

REPRODUCTIVE SEASONALITY OF SEVEN NEOTROPICAL PASSERINE SPECIES

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Abstract. We investigated gonad sizes, nesting patterns, and plasma hormone concentrations of seven Neotropical passerine species in a lowland tropical rainforest (Panama) at 9°N latitude over at least one annual cycle. All species had entirely regressed gonads for several months of the year (October to January), coinciding with the end of heavy rainfall. Gonadal recrudescence started in the dry season between January and March. Nesting began earlier (March) for open-habitat species than for forest-interior species (April), and lasted until August or December, respectively. Species differed widely in maximal relative testes sizes and reproductive hormone concentrations, but both measures were lower than in most temperate-zone species. Although we cannot provide a phylogenetically controlled comparison, polygynous and group-living species appeared to have larger testes than monogamous species, possibly indicating sperm competition. Testosterone concentrations were highest in polygynous species, intermediate in socially monogamous species, and lowest in a group-living species, indicating that testosterone is more influenced by social systems than by gonad cycles. Tropical birds may generally maintain low testosterone concentrations and relatively small gonads to decrease overall energy expenditure compared to temperate-zone relatives.

Key words: breeding season, gonad cycles, hormones, Panama, rainforest, seasonality, tropical.

Estacionalidad Reproductiva de Siete Especies Passeriformes Neotropicales

Resumen. Investigamos los tamaños de las gónadas, los patrones de nidificación y las concentraciones hormonales plasmáticas de siete especies de aves paserinas Neotropicales en una selva lluviosa tropical de tierras bajas en Panamá (9°N) durante por lo menos un ciclo anual. Todas las especies tenían gónadas enteramente retraídas por varios meses del año (octubre a enero), coincidiendo con el fin del periodo de precipitación lluviosa pesada. El crecimiento gonadal comenzó en la estación seca, entre enero y marzo. La nidificación comenzó primero en las especies de hábitat abierto (marzo) que en las especies de interior de bosque (abril) y duró hasta agosto y diciembre, respectivamente. Las especies difirieron extensamente en los tamaños relativos máximos de las gónadas y en las concentraciones de la hormona reproductiva, aunque ambas medidas fueron menores que para la mayoría de las especies de la zona templada. Aunque no podemos proveer una comparación controlada por filogenia, las especies poliginias y las especies que viven en grupo tenían testículos más grandes que las especies monógamas, lo que posiblemente podría estar indicando competencia espermática. Las concentraciones de testosterona fueron mayores en las especies poliginias, intermedias en las socialmente monógamas, y menores en las especies que viven en grupo, indicando que la testosterona estaría más influenciada por el sistema social que por los ciclos de las gónadas. Las aves tropicales podrían generalmente mantener niveles bajos de testosterona y tamaños relativamente pequeños de gónadas con el fin de disminuir los gastos energéticos totales en comparación a las especies emparentadas de las zonas templadas.

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INTRODUCTION

In most temperate-zone birds, gonadal recrudescence, territoriality, aggression, and reproduction co-occur during a relatively short period in spring and early summer (Lofts and Murton 1973, Murton and Westwood 1977, Searcy and Wingfield 1980, Balthazart 1983, Silverin et al. 1989, Ball 1993, for exceptions see Logan and Wingfield 1990, Soma and Wingfield 1999, Canoine and Gwinner 2002). In contrast, wet tropical habitats typically allow longer breeding seasons, year-round residency, and year-round territoriality (Baker 1938, Miller 1955, Wikelski et al. 2000, Stutchbury and Morton 2001). However, we have recently demonstrated that a near-equatorial bird from the rainforest understory uses a seasonal breeding strategy, much like temperate-zone birds (Wikelski et al. 2000). Is breeding seasonality a general pattern for birds living in the lowland tropics? Here we concentrate on three sets of interrelated questions on the interaction between reproduction, territoriality, and seasonality.

Are tropical birds physiologically capable of reproducing year round? Potentially unconstrained by low food supplies and cold temperatures of temperate winters, birds from the near-equatorial tropics might conceivably breed at any time of year. It is so far largely unclear if tropical birds are physiologically capable of breeding year round or not. Only very few studies provide the data necessary to determine reproductive capacity of free-living, near-equatorial birds throughout an annual cycle (e.g., Stiles 1980, Dittami and Gwinner 1985, 1990, Dittami 1986, 1987). One needs to directly determine the physiological state of reproductive organs (testes and ovaries) to understand if birds retain the potential to breed throughout the year. Only if the gonads are kept in a near-functional state throughout the year are birds truly capable of reproducing continuously. Once gonads are fully regressed, it takes 4–6 weeks before sperm can be produced or follicles can be ovulated (Wingfield and Farner 1993). To distinguish between these two possibilities we assessed gonad sizes in the field using laparotomy (Wikelski et al. 2000).

Do tropical birds that are territorial year round maintain high testosterone concentrations year round? The duration of territoriality often differs between tropical and temperate-zone

birds. Many tropical birds stay on their territories year round (Moreau 1950, Willis 1967, 1972, Skutch 1969, Morton 1980, Levin and Wingfield 1992, Dittami 1996), while most northern temperate zone birds abandon their territories in winter. In the temperate zone, territoriality during the breeding season is usually coupled with high concentrations of circulating androgen hormones, mostly testosterone (Wingfield et al. 1987, Wingfield and Hahn 1994). However, not all temperate-zone birds need testosterone to be aggressive during the nonbreeding season (Schwabl 1992, Gwinner et al. 1994, Wingfield 1994, Soma and Wingfield 1999, Canoine and Gwinner 2002). It is presently unclear for most tropical birds whether year-round territoriality requires androgen concentrations to be elevated year round, or whether in some birds the role of testosterone in reproduction has become dissociated from that in aggression.

Do physiological traits of a particular species correspond to its ecological characteristics? So far, only a handful of near-equatorial tropical bird species have been investigated with respect to the seasonality of both gonadal and hormonal patterns underlying reproductive behavior (summarized in Wikelski, Hau, and Wingfield 1999). Most of these species were insectivorous, territorial, and socially monogamous. Although no single empirical study can provide a sufficiently high sample size of bird species to compare many different ecological groups, we aimed at increasing the diversity of tropical bird species for which ecological and physiological traits are investigated in combination. We focused on species that cover a range of habitats (rainforest interior to secondary growth) within an 8-km radius, social systems (social monogamy to lek mating), and territorial systems (year-round territoriality, seasonal territoriality, and non-territoriality). Our objective was to describe the reproductive seasonality of an ecologically diverse group of tropical species, not to generate phylogenetically controlled comparisons.

We investigated the relationships among reproduction, territoriality, diet, and habitat in seven bird species in Panama (9°N latitude) by measuring gonad sizes and testosterone levels throughout at least one year. We hypothesized that despite year-round territoriality, tropical birds would generally keep testosterone concentrations low due to potential costs of constantly elevated testosterone (Dufty 1989, Ketterson et

TABLE 1. Main ecological characteristics of the seven species studied in Soberania National Park, Panama, 1996–1997.

Common name	Mass (g)	Habitat	Food	Social system	Territoriality
Spotted Antbird	18	Forest	Insects	Socially monogamous	Year round
Bicolored Antbird	31	Forest	Insects	Socially monogamous	Year round, commuting to ant swarms
Song Wren	25	Forest	Insects	Family groups	Year round
Red-capped Manakin	14	Forest	Fruit	Leks	Short, lek
Golden-collared Manakin	18	Edge	Fruit	Leks	Short, lek
Blue-gray Tanager	32	Open	Fruit, omnivorous	Small groups	Not territorial
Clay-colored Robin	74	Open	Omnivorous	Mating aggregations, leks	Short, local display court

al. 1992, Zuk 1996, Hillgarth and Wingfield 1997, Hillgarth et al. 1997). We also expected that tropical birds would restrict their reproductive capacities to those times of the year when environmental conditions are most favorable; that is, when the most energy is available for demanding reproductive activities. Lastly, we hypothesized that bird species in which males face strong intrasexual competition for mating opportunities would have higher peak testosterone concentrations and larger maximum testes sizes than those species that live in large groups or in family groups.

METHODS

We studied birds between November 1996 and December 1997 in Soberania National Park and adjacent woodlands around the village of Gamboa, in the Republic of Panama (Table 1). Five of these species were also studied at various times throughout 1996, but not as regularly as in 1997. Soberania National Park is a lowland, 22 000-ha moist forest (Holdridge 1967) in central Panama (9°N, 79°W), bordering the Panama Canal (Leigh et al. 1982). The forest consists of a mixture of secondary and primary forest. There is about 2600 mm of rain per year, with 90% falling during the late-April to mid-December wet season (Windsor 1990, Robinson, Brawn, and Robinson 2000). Mean daily low temperatures are 23°C; highs average 29°C in the wet season and 32°C in the dry season.

The seven study species discussed here differ in at least two major life-history attributes: habitat type and social system (Table 1). Four species inhabit mostly forested habitats: Spotted Antbird (*Hylophylax n. naevioides*; Willis 1972,

Hau et al. 1998), Bicolored Antbird (*Gymnophrys leucaspis bicolor*; Willis 1967), Song Wren (*Cyphorhinus phaeocephalus*; Robinson, Robinson, and Edwards 2000, Robinson and Robinson 2001), and Red-capped Manakin (*Pipra mentalis*; Worthington 1982). The remaining species, termed “edge” or “open habitat” species here, occupy second growth (Golden-collared Manakin, *Manacus vitellinus*, Worthington 1982) or open woodland (Blue-gray Tanager, *Thraupis episcopus*, Brawn et al. 1996; Clay-colored Robin, *Turdus grayii*, Morton 1971, Stutchbury and Morton 1995, 2001). Spotted Antbirds and Bicolored Antbirds are socially monogamous. Song Wrens (Robinson, Robinson, and Edwards 2000) and Blue-gray Tanagers live in groups, Clay-colored Robins display in groups, and the two manakin species breed in leks. Little is known about the sociobiology of the Blue-gray Tanager, but available data indicate that birds always travel in groups and have no territories in the usual sense (Brawn et al. 1996; E. S. Morton, pers. comm.; WDR, pers. obs.).

PHYSIOLOGICAL MEASUREMENTS

We measured birds at about bimonthly intervals throughout 1997 (and 1996 for some species). Birds were captured in mist nets set up either at the edge of a woodlot in Gamboa in proximity to a bird feeder, or in the forest adjacent to Pipeline Road. Except for Spotted Antbirds, we did not use sound playback to attract birds to the net. A few individuals were recaptured twice during the study, with the exception of Spotted Antbirds. Upon capture, a small blood sample (max. 300 µL) was collected within 30 min by

puncturing the alar wing vein with a 26-gauge needle; birds were then color banded with individual band combinations, weighed to the nearest 0.2 g, and checked for wing molt. Blood was collected in heparinized microcapillary tubes and kept cool (4°C) until centrifugation. Length and width of the left testis or 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 anesthesia (for details on standard laparotomy procedures see Wingfield and Farner 1976, Hau et al. 1998). We refer to gonads when talking about both testes and follicles and use testes only for males and follicles only for females. Testis volume was calculated using a formula for ellipsoid cylinders ($V = [4/3] \pi a^2 b$), where a is half the testis width and b half the length). Relative testis volume was calculated for each individual at each capture by dividing testis volume by body mass. We then calculated monthly means from the individual means. We considered male birds in reproductive condition when average testes sizes reached half their maximum values, because mature sperm can generally be found in testes of such large sizes (Wingfield and Farner 1993). For females, we used an average size of 1 mm for the largest follicle as indicator of reproductive readiness because follicles of such size can rapidly deposit yolk for egg laying (within 2–3 weeks, Wingfield and Farner 1993). We are aware that our use of a threshold for follicle size does not adjust for different body sizes of the species investigated. However, follicle growth in avian females appears to follow a step function, with slow growth until the threshold follicle diameter is reached (1–2 mm, almost independent of female body size) and rapid growth, again independent of species, beyond the threshold size (Murton and Westwood 1977).

Birds were kept for approximately 10 min after the laparotomy to allow for recovery before release. Recapture rates for laparotomized birds were indistinguishable from those of birds captured and bled only. Thus, laparotomy did not increase mortality beyond that of controls (WDR, unpubl. data). Plasma was separated from red blood cells by centrifugation at 6000 rpm for 4 min and treated with 10 μ L of 0.2% β -propiolactone solution of a pH of 7.0 at 4°C to kill viruses, according to USDA import regulations for avian blood (Wikelski et al. 2000).

Samples were then stored at -20°C and transported to the United States on dry ice for hormone analysis under permits from Panamanian and United States authorities.

RADIOIMMUNOASSAYS

Plasma concentrations of testosterone were measured with a radioimmunoassay after separation of steroid hormones by column chromatography (Wingfield and Farner 1975, Hau et al. 1998). Water blanks were taken through the entire assay procedure and were usually below detection limit. The accuracy of the hormone standards was 6.9%. Intra-assay variation was 2.3% (mean of 6 assays). Interassay variation was 4.6% ($n = 6$ assays). The lower sensitivity threshold of the assay was 0.15 ± 0.06 ng mL $^{-1}$ for testosterone (see Wingfield and Farner 1975 for methods). When testosterone concentrations were below detection limit, we set them at 0.15 ng mL $^{-1}$ as a conservative estimate for statistical comparisons.

BREEDING SEASONS AND BEHAVIORAL OBSERVATIONS

We documented actual breeding activity by searching our study areas for nests on a weekly basis from March through August and on a bi-weekly basis from September through February. We also monitored breeding activity by examining adults captured in mist nets for the presence of brood patches. Birds were captured every 2 weeks throughout the year in the forest study site in Soberania National Park and at least once per month in the second-growth habitats of Gamboa (Robinson, Brawn, and Robinson 2000). Active brood patches were defined as those that were edematous and highly vascularized. Ventral aspects of tropical birds often lack feathering even when individuals are not breeding, but our experience with many of these species indicates that the bare skin of inactive brood patches often is flaky and not obviously vascularized.

STATISTICAL ANALYSIS

We included in our analysis only those individuals for which the time between capture and blood sampling was less than 30 min. Plasma concentrations of gonadal steroids usually remain unchanged during this time (Wingfield and Farner 1993). Data were processed with SPSS 10.0 for Windows (SPSS Inc. 1991). Two-tailed

test statistics were used throughout. Because recaptures of individual birds were very infrequent (except for Spotted Antbirds), we treated all captures as independent data points. We conducted general linear models to test for differences between sampling occasions, except for Spotted Antbirds where we used repeated-measures ANOVA. Hormonal data were log-transformed for statistical analysis because they violated the assumption of normality due to the existence of a lower detection limit (Hau et al. 1998). However, we show means of untransformed data in the figures to make our data comparable to previously published data (Dittami and Gwinner 1990, Wikelski, Hau, and Wingfield 1999). We only analyzed sampling occasions in which we captured 3 or more individuals of a given species, but show all data in the figures even if fewer were captured. Data are reported as means \pm 95% confidence intervals when sample size is 3 or higher, or as single data points. We connect data points by lines in figures whenever the sampling intervals were less than three months. Sample sizes differ among sampling occasions and measures as indicated in the figures because not all data could be collected for all individuals.

RESULTS

GONAD CHANGES AND MOLT

All species showed seasonal changes in testes and follicle sizes, as well as in molt (Fig. 1). Clay-colored Robins, Golden-collared and Red-capped Manakins, and Blue-gray Tanagers started to enlarge their testes during the dry season (in February or March) and reached their peak testis sizes in May (Clay-colored Robin and Blue-gray Tanager) and June (Golden-collared Manakin). For each of the following species we found seasonal changes in gonad sizes within each sex: Clay-colored Robin (males: $F_{4,41} = 34.8$, $P < 0.001$, females: $F_{3,21} = 6.1$, $P = 0.004$); Golden-collared Manakin (males: $F_{4,27} = 5.5$, $P = 0.001$, females: $F_{2,31} = 3.2$, $P = 0.02$); Blue-gray Tanager (males: $F_{3,24} = 7.8$, $P = 0.001$, females: $F_{2,25} = 4.2$, $P = 0.02$). Females had a similar seasonal follicle development but in two species showed earlier peaks than males, Golden-collared Manakins in April and Blue-gray Tanagers in February. Spotted Antbirds also showed a seasonal pattern in gonadal recrudescence and total regression, but the start of gonadal growth and the peak in maximal gonad

size occurred approximately 2 months later than in the dry-season breeders (Wikelski et al. 2000). The seasonal pattern for Bicolored Antbirds is not entirely resolvable because of lack of data from July through November (males: $F_{6,41} = 2.4$, $P = 0.02$, females: $F_{6,39} = 7.7$, $P < 0.001$). Song Wrens had a prolonged period of increased testis and follicle sizes which ranged from approximately April until October (males: $F_{3,21} = 3.1$, $P = 0.03$, females: $F_{3,23} = 3.1$, $P = 0.03$).

The molting patterns were also seasonal in all species and generally followed the cessation of reproductive activities. It should be noted that for some species on the population level there was temporal overlap of molt with large gonad sizes (e.g., Spotted Antbird, July 1996). However, most of the individuals for which we had data showed no breeding-molting overlap (Wikelski et al. 2000). Instead, individual birds generally started to molt once they ceased their annual reproductive period. We found a large variation in molt duration between the species. Whereas Bicolored Antbirds could be found molting anytime between May 1996 and February 1997, Red-capped Manakins and Song Wrens showed a fairly tight synchronization of molt (June to August in 1996 and September to October in 1997). Blue-gray Tanagers and Clay-colored Robins showed intermediate molt durations, lasting from June to September (Fig. 1).

The maximum relative testes sizes differed between species. Clay-colored Robins, Blue-gray Tanagers, and Golden-collared Manakins had the largest testes relative to their body mass (Fig. 2), while Bicolored Antbirds, Song Wrens, and Spotted Antbirds had much smaller relative testes sizes ($F_{7,37} = 7.9$, $P = 0.01$).

LENGTH OF REPRODUCTIVE SEASON

The duration of seasonal reproductive capacity, as defined by the period that testes were found at or above half-maximum size (Fig. 3), was longest for Song Wrens (mid-March to early November, 7.1 months) and Bicolored Antbirds (late February to early September, 6.1 months) and shortest for Clay-colored Robins and Blue-gray Tanagers (early March until mid-June, 3.1 months, Fig. 3). The average (\pm SE) length of reproductive capacity across all seven species was 4.3 ± 0.7 months (128 ± 14 days, 112 ± 20 for edge species, 141 ± 34 for forest species). This compares to the length of reproductive ac-

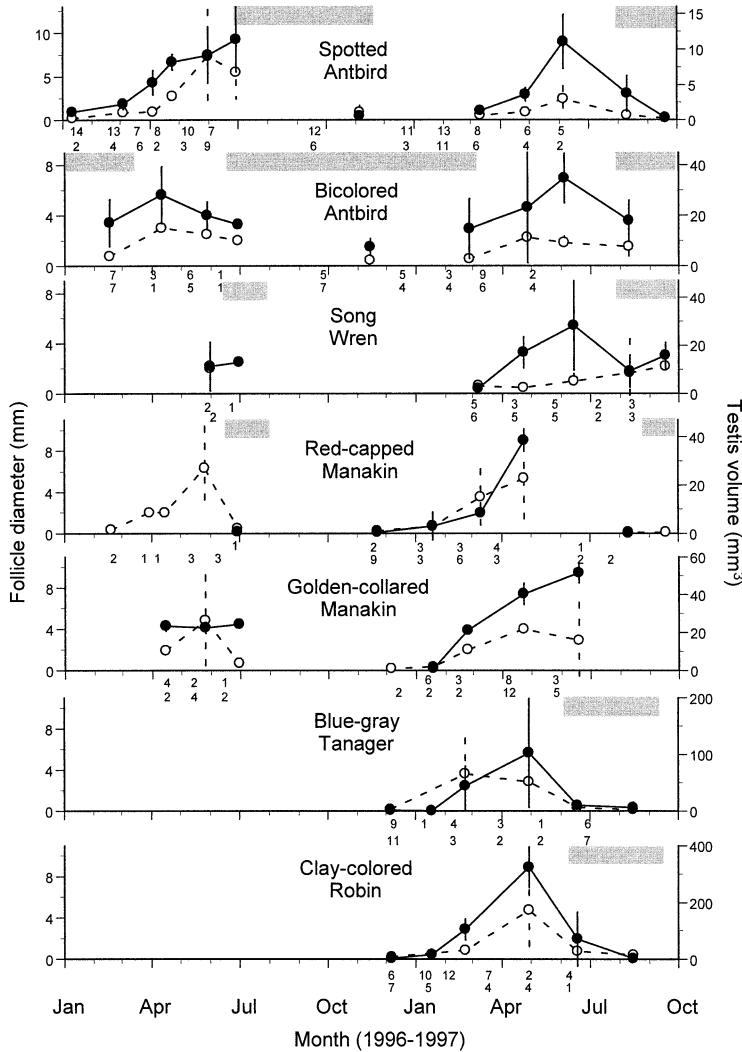


FIGURE 1. Changes in testis volume (filled circles) and follicle size (unfilled circles) of seven Neotropical passerine species throughout one or two annual cycles (January 1996 until October 1997) in central Panama. The shaded bars connect time points when molting individuals were captured. Note that the y-axes differ to account for differences in absolute gonad sizes (see Fig. 2). Data points show means \pm 95% CI. Sample sizes are indicated below each graph, males above females.

tivity in terms of active nests found of 136 ± 10 days (121 ± 15 for edge species, 148 ± 23 for forest species) and in terms of active brood patches of 176 ± 17 days (134 ± 24 for edge species, 210 ± 30 for forest species). Thus, we found a fairly close temporal association between potential reproductive capacity and realized reproduction.

TESTOSTERONE AND TERRITORIALITY

None of the females of any species showed significant changes in testosterone concentrations

over the seasons, and all had very low testosterone concentrations (all $P > 0.35$, Fig. 4), even though females in some of the species are quite aggressive and actively defend territories (e.g., Spotted Antbird, Bicolored Antbird, Song Wren). Only Clay-colored Robin and Golden-collared Manakin males showed significant seasonal changes in testosterone concentrations, while males of the other five species did not (Red-capped Manakins were not sampled). Clay-colored Robins had a marked increase in

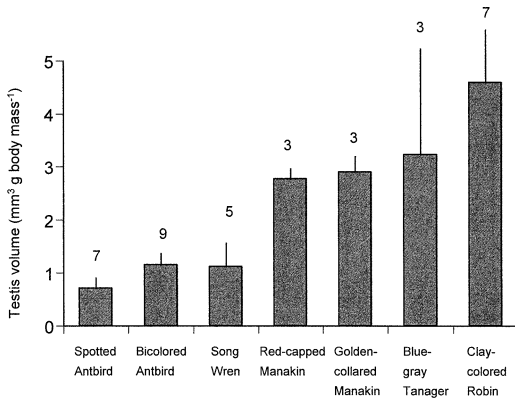


FIGURE 2. The relative maximum testis volume, calculated as maximum testis size for each individual divided by its body mass, differed between seven Neotropical passerine species. Bars indicate means \pm 95% CI; sample sizes appear above bars.

testosterone at the beginning of their territorial period in January ($F_{4,39} = 3.7, P = 0.04$, Fig. 4) with testosterone peaking in April and decreasing along with testes regression in June. Golden-collared Manakins, on the other hand, established their lek territories in January and February. This may have been in the absence of detectable testosterone, which peaked during the

onset of the mating season about April, and then decreased until the end of the lekking season in June ($F_{3,24} = 2.7, P < 0.05$). Blue-gray Tanagers were not territorial and had baseline testosterone throughout the year, despite their large relative testes sizes ($F_{2,21} = 2.7, P = 0.1$). Spotted Antbirds had very low testosterone concentrations throughout the year, even though they were highly territorial and aggressive year round (Hau et al. 2000). Song Wrens, which live in family groups, are also territorial throughout the year and showed no significant seasonal changes in testosterone ($F_{3,19} = 0.4, P = 0.85$). The plasma testosterone concentrations of some individual Bicolored Antbirds rose slightly during the early wet season, but we found no significant difference at the population level ($F_{6,36} = 1.1, P = 0.34$, Fig. 4). Bicolored Antbirds are territorial year round, but have to forage around army ant swarms, for which they often have to intrude upon territories of conspecifics.

BODY MASS

Male body mass was fairly stable throughout the year for all species, at least when compared to north-temperate species, many of which migrate and deposit fat seasonally. Nevertheless, we

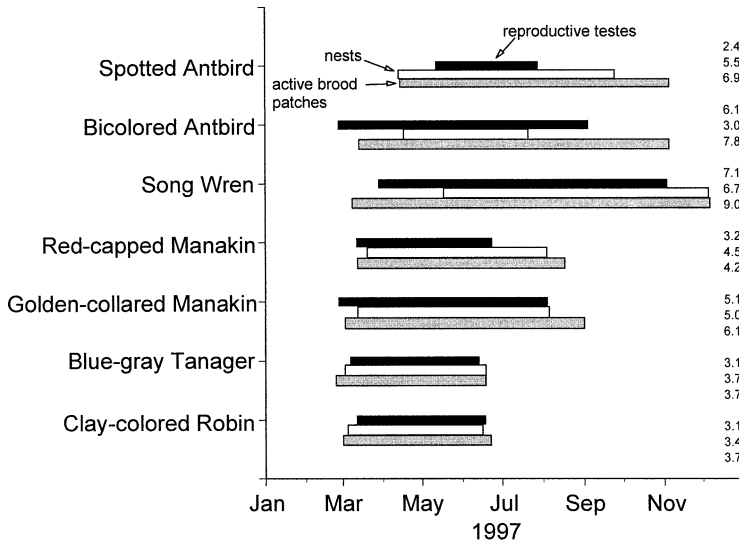


FIGURE 3. The length of the reproductive season varied between approximately 2.4 and 7.1 months in seven Neotropical passerines in central Panama. Black bars indicate when males of each species had on average testes that were half their maximum size or larger, which we used as an indicator for mature reproductive capacity. The white bars show when nests of a particular species were found (modified after Robinson et al. 2000). Gray bars indicate when birds with active brood patches were caught. Numbers inset at right of graph indicate the average duration of reproductive activity in months.

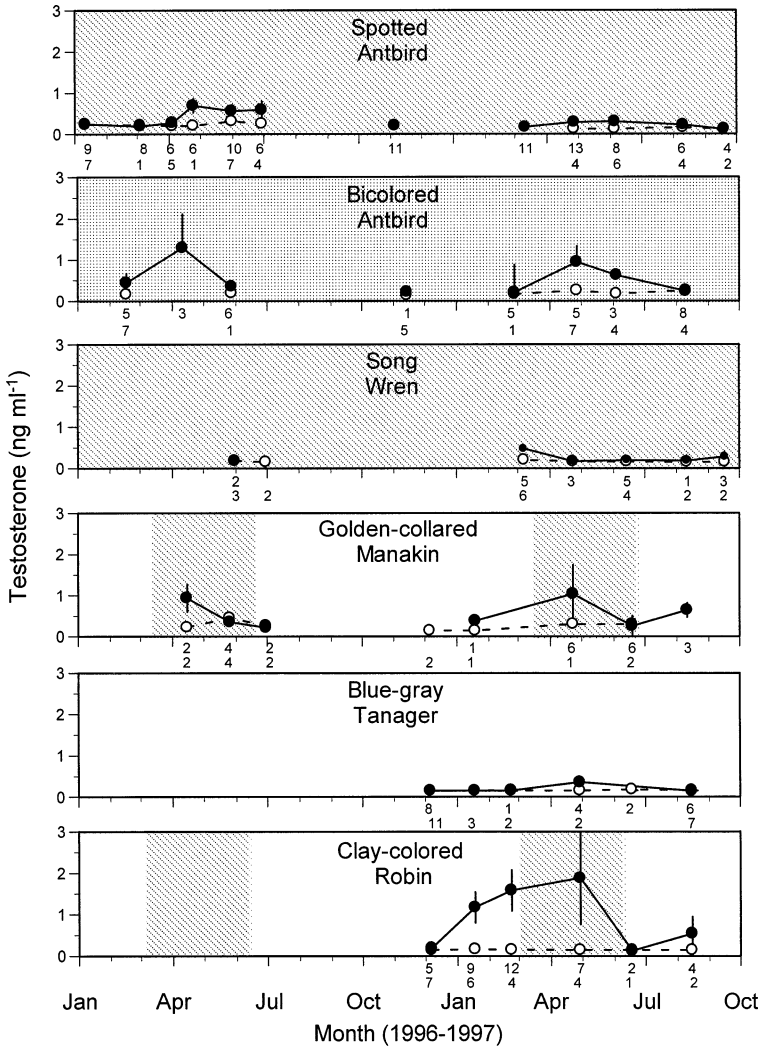


FIGURE 4. Seasonal changes (means \pm 95% CI) in testosterone concentrations of males (filled circles) and females (unfilled circles) of six Neotropical passerines. Shading indicates the extent of territorial behavior. Bicolored Antbirds are territorial but also commute into territories of conspecifics to forage around army ant swarms. Sample sizes are indicated below each graph, males over females. Red-capped manakins were not sampled because of their small body mass.

found significant differences in male body mass in three species (Fig. 5; Blue-gray Tanager: $F_{3,24} = 11.2$, $P < 0.001$, Clay-colored Robin: $F_{4,41} = 14.5$, $P < 0.001$, and Spotted Antbird, results in Wikelski et al. 2000) while in the other species males showed no seasonal difference in body mass (Golden-collared Manakin: $F_{5,39} = 0.7$, $P = 0.6$, Bicolored Antbird: $F_{7,51} = 0.3$, $P = 0.9$, Song Wren: $F_{3,21} = 2.5$, $P = 0.1$). The average \pm SD difference (in % maximum body mass for each species) between lowest and highest body

mass among the seven species was $9.9 \pm 4.5\%$. We did not analyze annual variation in female body mass because their body mass varies greatly during egg production, obscuring seasonal pattern.

DISCUSSION

We compared reproductive seasonality of seven species of Neotropical passerines that differ in territorial and social systems as well as in diet and habitat characteristics. Despite their diverse

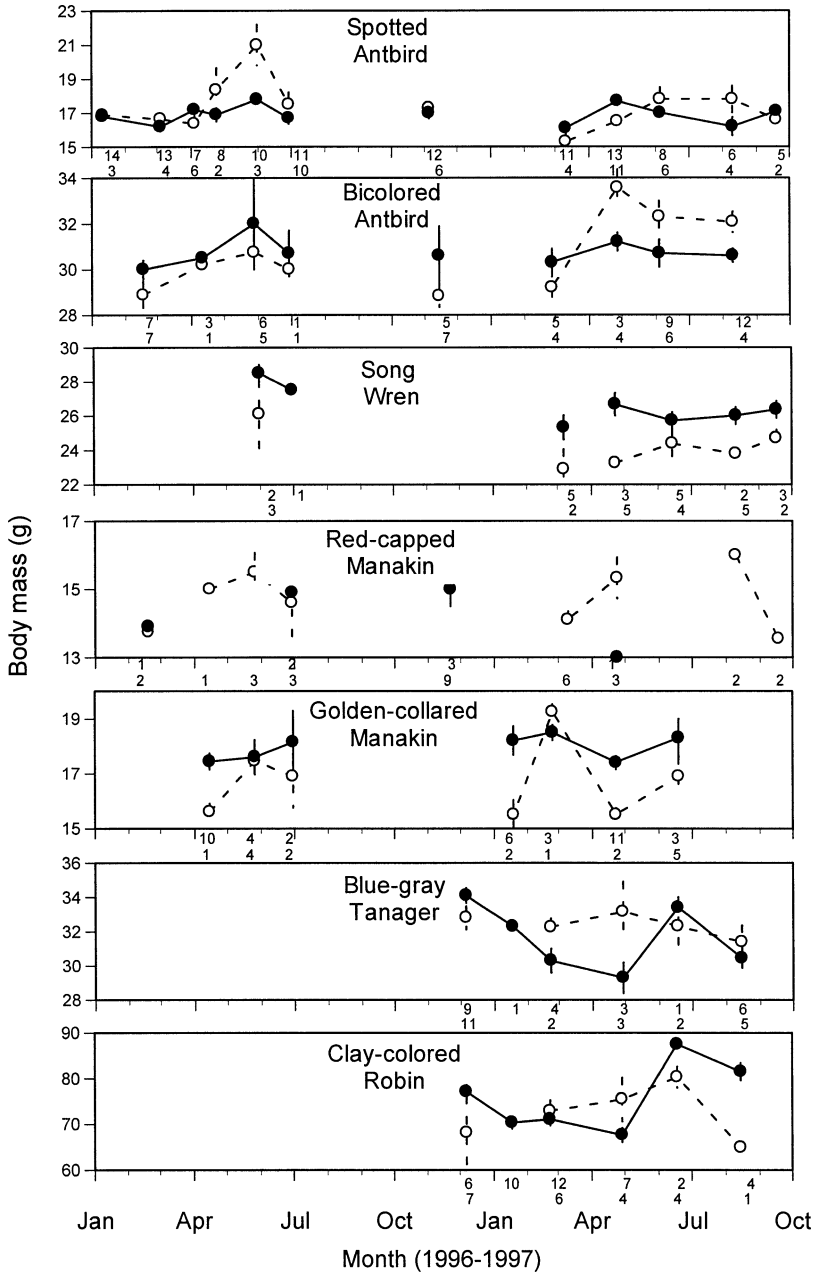


FIGURE 5. Seasonal changes (means \pm 95% CI) in body mass of males (filled circles) and females (open circles) of seven Neotropical passerines in central Panama, 1996–1997. Sample sizes are indicated below each graph, males over females.

ecological and phylogenetic backgrounds, these seven species showed similarities in (1) the general pattern of reproductive seasonality, (2) the synchrony of gonadal recrudescence, and (3) their low plasma testosterone concentrations

compared to temperate-zone birds of similar size. The seven species differed, however, in their degree of variation in testosterone concentrations throughout the year and in their relative testicular volumes: group-living and socially

monogamous species appeared to have low or no seasonal testosterone changes. However, group-living species that do not live in family groups (Blue-Gray Tanagers) and potentially polygynous (lekking) species (Manakins, Clay-colored Robins) may have large relative testes volumes compared to socially monogamous species or those that live in family groups (Song Wrens). Furthermore, our data suggest that edge species nest earlier than forest species and that gonad sizes of edge species regress earlier than in forest birds. An earlier onset of reproductive inactivity in edge species may also be indicated by their earlier onset of molt.

SIMILARITIES AMONG SPECIES: SEASONAL GONAD CHANGES

To our surprise, individuals of all species had entirely regressed gonads during some part of the year. For several species, gonads were entirely regressed for up to half a year (i.e., Spotted Antbird, Blue-gray Tanager, Clay-colored Robin). Such a reproductive strategy is markedly different from an opportunistic one where birds presumably keep gonads in a (near-) functional state year round (Immelmann 1971, Zann et al. 1995, see also Hahn 1995, 1998, Hau 2001). However, it is important to remember that our sampling scheme could not determine the exact duration of gonad regression because we had gaps between our sampling periods. Another commonality among species was that gonads generally recrudesced in the first months of the year. The breeding season for any particular species appeared to be long compared to the reproductive seasons of many temperate species. However, individuals of a given species may not breed synchronously, and thus the actual time spent breeding by individual birds within a population may be much shorter (Ricklefs 1968, 1969).

Several nonexclusive reasons may ultimately contribute to the fact that all seven Neotropical bird species recrudesced their gonads in the first few months of the year. First, migrants from the north-temperate zones could increase competition for food on their tropical wintering grounds and thus preclude gonadal recrudescence in tropical residents (Moreau 1950, Morton 1980). However, in Panama the total density of migrants wintering at sites in Soberania National Park is less than 3% of the total avian density (Robinson, Brawn, and Robinson 2000); thus in-

tense competition from migrants is unlikely. A second explanation for synchronized breeding in March and April may be the coincidence of increasing day length (Hau et al. 1998) and the increased food abundance during the first months of the year (Wolda 1989, Windsor 1990). A third reason for gonad recrudescence in spring could be changes in predation pressure; for example, if mammalian predators are highly food limited during the dry seasons (first months of the year) or if reptilian predators are more active during the hot dry seasons at the beginning of each year (Morton 1971, Huey and Slatkin 1976, Sieving 1992, Robinson, Robinson, et al. 2000). We cannot presently distinguish between these hypotheses but consider food peaks as the most likely selective agent.

DISSIMILARITIES AMONG SPECIES: TESTES SIZE, TESTOSTERONE LEVEL, AND GONAD REGRESSION

The seven species had large differences in relative testes size, which presumably reflect their respective mating systems (Stutchbury and Morton 1995). Year-round pair-bonded Spotted Antbirds showed the smallest relative testes volumes (about 0.7 mm³ per g body mass), while the polygynous Clay-colored Robins and Golden-collared Manakins had the largest and third-largest relative testes volumes, respectively (Fig. 2). Group-living Blue-gray Tanagers also had large relative testes volumes, which we speculate might be related to high sperm competition in Blue-gray Tanager groups (Stutchbury and Morton 2001), similar to Superb Fairy-wrens (*Malurus cyaneus*; Mulder and Cockburn 1993).

Interestingly, we found no relationship between mean maximal testes volume and plasma testosterone concentration. Relatively large testes did not secrete more testosterone than smaller testes. This lack of a relationship may be proximately explained by the fact that only a small and variable portion of the testes, the Leydig cells, produce testosterone (Murton and Westwood 1977). The largest tissue fraction of active testes are seminiferous tubules that are responsible for spermatogenesis (Lofts and Murton 1973). In addition to the quantitative uncoupling of plasma testosterone concentrations from testes volumes, we also found a temporal uncoupling of testes sizes and territoriality: Spotted Antbirds were territorial outside of the breeding season. Our data also suggested a difference in

the timing of gonadal regression, with edge species tending to terminate reproductive activities earlier than forest-interior species. We suggest that food supply, climatic conditions, or nest predation could be responsible for the differences.

HORMONAL CHANGES AND TERRITORIALITY

Territoriality occurred despite low testosterone concentrations in some tropical birds, confirming previous investigations. In a case study on the Neotropical Spotted Antbird we showed that high androgen concentrations only occur during brief bursts of territorial aggression, but not during the entire reproductive season (Wikelski, Hau, et al. 1999, Hau et al. 2000). However, it is unclear if this pattern is particular for this antbird species or whether it holds more generally. Few studies on tropical birds offer combined data on gonadal states, hormone concentrations, and territoriality for comparison with temperate-zone patterns. Dittami (1986, 1987) and Dittami and Gwinner (1990) compared six species of Afro-tropical birds. They found that in a seasonal tropical savannah at the equator, seasonal breeding seems to be the rule rather than the exception. Testosterone also changed seasonally in most of the species they studied, and overall testosterone concentrations were lower than for most temperate-zone birds. However, territorial aggression was uncoupled from testosterone in the Afro-tropical, near-equatorial White-browed Sparrow Weaver (*Plocepasser mahali*, Wingfield et al. 1991, 1992, Wingfield and Lewis 1993). These group-living birds are territorial year round, but show practically no increase in testosterone except for a short and modest rise in mid-breeding season. Similarly, Levin and Wingfield (1992) reported that Neotropical Bay Wrens (*Thryothorus nigricapillus*) were highly aggressive year round, but never had elevated testosterone concentrations. Spotted Antbirds reacted aggressively toward playback during any time of the year, even when they had no detectable plasma testosterone concentrations (Hau et al. 1998, 2000). Overall, this supports a flexible relationship between plasma testosterone and territorial aggression (Canoine and Gwinner 2002).

Our data double the number of tropical species for which annual changes in gonadal size and testosterone concentrations are now available (Dittami and Gwinner 1990, Wikelski, Hau,

and Wingfield 1999) for comparison with subtropical species (Ralph and Fancy 1994, McDonald et al. 2001). Although the total number of tropical species investigated is still very low, we suggest that a variety of interesting adaptive solutions exist for the interaction of hormones, behavior, and life history in tropical birds that goes beyond what is generally known for temperate-zone species (Stutchbury and Morton 2001, Wikelski and Ricklefs 2001, Ricklefs and Wikelski 2002).

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