Organization of vertebrate annual cycles: implications for control mechanisms

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The majority of vertebrates have a life span of greater than one year. Therefore individuals must be able to adapt to the annual cycle of changing conditions by adjusting morphology, physiology and behaviour. Phenotypic flexibility, in which an individual switches from one life history stage to another, is one way to maximize fitness in a changing environment. When environmental variation is low, few life history stages are needed. If environmental variation is large, there are more life history stages. Each life history stage has a characteristic set of sub-stages that can be expressed in various combinations and patterns to determine state at any point in the life of the individual. Thus individuals have a finite number of states that can be expressed over the spectrum of environmental conditions in their life spans. Life history stages have three phases—development, mature capability (when characteristic sub-stages can be expressed) and termination. Expression of a stage is time dependent (probably a minimum of one month), and termination of one stage overlaps development of the next stage. It follows that the more life history stages an individual expresses, the less flexibility it will have in timing those stages. Having fewer life history stages increases flexibility in timing, but less tolerance of variation in environmental conditions. To varying degrees it is possible to overlap mature capability of some life history stages to effectively reduce ‘finite stage diversity’ and maximize flexibility in timing. Theoretical ways by which this can be done, and the implications for neuroendocrine and endocrine control mechanisms are discussed. Twelve testable hypotheses are posed that relate directly to control mechanisms.

Keywords: life-history stage; moult; migration; reproduction; phenotypic flexibility

1. INTRODUCTION

No free-living organism lives in a truly constant environment. All are exposed to fluctuations in environmental conditions, some of which may be extreme. Examples include Arctic habitats where temperature, food availability and snow cover vary dramatically in a yearly seasonal cycle. Dry and rainy periods occur at specific times of year in many subtropical and tropical environments, but the amount and duration of rain and drought may vary. Even in localities that appear unchanging, such as in caves where yearly temperature fluctuations may be on the order of 2°C, seasonal flooding occurs providing changes in the nutrient input from non-cave sources (Poulson 1964). The deep oceanic abyss also experiences ‘benthic storms’ caused by surface winds that can change currents even at great depths (Gage & Tyler 1991). Since global climates are changing, a thorough understanding of the processes by which organisms use environmental signals to adjust changes in morphology, physiology and behaviour over the course of their annual cycles is urgently needed.

With a few exceptions, vertebrates that reach adulthood have a life expectancy of at least 1 year and within the period of a single lifespan environmental conditions will probably fluctuate (cycle) many times.

For this reason, phenotype switching between generations—the polyphenism type of phenotypic plasticity common in invertebrates—is not widespread in vertebrates (Stearns 1989; West-Eberhard 1989). Given that every organism must respond to environmental change at some stage in its life, an overarching question becomes: how do they organize their life cycles? This includes timing of components of those cycles and their synchronization with other individuals. In general, an organism must respond to two major types of environmental change: the predictable such as seasons, high tide and low tide, and the unpredictable such as storms, human disturbance, predators, etc. Because no individual experiences the environment in exactly the same way as another, it is important to customize individual responses to unique exposure to environmental events. This raises problems of how environmental change is perceived and transduced into responses (morphological, physiological and behavioural), as well as the degree of phenotypic flexibility an individual can express to cope with these changes.

The focus here will be on the predictable changes in the environment, particularly in relation to the annual cycle of day length, temperature, rainfall and associated fluctuations in food abundance. The entire annual cycle will be considered including migrations, breeding, moult and non-breeding (winter), all of which must be timed and integrated with changing seasons. Unpredictable perturbations of the environment requiring rapid facultative responses, called the emergency life-history stage, will not be discussed

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Figure 1. Fitness of phenotypes living in environments with different degrees of environmental variation over the year (see also [Levins 1968](#)). In (a) there is small environmental variation and this phenotype has a high fitness at all times. (b) If environmental variation over the year increases, then this phenotype has much less fitness at some times of year (extremes of the environmental variation). (c) If the environmental variation is very large, then this one phenotype has greatly reduced fitness over much of the year. (d) Life-history theory would predict that this genotype would express different phenotypes each with greatest fitness at different types of the year (adapted to environmental conditions at that time).

further here. For in-depth discussions of responses to the unpredictable, see [Sapolsky *et al.* \(2000\)](#) and [Wingfield \(2004\)](#).

Vertebrates, particularly long-lived species, have generation times and lifespans that may be many times greater than the temporal scale of seasonal environmental change. Unless the environmental fluctuations of the annual cycle are very small, an organism must therefore modify at least some components of its morphology, physiology and behaviour to survive as conditions change ([Prosser 1986](#)). These adjustments within the individual are reversible, usually cyclic and timed so as to acclimate to repeated environmental fluctuations ([Prosser 1986](#)). This raises the concept of life-history stages that allow adaptation to the annual cycle ([Jacobs & Wingfield 2000](#)).

2. LIFE-HISTORY STAGES

Fitness curves (expected reproductive success) for phenotypes living in environments with different degrees of environmental variation over the year are depicted in [figure 1](#) (see also [Levins 1968](#); [Jacobs 1996](#); [Jacobs & Wingfield 2000](#)). If there is small environmental variation ([figure 1a](#)), this phenotype has high fitness at all times ([Levins 1968](#)). If environmental variation over the year increases ([figure 1b](#)), then this phenotype has much lower fitness at some times of year (extremes of the environmental variation). If the environmental variation is very large, then this one phenotype has greatly reduced fitness over much of the year ([figure 1c](#)). Life-history theory would therefore predict that this genotype would express different phenotypes having greater fitness at different times of the year (adapted to environmental conditions at that time, [figure 1d](#); see [Levins 1968](#); [Stearns 1989](#); [West-Eberhard 1989](#)). However, if an individual has

a lifespan equal to or greater than the duration of the annual cycle (as most vertebrates do), then there should be selection for changes in morphology, physiology and behaviour to maintain high fitness as the environment also changes. [Jacobs & Wingfield \(2000\)](#) suggested the term life-history stage to describe specific phenotypic stages within an individual at different points on the spectrum of annual environmental change resulting overall in high fitness. An extension of the phenotypic models in [figure 1](#) can be made to life-history stages that take the place of phenotypes because here we are referring to individuals ([figure 2](#)).

One way for the individual to maximize fitness is to express two life-history stages even in an environment with small annual variation ([figure 2a](#)), each with their own fitness curve. Note that these two life-history stages are expressed by the same phenotype (unlike in [figure 1](#) in which two different phenotypes are expressed). This is called phenotypic flexibility—the ability of a single phenotype to change morphology, physiology and behaviour as the environment changes or in anticipation of such events—([Piersma & Drent 2003](#)). If the cost of transition between life-history stages is relatively small, overall fitness can be maintained at a high level by expressing yet more life-history stages over the annual cycle. Since environmental variation increases, so does phenotypic flexibility with three ([figure 2c](#)) and five ([figure 2d](#)) life-history stages expressed.

Note that a mixed phenotype (broken line, i.e. a phenotype that expresses all morphological, physiological and behavioural traits of all the life-history stages simultaneously) would have reduced fitness because the costs of maintaining all these traits at the same time would be prohibitive ([figure 2](#)). In some cases, mixed

Figure 2. (a) The fitness of a phenotype in an environment with small annual variation (from figure 1). (b) One way for the individual to maximize fitness is to express two life-history stages, each with their own fitness curve. Note that these two life-history stages are expressed by the same phenotype (unlike in figure 1 where two different phenotypes are expressed). This is called phenotypic flexibility (Piersma & Drent 2003). As environmental variation increases, so does phenotypic flexibility with (c) three and (d) five life-history stages expressed. Note that a mixed phenotype (expressing all morphological, physiological and behavioural traits of all life-history stages simultaneously, broken line) would have reduced fitness.

phenotypes would not be possible because morphological, physiological and behavioural traits would be in conflict. For example, rock ptarmigan, *Lagopus mutus*, and snowshoe hares, *Lepus americanus*, change colour of the integument from brown and cryptic in summer to white and cryptic in winter (Pielou 1994). The mixed phenotype, presumably with a 'beige'-coloured integument, would be conspicuous at all times of year and thus would have reduced fitness (Jacobs 1996; Jacobs & Wingfield 2000). Other examples of life-history stages are adaptations to winter and summer temperature ranges (e.g. the American goldfinch, *Carduelis tristis*; Buttemer 1985), and life-history processes associated with migration, reproduction and moulting (e.g. Farner 1985; Gwinner 1986). The temporal progression of life-history stages, their durations and seasonality, is driven by environmental cues and endogenous rhythms usually in relation to changing seasons. During a complete lifespan, the organism may pass through a number of cycles of stages that are characteristic of the species. Stages can overlap, but usually are temporally separated and sometimes are mutually exclusive (e.g. nesting and migration in birds).

There are two major classes of life-history stages. During ontogeny, different stages are expressed during growth, differentiation of cells, tissues and organs, and sex is usually determined at this time (Jacobs & Wingfield 2000; Wingfield 2004). This process leading to a particular phenotype is not reversible. In contrast, once an adult, a different set of life-history stages are expressed, especially as annual environmental variation increases. Again, there are growth and differentiation of cells, tissues and organs, but this time they are reversible (i.e. they are independent of age) and sex change may also occur in some species (phenotypic flexibility).

Further discussion of ontogenetic stages is beyond the scope of this paper (see Wingfield 2004, 2006).

3. HOW DO WE DEFINE LIFE-HISTORY STAGES?

In behavioural ecology and evolutionary ecology, suites of correlated traits are called 'syndromes'. These can be variable behavioural traits expressed by individuals in specific situations (e.g. Sih *et al.* 2004), or broader suites of traits including physiology and morphology typical of life-history events such as breeding, migration, etc. (Dingle 2001; Roff 2001). Whereas behavioural syndromes have been proposed to describe the interindividual spectrum of behavioural traits in 'situations' such as breeding and non-breeding (Sih *et al.* 2004), here it is proposed that life-history stages can be defined as syndromes of correlated morphological, physiological and behavioural traits related to a specific process, often at a particular time of year. For example, a breeding life-history stage would involve morphological changes such as gonadal development and growth of secondary sex characters; physiological traits such as yolk formation and deposition; and behavioural traits such as sexual and parental behaviour. All of these are correlated and specific to reproduction. In contrast, the non-breeding (winter) life-history stage usually involves regressed and non-functional gonads and accessory organs, enhanced fat storage and a characteristic integumental change (e.g. plumage/pelage colour and quality); physiological changes related to elevated metabolism; and behavioural traits such as dominance hierarchies in flocking/herding or a switch in territory type. Thus far, the following life-history stages have been identified as syndromes of correlated morphological, physiological

and behavioural traits expressed, to varying degrees, at specific times of year: non-breeding (e.g. winter including hibernation), vernal migration, breeding, various moults and autumnal migration (see also [Jacobs & Wingfield 2000](#)). The syndrome of traits within a life-history stage includes a suite of sub-stages that can only be expressed within that life-history stage, but can occur in various combinations and sequences ([Wingfield & Jacobs 1999](#); [Jacobs & Wingfield 2000](#); [Wingfield 2004](#)).

There are, of course, many morphological, physiological and behavioural traits that are common to all life-history stages in an individual's life cycle (e.g. legs, fins, wings associated with movement, osmoregulatory mechanisms, feeding behaviour, etc.), but even these may show some changes with life-history stage and season. For example, muscles powering migratory movements change, osmoregulatory functions may differ depending on whether the individual is in fresh water or seawater, wet season or dry season, and foraging behaviour can be modified if food sources also change with season. Given these common traits and those specific to particular times in the annual cycle, there is a set number of life-history stages for each phenotype each with a specific number of sub-stages. State of the individual at any point in the lifespan is a function of the expression, in various combinations and sequences, of life-history stages and their sub-stages. Since the numbers of these are fixed for any given phenotype there is, therefore, a finite number of states, hence the term finite state machine ([Jacobs & Wingfield 2000](#)). Again, the progression of life-history stages is analogous to the switching of phenotypes at the population level, only the 'switch' occurs within an individual.

[Piersma *et al.* \(2005\)](#) argue that such definitions for migratory syndromes might not be very clear because many traits are controlled differently across species, or because migrants express several traits (e.g. orientation, fat deposition) in other life-history stages. This is absolutely true, but here it is proposed that the syndrome concept can be used to define life-history stages within a population. Groups of species within a habitat may have similar life-history stages, but the suite of sub-stages and the ways in which they are expressed may be completely different. The fact that some traits such as fat deposition, orientation, territoriality and many others may be expressed in different life-history stages poses the interesting question of whether they are regulated by different mechanisms. [Piersma *et al.* \(2005\)](#) point out some examples where this may be the case when comparing migration traits with other life-history stages.

These tenets of the finite state machine raise a number of questions, some of which will be dealt with below. At first, it seems 'restrictive' that an individual would have a fixed number of states. However, this number is highly variable dependent upon how many life-history stages a phenotype has and how complex those stages are. Note that the combinations of sub-stages expressed, when and in what combinations they are expressed, are also influenced by maternal and environmental effects during ontogeny, as well as experience and learning throughout the individual's lifespan. However, any phenotype will still be restricted

in how many states it can express by the life-history stages and their sub-stages characteristic of the genotype. The finite state machine described here also has many parallels with annual routine models proposed by [McNamara & Houston \(1996\)](#) (see also [McNamara *et al.* 1998](#)) that predict adaptation strategies to the environment. The major intent of this paper is to present the machine as a framework specifically to generate hypotheses relating to control mechanisms within a population rather than to simply describe morphology, physiology and behaviour across species.

Examples of adult life-history stages from selected vertebrates are presented in [figure 3](#). Some, such as coral reef fishes, live in environments with small annual variation in environmental conditions and thus need few (two) life-history stages. This provides great flexibility in timing but tolerance of environmental variation will be low. In others (e.g. migratory birds), much greater environmental variation can be tolerated because they express up to six or even seven life-history stages. However, because each stage requires time to develop, be expressed and then terminated, flexibility in timing of those stages is reduced. This suggests a trade-off of numbers of life-history stages (phenotypic flexibility and ability to cope with broad environmental change) and flexibility of timing of those stages (ability to determine, for example, when the best time is to breed or moult, or even when to overlap them). Intermediate numbers of life-history stages (e.g. for a lizard or snake, [figure 3](#)) provide flexibility in timing of life-history stages, as well as tolerance of variation in annual environmental conditions (from [Wingfield 2004, 2006](#)). By arranging adult life-history stages according to time of year, it becomes clear that the developmental phase of a life-history stage must overlap the termination phase of the previous stage (see also [figure 7](#)), and that the more life-history stages expressed (e.g. [figure 4c](#) with six stages in migratory birds) means that flexibility in timing may be even lower. Others, such as coral reef fishes ([figure 4b](#)), have greatest flexibility, but their tolerance of environmental variation is low (after [Ramenofsky & Wingfield 2006](#); [Wingfield 2006](#)).

The simplest finite state machine is a single life-history stage, but apparently this is rare in vertebrates. Humans may have only one life-history stage because once adult, reproduction can be constant, we neither have a moult period nor show regular migration patterns that exclude other functions. Seasonal patterns in human births have been shown for virtually every population worldwide, and they tend to be more pronounced in regions with summer heat or at extreme latitude. This suggests at first glance that there may be breeding and non-breeding stages in humans. However, despite up to 45% difference in the high and low birth rates, women menstruate in all seasons although the length of the cycle may vary, but not significantly ([Rosetta 1993](#)). Semen quality and testosterone levels in human males also change but only by $\pm 10\%$ over a year ([Dabbs 1990](#); [Levine 1994](#)). Although many organisms use micro-environments to reduce variation in environmental conditions, humans have the unique ability to create their own

Figure 3. Examples of adult life-history stages from selected vertebrates. (a) Some, such as coral reef fishes, live in environments with small annual variation in environmental conditions and thus need only two life-history stages. This results in much flexibility in timing of life-history stages but tolerance of environmental variation will be low. (d) Humans have only one life-history stage yet are able to live in many different environments, but only if they are able to regulate their micro-environment by using clothes, heat, and by controlling their food supply. (c) In others (e.g. migratory birds), much greater environmental variation results in up to six or even seven life-history stages. This allows adaptation to greater ranges of annual environmental variation, but because each stage requires time to develop, be expressed and then terminate, then flexibility in timing is reduced. (b) Intermediate conditions in which three life-history stages are found (e.g. for a lizard or snake) may provide greater flexibility in timing of life-history stages, as well as tolerance of intermediate variation in annual environmental conditions. Adapted from Wingfield (2004, 2006), Elsevier Press, New York.

Figure 4. By arranging adult life-history stages according to time of year, it is clear that the more life-history stages expressed (e.g. c with six stages in migratory birds) then flexibility in timing is low. Note that the developmental phase of a life-history stage overlaps with the termination phase of the previous stage. (a) Humans and (b) coral reef fishes have greatest flexibility, but their tolerance of environmental variation is low (after Ramenofsky & Wingfield 2006, Springer, Berlin).

Figure 5. An example of adult life-history stages and their sub-stages in a migratory bird. Note that the stages have a sequence that cannot be reversed (e.g. [Jacobs & Wingfield 2000](#); [Wingfield 2004](#)), and the temporal sequence is fixed (life-history stages cannot be skipped). Sub-stages can be expressed in much more flexible subsequences (see below), can be skipped or reversed within a life-history stage. State of the individual at any point in the life cycle is determined by the combination of life-history stages and their sub-stages expressed at that time. Since each phenotype has a set number of life-history stages each with a characteristic set of sub-stages, then there must be a fixed number of states. That is, the individual is a finite state machine. (Adapted from [Jacobs & Wingfield 2000](#); [Wingfield 2004, 2005](#), Cambridge University Press, Cambridge.)

micro-environments and maintain it by artificial means even in very severe environments. This has allowed us to colonize virtually all regions on Earth ([Farhi 1987](#)). Clothing allows us to maintain a subtropical environment (at least at the skin surface, i.e. under clothing), and artificial heating and cooling allows us to maintain an ideal temperature in houses and work places. Thus, we do not need to migrate or moult and we are able to survive with a single life-history stage in extremely variable environments ([Wingfield 2004](#)). We also control our food supply through agriculture and the means to transport large amounts of food wherever we wish. Without our ability to control our living environment precisely, a naked human would only be able to survive in a few tropical environments with low variation in conditions.

The boundaries of the temporal sequence of life-history stages can be defined at many levels such as day, month, tidal fluctuation, length of wet/dry seasons, a year or longer ([Jacobs & Wingfield 2000](#)). Duration of each life-history stage can be measured directly from field observations. In migratory birds ([figure 4](#)), individuals may be in breeding condition for one to three months, whereas prebasic moult may be restricted to one month ([Wingfield *et al.* 1999](#)). In lizards and snakes, it may not be possible to separate moult from the breeding and non-breeding stages at all ([figure 3](#)). The degree of overlap of life-history stages varies too. In general, some life-history stages (such as winter and moult) may be more compatible in terms of overlap whereas others such as migration and breeding may be mutually exclusive. Obviously for a bird, it is not possible to build a nest

and incubate eggs while covering long distances on migration, but it may be possible to be gravid or pregnant and migrate in some fishes and mammals.

A schematic of the sub-stages of breeding life-history stages in different avian species, as well as other life-history stages are given in [figures 5 and 6](#). Note that connectivity of all sub-stages within a stage is limited resulting in specific sequences of stages (such as transitions from sexual sub-stages to parental sub-stages in [figure 6a](#)). Multiple-brooded species that show parental care are most complex whereas single-brooded species or brood parasites (with no parental care) are less so ([figure 6c](#)). Other life-history stages may be simple as well, e.g. winter and moult life-history stages ([figure 6](#); from [Wingfield & Jacobs 1999](#); [Wingfield 2004](#)).

Each life-history stage has a developmental phase in which morphological, physiological and behavioural characteristics of that stage are developed (in this case, the breeding life-history stage of a bird, [figure 7](#)). This results in mature capability when the stage can be expressed. Here a complex combination of breeding sub-stages are possible (e.g. sexual and/or parental behaviour), and may be repeated if environmental variation allows. The termination phase follows as the next life-history stage develops (from [Wingfield 2004, 2006](#)). This overlap of developmental phase of one life-history stage and the termination of another results in 'superstates', which may be energetically costly ([Wingfield & Jacobs 1999](#); [Jacobs & Wingfield 2000](#)) but usually are short lived (days to a few weeks). Superstates may be maintained for longer (including overlap of otherwise exclusive life-history stages such as

Figure 6. A schematic of the sub-stages of breeding life-history stages in different avian species, and sub-stages of other life-history stages. Note that connectivity of all sub-stages within a stage is limited resulting in specific sequences of stages (such as transitions from sexual sub-stages to parental sub-stages in *a*). (*c–e*) Multiple-brooded species that show parental care are most complex, whereas single-brooded species or brood parasites (with no parental care) are less so. Other life-history stages may also be more simple, although much more work needs to be done on the natural history of sub-stages. Adapted from Wingfield & Jacobs (1999); Wingfield (2006), Elsevier Press, New York.

Figure 7. Life-history stages have a development phase leading to mature capability when onset of the life-history stage with all its sub-stages can occur. The termination phase overlaps with the development phase of the next life-history stage (Jacobs & Wingfield 2000). Initial predictive information from the environment triggers onset of the development phase and maintains mature capability. Timing of the termination phase is also determined by initial predictive information. Local predictive information is of two types—inhibitory and acceleratory to all phases of the life-history stage. These serve to slow down the effects of initial predictive information (e.g. delay reproductive development in a cold spring) or accelerate it (e.g. early onset of breeding in a warm spring). Behavioural interactions also can influence all phases of a life-history stage serving to synchronize individuals in a pair or group and to integrate transitions among sub-stages (e.g. sexual to parental behaviour sub-stages when breeding). Modified from Wingfield (2006), Elsevier Press, New York.

moult and migration) if food supply is sufficient. Ways by which individuals may be able to do this will be discussed below.

4. THE FINITE STATE MACHINE MODEL

The concept of finite state machines has been used in the computer programming literature to describe the decision making process of a program (Gill 1962) and it conforms to several basic assumptions (Gill 1962;

Jacobs & Wingfield 2000). Three different types of variables are involved in a finite state machine.

- (i) Excitation variables (e.g. environmental cues) provide the stimulus for the machine.
- (ii) Response variables are the outputs of the system, the morphological, physiological and behavioural states involved in, for example, transitions between life-history stages—begin gonadal recrudescence, initiate migration or

they may be changes in physiological state within a life-history stage, i.e. sub-stages such as increase growth, increase fat stores, begin nesting, or shiver to increase body heat.

- (iii) Intermediate variables occur within the machine, and in this context probably represent internal mechanisms and neural pathways by which excitation variables are processed.

The machine has a finite number of inputs (excitation variables) and outputs (response variables). Whether the intermediate variables that represent mechanisms at cell and molecular levels that determine the actual state at any point in the life cycle are also finite remains to be determined. The finite state machine model may thus allow generation of hypotheses (see below) to explore cell and molecular mechanisms.

The view that an animal's lifespan is a series of discrete life-history stages repeated on a usually annual cycle has the potential to provide a framework for investigating control mechanisms at the neural and endocrine levels. It may also be useful for assessing control mechanisms across diverse taxa and in relation to multiple time frames within the annual cycle (long versus short seasons, etc.). Evidence to date strongly suggests that for phenotypes with more than two life-history stages, the progression of stages is unidirectional, and long-lived organisms will progress through all stages several times in a preordained sequence (figures 3 and 4). As far as I am aware, there is no evidence that the sequence can be reversed. For example, the only way for a migratory bird to go from the reproductive life-history stage to vernal migration is through all the other life-history stages (figures 3 and 4). Experiments on photoperiodic control of life-history stages and the expression of endogenous circannual rhythms supports this (e.g. Gwinner 1996; Wingfield & Silverin 2002). It is also proposed that life-history stages are not omitted or repeated out of sequence. Even in cases when animals may appear to skip reproduction, and may even appear not to migrate, further investigation shows that reproductive systems in these cases show at least partial development, and that preparations for migration (muscle hypertrophy, fattening) also occur (see Wingfield & Silverin 2002 for several examples). It is possible to induce an apparent moult by plucking feathers at any time of the annual cycle. However, this represents adventitious replacement of feathers (restricted to those actually lost) and does not induce a complete or other type of moult life-history stage.

The tight linkage of life-history stages to the environment means that a given stage is only appropriate at a specific season. For each organism, it is proposed that a finite state machine of characteristic life-history stages occurs in a fixed sequence and usually on a schedule determined by, for example, the changing seasons. Because predictable changes in environmental conditions occur in a more or less cyclical progression, then it follows that the temporal sequence of life-history stages is also cyclic. It should be borne in mind that although the sequence of life-history stages is fixed and cyclic, it can be accelerated

by artificial manipulation of photoperiod resulting in several 'cycles' per year (see Farner 1985).

Sub-stages are unique to each stage and their expression is by no means random (figure 5). They can be expressed in many sequences and combinations but generally they can also be repeated or reversed (figure 6, Jacobs 1996; Wingfield & Jacobs 1999; Jacobs & Wingfield 2000). As a result, a number of potential states can be manifest within each life-history stage. These represent not only the actual life-history stage and the combination of sub-stages, but also factors often included in the so-called extended phenotype (Dawkins 1982) such as territory, presence of a mate and social interactions that result (see Wingfield (2006) for references to many vertebrate systems).

State will vary with time, associated with changes in the 'extended phenotypic factors', as well as adjustments in morphology, physiology and behaviour of the organism as it acclimates to fluctuations in its environment. It is possible that the number and sequence of life-history stages, and the complexity of sub-stages within them are genetically determined for each individual. However, there are varying degrees of flexibility in the timing of development, onset and termination of those life-history stages, and the combination of sub-stages expressed at any moment in that stage. This is critical for the individual to adjust to local environmental and social conditions. It should be remembered that the repertoire of sub-stages is unique to a life-history stage and cannot be expressed at other times (Jacobs & Wingfield 2000).

The concept of states is not new and has been used by Mangel & Clark (1986), Houston & McNamara (1992) and McNamara & Houston (1996), including cyclic expression of states in an 'annual routine' (McNamara *et al.* 1998). But there are also important distinctions. The finite state machine framework proposed here is based on observations of life cycles and the experiments that have been done to determine how they are controlled by environmental cues. In contrast, the other concepts of states use underlying state variables to predict annual routines. A future combination of these two approaches may potentially enhance investigations of control mechanisms.

5. TIMING OF LIFE-HISTORY STAGES AND SUB-STAGES IN THE ANNUAL CYCLE

Timing of life-history stages and sub-stages is critically important in a changing environment. Cues from the environment that can be used as signals to trigger onset of a life-history stage or sequence of sub-stages will occur at more or less predictable times and the responses must coincide with appropriate conditions. Biological clocks are responsive to these environmental cues and their timing in the absence of environmental signals is usually different from timing in their presence, i.e. if a clock does not receive synchronizing signals that entrain it to the environment, it drifts or free runs (Farner & Gwinner 1980; Farner 1985; Gwinner 1996). In an environment with predictable components, each life cycle shows a progression of events (life-history stages), driven by environmental signals. These cues come in five basic classes:

developmental, initial predictive, local predictive, synchronizing and integrating, and perturbation (modifying) factors. These classes of cues combine to regulate the life cycle in relation to all environmental contingencies (Wingfield 1983; Wingfield & Kenagy 1991; Wingfield *et al.* 1999).

- (i) Developmental (ontogenetic) cues come in several different types, most based on intrinsic factors including genetic programmes: growth factors/morphogens, tissue interactions, etc. They usually originate from the internal environment of the embryo, but there are also extrinsic cues that come directly from the external environment. An example would be low environmental temperature that tends to slow down embryonic development in ectotherms. Note also maternal/paternal effects, experience and external environmental cues that influence development and adult phenotype.
- (ii) Initial predictive information includes environmental signals that allow the organism to make long-term predictions about the habitat and regulate timing of adult life-history stages. Photoperiod is a good example of a cue that provides information on future events in diverse environments. Increasing day length is an excellent predictor of the approach of spring and summer, and triggers gonadal development in the anticipation of the breeding season in many species (Follett 1984; Farner 1985; Gwinner 1986).
- (iii) Local predictive information such as food availability, rainfall and temperature provides fine-tuning for responses to initial predictive cues, and also gives short-term predictive information about the environment (Marshall 1959; Wingfield & Kenagy 1991). As the initial predictive information only provides a general clue of what the environment might be like in the future, local predictive information is important to ensure the organism makes the appropriate response at the correct time. In other words, they can accelerate or inhibit responses to initial predictive cues (figure 7).
- (iv) Synchronizing and integrating information encompasses social stimuli provided by other members of the population (Hinde 1965; Lehrman 1965). They ensure that the animal's responses to the external environment are appropriate to social status and condition of the other conspecifics.
- (v) Labile perturbation factors, or modifying factors, are unpredictable events in the environment such as inclement weather, flood, predation attempts, etc. (Jacobs 1996; Wingfield 2004), some of which can lead to stress (Wingfield & Ramenofsky 1999). For an event to be a labile perturbation factor, the organism must be qualitatively and quantitatively unable to cope with the event in the current life-history stage. Labile perturbation factors stimulate the expression of an alternate strategy, the emergency life-history stage

(Wingfield *et al.* 1998), but this will not be discussed further here.

Note that experimental evidence to date suggests that initial predictive information triggers development of a life-history stage and sustains mature capability (figure 7) so that other cues can regulate onset. Termination of the life-history stage is also regulated by initial predictive information (figure 7). Local predictive information and synchronizing and integrating information can also regulate all phases of the life-history stage (figure 7), but these effects are dependent on the action of initial predictive information (Wingfield & Kenagy 1991).

6. FINITE STAGE DIVERSITY—STRATEGIES TO TOLERATE LARGE ENVIRONMENTAL VARIATION WHILE MAINTAINING MAXIMUM FLEXIBILITY IN TIMING

From figure 4, it is clear that the number of life-history stages is not always a good index of 'finite stage diversity' (FSD), because these stages vary as a function of duration, and in many cases mature capability of at least two life-history stages may overlap. To analyse this variation, the Shannon diversity index (Pielou 1969, 1975) has been applied to finite-state machines of life-history stages (Wingfield & Jacobs 1999; Wingfield 2005). As with analyses of species diversity (e.g. MacArthur 1964), in which the formula expresses not only the number of species but also the relative distribution of individuals among species, it can be used to generate a measure of the diversity of life-history stages as a function of their number, duration and degree of overlap.

The temporal sequence of life-history stages is 1 year with intervals of months (i.e. 12 intervals in figure 8). The vertical axis is made up of different life-history stages (for example two to six stages in figure 8). For these temporal sequences of life-history stages, the mean stage interval diversity (MSID) can be calculated as a measure of the variation in duration of each life-history stage; and the temporal stage diversity (TSD) as a measure of the number of life-history stages in relation to degree of overlap. For example, in the rock dove, *Columba livia*, the breeding stage occurs in up to 10 months and the moult in 6 months. This gives a MSID of 8.5 (both are relatively long in duration) and a TSD of 1.3 (very few stages but this time with considerable overlap, figure 8). Although there are two life-history stages, owing to variation in duration and overlap in timing, the TSD is less than 2.

In the non-migratory white-crowned sparrow, *Zonotrichia leucophrys nuttalli* (figure 8b), the four life-history stages are of shorter duration with no overlap giving a MSID of 3.8 and a TSD of 3.1. The rock ptarmigan (figure 8c) has seven life-history stages with some degree of overlap. In this case, MSID = 2.4 and TSD = 4.9. Wingfield & Jacobs (1999) proposed that the ratio of TSD to MSID is a measure of finite stage diversity (FSD). In figure 8, the rock dove has the lowest FSD and the rock ptarmigan the highest. Clearly the numbers, duration and degree of overlap of life-history stages need to be taken into account when describing the diversity of finite state machines rather

Figure 8. Finite stage diversity for the three avian species. Each column represents an interval in a temporal sequence of life-history stages (i.e. months in a year). The rows represent life-history stages that vary according to species. The shaded circles indicate in which interval a life-history stage is expressed by an individual in a given population. (a) In the rock dove, *Columba livia* there are two life-history stages with relatively long durations and considerable overlap. Mean stage interval diversity (MSID) is high and temporal stage diversity (TSD) is low. (b) In the white-crowned sparrow, *Zonotrichia leucophrys gambelii*, and (c) rock ptarmigan, *Lagopus mutus*, there are more life-history stages with shorter durations and varying degrees of overlap. Here the MSID and TSD values for each taxon are similar. See text for details (Adapted from Wingfield & Jacobs 1999). FSD, finite-stage diversity of the annual cycle, i.e. TSD/MSID, the number of life-history stages weighted for duration and overlap. Adapted from Wingfield (2005), Springer-Verlag, Berlin.

than just the number. Since each life-history stage has the three phases of development, onset and termination, there is a time restraint on the duration of each stage. Thus, the higher FSD is, the less flexibility in timing of stages of the life cycle.

A potential drawback in this approach is that in some cases very different temporal sequences of life-history stages can give similar MSID and TSD values, as has been encountered by ecologists when using this formula to determine species diversity (Pielou 1969, 1975). For these reasons, this approach can be criticized; but on the other hand, these indices may still provide useful information to form hypotheses and predictions about adaptation to the annual cycle and the underlying mechanisms. It is possible that although the number and temporal sequence of life-history stages in some species may appear to be different superficially, the FSD (ratios of TSD and MSID values) suggest that they may be similar at least in terms of control mechanisms. These hypotheses are testable and, bearing in mind phylogenetic issues, may allow us to determine whether mechanisms differ or show convergence accordingly.

Finite state diversity can also be assessed among closely related taxa such as subspecies of the white-crowned sparrow that show varying degrees of migratory behaviour and thus numbers of life-cycle stages (figure 9). Natural history data (from Blanchard 1941;

Blanchard & Erickson 1949; Mewaldt & King 1977; Wingfield & Farner 1978a,b) show that the life-history stages vary in duration and may overlap in some cases giving diverse MSID and TSD values. Note that the FSD is lowest in the non-migratory *Z.l. nuttallii* and higher in the two migratory forms *Z.l. pugetensis* and *Z.l. gambelii* (figure 9). This analysis then sets up the hypothesis that timing of life-history stages in *Z.l. nuttallii* will be more flexible than in the other two forms—a very testable proposition. Indeed, comparisons of the effects of temperature on photoperiodically induced gonadal growth uphold these predictions. Low and high environmental temperature can inhibit or accelerate (respectively) photoperiodically induced gonadal growth in *Z.l. pugetensis*, but not in *Z.l. gambelii* (Wingfield *et al.* 1996, 1997). The latter taxon has a higher FSD (figure 9) although both have the same number of life-history stages.

7. USING FINITE STATE DIVERSITY TO GENERATE HYPOTHESES AND TESTABLE PREDICTIONS

Life-history stages and their characteristic sub-stages provide a finite number of states an individual may express throughout its life cycle. Analysis of FSD in relation to not only the number of stages, but also their duration and overlap allows us to compare finite state machines in different phenotypes within a genotype

Figure 9. Mean stage interval diversity and temporal stage diversity in relation to the number of phenotypic stages within a single species. (a) A non migrant, *Z. leucophrys nuttallii*; (b) a short-distance migrant *Z.l. pugetensis* and (c) a long-distance migrant *Z.l. gambelii* (Blanchard 1941; Blanchard & Erickson 1949; Mewaldt & King 1977; Wingfield & Farner 1978a,b). As the number of life-history stages increases, MSID decreases and TSD increases resulting in a net increase of finite stage diversity and less flexibility in overall timing of the life cycle. *Z.l. pugetensis* represents a compromise in that it has the same number of life-history stages as *Z.l. gambelii*, but by overlapping more stages it reduces finite stage diversity allowing more flexibility in timing. MSID, mean stage interval diversity; TSD, temporal stage diversity; FSD, finite-stage diversity of the annual cycle, i.e. TSD/MSID, the number of life-history stages weighted for duration and overlap. Adapted from Wingfield (2005), Springer, Berlin.

and across species in general. This may represent a classic trade-off because overlapping mature capability of two or more life-history stages incurs greater costs, but the reduction of FSD increases flexibility in timing that would be an advantage if environmental conditions become more variable. Although overlap of mature capability of life-history stages is energetically costly, it may be tenable at times of year when food resources are abundant. Note that when mature capability of life-history stages occurs only one life-history stage can actually be expressed at a time but either one can be switched on or off rapidly because the capacity to do so is already developed. This is different from the overlap of development phase of one stage and termination phase of the previous stage (Wingfield 2005).

An example in which FSD may vary in one genotype is a hypothetical bird in figure 10 (see also Wingfield 2005). The genotype may express several phenotypes such as (a) a non-migrant form, (b) a migratory form, (c) a partial migrant in which some members of a population may migrate whereas others do not, and (d) a population in which there is also a moult migration in which individuals move to a separate locality solely to moult. Clearly there is an increase in the number of life-history stages from (a) to (d) that could potentially decrease flexibility in timing (see Wingfield & Silverin 2002 for review). In the partial migrant (c), it is possible

that social and internal cues determine whether an individual migrates or not. In figure 10d, it is possible that a new life-history stage, moult migration, exists. However, rather than increase the number of life-history stages (and thus FSD), it may also be possible to overlap the mature capability phases of some life-history stages such as moult and autumn migration, or autumn migration and winter, so that one or other can be expressed rapidly as environmental conditions dictate without necessarily invoking new life-history stages (Wingfield 2005). Note that if an individual does migrate in autumn then it automatically must also incorporate an additional life-history stage—vernal migration—to return it to the breeding ground, thus increasing FSD even further (Wingfield 2005). This is a testable scenario as has been shown by elegant genetic experiments of different migratory forms of old world-warblers (e.g. Berthold 1999).

We have seen earlier how the FSD of the non-migratory bird is less than that of a migratory phenotype (figure 9; Wingfield 2005). However, if the individual can overlap vernal migration with breeding, or autumn migration with winter, then FSD is reduced to a level similar (even less than) that of the non-migrant (figure 11). Although mature capabilities of vernal migration and breeding overlap, only onset of one or the other can be triggered at any one time

Figure 10. Life-history stages of birds showing (a) no migration, (b) regular spring and autumn migrations, (c) partial migration in which certain individuals in a population migrate and others do not, and (d) a complex interaction of moult and autumn migration suggesting a new LHS—moult migration—may exist. Adapted from Wingfield (2005), Springer-Verlag, Berlin.

Figure 11. Finite stage diversity (FSD, finite-stage diversity of the annual cycle, i.e. TSD/MSID, the number of life-history stages weighted for duration and overlap) of avian life cycles including migration life-history stages (LHSs). Stages vary in number from (a) three in the non-migratory population to (b and c) five in migratory populations. The interval is one month (= 12 for the year) and the closed circles represent the months in which each LHS is expressed. Using formulae associated with the Shannon index, it is possible to calculate the mean interval for each LHS as a function of duration and number (mean stage interval duration, MSID), and the mean number of LHSs in each population as a function of number and duration (temporal stage duration, TSD). If the number of LHSs increases (a and b) then MSID decreases and TSD increases. The ratio of the two is finite stage diversity (FSD) that increases. Some avian populations show partial migration in which some individuals migrate and others do not. Here we model this as overlap of mature capabilities of vernal and autumnal migration LHSs with winter and breeding (c). Now MSID increases again and TSD is reduced resulting in a FSD similar to that of non-migrants. Adapted from Wingfield (2005), Springer-Verlag, Berlin.

because, for example, birds would not be able to migrate if incubating eggs in a nest. However, individuals can develop the reproductive system and form pair bonds while migrating so that they can then initiate onset of nesting quickly after arrival in the breeding area. Conversely, if birds begin a nesting attempt but fail owing to deteriorating conditions, if they are still in mature capability for migration they can move on quickly. Similarly with autumn migration and wintering life-history stages, mature capabilities may overlap, but under certain environmental conditions, one individual might trigger autumn migration whereas another might not and stay in the winter life-history stage. This flexibility would allow one individual to migrate 1 year and not in another year depending upon how it experiences its environment. Eventually the autumn migration life-history stage will be terminated and then all individuals in the population will be in winter life-history stage (figure 11; Wingfield 2005).

Another example of how FSD may influence flexibility of timing in the life cycle is the moult migration phenomenon. Some species migrate after breeding to a specific moulting area. Autumn migration to the wintering area follows completion of the moult (see Wingfield & Silverin 2002 for discussion, and Barta *et al.* (2008), this volume for optimization strategies as to why moult and migration strategies vary). If mature capability phases of prebasic moult and autumn migration life-history stages overlap, then one or the other could be expressed as environmental conditions and location require. In this scenario, a separate moult migration life-history stage need not be invoked thus reducing FSD by half and enhancing flexibility in timing (Wingfield 2005). Clearly, the overlap of two life-history stages has the potential to increase flexibility in timing. Note also that birds, and other animals, may show additional facultative migrations (e.g. irruptions) in response to labile perturbation factors. This type of migration is common but not a part of the predictable life cycle (Wingfield 2005).

8. ASSOCIATED-DISSOCIATED LIFE-HISTORY STAGES

Another way in which flexibility in the timing of life cycle events may be achieved is by dissociation of some sub-stages of a life-history stage and overlap with other stages. Expressions of sub-stages within a life-history stage are usually associated with mature capability and onset of the stage. For example, gonadal development precedes mating that then occurs when gametes are mature (Crews 1984, 1987). Parental care may follow (e.g. Wingfield & Silverin 2002) and multiple breeding attempts will occur if the breeding season is long. In some cases, breeding may be essentially continuous (at least the mature capability phase) and thus mating always occurs when the gonads are mature (Crews 1984, 1987). In other cases, gonadal development and mating behaviour are not associated, an example being the garter snake, *Thamnophis* sp. Some populations spend the winter in deep caves, and on emergence in spring copulation acts to increase secretion of gonadotrophins to initiate ovarian development. Sperm

obtained during copulation are stored in the oviduct until ovulation later in summer (Crews 1984, 1987). Eggs fertilized by stored sperm develop within the oviduct of the female (ovoviviparity) and young are born in late summer. In males, spermatogenesis also begins after emergence and copulation, and the resulting sperm are stored until the next year. Thus both male and female garter snakes show a dissociated cycle of gametogenesis and mating. One or both sexes of a broad spectrum of vertebrates can show either strategy of dissociated/associated cycles of gonadal development and mating (Crews & Moore 1986).

This strategy would spread out energetic costs of breeding over a longer period thus reducing costs of reproduction at any point in the year, as well as reducing FSD (figure 12; Wingfield 2005). Also, the onset of parental care in some species may be coincident with rapid regression of the gonads (figure 12). Dissociation of sub-stages of the breeding life-history stage may be a widespread potential mechanism to increase flexibility of timing. It is intriguing to speculate that this may also occur in other life-history stages as well.

9. VARIATION OF INTENSITY OF LIFE-HISTORY STAGE EXPRESSION TO INCREASE FLEXIBILITY IN TIMING

When two life-history stages overlap mature capability, both cannot be expressed at full capacity (Wingfield 2005), but it may be possible to express both at a lower capacity that does not exceed the energetic costs an individual can bear. An example is reduced rate of moult so that other life-history stages can be expressed simultaneously. In many tropical birds, moult may be very slow (e.g. one or two primaries at a time) allowing considerable overlap with reproduction (Foster 1975; Stutchbury & Morton 2001). It is also possible that if clutch size is also reduced from, for example five to two or three, then this would also allow more overlap (Stutchbury & Morton 2001). There is much to be explored here, and models to determine how much flexibility could be gained while retaining tolerance of a wide range of environmental conditions could be very useful for designing field studies and laboratory experiments to determine mechanisms.

Mechanisms for reducing finite state diversity may also have implications for how organisms will tolerate global warming. If an organism has few life-history stages then it has great flexibility in timing (low FSD), but the range of environmental tolerance is reduced. If an organism has more life-history stages, then it can tolerate a greater range of environmental variation, but flexibility in timing is reduced (high FSD). The concept of finite stage diversity addresses ways by which organisms can balance number of life-history stages to maximize tolerance of environmental variation while at the same time using various strategies to overlap life-history stages (associated/dissociated stages, reduced intensity of expression) to reduce FSD (Wingfield 2005). Thus in tropical regions, many species may be vulnerable to global climate change because they have low FSD and thus cannot tolerate environmental variation beyond the narrow

Figure 12. Extension of the associated–dissociated concept of Crews (1984, 1987) and Crews & Moore (1986) to the reproductive life-history stage of a vertebrate, but including the parental sub-stage. (a) An associated breeding life-history stage typical of most vertebrates including birds. (b) In some avian species with very brief breeding season the breeding life-history stage may become partially dissociated because the mating period and parental sub-stage do not overlap (compared with a). (c) A theoretical scenario in which gonadal development and regression, mating period (with territorial behaviour) and the parental period showing complete dissociation. This may occur in some vertebrates including birds such as sea birds in which egg production and mating do not always completely overlap. By the time the parental phase is underway the gonads may have already regressed. In this way, it is possible to spread the costs of reproduction over a much longer period, overlapping with other life-history stages such as moult. The result will be reduced finite stage diversity (FSD) and thus greater flexibility in the timing and integration of the life cycle. Adapted from Wingfield (2005), Springer-Verlag, Berlin.

limits of their habitat. At high latitudes, increased life-history stages mean high FSD and reduced flexibility in timing. Hence, these species will also be vulnerable to global climate change because they may not be able to adjust timing of crucial events such as breeding, migration and moult if the appropriate time of year changes. Trade-offs of FSD and costs of overlapping life-history stages in relation to global climate change may be most widespread at mid-latitudes—organisms have intermediate or high numbers of life-history stages, but use various strategies for reducing FSD so they can maximize flexibility in timing while being able to tolerate a wider range of environmental variation. These species may be more able to tolerate global climate change than tropical or high latitude species.

10. IMPLICATIONS FOR ENDOCRINE CONTROL MECHANISMS

Endocrine secretions regulate many aspects of transitions in morphology, physiology and behaviour in relation to predictable changes in the environment. However, the number of life-history stages, their durations, and the degree of overlap with other stages, varies from species to species and from population to population (finite stage diversity). As hormones regulate the development and onset of each stage and its termination, then the number of stages and the degree of overlap with other stages may influence neuroendocrine and endocrine mechanisms and their control by environmental cues. For example, the need for accurate timing of the transitions from one stage to the next in ptarmigan may be more important than

in the rock dove owing to different degrees of diversity in the stages (figure 8). The annual change in photoperiod acting through neuroendocrine and endocrine secretions regulate at least some of the life-history stages of rock ptarmigan (e.g. Stokkan *et al.* 1986, 1988). In contrast, regulation of breeding and moult appear to be independent of photoperiod in the rock dove (Lofts & Murton 1968). Finite stage diversity may help identify where possible differences, or similarities, in environmental and endocrine mechanisms may exist, and also indicate what experiments need to be performed.

Overlap of life-history stages decreases FSD potentially leading to increased flexibility in timing that in turn means that more environmental signals need to be monitored to regulate development, onset and termination of stages and thus maximize fitness (e.g. Wingfield *et al.* 1992, 1993). We know very little of how vertebrates perceive and transduce environmental cues other than photoperiod into neuroendocrine and endocrine secretions that regulate the processes of changing morphology, physiology and behaviour, or how they integrate different types of environmental information. Analyses of these types will probably provide an objective way of comparing populations experimentally to determine mechanisms underlying neural pathways for these environmental signals.

Using the finite state machine framework, 12 hypotheses have been formulated below that potentially have fundamental influences on hormone systems at all levels. This list is by no means exhaustive and others may come to light, or some may prove to be invalid as the predictions are tested. These hypotheses are meant to

initiate a critical analysis of principles of environmental endocrinology that may guide us in the future.

The hypotheses are as follows.

- (i) Owing to frequently conflicting physiology and behaviour, and the energetic costs of maintaining morphological characters, there are limits to the number of life-history stages that can be expressed simultaneously.
- (ii) Each stage has development, onset and termination phases that impose time restrictions. Thus there is a limit to how many may be expressed within a year even though development of the next life-history stage overlaps with termination of the last.
- (iii) More life-history stages (finite state diversity) means less flexibility in timing because the development and termination periods are time dependent and must be expressed in the correct temporal sequence. This in turn determines how specific neuroendocrine and endocrine control mechanisms of an individual respond to environmental cues used to pace the life cycle.
- (iv) Life-history stages cannot be omitted completely, but the expression of sub-stages at 'mature capability' may be suppressed (e.g. onset of breeding or migration).
- (v) The temporal sequence of stages continues even if the life-history cycle is interrupted by an unpredictable event (e.g. stress, extreme environments). During this interruption, an emergency life-history stage is expressed (see Wingfield *et al.* 1998, 1999) and mature capabilities of other life-history stages are suppressed. Once the unpredictable event passes, the life-history stage appropriate for that time of year will be assumed.
- (vi) The expression of sub-stages within a life-history stage is not random. However, despite certain sequences of sub-stages, there are varying degrees of flexibility. In contrast the temporal sequence of life-history stages is rigid. This implies that the timing and integration of life-history stages and sub-stages are fundamentally different.
- (vii) The longer a life-history stage is expressed in time, the greater flexibility of activation of sub-stages and combinations of sub-stages.
- (viii) Transition from one life-history stage to the next can vary in complexity as a function of the combination of sub-stages expressed just prior to the transition. In some cases, the transition may be rapid and simple, whereas in others it may be complex with a longer period of overlap. In contrast, transitions between sub-stages are usually rapid and reversible.
- (ix) The neural pathways by which environmental signals are perceived and transduced into neuroendocrine and endocrine secretions may not be the same among different phases of the life-history stage, or among different life-history stages, even though the environmental factors that regulate these processes may be similar. Selection may have acted on onset and termination of life-history stages separately thus resulting in different mechanisms.
- (x) Given a conserved and limited repertoire of endocrine systems (over 80% of hormone types are conserved from fishes to humans; Wingfield 2006), some specific hormones may act sequentially during development, onset and termination of a life-history stage. In these cases identical mechanisms of action of that hormone at each phase are unlikely. Multiple receptor types for specific hormones are well known and may form the basis of different mechanisms of the same hormone acting at different phases of the life-history stage.
- (xi) Apparently identical physiological processes and behaviour expressed in different life-history stages may not have the same hormone control mechanisms. This has been tested and shown to be so for control of territorial behaviour in songbirds when breeding and non-breeding (e.g. Wingfield *et al.* 2001).
- (xii) When life-history stages are expressed for long periods (i.e. if there are few life-history stages in a cycle), there are dramatic costs to prolonged high circulating levels of hormones characteristic of that stage. Many novel mechanisms may have evolved to minimize these costs. Some have been tested such as the trade-offs of the actions of testosterone—costs versus benefits (Wingfield *et al.* 2001).

These hypotheses stem directly from the finite state machine framework and have clear predictions that can be tested experimentally to explore possible common and basic neuroendocrine and endocrine mechanisms by which organisms deal with their environments.

11. SUMMARY

All organisms have to cope with changing environments. Since most vertebrates have a lifespan of greater than 1 year, individuals must be able to change morphology, physiology and behaviour to adapt to the annual cycle of changing conditions. They do this through phenotypic flexibility in which an individual switches from one life-history stage to another to maximize fitness at any point in the annual cycle of environmental change. If the range of environmental variation is low, then few life-history stages will be needed. If environmental variation is large, then more life-history stages will be required to adapt to the annual cycle. Each life-history stage has a characteristic set of sub-stages that can be expressed in various combinations and patterns to determine state at any point in the annual cycle. Since the number of life-history stages and sub-stages in an individual is fixed, the organism can be regarded as having a finite number of states that can be expressed over the spectrum of environmental conditions in its lifespan.

Life-history stages have three phases—development, mature capability (when characteristic sub-stages can be expressed) and termination. This means that expression of each stage is time dependent (probably a minimum of one month), and the termination phase

of one stage overlaps with the development phase of the next stage. For these reasons, the more life-history stages an individual expresses the less flexibility it will have in timing those stages. Fewer life-history stages mean more flexibility in timing but less tolerance of variation environmental conditions. This may have some significance for global climate change and which organisms will be able to adapt.

One way an organism can retain more life-history stages, so as to tolerate a greater range of environmental variation and yet maintain flexibility in timing, is to overlap mature capability of some life-history stages. This will effectively reduce 'finite stage diversity' and maximize flexibility in timing. Possible strategies by which this can be done, and the implications for neuroendocrine and endocrine control mechanisms are discussed. Using this finite state machine approach, 12 testable hypotheses are posed that relate directly to control mechanisms.

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