
# CHAPTER 12: Concluding Remarks

The primary purpose of this study, including the publications stemming from it, has been to enlarge our understanding of avian migration and reproductive biology. Ideally, the data and conclusions will apply not only to White-crowned Sparrows summering in the subalpine, but also to many other species by disclosing details of natural history and life history that will prove to be shared in common. The data should thus be useful for comparative purposes and for identifying new avenues of research. And they should also help to reveal some of the principles that underlie environmental adaptation.

One principle that seems to have emerged is that challenges posed by environmental variation often can be met with existing behavioral and physiological responses; adaptation occurs through flexibility rather than through acquisition of new abilities or mechanisms. Furthermore, and undoubtedly due to their differing biological roles, strategies adopted by males and females to cope with these challenges may differ.

An example was in the way gonadal development occurred in relation to migration schedule and to snow conditions at the breeding area (Chapter 5). Testicular enlargement continued for about a month after males had reached Tioga Pass but ovaries remained small, barely above wintertime size, and did not achieve maximal mass until the first ovulation. About 75% of testicular growth and more than 90% of ovarian growth was post-migrational. This helped to minimize the mass being transported during migration but did not appear to compromise function in males because their early-season plasma testosterone levels were high and they were fertile. In most years post-arrival gonadal developmental proceeded quickly in both sexes but if snow cover prevented nesting, physiological flexibility was displayed by females in that further ovarian growth was inhibited. And ovaries could remain in what appeared to be an undeveloped, arrested condition for six weeks or more. This energetically efficient response did not seem to compromise reproductive capabilities of females, however, because if nesting sites were provided by investigators or became available naturally they were able to begin laying within only a few days. If storms occurred before nesting was under way members of both sexes ceased efforts to acquire mates and territories in favor of a temporary move to lower altitude where conditions were milder.

Once the nesting season was in progress, another highly adaptive response that directly affected reproductive success and that required large adjustments in both physiology and behavior occurred when nesting was interrupted. Almost immediately endocrine pathways were reactivated, courtship was renewed, and females built a new nest and re-acquired enough nutrients to begin laying. Modal elapsed time for this complete sequence to occur was only 5 d and, if necessary, it could be repeated as many as four times in a season.

Additional behavioral flexibility was exhibited by females when snow cover was persistent in that their choice of nest sites was altered (Chapter 10). In light snow years as few as 10% of nests were built above ground in pines and willows, but in heavy snow years when open ground with places to hide nests were scarce up to 70% of nests were placed above ground. This helped to minimize the seasonal delay in nesting onset, which was important because the longer nesting was delayed the shorter the period available for renesting attempts and the fewer young produced.

Another principle is that adaptive responses can have costs; they may involve various kinds of trade-offs. For example, building nests in elevated sites can lessen delays caused by persistent snow cover, but females incubating in those nests weigh 5% less than those with ground nests, probably because they must combat an increase in convective cooling by producing more heat through shivering. Also, according to our thinking, a single, efficient regulatory process acts to regulate both clutch size (via termination of laying) and onset of incubation. Hatching asynchrony results from this process and it is a cost because it can sometimes facilitate unnecessary mortality in nestlings. Another possible trade-off, not yet explored in wild birds, is that accelerated molt, such as the one that allows females nesting late in the season to catch up with other adults, may compromise survival because quickly grown plumage is of poorer quality (see Dawson et al. 2000).

Along with revealing underlying principles of environmental adaptation, such as the two mentioned above, this study has also shown that experience counts for very little in passerine reproduction: there was no effect of age on egg size, clutch size, clutch volume, or number of fledglings produced (reproductive success). Perhaps the latter should be expected because the modal number of broods fledged, both annually and per lifetime, was one. There must be strong selection for maximal reproductive performance by yearlings. Only two age-related effects were found. One was that between-year breeding dispersal decreased with age, and the other was that incubation period was shorter if females were at least three years old. Interestingly, these phenomena appear to be related. Decreased dispersal by older females may signal their attainment of a favored nesting location. One expression of this optimal condition could be increased foraging efficiency, which, in turn, permits increased attentiveness and a shortened incubation period.

These are a few examples of how *oriantha* responded to high altitude conditions and they help to distinguish the relative roles of environmental factors, such as photoperiod, that act as initial predictive information from those, such as nutritional plane and availability of nesting sites, that act as supplementary information. These examples also serve to remind us that dividing physiology and behavior into separate categories is more a matter of convenience than reality. In truth, the more we learn about the lives of organisms and the ways they react to ecological conditions, the clearer it becomes that the two act together in complementary, reciprocal fashion and are often functionally inseparable.

Many possibilities for additional research arise from the *oriantha* data. One of the more interesting, and possibly intractable, ones is the cause and effect relationship that occurs in hatching asynchrony. We have hypothesized that asynchrony is an epiphenomenon, an unselected by-product of a mechanism that has evolved to turn off a physiological phase of reproduction (egg laying) while simultaneously turning on a behavioral one (full-time attentiveness). The competitive inequalities in siblings that stem from a staggered hatching pattern imperil the smallest chick(s) and adaptation to this problem may occur in at least three ways: (1) females minimize the hatching spread by maintaining high levels of attentiveness during the hatching period, even though they lose considerable body mass in the process (Chapter 6); (2) the last egg is the clutch tends to be relatively large, thereby producing a chick that is better able to compete with its older siblings (Chapter 7); and (3) from other studies, yolk testosterone concentrations increase with laying order (Schwabl 1993, Lipar et al. 1999), which may also help last-hatched young to compete. Like many of these questions that involve evolutionary history, ultimate causation is inferred from proximate results, and the reason asynchrony developed in the first place may never be settled to everyone's satisfaction. Nonetheless, investigations of the regulatory processes that occur toward the end of the ovulatory sequence, when clutch size is determined, are likely to produce important new information (see, for example, Sockman et al. 2000).

Investigations of how habitat quality and mate quality affect settlement patterns of females and their choices of nesting area over a lifetime should also be enlightening, especially when coupled with paternity data. Intrasexual aggression appears to be an important component of this site selection-breeding dispersal interplay and the straightforward method of trapping with decoys (Chapter 3) would seem to be a useful approach for measuring levels of aggression during territory acquisition and defense in both sexes.

There are many other results from the Tioga work which suggest that additional inquiry may be in order. For example, we expected that red blood cell synthesis would be stimulated by exposure to high altitude conditions, thereby causing hematocrits to increase during the summer. In fact, the opposite occurred, and the relative contributions of various underlying factors that could be responsible, such as changes in water balance and hemopoiesis, are unknown. Some fundamental adjustment in circulation dynamics related to migration biology seems to be occurring, however.

Another regulatory system worthy of a better look, and one that has potential for broad applicability in vertebrates, is the shift to hyperphagia that occurs at the onset of premigratory fattening. This change in food intake appears to be abrupt and massive and migratory birds should, therefore, be good models or preparations for detecting the mechanisms underlying appetite regulation.

The field observations also indicate that great opportunities exist for discovering metabolic costs of reproduction not only for broad categories, such as egg laying, incubation, and feeding nestlings, but also for times that could be crucial for survival or for when energy balance may be in jeopardy because of conflicting or overlapping functions. What happens to energy balance, for example, when pre-breeding altitudinal movements occur, when nesting sequences are disrupted by storms, or when molting begins during the parental phase? How stressed are females when incubating in above-ground nests, when their attempts to hatch out the last eggs in the clutch conflict with self maintenance, when they are engaged simultaneously in building replacement nests and preparing to ovulate, or when they are performing all care of offspring by themselves? There is no need to continue along these lines. Hopefully, thoughtful young scientists will come to their own conclusions about the data and hypotheses presented in this monograph and will be stimulated to design and pursue follow-up investigations of their own.