

SEASONALITY OF REPRODUCTION IN A NEOTROPICAL RAIN FOREST BIRD

MARTIN WIKELSKI,^{1,2,3} MICHAELA HAU,^{1,2,3} AND JOHN C. WINGFIELD¹

¹Department of Zoology, Box 351-800, University of Washington, Seattle, Washington 98195 USA

²Smithsonian Tropical Research Institute, Apto. 2072, Balboa, Republic of Panama

Abstract. Tropical wet forests are commonly perceived as stable and constant environments. However, many rain forest organisms reproduce seasonally. To understand the proximate regulation of life history events in tropical organisms, we asked three questions: (1) How predictable are seasonal changes in the tropical rain forest? (2) Can tropical organisms anticipate environmental seasonality, despite the presumed lack of long-term environmental cues in near-equatorial areas? (3) What environmental cues can tropical organisms use? We studied Spotted Antbirds, monogamous understory insectivores, which started breeding in Panama (9° N) in May (wet season) and continued until September/October. Breeding patterns were consistent between years, indicating that tropical seasons were as predictable for Spotted Antbirds (predictability 70%) as they are for many north temperate birds. Individual Spotted Antbirds shut down reproductive capacity (i.e., decreased gonad size) from October until February. In March, during the height of the dry season and about six weeks ahead of the wet season, gonads started to grow again. The growth rate of gonads was influenced by the amount of rainfall, which has been shown to correlate with food abundance. Gonad growth was paralleled by changes in luteinizing hormone, but not in testosterone, which remained at very low plasma levels year-round. The latter contrasts with the pattern for most migratory temperate-zone birds. Seasonal changes in reproductive activity correlated strongly with changes in the tropical photoperiod, but weakly with light intensity and rainfall, and not with temperature. Thus, Spotted Antbirds likely anticipated rain forest seasonality using long-term cues (tropical photoperiod) and fine-tuned their reproductive activities using short-term cues (food/rainfall). The use of long-term environmental information could apply to most vertebrate species that live in the tropics.

Key words: environmental cues; food supply; gonad growth; hormonal changes; *Hylophylax n. naevioides*; photoperiod; predictability of tropical seasons; rainfall; rain forest; seasonal reproduction; Spotted Antbird; tropics.

INTRODUCTION

Tropical rain forests, once thought to provide relatively constant environmental conditions year-round, have mostly been found to be seasonal environments. For example, there exist pronounced dry and wet seasons (Leigh et al. 1982, Wright and Cornejo 1990, Peres 1994), flood pulses (e.g., in Amazonia; Bodmer 1990), or seasonal changes in biotic interactions (e.g., seasonal migrations; Sinclair 1978, Morton 1980, Bolster and Robinson 1990, McNaughton 1990, Levey and Stiles 1992, Poulin and Lefebvre 1996). How do tropical organisms arrange their life history events in relation to these seasonal changes in environmental conditions? We studied the temporal organization of reproduction in a tropical bird because reproduction is very energy demanding, and therefore needs precise timing to coincide with good environmental conditions (Lack 1968,

Perrins 1970, Price et al. 1988, Van Noordwijk et al. 1995). To understand the life history decisions of tropical birds, we ask (1) how predictable the changes in the tropical environment are; (2) whether birds can *anticipate* changes in the environment, or if they only *react* to environmental changes; and (3) what environmental cues tropical birds can use to anticipate, or to react to, good conditions.

The temporal organization of life history events depends on how predictable seasonal changes in an environment are: in environments where good conditions can occur at any time, many organisms are quite flexible in their life histories. For example, Zebra Finches (*Taeniopygia guttata*) have been considered capable of breeding opportunistically at any time of the year in the Australian deserts, where rains can fall during any month of the year (Immelmann 1971, Sossinka 1980, Wyndham 1986). However, Hahn (1998) showed that another “opportunist,” the Red Crossbill (*Loxia curvirostra*), is not entirely flexible, but rather exhibits a high level of flexibility superimposed upon an underlying pattern of seasonal reproduction (see also Bertold and Gwinner 1978, Hahn 1995, Hahn et al. 1995).

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³ Present address: Department of Ecology and Evolutionary Biology, Guyot Hall, Princeton University, Princeton, New Jersey 08544 USA. E-mail: wikelski@princeton.edu

The same may apply to Zebra Finches (Zann et al. 1995, Zann 1996) and to some tropical frogs (Emerson and Hess 1996). In contrast, if environments are highly predictable, it pays off to time reproduction very precisely. For example, birds breeding at high latitudes, such as Lapland Longspurs (*Calcarius lapponicus*), arrive at their arctic breeding grounds in tight synchrony. Territory establishment and courtship last for only two days in May each year for the entire population, and egg-laying starts immediately thereafter (Hunt et al. 1995). Although it is intuitively obvious that changes in the arctic environment are more predictable than in the Australian desert, a quantification of the predictability can only be achieved by determining the reaction of organisms to environmental changes. Colwell (1974) quantified environmental predictability by analyzing the regularity with which reproductive events occur in organisms. Wingfield et al. (1992a) applied this model to avian data and found that environmental predictabilities range from 50% for apparently opportunistically breeding birds (Darwin's ground finches, *Geospiza* spp.) up to 82% for the highly seasonal White-crowned Sparrow (*Zonotrichia leucophrys gambelii*) breeding in arctic Alaska.

The degree of environmental predictability has important consequences for the reproductive physiology of organisms. Opportunistic breeders must keep their reproductive organs in a near-functional state in order not to miss the narrow time window during which reproduction is possible (Farner and Serventy 1960, Serventy 1971, Sossinka 1980, Emerson and Hess 1996, Hahn 1998). This is usually a costly strategy, because being prepared is energetically demanding (Murton and Westwood 1977). In contrast, seasonal breeding allows the total regression of reproductive organs and allocation of vital resources to other organismal functions, e.g., the buildup of flight muscles in migrating birds (Bairlein and Gwinner 1994, Gwinner 1996). It has been largely unclear which of these two breeding strategies birds in the tropical rain forests are more likely to use. Several reports suggested that at least some bird species are found breeding more or less year-round in tropical forests (Baker 1938, Skutch 1969). However, there are also good data for seasonal breeding patterns among tropical bird species (Moreau 1950, Skutch 1950, Snow and Snow 1964, Ward and Poh 1968, Ward 1969, Fogden 1972, Snow 1976, Murton and Westwood 1977, Stiles 1980, Bell 1982, Gradwohl and Greenberg 1982, Dittami 1986, 1987, Grant 1986). One should keep in mind that, for a given species, even if breeding birds are found year-round, this does not imply that all individuals retain their reproductive capacity year-round. It is conceivable that individual pairs are out of synchrony with other pairs, which gives the (false) impression of year-round reproduction on the individual level (Miller 1965, Wingfield et al. 1997a). It is therefore important to observe individual, rather than spe-

cies-specific, breeding seasons in tropical environments (see also Wingfield et al. 1991, 1992b).

Although seasonal reproduction occurs in many tropical organisms, it remains largely unclear *how* seasonal timing is achieved (Gwinner and Dittami 1985). Most temperate zone organisms are able to use the regular changes in photoperiod as a long-term cue (Murton and Westwood 1977, Farner and Follett 1979, Follett et al. 1985, Gwinner 1986, Gwinner and Dittami 1990). However, until recently, the tropical photoperiodic changes were regarded as too small to be used as a seasonal cue (Voous 1950, Miller 1965), although there was scattered evidence that some insects (Tanaka et al. 1987), fish (Burns 1985), and mammals (Wayne and Rissmann 1991; see also Heidemann and Bronson 1993) may be able to use tropical photoperiod as cue in their natural habitat (but see Heidemann et al. 1992, Heidemann and Bronson 1994). It was therefore assumed that tropical organisms use mostly short-term cues like rainfall to learn about, and react to, changes in environmental conditions (Immelmann 1971). We approached the question of what cues Spotted Antbirds use from two angles. First, we measured environmental parameters in the understory of the rain forest and correlated the changes in these parameters with changes in reproductive function of the birds. Second, we determined hormone levels of individual birds in the field.

Hormones transduce environmental information into physiological signals; thus, one can infer the perception of an environmental stimulus from correlated changes in relevant hormone levels (Balthazart 1983, Ball 1993, Wingfield and Farner 1993). In the temperate zone bird "model," luteinizing hormone (LH) is secreted by the pituitary as a response to the photoperiodic increases of day length in spring (Follett et al. 1985). LH, in concert with follicle-stimulating hormone (FSH), orchestrates gonad growth and the release of sex steroids such as testosterone (Scanes 1986). Testosterone levels are low during winter, increase as soon as temperate zone birds arrive at the breeding grounds, and decrease again after breeding (Wingfield and Farner 1993). In contrast, we largely lack information on how year-round territoriality in tropical rain forest birds is physiologically regulated (but see Wikelski et al. 1999a, b, Hau et al. 1999). Paradoxically, most tropical birds investigated thus far show only very low testosterone levels, but are nevertheless highly aggressive (Dittami and Gwinner 1990, Levin and Wingfield 1992, Wingfield et al. 1992b, Wingfield and Lewis 1993).

It was our aim to investigate the control of breeding in a tropical, near-equatorial, understory rain forest bird, as an example of how a purely tropical organism perceives seasonal environmental information and transforms it into physiological signals that trigger specific life history events.

1) We studied how predictable environmental conditions are for Spotted Antbirds by applying Colwell's (1974) predictability model, which evaluates how a

species perceives environmental changes (see also Wingfield et al. 1992a, 1993).

2) We determined gonad sizes of individual Spotted Antbirds in the field to see if individual birds are always prepared for breeding, or, alternatively, if they show seasonal changes in gonad sizes. This also allowed us to evaluate whether birds anticipate favorable environmental conditions by growing their gonads ahead of these periods.

3) We investigated how the levels of reproductive hormones change over the seasons, as an indication of how the brain transfers environmental information into physiological signals. At the same time, we measured relevant environmental factors and correlated their occurrence with reproductive changes. We used this to generate hypotheses regarding the signals that could be used as seasonal cues by tropical bird species.

Background natural history

Spotted Antbirds (*Hylophylax n. naevioides*, family *Thamnophilidae*) are small (17 g) suboscine passerines, with a presumably purely neotropical phylogenetic history (Sibley and Monroe 1990). Spotted Antbirds facultatively follow army ant swarms as these pass through their territories in the forest understory. In the Republic of Panama, pairs of Spotted Antbirds defend territories year-round but breed only during the rainy season (Willis 1972, Sieving 1992, Hau et al. 1998, 1999, Robinson et al. 2000), which lasts, on average, from 5 May to 18 December (official data from the Panama Canal Commission; S. Patton, Smithsonian Tropical Research Institute, *personal communication*).

METHODS

Study site and birds

We studied Spotted Antbirds along Pipeline Road (between km 2 and 6) in Soberania National Park, a lowland 22 000 ha moist forest in central Panama (9° N, 79° W) bordering the Panama Canal. The forest consists of a mixture of secondary forest (20–80 yr old, mostly around the gravel road) and primary forest.

We initially encountered Spotted Antbirds by slowly walking through the forest while playing back the tape-recorded song of a male Spotted Antbird. As soon as a bird responded, we put up one to five 12-m mist nets and repeated the playback until the birds were caught. Playbacks attracted both male and female Spotted Antbirds, but females reacted less to male playback (M. Hau and K. Soma, *unpublished manuscript*). We always tried to catch both the male and female on a territory. We captured a total of 88 individuals, 54 males and 34 females. Individual males were recaptured 2.2 ± 2.0 times (mean ± 1 SD), and individual females were recaptured 1.76 ± 1.3 times. Our sample included 13 known territorial pairs and five territorial males whose mate we never caught. We did not know the age of

birds. However, breeding birds are almost always >1 yr old (Willis 1972). To map territories of Spotted Antbirds, we approximated territorial boundaries at those sites where neighboring birds were countersinging. To recapture birds for repeated assessments of their reproductive activities (i.e., gonad sizes), we put up five 12-m mist nets in the middle of a bird's territory in the late afternoon. Nets were kept closed overnight and opened before dawn, i.e., around 0500–0530. Then, we used playback to lure birds into the nets. Playback times ranged from ~ 3 min to 3 h (37.4 ± 4.24 min, mean ± 1 SE). Only playback times of >2 h increased plasma T levels in Spotted Antbirds (Wikelski et al. 1999b); thus, data of five birds caught after >2 h were discarded from seasonal hormonal analysis. Birds were in the mist nets for a mean of ~ 8 min (1–30 min) before blood sampling. In addition to this capture technique, we sometimes used passive mist-netting (playback time 0 min).

At first capture, we banded birds with a numbered aluminum band and up to three color bands. At each capture, we determined whether birds had an active brood patch (both parents incubate the eggs). Birds were also weighed to the nearest 0.2 g with spring balances. In addition to captures, we systematically searched the forest for nests of Spotted Antbirds. The cup-shaped nests were usually located in branches of small saplings (see also Willis 1972, Sieving 1992).

Environmental parameters

A light sensor (photoresistor, Conrad Electronic, Munich, Germany, calibrated to measure Einsteins per square meter [$1 \text{ E} = 1$ mole of photons]) with a lower illuminance sensitivity threshold of ~ 0.2 lux was mounted in the forest understory onto a horizontal liana stem (1 m from a tree of 25 cm dbh) at ~ 1.5 m height. Data were stored on-site by a HOBO logger (Onset, Pocasset, Massachusetts, USA). Photoperiod was calculated as the daily interval between the first and the last positive reading of the light sensor (see also Hau et al. 1998). Standard operative temperature (Bakken 1992) was measured at the same site using a thermoprobe contained in a black 15 cm diameter copper bulb. To measure precipitation, we put up a metered rain gauge at Juan Grande bridge along Pipeline Road in spring 1996. We then regressed weekly rainfall data against data collected on Barro Colorado Island (BCI), Panama, by the Smithsonian Tropical Research Institute as part of a long-term environmental monitoring program (S. Patton, *personal communication*). Rainfall was tightly correlated between the two sites, with ~ 13 mm more rainfall per week on BCI (by linear regression, rain on pipeline road = 13.9 ± 9.5 plus 1.0 ± 0.1 mm/wk (mean ± 1 SE) rain on BCI; $F_{1,24} = 36$, $P < 0.001$, $r^2 = 0.61$). Higher rainfall on BCI was expected from the trans-isthmian gradient of increasing rainfall toward the northern (Atlantic) side of Panama (Windsor 1990). For our calculations, we used the cor-

TABLE 1. Frequency matrix for breeding seasons of the Spotted Antbird (*Hylophylax n. naevioides*) in central Panama, by month.

Spotted Antbird breeding status	J	F	M	A	M	J	J	A	S	O	N	D
Clutches present	0	0	1	2	4	4	4	4	2	1	0	0
No clutches present	4	4	3	2	0	0	0	0	2	3	4	4

Notes: Data from this table were used to calculate predictability, constancy, and contingency of the tropical understory environment as perceived by Spotted Antbirds. Pr (predictability) = 0.7, C (constancy) = 0.007, and M (contingency) = 0.69; $n = 4$ years.

rected precipitation data from BCI, because time series data are complete there. To determine the length of the dry and wet seasons, we relied on the official definitions of the Panama Canal Commission, which take several climate factors, but most prominently rainfall, into account. Onset and offset of the wet season can vary by up to 11 weeks between years (15 March to 10 June for wet season onset; Windsor 1990). The variation of rainfall within the dry season is extensive. Long-term (74-yr) climate records for monthly rainfall (mean \pm 1 SD) are as follows: January, 73 ± 90 mm; February, 40 ± 20 mm; March, 23 ± 23 mm; April, 107 ± 113 mm; May, 270 ± 125 mm (Windsor 1990).

We used Colwell's (1974) information theory model, and its application to avian breeding seasons by Wingfield et al. (1992a), to determine how predictable the tropical environment was for Spotted Antbirds in Panama. For this, we obtained data for the occurrence of nesting during all months of the years 1961 (Willis 1972), 1994–1995 (B. Poulin and G. Lefebvre, *personal communication*), 1996, and 1997 (T. R. and W. D. Robinson, *personal communication*; M. Wikelski and M. Hau, *unpublished data*; see Table 1). If data on nesting were not available, we used the occurrence of active brood patches in captured birds as a surrogate of actual nesting activity. This is justified because we could always determine, without doubt, whether a brood patch was active or not (i.e., when we detected heavy wrinkling of the ventral skin).

Predictability was calculated from the breeding activity of a Spotted Antbird population over four annual cycles. Birds were assigned as either breeding or not for each month, and the occurrence of breeding in each year was added for each row (Table 1). Thus, if birds reproduced each year in June, the value for breeding was four and the value for nonbreeding was zero. Using Shannon information statistics, we calculated the uncertainty with respect to time (U_{time} , columns) and with respect to breeding state (U_{state} , rows). Constancy is maximal if all rows are the same, and is defined as $1 - U_{\text{state}}/U_{\text{time}}$. Contingency (regular seasonality) is minimal if all columns are homogeneous, and maximal if there is exactly one nonzero value entry in each column (thus, if there is always only one state per month).

Predictability is then defined as constancy + contingency, or as $1 - (U_{\text{state} \times \text{time}} - U_{\text{time}})/U_{\text{state}}$.

Physiological measurements

Length and width of the left testis for males and diameter of the largest follicle for females were measured to the nearest 0.1 mm below 1 mm length, and to the nearest 0.2 mm above 1 mm length, by unilateral laparotomy under Isoflurane anesthesia (for details on standard laparotomy procedures see Wingfield and Farner 1976, Hau et al. 1998). Testis volume was calculated using a formula for ellipsoid cylinders ($4/3\pi a^2 b$, where a is half of the testis length and b is half of the width). We assumed that gonads were functional, i.e., produced sperm, at half-maximum size (Gwinner 1986). Blood samples were obtained by puncturing a superficial wing vein with a 26-gauge needle. Blood was collected in heparinized microcapillaries and kept cool until centrifugation. Birds were kept for ~5–10 min after the laparotomy to ameliorate effects of anesthesia (Oring et al. 1988). Plasma was separated from red blood cells by centrifugation at 588×10^2 m/s (6000 r/min) for 4 min. Plasma was subsequently treated with 10 μ L β -propiolactone solution according to U.S. import regulations for avian blood. Samples were then stored at -20°C and transported to Seattle on dry ice for hormone analysis, under permission of Panamanian and U.S. authorities.

Hormone assays

Luteinizing hormone (LH) was measured using the post-precipitation, double-antibody radioimmunoassay (RIA) for avian LH developed by Follett et al. (1972) and Sharp et al. (1987). Plasma levels of T, androstenedione (A_4), estradiol (E_2), and dihydrotestosterone (DHT) were measured with an indirect RIA after separation of hormones on a chromatography column (Wingfield and Farner 1975, 1976). To determine plasma levels of A_4 , the protocol differed from that described in Wingfield and Farner (1975) in the following way. Diatomaceous earth (6 g) was mixed with 1.5 mL propylene glycol and 1.5 mL ethylene glycol to manufacture chromatography columns. Hormones were eluted from columns using a mixture of ethyl acetate in iso-octane. We discarded 4 mL 0% fraction. The fractions collected were A_4 (4 mL 2% fraction), DHT (4.5 mL 10% fraction), T (4.5 mL 20% fraction), and E_2 (4.5 mL 40% fraction). Recoveries were collected for all steroids and were $60 \pm 5\%$ for A_4 , $69 \pm 8\%$ for DHT, $73 \pm 8\%$ for T, and $64 \pm 6\%$ for E_2 (mean \pm 1 SD). Water blanks were taken through the entire assay procedure and were usually below detection limit. The accuracy of the T hormone standards was 6.9%. Intra-assay variation was 1.7% ($n = 4$ assays). Inter-assay variation was 4.6% ($n = 6$ assays). Assay sensitivity was at 0.2 ± 0.06 ng/mL except for A_4 (0.25 ng/mL; see Wingfield and Farner 1975 for methods). Whenever samples were below detection limit, they were set at

0.2 ng/mL (0.25 ng/mL for A_4) as the highest possible value. This provided a conservative estimate for statistical comparisons.

Statistical analysis and data presentation

Data were processed with SPSS for Windows (SPSS 1991). Two-tailed test statistics were used. Data are given as means \pm 1 SD if not indicated otherwise, except for regression equations (mean \pm 1 SE). To generate hypotheses about the environmental factors that control gonad growth and regression, we used temporal cross-correlation analyses (Marmarelis and Marmarelis 1978, Sinclair et al. 1993). To analyze individual changes in gonad volumes across seasons, we used repeated-measure statistical tests whenever we had more than seven individuals for which we had nearly complete data sets for two years. We substituted the population mean for missing data points (not more than two for each individual). For all other tests, we included the data set for the entire population. We used repeated-measures ANOVAs and least significant post hoc tests whenever data were normally distributed. When data sets were not normal and whenever we had lower detection limits in our data sets (as for many "baseline" hormone values), we applied nonparametric (Friedman two-way) ANOVAs and least significant post hoc tests. Significance for all tests was accepted at the $\alpha = 0.05$ level. To demonstrate the tight temporal synchronization within the population, we plotted the data for the entire population (Figs. 1 and 2).

RESULTS

Environmental predictability

Nesting only occurred between March and October and there was little interannual variability in the onset and end of the nesting period (Table 1). The environmental predictability was 0.7 (G statistics = 575, $P < 0.001$) and consisted of the additive components of constancy = 0.007 ($G = 0.51$, $P > 0.05$) and contingency = 0.69 ($G = 574$, $P < 0.001$; degrees of freedom for each value were $n - 1 = 11$). The low G values for constancy showed that only contingency significantly contributed to the environmental predictability for Spotted Antbirds (Colwell 1974). The environmental information factor I_e was 92 ($I_e = \text{contingency}/\text{constancy}$). Such a high value predicted that Spotted Antbirds should use both long-term "initial" predictive information and short-term "supplementary" information (Wingfield et al. 1992a).

Seasonal changes in gonad, hormonal, and blood profiles

Males.—The size of the birds' testes changed seasonally from a low of 0.8×0.8 mm to a maximum of 3.0×5.0 mm (width \times length). Male Spotted Antbirds had very small, regressed gonads from about September until March (Fig. 1a). Gonads started to grow in

March, which is still the middle of the dry season (repeated-measures ANOVA $F_{1,7} = 7594$, $P < 0.001$; least significant differences between gonad sizes are indicated in Fig. 1). In a comparison between years, gonads started to grow at the same time (March). However, gonad growth rates differed between the two years (Fig. 1a). This is best illustrated by the fact that mean gonad sizes in April 1996 were already 50% larger than at approximately the same time in April 1997. The fast gonad growth in 1996 coincided with a very wet dry season and an early wet season, whereas the slow gonad growth in 1997 corresponded with a very pronounced and prolonged dry season in that year (see dry and wet season bars in Fig. 1a).

Plasma levels of LH were low (1 ng/mL) at the end of the wet seasons and into the early dry seasons (Fig. 1b). However, LH had already increased during the dry seasons in both years. LH levels were higher in March 1996 than in March 1997, reflecting the difference in dry season rainfall between years (repeated-measures ANOVA $F_{1,7} = 631$, $P < 0.001$; least significant differences are indicated in Fig. 1b).

Overall T levels were very low: the highest value ever measured was 1.57 ng/mL (Fig. 1c). There were seasonal differences in the plasma levels of T (Friedman two-way ANOVA, $\chi^2_{1,8} = 57$, $P < 0.001$; least significant differences are indicated in Fig. 1c). However, the seasonal pattern of increased T during the wet season in 1996 was not repeated during the following wet season in 1997. The low plasma levels of the androgen T were not compensated for by the other known plasma androgens DHT or A_4 . Both androgens were found in the plasma of Spotted Antbirds, but levels were always lower than T and were significantly correlated with T values. For DHT, by linear regression, $\text{DHT} = 0.13 (\pm 0.08) + 0.62 (\pm 0.10) \times T$ ($F_{1,13} = 34$, $P < 0.001$, $r^2 = 0.72$). For A_4 , a logarithmic regression fitted better than a linear one: $A_4 = 0.84 (\pm 0.11) + 0.25 (\pm 0.11) \ln(T)$ ($F_{1,13} = 5.1$, $P = 0.044$, $r^2 = 0.28$). We therefore concluded that the physiological role of T was not taken over by other known androgens in these tropical birds. The levels of E_2 were very low in all samples (usually at baseline levels of 0.2 ng/mL), and showed no seasonal variation.

Body mass changed significantly during the two years and was lowest in March, at the end of the dry season (repeated-measures ANOVA, $F_{1,7} = 29152$, $P < 0.001$; least significant differences are indicated in Fig. 1d). The spontaneous song activity of Spotted Antbirds appeared to show seasonal differences, with slightly higher song rates during the late wet and early dry season. However, these differences were not significant (Fig. 2; Kruskal-Wallis ANOVA, $c^2_{1,39} = 10$, $P = 0.34$).

Females.—As in males, female gonads (follicle diameters) were minimal during the dry seasons and increased at the beginning of the wet seasons in tight synchrony with the gonad increase in males (ANOVA

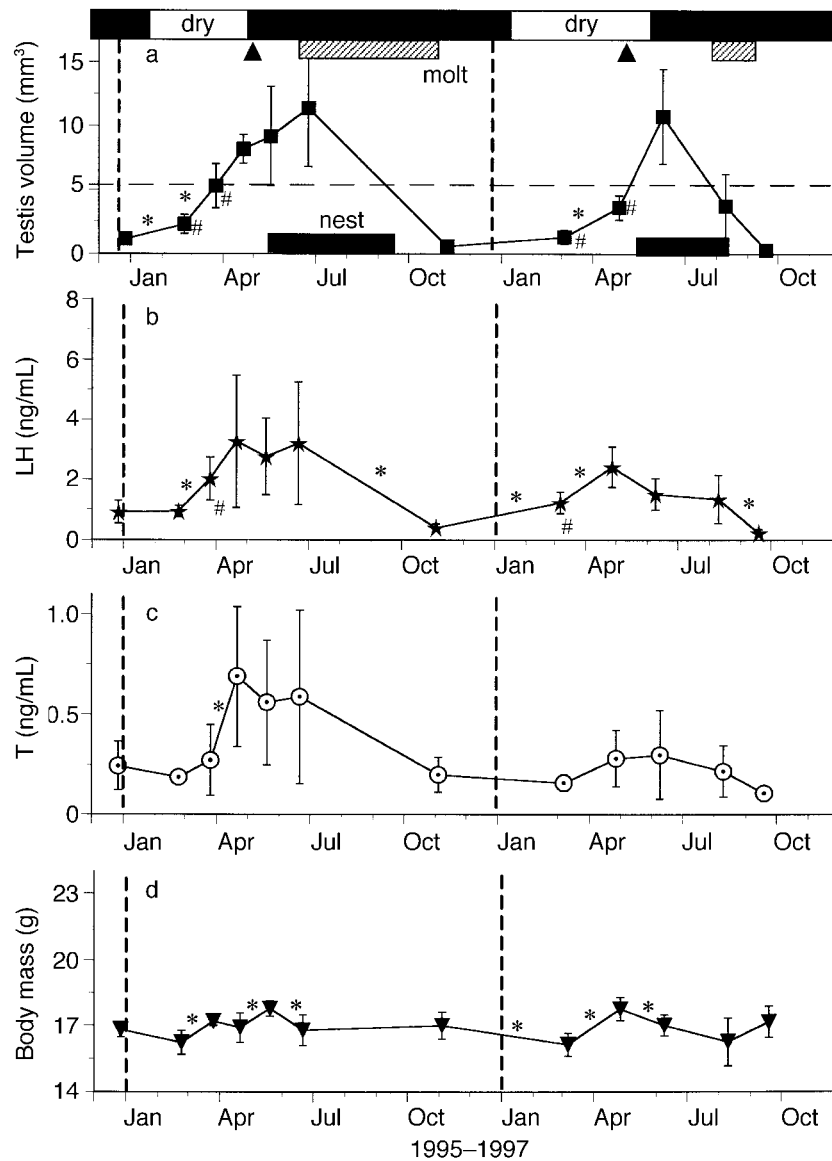


FIG. 1. Seasonal changes in reproductive parameters for a population of male Spotted Antbirds in central Panama over a period of two years. Data show means and 95% confidence intervals for (a) testis volumes, (b) plasma levels of luteinizing hormone (LH), (c) plasma levels of testosterone (T), and (d) body mass. Horizontal bars above (a) indicate wet (black) and dry (white) season as determined by the Panama Canal Commission and the population-wide duration of molt (hatched). Triangles show the 74-yr average onset of the wet season. In (a), the horizontal black bar at the base of the graph shows the duration of the nesting season; the horizontal broken line indicates the minimum functional gonad volume. Vertical broken lines in all graphs separate the years. Asterisks indicate significant differences ($P \leq 0.05$) between samples on either side of the asterisk, whereas # signs indicate that values differed between the two years. Significance was determined from repeated-measure ANOVAs and subsequent least significant difference tests for seven individual males. Sample sizes for the plotted values are as follows, from left to right: (a) 14, 13, 7, 8, 10, 7, 12, 11, 13, 8, 6, 5; (b) 14, 13, 7, 8, 6, 12, 9, 5, 4, 6, 4; (c) 9, 8, 6, 6, 10, 6, 11, 13, 8, 6, 4; and (d) 14, 13, 7, 6, 10, 11, 12, 11, 13, 8, 6, 5. Variation in sample size is due to difficulties in recapture.

$F_{11,57} = 5.4, P < 0.001$; least significant differences between follicle sizes during the same season between different years are indicated in Fig. 3a). Plasma LH levels in females also paralleled the seasonal changes in gonad sizes and were comparable to seasonal LH changes in males (Kruskal-Wallis ANOVA, $c_{11,43}^2 =$

20, $P = 0.04$; Fig. 3b). Plasma levels of T, E_2 , and A_4 in females were very low (usually baseline) throughout the year and are not reported here. As for males, body mass of females changed significantly during the two years and was lowest in March, at the end of the dry season (Fig. 3c; ANOVA, $F_{11,60} = 3.4, P = 0.002$).

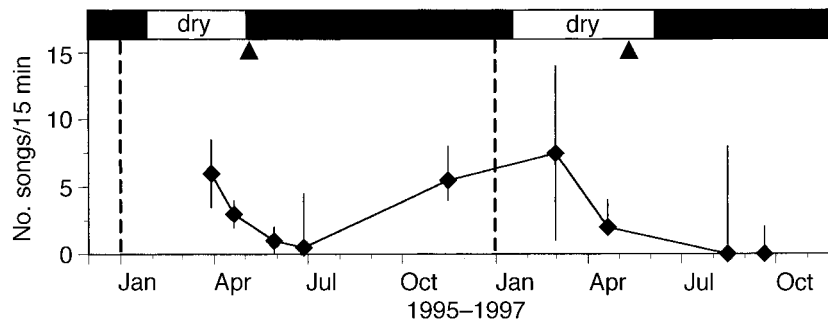


FIG. 2. The 15-min average number of spontaneous songs per territory (\pm interquartile ranges), recorded between 0600 and 0630 during March 1996 until September 1997). Sample sizes were, from left to right: 4, 4, 2, 4, 5, 7, 5, 5, and 4. Symbols are as in Fig. 1.

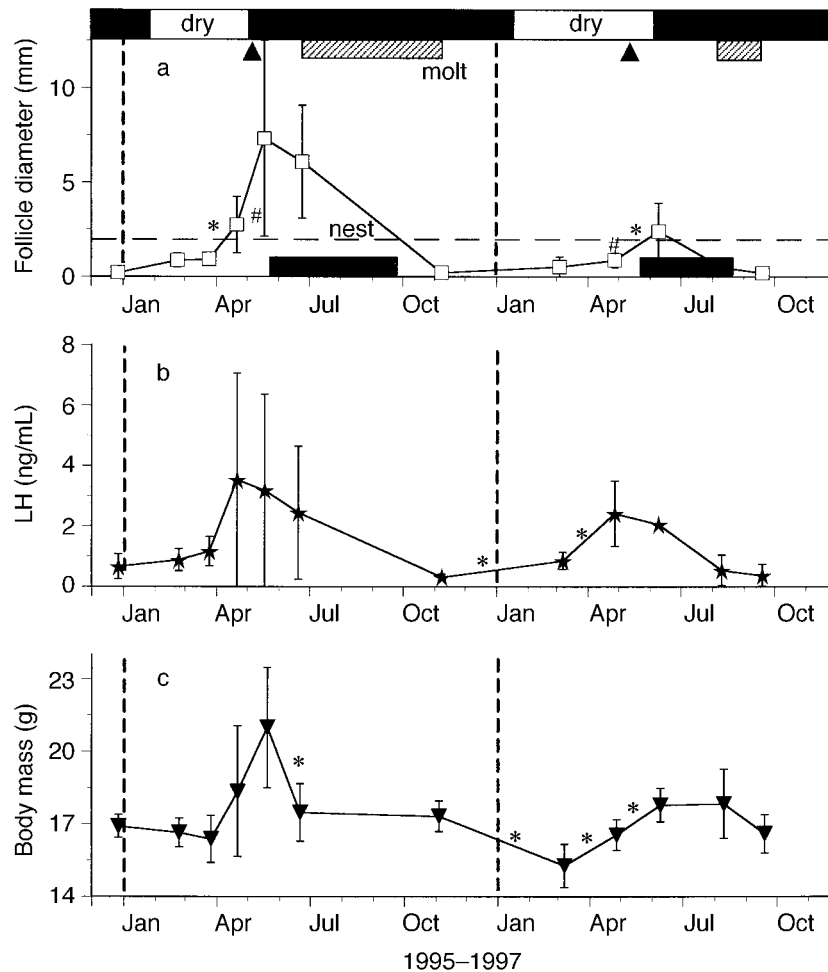


FIG. 3. Seasonal changes in reproductive parameters for female Spotted Antbirds (means \pm 95% CI). (a) Follicle diameters, (b) plasma levels of luteinizing hormone (LH), and (c) body mass. Symbols are as in Fig. 1. In (a), the horizontal broken line shows the follicle diameter above which egg-laying is possible within a few days. Sample sizes for the plotted values are, from left to right: (a) 2, 4, 6, 2, 3, 9, 6, 3, 11, 6, 4, and 2; (b) 4, 4, 6, 2, 2, 7, 4, 3, 7, 1, 2, and 2; (c) 3, 4, 6, 2, 3, 10, 6, 4, 11, 6, 4, and 2. Variation in sample size is due to difficulties in recapture.

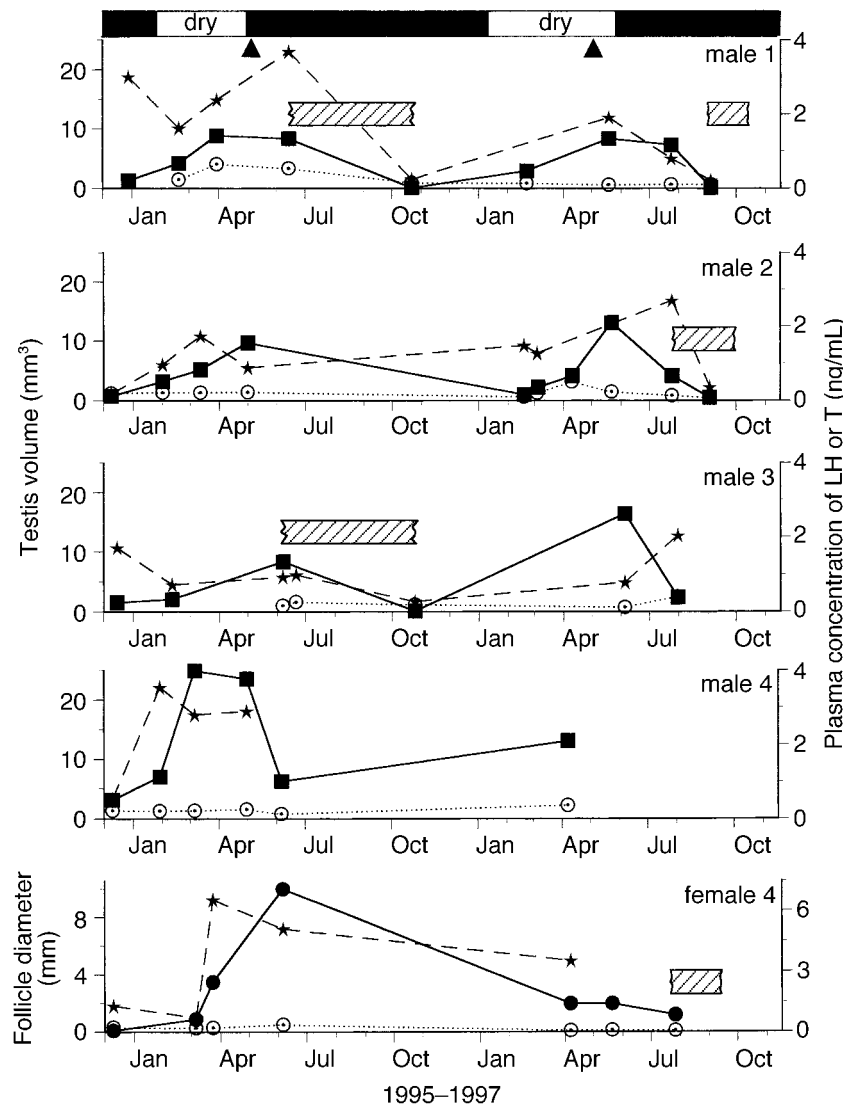


FIG. 4. Seasonal changes in individual testis sizes (solid squares), plasma levels of luteinizing hormone (LH; stars), plasma levels of testosterone (T; open circles), and follicle diameters (solid circles in bottom panel). Hatched bars show the approximate duration of molt; black and white bars at the top of the figure show climatic patterns, as in Fig. 1. Note that reproductive patterns are strongly seasonal and highly synchronized among individuals.

Individual gonad changes.—The changes in gonad sizes observed at the population level were also reflected in individual Spotted Antbirds (Fig. 4). T levels of male 1 showed a small increase during the first breeding season, but stayed low throughout the entire 1997 season (see also Wikelski et al. 1999b). In males 1 and 3, LH levels were high in the late wet season (December 1995), decreased further toward the dry season, and increased again (in male 1) ahead of the wet season. In males 2 and 4, LH increased in February and March 1996, respectively, in synchrony with their gonads, but there were no changes in T levels throughout the season. However, in the second year (1997), T levels increased in male 2 in April. All values were low again in fall 1997, toward the end of the rainy

season (about September). Pair 4 showed a synchronized pattern of gonad development. Again, note that T levels in the male remained low in the first year, despite peak levels in LH and gonad size.

Environmental factors used for seasonal timing

We used temporal cross-correlation statistics to generate hypotheses as to what environmental factor(s) Spotted Antbirds could use to anticipate the seasonal changes in environmental conditions in their understory rain forest habitat. For this analysis, we only used male testes volumes, because quantitative changes in testes were more pronounced and easier to quantify than were follicle diameters for females. We computed mean monthly values for all parameters and, if nec-

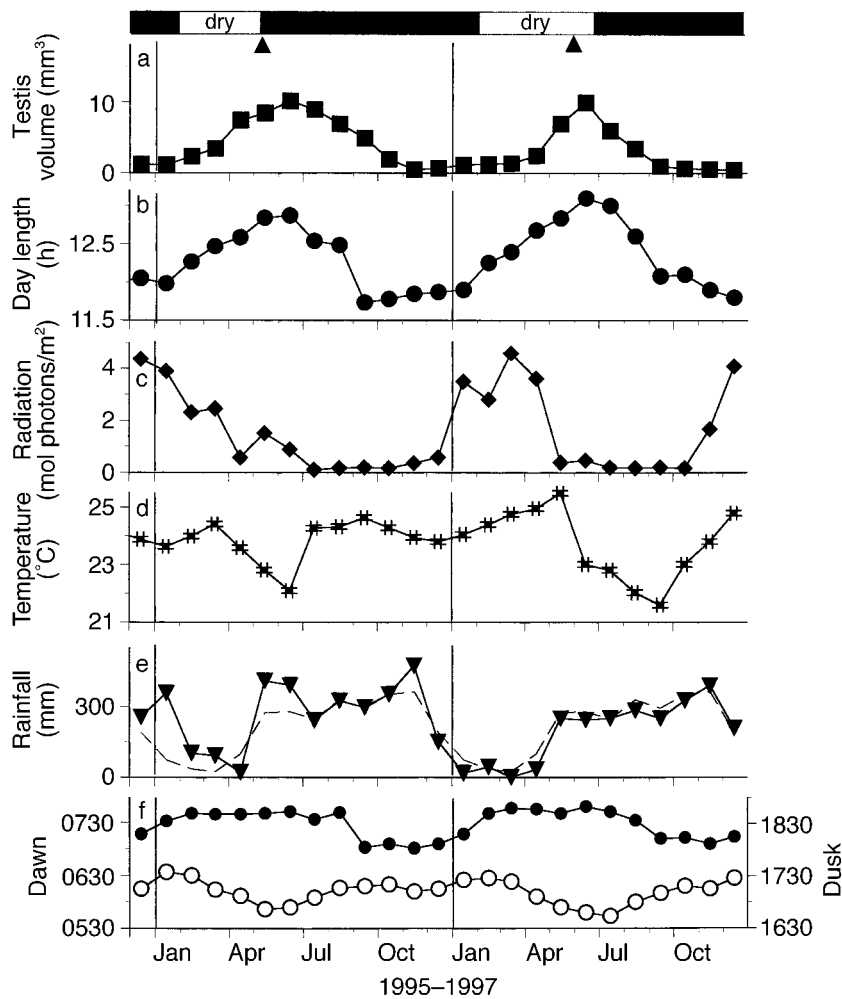


FIG. 5. Monthly running means of (a) the testes volumes, and mean monthly environmental parameters: (b) day length; (c) radiation intensity (measured in Einsteins, $1 \text{ E} = 1 \text{ mole of photons}$); (d) standard operative temperature; (e) rainfall (triangle and solid line) and 74-yr average rainfall on BCI, Panama (broken line); and (f) time of dawn (open symbols) and dusk (closed symbols). Symbols are as in Fig. 1.

essary, interpolated between means to achieve a continuous time series data set (Fig. 5). We set the periodicity to 12 mo and allowed a maximal lag of 6 mo. Because we computed several cross-correlations, we corrected the P values according to the Bonferroni method. The interval between the time of dawn and dusk (Fig. 5f) determines day length (Fig. 5b); thus, we did not compute cross-correlations between gonad sizes and times of dawn and dusk. There was a highly significant, positive cross-correlation between gonad size and day length, with a correlation coefficient of $r = 0.8$ and a time lag of about -1 mo. This indicates that the gonads started to grow ~ 1 mo after the shortest day of the year, i.e., in late January.

There was also a weakly significant relationship between gonad cycles and both rainfall ($r = 0.5$, time lag 3 mo) and light intensity ($r = 0.6$, time lag 4 mo). The time lag for both variables indicated that gonads were already growing 3 and 4 mo ahead of changes in pre-

cipitation and light intensity, respectively. There was no significant relationship between changes in temperature and changes in gonad sizes (all values below 95% confidence limits).

DISCUSSION

Our data show that the environmental changes in a tropical moist forest are as predictable for an insectivorous understory bird as they are for many temperate zone bird species. The gonads of individual Spotted Antbirds showed a seasonal decline and subsequent recrudescence in anticipation of favorable environmental conditions. This pattern was repeated in two years. The start of recrudescence was best predicted by changes in the tropical photoperiod, indicating the use of long-term information for seasonal reproduction. However, the rate of gonad growth differed between two years, depending on the amount of rain in the dry season, and thus presumably on the food abundance

during the recrudescence period (although food abundance was not measured in our study; but see Levings and Windsor 1982). This indicated the additional use of short-term information for the temporal fine-tuning of reproduction. The transduction of environmental information from the brain into physiological signals in these tropical birds appeared similar to that in temperate zone birds, in that LH increased with the increase in day length in spring and thus co-triggered gonad development. However, relative gonad sizes were much smaller in Spotted Antbirds than in temperate zone birds, and T levels could be low at all times of the year.

Predictability of a tropical rain forest environment

Little is known about how predictable tropical rain forests are for their inhabitants. Many organisms reproduce seasonally even in tropical forests, which are supposedly among the more "constant" environments (Leigh et al. 1982, Windsor 1990). Because these breeding events occur at more or less regular times of the year, this implies that environmental conditions are to some degree predictable in rain forests (Colwell 1974, Poulin et al. 1992). The predictability of an environment can be captured mathematically as the sum of the environment's constancy and its regular seasonality (termed contingency; Colwell 1974, Wingfield et al. 1992a). Thus, the predictability may either be high because the environment constantly supplies organisms with sufficient energy for breeding (e.g., Sooty Terns *Sterna fuscata* on Ascension Island; Chapin 1954, Ashmole 1963), or because the occurrence of good environmental conditions is very regular, as in the arctic spring, for example (Hunt et al. 1995). Predictability values are calculated from the phenological breeding pattern of a population (Colwell 1974, Wingfield et al. 1992a) and thus quantify the predictability as perceived by the organisms. It is astonishing that the neotropical Spotted Antbird showed a relatively strong reproductive seasonality, and that therefore the environment seemed highly predictable for this understory bird.

The predictability value of ~70% for Spotted Antbirds compares to 72% for central California White-crowned Sparrows (*Zonotrichia leucophrys nuttalli*) in central California, 77% for Song Sparrows (*Zonotrichia melodia morphna*) in western Washington, or 50% for Darwin's ground finches (*Geospiza* spp; Wingfield et al. 1992a). The very low values of environmental predictability for Darwin's finches may result from the fact that they live in arid tropical areas, which are often highly variable in terms of rain and subsequent food availability (Grant and Boag 1980). As a consequence, many organisms apparently use opportunistic breeding strategies in such erratic environments. However, the physiological mechanisms underlying such opportunism are largely unknown, but are presently under investigation; (M. Hau, M. Wikelski, and E. Gwinner, *personal observations*). It is quite likely that pure op-

portunism as suggested for Zebra Finches (Immelmann 1971) does not exist. Instead, breeding pattern may be better described as seasonal reproduction with high levels of flexibility. This was demonstrated for the Red Crossbill (Hahn 1998). Because of the general lack of detailed breeding data for tropical rain forest birds, it presently cannot be determined how general are the high predictability values that we found for Spotted Antbirds. It is important to emphasize, however, that organisms are more likely to use a seasonal breeding strategy in predictable environments. Therefore, we expected that Spotted Antbirds are not opportunistic breeders, but rather stop allocating energy into reproductive function during those times of the year when reproduction is unsuitable.

Seasonal changes in reproductive parameters

Individual Spotted Antbirds indeed had entirely regressed gonads from October until February, which confirmed that they are not opportunistic, but rather use a seasonal breeding strategy (Figs. 1a and 3a). Although overall gonad volumes were small, a 140-fold increase in gonad volume from 0.8×0.8 mm (0.27 mm³) to 3×6 mm (39 mm³) appears to be quite important. We used half-maximum gonad size to estimate the onset of spermatogenesis. There is good empirical evidence for this from a variety of temperate zone birds (Gwinner 1986, Wingfield and Farner 1993) and tropical birds (Foster 1987). Seasonal changes in gonad volume imply that the seasonal environmental changes in this tropical forest occurred regularly enough that it was advantageous for Spotted Antbirds to anticipate them physiologically, i.e., by starting to grow their gonads about 6–8 wk ahead of the wet season. Surprisingly, gonad growth among the individuals of our population was tightly synchronized, which indicates that all individuals probably reacted to the same environmental cues.

It is presently unknown what ultimate selection pressures restrict breeding seasons in Spotted Antbirds and why birds started to breed in synchrony at the onset of the wet season. One important reason may be that insect food abundance is much higher during the early rainy season than during most other parts of the year (Wolda 1989, Windsor 1990). There is also evidence that predation pressure may be very important in determining breeding seasons for tropical organisms, for example in the Clay-colored Robin *Turdus grayii* (Morton 1971; see also Young 1994). Our study did not attempt to quantify these selection pressures. However, the seasonal changes in body mass of Spotted Antbirds support the hypothesis that energy supply influences reproductive decisions. As expected from the relationship between rain and insect abundance, body masses were about ~8–15% lower during the late dry season as compared to all other times of the year. Another energy-demanding life history stage in birds, molt, also started during the early part of the wet season. It is important

to note that molt and breeding overlapped at the population level (Figs. 1a, b and 3a, b). However, we never found *individual* birds that had active brood patches and molted their primaries at the same time (but see Foster 1975). Thus, the population-wide overlap of nesting and molt in our study was generated by the fact that individual pairs of Spotted Antbirds initiated molt after raising a successful brood, whereas other pairs continued breeding, e.g., after the loss of a brood to predators (Morton 1971, Willis 1972, Sieving 1992, Roper 1996). Such variability of nesting success and re-nesting attempts could also contribute to annual differences in hormonal profiles, but our data set does not allow us to analyze this question in detail.

Environmental factors used for seasonal timing

Our study shows clearly that the environment was predictable for Spotted Antbirds and that individual birds anticipated good conditions by growing their gonads in anticipation of the breeding season. However, what cue could tropical organisms use to predict long-term changes in the rain forest? It has been suggested that day length provides the best long-term signal about environmental changes in the temperate zone, because it shows a lower signal-to-noise ratio than most other possible long-term cues, e.g., temperature (Gwinner 1986). However, it has been suggested that the photoperiod of tropical or equatorial latitudes would provide no useful seasonal cue because its changes are supposedly too small to be perceived by tropical organisms (Voous 1950, Miller 1965). Our correlational data (Fig. 5) contradict this statement by suggesting that day length can be used as long-term cue even in near-equatorial rain forests (Rollo and Domm 1943). This hypothesis receives strong support from our experimental evidence that Spotted Antbirds can indeed measure the slight photoperiodic changes characteristic of their natural tropical habitat (Hau et al. 1998).

It appears that the transduction of photoperiod into physiological signals could be similar in Spotted Antbirds to that in temperate zone birds (Wingfield 1980, Wingfield and Moore 1987), occurring by an increase of gonadotropins in spring. LH usually co-occurs with FSH and both hormones orchestrate gonad growth and maturation (Hadley 1992). It is yet unclear if LH levels are also influenced by non-photoperiodic cues such as good environmental conditions. Such a hypothesis is warranted by the fact that LH levels (at least in males) were higher during the unusually wet dry season of 1996 than during the entirely dry dry season of 1997. Higher LH levels may reflect the faster gonad growth rates in 1996 compared to 1997. However, we want to emphasize that only the onset of the LH increase was slightly different between years, not the overall magnitude of the seasonal LH response.

Year-round territoriality, seasonal reproduction, and facultative testosterone increases

In most temperate zone birds, territoriality, peak levels of T, and reproduction occur more or less at the

same time. For example, migratory White-crowned Sparrows show high T levels when establishing territories in spring, whereas T levels decrease after egg-laying to allow for brood care by the male (Wingfield and Farner 1993). In contrast, autumn territoriality in several temperate zone bird species was thought to be uncoupled from circulating T, e.g., in the Song Sparrow (*Melospiza melodia*, Wingfield and Monk 1991) and the European Robin (*Erithacus rubicula*, Schwabl 1992). However, recent results on Song Sparrows suggest that autumn territoriality is also controlled by T (Soma and Wingfield 1999). Thus, the hormonal mechanisms regulating aggression at low overall plasma T levels (Hau et al. 2000a) may not be unique to tropical birds. The year-round low T levels of Spotted Antbirds help to avoid the costs of constantly elevated T, such as immuno-suppression, injury, and interference with parental care (Hillgarth et al. 1997, Hillgarth and Wingfield 1997, Wingfield et al. 1999). Song activity, another measure of reproductive activity, which is also T sensitive (Hunt et al. 1995), did not show significant seasonal changes on the population level.

Comparison between tropical and temperate-zone bird models

We deliberately chose Spotted Antbirds as a purely tropical model system in order to understand how a typical tropical bird species from the rain forest understory copes with the fluctuations in its environment. A comparison between Spotted Antbirds and temperate zone birds may be confounded by phylogeny (Harvey and Pagel 1991). However, the endocrine system is well conserved in all vertebrates, and it is therefore likely that deviation from the general vertebrate model represent adaptations rather than phylogenetic constraints (Wingfield et al. 1997b). Therefore, we relate the data from Spotted Antbirds to data on temperate zone birds in order to generate hypotheses as to what factors may have caused similarities and differences on an evolutionary scale (Fig. 6). Spotted Antbirds share a regular seasonal pattern of gonad regression and recrudescence with most temperate zone birds (Murton and Westwood 1977), indicating that environmental conditions vary in a predictable way in both habitats. We obtained indications for the first time that a near-equatorial tropical bird uses photoperiod as initial predictive information to anticipate seasonal changes (Fig. 5; Hau et al. 1998). The transduction of seasonal information into physiological signals in Spotted Antbirds was similar to that in temperate zone birds, with increases in LH after reception of the adequate environmental signal. In contrast to the seasonal changes in LH levels, increased levels of T were only found during social challenges (Wikelski et al. 1999b). Thorough investigations on photoresponsiveness and brain pathways are necessary to evaluate such comparisons further.

Similar to many temperate zone birds, Spotted Antbirds relied heavily on supplementary environmental

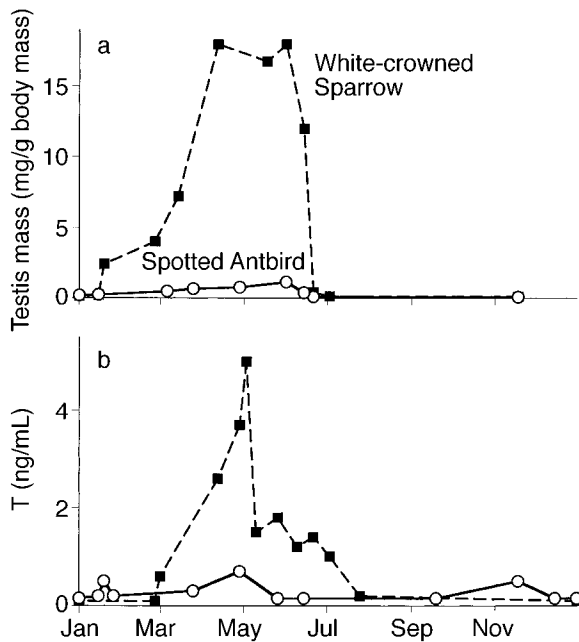


FIG. 6. Schematic comparison of (a) gonad sizes and (b) plasma testosterone levels of White-crowned Sparrows (north temperate zone, 50° N latitude; solid squares) and Spotted Antbirds (tropical Panama, 9° N latitude; open circles). Note that testosterone levels in Spotted Antbirds can stay at baseline throughout the year or increase at any time of the year during times of social instability.

information to initiate breeding. This was indicated by the fact that gonad growth was much slower in the dry (and thus presumably meager) year of 1997 (Figs. 1a and 3a). Temperate zone birds are also known to fine-tune breeding to local food abundances (Hahn et al. 1995, Nager and Van Noordwijk 1995). However, Spotted Antbirds had a very high environmental information factor (constancy/contingency ratio). This means that these birds should also rely on supplementary cues to fine-tune breeding (Wingfield et al. 1993). Indeed, captive Spotted Antbirds adjusted reproductive activity to variations in food abundance and quality (Hau et al. 2000b).

Our results on Spotted Antbirds also highlight differences between temperate zone and tropical birds. Despite the seasonal increases in gonad sizes, Spotted Antbirds had ~10 times smaller relative gonad sizes than most temperate zone birds. This is consistent with an analysis by Stutchbury and Morton (1995), who suggested a general latitudinal trend in gonad sizes. The proximate and evolutionary reasons underlying this difference are still debated. It is conceivable that both the densities of tropical birds and their extra-pair fertilization rates are much lower than in temperate zone birds. In combination, these factors may be responsible for the low maximal T levels (Figs. 1 and 6) and the small gonad sizes of tropical birds (Stutchbury and Morton 1995).

Our study suggests several important differences between Spotted Antbirds and most temperate zone birds in the physiological regulation of reproduction (Wingfield and Hahn 1994). We hypothesize that these divergent patterns reflect differences in ecological conditions between these habitats, and that they have evolved as response to these conditions (Wingfield et al. 1990). However, these patterns still need to be confirmed experimentally.

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