



CHAPTER 11: Late-season Events

GONADAL PHOTOREFRACTORINESS

Among migratory birds inhabiting the temperate zone, the nesting season must eventually come to a close so they can molt and prepare metabolically for migration before deteriorating environmental conditions reduce the chances of survival for young and adults alike (Immelmann 1973). In photoperiodic species, such as White-crowned Sparrows, breeding activity ceases because the system that controls the stimulation and maintenance of the reproductive organs becomes insensitive or refractory to the stimulatory effects of long days (Nicholls et al. 1988, Wilson and Donham 1988). The efficacy of this photorefractory response and its timing have presumably been acted on by natural selection such that seasonal reproductive efforts are terminated optimally (Farner and Lewis 1971, 1973; Farner et al. 1983, Farner 1986). Although terminating mechanisms are adaptive and comparable in significance to those that initiate and maintain periodic gonadal function, they have received little attention, particularly in field studies.

Gonadal regression

Logically, the onset of photorefractoriness should be followed closely by a decrease in gonadal size and functional ability. Spontaneous gonadal regression is, in fact, generally used by experimentalists as proof that refractoriness has set in (Wilson and Follett 1974). As can be seen from testis and cloacal protuberance lengths in *oriantha*, regression occurred in males between 10 July and 10 August (Fig. 5.1). This appears to be identical to the schedule followed by two migratory conspecifics, *gambelii* breeding in Alaska (King et al. 1966) and *pugetensis* breeding on the coast of Washington (Lewis 1975b). This is a surprise, given the latitudinal spreads involved and their respective photoperiods, because it is well known from studies of captives held under controlled conditions that the time of regression is an inverse function of daylength; the longer the days during photostimulation, the sooner involution occurs (Storey 1976, Moore et al. 1983). Furthermore, once the threshold daylength for the induction of photorefractoriness is exceeded, its rate of development becomes directly related to daylength (Nicholls et al. 1988). As Moore et al. (1983) pointed out, however, the onset time of regression is fixed relatively early in gonadal growth. Substantial gonadal development often occurs in migrants before they arrive at their summering areas, so if these three subspecies experience similar photoperiods at that time in the cycle, presumably while they are still on wintering areas or in transit to the breeding grounds, regression might very well be programmed to the same schedule in all of them. Implicit in this reasoning is that environmental feedback has not operated as yet to tailor optimally refractoriness onset for the separate breeding environments used by this subspecies cluster. The ovary is not as easy to evaluate *in situ* as the testis but, based on decreases in follicle diameter, loss of ovarian function occurred in *oriantha* within the same time frame as testicular regression (Fig. 5.1).

Although the refractory condition is usually assessed from data on gonadal condition, its functional advancement in wild birds can also be deduced from their renesting schedules. The rationale here is that if a mated pair is photosensitive, or at least the female is, and their nest is lost, she will replace it. If she has become photorefractory, she will not. The proportion of females failing to renest,

TABLE 11.1. PERCENT OF *Oriantha* FEMALES THAT RENESTED IN RELATION TO CALENDAR INTERVAL THAT LOSS OF EGGS OR NESTLINGS OCCURRED

Calendar interval	N	Percent that renested
20–25 June	32	100.0
26–30 June	52	100.0
1–5 July	37	100.0
6–10 July	21	100.0
11–15 July	24	91.7
16–20 July	20	90.0
21–25 July	11	36.4
26–31 July	7	14.3
1–5 August	8	12.5
6–10 August	8	0.0

therefore, should be directly related to the prevalence of refractoriness in the population. These assumptions seem correct because the data on renesting propensity yield the same temporal scale for refractoriness as those for ovarian collapse (Table 11.1). Before 10 July all females built replacement nests, but thereafter their tendency to do so decreased. There was no renesting if a nest was lost after 5 August and the tendency to renest toward season's end was not dependent upon a specific nesting stage. That is, renesting and its absence both occurred when nests were lost either with eggs or with nestlings.

Nesting termination

Another approach to identifying the termination of reproduction under field conditions is to examine the seasonal change in number of clutch starts or first-egg dates; their waning can be taken as a measure of refractoriness onset in the population (Fig 11.1). It is instructive also to look simply at the distribution of

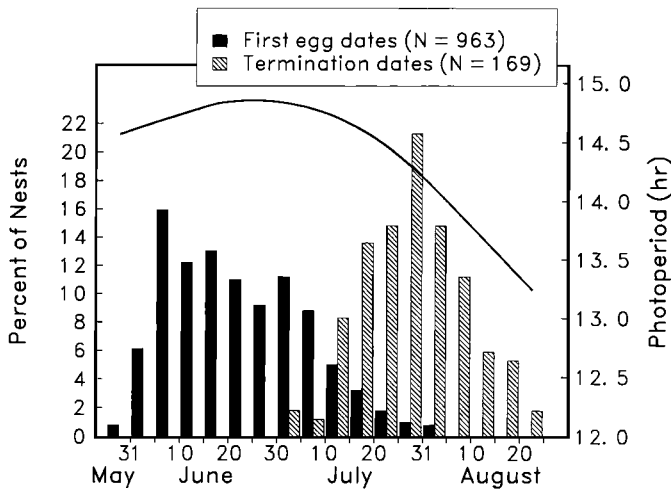


FIGURE 11.1. Seasonal schedule of clutch starts (first egg dates) and nesting termination dates (fledging or loss of nest without renest attempt) in *oriantha*. Line shows seasonal change in photoperiod at Tioga Pass.

all nesting terminations as they occurred, either from nest failures or from fledging events that were not followed by additional nestings (Fig. 11.1).

As would be expected from the data on ovarian stages (Fig. 5.1) and on re-nesting propensities (Table 11.1), egg laying ceased in early August. Previous to that time, of course, many females had already terminated reproduction (Fig. 11.1). These data raise several points for consideration. One is that photorefractoriness might productively be thought of as a trait that has considerable variation. It varied among female members of the population, for example, by at least a month (Table 11.1, Fig. 11.1). A second is that refractoriness may develop only gradually in the population. The seasonal decline in clutch size was previously pointed to as a possible symptom of this (Chapter 7). A third is that refractoriness is subject to modification by environmental or supplementary cues. For example, breeding tended to be prolonged in heavy snow years because the melt-off from large drifts kept the meadows wet and green until late in the summer (Morton et al. 1972b). Even in moderate snow years, late-season nestings sometimes occurred in a few territories that contained sumps, springs, or streamlets that helped to prolong green-vegetation conditions (Morton 1978). In *nuttalli*, nesting was extended later in summers that had been preceded by winters of heavy rainfall, probably in response to increased food availability (DeSante and Baptista 1989). And using an experimental approach, Runfeldt and Wingfield (1985) found that estradiol implants caused sexual activity to be extended in female Song Sparrows. Interestingly, testicular regression in their mates was substantially delayed. These studies suggest that the onset and perhaps the progression of refractoriness can be modified by supplementary cues such as food quality and quantity and by social interactions. It would seem that females are particularly sensitive to the former and males to the latter.

Beyond this, photorefractoriness itself can be shown to have a considerable range in efficacy. In some species in captivity, such as White-crowned Sparrows and European Starlings, it has been found to be “absolute” because it induces gonadal regression even if daylengths remain long and without decrease. Other species, such as Japanese Quail (*Coturnix japonica*), are “relatively” refractory because regression can be halted or reversed if the birds remain on constant long days (Hahn and Ball 1995, Hahn et al. 1997). In earlier years, this interspecific variation in the terminating mechanism was often described as being an expression of separate evolutionary pathways (Immelmann 1973, Farner et al. 1983). Recently, with the benefit of new information gained from molecular and neurobiological studies, it has become clearer that this variation or flexibility may be due simply to differences in the expression of a common underlying control system. For example, gonadotropin releasing hormone synthesis is inhibited in cases of absolute refractoriness, whereas its release is inhibited in relative refractoriness (Ball and Hahn 1997, Hahn et al. 1997). As stated by these authors, it seems likely that small changes in information processing could greatly alter the responses of this control system to supplementary information.

Understanding how breeding is terminated has been a mystifying problem that has been resistant to clarification. It has been difficult, for example, to separate experimentally the autumnal sequence of events that occur in migratory birds (gonadal regression, molting, and premigratory fattening) into individually regulated entities; physiologically, they seem to be very tightly coupled. Still, progress

is occurring. There is evidence in some species, such as White-throated Sparrows (Harris and Turek 1982), House Sparrows (Dawson 1991), and Song Sparrows (Wingfield 1993), for example, that a decreasing photoperiod is an important source of information to the expression of photorefractoriness. In keeping with this, note that loss of reproductive ability did not occur in *oriantha* until after the summer solstice (Fig. 11.1). It seems possible, then, that their reproductive system shut-down is being cued by decreasing daylengths. If this is true, one would expect time measurement through the use of an endogenous program or clock to be a functional component of the photorefractoriness mechanism (Robinson and Follett 1982, Wingfield 1993). It should be mentioned that although refractoriness is commonly expressed when days are getting shorter, in some species this can happen even before the solstice (Hahn et al. 1997).

Another intriguing line of inquiry has to do with the role of thyroid hormones in organizing the expression of refractoriness: thyroidectomy causes the reproductive system to become unresponsive to photoperiod change (Dawson 1993), thyroxine must be present in order for gonadal growth to occur under long days (Dawson 1989), and an intact thyroid is essential for photorefractoriness to develop (Goldsmith and Nicholls 1984). Wilson and Reinert (1993, 1995, 1998) have suggested that thyroxine and long days interact during a critical period, early in the gonadal cycle, to program organizational effects on photoperiodic control circuits in the brain. This would be further support for the hypothesis that the onset of refractoriness is determined during the time that daylengths are increasing rather than decreasing. In a thorough review of endocrine mechanisms operating in wild species, Wingfield and Farner (1993) concluded that photorefractoriness lies at the hypothalamic level or higher in the central nervous system, with the exact location still awaiting discovery.

MOLT

Molting, the shedding and regrowing of feathers, is a lengthy and energetically expensive process, but a necessary one if the plumage is to be retained in a condition that is functionally optimal for insulation and flight. The integration of molt into the annual cycle, along with control of its timing and rate, is of considerable interest to avian and comparative physiology (Payne 1972). In many species of migratory passerines, adults undergo a postnuptial (prebasic) molt before they fatten and depart on migration. In *oriantha* this molt is complete; that is, the entire plumage is renewed. This does not cause a change in coloration or markings so adults do not change in appearance from one molt to the next; they look the same on both summering and wintering grounds. Juveniles also molt before migrating but their molt, the postjuvinal (first prebasic) molt, is incomplete or partial. It does not involve the flight or contour feathers of the wing and tail, the remiges and rectrices, only those of the body. Their flight feathers are still very new at that time and are not in need of replacement. Postjuvinal molt does cause an appearance change because the buff-colored feathers on the heads of fledglings are replaced by brown and tan stripes. Young birds carry these through the winter until they are replaced by the black and white ones, typical of adults, in their first prenuptial molt, prior to departure from the wintering area.

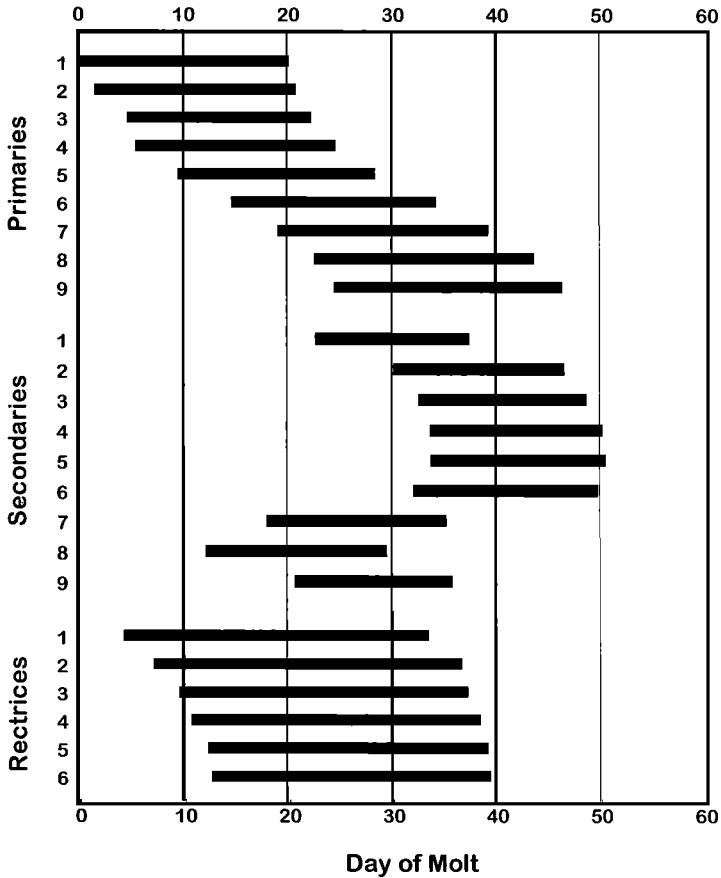


FIGURE 11.2. Timing and duration of growth for individual flight feathers during the postnuptial molt in *oriantha*.

Postnuptial molt

Postnuptial molt began about when the first primary (P_1) was shed and this easily observed event was used to mark its onset. Molting proceeded centrifugally in the wing from P_1 through P_9 , and soon the other flight feathers, the secondaries and rectrices (Fig. 11.2), along with the body feathers began to be replaced. During the first six weeks of molt we found that up to seven primaries could be growing simultaneously (Morton and Morton 1990, Morton 1992a), although the number was usually between two and five. Molt of body feathers peaked in intensity about midway through the molting period (Morton and Welton 1973).

While in molt, adults remained on their breeding territories, but they were quiet and unobtrusive and spent much of their time within and beneath vegetation, especially willows. At three to four weeks into molt, when the rectrices were about half-grown and many primaries and secondaries were in various stages of growth (see Fig. 11.2), they became reluctant to fly and when released from traps they would sometimes run to cover instead of flying. Still, all those tested could fly when released from the hand. Flight was labored, however, and those in heaviest molt also showed an inability to control their momentum when landing. Upon

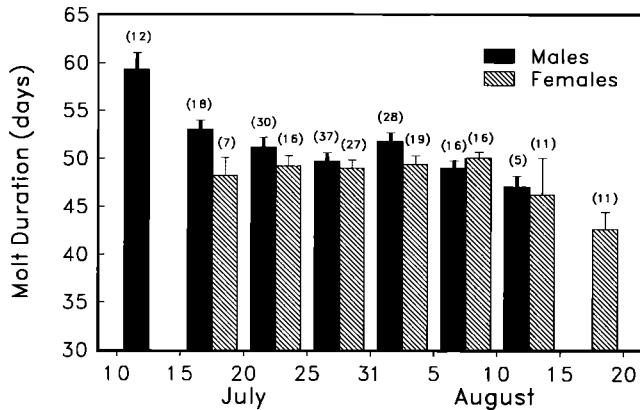


FIGURE 11.3. Duration of postnuptial molt in *oriantha* in relation to day when molt began. Bars show mean (+1 SE); sample sizes in parentheses.

approaching a perch they descended in a downward arc rather than the usual upward one. Within a few weeks after starting molt many individuals had gained 10% or more in body mass because of an increase in blood volume needed for circulation to the growing plumage (Chilgren and DeGraw 1977, DeGraw and Kern 1985). This greater mass probably contributed to their flight control problems. An additional sign of reduced mobility during the time of heavy molt was a marked decrease in trapping rates of both males and females (Morton and Morton 1990). *Oriantha* in heavy molt probably seek sheltered microenvironments in order to reduce both thermoregulation costs (due to having blood-filled quills and a sparser plumage) and vulnerability to avian predators (due to impaired flying abilities).

As can be seen in Fig. 11.2, secondaries 4 and 5 were the last of the flight feathers to complete their growth, and they did so about 50 days after molt onset. Growth in body feathers was usually also completed at about that time.

When the whole population was compared, males were found to begin molt five d earlier than females, and in 105 mated pairs mean onset was 5.5 d earlier in the males. A few females did start molting before their mates, but usually they were later (Morton and Morton 1990). In one extreme case, a female began molting 23 d after her mate (Morton 1992a). Mean duration of molt was 50.9 d (SD = 5.3 d, N = 148) in males and 48.2 d (SD = 4.5 d, N = 107) in females. This difference of 2.7 d was highly significant ($t = 4.28$, $P < 0.001$).

Date of postnuptial molt onset varied in the population by more than a month, and there seemed to be an underlying seasonal component to its duration. For example, the longest mean duration, 59.2 d, occurred in males (N = 12), that started before 15 July (Fig. 11.3). Eight of these males were known to be one-year-old non-breeders or floaters. Floaters also molted earliest in *gambelii* (Wingfield and Farner 1979). The shortest mean duration of molt, 42.9 d, occurred late in the season in females (N = 11) that started molting after 15 August (Fig. 11.3). Although delayed in their molt, probably because of stimuli emanating from the young and/or interactions with mates, as well as high gonadal steroid levels, all of which can delay the onset of postnuptial molt almost indefinitely (Hahn et al. 1992, Nolan et al. 1992), when released from parental care, these females were

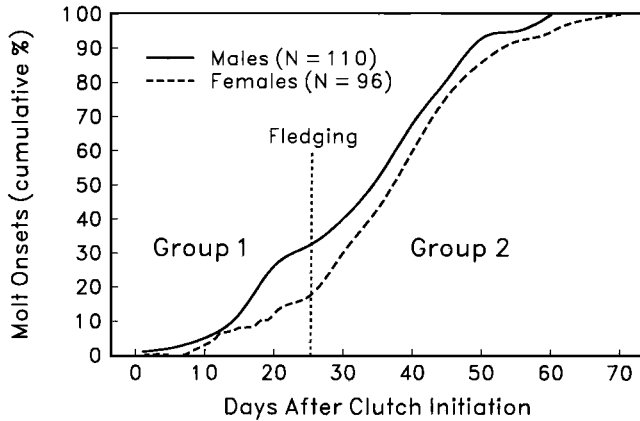


FIGURE 11.4. Onset of postnuptial molt in *oriantha* in relation to reproductive schedule. All data were obtained from mated birds and their date of molt onset was standardized by setting it in relation to the date of the first egg in their last nest of the season. Note that Group 1 birds were ones that started molting at any time before fledging of their young had occurred and Group 2 birds began molting at any time after fledging had occurred.

able to accelerate their molt and to catch up with other members of the population. There is evidence that a trade-off could be involved in this type of response, however. Dawson et al. (2000) have shown that accelerated molt in European Starlings (induced experimentally with shortened daylengths) results in the growth of poorer quality plumage. They suggest that this could diminish survival through decreased flight performance and increased thermoregulatory costs.

Overlap of molt and reproduction

Migrants have traditionally been characterized as proceeding step-wise through three major events on their summering grounds: reproduction, molt, and pre-migratory fattening. Because each of these involves major physiological and morphological changes and entails considerable time and energy expenditure, it has been usually assumed that there should be selection for their temporal separation (Farner 1983, 1986). Field studies have begun to show, however, that substantial overlap in reproductive and molting schedules sometimes occurs (Payne 1969, 1972; Verbeek 1970, Foster 1975a, Samson 1976a, Morton and Morton 1990, Hahn et al. 1992, Underhill et al. 1992, Hemborg 1999a). In *oriantha*, for example, about 20% of the females and 30% of the males began molting before their nestlings were fledged (Fig. 11.4). A few males even dropped P_1 while their mates were still ovulating. However, no females were known to start the molt until laying had been completed. Allowing for the period of post-fledging parental care (about three weeks), and assuming that both parents cared for fledglings, then molt and reproductive efforts actually overlapped in 71% of the females and 76% of the males. This was an unexpected result and it was motivation to look further into the data on molt timing and progression.

One approach was to compare molt parameters in adults known to be heavily engaged in reproduction while molting, designated as Group 1, with another that had less overlap between the two, Group 2 (Fig. 11.4). The time of fledging was established arbitrarily as the dividing point between the groups because beyond

TABLE 11.2. PARAMETERS OF POSTNUPTIAL MOLT IN GROUP 1^a AND GROUP 2^b *Oriantha* AT TIOGA PASS

	Group 1 ^a			Group 2 ^b			P
	Mean	SD (d)	N	Mean	SD (d)	N	
Males							
Molt onset date	28 July	6.9	36	31 July	7.6	74	ns
Molt completion date	17 Sept	8.0	36	19 Sept	7.6	74	ns
Molt duration (d)	51.1	4.6	25	50.4	5.8	51	ns
Females							
Molt onset date	1 Aug	8.6	18	4 Aug	9.6	77	ns
Molt completion date	20 Sept	9.2	18	20 Sept	9.3	78	ns
Molt duration (d)	49.9	4.9	18	47.1	4.8	47	0.048

^a Molt began prior to fledging of their young.

^b Molt began subsequent to fledging of their young.

that time parental effort decreased as the fledglings learned to feed themselves and because there was often uncertainty about the efforts of male parents during the postfledging period. Note that in Group 1 birds the temporal overlap between molt and reproductive activities could be on the order of 30–40 d, well over half of the molting period. In Group 2 birds, overlap could range from zero to a maximum of about 20 d.

In terms of molt timing (onset and termination) and duration, there were no differences between Group 1 and Group 2 males (Table 11.2). There were no differences in timing in females either, but molt was extended in duration by 2.8 d in Group 1 females, a significant difference (Table 11.2).

Molt characteristics of individuals also indicate that a few Group 1 males and females that were feeding fledglings were being stretched energetically. Although it began on time, their molt was greatly slowed or arrested, at least during the first 17 days. Some Group 1 individuals had only just shed P₃ at that juncture instead of being on the pace of those in Group 2, which were already growing in P₆ (Fig. 11.5). So there were signs that molt was sometimes slowed when *oriantha* were concurrently engaged in parental care. This is not surprising. The co-occurrence of increased self-maintenance costs (feather growth and thermo-regulation) and season-high foraging efforts, all the while in a condition of compromised flight efficiency, would seem certain to impose substantial energy balance problems.

One way to evaluate the energetic costs associated with life history events is to track changes in body mass associated with them. For example, female *oriantha* become extremely lean when feeding young, and are undoubtedly in or near negative energy balance during that time (Morton et al. 1973, Morton 1976). Males were also lean, but they began recovering mass about a month sooner than females. In addition, opposing patterns emerged when body mass changes in Group 1 birds were compared to those in Group 2. Group 1 females were lighter than those in Group 2 and since the former had much more overlap between molt and parental duties than the latter, this does not seem illogical; engagement in two energetically costly functions simultaneously might easily produce this result. Group 1 males, however, were consistently about 1 g heavier throughout the whole molting period than those in Group 2. This can be interpreted to mean that

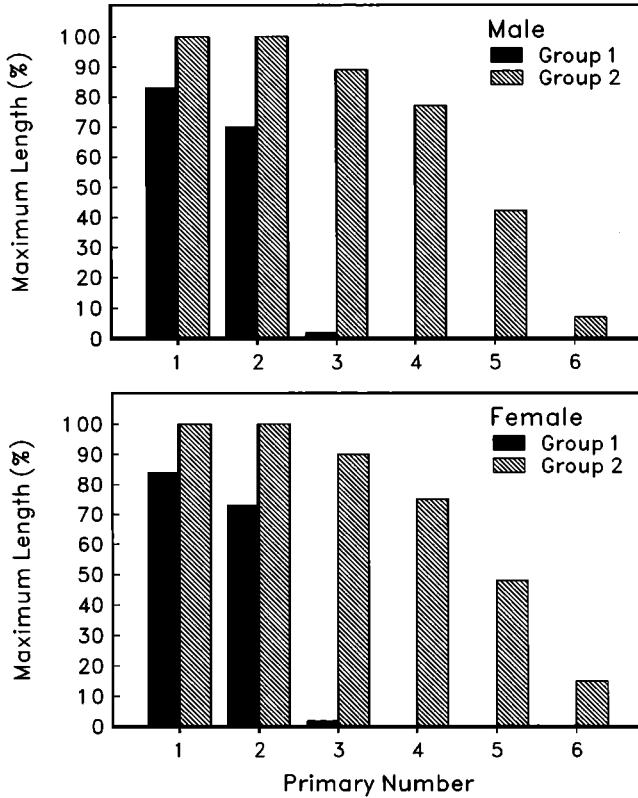


FIGURE 11.5. Percentage of maximum length attained in primaries 1–6 on 17th day of postnuptial molt in two males (one of Group 1 and one of Group 2, upper panel) and two females (one of Group 1 and one of Group 2, lower panel).

parental care declined or ceased altogether in males that began molting in the pre-fledging period. Lacking help from mates, females catabolized even more of their own tissues than usual in order to raise the young. If this construct is true (and it should be emphasized that parental feeding efforts by Group 1 and Group 2 individuals have not been well-quantified), then one might expect reproductive success to be lower for Group 1 birds. And it was. Males had significantly fewer nests that fledged young (Group 1 = 52.9%, Group 2 = 74.9%), and fewer chicks were fledged per nest (Group 1 = 1.29, Group 2 = 2.49). Similar effects were observed in females: 61.1% vs. 79.2% and 1.72 vs. 2.54 (Morton and Morton 1990). Group 1 birds, of course, were mostly individuals attempting to renest toward the end of the season because they had been unsuccessful in their earlier attempts. Apparently reduced success was better than none at all. Note that this lower success could have been influenced by seasonal tendencies for clutch size to be reduced and declining food supplies, as well as a molt-parental care conflict.

To summarize: If a pair was still attempting to bring off a brood in mid-summer or later, they were likely to have an overlap between their reproductive efforts and molting because the onset of molt was usually not delayed. This had fitness consequences because those birds that started molt in the pre-fledging period (Group 1) were less successful than those starting it in the post-fledging period

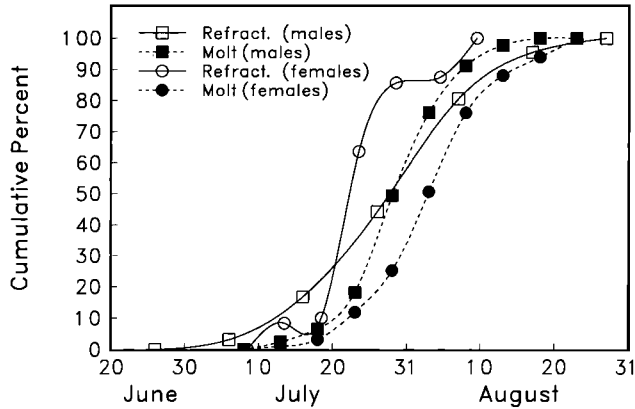


FIGURE 11.6. Temporal alignment of onsets of photorefractoriness and of postnuptial molt in male and female *oriantha*.

(Group 2). It is suggested that this occurs, at least in part, because molting males reduced their parental care (Chapter 8) and females were then unable to provide adequately for the whole brood on their own.

Molt and photorefractoriness

The foregoing shows that no fixed phase relationship existed between reproduction and molt onset, and that molt could begin at any time once egg laying had occurred. On the other hand, no female in molt, even in its earliest stages, ever initiated a nesting cycle. This argues that molt begins after reproductive capability has ended, in other words, at the same time as, or after the onset of photorefractoriness, but never before it. This agrees with the generalization of Nicholls et al. (1988) that the onset of molt signals that the bird has already entered the refractory state.

The graphical representation of refractoriness onset, as shown by testicular involution for males and decline in clutch initiations for females, and of molt onset, with all functions shown as cumulative percentages of occurrence through time, indicates that the two occurred nearly simultaneously in males (Fig. 11.6). In females refractoriness clearly led molt, often by about 10 d. This is in general agreement with Wingfield and Farner's (1978a) observation that molt follows gonadal regression in *gambelii*. Dawson and Sharp (1998) have discovered that prolactin secretion is at its seasonal maximum in European Starlings when refractoriness and postnuptial molt occur. They suggest that prolactin does not itself cause refractoriness but it may accelerate gonadal regression and it is required for the induction of molt.

As noted above, the onset of photorefractoriness was independent of reproductive stage because it could occur at any time in the nesting cycle. Since postnuptial molt began with refractoriness, or followed closely on its heels, it too should show independence from reproductive activities. We found, in fact, that the majority of the adult population was simultaneously involved in rearing young to independence and in replacing their worn plumage. This is contrary to a long-standing paradigm which suggests that these energetically costly events should not have overlapping schedules (Kendeigh 1949; Farner 1958c, 1964). The sup-

position has been that breeding birds must struggle to maintain a positive energy balance. In fact, this may not be so. As King and Murphy (1985) have warned, the limits of tolerance of organisms to nutritional and energetic demands have often been underestimated, and it is best to evaluate them under natural conditions in order to reveal their true scope.

It is my perspective that the terminology traditionally used to discuss the reproduction–molt overlap issue has been used a bit too vaguely for at least 50 years now. The contention that these two are usually separated temporally seems actually to mean that molt does not occur until reproductive *capabilities* have been lost. In other words, molt does not take place until gonadal regression or photorefractoriness has occurred, which seems to be true. The underpinnings of this logic are that it is more efficient to separate energetically expensive events than to have them co-occur, but its purveyors are ignoring the fact that birds can be heavily engaged in reproductive *activities* well beyond the time when they become refractory. I propose that if molt occurs at any time from nest building through feeding of fledglings, that it be described as overlapping with reproduction. Furthermore, I predict that many more cases of overlap will be found in temperate zone breeders as the data come in from other field studies (see Hahn et al. 1992).

Under what circumstances would this overlap be expected? As pointed out by Foster (1975b), if sufficient resources are present, then species may evolve a temporal pattern wherein costly events occur simultaneously, energy is simply allocated between them. This pattern should be highly adaptive in environments such as high altitude and high latitude where summer is relatively brief, providing that food is abundant. One promising line of inquiry has already been utilized, the examination of molting patterns in species with large latitudinal breeding ranges. For example, Mewaldt and King (1978) found that postnuptial molt duration decreased as latitude increased in *nutalli* and *pugetensis* living along the Pacific coast. Molt took 83 d at 35.2°N and only 47 d at 48.9°N. This was a decrease in duration of 2.6 d per degree of latitude. Underhill et al. (1992) observed that onset of molt was delayed by 3.5 d per degree of northward progression in Willow Warblers in Europe. Furthermore, there was overlap between breeding and molt at the higher latitudes. Reproduction and molt can be lengthy affairs and if they overlap instead of occurring end-to-end, considerable time can be saved, time that is potentially available for reproduction attempts and, at the end of the season, for fattening and migration prior to arrival of winter conditions.

Postjuvenal molt

Soon after fledging, at about 12–14 d of age, the last traces of natal down disappeared and young *oriantha* assumed their juvenal plumage. This plumage was never present in a completely finished condition, however, because many of the flight feathers, especially the rectrices, were not fully grown in before replacement of the natal body feathers was initiated by the postjuvenal molt (Morton et al. 1972b). Apparently, this pattern is pervasive in fringillids, having been observed in all 11 species studied by Sutton (1935).

To evaluate accurately the progress of molt, one must examine repeatedly the plumage of the same individuals. After many years of trapping, good information was obtained on the parameters of postjuvenal molt in *oriantha* of known age.

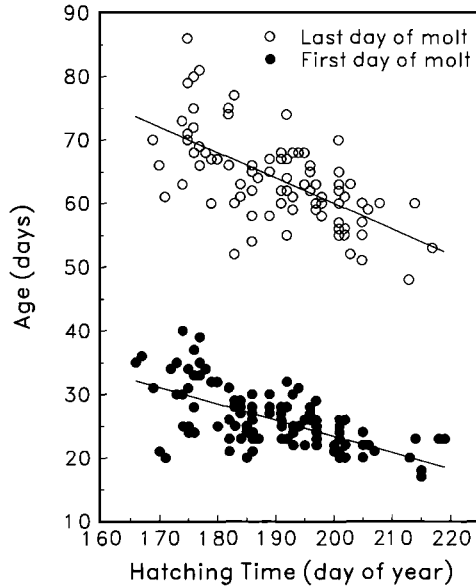


FIGURE 11.7. Age (in days) at onset and termination of postjuvinal molt in *oriantha* in relation to day of birth (hatching time). Data are from 136 individuals. Regression lines were fitted by least squares.

We found, for example, that this molt had about the same seasonal schedule as the postnuptial molt (Morton 1992a), and that a regular relationship existed between days of age and the growth of brown feathers into the crown (Morton et al. 1991).

Mean age at molt onset for all birds examined was 26.0 d (SD = 4.8 d, N = 110), and mean age on the last day of molt was 63.8 d (SD = 7.1 d, N = 87). The difference between these two means, 37.8 d, can be taken as a measure of postjuvinal molt duration. Another measure, and probably the best one, was obtained when both the first and last days of molt were known in the same individuals. This was 37.2 d (SD = 5.3 d, N = 62). These durations were in close agreement and were both substantially longer than the one of 32.4 d found in seven captives (Morton et al. 1972b). This was not a major surprise because the caged birds were fed an *ad libitum* high-protein diet and they even fattened somewhat because of the energy surplus. One result from these investigations of free-living birds was surprising, however. It was discovered that the later in the season that a bird hatched, the younger it was when its molt began and ended (Fig. 11.7). Late-hatched young began molting about 13 d of age earlier and completed molt about 18 d of age earlier than those hatched at the beginning of the season. (The five-day difference between these two measures suggests that molt duration also decreased seasonally, but the difference was not statistically significant, $P = 0.060$).

The younger age of molt onset in juveniles with seasonal progression indicates that their response was not strictly developmental; in other words, it was not the result of a genetically-based program that was expressed at a certain age. Rather, the flexibility in onset suggests that environmental factors were serving to cue

the beginning of molt. The obvious candidate in this case, because of the time period in question, would be decreasing daylength. Might young birds, only a few days old, be sensitive to this environmental signal? Evidence is accumulating which suggests that this could be the case. For example, Berthold et al. (1970) and Berthold (1988) showed that development, including molt, of hand-raised juvenile Blackcaps (*Sylvia atricapilla*) and Garden Warblers (*Sylvia borin*) could be speeded up by either an increasing or decreasing photoperiod. Additionally, Kroodsma and Pickert (1980) found that the song-learning period of Marsh Wrens (*Cistothorus palustris*) varied substantially with hatching date; those born late in the season delayed their learning until the next spring when the adults had resumed singing. And, directly relevant to the *oriantha* study, postjuvinal molt began at an earlier age (by 17.5 d) and took less time (by 6.5 d) in young Marsh Wrens held on a simulated August photoperiod than in those held on a June photoperiod. Previously, Haukioja (1969) had stated that postjuvinal molt occurred more rapidly in Reed Buntings (*Emberiza schoeniclus*) born late in the season, although no corroborating data were presented. In adult *gambelii*, postnuptial molt and autumnal fattening occurred more rapidly as days became shorter, helping late-starting individuals to be prepared on time (Moore et al. 1982). So the molt-accelerating effect of decreasing daylengths occurs in adults as well as juveniles. Lastly, a series of experiments designed to reveal the ontogeny of photorefractoriness in European Starlings showed that they could distinguish between long and short days early on, even before three weeks of age (Dawson and McNaughton 1992, McNaughton et al. 1992).

There is a long-standing hypothesis that autumnal events in migrants are cued indirectly by increasing photoperiods experienced in the spring (Farner 1964, Farner and Follett 1966). This paradigm cannot apply to juveniles, of course, because they are not even alive until later in the summer and they usually go through the first sequence in their life of molt, fattening, and migration while experiencing only decreasing photoperiods.

TIMING OF SEASONAL BREEDING

Cockrem (1995) has proposed a model to explain the timing of seasonal breeding in birds. It suggests that most or all of them are photoperiodic and possess an internal rhythm of reproduction that is synchronized with the environment by external factors. He suggests that avian breeding seasons begin with recovery from photorefractoriness in late autumn or early winter and are timed thereafter primarily by daylength increases following the winter solstice, with supplementary information being derived from social cues, food availability, ambient temperature, etc.

Given our current knowledge, this model is sensible and appealing, but it would have greater utility, and be more unifying, if it were expanded to account for the biology of hatching-year birds along with the major events in the annual cycle. Without this we are left to wonder if the young birds are supposed to have a unique control system that is used only once (to time their first schedule of molt, fattening, and migration) then discarded for something different when they become adults. This seems unlikely. The data on Blackcaps, Garden Warblers, Marsh Wrens, Reed Buntings, European Starlings, and Mountain White-crowned Sparrows all indicate that decreasing photoperiods have functional consequences in

young birds such as repression of gonadal activity, rescheduling of the sensitive period for learning conspecific song, and stimulating the early onset and/or increased pace of molt (the latter so that late-born young can catch up and migrate at the appropriate time).

I suggest that Cockrem's model might be modified to give it broader applicability as follows: Birds have a genetically controlled circannual rhythm of sequentially arranged components that are cued both by increasing and decreasing photoperiods (Aschoff 1955; Gwinner 1977a, 1986, 1996). All the major events of the annual cycle are included in this rhythm and their expression is dependent upon neuroendocrine axes that are finely tuned in their activity by proximate, ecological conditions. Furthermore, this rhythm begins at a very young age, in the egg or at hatching. Young are born in the photorefractory condition (see Dawson and McNaughton 1992) and perceive daylength changes from the beginning. Their first molt, fattening response, and migration departure are all cued by the (usually decreasing) photoperiod. Eventually, upon sufficient exposure to the short days of late autumn, they become photosensitive and are now in phase with adults. The rhythm then continues, more-or-less in synchrony for all members of the population, regardless of age, through the remainder of life.

PREMIGRATORY FATTENING

Birds commonly fatten prior to their initial migratory movement from wintering or summering areas and during pauses or stopovers that occur along the way. The positive energy balance required for this response is achieved by an active, hypothalamically-regulated hyperphagia which leads to fat accumulations that can approach 50% of total body mass in some species (Kuenzel and Helms 1967, 1970). This impressively obese condition is highly adaptive because the fat is both fuel for flight and a buffer against bad weather and uncertain food supplies that are sometimes encountered (King and Farner 1965). The pattern of fattening in relation to migration itinerary is highly variable (King 1972) but, in general, increased lipid stores are associated with increased speed of migration and with greater flight and migration distances (Berthold 1975, Blem 1990, Kaiser 1992). Hyperphagia and lipogenesis are facilitated throughout the migration period by a hormonal milieu that involves elevated levels of corticosterone (Holberton et al. 1996).

Premigratory hyperphagia, as expressed by rapid weight gain, began near the end of the postnuptial molt in *oriantha* adults. The best way to detect this phenomenon was to examine and weigh repeatedly the same individuals at short time intervals, daily if possible. Data from one such frequently captured male illustrate this principle (Fig. 11.8). It can be seen that this male (band number 125135996) was present on the study area for six years (1980–1985). During that time, he began molting between 23 July and 1 August and finished between 11 and 28 September. Because of changes in blood volume, his body mass increased slightly then decreased during the molting period. Recapture intervals became lengthened at mid-molt, a time when *oriantha* were often relatively immobile and reclusive. Every season, as the molt waned, body mass of this male veered to an upward trajectory. Presumably this was the result of a shift to a new and higher set point for appetite. Close inspection of the body mass records reveal that this regulatory change must have occurred suddenly, perhaps within a single 24-hr period.

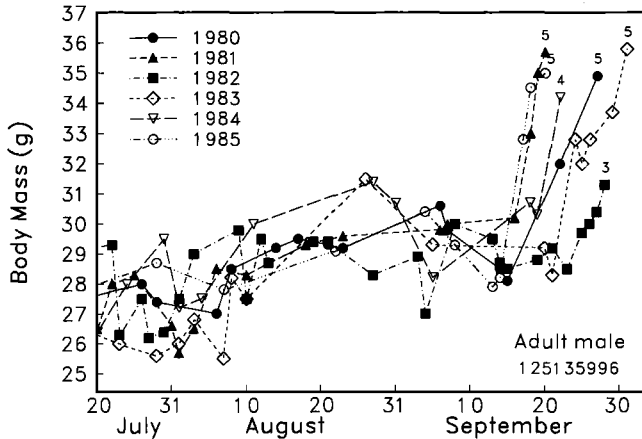


FIGURE 11.8. Changes in body mass of an adult male *oriantha* during six seasons from the time that molt began to when premigratory fattening and migration occurred. Numerals indicate fat class on the last capture of the season.

This insight on the switch to hyperphagia is different from the one that might be gathered from perusing the records of body mass in captives. In them mass appears to increase much more gradually than in the wild birds. There are several reasons for this: captives tend to put on fat in the presence of *ad libitum* food, even before they are hyperphagic; they have traditionally been weighed only at weekly or, at the most, semiweekly intervals; and, despite asynchronies in their schedules, their body mass changes have usually been presented collectively as means. In combination, these factors tend to portray mass gain in hyperphagic birds as being more gradual than it actually is (King et al. 1965, Morton et al. 1973). Much the same method of presenting body mass changes has also obscured how suddenly appetite is re-set in hibernators as they prepare metabolically for hibernation (Morton 1975; Mrosovsky 1975, 1976).

In recent years there has been an attempt to discover if food intake in White-crowned Sparrows is affected by various metabolites and hormones. In many of these experiments feeding activity was either undisturbed or inhibited. Cholecystokinin injections, for example, suppressed food intake (Richardson et al. 1993). In another set of experiments, feeding was unaffected by manipulations of carbohydrate metabolism and it decreased after plasma lipids were elevated through administrations of insulin and glucagon (Boswell et al. 1995). Unlike mammals, White-crowned Sparrows do not increase food intake in response to carbohydrate utilization and they appear to be more sensitive to signals from lipid metabolism than to those from carbohydrate metabolism (Boswell et al. 1996). At least one promising result has been obtained, however, and it typifies the type of information needed for understanding how environmental signals can be transduced to sudden increases in appetite. Richardson et al. (1995) found that neuropeptide Y (a member of the pancreatic peptide family that is widely distributed in the vertebrate brain) stimulated feeding when injected into the third ventricle of *gambelii*. The feeding response occurred on both short and long photoperiods, although sensitivity to neuropeptide Y appeared to be greater when the birds were being held on long days. At some time in the future it may be possible to monitor the

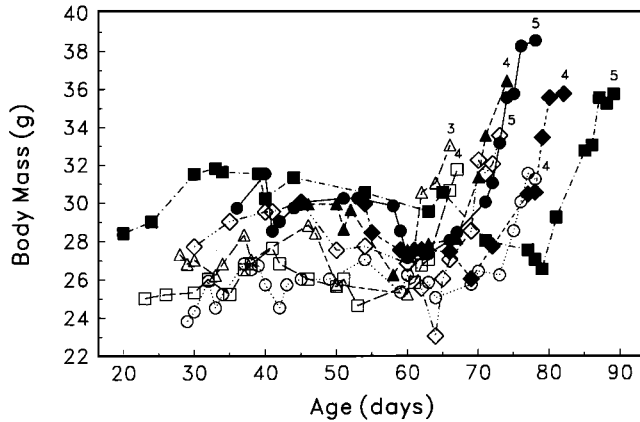


FIGURE 11.9. Changes in body mass of four male (solid symbols) and four female (open symbols) *oriantha* juveniles according to their age (in days). Numbers indicate fat class on the last capture of the season.

brain chemistry of migrants, such as *oriantha* and *gambelii*, as they transit from normal, homeostatic weight regulation to hyperphagia. Changes in neurochemical activity at that time should help us to understand how such large shifts in appetite and weight regulation can occur so quickly in migrants.

Body mass increased in *oriantha* juveniles until they reached adult size at about four weeks of age. They then completed the postjuvinal molt and eventually became hyperphagic and fattened. Data from eight juveniles (four males and four females) whose birth dates were known, and that had multiple captures, show that their fattening response had the same configuration as the one observed in adults, an abrupt inception, preceded by a slight decrease in mass that occurred at the end of molt (Fig. 11.9). The average gain per day, as a percent of initial body mass, was 2.3 to 2.6% in both juveniles and adults (Table 11.3). One exceptional juvenile male went from 26.5 to 30.4 g in 22.5 hr, a 14.7% increase. Fat classes in these frequently handled birds was usually 4 or 5 (see Table 6.3) on the day they were last captured (Figs. 11.8, 11.9).

Onset of the fattening response was not age-specific in juveniles and varied in occurrence from about 55 to 90 days of age. Mean duration of the response was eight or nine days, no matter the age or sex (Table 11.3). Females were about

TABLE 11.3. DURATION OF AUTUMNAL PREMIGRATORY FATTENING PERIOD IN *Oriantha* AND AVERAGE GAIN IN BODY MASS PER DAY (IN G AND AS % OF INITIAL BODY MASS)

	Duration of fattening period (d)			Gain in body mass per day (g)	Gain per day (% of initial body mass)
	Mean	SD	N		
Juveniles					
Males	9.29	2.84	103	0.66	2.3
Females	8.59	3.25	73	0.68	2.6
Adults					
Males	9.05	3.31	74	0.69	2.4
Females	8.22	2.88	46	0.61	2.3

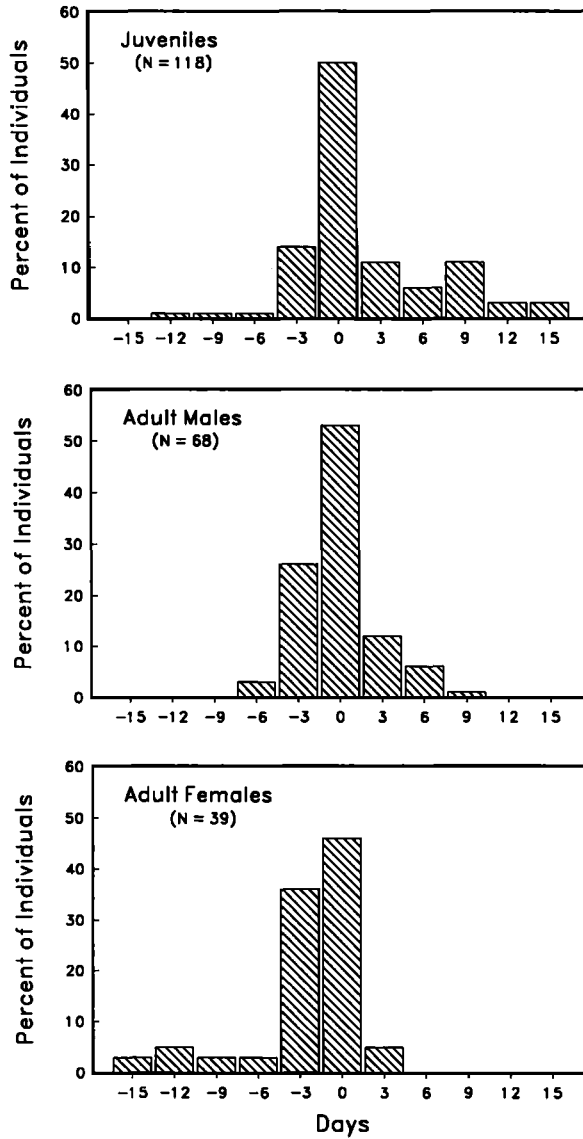


FIGURE 11.10. Onset of premigratory fattening in *oriantha* in relation to the end of molt. Negative numbers indicate days of molt remaining, day 0 equals end of molt, positive numbers indicate number of days molt had been completed before fattening began.

10% smaller than males and they tended to top out at lower masses, 32–34 g vs. 36–38 g, although individuals of both sexes and age groups were known occasionally to exceed these levels by 2 g or more.

The inflection point in the curve showing when body mass began to increase abruptly—the onset of premigratory fattening—occurred in most *oriantha*, juveniles and adults alike, just about the time when molt was being completed (Fig. 11.10). There were some cases, as in adult females rearing fledglings late in the season, where the two functions overlapped by as much as two weeks. Conversely,

molt had also been completed for about two weeks in a few juveniles before fattening began (Fig. 11.10). Still, fattening began in most birds when molt was ending and overlap between these two functions was not extensive. Molt termination itself is probably not utilized to regulate fattening onset because the two have been separated experimentally by Lindström et al. (1994). They found that simulation of autumn conditions, achieved by advancing the photoperiod by one month, did not affect molt dynamics in captive Bluethroats (*Luscinia svecica*), but fat deposition was shifted. It began early, right in the middle of molt in the experimental birds, rather than at the end, as is usual in this high latitude migrant.

Frequently retrapped, hyperphagic *oriantha* disappeared about the time their fat scores had reached class 4 or 5. Only occasionally did one in this completely fattened condition remain on the study area for even a day or two (see examples in Fig. 11.9).

MIGRATION DEPARTURE

The precise moment that any of the birds in this study began their autumnal flight to wintering areas was unknown. Yet this time could be deduced to within a day or two from frequently trapped individuals because, as stated above, they were seldom recaptured after reaching a peak mass. They fattened and left. This would seem to be a highly suitable response because birds should not depart until well supplied with energy reserves, nor should they linger, once appropriately obese, since fat reserves are costly to maintain (Hurly 1992).

Migration dynamics were obtained during seven years wherein trapping (using seed for bait) was conducted three to five days a week through the time in October when all *oriantha* had disappeared from the study area. As a result, migration departure dates were determined for 241 juveniles and 199 adults. Their frequency of departures, according to calendar date, occurred in approximately normal distributions for both age classes (Fig. 11.11). There was no difference in migration schedule for males and females within the two age classes, but juveniles, on average, did leave 3.2 d earlier than adults (Morton and Pereyra 1994). The earliest departure was 8 September and the latest was 23 October. Both of these birds were juveniles. The range in departure dates was 45 d for juveniles and 37 d for adults, with most of the variation being traceable to interannual differences in reproductive schedules. Departure was delayed about one day for every two days that nesting had been delayed earlier in the summer by environmental conditions such as a persisting snow cover. Over the seven-year period, mean departure date varied by about 14 d in juveniles and eight d in adults. Consistent with the differential of 3.2 d mentioned above, mean departure date of juveniles was earlier than that of adults in six of the seven years.

Departures did not follow a predictable, repetitive pattern. In some years their frequencies resembled a normal distribution, in others it was bimodal or multimodal. One year a mass exodus occurred just ahead of a fierce snowstorm. Usually, though, there was fair weather when individuals set off and the number of birds visiting seed-baited traps dwindled steadily through time.

Mean age of juveniles at their time of departure was 76.7 d (SD = 7.2 d, N = 43). It ranged from 64 to 98 d and appeared to have no central tendency (Morton and Pereyra 1994). This ability of individuals barely two months of age to fatten and migrate at the regular time, rather than being delayed into late

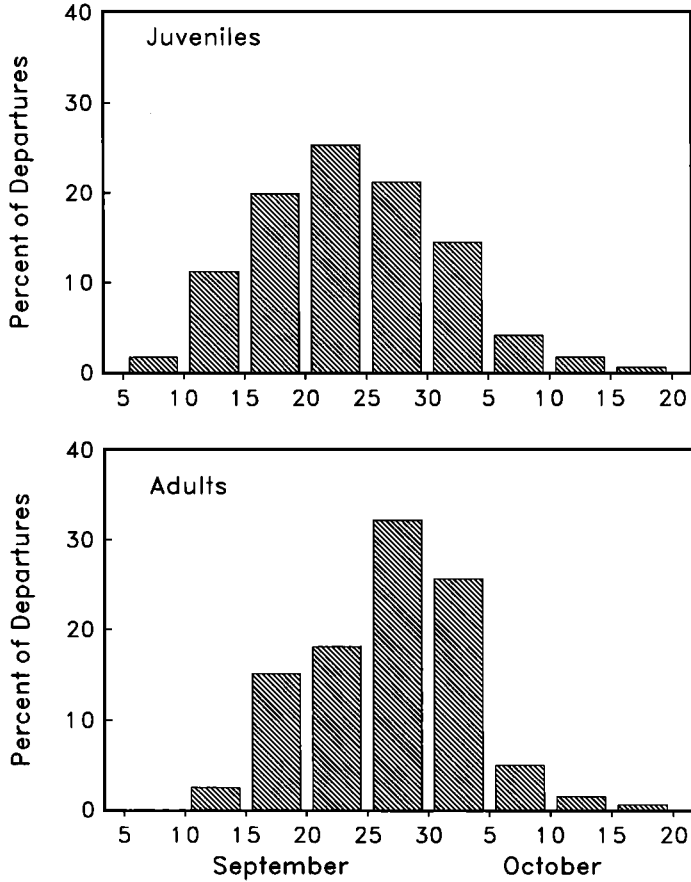


FIGURE 11.11. Migration departure schedules of juvenile ($N = 241$) and adult ($N = 199$) *oriantha*; seven yr of data.

October or early November, can be tied to the earlier observation that late-born young appear to be stimulated by decreasing daylengths to begin molting at an early age.

An overview of migration departure dates for the various age classes in the population shows that although juveniles tended to migrate ahead of adults, age was not a determining factor among adults of either sex (ANOVA $F_{5,122} = 1.08$, $P = 0.38$ for males; $F_{4,75} = 0.13$, $P = 0.97$ for females; Table 11.4).

THE STIMULUS FOR MIGRATION

The preceding data show clearly that *oriantha* did not tarry on the breeding meadows once they had fattened. Upon achieving what must have been energy reserves sufficient for their southward journey they departed, probably individually or in small flocks because dates of last captures were usually well spread out.

According to current wisdom, the urge to migrate in autumn is the expression of a genetically controlled circannual rhythm that is phased by the photoperiod so as to maintain its long-term accuracy (Gwinner 1971, 1977b, 1986, 1990, 1996;

TABLE 11.4. JULIAN DATES FOR MIGRATION DEPARTURE AND BODY MASS AT DEPARTURE IN *Oriantha*, ACCORDING TO YEAR OF AGE

Age	Males					Females				
	Departure date		Body mass (g)		N	Departure date		Body mass (g)		N
	Mean	SD	Mean	SD		Mean	SD	Mean	SD	
0 ^a	266.8	7.4	34.4	2.4	140	267.7	7.7	31.6	2.1	101
1	270.2	6.7	35.1	1.8	60	269.7	6.7	31.7	1.9	48
2	269.1	5.6	35.0	2.0	37	271.7	5.2	31.8	1.8	21
3	273.8	6.2	35.5	2.8	13	263.0	0.0	32.4	0.0	1
4	271.3	5.3	34.4	1.9	9	270.6	9.2	32.0	1.7	5
5	268.0	4.2	32.4	2.6	2	274.0	0.0	30.7	0.0	1
6	267.5	6.4	35.9	1.3	2	—	—	—	—	—

^a Juveniles.

King and Farner 1974; Berthold 1975, 1988; Gauthreaux 1996). So strong is this rhythm that captives kept lean by food deprivation will still show intense nocturnal locomotor activity, or *Zugunruhe*, the behavioral analog of migratory movement that is exhibited by individuals restrained in cages (King and Farner 1963, Lofts et al. 1963, Gwinner 1968, Berthold 1977). Pertinent to the present study is an older idea, one which proposes that achievement of a favorable migratory condition or disposition (in this case, being obese) could cause the release of migration behavior (Farner 1955a). Coalescing these ideas with the *oriantha* data leads me to suggest that an endogenous rhythm is involved in both the metabolic preparation for migration and in the propensity for migration behavior to be expressed, but the stimulus for beginning the journey itself is provided in free-living birds by the acquisition of appropriate amounts of stored fat. This could be facilitated, for example, by feedback from fat depots or from levels of circulating lipids.

Other than fattening, metabolic preparation for migration might also involve increasing the oxygen carrying abilities of the blood (important for skeletal muscle function during migration flights) through synthesis of additional erythrocytes. Wingfield and Farner (1980) found, for example, that hematocrit (packed erythrocyte volume) increased from about 52 to 57% during vernal migration in *gambelii*, a long-distance migrant, but did not increase in *pugetensis*, a short-distance migrant. *Oriantha*, a medium-distance migrant, had high hematocrits (57 to 59%) upon arrival at Tioga Pass and these then decreased and remained stable through the summer nesting period. Hematocrit dropped again during molt, in late July and August, to about 49%, then increased in late September to about 55% (Fig. 11.12). Some of this late-season increase was probably due to restoration of pre-molt plasma volumes, but increased erythropoietic activity could have been contributing as well. Interestingly, Lee (2000) discovered that hematocrit varies with photoperiod. It averaged 51% in *oriantha* held on short days (8L:16D) and 54% in those held on long days (16L:8D).

STOPOVER MIGRANTS AND THE MIGRATION SCHEDULE

In seven years TPM was trapped regularly during the fall months until all *oriantha* had disappeared. Other *Zonotrichia* that were stopping over during southward migration were also captured during that time. Nearly all of these were *gambelii* (which sometimes joined with *oriantha* to form mixed flocks), but a few

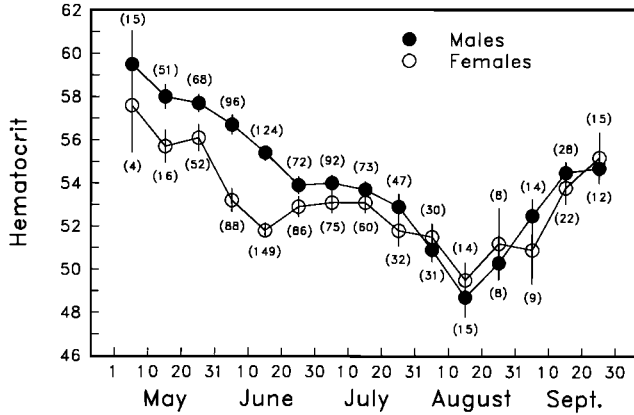


FIGURE 11.12. Seasonal changes in hematocrit of adult *oriantha* at Tioga Pass. Means \pm 1 SE; sample sizes in parentheses.

Golden-crowned Sparrows were also handled in most years and once a Harris's Sparrow. No *oriantha* were captured in autumn passage. Apparently those that summered to the north flew beyond Tioga Pass before stopping.

First captures of the season for stopover *gambelii* ranged between 7 and 17 September, with the mean date being 11 September. Dates of last captures for the season ranged between 5 and 23 October, with the mean being 11 October (Morton and Pereyra 1987). During September and October, therefore, both *oriantha* and *gambelii* appeared regularly in traps although from early October onward the majority of those captured each day were *gambelii* (Fig. 11.13). During their stopover period, which decreased in duration from an average of 7.6 d in early September to 2.5 d in late October, about 70% of the *gambelii* being trapped showed an increase in fat class and body mass. In many of the retrapped individuals a phase of rapid weight gain occurred that averaged about 0.4 g per d (Fig. 11.14).

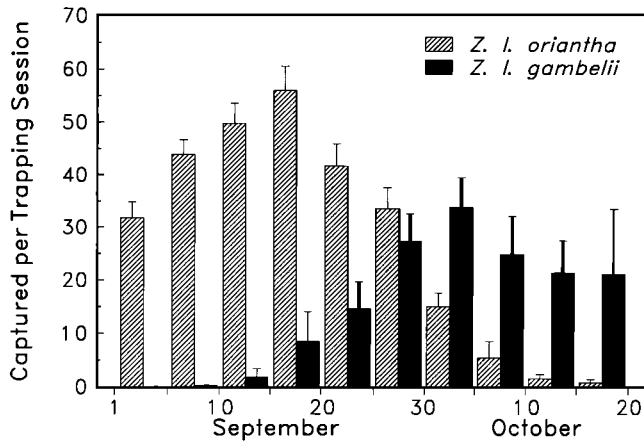


FIGURE 11.13. Mean number of *oriantha* and *gambelii* captured per trapping session on TPM in September and October during seven yr (1979–1985). Number of trapping sessions per five-day interval during those seven years ranged from six to 27. Bars show mean (+1 SE).

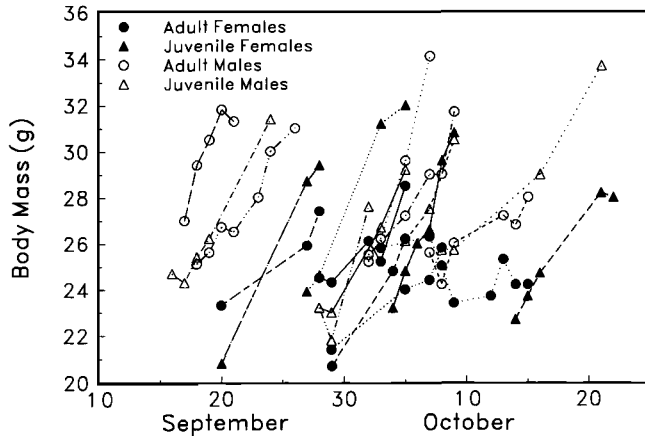


FIGURE 11.14. Body mass changes in *gambelii* retrapped during stopover periods on TPM.

Several points that are relevant to the migration biology of White-crowned Sparrows can be made at this juncture. Data from the stopover birds (*gambelii*) show that hyperphagia persisted beyond the initial episode of fattening that preceded departure from breeding areas. And, like individuals launching from summering areas, they seldom lingered once they had fattened. In other words, the initial migration movement, and those that occurred subsequently as the migration unfolded, bore close resemblance to one another when their pre-flight and departure characteristics were compared. Finally, the fact that close relatives of *oriantha* routinely stopped over on the study area well into October suggests that adequate food for a fattening response was still present on TPM after most of the *oriantha* had departed. Why not use this extra cushion of time to prolong the breeding season and produce more offspring? The answer must be that survival is poor in late-hatched young and, perhaps, in adults that must provide care for them. Insects, the primary food needed for nestling growth and nutrition, became scarce in the fall, and although seeds of grasses and sedges were often abundant, they may have been only adequate for putting on fat. In addition, ambient temperatures dropped sharply in September and October, especially nocturnal ones (Table 1.1), and molting birds, with their diminished thermoregulatory capacities, would undoubtedly have been stressed by such low temperatures. Another factor is that the frequency of potentially debilitating storms began to increase (Table 9.1). When such storms occurred they had an effect on the propensity of *gambelii* to stay in the high altitude meadows. For example, in 1984 the autumnal weather was very mild, and a total of 507 *gambelii* was captured on TPM. In 1982, on the other hand, a series of storms began in late September and only 66 *gambelii* were taken. This is not to say that survival of *gambelii* was affected in 1982. In early October of that year we surveyed the brushy thickets and weed patches that occur along the Great Basin-Sierra Nevada interface and found them there in substantial numbers. It appears that *gambelii* utilize the ripe grasses and sedges of the high elevation meadows during autumnal stopovers and if a major storm moves in they simply drop to lower elevations and continue on with their migration. But molting *oriantha* have reduced mobility and probably could not easily exercise this option. They would have to remain and endure the bad weather (one

post-molt adult male was known to have spent the day of 11 September in lower Lee Vining Canyon, following a snowstorm in the previous night). It seems, then, that the timing of autumnal migration in *oriantha* has evolved with a built-in margin of safety. They become refractory and complete the season-ending functions of molt and fattening before the frequency of bad weather begins to increase. By the time the first powerful winter storms strike the high mountain breeding areas they have already departed for Mexico thereby improving the likelihood of their continued survival and participation in subsequent reproductive efforts.

