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### TIMING OF BREEDING IN TROPICAL BIRDS: MECHANISMS AND EVOLUTIONARY IMPLICATIONS

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**Resumen. – Estacionalidad reproductiva en pájaros tropicales: Mecanismos e implicaciones evolutivas.** – El momento apropiado para la proliferación es un importante componente en el proceso de la reproducción de casi todos los animales que viven en medios ambientes fluctuantes debido a cambios estacionales. El tiempo preciso para la reproducción depende de procesos fisiológicos complicados que detectan variaciones en las condiciones ambientales, las integran con información interna y, de acuerdo a estas, regulan el estado reproductivo. La mayor parte de nuestro conocimiento de la fisiología de la aves en relación a las estrategias reproductivas deriva de estudios de especies de climas templados. Estos estudios han acentuado las adaptaciones fisiológicas que las especies poseen para regular la reproducción en un medio ambiente con cambios estacionales regulares en condiciones abióticas y bióticas. Sin embargo, en otras partes del mundo, por ejemplo en latitudes tropicales, las variaciones en las condiciones ambientales frecuentemente ocurren con diferentes características y regularidades que difieren de las de altas latitudes. La fascinante diversidad de las aves tropicales nos da una oportunidad única para investigar los mecanismos fisiológicos que forman la base de las interacciones entre animales y medio ambiente, y para entender como tales sistemas fisiológicos evolucionan. Aquí presentamos un resumen de las observaciones recientes sobre la fisiología reproductiva y el período de reproducción en aves tropicales, enfocando especialmente a especies que habitan en regiones tropicales cercanas al ecuador. Discutimos las variaciones en estrategias reproductivas, las respuestas a señales ambientales y el funcionamiento del eje neuroendocrino reproductivo en especies que viven en diferentes hábitat tropicales. Intentamos de interpretar estos datos en un contexto evolutivo y sugerimos futuras líneas de investigación. Nuestro conocimiento de la evolución del periodo de reproducción y sus relaciones fisiológicas en aves es todavía rudimentario, pero esperamos que estudios con especies tropicales puedan jugar un rol importante en la comprensión de esta cuestión.

**Abstract.** – Appropriate timing of breeding is an important component of reproductive success for almost all animals world-wide that live in seasonally fluctuating environments. A precise temporal regulation of reproduction is achieved by intricate physiological processes that sense variations in environmental conditions, integrate them with internal information and regulate the reproductive state accordingly. Most of our knowledge of the physiology underlying avian reproductive strategies has come from studies in

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temperate zone species. These studies have highlighted the physiological adaptations that species possess to regulate reproduction in environments with regular seasonal fluctuations in abiotic and biotic conditions. However, in other parts of the world, for example at tropical latitudes, variations in environmental conditions often occur in different patterns and regularity than at higher latitudes. The fascinating avian diversity in the tropics provides us with the unique opportunity to investigate the physiological mechanisms that form the basis of animal-environment interactions, to better understand how these physiological systems evolve. Here we summarize recent findings on the reproductive physiology and timing of reproduction in tropical birds, focusing on near-equatorial tropical species. We discuss variations in breeding strategies, responses to environmental cues and the functioning of the neuroendocrine reproductive axis in various avian species living in diverse tropical habitats. We then interpret these data in an evolutionary context to suggest future lines of research. Our understanding of the evolution of the timing of breeding and its underlying physiology in birds is still rudimentary, but we expect that studies on tropical species can play a major role in making substantial progress on these issues. *Accepted 5 October 2007.*

**Key words:** Reproduction, gonad growth, photoperiod, food, social cues, rainfall, GnRH, seasonal breeding, opportunistic breeding, environment, tropics.

## INTRODUCTION

Almost all organisms experience some seasonal fluctuations in climate, food abundance, disease and social factors in their environment (Nelson *et al.* 2002, Dunlap *et al.* 2004). To cope with such variations, organisms possess physiological mechanisms that allow them to temporally coordinate energetically demanding stages in their life, for example reproductive events, with conditions in the environment (Murton & Westwood 1977, Bronson 1989, Wingfield & Kenagy 1991, Shine & Brown 2008). Research in the last several decades has uncovered many features of physiological systems that enable vertebrates inhabiting temperate zone habitats to time reproduction according to environmental variation (e.g., Gwinner 1986, Crews & Moore 1986, Wingfield & Farner 1993, Hahn *et al.* 1997, Goldman 2001, Dawson 2002, Ball & Balthazart 2002, Prendergast 2005). Hallmarks in the physiological control of reproduction in most temperate zone and high-latitude vertebrates are a seasonal activation of reproductive organs in advance of the breeding season, typically in response to stimulatory (increasing) day lengths, followed by a complete

regression of the reproductive system after the breeding season. However, the majority of vertebrate species live in the tropics, where environmental conditions often do not vary as regularly and/or vary in different climatic or biotic variables than at higher latitudes. How do animals from tropical habitats as diverse as lowland rainforests, mountainous regions, savannahs or equatorial desert islands temporally coordinate reproduction to coincide with favorable environmental conditions?

Here we review recent advances in our understanding of the physiological mechanisms that regulate reproduction in tropical birds. Bird species are immensely valuable study systems because birds show a dramatic seasonal reorganization in physiology, behavior and morphology (Murton & Westwood 1977, Follett 1984, Dawson 2002). Established methods allow us to assess this variation in physiology, behavior and morphology in free-living individuals and place it in context with seasonal environmental variations (Wingfield *et al.* 1992, 1993). Field endocrinological techniques (Wingfield & Farner 1976), complemented with laboratory studies allow the investigation of physiological processes that underlie interactions of

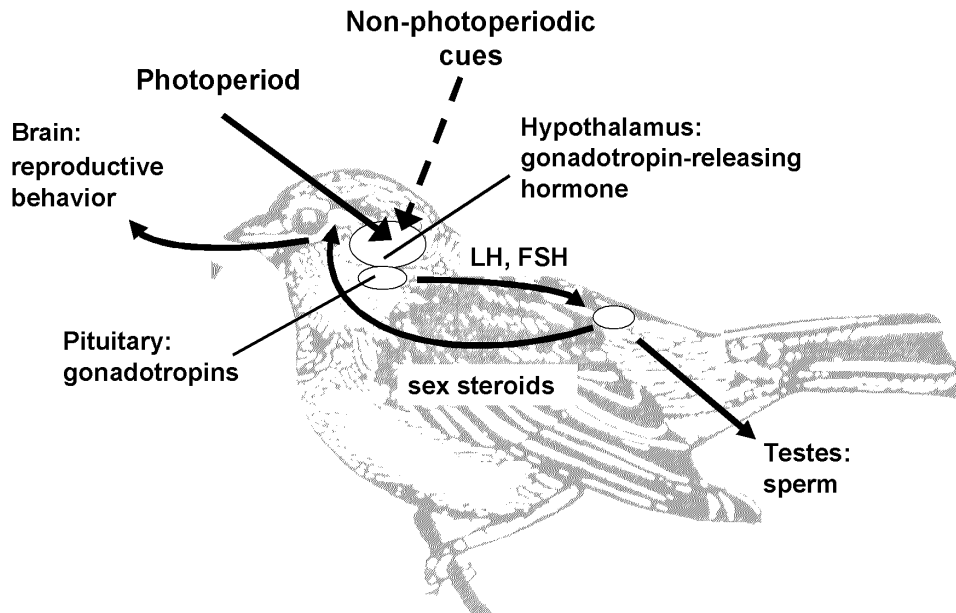


FIG. 1. Simplified model of the hypothalamo-pituitary-gonad (HPG) axis in temperate zone birds. Photoperiodic information is detected and decoded in the hypothalamus. Stimulatory (increasing) day lengths stimulate the release of gonadotropin-releasing hormone (GnRH) from the hypothalamus, from where it travels via a portal system to the pituitary gland. In the pituitary GnRH stimulates the release of gonadotropins (luteinizing hormone, LH and follicle stimulating hormone, FSH), into the circulation, which trigger the growth of the reproductive organs (the testes in male birds in this example). Once activated, the testes begin to produce mature sperm, and release sex steroid hormones such as testosterone and estradiol into the general circulation. These hormones act on receptors in the brain to promote the expression of reproductive and aggressive behaviors. Arrow with dotted line indicates the actions of non-photoperiodic cues on the HPG axis by mechanisms still to be identified; non-photoperiodic cues in most species only are effective after photostimulation.

individuals with their environment at various levels (Fig. 1). We emphatically support Stutchbury & Morton's (2001) proposition that the unparalleled diversity in habitat types and avian species in the tropics provides a large and mostly untapped resource as well as a natural laboratory for increasing our understanding of the way in which physiological systems function in animals from different environments (see also Levin & Wingfield 1992, Hau 2001, Goymann *et al.* 2004, Moore 2005, Hau 2007; for reviews on subtropical bird species see e.g., Chandola-Saklani *et al.*

1990, Cockrem 1995, Astheimer & Buttemer 2002).

#### THE TEMPERATE ZONE MODEL: SEASONAL BREEDING

Most temperate zone bird species live in environments that undergo considerable and highly predictable seasonal changes in environmental factors (e.g., day length, ambient temperature, rainfall) that are related to food availability. Hence, an appropriate timing of energetically demanding life-cycle stages such

as reproduction is essential for maximizing fitness (Perrins 1970, Price *et al.* 1988, Nilsson 1999, McNamara *et al.* 2004, Visser *et al.* 2004). Since variations in environmental conditions are so predictable, temperate zone birds have evolved a strong reliance on photoperiodic (day length) signals to determine the time of year and to regulate reproduction accordingly (Follett 1984, Hahn *et al.* 1997, Wilson & Donham 1998, Dawson *et al.* 2001, Sharp 2005). This high environmental predictability also allows temperate zone birds to seasonally regress reproductive organs, which might be an adaptation for minimizing energy expenditure during the non-breeding season (e.g., King 1973, Nicholls *et al.* 1988, Dawson *et al.* 2001).

The physiological system that enables birds, and other vertebrates, to assess environmental information and translate it into physiological signals that regulate the growth and the regression of reproductive organs is the hypothalamo-pituitary-gonad (HPG) axis (Fig. 1; Ball & Hahn 1997, Ball & Bentley 2000, Dawson *et al.* 2001, Sharp 2005). In birds, day length information is perceived primarily by photoreceptors embedded in the brain (e.g., Saldanha *et al.* 2001). Many species of temperate zone birds have become evolutionarily so reliant on day length as a seasonal cue that they require stimulatory (typically increasing) day lengths to activate the HPG axis (Follett 1984, Wilson & Donham 1998, Dawson *et al.* 2001). Other species possess endogenous circannual rhythms that can regulate the HPG-axis in the absence of environmental cues, but that respond to day length as a synchronizing factor (Gwinner 1986).

Stimulating environmental (day length) or internal (circannual rhythms) cues increase the production and secretion rates of gonadotropin-releasing hormone (GnRH), the protein hormone that functions like an on/off switch for an entire endocrine cascade that eventually activates the reproductive

organs and results in their seasonal gonadal growth (Ball & Hahn 1997, Ball & Bentley 2000, Dawson *et al.* 2001, Sharp 2005). GnRH released from the median eminence of the hypothalamus travels via the portal blood system to the anterior pituitary where it induces the release of two gonadotropins – follicle-stimulating hormone (FSH) and luteinizing hormone (LH). These two hormones act in concert to stimulate the growth and maturation of the ovary in female and the testes in male birds. The gonads will then increase the production of sex steroids such as estradiol and testosterone, which act on receptors in the brain to promote the expression of reproductive (song, courtship, copulatory) and aggressive (song, territory defense) behavior (Fig. 1; Ball & Balthazart 2002, Wingfield & Silverin 2002).

Once the HPG axis has been stimulated by long days, other environmental cues such as ambient temperature, food abundance, social factors and others can further stimulate or inhibit its seasonal growth and overall functioning (Ball 1993, Wingfield & Kenagy 1991, Wingfield *et al.* 1992, Schoech *et al.* 2004, Voigt *et al.* 2007). These types of cues allow the animal to fine-tune timing of reproduction to the local environment (Perfito *et al.* 2004). However, the precise mechanisms by which these ‘supplementary’ cues (Wingfield *et al.* 1992) affect the functioning of HPG axis are still largely unclear (e.g., Hau 2001).

## BREEDING SCHEDULES IN NEAR-EQUATORIAL TROPICAL BIRDS

Based on the general template of the physiological organization of seasonal breeding in temperate zone and high-latitude birds described above, we can now test in comparative studies whether the functioning of the HPG axis is similarly organized in species inhabiting divergent environments (Wing-

field *et al.* 1992, Hau 2001, Moore 2005, Hahn & McDougall-Shackleton 2008). A seasonal regulation of reproductive capacity coupled with advanced recrudescence of the reproductive system before environmental conditions improve intuitively appears beneficial in environments that annually undergo reliable and large-amplitude variations in environmental conditions (though its adaptive value has hardly been tested in a natural setting, Wikelski *et al.* 2008). However, patterns of variation in environmental conditions can be dramatically different in non-temperate environments such as the near-equatorial tropics (and also within temperate zone and subtropical habitats, see Hahn *et al.* 1997). Is it likely that breeding schedules and reliance on environmental cues are evolutionarily adjusted to different types of habitats (Wingfield *et al.* 1992, 1993; Hau 2001, Moore 2005, Hahn & McDougall-Shackleton 2008), though learning might also play a role (Grieco *et al.* 2002). For example, ambient temperature strongly affects seasonality in food abundance (especially insect availability) in temperate areas, but temperature tends to vary much less in near-equatorial tropical habitats (e.g., Leigh *et al.* 1996, Wikelski *et al.* 2000, Hau *et al.* 2004). Instead, rainfall is probably a stronger determinant of food abundance in many areas close to the equator (e.g., Grant & Boag 1980, Leigh *et al.* 1996, Ahumada 2001). And while rainfall may arrive on a fairly predictable annual schedule in some areas (Leigh *et al.* 1996, Wikelski *et al.* 2000), its occurrence might be hard to predict in others (Grant 1999). Finally, even though day length does change in some near-equatorial habitats (e.g., Hau *et al.* 1998), the amplitude of this variation is small and almost vanishes towards the equator (Gwinner & Dittami 1985, Hau *et al.* 2004, Moore *et al.* 2005).

The past decade or so has seen an increased interest in environmental physiology in tropical birds and in continuation we

will review some of these advances. Here we will not attempt a comprehensive overview of the large literature in this field, but instead will present select studies to illustrate where significant progress has been made and to outline areas in which we still lack important information. Within avian environmental physiology, we will concentrate on the perception and integration of environmental information by tropical birds; the regulation of behavior in tropical birds has already been reviewed elsewhere (e.g., Levin & Wingfield 1992, Hau 2001, Stutchbury & Morton 2001, Goymann *et al.* 2004, Moore 2005, Hau 2007). In the following, we will primarily discuss work conducted on near-equatorial species (within 10° of the equator), but supplement with select studies on tropical species from other areas. We will also include laboratory studies conducted on one of the most widely-used avian laboratory model, the Zebra Finch (*Taeniopygia guttata*), because of their relevance to our understanding of the physiological organization of the reproductive axis; the Australian subspecies, *Taeniopygia g. castanotis*, ranges from about 12 to 38°S, just reaching into temperate latitudes (Zann 1996).

*Seasonal breeding in tropical birds.* Long-term studies have delineated the seasonal regulation of reproduction in a suboscine passerine, the Spotted Antbird (*Hylophylax n. naevioides*) from a humid forest in Soberania National Park in central Panama (Hau 2001). The climate in central Panama (latitude 9°N) is characterized by a long rainy season from about May to November, each year with about 300 mm of rainfall per month, followed by a dry season between December and April during which hardly any rain falls (Leigh *et al.* 1996, Wikelski *et al.* 2000). Food abundance for insectivorous Spotted Antbirds increases dramatically during the early rainy season, which marks the onset of their breeding season (Willis 1972,

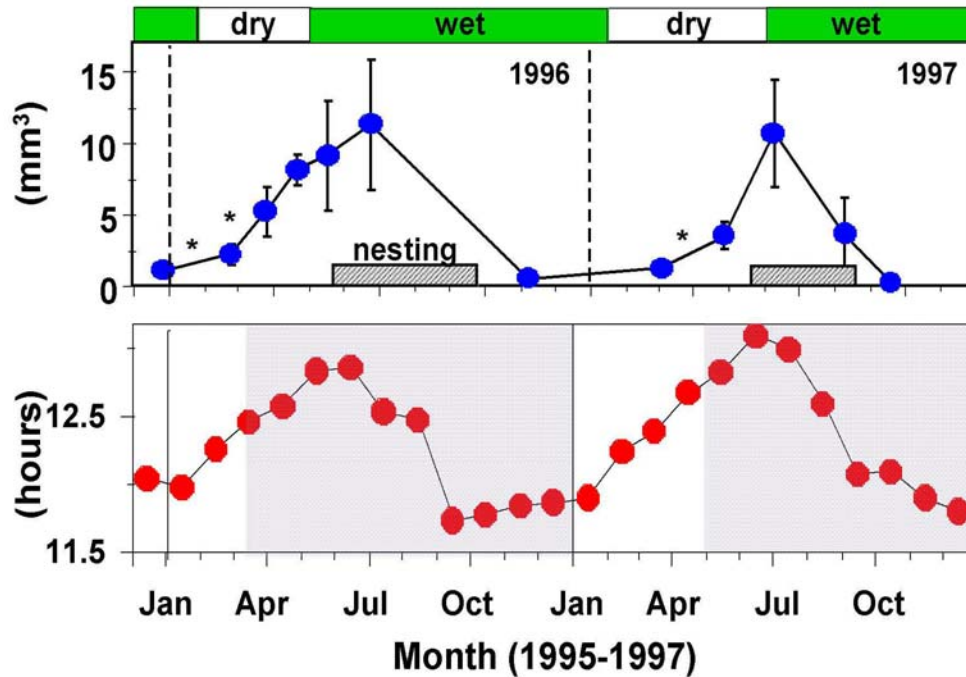


FIG. 2. Upper panel: Seasonal variation in testis sizes (in  $\text{mm}^3$ , means  $\pm$  95% CI) over two years of free-living male Spotted Antbirds from a lowland humid forest in central Panama. Horizontal bars above graph indicate dry (open) and wet seasons (dark grey). Hatched horizontal bars inside graph indicate nesting periods each year. Asterisks denote significant increases in testis sizes between sampling periods. Lower panel: Monthly averages of day length (h) as determined from a light logger positioned within a Spotted Antbird territory. Grey shading indicates periods of lower light intensities as determined from the light logger, while clear areas indicate periods of high light intensities during the day. Data compiled from Wikelski *et al.* (2000).

Wikelski *et al.* 2000). By assessing the size of the gonads in free-living male and female Spotted Antbirds at regular intervals via laparotomy, it was demonstrated that these birds express regular seasonal cycles of gonad growth and regression (Hau *et al.* 1998, Wikelski *et al.* 2000; Fig. 2). Much like temperate zone birds, Spotted Antbirds started to grow their gonads 1–2 months in advance of the onset of the breeding (rainy) season, while during the non-breeding season these birds had fully regressed reproductive organs (Wikelski *et al.* 2000). Hence, in a seasonally predictable habitat, even though close to the

equator, birds did display regular cycles in gonad size, and an anticipatory physiological preparation in advance of the breeding season, similar to many temperate zone birds (Hau 2001). Regular cycles in gonad sizes and seasonal breeding have also been shown by other near-equatorial tropical species, for example Stonechats (*Saxicola torquata axillaris*) from an equatorial population in Kenya (Gwinner & Dittami 1985, Dittami & Gwinner 1985). Likewise, Rufous-collared Sparrows (*Zonotrichia capensis*) from Ecuador display seasonal cycles of reproduction and associated variations in gonad size, reproduc-

tive hormone levels, the GnRH system, and the neural song control system (Moore *et al.* 2004, 2005, 2006).

*Continuous breeding in tropical birds.* The regular seasonality in gonad sizes shown by Spotted Antbirds differs from the regulation of reproductive activity found in a columbid species from central Venezuela, the Scaled Dove (*Columbina squammata*; Bosque *et al.* 2004). Even though living at a similar latitude (8°N) as Spotted Antbirds and also experiencing regular seasonal alternations between wet and dry seasons in their savannah habitat, male Scaled Doves never fully regressed their testes to a size at which sperm production was arrested (Bosque *et al.* 2004). Likewise, female Scaled Doves did not show clear seasonal cycles in follicle sizes. However, nesting in this species was seasonal and occurred primarily in the dry season when seed availability was highest. This strategy might be interpreted as continuous breeding, which is the strategy displayed by many columbid species (Wingfield *et al.* 1992), in which actual nesting is inhibited by low seed abundance during the wet season. Two related *Columbina* species living in the same habitat (*C. talpacoti* and *C. minuta*) showed more pronounced cycles in testis and follicles sizes, but out of phase with those of Scaled Doves (Bosque *et al.* 2004).

Continuous breeding may be possible in situations where food is not seasonally limited as has been demonstrated by an experimental study on the Seychelles Warbler (*Acrocephalus sechellensis*) at latitude 4°S (Komdeur 1996). Komdeur elegantly designed an experiment within a conservation effort and found that pairs that originated from islands with seasonal food availability and seasonal nesting showed continuous nesting activity after transfer to on new islands with more constant food abundance and low population densities (Komdeur 1996).

*Opportunistic breeding in tropical birds.* Examples of a habitat with seasonally unpredictable climatic fluctuations are the low-lying equatorial islands in the Galápagos archipelago off the coast of Ecuador (Grant & Grant 1989, Grant 1999). These islands (especially the lower elevations) are predominantly arid. Reproduction in Darwin's finches (*Geospiza* spp.), although some species can initiate breeding on pollen availability alone (Grant 1996), is strongly dependent on rainfall (Grant & Boag 1980, Grant *et al.* 2000), which can lead to an increase in insect food abundance within only 10 days (Grant & Grant 1989). The occurrence of rainfall on Galápagos has a seasonal component as it typically occurs between December and July each year. However, it is unpredictable as to when, whether and how much rain will fall during that period (Grant 1999, Hau *et al.* 2004). The large inter-annual fluctuations in rainfall are due to infrequent El Niño-Southern Oscillation (ENSO) events that bring rainfall of extended durations and amounts to the islands; ENSO events are typically followed by 'La Niña' years in which rainfall can be completely lacking. As birds cannot predict and prepare for such erratic rainfall, the best physiological strategy in such environments apparently is to breed opportunistically, i.e., to breed whenever environmental conditions permit (Farner & Serventy 1960, Immelmann 1971, Hahn *et al.* 1997, Astheimer & Buttemer 2002). For a long time it has been thought that one important physiological requirement of opportunistic breeding is a continuously activated HPG axis (much like in continuous breeders). Only such a physiological strategy would enable such species to rapidly initiate nesting whenever possible (Farner & Serventy 1960, Farner 1967). This view is derived from studies on the prime example of opportunistic breeding, the Zebra Finch. Indeed, populations of Zebra Finches from the arid interior of Australia where rainfall is erratic show enlarged

gonads over prolonged periods of time (Davies 1977). However, new data from this and other species question the notion that opportunistic breeding requires semi-activated gonads. Small Groundfinches (*Geospiza fuliginosa*), a species of Darwin's finch, showed full gonadal regression after the termination of the breeding season and throughout a 10-month drought period (Hau *et al.* 2004). Furthermore, Australian Zebra Finches from the southern part of their range also fully regressed their gonads during non-breeding in winter (Perfito *et al.* 2007).

#### HOW DO TROPICAL BIRDS KNOW WHEN TO BREED?

How do tropical bird species from various habitats assess environmental conditions, (i.e., which environmental stimuli do they respond to for timing reproductive events)?

*Responses to photoperiodic variations.* Responsiveness to photoperiodic cues is a physiological capacity that is ubiquitous among bird species inhabiting higher latitudes (Murton & Westwood 1977, Follett 1984, Wilson & Donham 1988, Hahn *et al.* 1997, Dawson *et al.* 2001, Sharp 2005). Curiously, several near-equatorial bird species that have been examined were also able to respond to the large photoperiodic changes characteristic of temperate latitudes (see summary in Hau *et al.* 1998). For example, Rufous-collared Sparrows from Colombia became photoperiodic when moved to the higher latitude, and associated changes in day length, of the Univ. of California, Berkeley campus (Miller 1965). The native population exhibited year-round breeding with two peaks while the transplanted population exhibited a typical high-latitude pattern of breeding in the spring (Miller 1959, 1962). Likewise, equatorial African Stonechats showed similar responses to temperate-zone photoperiodic variations as

European Stonechats (Gwinner & Dittami 1985, Gwinner & Scheuerlein 1999). The existence of such responsiveness to day length was considered paradoxical because sedentary near-equatorial species would never experience such large annual variations in day length in the wild, and the actual variations in day length at tropical latitudes were considered too small to be detected (e.g., Gwinner & Dittami 1985).

However, photoperiodic experiments in captive Spotted Antbirds from Panama revealed that near-equatorial birds are able to detect small variations in photoperiod (Hau *et al.* 1998): Spotted Antbirds increased gonad sizes and song activity in response to an abrupt increase in day length of one hour (the maximal natural change in photoperiod at their latitude), as well as by an increase of only 17 min (Hau *et al.* 1998). Since this finding, a subtropical Estrildid and an Emberizid from India (Chandola-Saklani *et al.* 2004, Rani *et al.* 2005), and the European Starling (*Sturnus vulgaris*) from Britain have been shown to be as highly photosensitive as Spotted Antbirds (Dawson 2007; see also discussion on evolution of photoperiodism below).

Photoresponsiveness might indeed be an adaptive physiological capability for species like Spotted Antbirds that live in seasonally predictable habitats, because changes in day length could be used to stimulate gonadal growth in anticipation of the rainy season (Hau *et al.* 1998, Wikelski *et al.* 2000). Such preparatory gonad growth would ensure that the birds are physiologically ready when the rainy season starts. It is unclear whether responsiveness to photoperiodic changes is beneficial for species in which changes in day length do not correspond with rainfall patterns or seasonal changes in food availability. Interestingly, it has recently been shown that even opportunistic breeders such as Zebra Finches can respond to large photoperiodic signals (Bentley *et al.* 2000a; see also Meijer *et*



*al.* 1996), suggesting that this trait is highly conserved among avian species, even in those that inhabit areas with unpredictable climatic variations.

*Responses to light intensity variations.* Even though populations living right at the equator might possess the physiological capability to respond to photoperiod, they are unlikely able to detect the slight variations in day length in their habitat. According to astronomical charts, annual variations in day length variations at the equator are less than 4 min (e.g., for equatorial Ecuador, Moore *et al.* 2005) although actual measurements at an equatorial site in Kenya showed annual day length variation up to 35 min (Dittami & Gwinner 1985). However, they might be utilizing seasonal variations in other photic environmental information such as in light intensity (Gwinner & Scheuerlein 1998). In many tropical habitats, light intensity during the day is substantially higher during the dry season, when cloud cover and humidity are low (and deciduous trees may lose their leaves in forested areas) compared to the rainy season. Indeed, experiments on captive equatorial Stonechats from Kenya have provided evidence that these birds can synchronize their circannual rhythms in reproductive activity accordingly (Gwinner & Scheuerlein 1998). Birds were held under a constant photoperiod but with bi-annual variations in light intensity during the day. This experimental schedule led to a synchronization of their circannual reproductive rhythms in such a way that they increased gonad sizes during the late dry season in advance of the rainy season during which they breed (Gwinner & Scheuerlein 1998). These findings suggest that even equatorial birds may be able to use photic information to predict seasonal variations in the environment, via measuring light intensity. Indeed, climatic variation in the habitat of Stonechats in Kenya are fairly regular between years, and

the combination of possessing circannual rhythms (Gwinner & Dittami 1990) with a sensitivity to long-term cues such as light intensity might enable these birds to breed seasonally even at the equator (Gwinner & Scheuerlein 1998).

Apart from functioning directly as a seasonal cue, light intensity might also influence the perception of day length in birds, by as yet unknown mechanisms. In temperate-zone birds held at fixed photoperiods high light intensities during the day can elicit responses that are usually shown in response to longer day length whereas low light intensities can elicit responses more similar to those under short photoperiods (Bissonette 1931, Bartholomew 1949, Bentley *et al.* 1998; see also Kumar & Rani 1996, Misra *et al.* 2004). Hence, seasonal variations in light intensity could amplify slight variations in photoperiod and thus facilitate their detection in near-equatorial habitats. Indeed, correlational data for Spotted Antbirds from Panama show that light intensity is highest during the early part of the year when birds start growing their gonads, perhaps amplifying the small increases in photoperiod that occur at that time (Fig. 2, Hau unpubl. compiled from Wikelski *et al.* 2000).

*Responses to variations in sunrise and sunset times.* A third photic signal that might be available even to equatorial populations is regular seasonal variations in sunrise and sunset times (Gwinner & Dittami 1985, Borchert *et al.* 2005). Even though day length hardly varies directly at the equator, the times of sunrise and sunset change annually by about 30 min (Borchert *et al.* 2005). These variations have long been proposed to provide potential seasonal cues, but only recently have data been published that support this hypothesis. A compilation of flowering data of various species of tropical trees suggested that these trees may synchronize their flowering times with

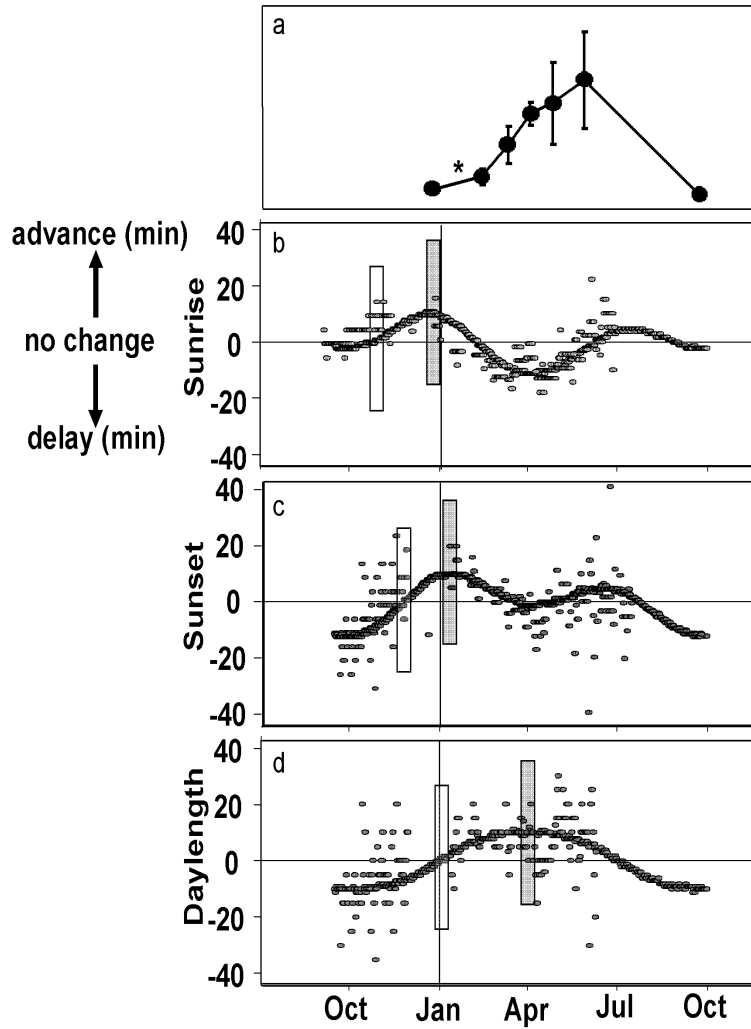


FIG. 3. Variations in testis volume of male Spotted Antbirds from Panama (a, in mm<sup>3</sup>, means  $\pm 9.5\%$  CI from the first year, asterisk (\*) denotes the first significant increase in testis sizes in the population) relative to seasonal changes in sunrise times (b), sunset times (c), and day length (d, all in minutes, and all 20-day running average, following Borchert *et al.* 2005). The thick line in b-d represents data obtained from astronomical charts. Individual data points are values obtained from a light logger positioned in a territory of a Spotted Antbird in the forest understory (note that data collection ceased in July). Light grey vertical bar indicate inflection points and dark grey vertical bars indicate periods of maximal changes of all photic variables (Hau unpubl.).

seasonal variations in sunset times (Borchert *et al.* 2005).

It is so far unknown whether animals have

the potential to detect annual variations in the times of sunrise and sunset. Equatorial Rufous-collared Sparrows do seasonally

change their daily activity period with seasonal changes in sunrise/sunset times (Moore unpubl.). An ongoing long-term experiment is currently testing this idea in captive equatorial African Stonechats (W. Goymann, I. Schwabl, B. Helm & I. T. Moore unpubl.).

To examine the possibility that sunrise and sunset times could provide seasonal information for near-equatorial Spotted Antbirds, 20-day differences of sunrise and sunset times as well as of daylength from astronomical charts were computed (solid lines in Fig. 3, following the methods of Borchert *et al.* 2005), and visually compared with seasonal variations in testis sizes of free-living males (Fig. 3a). The inflection points and the periods of maximal change for both sunrise and sunset times fall either before or within the period in which free-living Spotted Antbirds show the first significant increase in testis size (Fig. 3; Hau unpubl.). Since previous work had indicated that Spotted Antbirds can respond to slight variations in photoperiod (Hau *et al.* 1998), the present data suggest that they could obtain additional seasonal information from sunrise and sunset times as well. However, when data obtained from a light logger positioned in the forest understory where Spotted Antbirds live (individual data points in Fig. 3) were superimposed on the astronomical values, large daily variations in actual values became apparent. This variation is due to the fact that the logger (which has a lower threshold of sensitivity of about 0.2 lux; Wikelski *et al.* 2000) registers photic information influenced by natural events such as cloud and leaf cover. This raises several interesting questions that need to be addressed experimentally. For example, some of the natural scatter around the astronomical averages might function to amplify small changes in any of the three variables. For example the scatter in sunrise times between October and November appears to predominantly amplify the astronomically calculated advance in sunrise time (i.e., they are

more often above the line drawn from astronomical data; Fig. 3b), thus perhaps making the signal easier to detect. However, some of the variation is in both directions, for example in sunset times and day length (Figs 3c & 3d), probably obscuring actual changes in these variables and making it more difficult to detect the direction of change. Hence, we need to increase our understanding of how organisms cope with such daily variations and still potentially extract precise information on times of sunrise and sunset as well as day length using experimental methods. Other photic signals that might be available to near-equatorial birds as seasonal signals include the spectral composition of the light (e.g., Rani & Kumar 2000, Malik *et al.* 2001, Rani *et al.* 2001). It is conceivable that birds especially at near-equatorial latitudes use any signal available, and that the use of multiple signals improves the predictability of changes in the environment.

*Use of non-photoperiodic cues.* Environmental cues that show continuous and regular seasonal variations, such as day length and times of sunrise and sunset can be assessed at any point of the year and therefore are exquisitely suited for adjusting an individual's state in advance of actual environmental changes, if they reliably predict local environmental conditions. However, environmental conditions in tropical areas can show considerable year-to-year variation (Wingfield *et al.* 1992, Wikelski *et al.* 2000, Grant 1999), requiring additional mechanisms that allow individuals to tailor reproductive activity to local conditions.

A direct assessment of food availability would be the most direct means to evaluate whether environmental conditions are suitable for breeding. Food cues do not provide much advance notice for individuals that have completely regressed their gonads and hence would need some time to grow the gonads

before attempting to breed (which can take between 4 and 6 weeks in most temperate zone species, e.g., Farner & Wilson 1957). However, in species such as Spotted Antbirds in which the reproductive axis is activated by photoperiodic cues in advance of breeding, it can provide very precise information for adjusting the rate of gonadal development (Wikelski *et al.* 2000, Hau *et al.* 2000). Spotted Antbirds in Panama began gonadal development at similar times in two years that differed in the onset of the rainy season, as expected from the use of photoperiodic cues (Wikelski *et al.* 2000). However, in a year in which the rainy season was delayed by about 6 weeks compared to the previous year, the rate of gonadal development was slower, and males reached testis sizes that were assumed to be spermatogenic about one month later compared to a year with an earlier onset of the rainy season (Wikelski *et al.* 2000, Hau *et al.* 2000). Experiments on captive male Spotted Antbirds supported the hypothesis that food availability is used to adjust the rate of testis development: a group of males kept on an enriched diet grew their gonads faster and reached mature sizes within 3 weeks of food improvement, whereas individuals maintained on a standard diet did not develop their gonads further and did not develop fully mature gonads (Hau *et al.* 2000). Hence, food availability might provide a ‘supplementary cue’ (Wingfield & Kenagy 1991) for Spotted Antbirds to fine-tune the rate of gonadal development with environmental conditions in a particular year (see also Kumar *et al.* 2001). Likewise, in equatorial African Stonechats food abundance appears to function as a supplementary cue by modifying the actual nesting times within a given year; though food cues did not synchronize the circannual rhythm of reproduction and molt in free-living birds (Scheuerlein & Gwinner 2002).

Opportunistically breeding birds are

expected to rely heavily on short-term cues since long-term cues such as photoperiod, even where available, are not predictive of environmental conditions. Indeed, in captivity, Zebra Finches can breed year-round, suggesting that unlimited food in captivity and continuous social stimulation from having mates and other conspecifics in proximity (i.e., in a breeding colony) are sufficient to maintain reproductive activity (Oksche *et al.* 1963, Zann 1996). The use of short-term cues is also supported by experiments in wild Zebra Finches. Male Zebra Finches from southern Australia with completely regressed testes were brought into captivity and exposed to either short or long photoperiods (Perfito *et al.* 2007). However, despite the difference in photoperiodic treatment, both groups significantly and similarly increased their gonads, suggesting that cues other than photoperiod stimulated reproduction (Perfito *et al.* 2007). Those cues likely are related to food abundance – but could also be social – since males were kept in same-sex groups of four with visual and acoustic access to females. Experiments on the Lesser Sunda subspecies of the Zebra Finch (*Taeniopygia guttata*) corroborate that food cues are strong stimuli for reproductive activity (Perfito *et al.* 2008) and might be the actual stimuli that underlie the previously observed reproductive response to long day lengths in this species (Bentley *et al.* 2000a). This interpretation comes from an experiment showing that Zebra Finches exposed to long photoperiods significantly grew their gonads, while birds on the identical long photoperiod but with the amount of food restricted to short-day intake did not grow their gonads, similar to a group kept on short days (Perfito *et al.* 2008). Hence, it is possible that in this species reproductive activity is stimulated by extended feeding times or increased food abundance under long days, not by changes in day length *per se*, although in many other birds species it

has been confirmed that photoperiodic stimuli, and not extended feeding times stimulated reproductive activity (e.g., Ward 1972, Wingfield 1983, Dawson 1986, Hahn 1995).

Social cues are also probably of prime importance to tropical birds, especially those with socially monogamous mating systems (Kunkel 1974, Stutchbury & Morton 2001). Even the most seasonally breeding species of tropical bird are probably more flexible and asynchronous at the population level than high latitude birds due to a higher between-year variability in environmental seasonality. This situation makes coordination within pairs of utmost importance, especially for the male if he is to assure paternity of the offspring. In seasonally breeding, socially monogamous, Rufous-collared Sparrows in Ecuador, there is evidence that pairs synchronize seasonal growth of the gonads independent of the rest of the population (Moore *et al.* 2005). However, it is so far still unclear whether the male or the female is driving the synchrony.

Direct activation of the reproductive axis in avian species by social cues (e.g., song) is well known (for review, see Wingfield 1994). Interestingly, some of the best-studied species with respect to male song affecting female reproduction are in two continuous breeders: the Ring Dove (*Streptopelia risoria*; Lehrman 1965, O'Connell *et al.* 1981, Cheng and Zuo 1994) and the Canary (*Serinus canaria*; Hinde 1976, Bentley *et al.* 2000b), both of which inhabit temperate zone areas. Bentley and colleagues (2000b) found that male Canary song enhanced follicular development, advanced timing of egg-laying and total number of eggs laid in female Canaries. The extent to which social cues over-ride other environmental information in reproductive timing remains to be tested in tropical species. More generally, tropical species appear to show relatively high sensitivity to social, and other non-photoc cues, and thus represent ideal models for

understanding the pathways by which these cues are integrated by the HPG axis (see below).

## HOW DO CUES REGULATE REPRODUCTION IN TROPICAL BIRDS?

The GnRH system is considered the most important endocrine on/off switch in the brain for the HPG axis. Most vertebrates possess at least two forms of GnRH; birds in fact possess three: GnRH-I, -II and -III (Bentley *et al.* 2004). In temperate zone species, GnRH-I is regulated via photoperiodic information and appears to be strongly responsible for regulating the activity and regression of the HPG axis (Ball & Hahn 1997, Ball & Bentley 2000, Dawson *et al.* 2001, Sharp 2005). To date, we know very little about the GnRH system of tropical birds. Many species of tropical birds respond to injections of GnRH with increased secretion of luteinizing hormone (e.g., Wingfield *et al.* 1991, Levin & Wingfield 1992, Moore *et al.* 2002, O'Brien & Hau unpubl.). Furthermore, GnRH injections stimulate secretion of testosterone in males presumably from luteinizing hormone stimulation (Wingfield *et al.* 1991, Moore *et al.* 2002, Goymann & Wingfield 2004), suggesting that the endocrine cascade downstream from GnRH is not very different from that of temperate zone birds. However, how GnRH is regulated in the brain is unknown for the vast majority of tropical species. Therefore, we cannot yet assess whether GnRH-I is the main endocrine on/off switch in tropical birds as well, and whether the response of tropical birds to non-photoperiodic cues, especially in absence of photoperiodic cues transduced via GnRH-I or other forms of GnRH.

However, two recent studies have provided some insight into the regulation of the GnRH system in tropical birds. A recent

study in equatorial Rufous-collared Sparrows showed that the GnRH system is intact and functional, and that it is regulated by non-photoperiodic cues (Moore *et al.* 2006). Moore and colleagues studied two populations of Rufous-collared Sparrows that live on two opposite slopes of an Andean mountain in Ecuador, separated by only 25 km. Seasonal rainfall patterns on these two slopes are opposed, with one population receiving rainfall and hence breeding in September and the other population receiving rainfall, and breeding in February. In both populations, male birds had larger GnRH neurons during the breeding season compared to the non-breeding season regardless of the time of year; the antibody recognized both GnRH-I+II but based on the location of the cells were considered to be GnRH-I cell bodies (Moore *et al.* 2006). These data suggest that the GnRH system is up-regulated with reproductive axis activation. Since the two populations experience the same photic variations, environmental cues other than photoperiod must be regulating GnRH (Moore *et al.* 2006). However, one should keep in mind that studies measuring GnRH-ir with immunocytochemistry do not measure production and secretion rates directly.

In opportunistically breeding Zebra Finches, Perfito and colleagues obtained evidence that non-photoperiodic cues regulate GnRH-I and GnRH-II differently (Perfito *et al.* 2006). Zebra Finches were subject to a slow water restriction regime, which is the only known way in which the reproductive axis of captive Zebra Finches can be inhibited (Sossinka 1974, Vleck & Priedkalns 1985). Indeed, male Zebra Finches whose water availability was successively limited to 1 ml a week over the course of 9 weeks showed a reduction in gonad sizes and LH secretion (Perfito *et al.* 2006). However, the number of GnRH-I cells in the brain of birds kept under this water restriction regime for an additional

2 weeks was undistinguishable from those of birds taken directly from the breeding colony, from birds whose water supply had been restored to *ad libitum* levels, and from birds that were kept for the same amount of time and under the same experimental conditions but with continuous *ad libitum* water. Interestingly, GnRH-II cell numbers varied between experimental groups, such that only the individuals taken directly from the breeding colony had significantly more GnRH-II cells than all other groups (Perfito *et al.* 2006). Hence, water restriction does not account for the variation in GnRH-II cell numbers among experimental groups. In contrast, the fact that the group that was taken through the entire experiment with water available *ad libitum* had low GnRH-II cell numbers suggests that social cues might be regulating GnRH-II (Perfito *et al.* 2006). All experimental groups, except the group directly taken from the breeding colony, had experienced limited social interactions, since they were housed singly and only with other males nearby. Since GnRH-II stimulates sexual behaviors, at least in female songbirds studied to date (Maney *et al.* 1997, Bentley *et al.* 2006), it remains an exciting potential player in reproductive axis activation in tropical species.

## ECOLOGICAL AND EVOLUTIONARY IMPLICATIONS

What are the implications of the data reviewed above for our understanding of the ecological and evolutionary physiology of the timing of reproduction in birds? First, these data once again emphasize that tropical birds are valuable model systems, because their high diversity and distribution across a wide spectrum of habitats provides us with the opportunity for highly informative comparative studies. That said, there still are relatively few systems that have received sufficient attention to be able to draw some conclu-

sions. Second, even though we have made progress in understanding how tropical birds cope with seasonal variations in their environment, we are still far removed from understanding the evolutionary implications of these findings.

For example, the available data set suggests that several features of the HPG-axis are conserved. First, the general responsiveness to photoperiod appears at this point to be ubiquitous among avian taxa; although the new finding that in the Lesser Sundas finch extended feeding times or increased amount of food might be the actual stimuli underlying its response to long photoperiods suggests that some caution is required before making sweeping generalizations. Second, the major components and general functioning of the HPG-axis seem to be conserved as well. GnRH is present in tropical birds and correlates with reproductive activity, at least in seasonally-reproducing species like the Rufous-collared Sparrow; but perhaps is continually elevated in opportunistic breeders such as Zebra Finches. Furthermore, GnRH-release stimulates LH secretion like in temperate zone birds. Third, the general mechanisms that lead to a regression and growth of reproductive organs (either triggered by endogenous or exogenous cues) is present in tropical species as well, even in those that live in seasonally unpredictable habitats. It is likely, but remains to be established, that variations in GnRH-I secretion are at the basis of fluctuations in the size of reproductive organs.

It is presently unclear whether certain components of the system regulating reproductive physiology in tropical birds show evidence of evolutionary adaptation. The discovery of a high sensitivity to small variations in photoperiod in tropical birds (Hau *et al.* 1998, Chandola-Saklani *et al.* 2004, Beebe *et al.* 2005, Rani *et al.* 2005; see also Styrsky *et al.* 2004) has initially suggested that this might be an evolutionary adaptation in tropical birds to

utilize photoperiodic information close to the equator (Hau *et al.* 1998). However, the recent findings of a similarly high photosensitivity in European Starlings, which synchronized their reproductive cycles with a simulated photoperiod of 9°N (the latitude of Panama, which is outside their range of distribution; Dawson 2007), cast doubt on the interpretation that this capability is specific to species that live at low latitudes.

The apparent limitations in realistically interpreting the available data in an evolutionary context emphasize that we urgently need more, and in particular phylogenetically controlled studies, on the organization of reproductive physiology in birds (Moore *et al.* 2002, Hahn & McDougall-Shackleton 2008). Hahn & McDougall-Shackleton (2008) distinguish three scenarios that may account for interspecific variability in physiological organization, which need to be addressed experimentally to understand evolutionary patterns. (1) The adaptive specialization hypothesis assumes that evolutionary adaptation in a certain trait has actually occurred. (2) The conditional plasticity hypothesis assumes that physiological systems are plastic and can function well in diverse habitats. (3) The phylogenetic history hypothesis assumes that traits have been retained over evolutionary history, and have not been selected against. Only carefully designed comparative studies, in which phylogenetic relationships are being controlled for, can disentangle which of the three mechanisms generates the observed variability in breeding schedules and response to environmental cues (Hahn & McDougall-Shackleton 2008).

Hence, many evolutionary questions at present unfortunately remain unanswered. For example, why do we see an apparent conservation in some physiological traits such as a responsiveness to photoperiod? Is the near-ubiquity of this trait due to positive selection on photoresponsiveness for the temporal regulation of reproduction or other life-cycles

stages (molt, migration, etc.)? Or is it a phylogenetic relic that has not been selected against (Gwinner & Dittami 1985)? Perhaps the above-mentioned new data on the Lesser Sundas finch suggest that the responsiveness to photoperiod is not a phylogenetic relic but instead is under positive selection, even in near-equatorial species? Further, why do traits such as the composition and functioning of the HPG-axis show little variation between species? Is one reason that this system is highly complex, with many components depending on each other (e.g., Fig. 1)? It is conceivable that such complex systems require very strong selection pressures and long evolutionary times to change, because variations in the functioning of one part might impair the functioning of the entire system; but this is currently unknown.

Nevertheless, the lack of available data also emphasizes that there is much room for exciting new research, in which tropical species could play a prominent role. Future work on tropical birds will not only be crucial for understanding questions on the evolution of reproductive physiology, but also for increasing our knowledge on the mechanisms that underlie the responses of vertebrates to their environments. How are seasonal variations in light intensity perceived? Are they detected by a specialized mechanism separate from, but interacting with, the photoperiodic system? Or is the photoperiodic system inherently susceptible to light intensity cues as well (Gwinner & Scheuerlein 1998)? Can animals detect seasonal variations in sunrise/sunset cues and how do they accomplish this? How are food cues perceived, either in addition to or separate from, photoperiodic information (Hau *et al.* 2000, O'Brien & Hau 2005)? How do short-term cues such as food availability, rainfall, social cues etc. affect the HPG-axis? Studies on tropical birds have a high potential to make significant progress in our understanding of the

interactions of vertebrates with their environments.

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#### REFERENCES

- Ahumada, J. A. 2001. Comparison of the reproductive biology of two Neotropical wrens in an unpredictable environment in northeastern Colombia. *Auk* 118: 191–210.
- Astheimer, L. B., & W. A. Buttemer. 1999. Gonadal and hormonal patterns in the annual cycle of an Australian honeyeater. *Proc. Int. Ornithol. Congr.* 22: 1768–1783.
- Astheimer, L. B., & W. A. Buttemer. 2002. Changes in latitude, changes in attitude: a perspective on ecophysiological studies of Australian birds. *Emu* 102: 19–27.
- Ball, G. F. 1993. The neural integration of environmental information by seasonally breeding birds. *Am. Zool.* 33: 185–199.
- Ball, G. F., & J. Balthazart. 2002. Neuroendocrine mechanisms regulating reproductive cycles and reproductive behavior in birds. Pp. 649–798 *in* Pfaff, D. W. (ed.). *Hormones, brain and behavior*.



- ior. Volume 2. Academic Press, Amsterdam, The Netherlands.
- Ball, G. F., & G. E. Bentley. 2000. Neuroendocrine mechanisms mediating the photoperiodic and social regulation of seasonal reproduction in birds. Pp. 129–158 *in* Wallen, K., & J.E. Schneider (eds.). *Reproduction in context*. MIT Press, Cambridge, Massachusetts.
- Ball, G. F., & T. P. Hahn. 1997. GnRH neuronal systems in birds and their relation to the control of seasonal reproduction. Pp. 325–342 *in* Parhar, I. S., & Y. Sakuma (eds.). *GnRH neurons: gene to behavior*. Brain Shuppan, Tokyo, Japan.
- Bartholomew, G. A. 1949. The effect of light intensity and day length on reproduction in the English sparrow. *Bull. Mus. Comp. Zool. Harv.* 101: 433–476.
- Beebe, K., G. Bentley, & M. Hau. 2005. A seasonally breeding tropical bird lacks absolute photorefractoriness in the wild, despite high photoperiodic sensitivity. *Funct. Ecol.* 19: 505–512.
- Bentley, G. E., A. R. Goldsmith, A. Dawson, C. Briggs, & M. Pemberton. 1998. Decreased light intensity alters the perception of day length by male European Starlings (*Sturnus vulgaris*). *J. Biol. Rhythms* 13: 148–158.
- Bentley, G. E., B. D. Spar, S. A. MacDougall-Shackleton, T. P. Hahn, & G. F. Ball. 2000a. Photoperiodic regulation of the reproductive axis in male Zebra Finches, *Taeniopygia guttata*. *Gen. Comp. Endocrinol.* 117: 449–455.
- Bentley, G. E., J. C. Wingfield, M. L. Morton, & G. F. Ball. 2000b. Stimulatory effects on the reproductive axis in female songbirds by conspecific and heterospecific male song. *Horm. Behav.* 37: 179–189.
- Bentley, G. E., I. T. Moore, S. A. Sower, & J. C. Wingfield. 2004. Evidence for a novel gonadotropin-releasing hormone in hypothalamic and forebrain areas in songbirds. *Brain Behav. Evol.* 63: 34–46.
- Bentley, G. E., J. P. Jensen, G. J. Kaur, D. W. Wacker, K. Tsutsui, & J. C. Wingfield. 2006. Rapid inhibition of female sexual behavior by gonadotropin-inhibitory hormone (GnIH). *Horm. Behav.* 49: 550–555.
- Bissonnette, T. H. 1931. *Studies on the sexual cycle in birds. V: Effects of light of different intensities upon the testis activity of the European Starling (Sturnus vulgaris)*. *Physiol. Zool.* 4: 542–574.
- Borchert, R., S. S. Renner, Z. Calle, D. Navarrete, A. Tye, L. Gautier, R. Spichiger, & P. von Hildebrand. 2005. Photoperiodic induction of synchronous flowering near the Equator. *Nature* 433: 627–629.
- Bosque, C., M. A. Pacheco, & M. A. Garcia-Amado. 2004. The annual cycle of *Columbina* ground-doves in seasonal savannas of Venezuela. *J. Field Ornithol.* 75: 1–17.
- Bronson, F. H. 1989. *Mammalian reproductive biology*. Univ. of Chicago Press, Chicago, Illinois.
- Chandola-Saklani, A., K. K. Sharma, M. S. Bisht, & P. Lakhera. 1990. Ecophysiology of seasonal reproduction in the tropics: the Baya Weaver. Pp. 207–224 *in* Wada, M. (ed.). *Endocrinology of birds: molecular to behavioral*. Springer-Verlag, Berlin, Germany.
- Chandola-Saklani, A., A. Thapliyal, K. Negi, S. C. Diyundi, & B. Choudhary. 2004. Daily increments of light hours near vernal equinox synchronize circannual testicular cycle of tropical Spotted Munia. *Chronobiol. Int.* 21: 553–569.
- Cheng, M.-F., & M. Zuo. 1994. Proposed pathways for vocal self-stimulation: met-enkephalinergic projections linking the midbrain vocal nucleus, auditory-responsive thalamic regions and neurosecretory hypothalamus. *J. Neurobiol.* 25: 361–379.
- Cockrem, J. F. 1995. Timing of seasonal breeding in birds, with particular reference to New Zealand birds. *Reprod. Fert. Dev.* 7: 1–19.
- Crews, D., & M. C. Moore. 1986. Evolution of mechanisms controlling mating behavior. *Science* 231: 121–125.
- Davies, S. J. J. F. 1977. The timing of breeding by the Zebra Finch *Taeniopygia castanotis* at Mileura, Western Australia. *Ibis* 199: 369–372.
- Dawson, A. 1986. The effect of restricting the daily period of food availability on testicular growth of Starlings *Sturnus vulgaris*. *Ibis* 128: 572–575.
- Dawson, A. 2002. Photoperiodic control of the annual cycle in birds and comparison with mammals. *Ardea* 90: 355–367.
- Dawson, A. 2007. Seasonality in a temperate zone

- bird can be entrained by near equatorial photoperiods. *Proc. R. Soc. Lond. B* 274: 721–725.
- Dawson, A., V. M. King, G. E. Bentley, & G. F. Ball. 2001. Photoperiodic control of seasonality in birds. *J. Biol. Rhythms* 16: 365–380.
- Dittami, J. P., & E. Gwinner. 1985. Annual cycles in the African Stonechat *Saxicola torquata axillaris* and their relationship to environmental factors. *J. Zool. Lond.* 207: 357–370.
- Dunlap, J. C., J. J. Loros, & P. J. DeCoursey. 2004. *Chronobiology: biological timekeeping*. Sinauer, Sunderland, Massachusetts.
- Farner, D. S. 1967. The control of avian reproductive cycles. *Proc. Int. Ornithol. Congr.* 14: 107–133.
- Farner, D. S., & D. L. Serventy. 1960. The timing of reproduction in birds in the arid regions of Australia. *Anat. Rec.* 137: 354.
- Farner, D. S., & A. C. Wilson. 1957. A quantitative examination of testicular growth in the White-crowned Sparrow. *Biol. Bull.* 113: 254–267.
- Follett, B. K. 1984. Birds. Pp. 283–350 in Lammung, G. E. (ed.). *Marshall's physiology of reproduction*. Volume 1. Churchill Livingstone, Edinburgh, UK.
- Goldman, B. D. 2001. Mammalian photoperiodic system: Formal properties and neuroendocrine mechanisms of photoperiodic time measurement. *J. Biol. Rhythms* 16: 283–301.
- Goymann, W., & J. C. Wingfield. 2004. Competing females and caring males. Sex steroids in African Black Coucals, *Centropus grillii*. *Anim. Behav.* 68: 533–540.
- Goymann, W., I. T. Moore, A. Scheuerlein, K. Hirschenhauser, A. Grafen, & J. C. Wingfield. 2004. Testosterone in tropical birds: effects of environmental and social factors. *Am. Nat.* 164: 327–334.
- Grant, B. R. 1996. Pollen digestion by Darwin's finches and its importance for early breeding. *Ecology* 77: 489–499.
- Grant, B. R., & P. R. Grant. 1989. Evolutionary dynamics of a natural population: the large Cactus Finch of the Galapagos. Univ. of Chicago Press, Chicago, Illinois.
- Grant, P. R. 1999. *Ecology and evolution of Darwin's finches*. 2<sup>nd</sup> ed. Princeton Univ. Press, Princeton, New Jersey.
- Grant, P. R., & P. T. Boag. 1980. Rainfall on the Galapagos and the demography of Darwin's finches. *Auk* 97: 227–244.
- Grant, P. R., B. R. Grant, L. F. Keller, & K. Petren. 2000. Effects El Nino events on Darwin's finch productivity. *Ecology* 81: 2442–2457.
- Grieco, F., A. J. van Noordwijk, & M. E. Visser. 2002. Evidence for the effect of learning on timing of reproduction in Blue Tits. *Science* 296: 136–138.
- Gwinner, E. 1986. *Circannual rhythms*. Springer-Verlag, Berlin Heidelberg.
- Gwinner, E., & J. Dittami. 1985. Photoperiodic responses in temperate zone and equatorial Stonechats: a contribution to the problem of photoperiodism in tropical organisms. Pp. 279–294 in Follett, B. K., S. Ishii, & A. Chandola (eds.). *The endocrine system and the environment*. Springer-Verlag, Berlin, Germany.
- Gwinner, E., & A. Scheuerlein. 1998. Seasonal changes in day-light intensity as potential zeitgeber of circannual rhythms in equatorial Stonechats. *J. Ornithol.* 138: 407–412.
- Gwinner, E., & A. Scheuerlein. 1999. Photoperiodic responsiveness of equatorial and temperate-zone Stonechats. *Condor* 101: 347–359.
- Hahn, T. P. 1995. Integration of photoperiodic and food cues to time changes in reproductive physiology by an opportunistic breeder, the Red Crossbill *Loxia curvirostra* (Aves: Carduelinae). *J. Exp. Zool.* 272: 213–226.
- Hahn, T. P. 1998. Reproductive seasonality in an opportunistic breeder, the Red Crossbill (*Loxia curvirostra*). *Ecology* 79: 2365–2375.
- Hahn, T. P., T. Boswell, J. C. Wingfield, & G. F. Ball. 1997. Temporal flexibility in avian reproduction. Pp. 39–80 in Nolan Jr., V., E. D. Ketterson, & C. F. Thompson (eds.). *Current ornithology*. Volume 14. Plenum Press, New York, New York.
- Hahn, T. P., & S. A. MacDougall-Shackleton. 2008. Adaptive specialization, conditional plasticity, and phylogenetic history in the reproductive cue response systems of birds. *Philos. Trans. R. Soc. Lond. B* 363: 267–286.
- Hau, M. 2001. Timing of breeding in variable environments: Tropical birds as model systems. *Horm. Behav.* 40: 281–290.
- Hau, M. 2007. Regulation of male traits by testosterone: implications for the evolution of ver-

- tebrate life histories. *BioEssays* 29: 133–144.
- Hau, M., M. Wikelski, & J. C. Wingfield. 1998. A Neotropical forest bird can measure the slight changes in tropical photoperiod. *Proc. R. Soc. Lond. B* 265: 89–95.
- Hau, M., M. Wikelski, & J. C. Wingfield. 2000. Visual and nutritional food cues fine-tune timing of reproduction in a Neotropical rainforest bird. *J. Exp. Zool.* 286: 494–504.
- Hau, M., M. Wikelski, H. Gwinner, & E. Gwinner. 2004. Timing of reproduction in a Darwin's finch: temporal opportunism under spatial constraints. *Oikos* 106: 489–500.
- Hinde, R. A., & E. Steel. 1976. The effect of male song on an estrogen-dependent behavior pattern in the female canary. *Horm. Behav.* 7: 293–304.
- Immelmann, K. 1971. Ecological aspects of periodic reproduction. Pp. 341–389 *in* Farner, D. S., & J. R. King (eds.). *Avian biology*. Volume I. Academic Press, New York.
- King, J. R. 1973. Energetics of reproduction in birds. Pp. 78–120 *in* Farner, D. S. (ed.), *Breeding biology of birds*. National Academy of Science, Washington, D.C.
- Komdeur, J. 1996. Seasonal timing of reproduction in a tropical bird, the Seychelles Warbler: a field experiment using translocation. *J. Biol. Rhythms* 11: 333–346.
- Kumar, V., & S. Rani. 1996. Effects of wavelength and intensity of light in initiation of body fattening and gonadal growth in a migratory bunting under complete and skeleton photoperiods. *Physiol. Behav.* 60: 625–631.
- Kumar, V., S. Singh, M. Misra, & S. Malik. 2001. Effects of duration and time of food availability on photoperiodic responses in the migratory male Blackheaded Bunting (*Emberiza melanocephala*). *J. Exp. Biol.* 204: 2843–2848.
- Kunkel, P. 1974. Mating systems of tropical birds: the effect of weakness or absence of external reproduction-timing factors, with special reference to prolonged pair-bonds. *Z. Tierpsychol.* 34: 265–307.
- Lehrman, D. S., & M. Friedman. 1969. Auditory stimulation of ovarian activity in the Ring Dove (*Streptopelia risoria*). *Anim. Behav.* 17: 494–497.
- Leigh, E. G., A. S. Rand, & D. M. Windsor. 1996. The ecology of a tropical forest: seasonal rhythms and long-term changes. 2<sup>nd</sup> ed. Smithsonian Institution Press, Washington, D. C.
- Levin, R. N., & J. C. Wingfield. 1992. The hormonal control of territorial aggression in tropical birds. *Ornis Scand.* 23: 284–291.
- Malik, S., S. Rani, & V. Kumar. 2002. The influence of light wavelength on phase-dependent responsiveness of the photoperiodic clock in migratory Blackheaded Bunting. *Biol. Rhythm Res.* 33: 65–73.
- Maney, D. L., R. D. Richardson, & J. C. Wingfield. 1997. Central administration of chicken gonadotropin-releasing hormone-II enhances courtship behavior in a female sparrow. *Horm. Behav.* 32: 11–18.
- McNamara, J. M., R. K. Welham, A. I. Houston, S. Daan, & J. M. Tinbergen. 2004. The effects of background mortality on optimal reproduction in a seasonal environment. *Theor. Pop. Biol.* 65: 361–372.
- Meijer, T., J. Rozman, M. Schulte, & C. Stach-Dreesmann. 1996. New findings in body mass regulation in Zebra Finches (*Taeniopygia guttata*) in response to photoperiod and temperature. *J. Zool. Lond.* 240: 717–734.
- Miller, A. H. 1959. Reproductive cycles in an equatorial sparrow. *Proc. Natl. Acad. Sci. USA* 45: 1095–1100.
- Miller, A. H. 1962. Bimodal occurrence of breeding in an equatorial sparrow. *Proc. Natl. Acad. Sci. USA* 48: 396–400.
- Miller, A. H. 1965. Capacity for photoperiodic response and endogenous factors in the reproductive cycles of an equatorial sparrow. *Proc. Natl. Acad. Sci. USA* 54: 97–101.
- Misra, M., S. Rani, S. Singh, & V. Kumar. 2004. Regulation of seasonality in the migratory male Blackheaded Bunting (*Emberiza melanocephala*). *Reprod. Nutr. Dev.* 44: 341–352.
- Moore, I. T. 2005. Non-photoperiodic seasonality in a tropical songbird. Pp. 181–190 *in* Dawson, A., & P. J. Sharp (eds.). *Functional avian endocrinology*. Narosa Publishing House, New Delhi, India.
- Moore, I. T., N. Perfito, H. Wada, T. S. Sperry, & J. C. Wingfield. 2002. Latitudinal variation in plasma testosterone levels in birds of the genus *Zonotrichia*. *Gen. Comp. Endocrinol.* 129: 13–19.

- Moore, I. T., F. Bonier, & J. C. Wingfield. 2005. Reproductive asynchrony and population divergence between two tropical bird populations. *Behav. Ecol.* 16: 755–762.
- Moore, I. T., G. E. Bentley, C. Wotus, & J. C. Wingfield. 2006. Photoperiod-independent changes in immunoreactive brain gonadotropin-releasing hormone (GnRH) in a free-living, tropical bird. *Brain Behav. Evol.* 68: 37–44.
- Murton, R. K., & N. J. Westwood. 1977. Avian breeding cycles. Clarendon Press, Oxford, UK.
- Nelson, R. J., G. E. Demas, S. K. Klein, & L. J. Kriegsfeld. 2002. Seasonal patterns of stress, immune function and disease. Cambridge Univ. Press, Cambridge, UK.
- Nicholls, T. J., A. R. Goldsmith, & A. Dawson. 1988. Photorefractoriness in birds and comparison with mammals. *Physiol. Rev.* 68: 133–176.
- Nilsson, J. A. 1999. Fitness consequences of timing of reproduction. *Proc. Int. Ornithol. Congr.* 22: 234–247.
- O'Brien, S., & M. Hau. 2005. Food cues and gonadal development in Neotropical Spotted Antbirds (*Hylophylax naevioides*). *J. Ornithol.* 146: 332–337.
- O'Connell, M. E., C. Reboulleau, H. H. Feder, & R. Silver. 1981. Social interactions and androgen levels in birds. 1. Female characteristics associated with increased plasma androgen levels in the male Ring Dove (*Streptopelia risoria*). *Gen. Comp. Endocrinol.* 44: 454–463.
- Oksche, A., D. S. Farner, D. L. Serventy, F. Wolff, & C. A. Nicholls. 1963. The hypothalamo-hypophysial neurosecretory system of the Zebra Finch, *Taeniopygia castanotis*. *Zeitschr. Zellforsch.* 58: 846–914.
- Perfito, N., A. D. Tramontin, S. L. Meddle, P. Sharp, D. Afik, J. Gee, S. Ishii, M. Kikuchi, & J. C. Wingfield. 2004. Reproductive development according to elevation in a seasonally breeding male songbird. *Oecologia* 140: 201–210.
- Perfito, N., G. Bentley, & M. Hau. 2006. Tonic activation of brain GnRH immunoreactivity despite reduction of peripheral reproductive parameters in opportunistically breeding Zebra Finches. *Brain Behav. Evol.* 67: 123–134.
- Perfito, N., R. Zann, G. E. Bentley, & M. Hau. 2007. Opportunism at work: habitat predictability affects reproductive strategy in free-living Zebra Finches. *Funct. Ecol.* 21: 291–301.
- Perfito, N., J. Kwong, G. E. Bentley, & M. Hau. 2008. Cue hierarchies and testicular development in an opportunistic breeder (*Taeniopygia guttata*): Is food a far more potent stimulus than photoperiod?. *Horm. Behav.* In press.
- Perrins, C. M. 1970. The timing of birds' breeding seasons. *Ibis* 112: 242–255.
- Prendergast, B. J. 2005. Internalization of seasonal time. *Horm. Behav.* 48: 503–511.
- Price, T., M. Kirkpatrick, & S. J. Arnold. 1988. Directional selection and the evolution of breeding date in birds. *Science* 240: 798–799.
- Rani, S., & V. Kumar. 2000. Phasic response of the photoperiodic clock to wavelength and intensity of light in the Redheaded Bunting, *Emberiza bruniceps*. *Physiol. Behav.* 69: 277–283.
- Rani, S., S. Singh, M. Misra, & V. Kumar. 2001. The influence of light wavelength on reproductive photorefractoriness in migratory Blackheaded Bunting (*Emberiza melanocephala*). *Reprod. Nutr. Dev.* 41: 277–284.
- Rani, S., S. Singh, M. Misra, S. Malik, B. P. Singh, & V. Kumar. 2005. Daily light regulates seasonal responses in the migratory male Redheaded Bunting (*Emberiza bruniceps*). *J. Exp. Zool. A* 303: 541–550.
- Saldanha, C. J., A. J. Silverman, & R. Silver. 2001. Direct innervation of GnRH neurons by encephalic photoreceptors in birds. *J. Biol. Rhythms* 16: 39–49.
- Scheuerlein, A., & E. Gwinner. 2002. Is food availability a circannual zeitgeber in tropical birds? A field experiment on Stonechats in tropical Africa. *J. Biol. Rhythms* 17: 171–180.
- Schoech, S. J., R. Bowman, & S. J. Reynolds. 2004. Food supplementation and possible mechanisms underlying early breeding in the Florida Scrub-Jay (*Aphelocoma coerulescens*). *Horm. Behav.* 46: 565–573.
- Sharp, P. J. 2005. Photoperiodic regulation of seasonal breeding in birds. *Trends Comp. Endocrinol. Neurobiol.* 1040: 189–199.
- Shine, R., & G. P. Brown, 2008. Adapting to the unpredictable: reproductive biology of vertebrates in the Australian wet-dry tropics. *Philos. Trans. R. Soc. B*, in press.
- Sossinka, R. 1974. Der Einfluss von Durstperioden auf die Schilddruesen- und Gonadenaktivitaet

- und ihre Bedeutung fuer die Brutperiodik des Zebrafinken (*Taeniopygia castanotis* Gould). J. Ornithol. 115: 128–141.
- Styrsky, J. D., P. Berthold, & W. D. Robinson. 2004. Endogenous control of migration and calendar effects in an intratropical migrant, the Yellow-green Vireo. Anim. Behav. 67: 1141–1149.
- Stutchbury, B. J. M., & E. S. Morton. 2001. Behavioral ecology of tropical birds. Academic Press, San Diego, California.
- Visser, M. E., C. Both, & M. M. Lambrechts. 2004. Global climate change leads to mistimed avian reproduction. Adv. Ecol. Res. 35: 89–110.
- Vleck, C. M., & J. Priedkalns. 1985. Reproduction in Zebra Finches: hormone levels and effect of dehydration. Condor 87: 37–46.
- Voigt, C., W. Goymann, & S. Leitner. 2007. Green matters! Growing vegetation stimulates breeding under short day conditions in wild Canaries (*Serintis canaria*). J. Biol. Rhythms 22: 554–557.
- Ward, P. 1972. Appeal to physiologists reporting photoperiod experiments. Ibis 114: 275.
- Wikelski, M., M. Hau, & J. C. Wingfield. 2000. Seasonality of reproduction in a Neotropical rain forest bird. Ecology 81: 2458–2472.
- Wikelski, M., R. W. Kays, N. J. Kasdin, K. Thorup, J. A. Smith, & G. W. Swenson. 2007. Going wild: what a global small-animal tracking system could do for experimental biologists. J. Exp. Biol. 210: 181–186.
- Wikelski, M., L. B. Martin, M. T. Robinson, N. D. Robinson, A. Scheuerlein, M. Hau, & E. Gwinner. 2008. Avian circannual clocks: adaptive significance and possible proximate control by energy turnover. Philos. Trans. R. Soc. B 363: 411–423.
- Willis, E. O. 1972. The behaviour of Spotted Antbirds. Ornithol. Monogr. 10: 1–157.
- Wilson, F. E., & R. S. Donham. 1988. Daylength and control of seasonal reproduction in male birds. Pp. 101–119 in Stetson, M. H. (ed.). Processing of environmental information in vertebrates. Springer-Verlag, New York, New York.
- Wingfield, J. C. 1983. Environmental and endocrine control of reproduction: an ecological approach. Pp. 265–288 in Mikami, S., K. Homma, & M. Wada (eds.). Avian endocrinology: Environmental and ecological perspectives. Springer-Verlag, Berlin, Germany.
- Wingfield, J. C. 1994. Hormone-behavior interactions and mating systems in male and female birds. Pp. 303–330 in Short, R. V., & E. Balaban (eds.). The difference between the sexes. Cambridge Univ. Press, Cambridge, UK.
- Wingfield, J. C., & D. S. Farner. 1976. Avian endocrinology - field investigations and methods. Condor 78: 571–573.
- Wingfield, J. C., & D. S. Farner. 1993. Endocrinology of reproduction in wild species. Pp. 163–327 in Farner, D. S., J. R. King, & K. C. Parkes (eds.). Avian biology. Volume 9. Academic Press, London, UK.
- Wingfield, J. C., & G. J. Kenagy. 1991. Natural regulation of reproductive cycles. Pp. 181–241 in Pang, P. K. T., & M. P. Schreibman (eds.). Vertebrate endocrinology: fundamentals and biomedical implications. Academic Press, New York, New York.
- Wingfield, J. C., & B. Silverin. 2002. Ecophysiological studies of hormone-behavior relations in birds. Pp. 587–647 in Pfaff, D. W. (ed.). Hormones, brain and behavior. Volume 2. Academic Press, Amsterdam, The Netherlands.
- Wingfield, J. C., R. E. Hegner, & D. M. Lewis. 1991. Circulating levels of luteinizing hormone and steroid hormones in relation to social-status in the cooperatively breeding White-browed Sparrow Weaver, *Plocepasser mahali*. J. Zool. 225: 43–58.
- Wingfield, J. C., T. P. Hahn, R. Levin, & P. Honey. 1992. Environmental predictability and control of gonadal cycles in birds. J. Exp. Zool. 261: 214–231.
- Wingfield, J. C., T. P. Hahn, & D. Doak. 1993. Integration of environmental factors regulating transitions of physiological state, morphology and behaviour. Pp. 111–122 in Sharp, P. J. (ed.). Avian endocrinology. J. Endocrinology, Bristol, UK.
- Zann, R. A. 1996. The Zebra Finch. Oxford Univ. Press, New York.

