ENDOCRINE CONTROL OF LIFE-CYCLE STAGES:
A CONSTRAINT ON RESPONSE TO THE ENVIRONMENT?[1]

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Abstract. Most organisms live in seasonal environments that fluctuate on a predictable schedule and sometimes unpredictably. Individuals must, therefore, adjust so as to maximize their survival and reproductive success over a wide range of environmental conditions. In birds, as in other vertebrates, endocrine secretions regulate morphological, physiological, and behavioral changes in anticipation of future events. The individual thus prepares for predictable fluctuations in its environment by changing life-cycle stages. We have applied finite-state machine theory to define and compare different life-history cycles. The ability of birds to respond to predictable and unpredictable regimes of environmental variation may be constrained by the adaptability of their endocrine control systems. We have applied several theoretical approaches to natural history data of birds to compare the complexity of life cycles, the degree of plasticity of timing of stages within the cycle, and to determine whether endocrine control mechanisms influence the way birds respond to their environments. The interactions of environmental cues on the timing of life-history stages are not uniform in all populations. Taking the reproductive life-history stage as an example, arctic birds that have short breeding seasons in severe environments appear to use one reliable environmental cue to time reproduction and they ignore other factors. Birds having longer breeding seasons exhibit greater plasticity of onset and termination and appear to integrate several environmental cues. Theoretical approaches may allow us to predict how individuals respond to their environment at the proximate level and, conversely, predict how constraints imposed by endocrine control systems may limit the complexity of life cycles.

Key words: endocrinology, finite-state machine, follicle-stimulating hormone, life-history, predictability, prolactin, reproduction.

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. For example, in arctic environments, temperature, food availability, and the background color of the environment vary radically in a yearly seasonal cycle. In some tropical regions, the dry and rainy periods occur at specific times of year, but the amount of rain and severity of a drought may vary. Even in places that at first seem exceedingly stable, the environment fluctuates. In caves, where the yearly temperature may only fluctuate on the order of 2°C, seasonal flooding may occur, providing changes in the nutrient input from non-cave sources (Poulson 1964).

Unless the environmental fluctuations are very small, an organism must modify its morphology, physiology, and behavior to survive as conditions change (Prosser 1986). Although the term physiology can be used in a broad sense to include all the biological properties of the organism, including morphology and behavior (Eckert et al. 1988), we will use the term "state" to define this phenotypic expression of all three classes of traits. State can be adjusted in several ways to maximize survival in a fluctuating environment. Birds, particularly long-lived ones, have generation times and life spans that may be many times greater than the temporal scale of seasonal environmental change. They show dramatic changes in physiology within the individual, and these must be reversible or cyclic, so as to acclimate to repeated environmental fluctuations and for life-history stages to be expressed at appropriate times (Prosser 1986). These latter responses will be the focus here.

LIFE-HISTORY STAGES WITHIN INDIVIDUALS

With a few exceptions, most vertebrates have a life expectancy of at least one year. Within the period of a single life cycle, environmental conditions will probably fluctuate (cycle) many times. This makes the strategy of "hard-wired" phenotype switching between generations untenable; the polyphenism type of phenotypic plasticity common in invertebrates is not found in vertebrates (West-Eberhard 1987, Stearns 1989). Here we develop a model for state changes within an individual during its life cycle.

An individual must be able to survive a wide variety of environmental fluctuations. It does this by regulating gene expression to adjust state, i.e., morphology, physiology, and behavior, to track or anticipate environmental changes (Prosser 1986). In temperate or arctic species, the organism will often pass through a series of life-history stages, each appropriate for a part of the year, and the functions required at that time of year. Life-history stages are in many ways analogous to the phenotypic changes seen among individuals in a population, but they occur within an individual. For example, many animals undergo changes in coloration to adapt to seasonal fluctuations in the color of the habitat, or for thermoregulation and concealment. In the Willow Ptarmigan (*Lagopus lagopus*), changes in plumage coloration throughout the year match varying snow cover on the arctic tundra (Pielou 1994). Other examples of life-history stages include adaptations to different temperature ranges as in the American Goldfinch (*Carduelis tristis,* Buttemer 1985), or physiological changes associated with life-history processes such as migration, reproduction, and molting (Farner 1985). The temporal progression of life-history stages, their duration and seasonality are driven by time, usually in relation to changing seasons. During a complete life cycle, an animal will pass through a number of discrete stages that are species characteristic. Stages can overlap, but usually are temporally separated and sometimes are mutually exclusive.

For further discussions, a few terms need to be defined. A phenotype in vertebrates means the sum expression of all genes within all stages during the life cycle in a given individual. A number of phenotypic "sub-stages," defined by the different suites of extended phenotypes

(Dawkins 1982) in the various life-history stages, exist within each phenotype (Wingfield et al. 1997b, Wingfield and Jacobs 1999). Because different combinations of sub-stages can be expressed depending on local environmental conditions, they define state of the individual at that time. They may be altered further by, for example, changes in social status. 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.

An extension of Levins' (1968) phenotypic models can be made to life-history stages that take the place of phenotypes because we are now referring to individuals. If the cost of transition between life-history stages is relatively small, overall fitness can be increased by expressing more life-history stages rather than having a single mixed stage (Fig. 1). Transitions among life-history stages require a predictable component in the environment so individuals can anticipate change and activate the relevant stage, i.e., they must be timed so as to coincide with appropriate seasons. Information or cues from the environment (Levins 1968) permit organisms to anticipate these changes.

Environmental cues. In an environment with predictable components, each life-history stage shows a progression of events driven by cues from the environment. These cues come in five basic classes: developmental, initial predictive, supplementary, synchronizing/integrating, and modifying factors. All these classes of cues combine to orchestrate the life cycle in relation to all environmental contingencies (Wingfield 1983, Wingfield and Kenagy 1991, Wingfield et al. 1999a, 1999b).

(1) Developmental cues come in several different types: growth factors/morphogens, tissue interactions, intrinsic factors, and external factors. They most often originate from the internal environment of the embryo, such as growth factors, but extrinsic cues come directly from the external environment. An example would be low environmental temperature that tends to slow down embryonic development.

(2) Initial predictive cues are environmental signals that allow the organism to make long term predictions about the habitat. 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 trig-
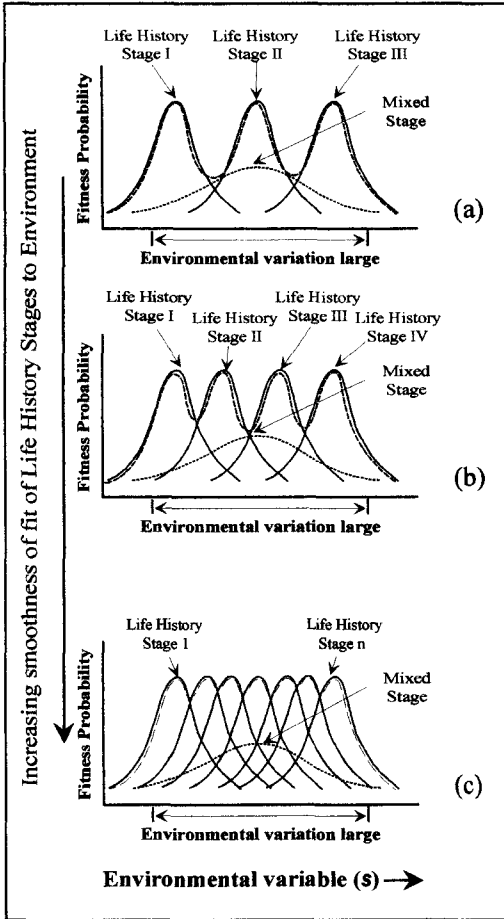
FIGURE 1. Fitness probability as a function of life-history stages. The dotted curve represents the fitness probability of a mixed stage, generalist phenotype that attempts to cover the entire range of environmental variability. As the number of life-history stages increases, the overall fitness also increases.

gers gonadal development in anticipation of the breeding season in many species (Follett 1984, Farner 1985, Gwinner 1987).

(3) Supplementary cues such as food availability provide fine tuning for responses to initial predictive cues, and also provide short term predictive information about the environment (Marshall 1959, Wingfield and Kenagy 1991). As the initial predictive cues only provide a general prediction of what the environment might be like in the future, supplementary cues are important to ensure the organism makes the correct responses at the correct time. In other words,

they can accelerate or inhibit the responses to initial predictive cues.

(4) Synchronizing/integrating cues are 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.

(5) Labile perturbation factors, or modifying factors, are unpredictable events in the environment such as inclement weather, frost, flood, predation attempts, etc. (Wingfield 1988, Jacobs 1996). Some labile perturbation factors can lead to stress (Wingfield and Ramenofsky 1999). For an event to be a labile perturbation factor, the organism must be qualitatively and quantitatively unprepared for the event otherwise it would be able to deal with it 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 will not be discussed further here.

TRANSITIONS BETWEEN LIFE-HISTORY STAGES

Development of a life-history stage usually requires stimulation of the cell cycle leading to cellular growth and differentiation such as in the recrudescence of gonads in seasonal breeding birds. This stimulation includes the action of hormones acting either via genomic receptors such as those of the steroids and thyroid hormones, or by slow acting membrane receptors that lead to stimulation of the cell cycle (Hadley 1996).

Timing of development of the stage, as well as the onset of mature capability, in which various sub-stages of the life-history stage can be expressed fully (Fig. 2) are regulated by supplementary, integrating, and synchronizing cues. These act as accelerators or inhibitors, speeding up or slowing down development of the life-history stage, as well as controlling the "pathways" among sub-stages within each stage and thus state at any given moment in the life cycle (Wingfield and Jacobs 1999). Onset of processes characteristic of sub-stages are regulated by environmental cues in the same categories, but presumably they act through different mechanisms. This is an important point for designing experiments to determine mechanisms. Onset of the life-history stage may be regulated by hormones acting via fast acting membrane receptors to reg-
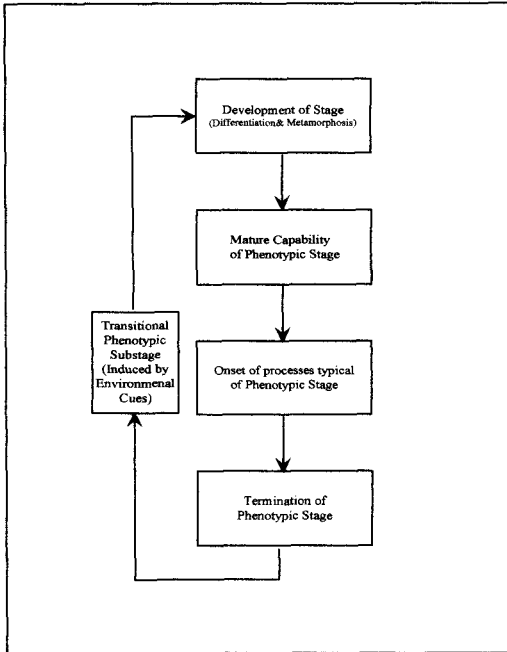
FIGURE 2. Cyclic nature of the development and expression of life-history stages. Environmental cues (usually initial predictive factors) trigger transitions to the next life-history stages. Development of the characteristics of the life-history stage may occur several weeks in advance of when the stage is timed to be expressed. This developmental period results in a "mature-capability" of the life-history stage and onset of that stage can begin at any time. Finally, the life-history stage is terminated and many morphological, physiological, and behavioral sub-stages, characteristic of the life-history stage, regress or are turned off. Termination of one stage and development of the next often overlap.

ulate the function of cells, rather than the slow acting effects via stimulation of the cell cycle. Termination of a life-history stage may be initiated by any of the cues including the unpredictable labile perturbation factors.

A number of potential states can be manifest within each life-history stage. These states represent not only the actual body condition of the organism, but also factors often included in the so-called extended phenotype such as territory quality and presence of a mate (Dawkins 1982). Obviously state will vary with time, associated with changes in the "extended phenotypic factors," as well as adjustments in morphology, physiology, and behavior of the organism as it acclimates to fluctuations in its environment. Note again that these changes are triggered by

environmental cues in a manner different from the transition between phenotypic stages.

It is possible to look at many different levels of life-history stages down to regulation of single genes and the states of all cells within the individual. This could generate an apparent infinite number of micro-states for an organism, but the vast majority of these will be functionally and selectively identical (or nearly so) and can be grouped into a finite number of states. Although all the individuals within a state will not be completely identical, their ability to interact with the environment will be largely indistinguishable.

THE FINITE-STATE MACHINE MODEL

Taking this view of an animal's life cycle as a series of discrete stages such as reproduction, migration, molting, we see that it occurs in a more or less cyclical progression, proceeding from one stage to the next in response to a wide number of environmental cues including social stimuli. Within a given life-history stage, the organism can express a finite number of functionally different states defined by a combination of appropriate sub-stages. The finite nature of these life-history stages and states within them allows us to view the animal's life cycle as a finite-state machine. These are similar to the concept of states as used by Mangel and Clark (1986) and Houston and McNamara (1992), including cyclic expression in an "annual routine" (McNamara et al. 1998).

Finite state machines (FSM) have been used in computer programming literature to describe the decision making process of a program (Gill 1962). Three different types of variables are involved in a FSM: (1) excitation variables provide the stimulus for the machine, (2) response variables are the outputs of the system, and could include various states, and (3) intermediate variables are often difficult to measure as they occur within the machine, and in this context probably represent internal mechanisms and neural pathways by which excitation variables are processed.

A FSM can be represented as a black box (Fig. 3). The "box" has a finite number of inputs (excitation variables) and finite number of outputs (response variables). The intermediate variables are inside the black box, and in biological systems they encapsulate the physiological mechanisms and cell functions within the
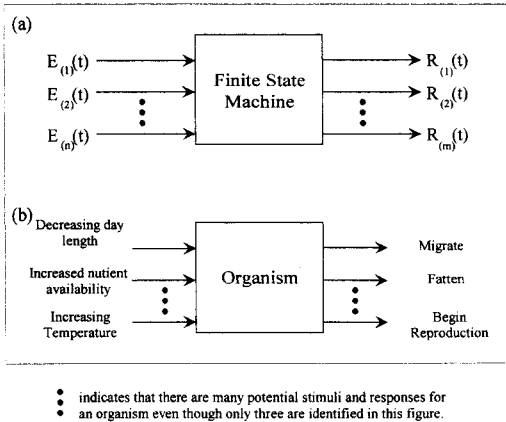
FIGURE 3.   Black box representation of a finite-state machine redrawn from Gill (1962). (a). Inputs enter the black box from the left, and responses leave on the right. Excitation variables are represented as "E," and response variables are represented as "R," where "t" is the sampling time, and "m" and "n" are the number of response and excitation variables, respectively. (b). A "biological black box." Although a vast number of excitations (stimuli) impinge on the organism, the individual has a finite number of responses to these excitations.

organism that determine the actual state at that time. Although their exact nature need not be understood to use the finite state model, they may indicate important lines of investigation to determine cell and molecular mechanisms of interest to a more reductionist approach.

In a biological system, the excitation variables are the environmental cues described above including initial predictive and supplementary cues such as increasing day length, food availability, and decreasing temperature. The response variables can be expressions of, and transitions between, life-history stages such as begin gonadal recrudescence, initiate migration. Or they may be changes in state within a life-history stage, i.e., sub-stages such as increase growth and fat stores, begin nesting, shiver to increase body heat (Fig. 3b).

Finite-state machines conform to several basic assumptions. The machine must be controlled by an independent entraining source, e.g., day length. The system variables are not measured constantly, but rather at discrete intervals when certain specific events occur, called entraining signals (e.g., onset of rainy season). These discrete time instances are called the sampling times. An additional assumption is that the be-

havior of the system at sampling time tV (where V is an integer indicating the time interval) is independent of the interval between tV and the previous interval $tV - 1$. Thus the system is not absolutely dependent on time, but rather on an ordinal number associated with the sampling times. This does not preclude events occurring at regular intervals, indeed information can come from internal biological clocks as well. This independence from the interval between samplings is important in biological systems because they are responding to their environment and not just to the ticking of a simple clock. Time may be critically important, but only in that the cues from the environment will occur at more or less predictable times and the responses must coincide with appropriate conditions. Although biological clocks have been documented in a large number of systems (Aschoff 1980, Gwinner 1987), these clocks are responsive to the environment, and timing in the absence of environmental cues is usually different from timing in their presence. Thus, if a biological clock does not receive entraining signals, it drifts or free-runs (Aschoff 1980, Gwinner 1987).

The current set of output response variables is uniquely determined by the present state of the machine and the excitation variables at that time. The previous history of the machine is only important in that it determines the present state of the machine. The state at the next sampling time is solely determined by the present state, and the excitation variables. Thus, the machine can be characterized by a state function and a response function:

$$response_i = f_{response}(excitaton_i, state_i)$$

$$state_{i+1} = f_{state}(excitation_i, state_i)$$

where $state\ i$ is the state of the machine at time ti ($i = 1, 2, 3, \ldots$), excitation i is the set of excitation variables received during interval i, $state\ i + 1$ is the state of the machine in the next time interval after i, and response i is the response of the machine at interval i. Both the response function (f response) and state function (f state) have the current state of the machine (state i) as a dependent variable, thus the response of the machine to a given excitation cannot be predicted, unless the state to which the excitations are applied (state i) is known, or the machine always has the same response to the
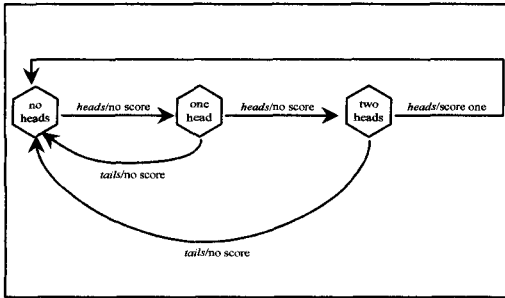
FIGURE 4. Transition diagram of a simple coin toss game. In this game points are awarded only for three consecutive coin tosses resulting in heads. States are enclosed in hexagons and excitations are in italics followed by the response.
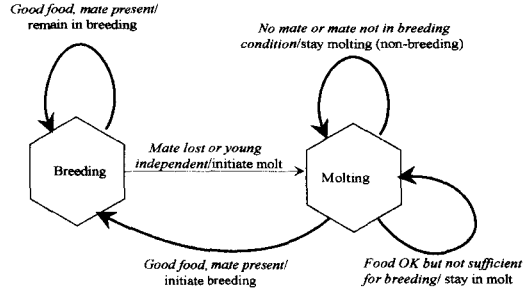

FIGURE 5. Transition diagram for a simple biological finite-state machine. An example of a simple finite-state machine is the life cycle of the Rock Dove (*Columba livia*). The two stages are represented by hexagons, and excitations are in italics. Responses of the machine are to the right of the slash marks for the corresponding excitation.

excitation. Note that some excitations do not cause the transition to another state, but act to maintain the current state or even inhibit transition to another state.

A simple example may better illustrate this state dependence. A coin toss game provides a very simple finite state machine (Fig. 4). The coin has two sides, heads and tails, and in this game points are only awarded for three heads in succession, without any intervening tails. The excitation variables are thus either heads or tails, and the response variables are score or no score. There are three states: no heads, one and two heads. The machine always responds to "no heads" (tails) in the same way (no score), and thus is always predictable regardless of whether the state of the machine is known or not. Both the response and the resulting state are ambiguous for "heads" unless you know the state of the machine. If you were to enter the room while the game was in progress, and the player flipped a "heads," you could not know whether a point was scored, without finding out from the players. You could not know whether the previous streak of heads was one, two, or zero, and thus could not predict the outcome (response) even though you knew the excitation (heads).

APPLICATION OF FINITE-STATE MACHINE MODELS TO BIOLOGICAL SYSTEMS

Let's now examine a simple biological example of a FSM. Consider the Rock Dove (*Columba livia*), with a simple FSM consisting of two life-history stages—breeding and molt (Fig. 5). These birds are commensals of humans, have

access to food at all times, and thus have the potential to breed continuously except under the worst environmental conditions, or if they lose a mate to a predator or competitor (Lofts and Murton 1968). For this example we will impose the limitation that while the doves are breeding, they cannot make the full transition into molt. As with all biological systems, the entraining source is the environment, and in this example habitat is the source as it provides food. Note that if food is present, many environmental changes may not be important so long as the food source is not affected. Therefore we would expect the organisms to ignore these changes (Wingfield et al. 1992, 1993). To summarize thus far, the environment changes through time, and this environmental variation provides the entraining signal. Environmental variation provides the excitation variables to the machine that then integrates these cues and responds appropriately to the state of the machine at that time. These correspond to a combination of morphological, physiological, and behavioral states.

In our simple Rock Dove FSM, the excitation variables are all supplementary cues: the presence or absence of food or a mate. The Rock Dove has three responses: to wait in breeding condition, get a mate and begin nesting, or to leave the breeding stage and molt. The "machine" has two stages: breeding and molting although there may be more states depending upon what combination of sub-stages are activated within a stage. During the breeding stage, the response set is to continue nesting as often as possible. During the molting stage, the re-

sponse set is to continue molting to completion then return to breeding. The reaction of the machine cannot be determined, unless the state of the machine at the time of the excitation is known. This factor cannot be over emphasized because it is important to all experimental manipulations of plants and animals. One can not predict the response of the system, unless you know both the physiological state of the organism, as well as the whole suite of excitations being experienced by the organism. A close examination of the transition diagram (Fig. 5) shows this quite clearly. The response to the presence of food or a mate is very different, depending on the current stage of the individual.

Some stages can be expressed simultaneously, and given that certain sub-stages within each stage can also be manifest concurrently, there is potential for very complex states at some times in the life cycle. This can be termed, in essence, a super-state for the FSM. In the Rock Dove example (Fig. 5), breeding and molt can overlap although the rate of molt is usually low if the individual is still breeding. This case represents the super-state of breeding and molting stages expressed simultaneously. Super-states can potentially be composed of any number of layers (overlap of life-history stages) and may encapsulate various additional layers of complexity during transitional periods in the life cycle. Intermediate variables, involving the central and endocrine mechanisms, in super-states may also be highly complex. It should be pointed out, however, that although super-states may be common, because of this complexity they usually are of short duration. It should also be noted that this complexity may be energetically costly and may incur other "costs" that would result in reduced fitness.

If we examine the life history of a more complex system, the migratory White-crowned Sparrow (*Zonotrichia leucophrys*), we see that the animal progresses through a number of discrete functional phases, such as migration, breeding, molting, and over wintering (Fig. 6). These also can be viewed as life-history stages, as they involve very different morphological, physiological, and behavioral expressions in the broad sense as described above, and are hence phenotypically different with respect to selection on the animal during the particular season (Fig. 6). For a seasonally breeding bird, such as the White-crowned Sparrow, the entraining source
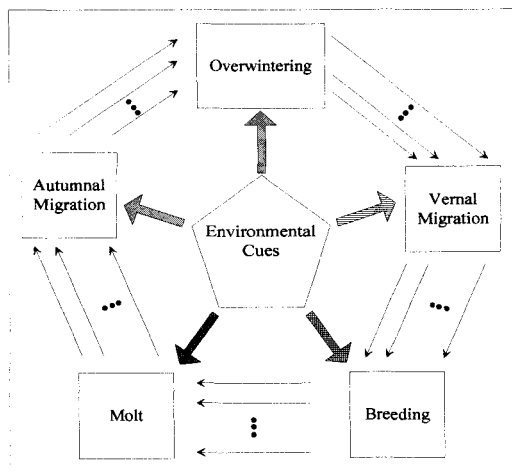

FIGURE 6. The seasonal life cycle of a migratory Gambel's White-crowned Sparrow (*Zonotrichia leucophrys gambelii*) diagrammed as a series of stages—finite-state machine. Each stage receives a number of excitations from the habitat in the form of environmental cues. These stimuli may be different for each stage as indicated by various shading patterns for the arrows. Note, however, that some environmental cues may also be similar or identical for different stages. The stimuli trigger a number of internal responses in the stages (intermediate response variables), and also trigger the transition from one stage to the next (indicated by simple arrows).

will be the progression of the seasons as driven by the movement of the earth around the sun. Again, at each step along the life cycle, the bird will receive excitations in the form of cues from the environment. In some cases these cues will be important individually, but in other cases the integration of several environmental cues may combine to form a single excitation.

The transition between life-history stages can follow several different paths and yield several different physiological states depending on both the integrated cues and state immediately before the transition (Fig. 7). Although each life-history stage contains a distinct set of sub-stages, combinations of which give states designed for specific tasks, the specific state expressed will be subject to constraints imposed by both the environment and the genome. The exact nature of the state at any one time will depend on such things as energy stores within the animal, quality of the territory, presence or absence of mate, and a whole set of morphological, physiological, and behavioral considerations as determined by the genome (Fig. 7). Again, excitation cues are im-
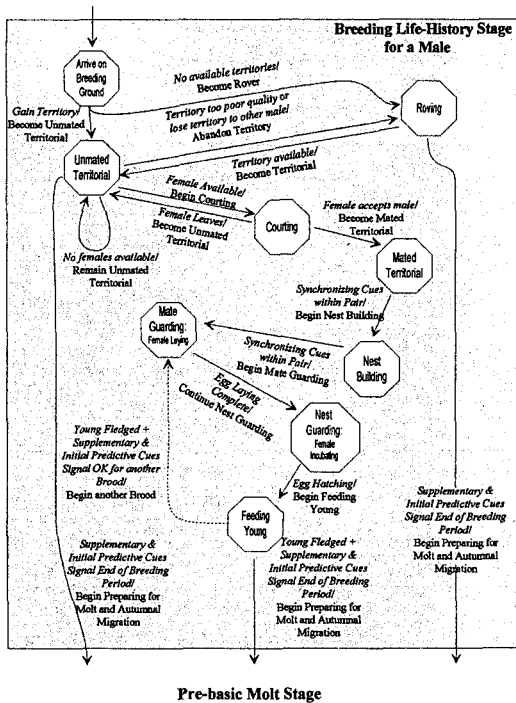
Pre-basic Molt Stage

FIGURE 7. Transition diagram of the breeding life-history stage for a male White-crowned Sparrow (*Zonotrichia leucophrys*). Note the complex transitions between sub-stages of the breeding life-history stage. This diagram does not depict every possible transition (Wingfield and Jacobs 1999).

portant in timing of the transition between life-history stages, but the state of the "machine"/individual is critical to the timing and direction of the transition. Therefore, this hypothesis predicts that for a seasonally breeding bird, the transition from one life-history stage to the next is unidirectional due to the seasonal nature of the excitation cues (Fig. 6). A bird that has migrated to the Arctic and started to breed, can not then begin vernal migration because the state of the animal does not allow a reverse transition to the vernal migration stage, in part because the bird is already at the end point of migration. The cues that normally trigger vernal migration are not present during the late summer and early autumn, and also not present on the arctic breeding grounds. It is possible to accelerate the pace of a life-history cycle by, for example, increasing photoperiod abruptly, but experimental evidence suggests that the sequence of life-history stages is set (Moore et al. 1983, Farner 1985).

These predictions are testable both in field and laboratory investigations. As all transitions depend on the state of the bird, there are several ways to make transitions between life-history stages, yielding different states within the next life-history stage. The resulting state depends on the initial state and the combination of excitations leading to the life-history stage transition. For example, breeding White-crowned Sparrows in Alaska make an abrupt transition from the breeding stage to pre-basic molt stage if the young are lost to a predator. However, if a breeding pair is feeding fledglings out of the nest, the transition to pre-basic molt is more gradual with birds initiating a slow molt while still feeding young. Later, the rate of molt is speeded up while the breeding stage is terminated quickly after the young become independent (Wingfield and Farner 1979).

Cycling of sub-stages can occur within a life-history stage such as in the case of multiple broods (Fig. 7), but after the bird has entered the next life-history stage, it must pass through the rest of the stages before returning to the one it just completed (Fig. 6). Sub-stages within a life history stage can cycle, or be expressed in many combinations (such as in the case of multiple-brooded birds), but only while in its specific life-history stage. The prediction that sub-stages generally cannot be expressed in other life-history stages raises some important issues for mechanisms. An individual will integrate initial predictive and supplementary cues at the cyclic transition point to determine if another cycle of sub-stages is feasible within the current life-history stage. If, for example, an initial predictive cue such as day length indicated that the season for the breeding life-history stage was nearly over, the bird would not initiate another brood even though supplementary cues such as food supply might be present. The same would be true if the food supply was insufficient for another brood. The bird would not nest again even though the initial predictive cues were correct. Furthermore, these predictions indicate that re-nesting after loss of the clutch or brood to a predator, and nesting attempts after successful raising of a brood are very different phenomena with possible separate control mechanisms (Wingfield and Farner 1979, Wingfield and Moore 1987). This is just one example of how application of finite-state machine theory may result in counter-intuitive predictions with po-

tentially profound implications for control mechanisms

HORMONES AND THE REGULATION OF LIFE-HISTORY STAGE TRANSITIONS.

How do animals integrate the signals from the environment and bring about both stage transitions, as well as changes from sub-stage to sub-stage? Neural integration is important in the initial collation of the sensory inputs, and for behavioral responses. Imagine if a signal must be sent to a large number of cells/tissues within the body, then this neural innervation of all the tissues would allow for immediate action on the integrated cues. But, such a system would have several limitations. First, the number of neural connections would be astronomical and would probably require a massive enlargement of both the brain and spinal cord. Second, it requires that the animal maintain a large network of neurons that have no function for most of the year as they would only be used during the transition periods and only a small portion of these regulatory neurons would be needed for any one transition. Clearly these constraints on both the complexity of the system and energy requirements to maintain such a network would be prohibitive.

The endocrine system may play one of its many roles in reducing the size and complexity of the regulatory systems of an animal. Hormones are carried throughout the body by the blood vascular system and stimulate their target cells at very minute concentrations (Hadley 1996). This non-directed transport of hormones may at first seem a problem because if all cells are exposed to the hormone, how can specific cells and tissues be regulated? As all hormones require receptor proteins in/on their target cells to have their actions, the easy answer to this specificity problem is that the receptors are found on only certain cells, and only at specific times (Hadley 1996). The distribution of hormone receptors does not wholly solve our problem, however, as we then need to know how the distribution of the receptors was determined.

Cells respond to cues from their environment just as do whole organisms. In many ways, cells within the body also function like finite-state machines. They respond to excitations from the environment in the form of hormones, growth factors, neurotransmitters, cell-cell interactions, morphogens, and concentrations of nutrients/

ions in the extracellular fluid (Prosser 1986, Hadley 1996). They also have specific responses to those excitations. The nature of the response is determined by both the excitation and the state of the cell. A nerve cell that has a strongly hyperpolarized resting potential will not generate a spike if exposed to a moderate amount of the appropriate neurotransmitter. If the resting potential of the same cell becomes depolarized to near threshold, an action potential will be generated in response to the same amount of neurotransmitter (Eckert et al. 1988). Clearly, if the neuron lacks receptors for a neurotransmitter then it ceases to be an excitation for the cell, even if depolarized to near threshold. The same is true for the action of hormones. If a cell lacks receptors for a hormone, the cell will not respond to that hormone. Part of the state of a cell will be the presence or absence of hormone receptors on or in the cell (Hadley 1996). Also important to the state of the cells will be the effect of cues from previous time intervals. If the cell becomes terminally differentiated into a red blood cell or a fused myotube, it is unlikely to respond to any hormone or growth factor by beginning to proliferate. The state of the second messenger systems within the cell will also be critical to that cell's response to a hormone. If the cell normally responds to a hormone by elevating endogenous c-AMP levels, and this cell has elevated phosphodiesterase that degrades c-AMP, then the hormone may have no effect on the response of the cell (Eckert et al. 1988, Hadley 1996).

The actual response of the cell will also depend on the nature of the hormone receptors it has. The expression of hormone receptors will be regulated by the genome, by cues from the environment, and the state of the cell. During the development of the animal, many of the most important cues will be of the developmental class because they will determine the location and final function of the cell within the animal. The number of receptors a cell has for a given hormone will vary over time in response to other hormones and concentrations of nutrients and ions within the extracellular fluids of the animal (Hadley 1996). Many hormones, such as the steroid and thyroid hormones, have permissive actions that set up the state within a cell so that a second hormone can then have a specific effect that was not possible without the prior action of the permissive hormone (Hadley 1996). Also,

many hormones have several types of receptors that have different affinities for the hormone and are activated at different hormone concentrations (Wingfield et al. 1997a).

This state dependence of cellular responses to hormones is crucial for regulating complex life-history stage transitions. This allows diverse cell types to respond to the same hormone in very different ways, and allows the same type of cells to respond to the same hormone differently at different times of year, depending on the state of the cell (Hadley 1996). For example, a molting bird would be in serious trouble if all of its cells (rather than just those of the skin) began to proliferate and grow in response to the thyroxine signal. Also, this same thyroxine signal has no similar role in other life-history stages.

The state dependent response helps to explain experiments on cellular responses to hormones that seem to be mutually exclusive, or inconsistent. Again, the response of the cell, even in culture, will be according to its state. If the cells are in a different state, possibly by growing in media with differing concentrations of permissive hormones, the action of the hormone to be tested may be different. Local specificity of cellular responses to hormones will be determined by the state of the cell as set-up by its developmental path, as well as the effect of other hormones. Thus a relatively small suite of hormones can serve to regulate very complex life-history stage transitions.

To reflect thus far, several ideas and predictions develop from using a FSM model to understand responses to a changing environment:

(1). Because the progression of life-history stages is unidirectional, long-lived organisms will progress through all stages several times in a preordained sequence (Fig. 6).

(2). The tight linkage of life-history stages to the environment means that a given stage is only appropriate at a specific season.

(3). Within each life-history stage (Fig. 7), a certain amount of predictable cycling between the sub-stages may occur such as initiating a second brood, or cycling may be due to unpredictable labile perturbation factors such as renesting after nest predation (Wingfield et al. 1998).

(4). The progression of sub-stages may follow a limited number of paths through the life-history stage and some may be unidirectional with a few predictable cyclic branches and possible

unpredictable set backs (Wingfield and Jacobs 1999). States are generally volatile and transition between states can occur rapidly. For example, a thirsty animal can quickly restore its water balance if given access to water. As the environment is changing constantly, so is the state control-system that is designed to maintain homeostasis in the face of such change.

(5). Life-history stages and the combinations of sub-stages may have profound implications for neuroendocrine and endocrine control mechanisms at the cell level. Conversely, states of cells and their limited ability to change their responsiveness to internal and external signals may place constraints on the degree of plasticity in life-history cycles.

ENDOCRINE AND PHYSIOLOGICAL CONSTRAINTS ON FINITE-STATE MACHINES AND THEIR SUB-STAGES

Endocrine regulation of growth, homeostasis, breeding, etc. requires time and energy. Therefore simultaneous expressions of all life-history stages may not be possible, especially if an organism has a large number of stages (Wingfield and Jacobs 1999). Thus, there are some constraints on the FSM imposed by limitations of endocrine and physiological systems as follows.

(1). There are limits to the number of life-history stages that can be expressed simultaneously. In some cases, super-states develop in which two or more life-history stages overlap, but if we look again at Figure 1, the generalist, mixed stage may have lower fitness because of the costs of expressing so many life-history stages simultaneously.

(2). Because each life-history stage has development and termination periods, there is a limit to how many may be expressed within a year. In other words it takes time to develop a state in which an individual can then migrate several thousand kilometers. Also, it takes about six weeks for a male White-crowned Sparrow to develop its gonads to the mature capability state when breeding can begin (Wingfield and Farner 1980, Follett 1984, Farner 1985). Similarly, there may be limits on the number of simultaneous sub-stages that can be expressed within a life-history stage.

(3). The more life-history stages that a population expresses, the less flexibility in timing transitions because of the constraints of 1 and 2 above. For example, Z. l. gambelii has five life-

history stages (Fig. 6), whereas the non-migratory *Z. l. nuttallii* of coastal California only has three (Wingfield and Jacobs 1999). We would then predict that the life-history stages in the latter have greater flexibility in timing and transitions than in the former. More tropical taxa such as *Z. capensis* may only have two life-history stages (Miller 1962) and should have even greater flexibility.

(4). Because expression of each life-history stage is regulated by endocrine secretions, there may be some form of feedback regulatory mechanism because there is mounting evidence that there are dramatic costs to high circulating levels of a specific hormone for prolonged periods (Wingfield et al. 1997b, 1999b). These costs may reduce reproductive success significantly, especially over the lifetime of the individual (Ketterson et al. 1996). For example, during the breeding life-history stage, the steroid hormone testosterone regulates spermatogenesis, development of reproductive accessory organs and some secondary sex characters, promotes muscle hypertrophy, activates sexual behavior and territorial aggression, and provides a negative feedback signal for gonadotropins (Wingfield et al. 1997b, 1999b). Clearly the multiple actions of testosterone are essential for normal male reproductive function. However, if the breeding life-history stage is prolonged, as in the tropics, then testosterone levels could potentially be high for much of the year. Emerging evidence indicates that many tropical birds have almost undetectable levels of testosterone in the blood throughout much of the breeding season, although it is present in the testes in large quantities. This is unlike avian species at higher latitudes with much more brief breeding seasons (Levin and Wingfield 1992, Wingfield et al. 1997b, Wikelski et al. 1999). This "absence" of high circulating testosterone for long periods may be a result of "costs" associated with prolonged exposure to testosterone. These include decreased paternal care of young, injury and/or increased predation, potential suppression of the immune system, impaired ability to maintain a pair bond, increased energetic costs, and possible oncogenic effects (Wingfield et al. 1997b, 1999b).

Such constraints may have important implications for the regulation and evolution of life-history stages in general. Additionally, the organization of FSMs may in turn have marked

influences on the control mechanisms. Closely related taxa such as within the genus *Zonotrichia* may provide valuable models for experimental testing of these predictions. A FSM approach to classifying life cycles may provide us with important new ways by which to develop appropriate hypotheses that are eminently testable either in the laboratory or field. Additionally, this model provides a number of insights into understanding animal's responses, and emphasizes a number of cautionary restrictions to investigators. To make conclusions about the response of an organism to a stimulus, the experimenter must be able to determine the state of the organism. If over-wintering animals are given an injection of testosterone, one cannot expect them to respond qualitatively and quantitatively in the same manner as the same animals during the breeding season. The experimenter also needs to know the normal excitations for the organism. Because excitations often result from an integration of multiple cues, isolating a single cue and presenting it to the organism may result in responses not normally expressed in the field. Thus the model proposed here provides a framework for investigating organismal responses to a changing environment.

EXAMPLES OF FINITE-STATE MACHINES AND COMPLEXITY OF EXCITATION AND RESPONSE VARIABLES

When investigating the excitation and response variables in populations with different FSMs, it is important to be able to compare all stages within the life cycle of each population. For example, within the species *Zonotrichia leucophrys,* there are populations with more life-history stages than others. Northern populations have two migratory periods, whereas the California coast population is sedentary. Length of the breeding season determines how long certain other life-history stages may be expressed. In other words, the FSM is a result not only of the number of life-history stages but also the degree of overlap of different stages and their duration (Wingfield and Jacobs 1999). We know of no studies in which any one population of organisms has been investigated this thoroughly. For this reason we focus on examples from the reproductive life-history stage in several species of closely related Emberizines. Nonetheless, it must be borne in mind that future research should address the excitation and response var-

iables of all life-history stages to test the concept of FSMs thoroughly.

Reproductive development in birds, as in any typical life-history stage, can be separated into two distinct phases with different control mechanisms. In the development phase, gonads grow from an immature state to near functional capacity. Mature capability followed by onset of nesting involves yolk deposition and rapid final maturation of ovarian follicles culminating in ovulation and oviposition. In contrast, the testes progress to functional maturity usually without a pause. Thus, these phases are distinct in females but not in males. The photoperiodic control of the first phase has received many decades of attention (Farner and Follett 1979, Nicholls et al. 1988). However, integration of supplementary information, as well as variations in responsiveness to these specific cues seen among populations, has not been well studied (Wingfield et al. 1992, 1993). How these cues may influence the two phases of ovarian development is even less well known.

Photoperiodic regulation of the first phase of reproductive development involves increased secretion of chicken gonadotropin-releasing hormone 1 (cGnRH-1), the major GnRH in passerines (Sherwood et al. 1987). This then regulates release of the gonadotropins luteinizing hormone (LH) and follicle-stimulating hormone (FSH) that in turn orchestrate gonadal growth and secretion of sex steroid hormones. The latter trigger development of secondary sex characters and reproductive behavior (Wingfield and Farner 1993). Increased levels of gonadotropins in blood are accompanied by elevated LHβ-subunit mRNA titers in the anterior pituitary, and a rise in LH and FSH receptors in the testes of White-crowned Sparrows (Ishii and Farner 1976, Kubokawa et al. 1994). In females, photoperiodic cues trigger release of the same reproductive hormones and ovarian maturation follows, but only to a sub-functional level (King et al. 1966, Wingfield and Farner 1980). In *Zonotrichia*, this rapid first phase of ovarian growth culminates when follicles are about 2–3 mm in diameter and contain white-yolk only. This development phase of the reproductive life-history stage requires 4–5 weeks to reach mature capability in the laboratory under artificial photostimulation and about 6 weeks under natural conditions.

Once mature capability has been attained, females generally will not progress beyond this phase unless the environment is conducive to nesting (King et al. 1966). A second set of supplementary factors regulates the second phase, rapid deposition of yellow yolk via the control of estradiol secretion, and egg laying (Wingfield and Farner 1980). The mechanisms by which these supplementary factors are perceived and then transduced into the intermediate variables of neuroendocrine and endocrine secretions are not well understood. Nonetheless, there is a limited literature on which cues can act as excitation variables and what the response variables are. Some examples are discussed next.

Predictability and the timing of life-history stages. The most energetically expensive, rate limiting, sub-stage or phase of the reproductive life-history stage is the parental sub-stage when young must be fed. Ultimate factors such as trophic level select those individuals that produce young at a time when resources can support such a high rate of provisioning. Clearly, predictability of the ultimate factor is crucial for determining when and how an individual prepares for the breeding season. Colwell's (1974) model allows us to ascribe a predictability value (Pr) to those resources essential for production and survival of young. There are two components to Pr—constancy (C): the uniformity of resource levels across time intervals within a year, and contingency (M): the temporal reliability of fluctuations in resource levels across time intervals within a year. The value of Pr can vary between 0, entirely unpredictable, and 1, entirely predictable. It is equal to the separate components C and M. Critical features of this model with respect to control of reproductive physiology are the total predictability (Pr), and the relative contributions to Pr of the separate components C and M.

What, then, does this tell us about patterns of reproductive function and environmental control of breeding? The total Pr is important because it indicates whether an organism will be able to rely on the resource level being in a certain range at a certain time of year that in turn determines whether breeding should be seasonal, constant, or opportunistic. The next question of whether and how organisms should use environmental information to regulate breeding pattern is addressed by Cohen (1967). He showed mathematically that if a future event such as onset of breeding or migration is certain in terms of timing, then it is optimal to respond to one or a few

reliable cues and ignore others. On the other hand, if the future event is less certain in terms of timing, then receiving more information about potential alternative decisions to inhibit or accelerate gonadal maturation can only lead to finer tuning of onset of breeding with local phenological conditions. Therefore, the relative contributions to Pr by C and M are important because firstly they indicate whether the organism requires any environmental information at all to anticipate what the resource level will be at a certain time. If C is very high, no external information will be required because the resource is not fluctuating (Wingfield et al. 1992, 1993). Secondly, the ratio of M and C in conjunction with Pr indicates the type of environmental information an organism should monitor to time life-history stages such as breeding. For example, an organism should use primarily initial predictive information if M is smaller than or nearly equal to C, or respond more to supplementary information when M is greater than C. Combinations of these responses are also possible. In this way the individual can anticipate changes in environmental conditions by triggering appropriate morphological, physiological, and behavioral adjustments. The relative contributions of M and C can be expressed conveniently as the M/C ratio, the environmental information factor (*Ie*), that is theoretically an indicator of the way in which organisms may integrate initial predictive and supplementary cues (Wingfield et al. 1992, 1993).

Effects of temperature. Temperature is a supplementary factor that regulates gonadal function in both phases of the breeding life-history stage. Mathematical models of egg-laying dates in sparrows indicate that species with a low *Ie* factor should be insensitive to supplementary environmental cues such as temperature and be driven primarily by photoperiod. Experimental results are consistent with these predictions (Wingfield et al. 1996, 1997a). *Z. l. pugetensis,* a species with a higher *Ie* factor, shows effects of increasing temperature on testicular and ovarian maturation. Furthermore, in females, exposure to 30°C results in deposition of yellow yolk and rapid final maturation of the ovary indicating onset of actual breeding. In contrast, *Z. l. gambelii,* a species with a low *Ie,* does not show these responses.

Although photoperiodically-induced rises in gonadotropins are mediated through the stimulation of cGnRH-1 from hypothalamic neurons (Follett 1984, Nicholls et al. 1988), the mechanisms by which temperature modulates this response remain unclear. In *Z. l. pugetensis,* we find no changes in plasma levels of LH or FSH in either sex despite profound effects on gonadal maturation in both phases (Wingfield et al. 1997a). These data suggest that temperature cues are signalized through a pathway other than the GnRH-gonadotropin axis. We have considered two alternatives: thyroid hormones and glucocorticosteroids. Low temperature does not increase circulating levels of thyroxine (T4) or triiodothyronine (T3). Thus it is unlikely that temperature effects on the first phase of gonadal maturation are mediated through the hypothalamo-pituitary-thyroid axis. Nor is it likely that the stress of low temperature is the mechanism that retards gonadal growth because plasma levels of corticosterone, an indicator of stress (Wingfield 1988) were similar in all groups. Our current hypothesis is that some other factor mediates the effect of temperature, presumably at the level of gonadal gonadotropin receptors, because plasma levels of gonadotropins, and presumably GnRH, were unaffected. Similarly, how temperature affects the second phase of ovarian maturation is unclear. Identical data have been obtained for male and female mountain White-crowned Sparrows, *Z. l. oriantha,* and Rufous Song Sparrows, *Melospiza melodia morphna,* both of which have high *Ie* values (Wingfield et al., unpubl. data), suggesting a true phenomenon and not a chance occurrence.

The above experiments were performed in environmental chambers in which males and females were housed together. Because it is well known that the presence of the opposite sex can enhance photoperiodically-induced gonadal maturation in both phases (Wingfield et al. 1994), experiments were conducted on *Z. l. pugetensis* in which sexes were isolated to remove intersexual social cues. Effects of temperature on testis growth persist (Wingfield et al. 1997a). However, isolation from males results in retardation of the first phase of ovarian development at temperatures of 5° and 20°C but not at 30°C. Temperature effects on the second phase of ovarian maturation are abolished in females isolated from males. These data clearly indicate that social cues and temperature interact to regulate development and onset of the reproductive life-history stage. It should also be noted that temper-

ature has marked effects on termination of the reproductive life-history stage. Low temperatures tend to prolong the stage whereas high temperatures result in earlier termination of breeding and subsequently earlier onset of the next life-history stage, pre-basic molt (Wingfield et al. 1997a).

Effects of food. Availability of food, quality of nutrition, and endogenous reserves of fat and protein can have profound influences on reproductive function (Follett 1984, Knobil and Neill 1994). However, the mechanisms by which food supply act as supplementary information remain equivocal (Wingfield and Kenagy 1991). Many experiments have been done, but they may not be relevant to an individual in its natural environment because severe food restriction is often the experimental paradigm (Wingfield and Kenagy 1991). In an apparent opportunistic breeder, the Red Crossbill, *Loxia curvirostra*, there appears to be a seasonal component to the reproductive life-history stage, probably regulated by photoperiod that brings the birds into breeding condition in July. There is another potential reproductive period in winter that is entirely opportunistic, controlled by factors other than day length and temperature because the former is still short and the latter is at a seasonal low in January (Hahn 1993, 1998). A regulatory role of food supply is unlikely to be simply caloric intake because captive Red Crossbills with ad libitum food fail to breed in winter. Photostimulated male Red Crossbills fed a laboratory diet equal to what they normally would eat on short days, show similar testicular growth to males fed ad libitum and much greater development than males held on short days (Hahn 1995). After food-restricted males on long days are given food ad libitum, testicular development is significantly greater than in males that have continuous access to ad libitum food. These exciting data suggest that perception of food availability may affect gonadal development. Body mass and food intake are similar among groups regardless of availability of food (Hahn 1995, 1998). This is a very interesting example because we have two apparent reproductive life-history stages separated by a pre-basic molt stage. Alternatively, it is possible that there is only one reproductive stage and the pre-basic molt stage overlaps completely with it. If the former is true, then FSM theory would predict that the excitation variables, and probably mech-

anistic intermediate variables, are different. If the latter is true, then we have a case of complete overlap of two life-history stages. These predictions could be tested experimentally.

Many avian species depend almost exclusively on arthropods in the diet to time onset of breeding and to feed young. Dry animal biomass gleaned from sweep nets in breeding habitat of Song Sparrows dramatically increases in spring and declines in autumn. There is great variation in this vernal increase among years at the same locality that is positively correlated with temperature and food availability. Associated with these changes are marked fluctuations in gonadal recrudescence and timing of clutch initiations (Wingfield et al. 1992, unpubl. data).

There also are differences in arthropod abundance and breeding schedule among localities. In Song Sparrows sampled at a mild Pacific Coast site, gonadal recrudescence is well underway by January, suggesting that these populations begin development in the shortest days of the year in December. In contrast, populations of the same race of sparrow breeding in the Cascade Mountains, 150 km to the east, do not begin gonadal recrudescence until late March. Onset of laying occurs in late February on the coast, but not until the third week of May in the mountains (unpubl. data). Other sites in between are intermediate. Note that because these populations are all at the same latitude, they are exposed to identical changes in natural photoperiod. Thus, here is an ideal comparison of Song Sparrow populations at the same latitude but with different breeding schedules. Further field work on these populations will provide critical correlations that we can then investigate experimentally in the laboratory.

CONCLUSIONS

All organisms pass through different life-cycle stages, each with characteristic morphology, physiology, and behavior. Variation in these traits among individuals within a population has received considerable attention, but mechanisms underlying changes in life-cycle stages in individuals, as well as variation in these mechanisms, have been less well investigated. Because most populations live in seasonally and often unpredictably fluctuating environments, individuals must adjust their morphology, behavior, and physiology to maximize their survival and reproductive success over a wide range of envi-

ronmental conditions. In birds, as in other vertebrates, endocrine secretions regulate these morphological, physiological, and behavioral changes in anticipation of future events. The individual thus prepares for predictable fluctuations in its environment by changing life-cycle stages. We have applied finite-state machine theory to define and compare different life-history cycles. Additionally, the ability of birds to respond to novel regimes of environmental variation may be constrained by the adaptability of their endocrine control systems. We have applied several theoretical approaches to natural history data of birds to compare the complexity of life cycles, the degree of plasticity of timing of stages within the cycle, and to determine whether endocrine control mechanisms influence the way birds respond to their environments. For example, although it is well known that the annual cycle in day length regulates gonadal development and regression, the mechanisms by which other environmental cues modulate reproductive function remain unclear. In North American sparrows of the genera *Zonotrichia* and *Melospiza,* photoperiod has dramatic effects on reproduction, particularly development of the reproductive system, onset of egg laying, and termination of breeding. Low temperature tends to slow down the gonadal cycle. High temperatures tend to speed up reproductive development, onset of breeding, and termination of reproductive function. However, these interactions of environmental cues on the timing of breeding are not uniform in all populations. Arctic birds which have short breeding seasons in severe environments, appear to use one reliable environmental cue to time reproduction, and they ignore other factors. Birds having longer breeding seasons exhibit greater plasticity of onset and termination and appear to integrate several environmental cues to time reproduction. Theoretical approaches may allow us to predict how individuals respond to their environment at the proximate level and, conversely, predict how constraints imposed by endocrine control systems may limit the complexity of life cycles.

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