

## HORMONAL CONTROL OF COURTSHIP IN MALE GOLDEN-COLLARED MANAKINS (*MANACUS VITELLINUS*)

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**Resumen.** – Control neural y hormonal del cortejo en el Saltarín Cuellidorado (*Manacus vitellinus*). – Muchos pájaros masculinos tropicales llevan a cabo elaboradas exhibiciones de cortejo. Estas exhibiciones pueden incluir señales visuales y acústicas implicando movimientos acrobáticos combinados con producción de vocal y sin vocal. Poco se sabe acerca de las adaptaciones hormonales y neuromusculares adyacente a las complejas exhibiciones en pájaros tropicales. Construyendo sobre las obras de los 1930s/40s por Frank Chapman y Percy Lowe, hemos estado investigando la fisiología del comportamiento del cortejo en el Saltarín Cuellidorado (*Manacus vitellinus*) de Panamá. Los saltarines masculinos producen exhibiciones diariamente en arenas dentro de leks de bosque para 6 o más meses. Usando video de alta velocidad, hemos analizado varios comportamientos del cortejo incluyendo múltiples movimientos complejos de baile y la producción de chasquidos resultando del rápido alzamiento de las alas. Los niveles de testosterona (T) en la sangre de los machos están generalmente elevados durante este periodo reproductor, están elementales por el resto del año, y están bajos en las hembras todo el año. Estos datos sugieren que T activa el cortejo del saltarín macho. Consistente con esta hipótesis, el tratamiento de pájaros no-reproductores con T activa varios comportamientos del cortejo. T probablemente estimula el cortejo por acciones en receptores de andrógeno. Receptores de andrógeno son expresados extensamente en el cerebro y la espina dorsal del saltarín, y tratamientos con flutamida bloqueadora de los receptores de andrógeno interrumpe el comportamiento normal del cortejo. Aunque T activa el cortejo, hay poca correspondencia entre el T circulante en un individuo y la frecuencia o intensidad de la actividad del cortejo. Los estudios están en camino a entender los factores que llevan a estas diferencias individuales en T y la tasa del despliegue.

**Abstract.** – Many male tropical birds perform elaborate courtship displays. These displays can include visual and acoustic signaling involving acrobatic movements combined with vocal and non-vocal sound production. Little is known about hormonal and neuromuscular adaptations underlying complex courtship displays in tropical birds. Building upon work from the 1930s/40s by Frank Chapman and Percy Lowe, we have been investigating the physiology of courtship behavior in Golden-collared Manakins (*Manacus vitellinus*) of Panama. Male manakins display daily on arenas within forest leks for 6 or more months. Using high-speed video, we have analyzed several courtship behaviors including multiple complex dance moves and the production of snapping sounds produced by rapid lifting of their wings. Blood levels of testosterone (T) in males are generally elevated during this reproductive period, are basal for the remainder of the year, and are low in females year round. These data suggest that T activates male manakin courtship. Con-

sistent with this hypothesis, T-treatment of non-reproductive birds activates several courtship behaviors. T likely stimulates courtship by actions on androgen receptors (AR). AR are expressed widely in the manakin brain and spinal cord and treatments with the AR-blocker flutamide disturb normal courtship behavior. Although T activates courtship, there is little correspondence between an individual's circulating T level and the frequency or intensity of courtship activity. Studies are underway to understand the factors that lead to these individual differences in T and display rate. *Accepted 2 November 2007.*

**Key words:** Steroids, testosterone, androgen receptors, hormonal control, vocalizations, courtship displays, Golden-collared Manakin, *Manacus vitellinus*.

## INTRODUCTION

This paper addresses the role of testicular hormones in controlling the complex courtship behavior of the Golden-collared Manakin (*Manacus vitellinus*) of Panama. It is important first to place these studies in the context of our current knowledge of this field if study.

*Hormonal control of courtship.* Gonadal hormones coordinate many facets of reproductive anatomy, physiology and behavior (Ball & Balthazart 2002, Wingfield & Silverin 2002). In male vertebrates, testosterone (T) is the dominant steroid secreted by the testes and T acts on a large number of neural and non-neural sites. We know a good deal about the behavioral neuroendocrinology of masculine reproduction in temperate breeding bird species. In these birds, T activates male-typical courtship and copulatory behaviors, as well as territorial aggressive behavior. This activation of behavior is often striking: in the absence of T in non-breeding or castrated birds, reproductive behaviors are absent, and the administration of T fully restores many behaviors (Ball & Balthazart 2002).

Recent work on tropical birds gives the impression that neuroendocrine control of behavior differs between tropical and temperate breeding birds (Borgia & Wingfield 1991, Moore *et al.* 2004, Goymann *et al.* 2004). Many birds of tropical lowlands are non-migratory, territorial year-round and, unlike temperate breeding male birds, T appears to circulate at

low levels throughout the year (Dittami & Gwinner 1990, Levin & Wingfield 1992, Wikelski *et al.* 2003, Goymann *et al.* 2004, Hau *et al.* 2004). Little is known about the neuro-hormonal basis of non-breeding territorial aggression in tropical birds though other hormones may be involved (Hau *et al.* 2004). Clearly we need additional studies of the physiology of behavior in tropical birds.

For the past several years, we have been examining neuromuscular and hormonal control of the unusual courtship display of the male Golden-collared Manakin (*Manacus vitellinus*). This *Manacus* species lives in forests of Panama and the males perform a spectacular courtship display. These fascinating birds and their unusual behaviors were first described in detail by Frank Chapman (1935). Stimulated by Chapman's fascination with the mechanics of manakin courtship (and using manakin carcasses sent to him by Chapman), Percy Lowe described specializations of the male Golden-collared Manakin musculoskeletal system that he thought might underlie their remarkable wingsnapping behavior (Lowe 1942). Since then, several investigators have examined these and related species, but the mechanisms of sound production is only just beginning to be understood (e.g., Bostwick & Prum 2003). Questions remain as to why and how these males are able to perform such distinctive behaviors for months on end. Presumably, access to females and copulation are the ultimate forces driving this behavior. Sexual selection is a fundamental evolutionary mechanism and the basis of a

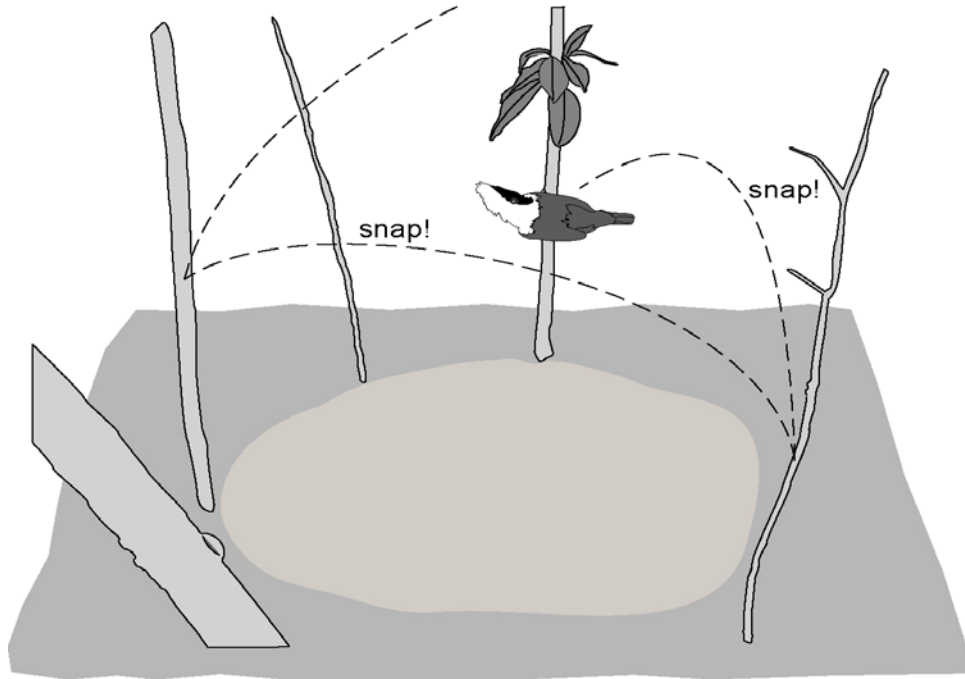


FIG 1. A schematic representation of the jump-snap display. Starting from a vertical sapling, the male jumps to another sapling producing a loud wing snap in midair. The males emit a “cheepoo” vocalization and other vocal and non-vocal sounds (from Fusani *et al.* 2007b).

significant body of research to understand how female preferences and male traits co-evolve (e.g., Coleman *et al.* 2004). We wonder, however, about hormonal and neuromuscular specializations that motivate male manakins to court and then allows them to perform the displays as they do.

#### COURTSHIP BEHAVIOR

The courtship display of the Golden-collared Manakin (*Manacus vitellinus*) includes unusual acrobatic dance moves punctuated by remarkably loud sounds produced by movements of their wings (Chapman 1935, Schlinger *et al.* 2001). These wingsounds occur singly as “wingsnaps” or in a series called “rollsnaps”. Males are brightly-colored yellow, black and green, whereas females and young males are

dull-green. In mid-January males gather into groups (leks) of 2–20 birds, each clearing and occupying one (rarely two) small courtship arenas (Fig. 1). The birds actively display daily until July when courting subsides to low levels from September to early January. We have identified and actively studied many manakin leks in forests near facilities run by the Smithsonian Tropical Research Institute in central Panama not far from Barro Colorado Island where Chapman did his work.

Many details of *Manacus* courtship are too rapid to distinguish with the naked eye making it virtually impossible to accurately describe the bird’s movements with convention recording equipment. We have used high-speed digital equipment in collaboration with Ted Goslow from Brown University and with

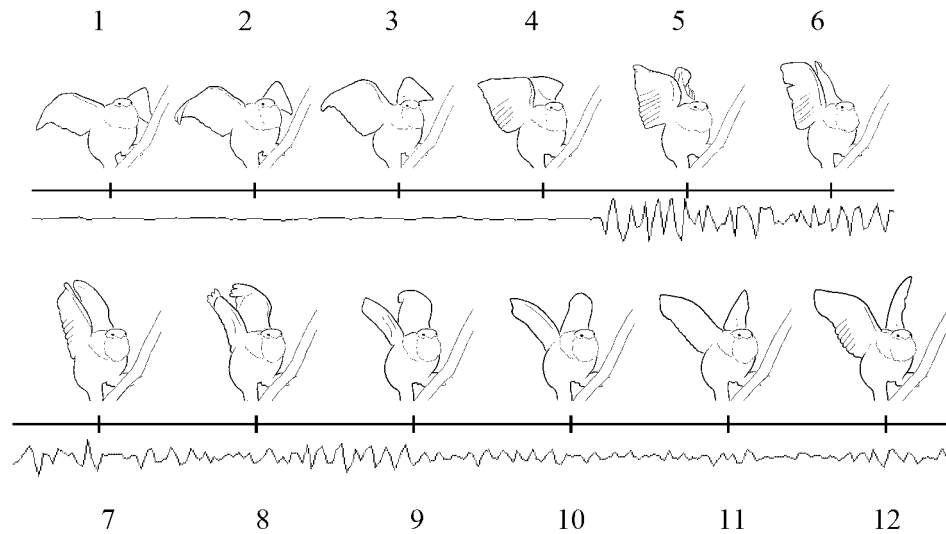


FIG. 2. Artists rendering of a frame-by-frame analysis of a single wingsnap within a longer manakin wingroll display. The synchronized sound oscillogram is below. These images were collected at 500 frames/s giving a 2 ms resolution for a total of 22 ms fully.

equipment similar to that used effectively to record behavior of other manakin species (Bostwick & Prum 2003). We established a connection between the strobe output from the camera and audio equipment creating a precise frame-by-frame synchronization of the high-speed camera with independent acoustic recording equipment. We have obtained a considerable number of video recordings of these birds in the field performing a full range of courtship behaviors, including individual wingsnaps, rollsnaps, dances involving males and females, and even copulations. Many of these were captured at 1000 frames/s (fps), with visual sequences synchronized with audio recordings giving a 1 ms accuracy for behavioral analyses. Figure 2 illustrates schematically a series of single frames of a single snap (in this case at 500 fps) within a longer wingroll display. Note this entire sequence lasts 22 ms; the snap appears between images 4 and 5 on the top panel.

The key features of these analyses are the following. Adult males perform their dance (flights and wingsnaps around the arena) with extraordinary speed, precision and grace. It is obvious that these displays demand great physical coordination and ultrafast visual and physical processing. Green birds (females but possibly also juvenile males) join adult males in the dance, but their performance is relatively uncontrolled. Young males may join adults to learn and to practice performing these difficult behaviors. To assess this possibility, we hope to capture repeated high-speed recordings of known (color-banded) young males as they mature. We have also documented new behaviors for this species including cartwheels (a midair half-twist jump from perch to the ground) and vertical hovering flights. Many of these behaviors have been recorded from multiple wild adult males and we have documented significant individual differences in the duration of jumps, the time required to assume beard-up posture after a

jump, and in jump speed (Fusani et al. 2007b). These differences probably indicate quality traits to females (neuromuscular coordination, physiological condition or age), and thus may form the basis for female mate choice. But questions still remain. For example, 1) how do neuroendocrine systems function over the course of the lengthy (6–8 month) courtship season, 2) which behaviors are aggressive or sexual, and 3) what physical adaptations allow male manakins to perform these behaviors? We are combining behavioral, physiological and anatomical studies in the lab and in the field in our efforts to answer these questions.

#### HORMONAL CONTROL OF AVIAN COURTSHIP

To understand the potential role of gonadal hormones, we must consider what we know of the hormonal control of behavior in other birds. First, we know that gonadal steroids can act during early development of birds to permanently masculinize or feminize some neural circuits (organizational actions) that control sex-specific reproductive behaviors (Schlinger 1998). In addition, gonadal steroids secreted during the breeding season transiently activate reproductive behaviors (activational effects). Studies of captive doves show that T did indeed activate courtship but likely after conversion into other steroidal compounds in brain. In the dove's brain, circulating T is converted into estradiol (E2) by the action of the estrogen synthetic aromatase; this E2 then binds to neural estrogen receptors (ER) to activate non-aggressive components of courtship (Cheng & Lehrman 1975, Hutchison & Steimer 1984). Aggressive components of courtship were stimulated by T or by 5 $\alpha$ -DHT (DHT) acting directly on androgen receptors (AR). 5 $\alpha$ -reductase is present in brain where it can convert circulating T into the potent androgen DHT. DHT

seems to be most important in activating courtship in other species as well, such as in the well-studied Japanese Quail (*Coturnix japonica*) (Ball & Balthazart 2002). In many oscine songbirds, aromatase and 5 $\alpha$ -reductase are present in brain allowing T action on both AR and ER, a requirement for full activation of courtship song (Schlinger & Brenowitz 2002).

Unlike doves, courtship in manakins is exceedingly complex with a remarkable mixture of visual and acoustic signals, including vocalizations, and sonations so it seems likely that hormonal control will be equally complex. Hormones likely act centrally to motivate males to perform displays, and then peripherally on many neuromuscular systems to facilitate the acrobatic performance. Different components of the displays may be associated with different motivational contexts that might be modulated by independent actions of androgens and estrogens. As in doves, androgens may activate behaviors that are aggressive in nature whereas estrogens may activate behaviors that attract or stimulate females (Cheng & Lehrman 1975, Hutchison & Steimer 1984). As with the hormonal control of territorial aggression, we expect there may be differences in the hormonal control of courtship between tropical and temperate breeding species as so few tropical forest species have been studied (Borgia & Wingfield 1991). We have now accumulated considerable evidence that T activates the complex courtship of male Gonden-collared Manakins. Our evidence comes from studies in both the lab and in the field; from measures of natural circulating steroid levels and behavioral studies in which hormones or their mechanisms of action are manipulated.

#### SEASONAL CHANGES IN CIRCULATING T

We have collected blood samples from many

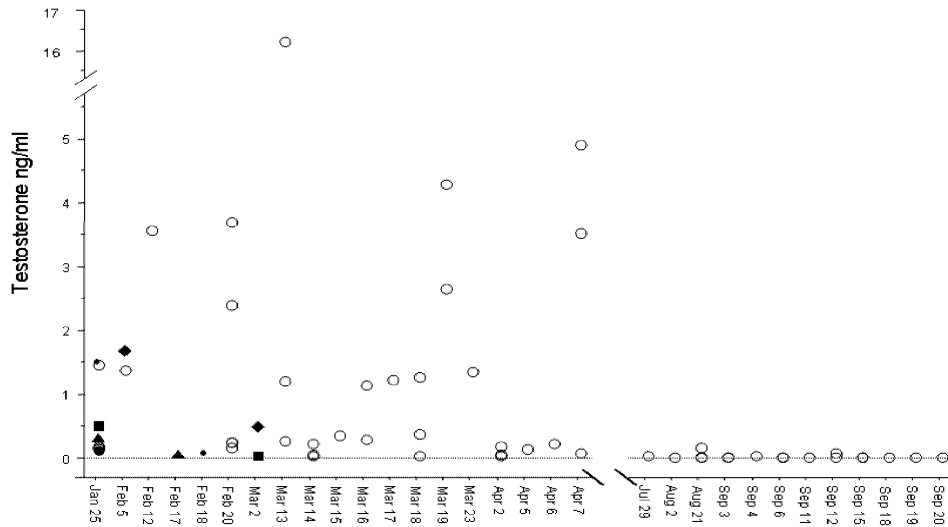


FIG. 3. Plasma T in wild male manakins during courtship (January–April) and non-courtship (July–September) seasons (from Day *et al.* 2007). Solid symbols represent individual males bled twice (see also Fig. 5).

males and females throughout much of the courting and non-courting seasons (Day *et al.* 2007). There are unequivocal sex and seasonal differences in plasma T levels in Golden-collared Manakins (Fig. 3). All birds bled during the non-courtship season (August to September) have very low or undetectable circulating T levels. In contrast, during the male courtship season (from mid-January through April), many adult males have elevated T in blood. During this same time females and juvenile males still have low to undetectable levels of circulating T. This pattern is not altogether different from what is seen in temperate breeding species. Given that T is elevated when males are establishing leks and initiating courtship, it suggests that T is responsible for activating courtship behavior. In temperate lekking species, T is typically elevated throughout the courtship season (Alatalo *et al.* 1996). On the contrary, T levels seem to decrease once leks are established and they become highly variable for the remainder of

the courtship season. This variability in T levels of adult male manakins collected while courting on leks does not fit with the idea that T is required to maintain courtship. Despite high levels of courtship activity, males have widely varying amounts of T in blood, with many males (~30%) having no measurable T in plasma (also Wikelski *et al.* 2003). These perplexing results require additional study.

#### EXPERIMENTAL MANIPULATIONS OF T

To test the hypothesis that T activates male courtship, we collected non-breeding birds, marked them individually with colored leg-bands, bled them for hormone analysis and gave them either blank or T-filled slow release implants. Some birds were brought to the lab; the remaining birds were released for field observations. Courtship behaviors were quantified for 3 weeks in the field (adult & juvenile males) by direct observation and in the lab

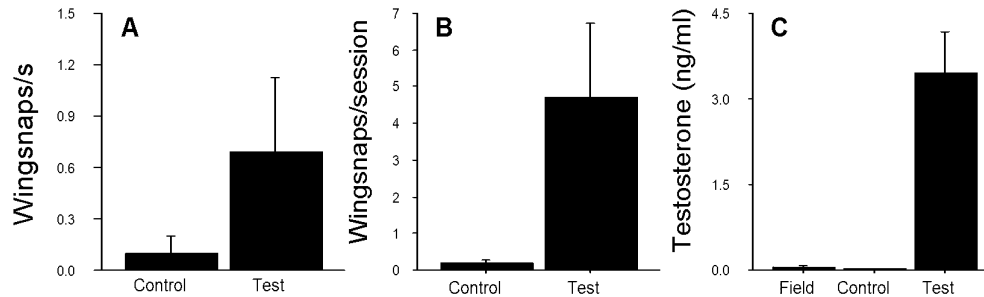


FIG. 4. Wingsnaps of male manakins during the non-breeding season in the field (A) and captivity (B) treated with implants that were blank (Control) or filled with T (Test). Plasma T levels (C) in males captured in the field, 11 days after receiving a blank implant (Control) or one filled with T (Test) (from Day *et al.* 2006).

(juvenile males) by watching videotapes captured 3 times daily. Captive birds were bled again 11 days after implantation. We used a PCR-based technique to identify the sex of green birds that were either females or juvenile males (Day *et al.* 2006). We knew that circulating T was low or undetectable in all birds at this time of year (Day *et al.* 2006) and, in both the field and in the lab (Fig. 4), control birds displayed very little courtship behavior. After 11 days of treatment, T was significantly elevated in T-implanted birds (Fig. 4) and both wild and captive T-implanted birds produced significantly more wingsnaps and rollsnaps than unimplanted birds (Day *et al.* 2006). These data fit well with the conclusion that T does indeed activate male manakin courtship behavior.

As we knew that T activated courtship in non-breeding males with low T levels, in another experiment we tested whether exogenous T could increase display behavior in adult “courting” males, some of whom we knew had very low levels of circulating T. Surprisingly, in both the lab and field, exogenous T had no effect on display behavior of adult males even if at the outset they had no detectable T in blood (Day *et al.* 2007). In this experiment, we also tested the effects of T on females and on juvenile males. As expected,

juvenile T-treated males displayed in captivity. Quite unexpectedly, T-treated females performed wingsnaps and rollsnaps, behaviors central to the masculine courtship display. It was a surprise to discover that T could activate these masculine courtship behaviors in female manakins. We do not believe that females ordinarily perform wingsnaps or rollsnaps in the wild, untreated females do not snap in captivity. However, females may snap in the wild and other researchers and we may have mistaken snapping females for juvenile males.

One conclusion we can make is that both males and females have the potential to wing- and rollsnap, so the neural circuits controlling these movements are probably not subject to organizational actions of hormones developmentally. Apparently, these two behaviors are under activational control by T. This observation is exciting to us, because it indicates that T might activate other behaviors of the male’s display in females. In our view, this would be surprising. Given the complexity of the behaviors involved, females would not need or want the additional neural circuitry that might be required to orchestrate male courtship. We might expect that gonadal hormones or direct genetic mechanisms might organize these circuits in males, but not in females, as is

the case for other avian reproductive behaviors (Arnold 2000). We have found sex differences in manakin spinal cord and wing musculature (Schultz & Schlinger 1999, Schultz *et al.* 2001), but assume now that they are transient differences directly or indirectly produced by T. Males of many manakin species (Pipridae) perform diverse and extraordinary courtship displays and several have anatomical adaptations presumably evolved for these behavioral performances (Bostwick & Prum 2003, 2005). Our results with female Golden-collared Manakins raise fundamental questions about the way in which these specializations develop in males of other manakin species.

#### SITES AND MECHANISMS OF T ACTION

We have evidence that T acts at least in part through androgen receptors (AR) to activate courtship (Fusani *et al.* 2007a). In field and lab experiments, we tested the effects of the AR blocker, flutamide, on the expression of courtship behavior. Birds were bled to obtain hormone measures, then implanted with flutamide or control pellets, retained in captivity or released, behavioral tested for about 3 weeks, and bled a second time when behavioral observations were completed. Importantly, at the end of the experiments, plasma T levels were the same as or lower than at the start, indicating the flutamide did not disturb hypothalamic control of pituitary and gonadal function. In wild birds, courtship behaviors of flutamide-treated birds were significantly lower than control-treated birds. After 2 weeks of flutamide treatment, levels of courtship behavior increased and by the 3rd week courtship was significantly elevated compared to control birds or to the behaviors of flutamide-treated birds during week one. The effects during week one are fully consistent with the view that interfering with AR

reduces courtship. The results in weeks 2 and 3 are more difficult to interpret but flutamide likely begins acting as an AR agonist. Nevertheless, it is clear that disturbing the normal function of AR in male manakins disturbs the normal performance of courtship behavior.

AR seems to be expressed uniquely in the manakin CNS (Fusani unpubl.). We have examined potential sites of sex steroid action in manakins by mapping the distribution of AR, ER and aromatase in the brains and spinal cords of adult males and females. Previously, we found that  $^3\text{H-T}$  accumulated in the spinal cords with greater accumulation in males than in females, particularly in the cervical enlargement (Schultz & Schlinger 1999). We have since mapped the spinal distribution of the motor neurons controlling the principal wing muscles, the pectoralis, SC and SHC by injecting these muscles with retrogradely transported fluorescent dyes (unpublished observations). We combined tracer experiments with *in situ* hybridization using avian probes to AR and found that the motor neurons innervating these wing muscles all express AR. Indeed, we have performed *in situ* hybridization for AR, ER and aromatase on spinal cords and on brains of male manakins and compared these distributions to other birds (unpubl.). Whereas the distributions of ER and aromatase were similar across species, AR was expressed at decidedly greater levels in several regions of the manakin brain, especially throughout the arcopallium, in cerebellar Purkinje cells and in the midbrain nucleus intercollicularis. These sites may be particularly important for controlling manakin courtship.

#### MAINTENANCE OF COURTSHIP

Once activated, courtship behavior may persist independently of gonadal T. Not only do



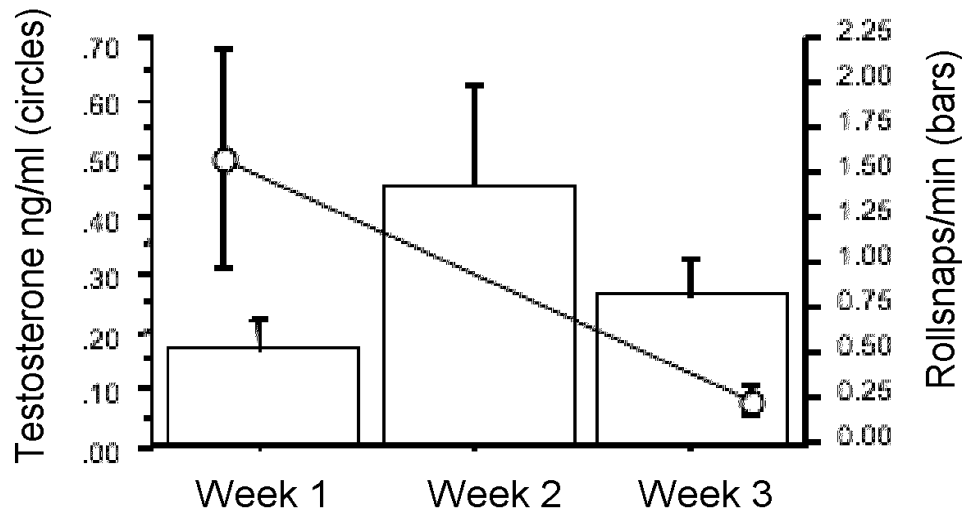


FIG. 5. Plasma T levels (ng/ml, mean  $\pm$  SEM, left axis, open circles) and rollsnaps per min (right axis, bars) of individually marked adult male manakins at the onset of lek formation in Jan (from Fusani *et al.* 2007a).

many courting males have low T in blood, but we also have direct evidence for this conclusion. Males captured at the onset of the breeding season (late January) were bled for hormone analysis, released, and their behavior observed for 3 weeks. After this time they were recaptured and bled again. Compared to non-breeding birds, plasma T levels were elevated initially (Figs 3 & 5) and males displayed high levels of courtship behavior, similar to T-treated non-breeding males (Day *et al.* 2006). After 3 weeks, however, plasma T levels declined in all birds to near basal levels, though males were on their arenas and actively engaged in courtship behavior (Fusani *et al.* 2007a). Indeed, courtship activity remains essentially unchanged from late January levels until at least mid-April (anecdotally courtship activity seems to remain elevated as late as early July).

It is likely that simple models of hormone activation derived from temperate breeding species may not apply to male manakins. We wonder if other steroid hormones control

manakin courtship when T is basal, or if non-hormonal factors maintain courtship after initial activation by T. Our future experiments will target these hypotheses.

## CONCLUSION

In summary, the elaborate and physically challenging courtship display of the male Gonden-collared Manakin appears to be activated by T at the onset of the courtship season. Whether courtship remains dependent on T throughout the long courtship season is unknown. Courtship is likely activated by androgens because AR are expressed in abundance and uniquely in the manakin CNS, and an androgen receptor blocker flutamide can modulate courtship behavior. Remarkably, once treated with T, females can perform some of the ultrafast wingsnapping behaviors typical of males. The larger sizes and different chemistry of the muscles that lift the wings in males probably arise from their differential usage rather than functioning as adaptations

needed for fast contraction. Finally, we still do not understand the physics underlying the acoustics of manakin wingsnapping nor do we know just how manakin neuromuscular systems function to create this phenomenal set of behaviors. Manakins will captivate us and stimulate scientific investigation for years to come.

#### ACKNOWLEDGMENTS

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