

CHAPTER 5: Gonadal Condition

Of central importance in the biology of migratory passerines is the great change that occurs seasonally in the size and functional status of their gonads. Enlargement of testes and ovaries from a regressed, quiescent condition begins while individuals are still on their wintering areas. Development continues apace during the vernal migration (King et al. 1966), but is often only partially completed when the birds arrive on their summering areas. What happens there, as the cycle continues to full sexual capability, is an opportune time for discovering how the energetic costs to the bird of migrating with enlarging gonads are traded off with the necessity of being able to breed without delay, and how social and ecological cues interact to affect the metamorphosis of the reproductive organs.

GONADAL CHANGES

There are several ways to characterize the annual cycle of gonadal growth or recrudescence. For example, its progress in male *oriantha* on the breeding grounds was assessed by measuring the length of the left testis during laparotomy as well as by the length of the cloacal protuberance (Fig. 5.1A). The latter contains the seminal vesicles and it allows sperm to be stored externally at lower than core body temperature (Wolfson 1954). Seasonal changes in these two structures were

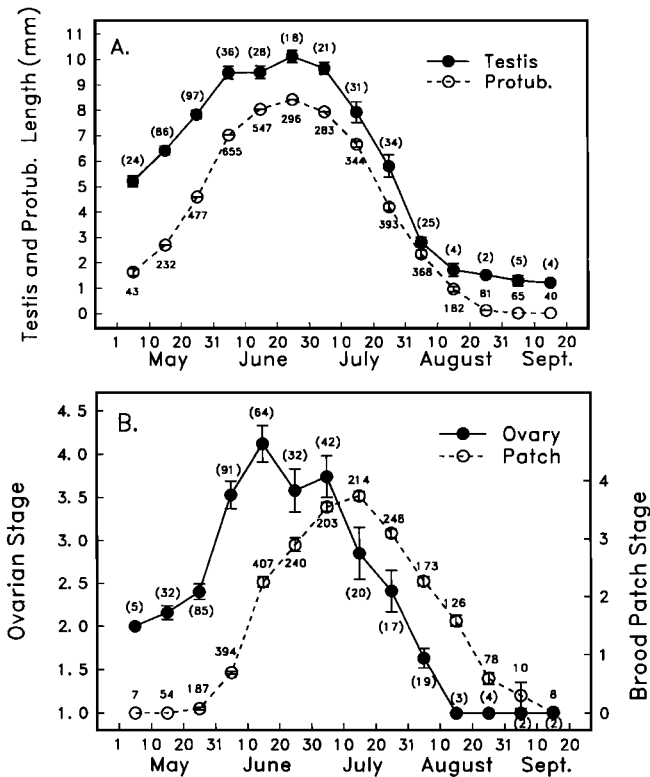


FIGURE 5.1. Seasonal changes in length of left testis and in cloacal protuberance (A) and in ovarian and brood patch development (B) in *oriantha*. Sample sizes for gonadal condition are in parentheses and those for cloacal protuberances and brood patches are without parentheses. Testis lengths and ovarian stages were determined during nine different years (by laparotomy), protuberances and patches during 22 yr.

similar and highly correlated ($r^2 = 0.605$, $df = 401$, $P < 0.001$). In females the diameter of the largest ovarian follicles were measured during laparotomy and categorized by stages as follows. *Stage 1*: follicles in winter condition; 0.4 mm or less in diameter. *Stage 2*: follicles 0.5–1.0 mm. *Stage 3*: follicles 2–3 mm; no yellow yolk. *Stage 4*: follicles 4–10 mm; yellow yolk present. *Stage 5*: about to ovulate or egg in oviduct (Fig. 5.1B). The condition of brood patches was also defined by stages (see below).

Growth of the testes continued for about a month after males had begun to arrive at Tioga Pass. They reached maximum size in June, began to regress in July, and were near their wintertime minimum by early September (Fig. 5.1A). Cloacal protuberance length followed much the same pattern. Fluctuations in protuberance size provided a rough estimate of testicular secretory activity because growth of this structure is stimulated by testosterone (Witschi 1961), and its congruence with the testicular cycle, with a slight lag, is to be expected.

Ovarian follicles grew slowly during May then increased rapidly in size as females began nesting. Their collapse to minimum size was completed by mid-August, about the same schedule observed in males. Incubation or brood patch development and regression is a function of circulating estrogen levels (Kern 1979), so, like the cloacal protuberance, its status is an easily obtained measure of gonadal activity in the bird under examination. The seasonally consistent, two- to three-week lag of patch condition behind ovarian condition (Fig 5.1B) was probably a function of both ovarian secretion rates and the time it took for the extensive morphological changes involved in brood patch cycling.

INCUBATION (BROOD) PATCH

The incubation or brood patch of White-crowned Sparrows has been described in detail by Bailey (1952). He and Hinde (1962) point out that three notable changes occur in the ventral surface of female passerines when they prepare for incubation of eggs and, eventually, brooding of nestlings: defeathering, vascularization, and edema. Loss of feathers from the ventral surface occurs four or five days before the first egg is laid. Immediately following defeathering, blood vessels in the dermis of the ventral apertium begin to increase in size and number and vessels become large enough to be seen with the naked eye. Toward the end of laying and on through incubation the dermal tissue becomes edematous and thickened.

We found that this description only applied to first nests of the season, however. If a nest was lost during incubation the dermal fluid was withdrawn, exposing large blood vessels to view, and the patch became dry and wrinkled in appearance. It became edematous again if a new nest and clutch appeared.

Through the use of implants, Bailey (1952) was able to show that exogenous estrogen could induce brood patch formation in wintering females, and that if the birds were hypophysectomized, prolactin injections were synergistic. He deduced that estrogen stimulates increased vascularity in the dermis and, when estrogen is present, prolactin stimulates defeathering and dermal edema. In a review of the endocrinology of patch formation, Jones (1971) suggested that patch formation is completed through the influence of escalating prolactin levels on the female's estrogen-primed skin.

The relationship of brood patch condition to the reproductive status of *oriantha*

females was as follows. The first loss of feathers from the distal region of the abdomen (stage 1) occurred in females engaging in their first nesting effort of the season. It was observed in females that were building nests, had nests already constructed, or, in a few cases, had even begun to lay. A completely defeathered patch, with a trace of vascularity but without edema (stage 2), was found in laying birds and those in the first day or two of incubation. Sometimes edema was already present in individuals entering incubation and they were designated as being in a stage 3 condition. Stage 4, when the patch had accumulated enough fluid to be described as moderately edematous, was noted in some females making the transition to full-time incubation. The stage 5 patch, one that was highly vascularized and fully edematous, was found in females that were well into incubation or that had hatchlings.

As the season wore on, brood patch condition changed in accordance with nesting success and, eventually, the onset of postnuptial molt. The same classification system was used but the etiology of patch condition was different. For example, the partially defeathered condition (stage 1) occurred late in the season when the patch was being refeathered during the molt. Eventually it was completely obliterated by new feathers and became stage 0, the same condition observed early in the season before commencement of nesting activities. Females with fledglings had stage 2 patches because the fluid had been reabsorbed, and those that had recently lost a nest could be diagnosed because they had regressed to a stage 3 condition, and the rich vascular bed, normally present during stages 4 and 5 but obscured by the thick layer of fluid, was now highly visible.

ROLE OF ENVIRONMENTAL CUES IN ANNUAL CYCLES

Environmental influences on annual cycles, especially those portions involving reproduction, have intrigued avian biologists for many years. Early in its history this field of study benefited greatly from a theoretical framework envisioned by J. R. Baker (1938a, b). He described environmental factors as being either ultimate or proximate in their effects on the timing of reproduction. Ultimate factors or causes give survival value to the adjustment of the bird's cycle to that of the environment and proximate factors provide the actual timing that brings the adjustment into play (Thomson 1950).

The availability of an adequate food supply for the parents and young is nearly always identified as being the most potent of ultimate factors, but others such as competition, nesting conditions, predation pressure, and weather patterns can, under certain circumstances, exert ultimate control by selecting for a breeding schedule that will maximize the number of reproductively viable young produced (Immelmann 1971, 1973). Environmental events such as those listed above occur too late in the season, however, to serve as information for timing the onset of gonadal maturation (Immelmann 1973, Rand 1973). Thus, the need arises for proximate factors that can act through the endocrine and neuroendocrine systems to provide a finer control of the correct timing and temporal sequence of stages in the reproductive cycle. This input is essential because of intra- and interannual variations in ecological conditions on the breeding grounds, variations that can affect the most propitious fit between environmental and reproductive schedule by at least several weeks in birds summering at mid- to high latitude or at high altitude. This would apply to all species migrating to rigorous climes even though the

mechanisms controlling their basic rhythm and preparation for migration and reproduction might vary from being totally endogenous to one that is driven strictly by changes in daylength (see reviews by Marshall 1960, 1961; Farner 1964, 1975, 1983; Farner and Follett 1966, 1979; Lofts and Murton 1968, Farner and Lewis 1971; Immelmann 1971, 1973; Elliott and Goldman 1981, Meier and Russo 1985).

During the last five decades there have been numerous investigations of environmental cues that are presumed to affect avian reproduction, especially those that are proximate factors since they are more amenable to testing than ultimate ones. An undesirable side effect of all this research has been the generation of considerable overlapping, redundant, and confusing terminology. This was rectified in a series of papers that systematically organized and defined the roles of proximate information, particularly as it affects reproduction in passerines (Wingfield 1980, 1983; Wingfield and Kenagy 1991; Wingfield et al. 1992). These definitions are as follows:

Initial predictive information

These factors initiate gonadal development and other vernal phenomena in anticipation of the ensuing breeding season but are insufficient by themselves to initiate nesting. They may also cause, indirectly, gonadal regression at the end of the breeding season. The most important factors of this type would be the annual cycle of photoperiod or daylength and endogenous circannual rhythms that are themselves entrained by exogenous cues such as photoperiod or rainfall (Gwinner 1986).

Supplementary information

These factors, usually perceived through visual and auditory systems (Ball 1993), supplement initial predictive information and, acting as short-term predictors, initiate the final stages of gonadal development. They help correct for inter-annual variation in environmental conditions and are crucial for coordinating the nesting phase with local phenologic progressions. They can regulate behaviors such as arrival schedules, territory establishment, and pair bonding, as well as the final stages of gonadal maturation. Inhibition or acceleration of these events can occur depending upon the immediate situation. Specific examples of supplementary factors are presence of a mate, availability of nesting sites, rainfall, ambient temperature, and nutritional plane. Together, the initial predictive and supplementary factors regulate the seasonal cycle of gonadal maturation and regression.

Integrating and synchronizing information

These factors become important once reproduction is actually under way. They serve to integrate events of the reproductive cycle so that the correct temporal sequence of nest building, copulation, oviposition, incubation, and feeding of young occurs. They also affect synchronization of the reproductive effort between members of a pair. Examples would be visual and tactile cues from the nest and eggs and auditory cues from nestlings, as well as reciprocal behavioral interactions between mates. Note that these categories are not necessarily exclusive; some factors such as interactions between the sexes could be functioning as more than one type of information.

Modifying information

These factors cause disruption of the nesting phase at any stage and are restricted temporally, by definition, to the nesting phase. Good examples of such factors would be predation and storms.

Thus far, studies of proximate factors controlling avian reproduction in North America have been focused mainly on those that provide initial predictive information, especially the photoperiod. Studies of photoperiodic effects on the gonadal cycle and associated functions, such as premigratory fattening and molt, have been highly effective lines of inquiry; they can be conducted indoors under controlled conditions, are amenable to experimental design and hypothesis testing, and often provide excellent quantitative results. Photoperiod experiments on *Zonotrichia* have been particularly productive because exposure to long days appears to be an essential requirement in their annual cycle (Follett et al. 1975, Sansum and King 1976), as well as that of many other temperate zone-breeding passerines (Gwinner and Dittami 1985). Nonetheless, the length of day provides only initial predictive information and no species of wild bird, even of *Zonotrichia*, is known to breed strictly under the influence of the vernal photoperiod; fine tuning in the form of essential supplementary information is required.

Despite enduring interest among avian biologists in proximate and ultimate factors, and continued efforts to unravel their interactions and individual efficacies, it has been much easier to postulate their roles in wild populations than it has been to actually show how they operate; it is difficult to separate cause and effect relationships when numerous, uncontrolled biotic and abiotic variables are interacting simultaneously. Conducting long-term studies of breeding birds through many annual cycles at locations with markedly variable environmental conditions, as in the present study, is one approach toward solving this problem.

PHOTOPERIOD EFFECTS

Among White-crowned Sparrows, the role of photoperiod in the control of annual cycles, such as the one in gonadal function, has most often been studied in *gambelii*. In them (and other *Zonotrichia*) gonadal development in both males (Farner and Wilson 1957, Farner 1964, Farner and Follett 1966) and females (Farner et al. 1966, Morton et al. 1985) is stimulated by long days perceived via encephalic photoreceptors. Gonadotropic activity is thought to occur when there is coincidence between the environmental photophase (daylight) and the sensitive phase of an entrained circadian rhythm in photosensitivity (Farner et al. 1981). In captive males with fully regressed testes weighing only 2–3 mg, full reproductive development, including spermatogenesis, has been routinely induced by exposure to photoperiods of 16 hr or longer for only a few weeks (Farner and Follett 1966). Peak mean mass of the paired testes in these captives was about 300–360 mg (King et al. 1966, Lewis 1975a, Farner et al. 1980), not quite as high as the 440–460 mg reported for breeding *gambelii* in Alaska and Washington (King et al. 1966). Long days are also stimulatory to ovarian growth in *gambelii*, but only from an initial mass of 5 mg up to about 50 mg (Farner et al. 1966, Morton et al. 1985). This is an order of magnitude change but still far less than the two orders that occurs in males. And the photoperiodically-driven growth of ovaries stops well short of the mean mass of 326 mg reported for females breeding

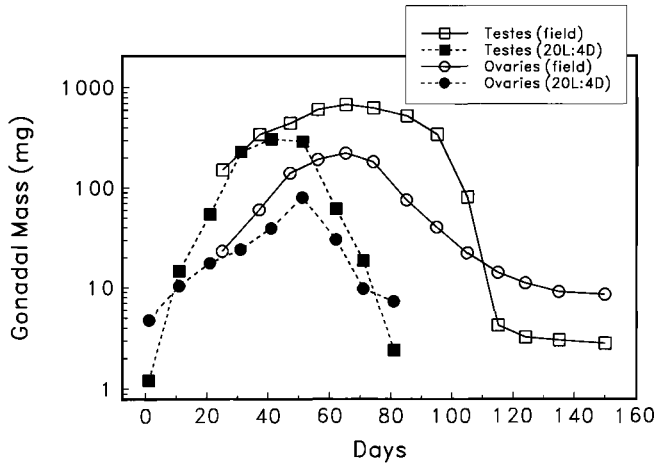


FIGURE 5.2. Mean gonadal mass in *oriantha* (log scale) collected between May and September at Tioga Pass (solid symbols) and in captives exposed to a 20L:4D regime beginning at day 0 of the abscissa. Sample sizes were 3–14 in the field and 2–5 in the lab.

in Alaska (King et al. 1966). So captive females, more so than males, ordinarily do not approach full gonadal development, as measured by changes in mass, when stimulated by photoperiod alone. There appears to be an initial phase of growth beyond which captives do not progress, at least during their first year after capture. Exposure to male song augmented ovarian growth rates in captive *gambelii*, but the final mean mass still did not exceed 50 mg (Morton et al. 1985). Life in the cage must be non-stimulatory for some reason, perhaps because of sensory deprivation and/or induction of fear (King et al. 1966). Furthermore, females are well known to be more strongly affected by modifying factors than are males (Farner and Lewis 1971). We have now learned more about how modifying and supplementary factors, all of which are non-photoperiodic, can operate in the natural setting. Next, we will pursue their importance, as revealed in our study of *oriantha*, with results from both the lab and field.

To test for the role of photoperiod, first-year *oriantha* were brought from the field to the laboratory on 30 September and placed in captivity on a short-day regime (8L:16D). On 11 December, well beyond the time required for them to become photosensitive (Farner and Mewaldt 1955), half were placed on long days (20L:4D), and the other half were retained on short days (8L:16D) as controls. For the next 40 to 50 days birds under long days exhibited gonadal growth (none occurred in the short-day birds). Involution then followed so that after 80 days of exposure, gonadal mass approached that of the controls (Fig. 5.2). Maximum mean mass of testes, achieved in the day 40 sample, was 305 mg, and of ovaries, achieved in the day 50 sample, was 80 mg (one ovary of 205 mg strongly influenced the mean).

Next to the data from these artificially photostimulated birds are juxtaposed those on gonadal mass, collected during four field seasons, at a place on the graph where gonadal size of captives and of field birds were similar. The data on field birds go from mid-May to late September and they illustrate about how much gonadal growth occurs after the birds reach their breeding areas. The mid-May

means were 155 mg for testes and 23 mg for ovaries. Based on mean maximum masses recorded during the breeding season (see below), more than 75% of testicular growth and 90% of ovarian growth in *oriantha* was post-migrational. This suggests that selection has acted to minimize the biomass that is carried during the migration itself. Some support for this view can be found in a study by Brooke (1979) on Northern Wheatears that migrate in spring to Wales. He had no actual data on gonad condition, but thought that a three-week pause that occurred between arrival and egg laying was probably necessary for development of the reproductive organs rather than for a need to build up energy reserves for egg formation.

The field birds (Fig. 5.2) had been photostimulated by shorter days than the lab birds, but for longer periods of time, so comparisons of the growth and involution schedules of the two groups is difficult. Also, one-year-old males are known to have smaller testes than older ones at all times during the reproductive cycle (Morton and Allan 1990, Morton et al. 1990). Nonetheless, substantial differences exist here that might tell us something about non-photoperiodic influences.

First, gonads of birds in the wild population grew to much larger sizes than those in captivity. Maximum mean mass in the wild was 220 mg for ovaries and 670 mg for paired testes and masses observed in individuals could be much larger. For example, on 27 June 1968 three males with 820, 849, and 976 mg testes were collected. Second, maximum mass was not retained for very long in 20L:4D birds. It is typical of captives that the longer the days they are held on, the sooner they are likely to regress once the enlarged condition has been achieved. Based on the study of Moore et al. (1983) on this phenomenon, the Tioga Pass birds, due to their exposure to natural daylengths (which are shorter), should have shown testicular regression from the photostimulated state about 10 days later than the 20L:4D birds. It was actually about 40 days later (see Fig. 5.2), so about one additional month of retention at peak functional condition occurred in the field birds beyond that expected from a purely photoperiod effect. Clearly, engagement in reproductive activities is stimulatory to gonadal growth and maintenance. Just what would some of these stimuli be?

The history of this field suggests that the fine-tuning of reproduction is achieved via complex, reciprocal behaviors between males and females, along with responses to local environmental conditions, especially by females (Lewis and Orcutt 1971; Moore 1982, 1983). To develop some understanding of this complicated mélange of stimuli, correlates of both social and ecological cues will be discussed next.

NON-PHOTOPERIOD EFFECTS

Social cues: Males

There is abundant experimental evidence that the reproductive condition of passerine males can be affected by the behavior of females. For example, Gwinner (1975) found that an endogenously programmed readiness for sexual activity in captive male European Starlings (*Sturnus vulgaris*) was enhanced when they were in the presence of females. Testicular regression was also prevented. Moore (1983) found that solicitation displays, which normally ceased during egg laying, could

be extended into the incubation period in female *pugetensis* by implanting them with estradiol. The mates of these females had significantly elevated plasma levels of testosterone and dihydrotestosterone. Moore (1983) also found that testosterone and luteinizing hormone increased in photostimulated captive males that were paired with estradiol-implanted females. These males copulated and also maintained enlarged testes for a longer time than control males paired with untreated, non-receptive females. Interestingly, males that had been maintained on short photoperiods also attempted to copulate when caged with implanted, soliciting females even though their testes were undeveloped and plasma testosterone and luteinizing hormone levels were basal. In a similar vein, Runfeldt and Wingfield (1985) found that testosterone was elevated and that territorial behavior was maintained for up three extra months in male Song Sparrows mated to females with estradiol implants. Gonadal activity and sexual behavior in male passerines, therefore, can be strongly affected by the behaviors of females.

Social cues: Females

As mentioned above, ovarian growth rates in *gambelii* were increased by exposure of females to male song during the initial phase of photostimulation (Morton et al. 1985), and it has now been shown that gonadotropin levels and ovarian development increase in *oriantha* females treated in a similar fashion (MacDougall-Shackleton et al. 2001). Aside from these studies on White-crowned Sparrows, however, there seems to be little evidence that social interactions with males affect gonadal function in females. To the contrary, the presence of a male enhanced neither estradiol secretion nor ovarian growth in photostimulated Great Tits (Jonsson 1994). Furthermore, Runfeldt and Wingfield (1985) found that although testosterone-implanted Song Sparrow males remained on territory and were responsive in song playback experiments well beyond the usual breeding season, their mates terminated reproductive activity at the regular time and went into molt. There are subtleties to the social cue-photoperiod interaction that need to be clarified, however. Specifically, a stimulatory effect of song on *gambelii* females was detectable when their schedule was 15L:9D, but not when it was 20L:4D. The latter was the same schedule used by Jonsson (1994) on Great Tits. It may be that very long photoperiods are so stimulatory to females that they swamp the relatively small effects that accrue from social input.

Ecological cues: Males

Berthold (1969) reported that testicular development was not affected in European Starlings exposed to bad weather at their breeding areas in Germany. On the other hand, exposure to prolonged spells of good weather caused advances in development of up to 10 days. He also found that testicular recrudescence was delayed in a Common Chaffinch (*Fringilla coelebs*) population prevented from arriving on their breeding area at the usual time by heavy snow conditions.

This last situation can also occur in *oriantha* when storms and deep snows converge to hinder their springtime occupancy of the breeding area meadows. In 1995, for example, we were present on the study area from 7 May onward, but no males were observed or captured until 17 May. Despite unfavorable environmental conditions, however, and unlike Berthold's chaffinches, testicular growth in these first arrivals was no different than that observed in 1988, a very mild

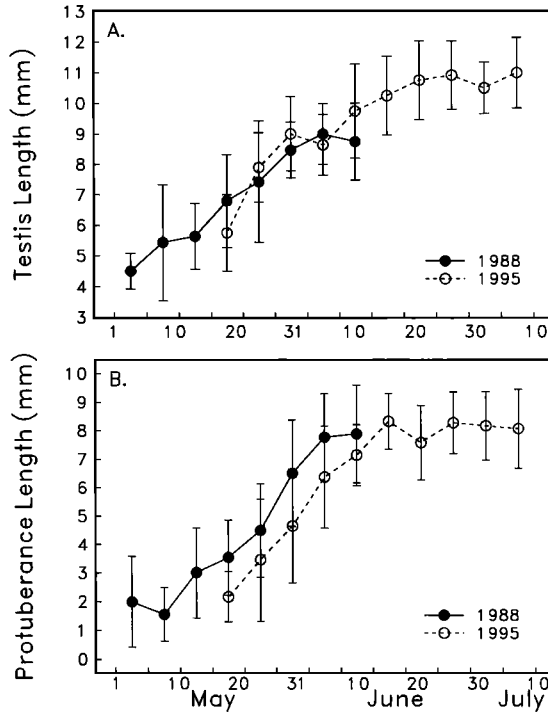


FIGURE 5.3. Testis (A) and cloacal protuberance lengths (B) in a year of mild weather (1988) and in one of inclement weather (1995). Data stop at each year when clutches were started. Symbols indicate means ± 1 SE; sample sizes = 4–8.

year when males began arriving on 3 May (Fig. 5.3A). The data in Fig. 5.3A were plotted up to the time that egg laying began at Tioga Pass, which was early June in 1988 and early July in 1995. Since males are capable of breeding well before testes reached maximum size, as in 1988, the testicular growth that occurs after migration arrival may have more to do with sperm competition than sperm viability.

Although testes were the same size during the 25-d period of overlap in May and June shown for the two years in Fig. 5.3A, cloacal protuberances were not. They lagged behind by about a week in the 1995 males (Fig. 5.3B). This suggests that testosterone secretion was inhibited in years when unfavorable weather prevented early settlement onto breeding territories. This inhibition could have been the result of a decrease in the intensity or frequency of reciprocal sexual behaviors or to the deep snowpack and weather, or combinations thereof. No additional data for passerines could be found, but testicular development was unaffected in Least Auklets (*Aethia pusilla*) forced to wait for nesting sites because of overlying snow (Sealy 1975).

Ecological cues: Females

Was gonadal maturation in females affected by environmental conditions in the same way as males? Clearly not, if one assumes that completion of this process includes ovulation and laying, functions that will not occur unless a nest is present,

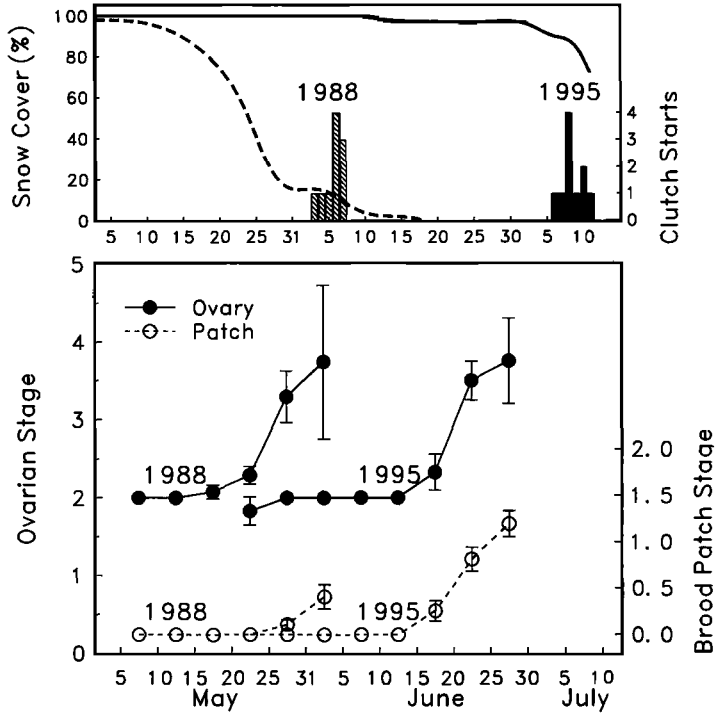


FIGURE 5.4. Upper panel: Snow cover on TPM (% of ground covered by snow) during 1988 (dashed line) and 1995 (solid line), along with dates of the first 10 clutch starts of the season on TPM for both years (histograms). Lower panel: Ovarian and brood patch development in 1988 and 1995; means ± 1 SE; sample sizes = 4–9. Data not shown beyond the time that first eggs were being laid (see upper panel).

which is an impossibility if all materials for building nests and places to hide them are buried under snow. Where then is development of the female tract arrested when breeding is long delayed? Again, the 1988–1995 comparisons are enlightening.

The schedules of snow melt-off and of the onset of egg laying for those years show that the much lighter pack in 1988 had mostly melted by early June, the time when females began to lay (Fig. 5.4, upper panel). Ovarian follicles in the 1988 females were at stage 2 in early and mid-May then began to enlarge as the time for nesting approached. Not until a few days before laying did their brood patches begin to develop (Fig. 5.4, lower panel). In 1995 the first females were not captured until 26 May and the first open ground available for nesting did not appear until the very end of June. Egg laying began almost immediately thereafter (Fig. 5.4, upper panel).

The 1995 data are important because they tell us what happens to females when nesting cannot proceed because of environmental conditions. It was pointed out previously that photostimulation causes ovaries to grow to about 50 mg in size with follicles that are usually 1 mm or less in diameter (a stage 2 ovary). This was the condition of females as they arrived on the breeding area in all years of the study, although a stage 1 was sometimes encountered. It appears that ovarian development was arrested at stage 2 for six or seven weeks in 1995 while the

females waited for conditions to ameliorate. This is far different than the response of female Least and Crested (*Aethia cristatella*) auklets. They appear unable to halt follicular maturation when nesting habitat is unavailable and will eventually lay their eggs right on the snow (Sealy 1975).

Note that brood patches developed earlier with respect to onset of nesting in 1995 than in 1988 (Fig. 5.4, lower panel). This shows that the 50 mg ovary is capable of secreting enough estrogen to stimulate patch development. Furthermore, it is a functional platform from which females can very quickly initiate ovulation if the opportunity arises.

This was shown in an experiment conducted in 1995. On 22 June two small patches of open ground were discovered on TPM that had thawed out that morning where subnivean streamlets had caused the overburden of snow to melt and collapse. Pine boughs were immediately cut and stacked to a height of 1 m on each of these open areas. Two hr later both of the brush piles were already being occupied and investigated by *oriantha* pairs. Nests were being constructed on the following morning from dried grass stalks gathered from a nearby knoll and both females ovulated on 26 June, 4 days after the nesting sites were provided (their first eggs appeared in the nests on the morning of 27 June). This was 9 days earlier than the first clutch starts for nests built in naturally-occurring locations. The 50 mg ovary, therefore, is an active endocrine gland that can be transformed within just a few days to an ovulation-capable structure, providing that environmental conditions are favorable. In 1995 the availability of nesting sites was the last remaining factor crucial to this transformation, a clear demonstration of its importance as supplementary information.

In summary, long photoperiods stimulate testicular growth to about one-half, or less, of maximum mass. The remainder of growth and the prolongation of functional condition appears to be heavily reliant upon stimuli received from females. Ovaries are still quite small (50 mg) when photo-induced growth ceases, but at that point this gland is actually a well-organized structure, poised to carry out its hormone- and gamete-producing roles at the opportune moment. Once this stage of their cycle is reached, females do not appear to be especially reliant upon stimuli from males for continuation into the actual process of nesting. For that step to occur they must experience favorable feedback from ecological factors.

In terms of maintaining gonadal mass, the sexes also follow different strategies. Testes grow on the summering grounds to a size that is close to three orders of magnitude above mid-winter mass (~ 1 vs. 1000 mg), and they are maintained at that level until the shift to photorefractoriness begins (see Chapter 11). Ovarian mass can also vary seasonally by about three orders of magnitude (~ 5 vs. 5000 mg), but maintenance at maximum size is confined to the relatively brief period when a clutch is being produced. Immediately before and after that time it is about 50 mg. This must represent a considerable energy saving for females during both spring migration and the breeding season.

Ambient temperature

One would expect photoperiodically-induced gonadal growth to be modulated by ambient temperatures (T_a) if they are being utilized as supplementary information that is being transduced by the central nervous system to influence the appropriate endocrine axis (Chapter 1). But it is important to remember that T_a ,

unlike other types of supplementary information, has a biological counterpart, body temperature (T_b). Therefore, T_a has the potential to be both an environmental cue and, when it is low, if it causes T_b to decrease, an inhibitor of metabolism. In fact, T_b of captive *gambelii* decreased by 3 to 6 C when they were exposed to a T_a of -10 C, a saving of about 18% in metabolic cost (Paladino 1986). The point is that if low T_a induce hypothermia in the field, which is most probable at night because that is when T_a are lowest and the birds are roosting and least active, thermosensitive cell-division processes in the developing gonads could be decelerated. This potential interaction between photoperiod, T_a , and T_b has not been studied, however.

Full-time T_b data on *oriantha* were not obtained in this study, nor even reliable information on their exposure to T_a . They occupy numerous microclimates during their daily activities, some of which could even be at much lower altitudes (Hahn and Morton 1995). A start in monitoring microclimate usage by *oriantha* at Tioga Pass has been made, however, by Sockman and Hahn (1996). They found that early in the season transmitter-bearing mated pairs left their territories at night to roost in tall pines, sometimes in the same one, on the periphery of the meadows. Once the females had nests they roosted or sat in them, but males did not leave the trees and begin roosting on their territories until late June, by which time nocturnal T_a had increased substantially.

Although T_a effects in the field are difficult to assess, they could very well be providing important supplementary information that affects the final stages of gonadal maturation and implementation of reproductive effort. This probably occurred nearly every spring at Tioga Pass when escalating T_a caused the snow to melt and the vegetation to develop. In 1983, for example, a massive snowpack was quickly dissipated by unusually warm weather and nesting was delayed much less than had been expected.

The effects of T_a on gonadal development during photostimulation (but without concurrent information on T_b) has been tested in the laboratory in *gambelii*, *pugetensis*, and *oriantha*, with mixed results. Lewis and Farner (1973) found that testicular growth rates increased slightly with T_a in *gambelii* but ovarian growth was unaffected in both *gambelii* and *pugetensis* (male *pugetensis* were not tested). Subsequently, Wingfield et al. (1997) showed that testicular growth did not vary in *pugetensis* on various temperature regimes (5, 20, 30 C). Follicular and brood patch development were enhanced at 30 C but only if males were present in the environmental room. These investigators also found no evidence for a temperature effect on either the gonads or accessory structures in male and female *gambelii* (Wingfield et al. 1996). On the other hand, gonadal growth in *oriantha* was slower in both sexes on 5 than on 20 or 30 C (5 C is well below the thermoneutral zone of *oriantha*; Maxwell and King 1976). Despite this, there was no parallel change in luteotropic hormone; it was the same at all T_a (J. Wingfield et al., unpublished data). Maney et al. (1999) have discovered that these seemingly inconsistent gonadal responses of White-crowned Sparrows to T_a are mirrored by changes in their plasma prolactin levels. Since these levels appear to follow thyroxine secretion, Maney et al. (1999) have suggested that temperature information may act through thyroxine to increase prolactin. Prolactin, in turn, may mediate gonadal development (as in mammals) by increasing gonadotropin receptors at the gonad.

This would explain why a gonadotropic effect sometimes occurs even though luteotropic hormone levels do not change.

Relevant to the discussion of the role of T_a is a mathematical model developed by Wingfield et al. (1992) to assess the predictability of an organism's environment, and the relative roles of initial predictive information (such as photoperiod) and the more short-term supplementary information (such as T_a) with respect to this predictability. To apply their model to birds, they used data on the time of year when clutches were initiated to generate a measure of environmental predictability (Ie). Ie is the ratio of the fluctuations in resource levels across time (M) to the constancy of those resources (C). They suggest that when Ie values are low (near zero), the environment is relatively constant and initial predictive information should be sufficient to time gonadal maturation. When Ie values are near 1, C and M make equal contributions and individuals utilizing those environments may be required to integrate supplementary information. The more that Ie values exceed 1, the more important supplementary cues, such as availability of nesting sites and T_a , become in the regulation of breeding. They hypothesized that migrants, as well as other species with precisely timed breeding seasons, would be less responsive to supplementary cues than sedentary species and those with more flexible breeding times. A test of the model was made by looking at the effects of T_a on photoperiodically-induced testicular maturation in a variety of avian taxa. True to their prediction, low T_a tended to inhibit gonadal development more in resident birds than in migrants.

Ie values have now been calculated for four subspecies of White-crowned Sparrows (Wingfield et al. 1992; J. Wingfield et al., unpublished data) and, consistent with the environmental predictability model, the largest value, 6.3, was found for *nuttalli*, the sedentary subspecies, and the smallest, 1.1, for *gambelii*, the one that migrates the greatest distances. The value for *oriantha* was 2.1, suggesting that they should be sensitive to supplementary information, a prediction that is borne out by the inhibitory effects of low T_a on their gonadal development in captivity (noted above). Since the Ie value obtained for *pugetensis*, the short-distance migrant, was 4.3, an intriguing corollary emerges from these data: migration distance is inversely related to environmental predictability.

GONADAL HORMONES

Despite having only partially grown testes, the plasma concentrations of testosterone in newly arrived males were already near their seasonal high (Table 5.1). The averages through the nest-building period for all ages combined was about 3.3 ng/ml, about the same as those found in both *gambelii* (Wingfield and Farner 1978a) and *pugetensis* (Wingfield and Farner 1978b).

Testosterone remained high in mated males until nests had been built, then decreased steadily thereafter with successive stages of the nesting cycle, from parental care through molt and premigratory fattening. If a nest was lost, testosterone levels increased again in males as the pair resumed sexual activity (mean = 1.42 ng/ml, SD = 1.87 ng/ml, N = 7).

This profile of testosterone secretion to the bloodstream is the usual one found in male migrants and it is correlated with their behaviors. At first they interact aggressively while establishing territories and obtaining and guarding mates, then the social system becomes more stabilized, the frequency of aggressive encounters

TABLE 5.1. PLASMA HORMONE LEVELS IN ADULT *Oriantha* IN RELATION TO STAGE OF THE REPRODUCTIVE SEASON

Stage	Testosterone (males, ng/ml)			Estradiol (females, pg/ml)		
	Mean	SD	N	Mean	SD	N
1. Arrival	2.98	3.60	111	84.6	52.8	34
2. Pre-nesting	3.32	3.46	41	82.8	34.6	18
3. Nest building	3.28	3.12	13	112.8	72.6	8
4. Pre-laying	1.89	1.92	8	112.9	125.1	16
5. Laying	1.13	1.46	30	88.6	51.9	40
6. Incubation	0.96	1.41	32	80.0	36.0	54
7. Nestlings	0.65	1.33	42	85.2	34.2	39
8. Fledglings	0.48	0.60	16	87.5	33.9	13
9. Molt	0.12	0.10	89	95.6	67.1	31
10. Fattening	0.19	0.19	23	83.0	26.9	8

Notes: Hormones were measured by radioimmunoassay (Wingfield and Farner 1975, 1976). Note that stages 3–8 in males could be determined only in individuals that were known to be mated and engaged in reproductive activities.

diminishes, and the birds move into phases of parental care and self-maintenance (Wingfield and Farner 1979; Wingfield 1984b, 1985; Wingfield et al. 1987, 1990; Wingfield and Wada 1989, Wingfield and Goldsmith 1990, Wingfield and Hahn 1994).

The relationship of aggression to testosterone in male *oriantha* can be illustrated by combining data from Tables 3.4 (responses to decoys) and 5.1 (testosterone concentrations). Six stages of the reproductive cycle are shared in common in these tables: pre-nesting, pre-laying, laying, incubation, nestlings present, and fledglings present. A plot of means obtained for those stages indicates that the two functions are related (Fig. 5.6). No statistics are given because the data are for means and were gathered from different males in different years, but the tie that is presumed to exist here between physiology and behavior is reinforced and the method of using decoys for evaluation of aggressive tendencies is supported.

As stated above, testes and cloacal protuberances were both smaller throughout the summer in one-year-old *oriantha* males than in older ones (Morton and Allan 1990, Morton et al. 1990), a disparity that has also been reported for Cassin’s

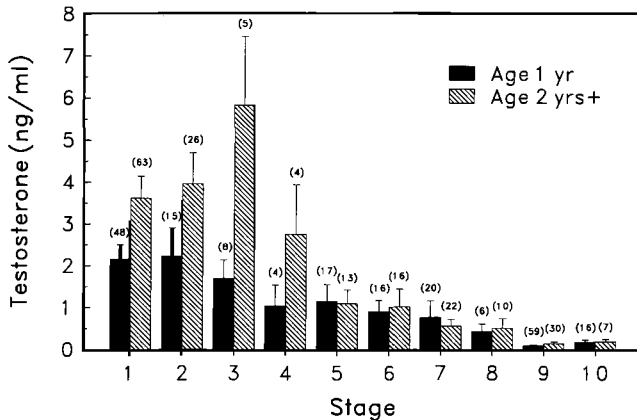


FIGURE 5.5. Mean plasma testosterone concentrations, according to age, in adult male *oriantha* in sequential stages of the reproductive season (stages are defined in Table 5.1). Line shows 1 SE; sample sizes in parentheses.

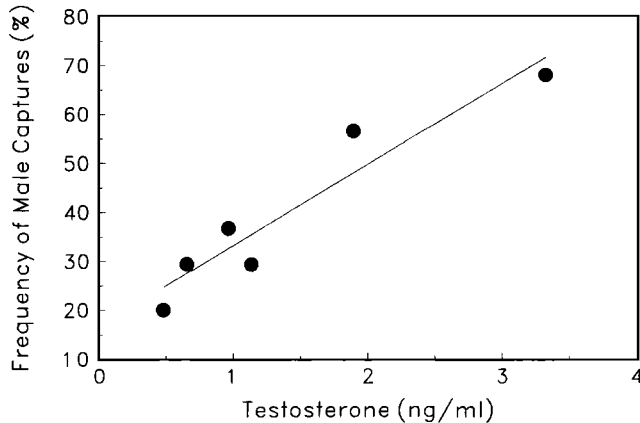


FIGURE 5.6. Percent of time male *oriantha* were captured when decoys were placed on their territories in relation to plasma testosterone levels. Means obtained during six different stages of the reproductive cycle are shown (see text). Data taken from Tables 3.4 and 5.1.

Finches (*Carpodacus cassinii*; Samson 1976b), Dark-eyed Juncos (Ketterson and Nolan 1992, Deviche et al. 2000) and Great Tits (Silverin et al. 1997). Early in the season, as suggested by the data on protuberances, there was a hormonal correlate of this difference: testosterone levels tended to be lower in one-year-old males (Fig. 5.5), the difference being significant during the arrival and nest-building stages ($t = 2.15$, $P = 0.034$; $t = 3.00$, $P = 0.012$, respectively), but not the pre-nesting stage ($t = 1.58$, $P = 0.122$).

It seems likely that this age-related effect occurs because the smaller testes of immature birds, undergoing hypertrophy for the first time, have lower secretory capabilities than the larger, recrudescing ones of the older males. Intra-testicular testosterone levels may not have been affected because fertility, as measured by hatchability of eggs, did not vary with male age. But the lower peripheral (plasma) levels of testosterone in young birds may have had functional ramifications; it may have been the physiological basis for their reduced competitiveness and why relatively more of them were unmated. Just how various male-male and male-female behaviors might be affected by these lower testosterone levels, or vice-versa, has not been investigated although it is known that a positive relationship exists between song rates and testosterone levels in both European Robins (*Eri-thacus rubecula*; Schwabl and Kriner 1991) and Willow Tits (*Parus montanus*; Rost 1992). It would be interesting to know if singing frequency, as well as other behaviors that might affect territory and mate acquisition and defense, varies with male age in *oriantha*. It could also be that young males, as a group, lacked social stimulation from females because many of them were unmated and without territories. Diminished behavioral interactions with females has been suggested as the cause of age-class differences in testicular size in Dark-eyed Juncos (Deviche et al. 2000).

Plasma estradiol levels were quite low in females and did not vary with stage of reproduction (ANOVA $F_{9,254} = 0.81$, $P = 0.688$; Table 5.1). Wingfield and Farner (1978a) found that estradiol and estrone levels were both at or above 300 pg/ml in *gambelii* females engaged in courtship, nest building, and laying. They

obtained similar results in *pugetensis* females for estrone, but estradiol levels hovered around 100 pg/ml (Wingfield and Farner 1978b), much the same as those observed in *oriantha*. Estradiol is metabolized readily to estrone (Common et al. 1968), and not having assayed for the latter, there is little we can say about total estrogen in relation to reproductive stages of females. Testosterone levels in females averaged 154 pg/ml of plasma during the pre-laying period (nest built and sitting empty), and between 50 and 100 pg/ml during the other stages. This variation was not significant (ANOVA $F_{9,254} = 1.44$, $P = 0.11$).

