

# A neotropical forest bird can measure the slight changes in tropical photoperiod

Michaela Hau<sup>1\*,2</sup>, Martin Wikelski<sup>1,2</sup> and John C. Wingfield<sup>1</sup>

<sup>1</sup>Department of Zoology, University of Washington, Seattle, WA 98195, USA

<sup>2</sup>Smithsonian Tropical Research Institute, Balboa, Republic of Panamá

Many tropical birds breed seasonally, but it is largely unknown which environmental cues they use to time reproduction. Changes in tropical photoperiod have been regarded as too small to be used as a proximate environmental cue. This hypothesis, however, has never been rigorously tested. Here, we report on experimental evidence that photoperiodic changes characteristic of tropical latitudes stimulate reproductive activity in a neotropical bird from the forest understory. In the central Republic of Panamá (9° N), photoperiod varies annually between 12 hours (December) and 13 hours (June). Free-living spotted antbirds (*Hylophylax n. naevioides*) had regressed gonads in December, but increased gonads ahead of the rainy (the breeding) season in May. Captive spotted antbirds exposed to a 'long' photoperiod of 13 hours increased gonadal size eight-fold and song activity six-fold over that of control birds remaining on a simulated 'short' photoperiod of 12 hours of daylight. Moreover, even a photoperiod of 12 hours 17 minutes was sufficient to stimulate gonadal growth in photostimulated birds over that of controls. The dramatic changes in gonadal development were not accompanied by similar changes in hormone titres such as luteinizing hormone and testosterone as expected from temperate zone birds. We propose a more general role of the tropical photoperiod in the regulation of seasonal events in tropical organisms, or in temperate zone species migrating to the tropics.

**Keywords:** neotropical bird, seasonal breeding, tropical photoperiod, avian reproduction, *Hylophylax naevioides*

## 1. INTRODUCTION

Evidence is accumulating that many, if not most, tropical birds show a distinct seasonal pattern in life history parameters such as breeding activity (for overviews, see Moreau 1950; Skutch 1950; Voous 1950; Snow & Snow 1964; Fogden 1972; Stiles 1980; Bell 1982; Dittami & Gwinner 1990; Tye 1991). Differences in food availability and in the degree of nest predation have been suggested to act as ultimate factors, concentrating avian breeding in the tropics to certain parts of the year (e.g. Skutch 1950; Morton 1971; Fogden 1972; Snow 1976; Sinclair 1978; Grant & Boag 1980; Worthington 1982; Poulin *et al.* 1992; Young 1994; Komdeur 1996). In contrast, the proximate environmental factors that regulate breeding events in tropical birds are still largely obscure. How do birds accomplish seasonal breeding in the tropics, an environment regarded as having a comparatively low seasonality?

In the temperate zones, most birds respond hierarchically to the two main types of proximate environmental information to regulate breeding on a seasonal basis: long-term cues such as photoperiod ('initial predictive information', Wingfield 1980) govern the gross hormonal and gonadal changes necessary for the transition between states of reproductive inactivity and activity (e.g. Murton & Westwood 1977; Farner & Follett 1979; Ball 1993;

Wingfield & Farner 1993), whereas short-term cues such as temperature, food, nest site availability, etc., mediate the more subtle physiological changes that lead to the actual reproductive events ('supplementary information', Wingfield 1980; Wingfield *et al.* 1992; Ball 1993; Nager & van Noordwijk 1995).

In view of the slight photoperiodic changes in the tropics (and their weak temporal association with seasonal climatic changes), it has been suggested that tropical birds might not be able to use daylength as a long-term cue to control breeding (e.g. Voous 1950; Miller 1959, 1965; Cockrem 1995). Instead, in many tropical bird species investigated so far breeding activity has been linked to short-term changes in food availability, possibly signalled by rainfall (Ward 1969; Jones & Ward 1976; Fogden & Fogden 1979). In this scenario, tropical birds would use fundamentally different environmental signals from many of their temperate zone counterparts (see also Wingfield *et al.* 1992).

However, the dismissal of the tropical photoperiod as a proximate cue for timing life history events in tropical birds has been based on a few and sometimes inconclusive experiments. Some tropical bird species have been tested for their capability to react to changes in daylength, but these studies often involved an exposure of tropical birds to exaggerated subtropical or even temperate zone photoperiods (Rollo & Domm 1943; Miller 1959, 1965; Wolfson & Winchester 1959; Disney *et al.* 1961; Epple *et al.* 1972; Chandola & Chakravorty 1982; Gwinner & Dittami

\*Author and address for correspondence  
(hau@zoology.washington.edu).

1985; Tewary & Dixit 1986) and so did not investigate the possible role of the tropical photoperiod. Other experiments had very small samples sizes (Rollo & Domm 1943), were lacking a control group for a non-intentional experiment on the effect of the tropical photoperiod (Disney *et al.* 1961), or yielded similar reactions in experimental and control birds (Rollo & Domm 1943; Marshall & Disney 1956; Lofts 1962).

Therefore, the present experiments were designed to test whether a neotropical bird species, the spotted antbird (*Hylophylax n. naevioides*) from a lowland moist forest of central Panama (9° N 79° W), can perceive the small changes in photoperiod of its natural habitat. Spotted antbirds (Family: Thamnophilidae) are small (17 g) subsocial passerines with a presumably purely neotropical phylogenetic history (Sibley & Monroe 1990). They are facultative followers of army ant swarms in the forest understory, where pairs defend year-round all-purpose territories (Willis 1972). In central Panamá, spotted antbirds breed within the rainy season (May–October; Willis 1972; Sieving 1992), which lasts on average from 19 December to 4 May. To investigate the photoperiodic sensitivity of spotted antbirds, we monitored two physiological measures that are direct indicators of breeding state (e.g. Murton & Westwood 1977; Wilson & Donham 1988; Ball 1993; Wingfield & Farner 1993): (i) gonadal size, and (ii) plasma levels of the reproductive hormones, luteinizing hormone (LH) and testosterone (T). In addition, as a behavioural parameter, song activity was recorded. To put the experimental data into the perspective of the natural situation, we studied the gonadal development in a free-living population of spotted antbirds.

## 2. METHODS

In February 1996, we mist-netted 28 spotted antbirds and randomly divided them into two groups, each of eight males and six females. Following capture, the birds were immediately housed in individual cages (35 cm × 30 cm × 30 cm) with water and food provided *ad libitum*. Experimental rooms (two adjacent wooden rooms in the basement of an apartment building) were built light-tight.

Photoperiodic conditions were simulated as closely as possible to the natural situation and adjusted to measurements taken at our field site on Pipeline Road in Soberania National Park, Republic of Panamá. For this, a light sensor (photoresistor, Conrad Electronic, München, calibrated for lux measurements) with a lower sensitivity threshold of about 0.2 lux was mounted in the forest understory onto a horizontal liana stem (1 m from a 25 cm DBH tree) at a height of about 1.5 m. Data were stored on-site by a HOBO logger (Onset Inc., Pocasset) and expressed as seven-day running means (figure 1).

Experimental photoperiods included two twilight periods and light illumination was always indirect (all light sources were mounted behind partly perforated cardboard shields). Two broad spectrum fluorescent light tubes (Phillips 40 W, 1 m long) lighted each experimental room with about 170 lux (measured at cage level) during the day. No light was given during the night. Twilight of 15 min duration was provided in the morning and in the evening by one incandescent light bulb (Phillips 25 W, about 0.2 lux). Temperature inside the rooms averaged 28 °C, which approximates to the mean temperature of the birds' natural habitat. Fans continuously ventilated the air. Fresh food was

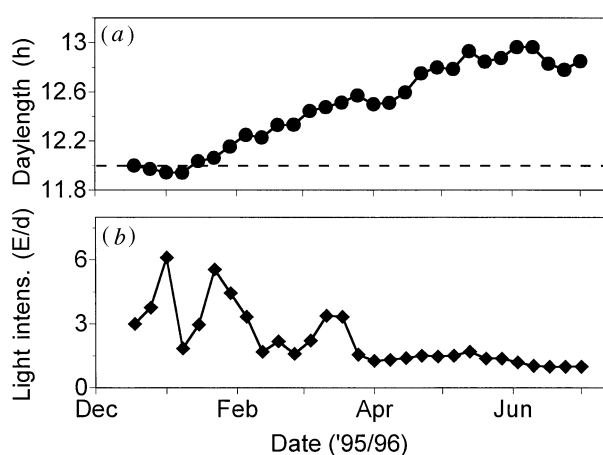


Figure 1. Weekly running means of climate parameters at the study site in Soberania National Park, Republic of Panamá, from December 1995 through July 1996. (a) Daylength; (b) light intensity.

offered twice a day and consisted of freshly made egg food (following Gwinner *et al.* 1987), live mealworms, and juvenile crickets. Spare mealworms and crickets were kept in dark containers in a distant room (and thus could not convey environmental information to the birds). Water was renewed daily, cages were cleaned every 3–4 days.

After being initially kept under a 'short' photoperiod of 12 h for at least eight days (maximally 18 days, depending on time of capture), one group was transferred to a 'long' photoperiod of 13 h on 20 February. The other group remained on 12 h of light per day. Gonadal sizes of all birds were determined before, and then four and seven weeks after photostimulation (see below). At these times, birds were also weighed and had a blood sample taken for subsequent analysis of plasma titres of LH and T. Another small blood sample for LH analysis only was taken on 29 February. For a second experiment, the 12 h group was randomly divided into two groups on 5 April. Five birds were exposed to a photoperiod of 12.28 h (a 17 min increase in photoperiod), the others remained on 12 h light per day. After three weeks, gonadal development of all birds was examined. Throughout the experiment, 30 min of song activity were measured at regular intervals in the morning (between 06:00 and 07:00 h) with Dictaphones. The birds were released after termination of the experiment.

Due to a delayed shipment of live crickets to Panamá, the birds could not be given crickets during a four-day period (in March, see arrow in figure 2c) in experiment 1. To replicate and experimentally induce the observed drop in song activity, in the second experiment the birds were deprived of crickets for a day at the times indicated by arrows in figure 3c.

At approximately monthly intervals, free-living spotted antbirds were caught in mist nets within their territories, laparotomized under anaesthesia (see below), and released again. Many individuals were caught and measured repeatedly.

Length and width of the left testis and diameter of the largest follicle 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 anaesthesia (for details on standard laparotomy procedures, see Wingfield & Farner 1976). Testis volume was calculated using a formula for ellipsoid cylinders ( $4/3 \pi a^2 b$ , where  $a$  is half the testis length and  $b$  is half the testis

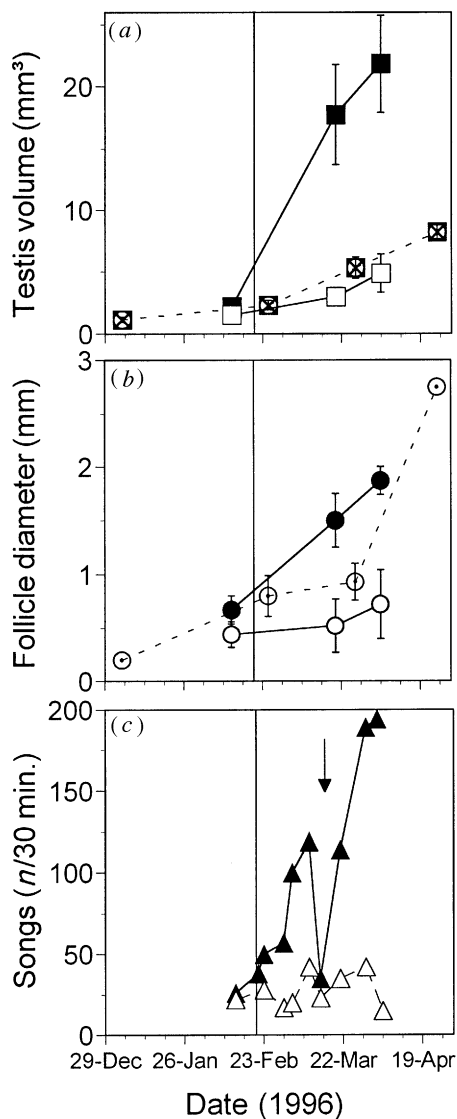


Figure 2. Changes in (a) testis volume (mean  $\pm$  s.e.), (b) follicle diameter (mean  $\pm$  s.e.) and (c) song activity of spotted antbirds during the first experiment. In panels (a) and (b) gonadal development of experimental birds is compared to that of a free-living population (mean  $\pm$  s.e., s.e. given only when sample size  $\geq 3$ ). Open symbols, 12 h group; closed symbols, 13 h group; half-closed symbols, free-living population. Vertical solid line indicates time of photostimulation of the 13 h group. The arrow indicates lack of crickets in the birds' diet.

width). 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. Plasma was separated, stored at  $-20^{\circ}\text{C}$  and transported to Seattle on ice for hormone analysis.

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 were measured with an indirect RIA. Aliquots of about 100  $\mu\text{l}$  plasma were equilibrated with 2000 cpm of  $^3\text{H}$ -testosterone overnight at  $4^{\circ}\text{C}$  for the determination of extraction efficiency. Samples were then extracted with 4 ml of dichloromethane, dried down in a  $40^{\circ}\text{C}$  water bath under nitrogen gas, and redissolved in 550  $\mu\text{l}$  of buffer. Samples were allowed to equilibrate

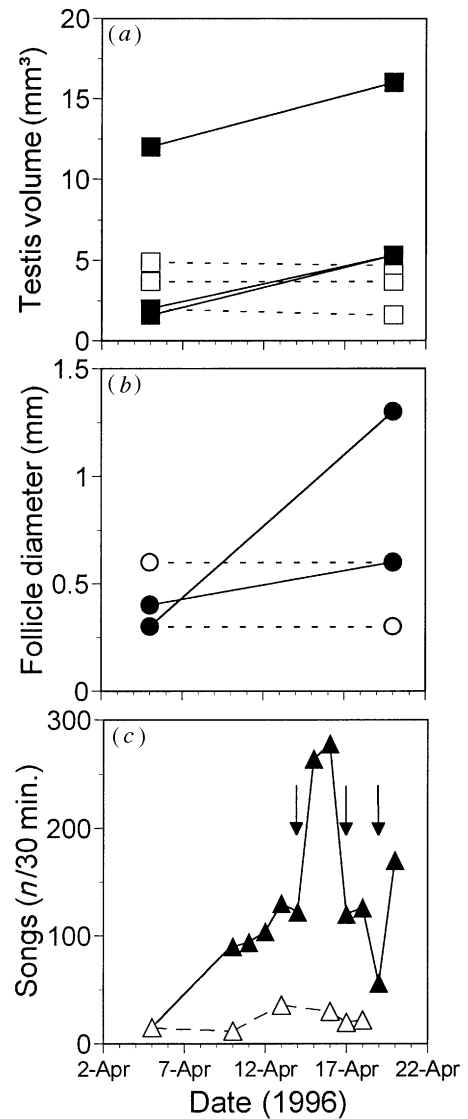


Figure 3. Changes in (a) testis volume, (b) follicle diameter and (c) song activity of individual spotted antbirds before and after photostimulation of the 12.28 h group during the second experiment. Closed symbols, solid lines, 12.28 h individuals; open symbols, broken lines, 12 h individuals. Arrows indicate lack of crickets in the birds' diet.

with buffer overnight at  $4^{\circ}\text{C}$ . 200  $\mu\text{l}$  fractions were taken for duplicates used in the RIA as described previously (e.g. Wingfield & Farner 1975). Fractions (100  $\mu\text{l}$ ) were directly counted for the determination of recovery. Mean ( $\pm$  s.d.) recovery was  $77.2 \pm 7.5\%$ . Two 400  $\mu\text{l}$  aliquots of distilled water (water blanks) and a total of four 400  $\mu\text{l}$  aliquots containing either 0.15, 0.25, or 0.5 ng of non-radioactive T standards were taken through the whole assay procedure to estimate non-specific interference, assay accuracy and intra-assay variation. Blanks were usually below detection limit, accuracy of the T standards was  $10 \pm 0.8\%$ , and intra-assay variation was 13%. Assay sensitivity was at  $0.15 \text{ ng ml}^{-1}$  (2 s.d. from lowest dilution). Since many samples in the T assay were below the detection limit, they were set at  $0.15 \text{ ng ml}^{-1}$  as the highest possible value for a conservative estimate for statistical comparisons.

We obtained continuous gonadal data from 22 experimental birds (6/8 male, 5/3 female, control/photostimulated birds,

respectively). Sample sizes for other measurements differ because not all variables could be measured in all individuals at all times (body mass, 6/8 males, 5/6 females; LH, 5/8 males, 3/4 females; T, 6/8 males, 5/6 females, respectively). Data were processed and analysed with SPSS for Windows (SPSS Inc., Chicago), using a repeated measures ANOVA after testing for normal distribution with a Kolmogorov–Smirnov test, unless stated otherwise. Data from male and female birds were always analysed in separate statistical tests. Gonadal data from the second experiment were analysed using a one-tailed Sign test. For free-living birds, a repeated measures ANOVA was conducted on the data from seven males that were caught repeatedly (at least three, and up to five times) during December 1995 to July 1996 (the significance level was adjusted by the lower-bound epsilon to correct for an apparent violation of the sphericity assumption). If an individual could not be caught during one period, the missing data point was substituted by the mean of the population during the respective capturing period (since the population was closely synchronized, see below).

### 3. RESULTS

A minimal daylength of 11.94 h was measured at the beginning of January 1996, whereas maximal daylength in the second week of June 13 was 12.96 h (figure 1a). It is noteworthy here that seasonal changes in photoperiod in the deep tropics do not vary symmetrically around 12 h. Highest light intensity levels ( $6.1 \text{ E d}^{-1}$ ) were recorded at the beginning of January 1996, and lowest light intensities ( $1.0 \text{ E d}^{-1}$ ) in June and July 1996 (figure 1b).

Gonads of all birds were small following capture from the wild (figure 2a,b). However, after photostimulation, the testis volume of 13 h-males increased eightfold over that of 12 h-males, an effect clearly visible already four weeks after photostimulation (figure 2a). Follicular diameter of 13 h-females increased more than threefold over that of 12 h-females (figure 2b). In both males and females, gonads of photostimulated birds were larger than those of controls (males,  $F_{1,12}=85.92$ ,  $p=0.003$ ; females,  $F_{1,6}=6.4$ ,  $p<0.05$ ). Only gonadal sizes of photostimulated birds increased over time (males,  $F_{2,24}=13.7$ ,  $p<0.001$ ; females,  $F_{2,12}=13.12$ ,  $p=0.001$ ), and differed from initial sizes already after four weeks (least significant difference *post hoc* test, both males and females  $p<0.01$ ). Both males and females sang in captivity. Song activity of all birds in the 13 h-group increased sixfold, whereas no change was observed in the 12 h-group (figure 2c).

Gonadal sizes of free-living spotted antbirds were determined during the periods (with sample sizes for males/females, respectively) from 20 December 1995–11 January 1996 (14/2), 12 February–4 March (13/4), 20 March–4 April (7/6), 7 April–24 April (8/2) (figure 2a,b). In free-living males, minimal gonadal sizes were found in December 1995, maximal gonadal sizes were reached in April 1996 ( $F_{1,30}=127.42$ ,  $p=0.011$ ). Gonadal sizes were monitored throughout July 1996, but no further increase beyond the April values was detected. Active nests of spotted antbirds were first found at the beginning of May 1996 at the start of the rainy season (T. R. Robinson, personal communication and observations). Male photostimulated birds reached larger maximal gonadal sizes than free-living conspecifics during the breeding season (*t*-test,  $p<0.01$ , see figure 2a).

In the second experiment, the size of gonads in all 12.28 h-birds increased ( $p=0.02$ ; figure 3), as did song activity as a response to an increase in photoperiod of only 17 min. The control group showed no changes ( $p>0.05$ ).

The body mass of all birds increased during the first experiment ( $F_{2,42}=38.22$ ,  $p<0.001$ ; table 1). There was no difference in male body mass between the two treatment groups ( $F_{1,12}=0.23$ ,  $p>0.6$ ), but there was a trend in photostimulated females to gain more weight than control females ( $F_{1,9}=5.15$ ,  $p=0.05$ ). We did not obtain continuous data on body mass during the second experiment. We could not detect significant differences in male LH levels between the two groups (table 1;  $F_{1,11}=4.38$ ,  $p=0.06$ ), nor within the two experimental groups (for all tests  $p>0.4$ ). Likewise, there were no difference in LH levels in females in any of the tests (for all tests  $p>0.1$ ). We did not obtain enough samples for the analysis of the LH or T pattern in experiment 2. T levels of all birds were low, most samples being below or around the detection limit (table 1). There were no differences in T over time nor within groups (table 1; males, for all tests  $p>0.2$ ; females, for all tests  $p>0.3$ ).

### 4. DISCUSSION

We conclude that spotted antbirds are able to perceive the one-hour difference between the longest and shortest photoperiod of their tropical habitat. After only four weeks of exposure to an increase in daylength of one hour, both males and females showed dramatically increased gonadal sizes and song activity over their initial values and over those of control and free-living birds. Even more surprising, these birds were able to respond physiologically and behaviourally to an increase in photoperiod of as little as 17 minutes. Such a sensitivity is extremely high and has, to our knowledge, not been reported in tropical species before. These results suggest that a bird species from the forest understory in the deep tropics possesses both the sensitivity and the physiological mechanism to exploit natural changes in tropical photoperiod as long-term seasonal information.

Gonadal size changed more dramatically after the one-hour prolongation of the experimental photoperiod as compared to the 17 minutes increase in daylength. However, the duration of photostimulation was also shorter in the second than in the first experiment (three versus seven weeks). Nevertheless, these data provide strong evidence that spotted antbirds can respond to very small photoperiodic changes because all photostimulated birds increased gonadal size and song activity. Despite the incomplete acoustic isolation of our experimental groups from each other or from the outside, no social (e.g. song) or other non-photoperiodic stimulation of the birds could be detected.

Our field data show that the remarkable photoperiodic capacity of spotted antbirds observed in an experimental situation does not remain a hypothetical mechanism. If the birds measure photoperiodic changes in the wild, we would expect them to undergo regular seasonal changes in gonadal state, i.e. to regress gonads during the non-breeding season as well as grow them again in advance of the breeding season, in a similar way to that of many temperate zone birds. Indeed, free-living spotted antbirds

Table 1. *Body mass (g, mean  $\pm$  s.e.), and plasma titres of LH and T (ng ml<sup>-1</sup>), median and inter-quartile ranges (in brackets) of control and photostimulated spotted antbirds*

	control				photostimulated			
	before	10 days after	4 weeks after	7 weeks after	before	10 days after	4 weeks after	7 weeks after
<i>(a) males</i>								
body mass (g)	16.72 $\pm$ 0.41	—	16.42 $\pm$ 0.62	18.72 $\pm$ 1.04	16.25 $\pm$ 0.31	—	16.52 $\pm$ 0.33	18.09 $\pm$ 0.55
LH (ng ml <sup>-1</sup> )	1.28 (0.91/2.33)	1.07 (0.87/1.47)	2.02 (1.47/2.74)	1.4 (0.64/1.73)	1.58 (1.07/3.56)	2.32 (2.0/2.78)	1.91 (1.78/2.35)	1.91 (1.55/2.39)
T (ng ml <sup>-1</sup> )	0.15 (0.15/0.18)	—	0.15 (0.15/0.15)	0.15 (0.15/0.15)	0.17 (0.15/0.28)	—	0.15 (0.15/0.31)	0.15 (0.15/0.18)
<i>(b) females</i>								
body mass (g)	16.8 $\pm$ 0.35	15.88 $\pm$ 0.28	17.43 $\pm$ 0.56	—	16.7 $\pm$ 0.41	16.14 $\pm$ 0.52	19.22 $\pm$ 0.42	—
LH (ng ml <sup>-1</sup> )	0.99 (0.95/1.18)	1.34 (1.05/1.65)	1.16 (0.79/1.6)	1.14 (0.69/3.22)	2.18 (1.06/3.68)	1.46 (2.0/2.18)	1.3 (1.1/1.58)	1.4 (1.01/1.43)
T (ng ml <sup>-1</sup> )	0.15 (0.15/0.15)	—	0.15 (0.15/0.15)	0.15 (0.15/0.15)	0.15 (0.15/0.15)	—	0.15 (0.15/0.15)	0.15 (0.15/0.15)

had uniformly regressed gonads during the non-breeding season and enlarged gonads ahead of the breeding season (see figure 2*a,b*). The finding that spotted antbirds started to increase gonadal sizes 1–2 months before the rainy (i.e. the breeding) season provides an additional indication that they make use of long-term environmental information in the wild.

Three observations from the present experiments suggest that food stimuli may serve as supplementary information for spotted antbirds, fine-tuning breeding events with local environmental circumstances (Wingfield 1980; Wingfield *et al.* 1992). (1) There was a consistent drop in song activity in both experiments when crickets were omitted from the birds' diet (see arrows in figures 2*c*, 3*c*). (2) Maximal gonadal sizes of birds experiencing a 13-hour photoperiod exceeded those of free-living conspecifics (figure 2*a,b*). (3) The slight gonadal development of control birds might have been caused by improved food availability in captivity (since body mass of all birds increased throughout the first experiment; table 1). In contrast, gonadal growth of 12-hour birds could have also been caused by endogenous annual factors (Gwinner 1986). These hypotheses are testable and will be subject to further studies.

The strong gonadal responses to photostimulation were not reflected by similar changes in plasma hormone titres of spotted antbirds. At present, we are not able to fully interpret these hormonal results, but four physiological mechanisms are possible: (1) captivity suppresses hormonal responses in spotted antbirds, as has been shown for some temperate zone birds (Wingfield & Moore 1987; Wingfield *et al.* 1992); (2) tropical birds have evolved different pathways for the transduction of environmental information (especially photoperiod) into physiological signals—these pathways might not involve the hormones identified in temperate zone birds; (3) spotted antbirds possess similar endocrinological pathways to those of temperate zone birds but the specific hormones exert different effects and functions (see, also, Levin & Wingfield 1992); and (4) spotted antbirds employ similar physiological mechanisms to those of temperate zone

birds, but changes in hormone levels occur at lower magnitudes. Previous field studies on hormonal processes in tropical birds indeed found similarities between temperate zone and tropical birds, with T being lower in tropical than in temperate zone species (see summaries in Dittami & Gwinner 1990; Levin & Wingfield 1992). Further studies are needed to understand the hormonal processes that transduce environmental information (such as photoperiodic changes) into physiological signals in tropical birds. For example, follicle-stimulating hormone (FSH) might be a better predictor of gonadal development than LH in spotted antbirds.

The high sensitivity of tropical birds to small-scale changes in photoperiod allows a precise seasonal time measurement and appears advantageous for organisms that live in seasonal environments. Other tropical organisms probably use similar strategies. A sensitivity to the slight changes in the tropical photoperiod seems to underlie the sexual maturation in juveniles of a tropical mammal (Wayne & Rissman 1991), the gonadal development of an insect (Tanaka *et al.* 1987), and the reproductive activity in two poeciliid fish species (Burns 1985). Although in a different experimental context, African stonechats (*Saxicola torquata axillaris*) are capable to distinguish photoperiods differing by 0.55 hours, as they only express circannual rhythmicity under 12.25 hours, but not under 12.8 hours (Gwinner 1996).

It is so far not generally appreciated that even temperate zone organisms can show high sensitivities towards changes in daylength. Such has been reported for circadian responses of temperate zone passerines (Wever 1967), photorefractoriness in house sparrows (*Passer domesticus*; Dawson 1991), the photoperiodic threshold for the expression of annual rhythms in European starlings (*Sturnus vulgaris*, e.g. Hamner 1971; Schwab 1971) and photoresponsiveness in Syrian hamsters (*Mesocricetus auratus*; Heideman & Bronson 1993). For temperate zone organisms, precise photoperiodic time measurement could be equally valuable for an exact timing of reproduction as well as for other life history events. For example, photoperiod has been reported to be the only environmental factor that affects the time-course of the

endogenous migratory programme of long-distance migrants such as garden warblers (Gwinner 1996). If the tropical photoperiod could be perceived by migratory birds, it would be a valuable mechanism to fine-tune initiation and termination of migration in tropical latitudes. The measurement of the tropical photoperiod could enable a bird to truncate its endogenous migratory time programme once it reached the appropriate latitude of its wintering site. Likewise, birds that happened to have wintered too far south in the tropics could use the local photoperiod to accelerate the initiation of spring migration (Gwinner 1996).

We thank E. Gwinner, W. D. Robinson, T. R. Robinson, J. Habersetzer, A. S. Rand, N. G. Smith, family C. Carrasco, B. Poulin, G. Lefebvre, L. Erckmann, E. S. Morton and the staff at STRI for invaluable help during the study, and P. R. Grant for the idea of using a 15 minute light increase. Four anonymous referees provided helpful critiques on the manuscript. IN.RE.NA.RE. kindly permitted our work in Soberanía National Park, Republic of Panamá. This study was supported by grants from the Deutsche Forschungsgemeinschaft, the Deutsche Ornithologen-Gesellschaft and the Max-Planck-Gesellschaft to M.H., by the Alexander-von-Humboldt Society and the Smithsonian Tropical Research Institute to M.W., and the National Science Foundation to J.C.W.

## REFERENCES

- Ball, G. F. 1993 The neural integration of environmental information by seasonally breeding birds. *Am. Zool.* **33**, 185–199.
- Bell, H. L. 1982 A bird community of lowland rainforest in New Guinea. 2. Seasonality. *Emu* **82**, 65–74.
- Burns, J. R. 1985 The effect of low-latitude photoperiods on the reproduction of female and male *Poeciliopsis gracilis* and *Pecilia sphenops*. *Copeia* **4**, 961–965.
- Chandola, A. & Chakravorty, K. 1982 Termination of seasonal breeding in the photoperiodic weaver bird. *J. Exp. Zool.* **222**, 169–172.
- Cockrem, J. F. 1995 Timing of seasonal breeding in birds, with particular reference to New Zealand birds. *Reprod. Fert. Dev.* **7**, 1–19.
- Dawson, A. 1991 Photoperiodic control of testicular regression and moult in male house sparrows, *Passer domesticus*. *Ibis* **133**, 312–316.
- Disney, H. J. de S., Lofts, B. & Marshall, A. J. 1961 An experimental study of the internal rhythm of reproduction in the red-billed dioch *Quelea quelea* by means of photostimulation, with a note on melanism induced in captivity. *Proc. Zool. Soc. Lond.* **136**, 123–129.
- Dittami, J. P. & Gwinner, E. 1990 Endocrine correlates of seasonal reproduction and territorial behavior in some tropical passerines. In *Endocrinology of birds: molecular to behavioral* (ed. M. Wada), pp. 225–233. Tokyo/Berlin: Japan Science Society Press/Springer.
- Epple, A., Orians, G. H., Farner, D. S. & Lewis, R. A. 1972 The photoperiodic testicular response of a tropical finch, *Zonotrichia capensis costaricensis*. *Condor* **74**, 1–4.
- Farner, D. S. & Follett, B. K. 1979 Reproductive periodicity in birds. In *Hormones and evolution* (ed. J. W. Barrington), pp. 829–872. New York: Academic Press.
- Fogden, M. P. L. 1972 The seasonality and population dynamics of equatorial forest birds in Sarawak. *Ibis* **114**, 307–343.
- Fogden, M. P. L. & Fodgen, P. M. 1979 The role of fat and protein reserves in the annual cycle of the grey-backed camaroptera in Uganda (Aves: Sylviidae). *J. Zool. Lond.* **189**, 233–258.
- Follett, B. K., Scanes, C. G. & Cunningham, F. J. 1972 A radioimmunoassay for avian luteinizing hormone. *J. Endocrinol.* **52**, 359–378.
- Grant, P. R. & Boag, P. T. 1980 Rainfall on the Galapagos and the demography of Darwin's finches. *Auk* **97**, 227–244.
- Gwinner, E. 1986 *Circannual rhythms*. Heidelberg: Springer.
- Gwinner, E. 1996 Circadian and circannual programmes in avian migration. *J. Exp. Biol.* **199**, 39–48.
- Gwinner, E. & Dittami, J. 1985 Photoperiodic responses in temperate zone and equatorial stonechats: a contribution to the problem of photoperiodism in tropical organisms. In *The endocrine system and the environment* (eds B. K. Follett, S. Ishii & A. Chandola), pp. 279–294. Tokyo/Berlin: Japan Science Society Press/Springer.
- Gwinner, E., Neusser, V., Engl, D., Schmidl, D. & Bals, L. 1987 Haltung, Zucht und Eiaufzucht afrikanischer und europäischer Schwarzkehlchen *Saxicola torquata*. *Gef. Welt* **111**, 118–120, 145–147.
- Hamner, W. M. 1971 On seeking an alternative to the endogenous reproductive rhythm hypothesis in birds. In *Biochronometry* (ed. M. Menaker), pp. 448–461. Washington, DC: National Academy of Sciences.
- Heidemann, P. D. & Bronson, F. H. 1993 Sensitivity of Syrian hamsters (*Mesocricetus auratus*) to amplitudes and rates of photoperiodic change typical of the tropics. *J. Biol. Rhythms* **8**, 325–337.
- Jones, P. J. & Ward, P. 1976 The level of reserve protein as the proximate factor controlling the timing of breeding and clutch size in the red-billed quelea. *Ibis* **118**, 547–574.
- 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.
- Levin, R. N. & Wingfield, J. C. 1992 The hormonal control of territorial aggression in tropical birds. *Ornis. Scand.* **23**, 284–291.
- Lofts, B. 1962 Photoperiod and the refractory period of reproduction in an equatorial bird, *Quelea quelea*. *Gen. Comp. Endocrinol.* **2**, 394–406.
- Marshall, A. J. & Disney, H. S. de S. 1956 Photostimulation of an equatorial bird (*Quelea quelea* Linnaeus). *Nature* **177**, 143–144.
- Miller, A. M. 1959 Reproductive cycles in an equatorial sparrow. *Condor* **61**, 344–347.
- Miller, A. M. 1965 Capacity for photoperiodic response and endogenous factors in the reproductive cycles of an equatorial sparrow. *Proc. Natn. Acad. Sci. USA* **54**, 97–101.
- Moreau, R. E. 1950 The breeding seasons of African birds. 1. Land birds. *Ibis* **92**, 223–267.
- Morton, E. S. 1971 Nest predation affecting the breeding season of the clay-colored Robin. *Science* **181**, 920–921.
- Murton, R. K. & Westwood, N. J. 1977 *Avian breeding cycles*. Oxford: Clarendon Press.
- Nager, R. G. & van Noordwijk, A. J. 1995 Proximate and ultimate aspects of phenotypic plasticity in timing of great tit breeding in a heterogeneous environment. *Am. Nat.* **146**, 454–474.
- Poulin, B., Lefebvre, G. & McNeil, R. 1992 Tropical avian phenology in relation to abundance and exploitation of food resources. *Ecology* **73**, 2295–2309.
- Rollo, M. & Domm, L. V. 1943 Light requirements of the weaver finch. I. Light period and intensity. *Auk* **60**, 357–367.
- Schwab, R. G. 1971 Circannual testicular periodicity in the European starling in the absence of photoperiodic change. In *Biochronometry* (ed. M. Menaker), pp. 428–447. Washington, DC: National Academy of Sciences.
- Sharp, P. J., Dunn, I. C. & Talbot, R. T. 1987 Sex differences in the responses to chicken LHRH-I and II in the domestic fowl. *J. Endocrinol.* **115**, 323–331.
- Sibley, C. G. & Monroe, B. L. Jr 1990 *Taxonomy and distribution of the birds of the world*. New Haven, CT: Yale University Press.
- Sieving, K. E. 1992 Nest predation and differential insular extinction among selected forest birds of central Panamá. *Ecology* **73**, 2310–2328.

- Sinclair, A. R. E. 1978 Factors determining the food supply and breeding season of resident birds and movements of palaeartic migrants. *Ibis* **120**, 480–497.
- Skutch, A. F. 1950 The nesting season of Central American birds in relation to climate and food supply. *Ibis* **92**, 185–222.
- Snow, D. W. 1976 The relationship between climate and annual cycles in the Cotingidae. *Ibis* **118**, 366–401.
- Snow, D. W. & Snow, B. K. 1964 Breeding seasons and annual cycles of Trinidad land-birds. *Zoologica NY* **49**, 1–39.
- Stiles, G. F. 1980 The annual cycle in a tropical wet forest hummingbird community. *Ibis* **122**, 322–343.
- Tanaka, S., Denlinger, D. L. & Wolda, H. 1987 Daylength and humidity as environmental cues for diapause termination in a tropical beetle. *Physiol. Entomol.* **12**, 213–224.
- Tewary, P. D. & Dixit, A. S. 1986 Photoperiodic regulation of reproduction in subtropical female yellow-throated sparrows. *Condor* **88**, 70–73.
- Tye, H. 1991 Reversal of breeding season by lowland birds at higher altitudes in western cameroon. *Ibis* **134**, 154–163.
- Voous, K. H. 1950 The breeding seasons of birds in Indonesia. *Ibis* **92**, 279–287.
- Ward, P. 1969 The annual cycle of the yellow-vented bulbul *Pycnonotus goiavier* in a humid equatorial environment. *J. Zool.* **157**, 25–45.
- Wayne, N. L. & Rissman, E. F. 1991 Tropical photoperiods affect reproductive development in the musk shrew, *Suncus murinus*. *Physiol. Behav.* **50**, 549–553.
- Wever, R. 1967 Zum Einfluss der Dämmerung auf die circadiane Periodik. *Z. Vergl. Physiol.* **55**, 255–277.
- Willis, E. O. 1972 *The behavior of spotted antbirds*. Ornithological Monographs 10. American Ornithologists Union.
- Wilson, F. E. & Donham, R. S. 1988 Daylength and control of seasonal reproduction in male birds. In *Processing of environmental information in vertebrates* (ed. M. H. Stetson), pp. 101–119. New York: Springer.
- Wingfield, J. C. 1980 Fine temporal adjustment of reproductive functions. In *Avian endocrinology* (ed. A. Epplé & M. H. Stetson), pp. 367–389. New York: Academic Press.
- Wingfield, J. C. & Farner, D. S. 1975 The determination of five steroids in avian plasma by radioimmunoassay and competitive protein-binding. *Steroids* **26**, 311–327.
- Wingfield, J. C. & Farner, D. S. 1976 Avian endocrinology—field investigations and methods. *Condor* **78**, 571–573.
- Wingfield, J. C. & Farner, D. S. 1993 Endocrinology of reproduction in wild species. In *Avian biology IX* (ed. D. S. Farner, J. R. King & K. C. Parkes), pp. 163–327. Academic Press.
- Wingfield, J. C. & Moore, M. C. 1987 Hormonal, social, and environmental factors in the reproductive biology of free-living male birds. In *Psychobiology of reproductive behaviour: an evolutionary perspective* (ed. D. Crews), pp. 149–175. New Jersey: Prentice Hall.
- Wingfield, J. C., Hahn, T. P., Levin, R. & Honey, P. 1992 Environmental predictability and control of gonadal cycles in birds. *J. Exp. Zool.* **261**, 214–231.
- Wolfson, A. & Winchester, D. P. 1959 Effect of photoperiod on the gonadal cycle in an equatorial bird, *Quelea quelea*. *Nature* **184**, 1658–1659.
- Worthington, A. 1982 Population sizes and breeding rhythms of two species of manakins in relation to food supply. In *The ecology of a tropical forest: seasonal rhythms and long-term changes* (ed. E. G. Leigh Jr, A. S. Rand & D. M. Windsor), pp. 213–225. Washington, DC: Smithsonian Institution Press.
- Young, B. E. 1994 The effects of food, nest predation and weather on the timing of breeding in tropical house wrens. *Condor* **96**, 341–353.

