

# Timing of Breeding in Variable Environments: Tropical Birds as Model Systems

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Animals need to adjust reproductive decisions to environmental seasonality. In contrast to species from the well-studied temperate zones, little is known for tropical birds about the environmental cues that stimulate reproductive activity and the physiological mechanisms that regulate reproduction. I am investigating the environmental and endocrine mechanisms that underlie the timing of reproduction in spotted antbirds from the near-equatorial Panamanian rainforest and in small ground finches from the equatorial arid Galápagos islands. Spotted antbirds live in a fairly predictable seasonal environment and show regular changes in gonad sizes and some reproductive hormones. Despite the small annual variation in photoperiod close to the equator, these birds can measure slight photoperiodic increases and use it to initiate reproductive activity. Spotted antbirds also respond to seasonal changes in food availability, which allows them to flexibly adjust gonad growth to environmental conditions. Testosterone is involved in regulating song and aggressive behavior in these year-round territorial birds, although it can remain at low plasma levels throughout the year. In contrast, small ground finches exposed to a rather unpredictable climate on Galápagos appear to grow their gonads whenever heavy rains fall and have regressed gonads during other times of the year. The lack of a physiological preparation for the breeding season and their response to short-term cues related to rainfall indicate a striking flexibility in the regulation of breeding in small ground finches. I suggest that tropical birds can serve as model systems to study the physiological adaptations to different environments. Unraveling the neuroendocrine mechanisms behind the flexibility in reproductive timing will clarify whether differences found between temperate and tropical birds represent variations of the same basic mechanism or instead reflect a fundamental divergence in physiological control systems. © 2001 Academic Press

**Key Words:** tropical bird; reproduction; seasonal

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breeding; gonad development; luteinizing hormone; testosterone; photoperiod; opportunistic breeding; food abundance.

## TROPICAL ANIMALS LIVE IN "UNCONVENTIONAL" ENVIRONMENTS

Evolutionarily, animals have adjusted the seasonal regulation of life history stages to the seasonality of environments in which they live. The control of reproduction is well documented for animals living at temperate, regular seasonal, latitudes (Baker, 1938; Murtton and Westwood, 1977; Bronson, 1987; Wingfield and Kenagy, 1991; Ball, 1993; Cockrem, 1995). In contrast, the timing processes of animals inhabiting environments with only slight seasonal fluctuations such as the tropics are poorly understood (Gwinner and Dittami, 1985; Bronson, 1987; Dittami and Gwinner, 1990; Wingfield, Hahn, Levin, and Honey, 1992; Hau, Wikelski, and Wingfield, 1999).

The two most critical features in the seasonality of an environment are the amplitude of the seasonal fluctuations and the precision with which these fluctuations occur each year (Colwell, 1974; Wingfield *et al.*, 1992). In general, there exists a decline from high to low latitudes both in the amplitude of seasonal fluctuations and in their year-to-year precision. Consequently, life history states in animals from higher latitudes are controlled by rather rigid seasonal processes. In contrast, animals of lower latitudes need a more flexible physiological control of life history states to cope with seasonal variability (see also Wingfield *et al.*, 1992).

In this article I suggest that tropical birds are appropriate model systems with which we can reach a deeper understanding of how seasonal processes are adapted to "unconventional" environments, i.e., to

habitats that differ in critical parameters from the typical temperate zones. Only by studying animal systems that deviate from the typical temperate zone systems can we test the general validity of existing concepts and uncover new principles that animals have evolved. Although I contrast temperate and tropical environments for this purpose, it is important to note that such an approach is not limited to a latitudinal comparison. Alternatively, one might investigate species that inhabit similar habitats, but experience special ecological circumstances rendering their subjective environment unusually variable (e.g., a reliance on irregular seed masts for breeding as in red crossbills; Hahn, Boswell, Wingfield, and Ball, 1997; Hahn, 1998), or live at different altitudes (Morton, 1994; Widmer, 1996).

## SEASONAL REPRODUCTION IN BIRDS: GENERAL PATTERNS

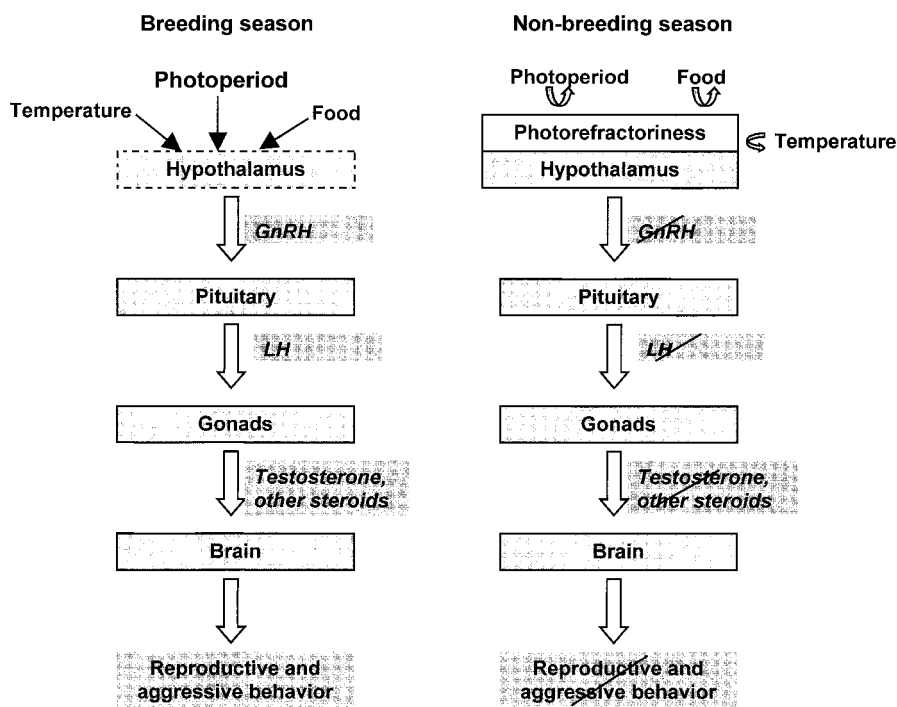
The physiological processes that underlie the timing of breeding in birds have been studied extensively in temperate zone species (Murton and Westwood, 1977; Follett, Foster, and Nicholls, 1985; Wingfield *et al.*, 1992; Ball, 1993; Cockrem, 1995; Hahn *et al.*, 1997) and are applicable to most arctic birds as well (Hahn, Wingfield, Mullen, and Deviche, 1995; Silverin, 1995). The regular seasonal fluctuations in temperate and arctic habitats are highly correlated with the pronounced seasonal changes in photoperiod. Thus, most temperate and arctic animals rely to a high degree on photoperiodic stimuli for controlling reproduction. Photoperiod regulates seasonal processes either directly by initiating or terminating them or indirectly by synchronizing endogenous timing mechanisms (e.g., Farner and Lewis, 1971; Follett *et al.*, 1985; Gwinner, 1986; Wilson and Donham, 1988).

An increase in photoperiod in spring starts the so-called "neuroendocrine cascade" (Fig. 1), which begins with the secretion of releasing hormones from the hypothalamus (gonadotropin-releasing hormone, GnRH). GnRH then stimulates the secretion of hypophysial hormones such as luteinizing hormone (LH) and follicle-stimulating hormone (FSH, not indicated in Fig. 1), which in turn induce gonad growth and steroid hormone production (Murton and Westwood, 1977; Ball, 1993; Wingfield and Farner, 1993). Gonadal steroids regulate important physiological changes and behaviors associated with reproduction (Balthazart, 1983; Wingfield and Ramenofsky, 1985; Wingfield, Ja-

cobs, Soma, Maney, Hunt, Wisti-Peterson, Meddle, Ramenofsky, and Sullivan, 1999). Only after the system has been "switched on" by photoperiod can additional or "supplementary" environmental stimuli such as food and temperature also influence the hypothalamo-pituitary-gonad (HPG) axis (Wingfield, 1983; Wingfield *et al.*, 1992). The reproductive period is usually terminated by a process called "photorefractoriness," in which the system becomes unresponsive to the stimulatory actions of long daylength and other stimuli, the neuroendocrine cascade is shut down, and the gonads collapse (Farner, Donham, Matt, Mattocks, Moore, and Wingfield, 1983; Follett *et al.*, 1985; Nicholls, Goldsmith, and Dawson, 1988; Wilson and Donham, 1988; Bentley, 1997).

There is ample evidence that this basic scheme of seasonal reproduction is adapted to different environments. For example, photoperiodic response thresholds differ between populations of birds living at different latitudes (Gwinner, 1989; Silverin, Massa, and Stokkan, 1993; Silverin *et al.*, 1995; Lambrechts, Blondel, Maistre, and Perret, 1997), ranging down to the subtropics (e.g., Chandola, Pavnaskar, and Thapliyal, 1975; Tewary and Dixit, 1986; Chandola-Saklani, Sharma, Bisht, and Lakhera, 1990). Also, the degree to which supplementary information is integrated into reproductive decisions tends to increase toward lower latitudes and environments with a high year-to-year variability in seasonality (Chandola *et al.*, 1990; Wingfield *et al.*, 1992; Wingfield, Hahn, and Doak, 1993; Svensson, 1995; Hahn *et al.*, 1997). But it is still unknown whether these mechanisms are useful in more extreme environments with only slight or variable seasonality. In particular, seasonal control mechanisms in near-equatorial habitats, where photoperiodic changes are minimal, are poorly understood. Some near-equatorial vertebrate species do show photoperiodic responses when exposed to temperate-zone-like daylength changes (reviewed in Gwinner and Dittami, 1985; Bronson, 1987; Hau *et al.*, 1999). Interestingly, new studies suggest a functional relevance for such photic responses in regulating seasonal breeding in near-equatorial birds (Hau, Wikelski and Wingfield, 1998; Gwinner and Scheuerlein, 1999).

In the following, I summarize data that collaborators and I have collected on two bird species from different near-equatorial habitats. Spotted antbirds (*Hylophylax n. naevioides*) live in a lowland humid forest in central Panama, an environment with a moderate seasonality and some year-to-year variability (Windsor, 1990; Leigh, Rand, and Windsor, 1996; Hau *et al.*, 1999; Wikelski, Hau, and Wingfield, 2000). Small



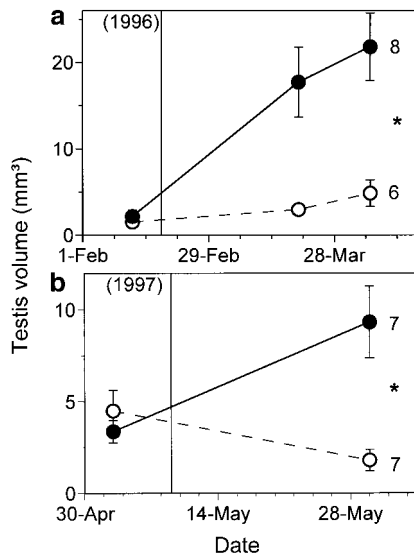
**FIG. 1.** Schematic representation of the seasonal regulation of reproductive physiology in a “typical” temperate-zone male bird. For further explanation of the neuroendocrine cascade see text. During the nonbreeding season most temperate-zone birds enter a state of photorefractoriness, during which the hypothalamo-pituitary-gonad (HPG) axis becomes unresponsive to formerly stimulating environmental cues (symbolized by arrows pointing away from the hypothalamus). During this time, the neuroendocrine cascade is shut down, hormone secretion ceases and behavioral processes associated with reproduction are no longer expressed. Note that only certain steps in the cascade are represented; many others are omitted for clarity.

ground finches (*Geospiza fuliginosa*) live on the Galápagos islands, Ecuador, and are exposed to strong seasonal fluctuations in temperature and rainfall that fluctuate widely from year to year (Grant and Boag, 1980; Grant, 1986; Grant and Grant, 1989). While the study on spotted antbirds is already advanced, only preliminary results can yet be presented for small ground finches. The purpose of this article is to highlight the seasonal adaptations that these species exhibit and to emphasize the potential for future research.

## PHYSIOLOGICAL CONTROL OF REPRODUCTION IN A SEASONAL TROPICAL RAINFOREST

The spotted antbird is an ideal model species for studying the timing and physiological regulation of reproduction in a tropical setting: It is a small subsocial passerine with a predominantly neotropical distribution (Ridgely and Tudor, 1994) and thus phy-

logenetically appears to be a genuine tropical species. The species inhabits a humid near-equatorial forest in central Panama (9°N), which is fairly seasonal but shows some year-to-year variability in seasonal environmental conditions (Windsor, 1990; Leigh *et al.*, 1996; Wikelski *et al.*, 2000). Spotted antbirds breed during the single long rainy season (May–December), when insect food is most abundant (Willis, 1972; Sieving, 1992; Wikelski *et al.*, 2000; Robinson, Robinson, Brawn, and Robinson, 2000). The rainy season begins roughly at the same time each year, but long-term data show that its onset can vary by up to 6 weeks between years (Windsor, 1990). The nesting behavior of spotted antbirds is seasonal (May–October; Willis, 1972; Wikelski *et al.*, 2000); however, the physiological processes regulating reproduction have so far been unknown. Combining data on free-living individual spotted antbirds with experiments on captive birds, we sought to elucidate their breeding strategy (e.g., seasonal or opportunistic breeding), their response to seasonal environmental cues, and the functioning of their endocrine system.



**FIG. 2.** Changes in testis volumes (mean  $\pm$  SE) of captive male spotted antbirds in response to (a) photostimulation with an increase in photoperiod by 1 h (after Hau *et al.*, 1998) and (b) increase in food abundance and quality (after Hau *et al.*, 2000a). Vertical lines indicate start of the experiment, numbers show sample sizes for each group, asterisks indicate a significant difference between the two groups ( $P < 0.05$ ). (a) The control group (open symbols, dashed line) remained on 12 h light per day throughout the experiment, while the second group (closed symbols, solid line) was exposed to an abrupt increase in photoperiod by 1 h. For further details see text and Hau *et al.* (1998). (b) The control group (open symbols, dashed line) was fed a standard diet for insectivorous birds including live mealworms such that they maintained their initial body mass. The “food-stimulated” group was kept on the same standard diet as the control group but got additional mealworms and also live crickets. Food-stimulated birds increased body mass by about 20% and also significantly increased gonad sizes. For further details see text and Hau *et al.* (2000a).

### Seasonal Breeding, Sensitivity to Photoperiod and Food Cues, and Year-Round Territoriality

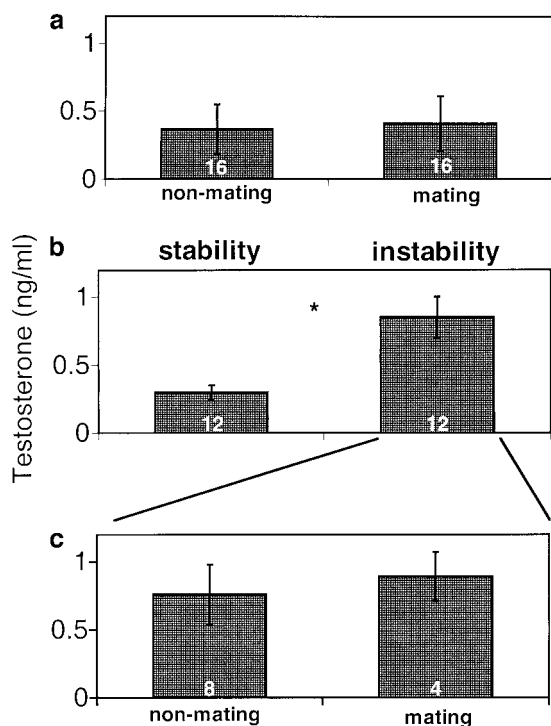
The available data suggest that spotted antbirds are regular seasonal breeders, much like temperate birds. This interpretation stems from the finding that both male and female spotted antbirds showed regular seasonal changes in gonad sizes and reproductive hormones such as LH in 2 subsequent years (Wikelski *et al.*, 2000). These birds also “anticipated” the breeding season by growing their gonads 1–2 months ahead of the beginning of the rainy (=breeding) season (Wikelski *et al.*, 2000). Seasonal breeding in this near-equatorial habitat is probably made possible by possessing an exceptionally high sensitivity to the slight seasonal changes in photoperiod at this latitude (maximal annual daylength change about 1 h; Fig. 2a; Hau *et al.*, 1998; Wikelski *et al.*, 2000). A response to photoperi-

odic cues enables these birds to physiologically prepare for the coming breeding season ahead of time. In addition to photoperiod, spotted antbirds are also very responsive to changes in food abundance and adjust (photoperiodically induced) gonad growth to food availability (Fig. 2b; Hau, Wikelski and Wingfield, 2000a; Wikelski *et al.*, 2000). Their response to food availability appears to be stronger than in most temperate birds (see Hau *et al.*, 1999, 2000a, for discussion) and could be interpreted as an adaptation to the variability in the onset of the rainy season as rain increases insect food abundance (Leigh *et al.*, 1996). Food abundance is perhaps measured by spotted antbird through some combination of seeing and handling live insects, as suggested from a laboratory experiment (Hau *et al.*, 2000a).

While the seasonal regulation of breeding at least partly resembles the situation in temperate birds, the hormonal control of song and aggressive behavior shows some interesting differences (see also, Wikelski, Hau, Robinson and Wingfield, 1999b). Despite seasonal changes in plasma LH secretion, plasma T levels are low in both sexes throughout the year (Fig. 3a; Wikelski, Hau, and Wingfield, 1999a; Wikelski *et al.*, 2000). In typical temperate zone male birds, plasma T titers increase dramatically during the breeding season and T is involved in important reproductive processes and behaviors, such as sperm maturation, song, courtship, and territoriality (Balthazart, 1983; Wingfield and Ramenofsky, 1985; Wingfield, Hegner, Dufty, and Ball, 1990). However, elevated plasma levels of T may also incur physiological costs (e.g., Dufty, 1989; Ketterson, Nolan, Cawthorn, Parker, and Ziegenfus, 1996; Hillgarth and Wingfield, 1997). Experiments revealed that spotted antbird males do increase plasma T levels in response to aggressive territorial challenges, during both the breeding and the nonbreeding seasons (Fig. 3; Wikelski *et al.*, 1999a). During socially stable conditions plasma T levels remain low (Fig. 3b; Wikelski *et al.*, 1999a). Further experiments on captive male spotted antbirds confirmed that T, or its estrogenic metabolites, are causally involved in regulating aggressive behavior and song (Hau, Wikelski, and Wingfield, 2000b).

## PHYSIOLOGICAL CONTROL OF REPRODUCTION IN AN UNPREDICTABLE, ARID HABITAT

Darwin’s ground finches (*Geospiza spp.*) are small emberizid finches endemic to the Galápagos archipel-



**FIG. 3.** Plasma T levels (mean  $\pm$  95% CI) of free-living territorial male spotted antbirds in different reproductive stages and social conditions (after Wikelski *et al.*, 1999a). “Nonmating”: males caught during the nonbreeding and the prebreeding (when gonads had started to grow to half-maximal sizes) seasons and during phases of parental care. “Mating”: males having at least half-maximal to maximal gonad sizes but no brood patches or active nests. (a) There was no difference in plasma T levels of males caught in nonmating versus mating phases. (b) However, circulating T levels were lower in territory owners experiencing social stability (only the territorial male was caught on his territory) compared to territory owners experiencing social instability (in addition to the territorial male we caught three or more conspecifics on his territory on that day indicating a territorial challenge). (c) Plasma T levels of males experiencing social instability were elevated both during nonmating and mating season.

ago, Ecuador (e.g., Grant 1986; Grant and Grant, 1989; Hau and Wikelski, 2000). The Galápagos islands lie directly at the equator at a latitude between 2°N and 2°S. Despite their equatorial location, the climate is quite seasonal and can be divided into a hot-and-wet (about January–May) and a cool-and-dry season (about June–December; Grant, 1986). Between-year variability in climatic events is high and becomes amplified by frequent El Niño events, which bring strong and extended rains to Galápagos. Small ground finches occur on most islands and also inhabit many different habitats (e.g., Grant, 1986).

Small ground finches are mainly granivorous. However, they raise their nestlings primarily on insect food

and thus are dependent on rainfall for reproduction (breeding season between about December–July). Caterpillar abundance can increase within 10 days after a substantial rainfall (Grant and Grant, 1989). The strong dependence of the ground finches on rainfall suggested that they are opportunistic breeders (Wingfield *et al.*, 1992; Hahn *et al.*, 1997; Grant, Grant, Keller, and Petren, 2000), but the physiological mechanisms were unknown. In fact, only limited physiological data exist for opportunistic breeders in general (Hahn *et al.*, 1997). Therefore, we initiated a field study to investigate the physiological breeding strategy and the response to environmental cues of small ground finches, using similar methods to those in the spotted antbird study (Hau, Gwinner, Wikelski, and Gwinner, in preparation).

### Opportunistic Breeding and Response to Rainfall

Small ground finches showed significant seasonal changes in gonad sizes. They had fully developed gonads during, and regressed gonads outside, the breeding season (Hau, Gwinner, Wikelski, and Gwinner, in preparation). In contrast to spotted antbirds, changes in gonad development did not occur at the same time in 2 subsequent years, and the birds did not anticipate the coming breeding season by growing their gonads in advance. These findings suggest that small ground finches are indeed opportunistic breeders. With regard to the regression of gonads after the breeding season, however, these birds differ from the prime example of opportunistic breeding, the Australian zebra finch (*Taeniopygia guttata*, e.g., Zann, 1996). Zebra finches keep their gonads in an at least a half-developed state throughout most the year (Sossinka, 1974; Davies, 1977; Vleck and Priedkalns, 1985).

Only rainfall, but not photoperiod, light intensity during the day, or ambient temperature correlated with the pattern in gonad development in small ground finches. Furthermore, three populations of small ground finches from habitats with different rainfall patterns (St. Fé lowlands and St. Cruz lowlands and highlands) grew their gonads when the rainy season began at their respective location (Hau, Gwinner, Wikelski, and Gwinner, in preparation). As rainfall is the prerequisite for an increase in insect (and later grass seed) abundance, we experimentally tested in captive birds whether improved food availability and not rain per se sets a signal for the suitability of environmental conditions for breeding. However, two groups of birds kept on diets with differing quality (low- versus high-quality diet) increased gonad sizes

**TABLE 1**  
Differences in the Environmental and Endocrine Regulation of Reproduction and Territorial Behavior between “Typical” Temperate-Zone and Two Near-Equatorial Tropical Bird Species

	Temperate-zone birds	Spotted antbird	Small ground finch
Breeding strategy	Seasonal	Seasonal	Opportunistic ?
Primary timing cue	Photoperiod	Photoperiod	?
Territorial behavior	Breeding season	Year-round	Breeding season
Increase in plasma T levels during aggressive encounters	Breeding season	Year-round	Breeding season

simultaneously (Hau, Schmidl, and Gwinner, in preparation). This increase in gonad sizes coincided with a very precocious onset of the rainy season, with heavy rains occurring about 2 weeks after the beginning of the experiment. Interestingly, at the termination of the experiment free-living small ground finches also had significantly grown their gonads. Based on these findings, our current working hypothesis is that the birds perhaps respond to rainfall cues directly. This prediction will be tested in future experiments.

## PHYSIOLOGICAL AND ENVIRONMENTAL CONTROL OF REPRODUCTION IN TROPICAL BIRDS: OPEN QUESTIONS

With regard to their reproductive physiology, spotted antbirds and small ground finches differ from the temperate bird model in some very interesting ways (Table 1). Figure 4 outlines possible scenarios and indicates future research avenues for spotted antbirds. Currently, the available data for small ground finches are too preliminary to make similar predictions as to the functioning of their seasonal system.

### *Seasonal Regulation of Reproductive Physiology*

Although spotted antbirds resemble temperate seasonal breeders in some aspects, it is still unclear whether these birds completely shut down reproductive activity during the nonbreeding season. From a functional viewpoint, as a sedentary species (i.e., without the need to prepare for migration while environmental conditions are still favorable), they may not need to shut down responsiveness to stimulatory environmental cues at a particular time of year. The lack of a refractory period might enable them to time the breeding season in a much more flexible way and to lengthen their breeding season past the summer sol-

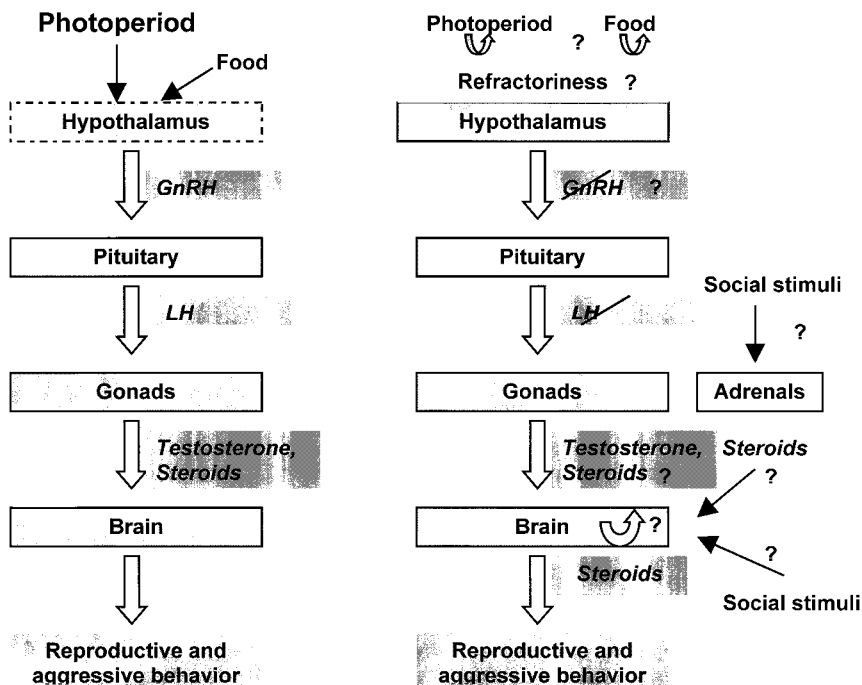
stice. If spotted antbirds retain sensitivity to environmental cues in the nonbreeding season, and these include social factors like territorial challenges, this could lead to their ability to secrete T throughout the year.

Small ground finches show an even stronger, perhaps opportunistic, flexibility in their timing of breeding than spotted antbirds. Darwin's ground finches have been recorded breeding at almost any time of the year (Grant, 1986; Grant and Grant, 1989). Our present data on gonad development strongly support this flexibility. It is therefore perhaps unlikely that small ground finches possess distinct reproductive “windows” and a fixed period of refractoriness, although this remains to be tested. Furthermore, in contrast to other opportunistic breeders such as zebra finches (Tordoff and Dawson, 1965; Berthold and Gwinner, 1975; Davies, 1977; Vleck and Priedkalns, 1985) and red crossbills (Hahn, 1995, 1998), small ground finches regress gonads after the breeding season. The differential regulation of gonad development among species with opportunistic breeding capabilities may indicate adaptations to special ecological circumstances, or life-history trade-offs. It may also call for a reexamination of earlier concepts of opportunistic breeding (see also Hahn *et al.*, 1997) and a renewed data collection on these species (e.g., Hahn, 1995, 1998; Bentley, Spar, MacDougall-Shackleton, Hahn, and Ball, 2000). For example, whether individuals actually keep their gonads active year-round or whether this is instead a population-level phenomenon is not clear.

### *Use of Environmental Cues*

Both spotted antbirds and small ground finches possess new and interesting adaptations for the use of environmental information as seasonal cues. The high sensitivity of spotted antbirds to slight changes in photoperiod and food abundance (Fig. 2) suggests that they might function as a model system to elucidate the

## Spotted Antbirds ?



**FIG. 4.** Schematic representation of the seasonal regulation of reproductive physiology in (male) spotted antbirds. For further explanation see the legend to Fig. 1 and text. Question marks indicate connections that are still hypothetical and remain to be investigated. During the breeding season, the physiological regulation of reproduction appears to be similar to temperate birds. However, spotted antbirds do not generally elevate plasma T levels during the breeding season. Instead, these birds keep plasma T levels low year-round and only increase it during periods of territorial instability (see text). It is not yet clear whether these birds possess a refractory period and whether they entirely shut down the HPG axis during the nonbreeding season. If the gonads remain somehow active during the nonbreeding season, perhaps they secrete T in response to territorial challenges. Alternatively, during the nonbreeding season or perhaps year-round the adrenals could secrete androgen precursors in response to aggressive social stimuli which are then converted to T in the brain.

sensory and integrative processes that enable this response. Among the possible scenarios could be an adaptation in the functioning of the circadian system to achieve a high photoperiodic sensitivity. Currently, the possibility that some temperate birds also possess high photoperiodic sensitivities cannot be excluded. Perhaps species that migrate to equatorial latitudes could use photoperiodic information to locate the wintering grounds or modify spring migration (cf. Hau *et al.*, 1998).

The way in which food exerts effects on the reproductive system is also largely unknown in many taxa. We are lacking important sensory, neuronal, and endocrine information about how food cues are integrated in addition to, or separately from, photoperiodic information. The increased song activity in response to seeing and handling live crickets in spotted antbirds (Hau *et al.*, 2000a) could serve as a behavioral assay to investigate these questions. If small ground finches really respond to rainfall as a seasonal

cue it would be very interesting to investigate the physiological pathway of this response. The use of rainfall cues is even less understood physiologically than the integration of food stimuli. It may also be possible that small ground finches have retained some photoperiodic capacity and use it as seasonal information to some extent, for example, to time molt. In this species, molt appears to occur on a more seasonal basis than gonad development, but its proximate regulation is still obscure (Hau, Gwinner, Wikelski, and Gwinner, in preparation).

### Endocrine Control of Seasonal Behavior

The available data suggest that even in year-round territorial birds such as spotted antbirds, T regulates male aggressive behavior and song year-round (Fig. 3; Hau *et al.*, 2000b; Wikelski *et al.*, 2000). It remains to be seen where T is produced during the nonbreeding

season. Perhaps the gonads secrete T year-round, even in a regressed state. Alternatively, T precursors could come from nongonadal sources (Adkins-Regan, Abdelnabi, Mobarak, and Ottinger, 1990; Tsutsui, Wingfield, and Bottjer, 1991; Wikelski, Lynn, Breuner, Wingfield, and Kenagy, 1999c; Soma, Tramontin, and Wingfield, 2000) and be converted to T in brain target sites (Schlinger and Arnold, 1992; Soma and Wingfield, 1999; Hau *et al.*, 2000b; Soma *et al.*, 2000). Moreover, spotted antbird females sing and are aggressive year-round like males (Hau, Wingfield and Soma, submitted), but have low plasma T titers throughout the year. Thus female spotted antbirds are ideally suited to investigate the endocrine regulation of female song and aggression. Currently, in small ground finches there exists only preliminary information on the endocrine control of seasonal behavior. In contrast to spotted antbirds, male small ground finches have elevated plasma androgen levels during the breeding season, and these levels are comparable to those of temperate species (Hau, Gwinner, Gwinner, and Wikelski, in preparation). This is in line with their seasonal expression of song and territorial behavior (Grant 1986; Grant and Grant, 1989; Wingfield *et al.*, 1990). Among other questions, further research will address how fast sex steroids can increase at the beginning of the breeding season.

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