were sometimes directly exposed to rain, hail, snow, and thermolytic winds while the tending female was away gathering food. Once the young and the nest became cold and wet, mortality sometimes ensued. But why the seasonality? More rainstorms occurred in July and August than in other summer months, but there were also fewer snowstorms (Table 9.1). The most important factor here may have been a decrease in provisioning by males. In many late-season breeding attempts nestlings were fed only by females.

The consequences of this shift in parental behavior can be seen in data on body mass obtained from six broods that hatched relatively late in the season, in the last week of July (Fig. 8.2). Growth curves shown in nests A and B were for broods of four and three, respectively, and they were representative of normal weight-change trajectories. Also shown is an example of brood reduction, even though both parents were bringing food (nest C). In that nest the youngest nestling was not competitive, it grew slowly and died at four days of age. It should be noted that runt nestlings gave every indication of being hungry because they begged incessantly. In three other nests (D, E, and F) the female was the sole provider. In nest D all three chicks fledged, although at reduced weight, whereas in E and F the youngest and smallest nestling died. In nest F the nestling died at seven days of age. Excluding predation, this was the latest that nestling death was observed except for the unusual situation, mentioned earlier, when lone nestlings were neglected because females were engaged in excessive brooding of inviable eggs (for specific examples see below).

HATCHING ASYNCHRONY

There have now been at least 17 hypotheses advanced in explanation of hatching asynchrony (Clark and Wilson 1981, Slagsvold and Lifjeld 1989, Magrath 1990, Amundsen and Slagsvold 1991, Ricklefs 1993, Murray 1994, Stoleson and Beissinger 1995). Most of these, including the brood-reduction hypothesis, have proposed that the hierarchy in nestling size generated by asynchrony is adaptive. But numerous field studies, many of which involved manipulations of brood and nestling size differences, have not provided convincing evidence that this hierarchy either increases offspring survival after hatching or reduces parental in-

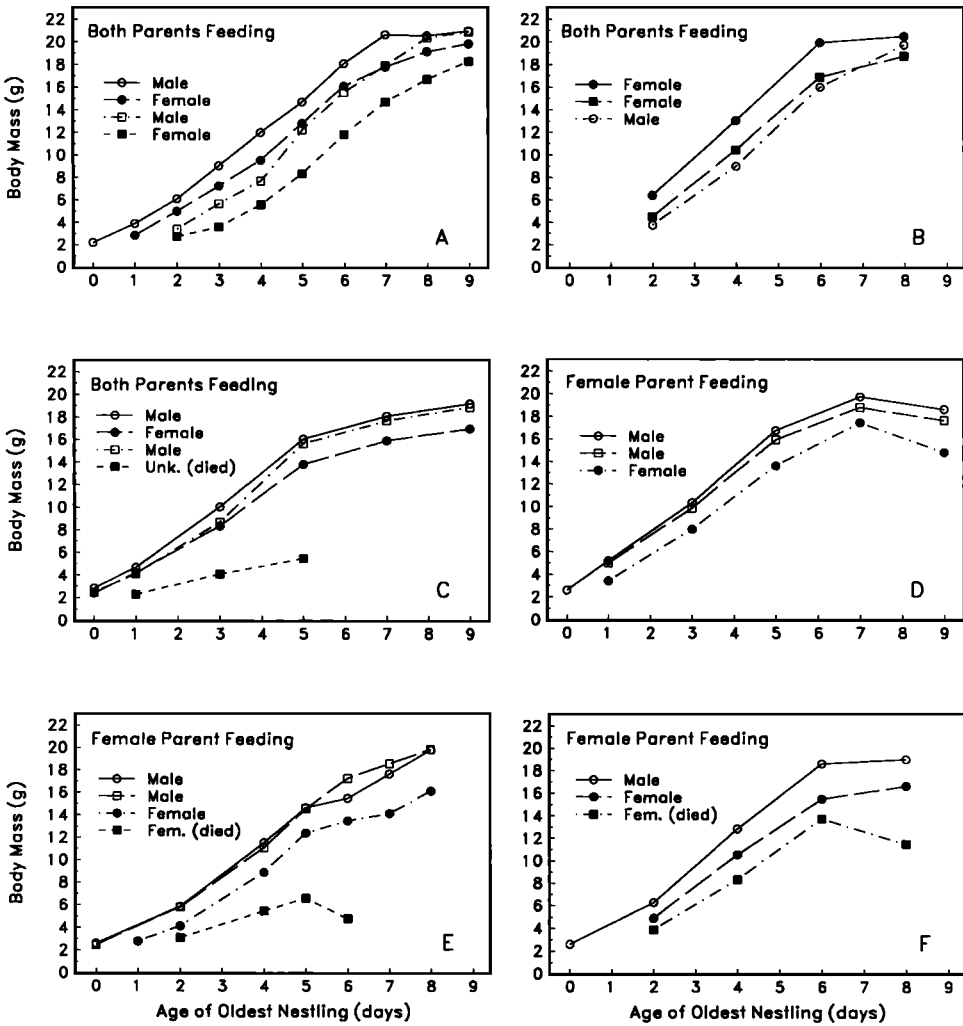


FIGURE 8.2. Body mass changes of *oriantha* nestlings in six different nests during late July. In nests A, B, and C both parents were known to be bringing food. In nests D, E, and F only the female was observed feeding the nestlings. The sex of each nestling is given in the legend.

vestment (Stoleson and Beissinger 1995). As Stoleson and Beissinger point out, studies that address hatching patterns have uniformly ignored the physiological, environmental, and social constraints that affect the onset of incubation and, other than the resultant effects on nestling size differentials, the possible adaptive significance of beginning incubation prior to clutch completion.

There are a few hypotheses which propose that early incubation is itself adaptive: it could maintain viability of first-laid eggs (Arnold et al. 1987), protect eggs from predators (Dunlop 1910), protect the clutch from brood parasites (Wiley and Wiley 1980), or protect the eggs during the day from potentially lethal solar heating and at night from freezing (Zerba and Morton 1983b). There are also two hypotheses which propose that hatching asynchrony is simply an epiphenomenon. One states that hatching patterns may reflect energy constraints experienced by

laying females (Stoleson and Beissinger 1995); the female's attentiveness pattern might vary indirectly with food availability, for example. The other, the hormonal hypothesis, suggests that hatching asynchrony is the by-product of a physiological mechanism that evolved originally for the dual purpose of stimulating incubation and terminating laying (Mead and Morton 1985). Next, I will elaborate on this hypothesis and provide a graphical model for consideration.

The hormonal hypothesis

To begin with, follicles do not mature synchronously in the avian ovary—there is a hierarchy in their size. At regular intervals, usually one day in laying passerines, the currently largest follicle is ovulated. This event is preceded six to eight hr by a surge in luteotropic hormone. The ovum or egg then spends about 24 hr in the oviduct before being laid. There is a close relationship between ovulation and oviposition (laying) in that ovulation of the next ovum in the hierarchy occurs 15 to 75 min after oviposition (Follett 1984, Birkhead 1996). Oviposition of the final egg in the clutch is not succeeded by an ovulation, of course. This means that at some point in the preceding 24 hr the sequence of ovulations was halted, presumably soon after the final ovum entered the oviduct. Although interest abounds in the regulation of clutch size, this key determining step in the mechanism responsible for termination of ovulation has not been thoroughly investigated, probably because most of the information about ovarian physiology has been derived from domestic fowl (Sharp 1980), and these particular birds have been artificially selected for continuous laying.

Stimulation of gonadal activity is controlled via the hypothalamus-anterior pituitary-gonadal axis, and we assume that the same regulatory pathway is also involved in gonadal inhibition, either through a decrease in gonadotropin secretion and/or the activation of some other inhibitory mechanism such as down-regulation of receptors. In any event, it appears in *oriantha*, and probably many other birds as well, that ovarian inhibition must be occurring at nearly the same moment as onset of full-time incubation behavior. This temporal coincidence, noticed first by Paul Mead, led to a conservative model (Mead and Morton 1985), which suggests that the early onset of incubation evolved because it was the result of an adaptive outcome, one wherein one mechanism, executed perhaps through the action of a single hormone, was selected both to turn off a physiological phase of reproduction (ovulation) and to turn on a behavioral phase (incubation). Hatching asynchrony resulted from this adaptation, but it was an unselected by-product. This idea can be visualized in a simple diagram (Fig. 8.3) in which the thresholds for these two functions are displayed amidst a changing hormonal milieu. The threshold for ovarian inhibition should be crossed shortly after the final ovum is ovulated, in other words, at about the time the penultimate egg is laid. As illustrated in Fig. 8.3, this would be the third egg in a 4-egg clutch. The inhibition threshold is characterized as being fixed because it should not vary appreciably among species of determinate layers. They must all shut down the ovulatory sequence at the proper time in order to exert control over clutch size. The threshold for incubation onset, however, is depicted as being adjustable (arrows). In *oriantha* it must be very close to where it has been drawn in Fig. 8.3 because both thresholds are crossed at about the same time.

An upward adjustment of the threshold for incubation onset would serve to

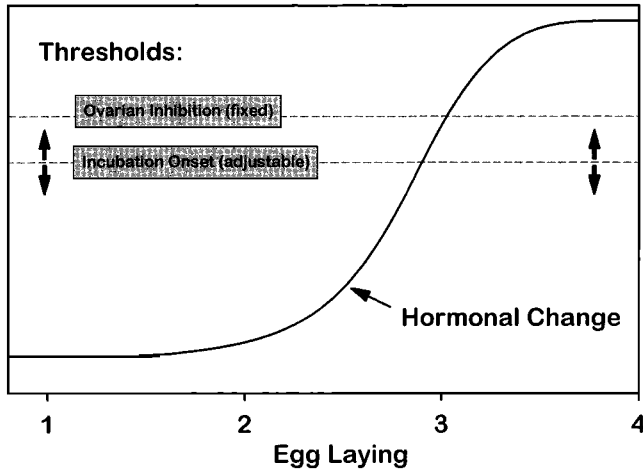


FIGURE 8.3. The hormonal hypothesis: model proposing the control of ovarian inhibition and onset of full-time incubation behavior by hormonal changes in relation to the time of egg laying in a 4-egg clutch.

decrease hatching asynchrony because incubation would begin closer to the time of clutch completion, and setting it lower would increase hatching asynchrony because incubation would begin closer to the time of clutch initiation. A change in the slope of hormone titer (secretion rate) might also be an effective regulation tactic. Realize here that ovarian inhibition sufficient to halt the ovulatory sequence is an all-or-nothing response whereas onset of incubation behavior often is not. There is abundant evidence that attentiveness in laying females can develop gradually and at different times during the egg-laying period (Lehrman 1961; Haftorn 1978a,b, 1979, 1981; Richter 1984, Morton and Pereyra 1985, Hebert and Sealy 1992, Hillstrom and Olsson 1994). We contend that the hormonal hypothesis describes the primitive condition, and the reason why hatching asynchrony evolved in the first place. Furthermore, the hatching-pattern dynamic that stems from it should prove to be the most commonly observed one, otherwise hatching asynchrony would likely increase with environmental instability and unpredictability, as with latitude or altitude (which it does not). This is not to deny that natural selection could still be acting on the hatching spread in some species. For example, and in concordance with hypotheses suggesting that brood reduction is adaptive, asynchrony might increase in localized regions where episodes of bad weather occur randomly during the nesting season. This could be the explanation for the highly asynchronous patterns observed in Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*) nesting in Iowa (Richter 1984). Our model allows for such perturbations and even suggests, in a mechanistic sense, which element of the system could be most easily modified to obtain individual patterns (in this case, by lowering the threshold for onset of incubation behavior).

What might be the hormone or hormones involved in this regulatory pattern? As pointed out earlier (Mead and Morton 1985), prolactin is a strong candidate because it is well known to have antigonadal effects. It has also been implicated in both the induction and maintenance of parental care (Ball 1991, Wingfield and Farner 1993), and its levels increase at the onset of incubation, much as we have

shown for a hypothetical hormone in our model. For examples, see studies by Goldsmith (1982) on the Common Canary (*Serinus canaria*) and Sockman et al. (2000) on the American Kestrel (*Falco sparverius*).

Progesterone is another hormone known to have potent effects on the female tract (Sturkie and Mueller 1976), and both increased (Lehrman and Wortis 1960, Lehrman 1961) and decreased levels (Sockman and Schwabl 1999) have been observed in relation to incubation onset. In 1987 progesterone was implanted subdermally in five laying *oriantha* (8 mm Silastic capsules) in the mid-morning. Although these females all had incomplete clutches when implanted (one or two eggs), and must have ovulated only a few hours earlier, none laid again. Three tended their nests for a few days, at least intermittently, and two abandoned immediately. It appears that the smooth muscle of their reproductive tracts was completely inhibited. One female was recovered in 1988 with an empty capsule still in place, the other four were never trapped again. Two other females provided with empty implants (controls) completed their clutches and incubated normally. Progesterone, therefore, is an unlikely candidate for stimulation of incubation in *oriantha* although it might be useful for control of clutch size.

Despite uncertainties surrounding the control mechanism (a recent study by Sockman et al. 2000, for example, has yielded equivocal results), this model provides a starting place for explaining a commonly observed hatching pattern and shows that in species wherein a different pattern might be selected for, all that would need to be modified would be the threshold for induction of incubation behavior. This might be as simple as altering the structure or activity of a gene coding for hormone receptors in the membranes or cytoplasm of neurons that control incubation behavior. Whatever the physiological signals turn out to be, or even the usefulness of the hormonal hypothesis itself, we agree with Stoleson and Beissinger (1995) that studies of hatching asynchrony should be shifted from the search for adaptive hatching patterns to the events that occur during egg laying because this may be where adaptation truly lies.

SEX RATIO

The sex ratio in *oriantha* nestlings was determined from 214 clutches wherein every egg hatched out and every individual in the brood was then sexed by laparotomy. There were 681 nestlings in the sample, 342 males and 339 females, a ratio that was not different from 1:1 (Chi-square = 7.14, df = 1, P = 0.712).

COWBIRD PARASITISM

Brown-headed Cowbirds (*Molothrus ater*) rarely parasitize White-crowned Sparrows (Lavers 1974, King et al. 1976). At Hart Mountain, Oregon, however, 6 of 42 *oriantha* nests (14.3%) contained cowbird eggs or nestlings (King et al. 1976). Within the last two decades Brown-headed Cowbirds have become increasingly abundant in and around campgrounds located in the lower end of Lee Vining Canyon, about 10–15 km from the Tioga Pass study area. They have probably propagated there from nearby pack stations and cattle ranches, and do well in the campgrounds because of numerous bird feeders put out by campers. Cowbirds were observed frequently on the lower parts of the study area, especially around Ellery Lake and along Lee Vining Creek, but they were known to have

TABLE 8.6. FOOD DELIVERY TRIPS PER HOUR, INCLUDING PERCENT OF TRIPS BY EACH PARENT, TO BROODS OF THREE OR FOUR *Oriantha* NESTLINGS, IN RELATION TO NESTLING AGE

Nestling age (d)	Number of broods	Feeding trips by adults		Percent of feeding trips	
		Mean trips per hour	SD	By males	By females
0	3	3.5	0.7	13.3	86.7
1	6	5.3	3.4	24.0	76.0
2	5	5.2	2.1	30.6	69.4
3	8	8.2	2.8	33.2	66.8
4	6	11.4	4.4	35.5	64.5
5	7	13.0	3.8	45.5	54.5
6	8	14.7	4.3	38.8	61.2
7	7	16.7	3.4	37.4	62.6
8	4	15.5	4.0	33.5	66.5
9	3	16.5	3.9	22.0	78.0

Notes: Data derived from 57 broods. Nestling age 0 refers to day that first hatchling appeared (a full brood may not have been present until the next day).

laid in only a few Dusky Flycatcher nests (Pereyra 1998) and in one *oriantha* nest, an attempt that was unsuccessful.

PROVISIONING RATES

Nestlings could make gaping movements within a few minutes of release from the egg and were sometimes fed by the female almost immediately thereafter. One chick even obtained food while lying on its back, still struggling to become free of the half-shell adhering to its dorsal surface. The very first feedings were always provided by females. In some cases a male approached with food while hatching was in progress but the female would not let him feed new hatchlings. She took the food from him and swallowed it or sometimes stood up and fed it to the hatchlings lying beneath her. This type of behavior by females ceased within the first day or two and males began to feed nestlings directly.

During 77 observation periods (mean = 2.9 hr, SD = 2.3 hr) made on 61 nests during nine different years at all times of the season, 1,799 deliveries of food to the nest occurred. Of these, 699 (38.9%) were made by males and 1,100 (61.1%) were made by females (Chi-square = 89.38, df = 1, $P < 0.001$). Although males usually brought food to the nest, females consistently made more trips throughout the nine-d nestling period (Table 8.6). It should be warned that males were sometimes less inclined than females to ignore an observer's presence. They took longer to settle down and resume normal activities when observation blinds were entered, and some inhibition of their intent to feed nestlings could have occurred despite our precautions. Still the downward trend in body mass observed in males, while not as pronounced as that of females (Fig. 6.4), indicates that care of nestlings was energetically stressful for both parents.

Close-up observations plus collections made from collared nestlings indicate that arthropods, adult insects and their larvae in particular, were the primary type of food being delivered to nestlings. On occasion a few bits of plants, including leaves, buds, and flowers, were also delivered.

A distinctive diurnal pattern of feedings per hour was observed at one nest containing three Day 7 nestlings that was observed from first light to last (Fig. 8.4). The parents began feeding about 45 min before sunrise and stopped feeding

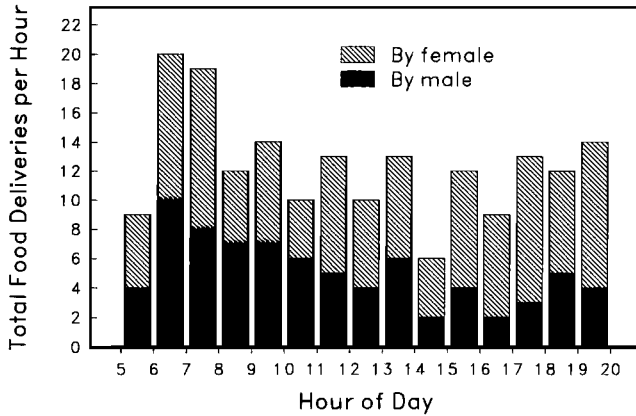


FIGURE 8.4. Diurnal pattern of parental provisioning in an *oriantha* nest with three Day 7 nestlings.

about 45 min after sunset. There were 186 food deliveries made during this one entire day, 77 (41.4%) by the male and 109 (58.6%) by the female. Two things stand out in this pattern. First, nestlings were fed most frequently in the early morning, the time when they were probably hungriest and begging most vociferously from the overnight fast. Second, parental care was shared about equally in the hours before noon but thereafter the male's contribution decreased substantially. Males were known to devote more time to territorial behavior in afternoon hours, especially to singing (Morton et al. 1972b).

As nestlings aged and grew, the rate at which food was delivered to the nest increased. Day 0 broods (those wherein at least one hatchling was present) were fed about three times per hr whereas those that were Day 7 and older were fed about 16 times per hr (Table 8.6). Note that these data were for deliveries to the whole brood, not to individual nestlings. Earlier, it was calculated that each nestling was fed about twice per hr on Day 0, and that this increased to about seven times per hr by Day 5 (Morton et al. 1972b). Also, as thermoregulatory abilities of nestlings improved, females spent less time brooding and more time feeding them. Eventually, feeding time was extended by about three hr, mostly in the early morning, the coldest time of day (Morton 1979).

NEST SANITATION

Nests were maintained in sanitary condition because the adults usually ingested the fecal sacs of nestlings, either at the nest or after carrying them away to a perch. Each nestling produced about 0.5 to 1 fecal sacs per hour from Day 0 through Day 9, with each sac weighing consistently about 2.5% of the nestling's total body mass throughout this time. A brood of four, therefore, produced more than 20 g of fecal sacs per day from Day 4 onward. Digestive efficiency of nestlings, especially of fats and proteins, improved substantially in the first two days after hatching, but because of the large volume of sacs involved, approximately 5 to 10% of the daily energy expenditure of the adults could be met from their consumption and recycling of nestling fecal material (Morton 1979).

PATTERNS OF PARENTAL CARE

As indicated above, males tended to show decreased parental effort toward the end of the season, as well as the end of the day. Delivery of food by male parents was highest in the earliest nests, remained fairly constant through July, then dropped precipitously in nests that were present in August. In 34 nests active in August that were observed from a distance with binoculars, the male was not delivering food at seven of them (20.6%). These seasonal effects, along with the extra demands imposed when double brooding occurred, caused considerable variation in patterns of parental care. Four seemed to be most common: 1) Both parents fed nestlings and fledglings. 2) Both parents fed nestlings and males took over care of fledglings when the female began a second nesting cycle (double brooding). 3) Both parents fed nestlings but only the female fed fledglings. 4) All parental care was provided by the female.

The necessity for biparental care is often described as an agent selecting for monogamy (Wittenberger 1976, 1982). Widowed females raise fewer offspring of lower quality, although the need for male assistance varies seasonally and/or interannually, depending upon food availability (Bart and Tornes 1989). Monogamy, therefore, could be a bet-hedging strategy, especially in unpredictable and fluctuating environments, such as those occupied by *oriantha* and Snow Buntings (Lyon et al. 1987). When food is dependably in surplus, females may provide all the parental care, as in Aquatic Warblers (*Acrocephalus paludicola*; Heise 1970), a species with a quasi-promiscuous mating system and high levels of multiple paternity (Schulze-Hagen et al. 1995).

When parental care is less demanding, as during times of exceptional food abundance, it has been suggested that males in monogamous mating systems should decrease their parental efforts to allow themselves more time and energy for extra-pair matings (Westneat 1988, Carey 1990, Westneat and Sherman 1993). Paternity exclusion data show that *oriantha* males engaged in extra-pair matings (Sherman and Morton 1988) and since they usually provided fewer than half of the feedings to nestlings (Table 8.6), there may have been time for extra-pair sexual activity during most of the reproductive season, especially in the afternoon hours (see Fig. 8.4). But the reduction, even total cessation, of parental care by males in the last nests of the season (patterns 3 and 4, above) suggests that other forces may be at work here.

Theoretically, males should not provide care to non-related young (Trivers 1972), but there is no reason to suspect that cuckoldry rates escalated at the end of the season. Furthermore, male birds apparently do not discriminate against non-related offspring (Kempnaers and Sheldon 1996, MacDougall-Shackleton and Robertson 1998). Why then would *oriantha* males withdraw parental care, particularly if it could be contributing toward mortality in their own offspring? It may be that their behavior is the solution to a conflict between their own long-term survival and the immediate survival of their young: current versus lifetime reproductive success. Mated males captured at season's end that were not feeding at the nest were invariably well into the postnuptial molt (Chapter 11). Once this molt was fully developed it may not have been feasible energetically for them to then begin caring for nestlings. It should be acknowledged, however, that females were sometimes known to be feeding fledglings while in the midst of heavy molt.

The outcome of opposing selective forces, parental care and self-maintenance, seems to be different, therefore, for adult males and females during this one period in the reproductive season. And this has a number of ramifications. For example, the seasonal reduction in clutch size and, thereby, the number of offspring that would eventually have to be cared for might have evolved as a hedge by females against decreasing parental efforts of males. This could be costly to females, however, because their survival rates decrease when males desert (Hemborg 1999b).

Sexual differences in pattern of reproductive investment occur in a variety of avian taxa and mating systems and it has been argued that these differences are primarily the result of sexual selection (Parish and Coulson 1998). It should be mentioned too that parental care by males might not be very important. For example, Freeman-Gallant (1998) discovered that the contribution of male Savannah Sparrows during the nestling stage was only weakly correlated with offspring quality and survival. Compensatory feeding by females may have been largely responsible for this result.

GROWTH AND THERMOREGULATION IN NESTLINGS

During their relatively brief time in the nest the altricial young of passerines typically undergo rapid changes in their morphology and physiology. Body mass increases by about an order of magnitude, a nearly complete plumage is grown, and transition from ectothermy to endothermy is accomplished. It is a period when differential abilities in parental care are likely to be exposed, as are the potential vulnerabilities of nest structure and nest site (the nest microenvironment) to effects of weather. In terms of survival, it is probably the most perilous time in a bird's life.

Earlier, basic information was presented on developmental changes in *oriantha*, including growth rates and thermoregulatory capacities of nestlings (Morton and Carey 1971). Here those data are bolstered with others and extended conceptually for their comparative value and for fresh insight on how variation in nestling growth and thermal responses may reflect both parental behavior and competitive interactions among nestlings.

Nestling development

The appearance and behavior of *oriantha* nestlings were very similar to those of *pugetensis* and *nuttalli*, as described in detail by Blanchard (1941) and Banks (1959), respectively. Supplementary observations are provided below for *oriantha*.

Day 0. Bodily movements were feeble and poorly coordinated except for the gaping response associated with begging. Nestlings could gape soon after hatching and were usually fed within the hour. In one case we observed a successful feeding 14 min after hatching. Gaping occurred when the female left the nest, sometimes while she was gone, and again when she or the male returned and hopped onto the nest rim.

Day 1. Wings and legs were flexed vigorously when nestlings were handled. Gaping occurred when the female left the nest and intermittently thereafter

until her return; vibration of the nest was a strong stimulus for the begging response.

Day 2. Motor coordination was improved. Some nestlings had enough strength and coordination to right themselves when placed on their backs. Gaping occurred as on Day 1, and a rudimentary alarm vocalization (a *cheep*) sometimes occurred during handling. The primaries had erupted by midday.

Day 3. Nestlings could locomote slightly through scrambling efforts when removed from the nest. Gaping occurred as before except that it sometimes now took place well before the adult hopped onto the nest, indicating that the ears were becoming functional. The eyes were still closed. Feather sheaths protruded slightly from the ventral and spinal tracts. The first noticeable increase in metabolic rate occurred (Morton and Carey 1971).

Day 4. Righting was now easily accomplished by most nestlings. Gaping tended to occur only when adults approached the nest. The eyes were starting to open. Feathers in all major tracts except the caudal tract had erupted. Nestlings made alarm calls and defecated when handled.

Day 5. Some nestlings gaped when handled and some crouched in an apparent fear reaction. The eyes were open in almost all individuals. The mean age at which eyes opened in 87 nestlings was 4.6 d. Rectrices were now erupted and barbs had broken through at sheath tips in the major body tracts. In terms of feather development, *oriantha* were about a day ahead of *nutalli*, as described by Banks (1959).

Day 6. Nestlings were alert and their movements were fairly well coordinated. They could sit erect and balance on their feet with wings held to the sides. When placed on a perch they maintained themselves, but awkwardly. Barbs had erupted from tips of sheaths in both flight and contour feathers. All nestlings exhibited a well-developed shivering response when exposed to cold air. They cued visually on the parents and sometimes gaped when an adult was still a meter or so away in its approach to the nest.

Day 7. Nestlings sometimes lifted up in the nest and exercised their wings. Many now defecated, gave an open-mouth threat display, or a loud fright-note when handled. This note caused siblings in the nest to hop out immediately and hide in nearby vegetation. They could survive overnight out of the nest at this age. Perching abilities were good and the insulative feather layer and control of metabolism were sufficient for maintaining a high body temperature. Oakeson (1954) noted one case wherein a disturbed *gambelii* chick left the nest on Day 7.

Day 8. The responses to handling were the same as on Day 7. When placed on the ground, nestlings were capable of running.

Day 9. Nestlings were very alert. When approached, they sometimes fledged by jumping out and running into cover. If tossed gently into the air, they flapped but usually did not make much horizontal progress. However, one chick flew about 10 m in a low ground-skimming flight when frightened from the nest. Most nestlings fledged on this day even when undisturbed. The last-hatched chick, although it was often age Day 8, generally fledged along with its older siblings.

TABLE 8.7. BODY MASS (G) OF NESTLING *Oriantha*

Age (d)	Mean	SD	N
0 ^a	2.65	0.36	173
1	4.16	0.71	229
2	6.33	1.04	194
3	9.08	1.45	175
4	12.02	1.71	203
5	15.21	1.61	134
6	17.60	1.88	123
7	18.64	1.81	96
8	19.71	1.80	94
9	20.70	2.09	30

^a Day of hatching.

Day 10+. A few nestlings remained in the nest beyond Day 9, usually because they were underweight and retarded otherwise in their development. Such retardation could usually be traced to exposure to bad weather, to being a lone hatchling, or, rarely, to disease or injury.

For the next three weeks of life, up to about one month of age, fledglings were dependent upon their parents for food. They gradually developed flying and foraging abilities (they could survive on their own in captivity beyond Day 19), and tended to disperse away from natal territories (Morton et al. 1972b). The role of the male parent was more variable than that of the female during this time. The newly fledged brood was usually split between the parents, but some males fed fledglings little, if at all, and the parent most likely to be seen caring for fledglings at the very end of their period of dependency was the female.

Growth rates

The mean body mass of *oriantha* nestlings taken in the morning, beginning with the day of hatching (Day 0), was 2.65 g, and at the time of fledging nine days later it was 20.70 g (Table 8.7). Converted to a logarithmic scale, mass changes appeared to follow a near-linear increase for the first few days of life, then declined in rate during the remaining two-thirds of the nestling period (Fig. 8.5). During these early days growth exceeded 40% per day, as is usual in various sparrows and buntings (Dawson and Hudson 1970).

Because nestlings grew in approximately log-linear fashion up to Day 4, logarithmic growth rate constants per day (K) were calculated for nestlings weighed at least twice during that time period. The K values, which are simply slopes, can then be used to inform us about the trajectory of growth and how it might vary with biological and environmental factors. For example, growth rate in young nestlings did not vary with sex (males: mean K = 0.158, SD = 0.023, N = 103; females: mean K = 0.155, SD = 0.026, N = 104; $t = 0.853$, $P = 0.190$), or with parent's age (male parent: ANOVA $F_{6, 256} = 0.74$, $P = 0.622$, N = 263; female parent: ANOVA $F_{4, 347} = 0.32$, $P = 0.861$, N = 352).

Nestling growth rates during these first few days of life did change with season, however. They were highest in June, then declined steadily thereafter (ANOVA $F_{5, 387} = 5.16$, $P < 0.001$; Fig. 8.6). They also varied with hatching order; the first chick that hatched grew slowest and the last chick the fastest (ANOVA $F_{4, 329} =$

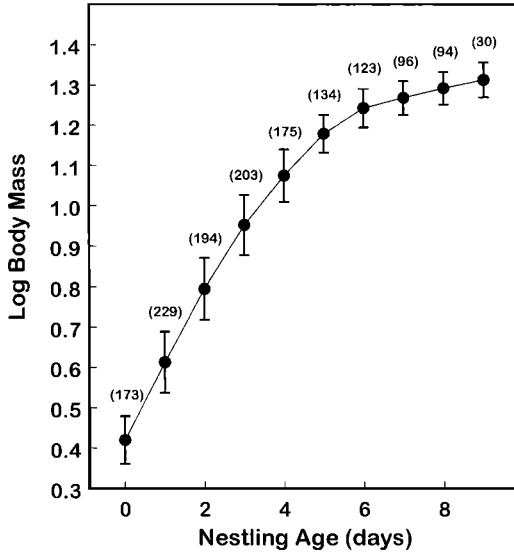


FIGURE 8.5. Semi-logarithmic plot of body mass in nestling *oriantha*. Means (± 1 SE); sample sizes in parentheses.

5.61, $P < 0.001$). This relationship was almost completely consistent through the hatching sequence, no matter the brood size (Fig. 8.7).

As can be deduced from Fig. 8.7, nestling growth rates tended to increase with brood size (ANOVA $F_{4,387} = 6.50$, $P < 0.001$; Table 8.8). Note that brood size refers to the number of nestlings alive at the time body masses were measured; it could be lower than clutch size if all of the eggs did not hatch. To summarize: as chicks were added to the nest due to hatching, growth rate in each newcomer was higher than that of its predecessor, and the larger the brood the higher the collective growth rate tended to be for members of that brood (Table 8.6, Fig. 8.7). There was also variation in growth rates obtained in different years. For example, in five years when substantial numbers of nestlings were weighed in the

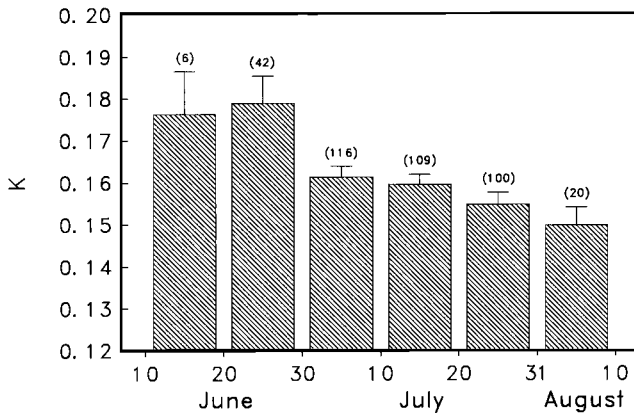


FIGURE 8.6. Growth rates (K) of *oriantha* nestlings during the first four days of life in relation to hatching date. Bars show mean ($+ 1$ SE); number of nestlings in parentheses.

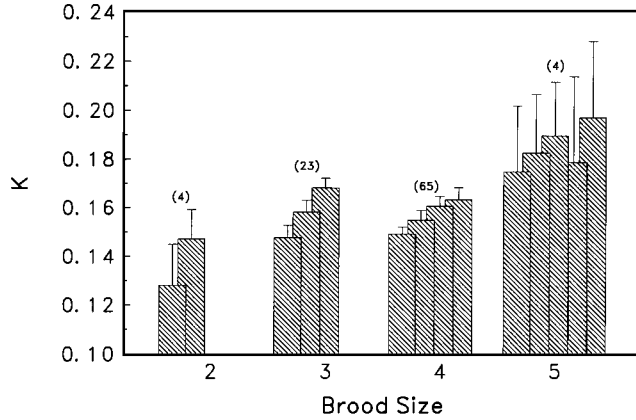


FIGURE 8.7. Growth rates (K) of *oriantha* nestlings during the first four days of life in various-sized broods, arranged first-to-last (left-to-right) in hatching order. Bars show mean (+1 SE); number of broods in parentheses.

first days after hatching, the mean value of K varied from 0.154 to 0.175 (ANOVA $F_{4,388} = 9.99$, $P < 0.001$; Table 8.9).

King and Hubbard (1981) compiled growth rate data in *gambelii* and *oriantha* from six populations and found that the growth curves for the whole of the nestling period were congruent and independent of brood size and locality. They took this constancy to mean that growth rates in White-crowned Sparrows are physiologically maximized. This might only be expected, however, when optimum ecological conditions prevail (Ricklefs 1968, 1973). As the data presented above show, growth in the period right after hatching does vary in *oriantha*, sometimes subtly, but one needs more than the limited data set applied by King and Hubbard to detect it. They were comparing mean body masses at various days of age and had inadequate information on interannual variation and none at all on growth rates according to parent age, hatching date, or hatching order.

What could be contributing to the growth rate variations observed in *oriantha*? One logical place to focus is on the energy budgets of nestlings. Their total metabolizable energy (TME) is equal to resting metabolic rate plus growth (energy put into tissue) plus the costs of activity and thermoregulation (Williams and Prints 1986, Weathers and Sullivan 1991). The scope of variation in these parameters will depend upon interactions among them and on how effectively the parents supply food. The growth rate of a nestling might vary, therefore, according to how much it is fed and to how it partitions TME. It appears that experience

TABLE 8.8. LOGARITHMIC GROWTH RATE CONSTANTS (K) DURING THE FIRST FOUR DAYS OF LIFE IN *Oriantha* NESTLINGS, IN RELATION TO BROOD SIZE

Brood size	Mean	SD	N ^a
1	0.143	0.016	3
2	0.148	0.027	31
3	0.160	0.025	136
4	0.161	0.030	197
5	0.197	0.042	15

^aNumber of nestlings weighed.

TABLE 8.9. LOGARITHMIC GROWTH RATE CONSTANTS (K) OF *Oriantha* NESTLINGS ACCORDING TO YEAR

Yr	Mean	SD	N ^a
1982	0.153	0.025	125
1991	0.154	0.028	47
1992	0.154	0.037	69
1993	0.175	0.023	84
1994	0.167	0.030	68

^a Number of nestlings weighed.

in food gathering for dependent offspring was not a factor in *oriantha* because nestling growth rates did not change with parent age.

The increase in growth rate with hatching order introduces additional variables to be considered: sibling competition and the female's brooding propensities. Sibling competition has been invoked as a dominant force in the evolution of avian growth rates (Werschkul and Jackson 1979), and although evidence for this hypothesis is not always robust, intense competition for food has often been observed among passerine siblings (Ricklefs 1982). Generally the larger, first-born young are the ones that obtain the most food, either because they are stronger or because they are fed preferentially by the adults (Lack 1956, Hussell 1972, Howe 1976). This leads one to expect that growth rates should decline with hatching order—exactly the opposite of what was observed (Fig. 8.7). How can this be explained?

As noted earlier, females sat tightly on the nest during the time of hatching, even though their body mass was declining, and fed first-hatched nestlings sparingly until all eggs in the clutch had hatched. When bad weather caused partial mortality so that only one or two eggs or hatchlings survived, or when its effects caused hatching asynchrony to be greatly exaggerated, prolongation of attentiveness typical of incubation occurred. For example, in a nest wherein only one egg out of four was viable the female brooded the hatchling and the three eggs almost continuously for at least five days. The lone nestling was fed irregularly and weighed 3.2 g on Day 5, about 20% of the mass expected at that age (see Table 8.7). It eventually reached 13.7 g on Day 11, two days beyond the usual fledging time, but was dead in the nest on the next day. In another nest with five eggs, three of the chicks hatched out three days before the other two. Again, the female was reluctant to leave the nest and growth of the early chicks was greatly retarded until the others hatched. At that time growth in all five began to proceed at the normal rate. The propensity to starve hatchlings in order to remain on the nest and supply heat to unhatched eggs has not, to my knowledge, been previously reported.

The maintenance of nest attentiveness typical of incubation during the hatching period, even though it puts females into negative energy balance and slows growth in hatchlings, suggests that it is important for females to minimize the hatching spread induced by the early onset of incubation behavior. I hypothesize that a trade-off is occurring here because, in the long run, hatching asynchrony probably increases nestling mortality.

More rapid growth with brood size is a response that calls for more investigation. Several factors, some of them clearly interdependent, may have contrib-

uted to this surprising pattern. For example, the presence of more nestlings could have stimulated a disproportionate increase in parental feedings. Also, defense of broods against cooling is known to improve as the number of chicks increases (within normal brood size ranges) because of the increased effectiveness of huddling (see below). This would spare more energy for incorporation into biomass and it could also increase the female's ability to provision because the chicks would require less brooding.

Although the ANOVA indicated that inter-brood growth rates varied, inspection of the data (Table 8.8) reveals that brood sizes of three and four, which comprised 87% of all broods measured, had similar K values. Most of the variation was due to differential rates in the smallest and largest broods. Chicks in broods of one and two grew the slowest and, as pointed out above, were sometimes neglected. In addition, because clutch size decreased seasonally, these broods tended to occur at the end of summer when insect food was diminishing (see below) and when care by male parents was unreliable. The high growth rates observed in broods of five could also have been related to food abundance. Recall that short-term environmental feedback operating during favorable trophic conditions seemed to favor the laying of 5-egg clutches (Chapter 7), so territories containing broods of five may have been optimal for parental provisioning and, consequently, for hatching growth.

It should be re-emphasized that growth rates were only measured during the first few days of nestling life, the most propitious time to detect differences that might occur because of variations in brooding and provisioning. It is unclear if these differences carried through to fledging or beyond, but perhaps they did not (see Fig. 8.2, A, B, C). A comparison of growth rates taken in the present study with those derived by other methods, such as the logistic conversion of asymptotic mass (Ricklefs 1967), would be instructive, especially if concurrent data were obtained on parental behavior and the type and volume of food being brought to nestlings.

The fact that growth rates declined with season (Fig. 8.6) should not be attributed to an increase in thermoregulatory demands because ambient temperatures ameliorate through the summer. Also, at the ages when growth rates were measured, nestlings were still ectothermic (see below), and their thermoregulatory costs must have been low. Aside from shifts in parental care, discussed above, it may be that appropriate food for nestlings also wanes in availability with season at Tioga Pass. Biomass of flying insects (adults) tended to increase until late July, or even into August in some years at Tioga Pass (Pereyra 1998, Fig. 24). Inter-annual variation was quite large, being on the order of a 20-fold difference. These data do not address abundance of insect larvae, which should decline well before that of adults, but they do indicate that variation in food supply could be influencing interannual and seasonal differences in growth rates of *oriantha* nestlings.

Ontogeny of thermoregulation

As nestlings added biomass, their surface-to-volume ratio decreased, insulation was added as feathers grew in and brushed out, and their thermogenic abilities increased. In a period of three or four days, midway the nestling period, they made the transition from ectothermy to endothermy. At the time they fledged, usually Day 9, they were homeothermic and could thermoregulate effectively

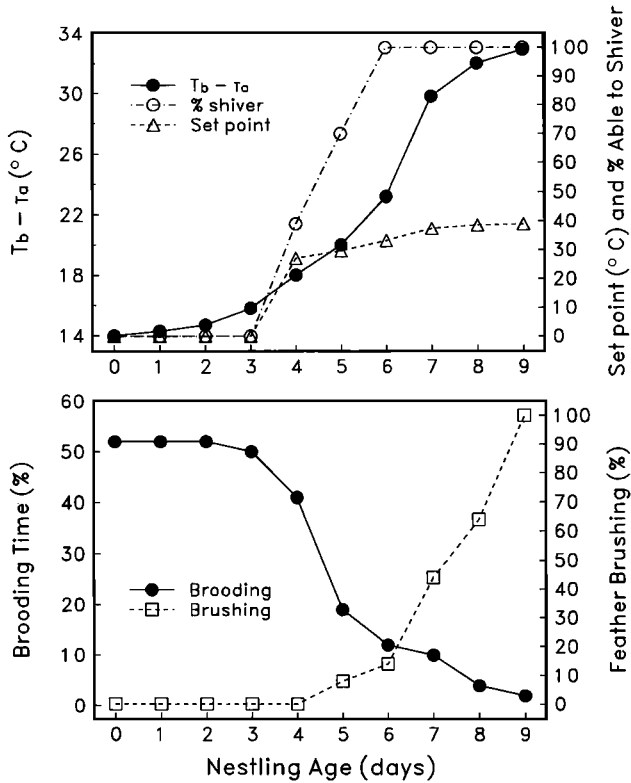


FIGURE 8.8. Parameters of thermoregulation and plumage development in *oriantha* nestlings, and of daytime brooding by tending females. Means are shown for each day of age. Chicks were cold stressed by exposing them individually to 5 C air temperature for 10 min. Sample sizes were 15–50. Adapted from Morton and Carey (1971).

enough to survive even sub-freezing temperatures on their own (Morton and Carey 1971). The first expression of incipient endothermy occurred about Day 4, the time when some of the chilled nestlings began to shiver, to open their eyes, and to grow less rapidly. If they were taken out of the nest in the early morning on Day 4 when ambient temperature (T_a) was about 5 C, their body temperature (T_b) decreased such that they were only 18 degrees warmer than T_a after 10 min (Fig. 8.8, upper). The $T_b - T_a$ gradient in cold-stressed nestlings increased to about 30 degrees over the next three days and on Day 7 they were already capable of resisting the cold and surviving premature fledging, should it occur.

On Day 4 about 40% of the nestlings tested were able to shiver and two days later all of them were doing it (Fig. 8.8, upper). This schedule was nearly two days ahead of that found in a close relative, the Song Sparrow, living at low elevations (Sogge et al. 1991). The T_b at which shivering began in *oriantha*, the manifestation of a hypothalamic set point, also showed some maturational changes within this time frame, increasing by 10 degrees from about 29 C to 39 C (Fig. 8.8, upper). In parallel with increasing thermogenic capacities, nestlings also became better insulated due to their new feathers becoming brushed out at the tips and covering the bare skin of their apteria (Fig. 8.8, lower).

These field experiments were performed to discover nestling thermoregulatory

TABLE 8.10. MEAN DECREASE IN BODY TEMPERATURE OF *Oriantha* NESTLINGS MEASURED IN THE NEST, AFTER EXPOSURE TO AMBIENT TEMPERATURE OF 10 C FOR 15 MIN

Nestling Age (d)	One Nestling			Four Nestlings		
	Mean	SD	N	Mean	SD	N
2	10.8	1.8	7	5.4	1.9	7
4	6.8	1.2	7	2.3	1.2	7
6	1.3	1.3	7	0.2	0.4	7
8	0.5	1.0	7	0.1	0.1	7

capacities, particularly their ability to avoid heat loss. Normally, of course, chicks benefit by being in the nest where they are surrounded by its walls and by siblings, and from being brooded by their mother (the duration of which she modified as they gained thermal independence; Fig. 8.8, lower). As a result, mean T_b of nestlings was actually quite stable. Measured *in situ*, with as little disturbance as possible, it varied only about five degrees, averaging 34 C in the youngest (Day 0) and 39 C in the oldest nestlings (Day 9).

Huddling

Huddling of neonates reduces the collective surface area exposed to the elements and the heat they produce also warms the immediate microenvironment, further affecting energy exchange rates (Hayes et al. 1992). When the air was cold, *oriantha* nestlings invariably packed themselves tightly against one another. To evaluate the effect of huddling, T_b was measured in intact broods of four and in lone nestlings when the female was kept away by our presence near the nest. It was found that Day 2 broods cooled by a mean of 5.4 degrees when subjected to early morning cold for 15 min whereas singleton nestlings decreased by 10.8 degrees, a significant difference ($t = 5.01$, $P < 0.001$; Table 8.10). Although this difference decreased as nestlings grew older (Table 8.10), the effectiveness of huddling by full broods helps to explain why brooding time of females in daylight hours decreased rapidly after Day 3 (Fig. 8.8, lower). The acquisition of functional endothermy by broods well ahead of individuals has often been noted in altricial birds (Dunn 1975, 1976, 1979; Sullivan and Weathers 1992, Pereyra and Morton 2001), and the ability of broods to function as thermoregulatory units that can buffer T_b decrease while the nest is untended probably contributes to their own health and to the time available for females to engage in self maintenance and food gathering (Verbeek 1995).

In recent years it has become possible to measure metabolic rates of nestlings with the doubly-labeled water (DLW) technique. One immediate revelation was that, because of thermoregulatory costs, energy budgets of nestlings were substantially higher in the field than in the lab. Even resting or basal metabolic rates of the field-tested nestlings were unexpectedly high (Williams and Hansell 1981, Williams and Nagy 1984, Williams and Prints 1986).

Sullivan and Weathers (1992) used DLW to measure nestling energy requirements in Yellow-eyed Juncos in relation to brood size and found that the modal clutch size (4) was also the most efficient brood size. Reducing the brood size increased the metabolic cost per nestling because benefits from huddling were lower. Augmenting the brood was also costly because the chicks no longer fitted

properly within the nest walls. Ambient temperature accounted for the greatest amount of the variation in field metabolic rates, 21.0%, but brood size was also a large factor, accounting for 17.5% of the variation. In the future it would seem important that data from the DLW studies of nestling thermoregulatory costs be taken into consideration when conclusions are being drawn about optimal clutch sizes and “benefits” of brood reduction.

Implications from the foregoing are that loss of heat subtracts from growth and survival, and that this might be of great concern in high altitude environments where cold is imposed nocturnally and summer storms are frequent. This is true, but it is also true that the thinned-out layer of water vapor in the atmosphere exacerbates the problem of overheating from solar radiation. Intra-nest temperatures can soar when exposure to direct sun occurs, causing mortality in eggs and nestlings within 20–30 min (Morton and Carey 1971, Zerba and Morton 1983b). Solar heating can also cause older nestlings to leave the nest temporarily to lower their discomfort and may even stimulate fledging itself if they are at the appropriate age.

If a nest is exposed to direct sun its contents can be protected in several ways. One is that females can stay on the nest and shade it, and attentiveness does increase as solar heating increases (Zerba and Morton 1983b). Another, at least for nestlings, is that some protection can be afforded by evaporative cooling from the respiratory tract. Active heat defense is well known in altricial birds and thermostatic controls can be observed at an early age (Dawson and Hudson 1970). For example, less than an hour after hatching, *oriantha* nestlings will pant when exposed to heat loads. The efficacy of this behavior has not been adequately examined, but the T_b set point for panting was found to be about 41 C and, most impressively, did not vary significantly from the day of hatching onward (Morton and Carey 1971). It should not be overlooked that the plumage of nestlings, including the downy feathers, may serve to deflect or exclude solar radiation (Verbeek 1988).

NATAL DISPERSAL

From the moment they leave the nest, young passerines begin a journey that will take them from their place of birth to where they will eventually settle and breed. In sedentary species, the total distance involved in this natal dispersal is ordinarily a few kilometers or less, and it is usually covered within the first few months of life, before the arrival of winter weather (Tompa 1962, Nilsson 1989). Because of the migration to and from wintering areas that intervenes, natal dispersal in migratory species is a temporally discontinuous process, and its distances and biology are poorly understood.

Oriantha fledglings remained hidden in vegetation close to the nest for the first few days after leaving it. If both adults were feeding them, each one tended to focus on part of the brood, repeatedly feeding the same one or two fledglings, for example, rather than all of them. Thus, the family became divided into subunits that after about a week, and coincident with the development of flying and foraging abilities in the fledglings, began drifting away from the area of the nest (Fig. 8.9). At about one month of age, some three weeks after fledging, the family subunits dissolved. By then the young were of adult body size, able to survive independently, usually living well away from their natal site (Fig. 8.9), and en-

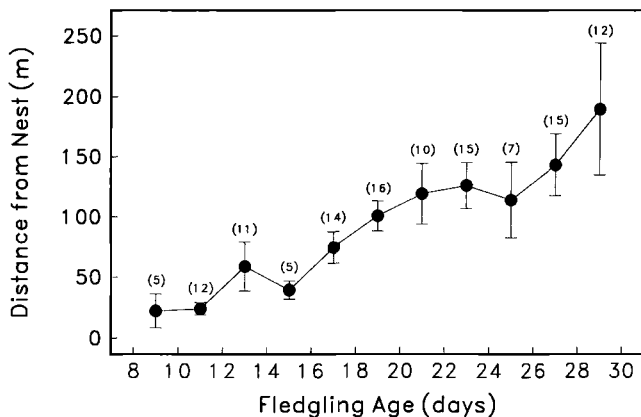


FIGURE 8.9. Mean distance moved (+ SE) with age by *oriantha* fledglings in relation to their nest. Sample sizes in parentheses.

tering the postjuvinal molt. Although no longer interacting with their parents, some siblings probably continued to travel together for several additional weeks because they were often trapped simultaneously at the same location.

Most of the observations on post-fledging movements were made on TPM and some of the juveniles that were born there stayed on that meadow until departing on migration. Most moved away or died, however, because they were no longer observed nor did they show up in traps. Another measure of mobility in juveniles was obtained from individuals banded as nestlings at locations 2–5 km from TPM that were subsequently captured on TPM. These nonlocal juveniles ranged in age from 32 to 78 d upon first arriving at TPM (mean = 52.8 d, N = 17 males and 15 females).

As summer progressed first captures of juveniles born on TPM (locals) declined, but members of the other cohort (nonlocals) began to increase. The frequency distribution for first captures of these two groups was about one month out of phase, and every year the nonlocals outnumbered the locals by about two to one (Fig. 8.10). The postjuvinal molt occupied the second month of life in juveniles and about 90% of the nonlocals were either in its final stages or had fresh plumage. Thus, most of the nonlocals were two months old or older when they arrived on TPM. It seemed likely that many had traveled more than 5 km to get there and may have moved in from watersheds outside the Lee Vining Creek drainage (Morton et al. 1991, Morton 1997).

Natal dispersal is a permanent movement from birth site to first breeding site, but, as pointed out above, it is discontinuous in migrants being separated into two stages, one between fledging and migration departure in the fall, the post-fledging period, and the other between arrival and settlement the next spring, the pre-breeding period (Morton 1992b, 1997).

Dispersing juveniles must locate suitable breeding habitat and then be able to settle there. Obviously, the first of these processes could take place during the post-fledging period whereas the second must wait until the pre-breeding period. It has been suggested, in fact, that the critical time for habitat imprinting in various species of passerine migrants is when they are only about 30 to 50 days of age, the very first few weeks after they have become independent and can travel alone

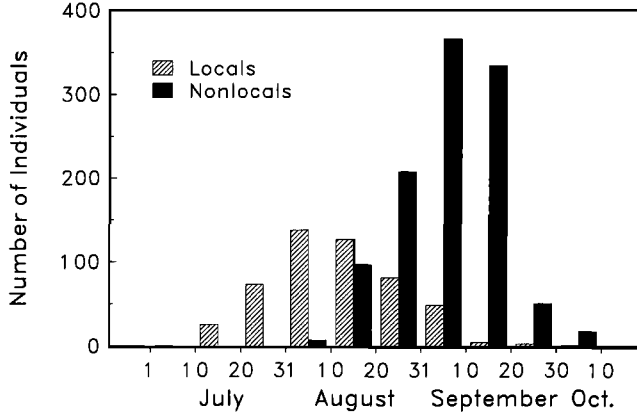


FIGURE 8.10. Distribution of dates of first captures of *oriantha* juveniles on TPM. Locals were born on TPM, nonlocals elsewhere. Samples were derived from 10 yr of data (1978–1987), $N = 506$ locals and 1,083 nonlocals.

(Löhrl 1959, Haukioja 1971, Van Balen 1979, Morton et al. 1991, Sokolov 1991). During post-fledging dispersal, juveniles could also be learning landmarks that would be useful to them the next spring when they return after an absence of eight months, and at a time when the habitat looks very different (Löhrl 1959, Wiltschko and Wiltschko 1978, Able and Bingman 1987). Furthermore, post-fledging meanderings may help young birds find enough food for growth, maintenance, and premigratory fattening (Morton 1997). In Green-tailed Towhees (*Pipilo chlorurus*), for example, such movements were longest during drought years (Morton 1991).

The trapping data reveal some additional subtleties about habitat imprinting in *oriantha*. For example, the return rate of birds to the study area as adults that had been banded there as juveniles was different for the sexes. In males it was 13.9% (124 of 894) and in females it was 10.0% (70 of 700), a significant difference (Chi-square = 5.50, $df = 1$, $P = 0.019$). This effect could be traced to differences in return rates that were related to the amount of time spent on TPM as juveniles. If males were in residency on TPM as juveniles for more than four weeks their return rate increased significantly, from 11.1% to 28.5% (Chi-square = 30.64, $df = 1$, $P < 0.001$; Fig. 8.11), but return rate did not change between these periods of residency in females, 10.3% vs. 8.4% (Chi-square = 0.35, $df = 1$, $P = 0.552$). The return rate of 28.5% for males that were sedentary as juveniles was extremely high in comparison to rates observed in other migratory species (Weatherhead and Forbes 1994), and nearly all of these particular individuals that survived the winter must have returned to TPM. Apparently the selection of breeding habitat was entirely completed by this group during the post-fledging period. The return rate of sedentary female juveniles (8.4%) was significantly lower than that of males (Chi-square = 15.49, $df = 1$, $P < 0.001$).

The lower return rates observed in females and in non-sedentary males (as compared to sedentary males) may simply be a function of some birds, females especially, traveling over greater distances than others during their post-fledging dispersal period. Thus, they were more scattered when returning the next spring as adults and not as many showed up on the study area.

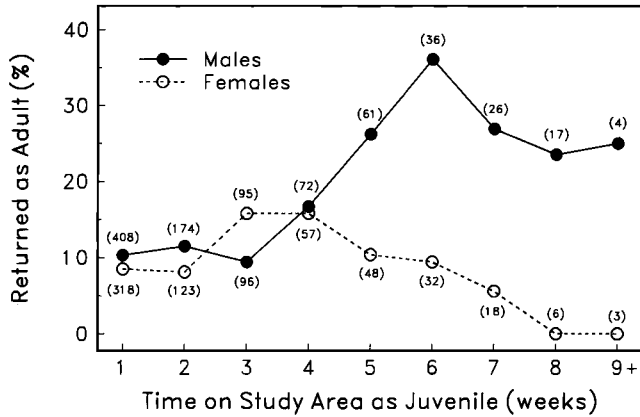


FIGURE 8.11. Return rates of *oriantha* adults to the study area in accordance with their duration of residency as juveniles in the previous year. Sample sizes in parentheses.

Despite limitations imposed by study area size (which invariably causes dispersal distances for a population to be underestimated) there were indications that *oriantha* females followed the pattern observed in most avian species in that they tended to disperse greater distances than males (Gauthreaux 1978, Greenwood 1980, Pusey 1987, Plissner and Gowaty 1996). Mean natal dispersal distance (distance from nest of birth to first nest as a one-year-old adult) was 1.7 km (SD = 1.1 km) in females (N = 15) and 1.2 km (SD = 1.0 km) in males (N = 25). Median dispersal distance was 1.7 km in females and 0.8 km in males. Although these differences were large, they did not reach statistical significance (Morton 1992b).

Did experiences gained during the post-fledging period subsequently affect reproductive success? This cannot be answered with certainty, but it can be pointed out that such exposure may have influenced recruitment or philopatric tendencies in the sexes. Of 188 one-year-old males known to have nests on TPM, 68 (36.2%) had been captured there the previous year as juveniles; in females it was 45 of 256 (17.6%), a significant difference (Chi-square = 19.75, df = 1, $P < 0.001$). Males were more philopatric than females.

