

Review

“Seasonal changes in the neuroendocrine system”: Some reflections



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ABSTRACT

This perspective considers first the general issue of seasonality and how it is shaped ecologically. It asks what is the relative importance of “strategic” (photoperiod-dependent) versus “tactical” (supplemental) cues in seasonality and what neural circuits are involved? It then considers recent developments as reflected in the Special Issue. What don’t we understand about the photoperiodic clock and also the long-term timing mechanisms underlying refractoriness? Are these latter related to the endogenous annual rhythms? Can we finally identify the opsins involved in photodetection? What is the present position with regard to melatonin as “the” annual calendar? An exciting development has been the recognition of the involvement of thyroid hormones in seasonality but how does the Dio/TSH/thyroid hormone pathway integrate with downstream components of the photoperiodic response system? Finally, there are the seasonal changes within the central nervous system itself – perhaps the most exciting aspect of all.

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1. Introduction

Adaptations to season are often viewed largely in the context of reproduction but as reviews collected in the present special issue indicate they encompass many other core physiological processes (metabolism (food intake and fattening), pelage changes, migration and hibernation). All these processes are regulated by a “timing mechanism” whose functions are to anticipate the optimal period when processes should take place and, if possible, minimize energy expenditure by separating them temporally. This perspective first includes a personal view on the topic of seasonality, and then considers the recent developments in the various Chapters within this special issue along with some other contemporary aspects of seasonality.

2. Seasonal rhythms: a personal view

Fig. 1 shows the sequence of annual life-history stages in birds (Williams, 2012a,b). The widely held view is that the different stages are orchestrated sequentially with minimum overlap but in reality there is much flexibility and a package has evolved to maximize lifetime fitness. Quite frankly we physiologists have barely contemplated how such complexity is managed in neural and neuroendocrine terms but it is at the core of why and how seasonality has evolved. Incidentally Fig. 1 raises the question as to whether there is a single timer acting as a “master calendar” with each physiological function tapping into the information or are there multiple timers, each regulating a sub-set of annual processes.

In practical terms research on seasonality tends to be undertaken either physiologically or ecologically, and this special issue is devoted to the former. Some articles are devoted to the “timing mechanisms” – photoreception and the timers themselves – but a majority focus upon the neural and neuroendocrine pathways leading to the downstream physiology. Five other articles reflect on the fascinating changes in the brain areas associated with neurogenesis, memory, and seasonal song in birds and mammals whilst one reminds us that other vertebrate groups also have seasonality by reflecting upon the auditory systems of fish. As in all branches of science the field continues to burgeon and recent reviews are available on the neuroendocrinology of seasonal breeding: Nakane and Yoshimura (2014), Dardente et al. (2014), Hut et al. (2014) and Wood and Loudon (2014). There is, I suspect, an assumption that the basic physiology of the various processes (reproduction, metabolism, etc.) is similar and that the key feature of seasonality lies in how the upstream timing mechanisms modify the individual physiological pathways.

Fig. 2 exemplifies how Fig. 1 can be played out in real life. Here I could have used a mammal or a bird but have chosen an example from colleagues in Oxford who are using modern telemetry to understand the remarkable Manx shearwater (*Puffinus puffinus*). This small pelagic seabird breeds on islands in the western parts of the UK, lays a single egg in a burrow (hence it is accessible) and migrates to the southern Atlantic (Guilford et al., 2009). The diagram implies a neat series of stages across the year but only two of these are inflexible (incubation and chick-rearing) and the others can be varied from year to year. Indeed, flexibility is the general key to lifetime fitness and as is often the case in birds

and hibernating mammals (Ozgul et al., 2010) reproductive success is improved if an individual breeds early relative to its conspecifics. So – and interestingly in view of our focus as physiologists – the period of gonadal maturation (the pre-laying period in Fig. 2) varies considerably and is also much influenced by the physiological state of the shearwater when it returns from South America. An equivalent figure for a hibernating rodent might focus upon its breeding period, its fattening and the long period of hibernation. Only gestation and lactation are largely inflexible in terms of duration and the other stages can be influenced by local conditions (Ozgul et al., 2010; Sheriff et al., 2011). By any measure annual cycles are remarkable and many of us were drawn to study the phenomenon either *physiologically* or *ecologically*.

How annual cycles were regulated became clear in the first half of the 20th century when experiments on plants and insects, and then higher vertebrates established that the key timer was the annual change in day length. Photoperiod offers a physically stable calendar and can be viewed as the *strategic* indicator of season. But as is evident from my earlier comments about flexibility of the seasonal program, photoperiod alone is not sufficient for fine-tuning and so other factors reflecting local conditions act as *tactical* indicators of season and are vital to adjust the precise time of, say, first egg, or entry into hibernation. Ecologists in particular focus upon these *tactical* factors which advance or delay a given function by a few days and are so important in evolutionary terms. Amongst physiologists John Wingfield has made this his especial focus (2008, 2015; Wingfield and Mukai, 2009). In his review for this special issue he elegantly summarizes the present situation and it complements this Introduction.

I suspect that differences between a physiologist's approach to seasonality and that of an ecologist are probably encapsulated in this idea of *strategic* (the “big picture”) versus *tactical* (“lifetime reproductive success”). Valiant efforts have been made to bring these approaches together (see Wingfield et al., 2008 “*Integration of ecology and endocrinology in avian reproduction: a new synthesis*”; Williams, 2012a; Williams, 2012b) but much more interaction is needed if we are to understand the neural and endocrine changes whereby tactical factors operate. If there is one key message for physiologists it is to understand how phenotypic flexibility, a concept central to ecology, is regulated in biochemical terms. One example may well be ovarian development and maturation in birds. Williams (2012a,b) emphasizes that development of the avian ovary is slow and largely pre-vitellogenic until only a week or so prior to egg-laying. Then major development occurs with the final steps (expansion of the ovarian follicles by yolk acquisition, oviduct maturation, egg-laying itself) being achieved in only a few days. Presumably it is at this point when the *tactical* factors (fine-scale tuning by supplemental factors) operate most powerfully c.f. the longer-term *strategic* photoperiodically-driven

processes. We really must learn more of the precise changes occurring in these last few days and how they alter the precise time of the first egg. Much of the flexibility in the annual variation in egg-laying can probably be handled by “simple” endocrine changes and this may well explain why so many evolutionary studies (e.g. Charmantier et al., 2008; Vedder et al., 2013) point to seasonal change being primarily phenotypic rather than genotypic. A similar situation may well exist in mammals. Sheriff et al. (2011) studied the phenological variation in the timing of hibernation in two populations of Arctic ground squirrels living 20 km apart and observed that entry into hibernation (and exit from) differed by more than a week: they concluded “*this variation is likely generated by plasticity of physiological mechanisms...*”. A particularly elegant case is the yellow-bellied marmot (*Marmota flaviventris*) whose population has doubled in a decade as a result of warming climate change in Colorado. The reasons are probably phenotypic – slightly earlier emergence from hibernation and, therefore a longer season to reproduce and fatten before entering hibernation in the fall. Survival is enhanced and population responses follow. This does not, of course exclude genotypic change as a response to climate alterations but in many vertebrates phenotypic responses are still adequate to explain the alterations in the last twenty years or so (O'Brien et al., 2013; Lehmann et al., 2012; Liedvogel et al., 2012). What is needed are quantitative physiological data that can be analyzed statistically and one applauds the Dutch group of Marcel Visser and colleagues who have an infrastructure whereby they can control breeding of great tits with precision and investigate the physiological and genetic alterations using sufficient numbers to allow statistical analysis (e.g. Schaper et al., 2013; Helm and Visser, 2013). Again comparable studies can be undertaken in small rodents and the elegant studies of Jay Storz and Roy Weber in Nebraska (e.g. Revsbech et al., 2013) show what is achievable. However, as Williams emphasized to me: “*we need more ecological and evolutionary context for the physiology we do... [which] probably means less deep brain research and more work on “peripheral” hormones working closer to the phenotypic traits of interest*”.

3. The photoperiodic “system”

3.1. The clock systems

Many of the papers in this issue consider the photoperiodic control of seasonal functions in mammals – from reproduction through sexual behavior to metabolism (food intake) and to immune function. Two papers consider in depth the photoperiodic clockwork in mammals (Coomans et al., 2015), and how the complex annual cycle in birds is regulated by day length (Dawson, 2015). Two other recent reviews are also slanted in this direction:

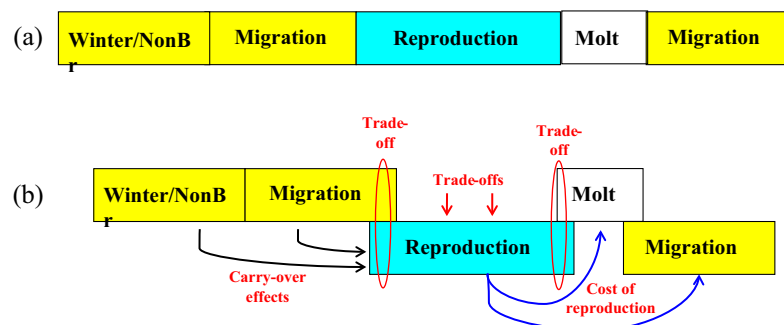


Fig. 1. Models for the organization and physiological analysis of life histories: (a) sequentially orchestrated stages, in which overlap between successive life-history stages is minimized; (b) a more realistic model with overlap between successive stages integrating trade-offs and carry-over effects among different stages. First published in Williams (2012a,b), reproduced with permission.

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