



Minireview

Behavior, natural history and neuroendocrinology of a tropical bird

Barney A. Schlinger^{a,*}, Lainy B. Day^b, Leonida Fusani^c^a Department of Physiological Science and the Laboratory of Neuroendocrinology of the Brain Research Institute, University of California, 621 Charles Young Drive South, Los Angeles, CA 90095-1606, USA^b Department of Biology, University of Mississippi, Oxford, MS, USA^c Department of Biology and Evolution, University of Ferrara, Ferrara, Italy

ARTICLE INFO

Article history:

Received 22 January 2008

Revised 21 May 2008

Accepted 22 May 2008

Available online 29 May 2008

Keywords:

Sex steroids
Reproductive behavior
Courtship
Testosterone
Manakins

ABSTRACT

Male Golden-collared manakins (*Manacus vitellinus*) of Panama perform an acrobatic and noisy courtship display, the result of an intense process of sexual selection. These birds have a lek mating system with the reproductive success of males depending almost entirely on their courtship. We have studied this remarkable behavior and investigated seasonal cycles of testosterone secretion, hormonal activation of courtship and neuromuscular adaptations that underlie the performance of male courtship behavior. We describe these studies in the context of the natural history of this fascinating lowland tropical species. Our studies have shown that manakin courtship requires a series of morphological and physiological specializations and represents an exceptional model system for studying the hormonal control of elaborate courtship displays.

© 2008 Elsevier Inc. All rights reserved.

1. Introduction

A particularly gratifying approach to studies in comparative biology is the capacity to focus on a single species relating an animal's ecology to phenotypic, anatomical, physiological, cellular, molecular and genetic characters that establish the full biology of that species. These kind of multidimensional studies of birds were enabled by pioneers in avian biology, such as Margaret Morse Nice. Although Nice published widely on a variety of bird species, her detailed accounts of the life history of the song sparrow established her as a leading ornithologist of the last century (e.g. Nice, 1943). She was one of a small cadre of biologists who shifted ornithological research from the collection and preparation of specimens and analyzes of museum study skins to the detailed investigation of the intimate facets of a bird's behavior and ecology in nature.

John Wingfield picked up where Margaret Morse Nice left off carrying the torch of song sparrow biology into the realm of comparative endocrinology and beyond (e.g. Wingfield, 1984a,b). In addition to his many interests and contributions in avian biology, Wingfield's advances in avian blood hormone analysis (Wingfield and Farner, 1976) came at a time when there was an explosion of technological advances in endocrinology, neurobiology and molecular biology. By casting these techniques with sound hypothesis driven questions, his work, more than any other, opened the

door for the next generation of avian biologists to perform physiological, neuroanatomical and molecular studies on wild birds to understand mechanisms underlying their behavioral and life history traits that intrigue so many of us.

We have used the foundation laid by pioneers in avian biology to build our own story about the biological basis of an individual species complex behavior and life history. The Golden-collared manakin (*Manacus vitellinus*) is a Panamanian forest bird belonging to a larger group of "bearded" manakins found elsewhere in South and Central America and the Caribbean. During their lengthy breeding seasons, males of these species gather in leks and perform elaborate courtship displays to attract females for copulations. Courtship includes rapid visual and loud acoustic elements produced by extraordinary physical movements involving extensive neuromuscular coordination. Birds living in the tropics can differ from their temperate counterparts with respect to the hormonal control of reproductive behavior (Goymann et al., 2004). With this in mind, and upon witnessing this remarkable behavior in the field, one is prone to ask many questions in basic biology. How has sexual selection shaped this elaborate courtship? Do males possess unique anatomical features enabling the behavior? Are there unique neural circuits that, like the neural circuits controlling song in oscine songbirds, orchestrate performance of these behaviors? Is the activation and maintenance of courtship dependent on testosterone as it is for lekking birds of temperate regions? Our studies over the past 12 years have examined the behavioral, endocrine, neural and muscular adaptations that underlie the remarkable courtship of manakins. Although we still have a long

* Corresponding author. Fax: +1 310 206 9184.

E-mail address: schlinge@lifesci.ucla.edu (B.A. Schlinger).

way to go, we can begin to answer some of these questions. The following sections provide details of Golden-collared manakin natural history and behavior. We then focus on our studies examining circulating testosterone (T), its role in controlling male courtship behavior and specialized sites where T may act to stimulate male behavior.

We recognize that our studies are grounded in the work of several important avian biologists. Frank Chapman gave the first descriptions of the life history, morphology and behavior of *M. vitellinus* (Chapman, 1935). His work on Barro Colorado Island in the Panama Canal, near our study sites on the mainland, relied extensively on logistical support from the Smithsonian Institute, as do ours now. Chapman's field studies were followed up by additional work by Percy Lowe (1942) who examined anatomical characters unique to male manakins. Additional extensive studies of the behavior of related *Manacus* species has contributed to our full understanding of the behavior of this group of birds (Snow, 1962; Lill, 1974; Bostwick and Prum, 2003). And of course we follow in the footsteps of the many elegant field studies in avian behavioral endocrinology, long a trait of the Wingfield lab. We draw upon the insight of all these investigators and others to fully understand the behavioral neuroendocrinology of *M. vitellinus* hereafter referred to as manakin.

2. Manakin life history

Manakins are a common understory species in forests of Central Panama. They are frugivores, feeding largely on berries and small fruits that they find from ground level to high in the canopy. Adult males are brightly colored with black, yellow and green with bright orange legs. They aggregate in leks and display on arenas that they construct by clearing leaves and debris from the forest floor between several small vertical saplings (Fig. 1). Individual arenas are used by the same male for many years on end. These display arenas are clustered together with those of other males in a patch of forest of varying size that depends on the number of males, anywhere from 2 to 20 birds, with arenas of individual males separated by 1–10 m (Chapman, 1935). Leaks are separated by several 100 m or more. Adult males arrive on their arenas near the beginning of the dry season usually in mid January (Fig. 1). Upon occupying their leks, males display daily, most actively in early morning and early afternoon, until July or August, when the displaying by adult males decreases. Thus, males remain on or near their courts through the dry season and into the wet season that begins typically in April and May. From July to September, many young males are found within the leks, but adult males begin to spend more and more time away from their arenas. From October to December, when rains are at their heaviest in Central Panama, the birds appear to disperse to search for fruit which, at this time of year, is difficult to find. Reliably they return the following January to their original leks. Chapman (1935) describes this seasonal movement as a "migration in miniature...the regular return to their mating grounds, at approximately the same time each year, to establish territories to which the female will be invited, is prompted by fundamentally the same motive that induces a migratory bird to return to its nesting grounds".

An important advantage to our studies is the strength of this site faithfulness shown by adult males. Males are strongly tied to their arenas and leks, they are highly tolerant of outside disturbance, including the frequent presence of curious STRI scientists, and we can gather behavioral and endocrine data repeatedly from the same male for years on end. Males do not abandon longheld arenas (manakins as a group are long-lived species e.g. McDonald, 2007) even when massive construction sites associated with Panama Canal maintenance are located meters from their lek with

roads cut and large trucks passing by throughout the day. A particularly productive lek that we have studied for many years is now located adjacent to an artificial Indian village with music and dancing created for tourists by an Eco-friendly hotel. Over the last dozen years, our research activity involving more than 15 different leks, including the collection of individuals for anatomical studies, has produced no evident effect on lek activity. In some cases, birds have been moved to captivity for behavioral studies. After release weeks to months later, males have returned to their original leks and appear to be behaving normally.

Female manakins and juvenile males are uniformly colored a dull green. They are impossible to distinguish in the field, which may have led to some misinterpretations by previous investigators (Chapman, 1935; and see below). Females are attracted to leks where they interact with and then choose males for copulations. Females depart and then engage in all nesting activities alone. Young males wander in and around leks, sometimes performing courtship displays away from arenas. Sometimes young males create arenas on the periphery of established leks and there seem to practice display elements. Young males may mimic females and join adult males in their courtship dance, perhaps to learn displays from successful adult males.

3. Male courtship behavior

The display of the male has been described in detail elsewhere (Chapman, 1935; Schlinger et al., 2001). Of importance here is that males generate exceptionally loud snapping sounds (wingsnaps) by rapid and forceful lifting of their wings. These single or rolled snaps occur when the wrists strike each other above the bird's back (Bostwick and Prum, 2003). The mechanism of sound production is still not fully understood, as it seems unlikely that the wingbones possess enough mass to create the sound simply by their impact. Chapman (1935) hypothesized that it was the primary wing feathers (remiges) striking each other that produce the snap, but our evidence described below argues against this conclusion. We are exploring mechanisms for this sound production using mathematical models and engineering "robotic" manakin wings.

Single snaps are produced in midair by males as they rapidly leap from sapling to sapling on their arenas. These "dances" around the arena are produced when females are present and observing the male. When a male on the lek is courting a female, other male's will descend to their own arenas and display presumably attempting to acoustically lure the female away from her current suitor. The female may join the male in the dance and then rarely, she allows a male to copulate. Specific features of these displays occur too rapidly for us to visualize with the naked eye. Portable high-speed video/audio recording equipment has enabled us to document multiple complete display sequences of a number of wild males (Fusani et al., 2007a). These recordings clearly reveal a number of important features. Most notably, the performance by the males is almost unbelievably fast, acrobatic and elegant. Moreover, we know that males differ significantly in the speed with which different aspects of the display are performed (Fusani et al., 2007a) with significant individual differences in the duration of jumps, the time required to restore their beard-up posture after a jump, and in jump speed (Fig. 2). Some of these differences are on the order of tens of milliseconds. For example, these "bearded" manakins have elongated gular feathers that they can extend downwards and forwards, appearing much like the dewlap display of many lizards. Males extend these feathers through much of the dance, as they soar between saplings and while perched between jumps. At each landing, the male twists in midair so that upon landing, he is still facing the female who has landed behind him. Males differ significantly in the time it takes to restore their pos-

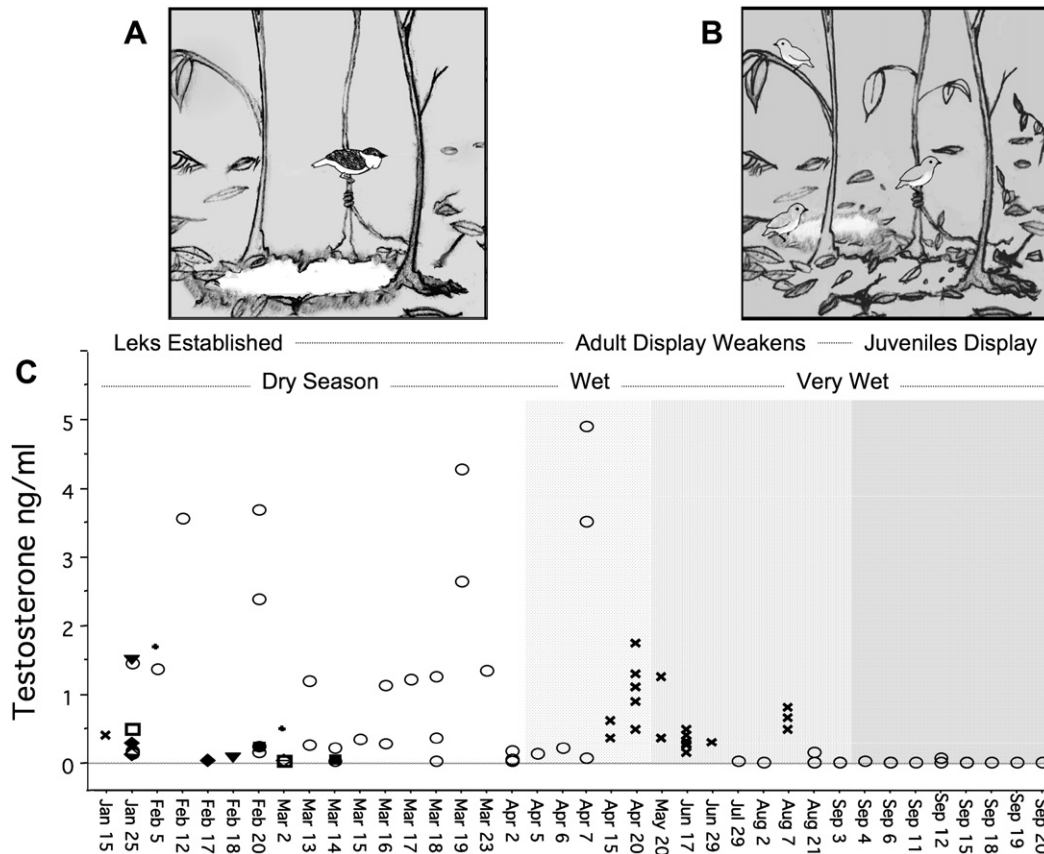


Fig. 1. Seasonal patterns of behavior, weather and testosterone (T) levels in Golden-collared manakins. In the dry season, (A) adult males scratch out an arena defended from other males where they display to attract females (not shown) for mating. Arenas are not defended by adult males during the wet season (B) but juvenile males occupy leks as shown displaying sporadically alone or in groups on old arenas, newly created arenas and in trees. (C) Testosterone levels of adult males only at indicated time points. Circles (o) = data from Day et al. (2006, 2007). Crosses (x) = values estimated from Wikelski et al. (2003). Other solid symbols indicate samples taken from the same individual at two time points with unique symbols for each individual (Fusani et al., 2007a,b). All of these individuals sampled twice had higher T levels in January/February than when sampled three weeks later February/March.

ture and elevate the beard upon landing at the end of each jump with the slowest male regularly taking about 63 ms and the fastest regularly taking about 43 ms (Fig. 2).

We believe that these differences are the basis of female choice. How the speed and accuracy of these physical movements provides information to females for sexual selection is unclear. We marvel at the processing capacity of the female's visual system allowing them to discriminate individual male behaviors. There is no doubt that this selection pressure is strong and has produced these spectacular and unique behaviors.

4. Hormones and behavior

Only males join leks and clear arenas; females seem to wander the forest in and around leks in search of food and nest sites, periodically visiting leks to examine males. To the best of our knowledge, in the field rolled snaps and the single wingsnaps of courtship dances are performed only by males (see also Chapman, 1935) and largely only between January and August surrounding dates when females nest and produce young. Thus, January through July/August is the breeding season for manakins leading to the expectation that during this period, the testes are enlarged and secreting testosterone (T) stimulating adult males to occupy leks, clear arenas and perform courtship behaviors. We have collected two lines of evidence to support this view.

First, we have collected blood samples from adult males and females and juvenile males during many months of the year (Fig. 1).

As expected from the hypothesis that T drives lek formation and activates courtship in males, in general, between January through April T levels are elevated in adult males when leks are occupied and lower in July through September when courtship wanes (Wikelski et al., 2003; Day et al., 2007). Compared to adult males, blood levels of T during the courtship season are significantly lower in both females who do not court and variable in juvenile males that do not yet occupy arenas (Day et al., 2007). Second, males displaying during the months of July–September that have low T levels have been collected, implanted with T or control (blank) implants and either held in captivity or released back into the wild. In both cases, birds treated with T showed significantly greater levels of several courtship behaviors as compared to control birds (Day et al., 2006) confirming that T can activate male manakin courtship and likely does so naturally in wild birds.

Although the data supports the general view that T activates courtship behavior in males, we also have evidence to suggest that the relationship between levels of T and behavior is weak. Surprisingly, many males taken from leks during the courtship season have low or even undetectable levels of T (Day et al., 2007). Furthermore, one group of individually marked males bled at the beginning and end of a one month period over which behaviors were recorded every 3 days showed a dramatic decline in T but their courtship behavior remained nearly constant (Fusani et al., 2007b; Fig. 1). We believe that T is elevated in males at the beginning of the dry season to motivate the onset of courtship; presumably, occupancy of arenas involves hormonal activation of

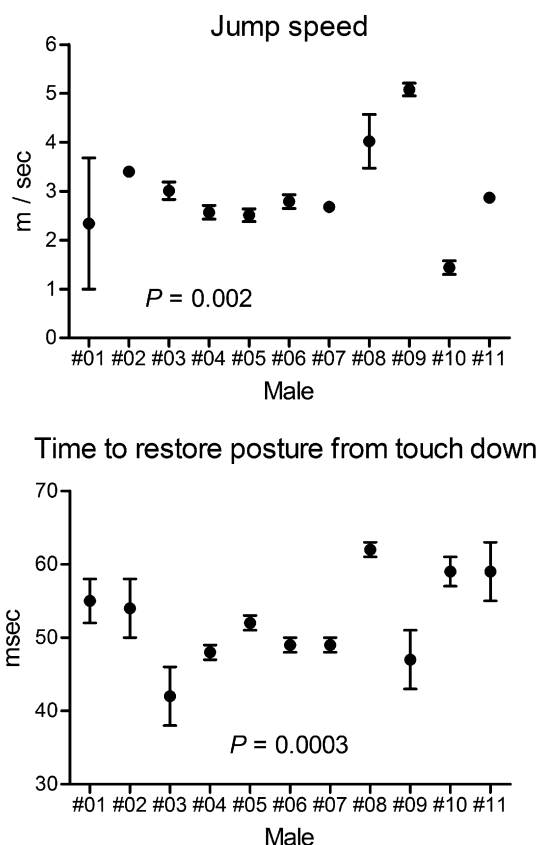


Fig. 2. Individual mean values (\pm SEM) for the variables jump speed (top) and time to restore posture after touch down (bottom) in male manakins. There are significant differences between individuals which could represent parameters of male quality and be used by female for mate choice. *P*-values are from Kruskal–Wallis non-parametric ANOVA. From Fusani et al. (2007a,b).

territorial behavior stimulating aggressive interactions with nearby adult males. Afterwards, however, T levels fluctuated widely, likely in response to interactions with males and with females, with no apparent decrement in the rate or quality of courtship behavior. This pattern of circulating T in manakins differs from that found in lekking species of temperate zones, which typically have elevated T levels throughout the lekking period. Persistent high T levels across this lengthy reproductive period of manakins is likely harmful to males (Goymann et al., 2004) so they may have evolved mechanisms to secrete just enough hormone to retain reproductive competence and courtship behavior while limiting the costs of high T. This perspective may have implications for our more general consideration of T in tropical birds. Generally, males of tropical wet lowland species have very low levels of T year round (Goymann et al., 2004; see also this issue). Male manakins and a few other species clearly have a season of elevated T, much like many temperate species (Wingfield and Farner, 1993). Nevertheless, there is substantial variability of T levels in breeding males likely reflecting interesting regulation of the hypothalamic–pituitary–gonadal axis required by a species with such a lengthy season of reproduction. We are pursuing additional studies to evaluate these ideas.

In some of these experiments we have implanted both males and females with T. Adult female and juvenile male *Manacus* have a similar dull green plumage and can be distinguished reliably only by genetic sexing or by laparotomy. Interestingly, after only a few days, females implanted with T can perform wing- and roll-snaps that are similar to the same sounds in males (Day et al., 2006). Thus, sex-differences in the expression of these courtship behav-

iors seems to depend largely on the activational effects of T, although the full courtship display has never been demonstrated in females. Apparently, and perhaps somewhat surprisingly, manakins do not possess permanent sexually dimorphic neuromuscular systems enabling wingsnapping. Such sex-differences underlie the performance of some vertebrate reproductive behaviors and are established developmentally by hormones or by constitutive sexually dimorphic growth (Schlinger, 1998). In this respect manakins are similar to some songbird species like the canary, in which females usually do not sing but song can be induced in adult females by T-treatment (Leonard, 1939).

Although T activates courtship, apparently it has little to do with the growth of the adult male plumage. Juvenile males (in green plumage) have been implanted with T when feathers from tracts that would ordinarily grow black or yellow have been plucked. In all cases, these feathers regrew green even though courtship behaviors were activated by T (Day et al., 2006). These results suggest that the plumage of adult males is acquired due to non-hormonal factors, including constitutive expression of sex-specific genes in feather follicles. Primary feathers of males differ from those of females (Chapman, 1935) and one primary feather was plucked from young males in these experiments. Before this feather was able to regrow these young males performed wingsnaps. Chapman (1935) hypothesized the flight feathers (remiges) were required for the wingsnap and there has been additional speculation that the thin pointed primaries of males are accelerated like a “bullwhip”, to produce a “sonic boom” that is the snap. Because females can wingsnap when treated with T and males missing a primary can still wingsnap, we believe this argues that the masculine remiges are not necessary for creation of wingsnaps and the sounds are not produced like a “whipcrack”. Interestingly, males do make an interesting shuffling sound when they fly and we believe the sexually dimorphic feather structures create this unique sound of male flight.

5. Sites and mechanisms of T action

Testosterone can activate targets as an androgen via androgen receptors with T binding directly to AR or after T is converted into the more potent androgen 5α -dihydrotestosterone (DHT). Alternatively, T can be converted into estradiol (E2) by the actions of the enzyme aromatase and this E2 can bind to estrogen receptors (ER) to stimulate target cells. Studies of less complicated courtship behaviors of captive doves and quail indicate that both ER and AR mediated pathways contribute to the activation of male courtship (Cheng and Lehrman, 1975; Hutchison and Steimer, 1984; Balthazart and Schumacher, 1985). Like doves and quail, aromatase is present in the manakin brain (Saldanha et al., 2000) so T could act in part through ER. We believe, however, that AR are most important. If reproductively active male manakins are implanted with the AR-antagonist flutamide they show significant decrements in courtship displays (Fusani et al., 2007b). These birds appear to make some physiological adjustment to the blocked AR because two weeks later the birds are displaying at significantly higher rates than untreated males. Clearly, interruption of AR contributes to a perturbation of male courtship behavior indicating the importance of the AR signaling pathway. We have not tested an ER-antagonist or aromatase-inhibitor to rule-out a role for estrogens. However, we have some evidence that estrogens might potentiate the actions of androgens. Reproductively inactive birds require a combination of E2 and DHT, administered in that sequence, to activate courtship and we have additional evidence that E2 might upregulate AR in some manakin tissues (unpublished data). Aromatization of T into ER might be involved in the details of the display structure which determine the success of a male, similarly to what has been described for the song of canaries (Fusani et al., 2003).

Typically, neuromuscular systems required for performance of male reproductive behavior are sensitive to androgens. In manakins, we predict that androgens act on a diversity of sites in the brain, spinal cord and peripheral muscles to activate the myriad of circuits involved in contractions of the full suite of muscles required by male courtship. We have evidence for the expression of AR in all three tissues. $^3\text{H-T}$ accumulates in the spinal cord, especially in the cervical enlargement where motor neurons are located that innervate wing muscles (Schultz and Schlinger, 1999). We believe these muscles might be especially important androgen targets since wingsnaps are such an important feature of the manakin display. Moreover, several muscles appear hypertrophied in manakins (Lowe, 1942) and two muscles that lift the wings are larger, with larger fiber size and unique fast myosin expression in males as compared to females and as compared to male zebra finches who do not perform a remarkable physical courtship (Schultz et al., 2001). Because females can perform wingsnaps after T-treatment, T may stimulate the muscle growth and myosin expression in females as is seen in typical males or the extensive practice of the display by males may increase muscle mass.

6. Summary

Our data support the view that T activates the remarkable courtship of male manakins by actions on the brain, spinal cord and peripheral muscles. Despite the overwhelming evidence that T activates male courtship, males do show variable T levels across the lengthy courting season. Social factors may contribute to such variability but they raise the question of how courtship is displayed when T levels are low. Perhaps elevated AR expression in diverse manakin neural circuits and muscles evolved to support the T-dependent performance of elaborate courtship but secondarily provided increased androgen-sensitivity so low levels of T remain activational. It is also possible that T acts to organize neuromuscular systems at the onset breeding that remain competent for many months irrespective of the presence of T. Such a mechanism would challenge the notion that activational effects of androgen are transient and require a constant and intense hormone exposure, as we know from breeding adults of temperate lekking species. There is increasing evidence that our traditional views of hormone action based on studies of temperate breeding species need to be reconsidered in view of recent studies on species with unique life-histories, especially those residing in wet tropical lowlands. We expect that continued studies of the Golden-collared manakin will contribute new concepts in behavioral neuroendocrinology.

Acknowledgments

Supported by NSF IBN 0213194 and the National Geographic Society. We thank Tim Gooch for assistance with the illustrations and the staff at the Smithsonian Tropical Research Institute, the Government of Panama, especially ANAM, for permission to perform these studies.

References

- Balthazart, J., Schumacher, M., 1985. Interaction of androgens and estrogens in the control of sexual behavior in male Japanese quail. *Physiol. Behav.* 35, 157–166.
- Bostwick, K.S., Prum, R.O., 2003. High-speed video analysis of wing-snapping in two manakin clades (Pipridae: Aves). *J. Exp. Biol.* 206, 3693–3706.
- Chapman, F.M., 1935. The Courtship of Gould's Manakin (*Manacus vitellinus vitellinus*) on Barro Colorado Island, Canal Zone. *Bull. Am. Mus. Nat. Hist.* 68, 472–521.
- Cheng, M.-F., Lehrman, D., 1975. Gonadal hormone specificity in the sexual behavior of ring doves. *Psychoneuroendocrinology* 1, 95–102.
- Day, L., Fusani, L., Hernandez, E., Wise, P., Schlinger, B., 2007. Testosterone and its effects on courtship in Golden-collared manakins: seasonal, sex and age differences. *Horm. Behav.* 51, 62–68.
- Day, L.B., McBroom, J.T., Schlinger, B.A., 2006. Testosterone increases display behaviors but does not stimulate growth of adult plumage in male golden-collared manakins (*Manacus vitellinus*). *Horm. Behav.* 49, 223–232.
- Fusani, L., Metzendorf, R., Hutchison, J.B., Gahr, M., 2003. Aromatase inhibition affects testosterone-induced masculinization of song and the neural song system in female canaries. *J. Neurobiol.* 54, 370–379.
- Fusani, L., Giordano, M., Day, L., Schlinger, B., 2007a. High-speed video analysis reveals individual differences in the courtship display of male golden-collared manakins. *Ethology* 113, 964–972.
- Fusani, L., Canoine, V., Day, L., Reineman, D., Schlinger, B., 2007b. Androgen and the elaborate courtship behavior of a tropical lekking bird. *Horm. Behav.* 51, 69–76.
- Goymann, W., Moore, I.T., Scheuerlein, A., Hirschenhauser, K., Grafen, A., Wingfield, J.C., 2004. Testosterone in tropical birds: effects of environmental and social factors. *Am. Nat.* 164, 327–334.
- Hutchison, J.B., Steimer, T., 1984. Androgen metabolism in the brain: behavioural correlates. *Prog. Brain Res.* 61, 23–51.
- Leonard, S.L., 1939. Induction of singing in female canaries by injections of male hormone. *Proc. Natl. Acad. Sci. USA* 41, 229–230.
- Lill, A., 1974. Sexual behaviour of the lek forming white-bearded manakin, *Manacus trinitatis*. *Z. Tierpsychol.* 36, 1–36.
- Lowe, P.R., 1942. The anatomy of Gould's manakin (*Manacus vitellinus*) in relation to its display. *IBIS* 6, 50–83.
- McDonald, B.B., 2007. Predicting fate from early connectivity in a social network. *Proc. Natl. Acad. Sci. USA* 104, 10910–10914.
- Nice, M.M., 1943. Studies in the life history of song sparrow II. The behavior of the song sparrow and other passerines. *Trans. Linn. Soc. NY* 6, 1–388.
- Saldanha, C.J., Schultz, J.D., London, S.E., Schlinger, B.A., 2000. Telencephalic aromatase, but not a song system, in a sub-oscine passerine, the golden collared manakin (*Manacus vitellinus*). *Brain Behav. Evol.* 56, 29–37.
- Schlinger, B., Schultz, J.D., Hertel, F., 2001. Neuromuscular and endocrine control of an avian courtship behavior. *Horm. Behav.* 40, 276–280.
- Schlinger, B.A., 1998. Sexual differentiation of avian brain and behavior: current views on gonadal hormone-dependent and independent mechanisms. *Ann. Rev. Physiol.* 60, 407–429.
- Schultz, J.D., Schlinger, B.A., 1999. Widespread accumulation of [(3)H] testosterone in the spinal cord of a wild bird with an elaborate courtship display. *Proc. Natl. Acad. Sci. USA* 96, 10428–10432.
- Schultz, J.D., Hertel, F., Bauch, M., Schlinger, B.A., 2001. Adaptations for rapid and forceful contraction in wing muscles of the male golden-collared manakin: sex and species comparisons. *J. Comp. Physiol. A* 187, 677–684.
- Snow, D.W., 1962. A field study of the black and white Manakin, *Manacus manacus*, in Trinidad. *Zoologica* 47, 65–104.
- Wikelski, M., Hau, M., Robinson, W.D., Wingfield, J.C., 2003. Reproductive seasonality of seven neotropical passerine species. *Condor* 105, 683–695.
- Wingfield, J., Farner, D., 1976. Avian endocrinology-field investigations and methods. *Condor* 78, 570–573.
- Wingfield, J.C., 1984a. Environmental and endocrine control of reproduction in the song sparrow, *Melospiza melodia*. II. Agonistic interactions as environmental information stimulating secretion of testosterone. *Gen. Comp. Endocrinol.* 56, 417–424.
- Wingfield, J.C., 1984b. Environmental and endocrine control of reproduction in the song sparrow, *Melospiza melodia*. I. Temporal organization of the breeding cycle. *Gen. Comp. Endocrinol.* 56, 406–416.
- Wingfield, J.C., Farner, D., 1993. Endocrinology of reproduction in wild species. In: Farner, D.S., King, J.R., Parkes, K.C. (Eds.), *Avian Biology*. Academic Press, New York, pp. 163–327.