

ROLE OF TESTOSTERONE ON BODY MASS, BODY MOLTS, PRIMARY FLIGHT FEATHERS, PLUMAGE REGENERATION AND TESTES IN BRAHMINY MYNA (*STURNUS PAGODARUM*)

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ABSTRACT

Three groups (1-3) of birds were subjected to non stimulatory photoperiod (9L:15D), and received olive oil (0.1 ml), 10 and 50 ig TP (Testosterone propionate) per bird on alternate day respectively. Next three groups (4-6) of birds were subjected to stimulatory photoperiod (15L:9D), and received olive oil (0.1 ml), 10 and 50 ig TP (Testosterone propionate) per bird on alternate day respectively. In total, fifteen injection were made. Groups (1-3) were transferred to stimulatory photoperiod (15L:9D) after 60 days. Body mass, testis volume, plumage regenerations, primary flight feathers and body molts also studied in this experiment. Observations were made at the beginning, fortnightly and end of the 30 day experiment.

The results of current study demonstrate the effect of TP on the testes, body weight, body molts, primary flight feathers and plumage regeneration in brahminy myna. Brahminy myna placed on 9L:15D did not induced testis growth till 60 days after that photoperiod of 9L:15D transferred to 15L:9D then the testis volume increased significantly and this clearly suggest that brahminy mynas were not sensitive to short photoperiod (non stimulatory photoperiod) and as expected, 15L:9D showed testicular response till 60 days then suddenly decreased and this can be taken to suggest that brahminy myna are a long day species and this study did not show an effect of prior treatment of testosterone hormone on photoperiodic induction of testicular growth.

Key words: Brahminy myna, Photoperiod, Testosterone propionate, gonads

INTRODUCTION

The steroid hormone testosterone (T) mediates the expression of many secondary sexual characters, including behaviors which influence male reproductive success. In males of many birds, territorial behaviors, such as song and aggressive displays, are regulated by the hormone, testosterone (Wingfield, 1994a; Hunt *et al.*, 1995; Hirschenhauser *et al.*, 2003). In male chestnut-collared longspurs, *Calcarius ornatus*, high plasma

testosterone may be more important in eliciting and maintaining sexual behavior than aggressive behavior (Lynn and Wingfield, 2008). Apart from the regulation of territorial aggression, increased plasma T levels are important for the expression of secondary sexual characters, sperm production, and sexual behavior in male birds (Balthazart, 1983; Ketterson and Nolan, 1994).

Exogenous administration of T to males in winter results in springtime plasma titers and

consequently enhances territorial aggression (Wingfield, 1994a). There appear two pathways by which T can influence behavior: (i) by binding to androgen receptors (Schwabl and Kriner, 1991; Labrie, 1993), and (ii) by being converted in the brain into 17- β estradiol (E2) by the enzyme aromatase (Schlinger and Arnold, 1991; Wade *et al.*, 1994). Existing correlational studies have yielded mixed results: in some year-round territorial Afrotropical birds (Dittami and Gwinner, 1985, 1990; Dittami, 1986, 1987) and in subtropical Rose-ringed parakeets (*Psittacula krameri*; Krishnaprasadan *et al.*, 1988) plasma T levels are continuously elevated (but usually remain below 2 ng/ml), perhaps indicating a coupling of T and territorial behavior. In contrast, in many other tropical species, which maintain territories year-round, males have baseline T levels throughout the year, even during the breeding season (Levin and Wingfield, 1992; Wingfield *et al.*, 1992; Wikelski *et al.*, 1999 a, b; Wikelski *et al.*, 2000). Moreover, in Afrotropical White-browed sparrow weavers (*Plocepasser mahali*) aggressive territorial behavior and song can be induced without concomitant increases in plasma T levels from baseline values (Wingfield *et al.*, 1992; Wingfield and Lewis, 1993). The photoperiodic condition and social context may modulate the effects of steroids on song control regions (SCR) and singing behavior in adult male songbirds in the fall (Strand *et al.*, 2008). In male song birds suppression of sickness behavior could occur when testosterone (T) is elevated to socially-modulated levels (Ashley *et al.*, 2009).

Role of gonadal steroids in the regulation of gonadal cycles has been studied in several Indian birds. The notable ones are: the weaver bird, lal munia, spotted munia, common myna, blossom headed parakeet, migratory redheaded bunting and yellow throated sparrow (Kumar and Kumar, 1990); White-crowned sparrow (Wikelski *et al.*, 1999; Moore *et al.*, 2002); House sparrow (Kumar, 2002; Greenman *et al.*, 2005); Japanese quail (Desjardins and Turek, 1977; Kumar *et al.*, 2009); Western Scrub-Jays (Bridge *et al.*, 2009); Weaver finch (Lofts, 1962); White throated sparrow (Turek *et al.*, 1980); Brahminy

myna (Kumar and Kumar, 1992). Studies on these species have revealed that, depending on the species, on the phase of the gonadal cycles, and on the dose administered, testosterone may stimulate, inhibit or produce no effect on gonadal cycles of Indian birds. Saxena (1964) studied the role of testosterone in testicular cycle of the Indian weaver bird. Testosterone, irrespective of its dose, inhibits weaver birds gonadal growth cycle. Similarly, the effects of testosterone on testicular cycle were studied in detail in the Indian weaver bird (Singh, 1982; Thapliyal *et al.*, 1983). In long-term experiments, high doses of testosterone were found to be gonadostimulatory, whereas low doses of the hormone induced either stimulation or inhibition of testicular activity, depending on the phase of the testicular cycle when the treatment was started. Gonadal hormones have also been reported to be involved in the regulation of photoperiodic responses and photorefractoriness in more Indian species (Singh and Chandola, 1981; Lal 1982; Thapliyal and Lal, 1983, 1984a,b). In male vertebrates, the hormone testosterone increases in the circulation during the breeding season (reviewed in Nelson, 2000). Testosterone promotes the development of many male secondary sexual characteristic (Emerson, 2000). The gonadotrophin-inhibitory hormone (GnIH) provides novel directions to investigate neuropeptide regulation of reproduction (Tsutsui *et al.*, 2009). The gonadotrophin-inhibitory hormone (GnIH) and its related peptides are important modulators of reproductive function at the level of the GnRH neurone, the gonadotroph and the gonads (Bentley *et al.*, 2009).

Post-nuptially, following the breeding season, many photoperiodic birds enter a photosensitive (photorefractory) state in which testicular growth is not initiated on exposure to long days. Administration of different doses of testosterone propionate (TP) to birds during this period should produce dose-dependent effects, similar to those described in photosensitive individuals (Turek, *et al.*, 1976). At low doses, circulating levels of testosterone remain normal or below normal and, therefore, TP produces an antigonadal response by the negative feedback

action on the hypothalamo-hypophyseal (h-h) system (Follett *et al.*, 1972; Stetson, 1972). But, once the circulating levels become sufficiently higher after administration of high doses, TP directly acts on the seminiferous tubules leading to stimulation and/ or maintenance of the growth of the regressed testes (Desjardins and Turek, 1977). In Mute Swans (*Cygnus olor*), molt is related to decreasing plasma prolactin, and is inhibited when plasma prolactin is increasing or high (Dawson *et al.*, 2009). The photorefractoriness in birds coincides with the period of post-nuptial molt (an event characterized by loss and regeneration of feathers). There exists a direct relationship between the gonads and the molt, and possibly this relationship is antagonistic (Schleussner, *et al.*, 1985). However, the dose-dependent effects of testosterone on the body weight in gonadally regressed birds have not been fully studied.

Therefore, in this study, we investigated the role of male hormone (testosterone) on the testes, body weight, body molts, primary flight feathers and plumage regeneration in brahminy myna.

MATERIAL AND METHODS

This experiment was performed on photosensitive, adult male brahminy myna (*Sturnus pagodarum*) procured locally at 29°N in meerut. This experiment began on 18 March 2007, and acclimatized to captivity conditions under natural day lengths (NDL) for 15 days before they were exposed to experimental conditions. The birds were given proteinaceous food and water ad libitum to all experimental birds and replenished twice daily during the day-time. Birds maintained good health under captive conditions and during the experimentation.

Three groups (1-3) of birds were subjected to non stimulatory photoperiod (9L:15D), and received olive oil (0.1 ml), 10 and 50 µg TP per bird on alternate day respectively. Next three groups (4-6) of birds were subjected to stimulatory photoperiod (15L:9D), and received olive oil (0.1 ml), 10 and 50 µg TP per bird on alternate day respectively. In total, fifteen injection were made. Groups (1-3) were transferred to stimulatory

photoperiod (15L:9D) after 60 days. Plumage regenerations, primary flight feathers and body molts also studied in this experiment. Observations were made at the beginning, fortnightly and end of the 30 days experiment.

All the birds were housed in wire mesh cages (size 45 x 25 x 25 cm³). An artificial light-dark (LD) cycles were provided by 14-watt fluorescent tubes (CFL). The room containing the light-tight photoperiod boxes was held in constant darkness and maintained at 23 ± 3 °C temperature. Observations on body mass and testis volume were taken at the beginning and at appropriate intervals of the experiment. Body mass was recorded on a top pan balance providing an accuracy of 0.1g. The size of the testis was measured as the testicular volume. For this, the dimension of the left testis of each bird were recorded by unilateral laparotomy performed under local anesthesia, and the testis volume was calculated using the formula $4/3\pi ab^2$, where a and b denote half of the long (length) and short (width) axes, respectively.

The data are presented as mean ± SE. They were analyzed using one way analysis of variance with repeated measures (1-way RM ANOVA) when the response of a group was compared as a function of time, followed by the Student Newman-Keuls post-hoc test if ANOVA indicated a significance of difference. We used 1-way ANOVA without repeated measure in comparing the means of the different groups on selected observation. Significance was taken at P<0.05.

RESULT

The results are shown in figure 1. The mean body mass was slightly increased among all the groups, exposed to 9L:15D and 15L:9D photoperiod throughout the experiment (1-way RM ANOVA: control 9L, $F_{3,12}=8.498$, $P=0.0027$; 10µg TP 9L, $F_{3,12}=16.54$, $P=0.0001$; 50µg TP 9L, $F_{3,12}=14.15$, $P=0.0003$; control 15L, $F_{3,12}=29.18$, $P<0.0001$; 10µg TP 15L, $F_{3,12}=14.62$, $P=0.0003$ and 50µg 15L, $F_{3,12}=13.39$, $P=0.0004$) (fig.1a&f).

Molt of body feathers (fig. 1b&g) in all groups of 9L:15D and 15L:9D photoperiod

showed significant variation (1-way RM ANOVA: control, $F_{6,18}=27.00$, $P<0.0001$; 10 μ g TP, $F_{6,18}=17.31$, $P<0.0001$; 50 μ g TP, $F_{6,18}=54.33$, $P<0.0001$; control, $F_{6,18}=23.31$, $P<0.0001$; 10 μ g TP, $F_{6,18}=6.643$, $P=0.0008$ and 50 μ g TP, $F_{6,18}=23.12$, $P<0.0001$) respectively.

Molt of wing primaries in these three groups of both photoperiod, showed significant variation (1-way RM ANOVA: 9L control, $F_{6,18}=3.000$, $P=0.0327$; 9L 50 μ g TP, $F_{6,18}=25.00$, $P<0.0001$ and 15L 50 μ g TP, $F_{6,18}=3.000$, $P<0.0327$) (fig. 1c) but in another three groups did not show significant variation (1-way RM ANOVA: 9L 10 μ g TP, $F_{6,18}=2.455$, $P=0.0652$; 15L control, $F_{6,18}=2.407$, $P=0.0694$; and 15L 10 μ g TP, $F_{6,18}=1.000$, $P=0.4552$) (fig. 1h).

Feather regeneration occurred in birds in all three groups (G1, G2 and G3) of 9L photoperiod and group 6 of 15L photoperiod but not in G4 and G5 of 15L photoperiod. Feather papillae did not emerge in 2, 1, 1 and 2 birds of G1, G2, G3 and G6 respectively. The day of the first emergence of papilla/papillae differed even amongst the groups in which feather regeneration occurred.

A few papillae found emerged on day 8 in one and day 24 in two birds of group 1; in G2, by day 24 in one but day 27 in three birds; in G3, by day 9 in one, by day 20 in two and by day 25 in one bird and in G6, by day 18, 22 and 32 each three birds of this group respectively. The sequence of average numbers of emerged papillae in groups were as follows G2>G3>G1>G6 (absent in G4 and G5). These data indicate that TP integrates with feather regeneration process in brahminy myna in a dose dependent manner. Some dose facilitate plumage regeneration, whilst other exert a negative effect.

There was significant gain in papillae regeneration in all groups of 9L:15D photoperiod (1-way RM ANOVA: control, $F_{45,180}=8.762$, $P<0.0001$; 10 μ g TP, $F_{45,180}=22.59$, $P<0.0001$ and 50 μ g TP, $F_{45,180}=82.38$, $P<0.0001$) (fig. 1d). Also significant gain in papillae regeneration in 50 μ g TP group of 15L:9D photoperiod (1-way RM ANOVA : 50 μ g TP, $F_{45,180}=5.835$, $P<0.0001$), rest

both group did not show significant changes (fig. 1i).

The testis volume of three groups of 9L:15D was unstimulated upto day 60 and then subjected to long photoperiod (15L:9D) then these three groups were fully developed upto day 90. There was a significant difference in testis volume of three groups of 9L:15D (1-way RM ANOVA: control, $F_{3,12}=80.26$, $P<0.0001$; 10 μ g TP, $F_{3,12}=111.6$, $P<0.0001$; and 50 μ g TP, $F_{3,12}=2041$, $P<0.0001$) (fig. 1e). Also there was a significant change in the testis volume of the three groups of 15L:9D (1-way RM ANOVA: control, $F_{3,12}=310.4$, $P<0.0001$; 10 μ g TP, $F_{3,12}=98.35$, $P<0.0001$ and 50 μ g TP, $F_{3,12}=728.9$, $P<0.0001$) (fig. 1j).

DISCUSSION

Previous studies on temperate population of house sparrow show that gonadal steroids inhibit growth of gonads; very high levels of testosterone but not of estradiol stimulate inactive gonads of both Indian and temperate population of house sparrows (Turek *et al.*, 1976; Thapliyal and Gupta, 1989). Low doses of testosterone, administered via 5- or 10-mm silastic capsules, induce complete gonadal atrophy. But high doses of testosterone, administered via 40-, 80-, or 120-mm silastic capsules, maintained paired testis weight and spermatogenic activity birds (Turek *et al.*, 1976). Effect of testosterone has also been studied in male blossom headed parakeets (*Psittacula cyanocephala*) (Maitra and Ghosh, 1981) during the breeding and post-breeding phase of the annual cycle. During the breeding season, a significant fall both in the testis weight and the diameter of the seminiferous tubules was observed. In the post-breeding phase, testes of all control birds were very small and in the state of regression. Testosterone treatment during the period when the gonads were inactive did not affect the testis weight. It is suggested that the differential effect of exogenous TP on the testes are due to its dose-dependent action (Turek, *et al.*, 1976). At low doses, circulating levels of testosterone remain normal or below normal and therefore, TP produces an antigonadal response by the negative feedback actions on the

hypothalamo-hypophyseal (h-h) system (Stetson, 1972). But, once the circulating levels become sufficiently higher after administration of high doses, TP directly acts on the seminiferous tubules leading to stimulation and/or maintenance of the growth of the regressed testes (Desjardins and Turek, 1977). In Western Scrub-Jays (*Aphelocoma californica*) birds with unpredictable food had slightly lower testosterone levels relative to controls, but there was no effect on estradiol or luteinizing hormone (Bridge et al., 2009).

Effect of TP has also been investigated in the migratory red headed bunting (*Emberiza bruniceps*) (Kumar and Kumar, 1990). TP declines food intake but dose not potentially affect the gain in fat and body mass. This suggested that photoperiodic effects on fattening and weight gain in *Emberiza bruniceps* were not exerted through hyperphagia. The authors argue that, probably, the hormones other than gonadal steroids (viz. prolactin, adrenal steroids) are involved in the control of fattening and weight gain in bunting.

There have been different accounts of the effects on TP on reproductively mature and active testis of different birds. Kumaran and Turner (1949) and Lofts (1962) suggested that the testosterone had no adverse effect on gonads in near maximum breeding condition, but spermatocytes. It is also suspected that the spermatokinetic effect of exogenous androgen is by way of direct action of the hormone on the testis (Lofts, 1962; Lofts et al., 1973). Studied performed by Davies and Bicknell (1976) and others on different avian species have also documented the possible activation of the hypothalamo-hypophyseal system, particularly in relation to the secretion of that exogenous testosterone may have either pro- or anti-gonadal effect depending upon the sexual status of the bird (Tewary et al., 1985). They are also consistent with the studies on some mammalian species, which suggest a dose-dependent differential effect of testosterone (Berndtson et al., 1974).

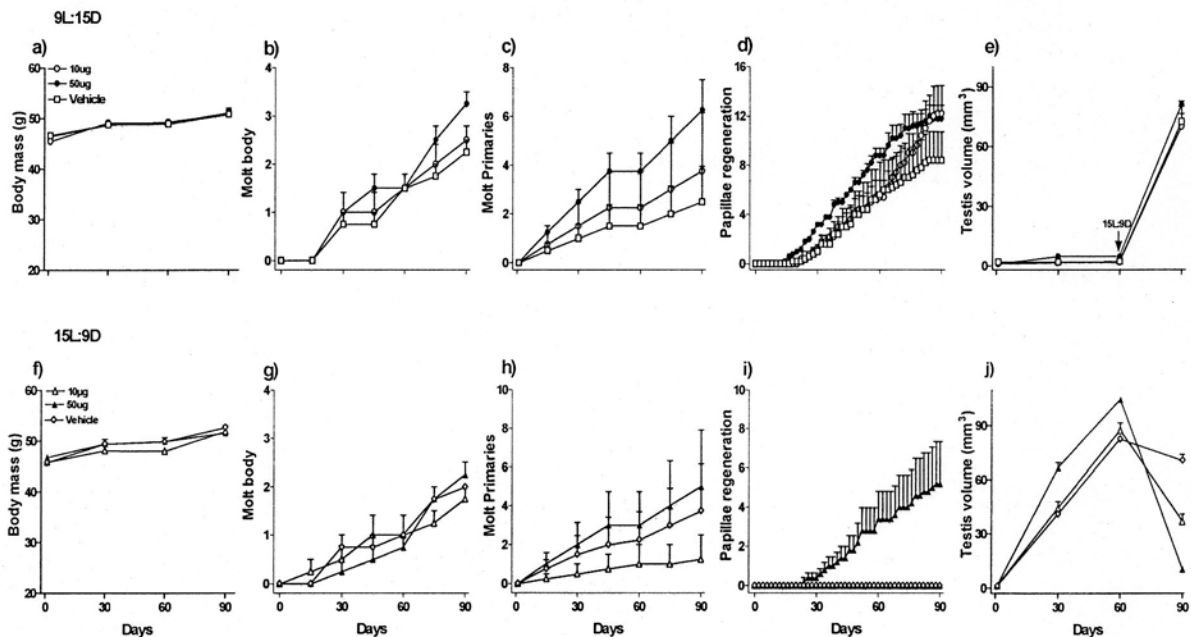


Figure 1: Changes (mean \pm SE) in body mass (a,f), molt body (b,g), molt primaries (c,h), feather papillae regeneration (d,i) and testis volume (e,j) of photosensitive male brahmimyna. Three groups (1-3) of birds were subjected to non stimulatory photoperiod (9L:15D), and received 0.1 ml olive oil, 10 and 50 μ g TP per bird on alternate day respectively. Next three groups (4-6) of birds were subjected to stimulatory photoperiod (15L: 9D), and received 0.1 ml olive oil, 10 and 50 μ g TP per bird on alternate day respectively. In total, each group received fifteen injections in the period of the experiment of 30 days. Groups (1-3) were transferred to stimulatory photoperiod (15L:9D) after 60 days. The experiment began on 18 march 2007. Each symbol represents the mean and the vertical line on it indicates the standard error.

The results of current study demonstrate the effect of TP on the testes, body weight, body molts, primary flight feathers and plumage regeneration in brahmyn myna. Brahmyn myna placed on 9L:15D did not induced testis growth till 60 days after that photoperiod of 9L:15D transferred to 15L:9D then the testis volume increased significantly (fig. 1e) and this clearly suggest that brahmyn myna were not sensitive to short photoperiod and as expected, 15L:9D (fig. 1j) showed testicular response till 60 days then suddenly decreased and this can be taken to suggest that brahmyn myna are a long day species.

Although most of the effects may be explained on the basis of either an increase in the level of the central set point or to decrease in the sensitivity of central mechanisms to feed back inhibition by the increasing levels of steroid. Changing levels of thyroid hormones may also play an important role in determining the type and extent of the effects of the testosterone on neuroendocrine-gonadal axis from the late quiescent phase to the reproductive phase of annual reproductive cycle.

In conclusion, it appears that the effects of gonadal steroids found in the current study as well as a number of previous studies is primarily through its feedback action on the central photo-neuroendocrine machinery. This may have a lot of adaptive implications. An internal control by testosterone would help an individual not to perform many avoidable activities at the time of reproduction. In seasonal breeder, reproductive window is too small and therefore, the animal needs to have an internal regulation. The advantage of having a testosterone-dependent mechanism is that an "avoidable activity" is slowed down, stopped or postponed only for the period when it is actually needed.

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REFERENCES

- Ashley, N.T., Hays, Q.R., Bentley, G.E. and Wingfield, J.C. (2009). Testosterone treatment diminishes sickness behavior in male songbirds. *Horm Behav.* **56**: 169-76.
- Balthazart, J. (1983). Hormonal correlates of behavior. In: *Avian Biology* (D. S. Farner, J. R. King and K. C. Parker, Eds.), Vol. VII, pp. 221–365. *Acad. Press.* San Diego.
- Bentley, G.E., Ubuka, T., Mcguire, N.L., Calisi, R., Perfito, N., Kriegsfeld, L.J., Wingfield, J.C. and Tsutsui, K. (2009). Gonadotropin-inhibitory hormone: a multifunctional neuropeptide. *J. Neuroendocrinol.* **21**: 276-81.
- Berndtson, W.E., Desjardins, C. and Ewing, L.L. (1974). Inhibition and maintenance of spermatogenesis in rats implanted with Polydimethylsiloxane capsules containing various androgens. *J. Endocrinol.* **62**:125-135.
- Bridge, E.S., Schoech, S.J., Bowman, R. and Wingfield, J.C. (2009). Temporal periodicity in food availability: effects upon the reproductive axis in Scrub-Jays. *J. Exp. Zoo.* **311**: 35-44.
- Davies, D.T. and Bicknell, R.J. (1976). The effect of testosterone on the responsiveness of the quail's pituitary to luteinizing hormone-releasing hormone (LH-RH) during photoperiodically induced testicular growth. *Gen. Comp. Endocrinol.* **30**: 487-499.
- Dawson A., Perrins C.M., Sharp P.J., Wheeler, D. and Groves, S. (2009). The Involvement of prolactin in avian molt: the effects of gender and breeding success on the timing of molt in Mute swans (*Cygnus olor*). *Gen. Comp. Endocrinol.* **161**: 267-70.
- Desjardins, C. and Turek, F.W. (1977). Effects of testosterone on spermatogenesis and luteinizing hormone release in Japanese quail. *Gen. Comp. Endocrinol.* **33**: 293-303.
- Dittami, J.P. and Gwinner, E. (1985). Annual cycles in the African stonechat and their relationship to environmental factors. *J. Zool. (Lond.)*. **207**: 357-370.
- Dittami, J.P. (1986). Seasonal reproduction, moult and their endocrine correlates in two tropical *Ploceidae* species. *J. Comp. Physiol. B.* **156**: 641-647.
- Dittami, J.P. (1987). A comparison of breeding and moult cycles and life histories in two tropical species: The blue-eared glossy starling *Lamprolornis chalybaeus* and Rüppell's long-tailed glossy starling *L. purpuropterus*. *Ibis.* **129**: 69-85.
- Dittami, J.P. and Gwinner, E. (1990). Endocrine correlates of seasonal reproduction and territorial behavior in some tropical passerines. In: *Endocrinology of Birds. Molecular to Behavioral.* 225-233.

- Emerson, S.B. (2000). Vertebrate secondary sexual characteristics: physiological mechanisms and evolutionary patterns. *Am. Nat.* **156**: 84-91.
- Follett, B.K., Scanes, C.G. and Cunningham, F.J. (1972). A radioimmunoassay for avian luteinizing hormone. *J. Endocrinol.* **52**: 359-378.
- Greenman, G.C., Martin, L.B. and Hau, M. (2005). Reproductive state, but not testosterone, reduces immune function in male house sparrows (*Passer domesticus*). *Physiological and biochemical Zoology*. **78**: 60-68.
- Hirschenhauser, K., Winkler, H. and Oliveria, R.F. (2003). Comparative analysis of male androgen responsiveness to social environment in birds: the effects of mating system and paternal incubation. *Horm. Behav.* **43**: 508-519.
- Hunt, K., Wingfield, J.C., Astheimer, L.B., Buttemer, W.A. and Hahn, T.P. (1995). Temporal patterns of territorial behavior and circulating testosterone in the Lapland longspur and other arctic passerines. *Am. Zool.* **35**: 274-284.
- Ketterson, E.D., and Jr. Nolan, V. (1994). Male parental behavior in birds. *Annu. Rev. Ecol. Syst.* **25**: 601-628.
- Krishnaprasadan, T.N., Kotak, V.K., Sharp, P.J., Schmedemann, R. and Haase, E. (1988). Environmental and hormonal factors in seasonal breeding in free-living male Indian rose-ringed parakeets (*Psittacula krameri*). *Horm. Behav.* **22**: 488-496.
- Kumar, P., Pati, A.K., Mohan, J., Sastry, K.V.H., Tyagi, J.S. and Chaturvedi, C.M. (2009). Effect of simulated hypo- and hyper-reproductive conditions on the characteristics of circadian rhythm in hypothalamic concentration of serotonin and dopamine and in plasma levels of thyroxine, triiodothyronine, and testosterone in Japanese quail, *Coturnix coturnix japonica*. *Chronobiology International*. **26**: 28-46.
- Kumar, V. (2002). *Biological Rhythms*. Eds. Narosa Publishing house. New Delhi, Chennai, Mumbai, Kolkata.
- Kumar, V. and Kumar, B.S. (1990). Effects of photoperiod, gonadectomy and testosterone therapy on food intake and body weight in male redheaded bunting, *Embriza bruniceps*. *J. Reprod. Biol. Comp. Endocrinol.* **2**: 80-87.
- Kumar, V. and Kumar, B.S. (1992). Termination of photorefractoriness in the brahminy myna, *Sturnus pagodarum*: Role of photoperiod and gonadal hormones. *Indian J. Exp. Biol.* **30**: 48-53.
- Kumaran, J.D.S and Turner, C.W. (1949). The endocrinology of spermatogenesis in birds. II effect of androgens. *Pout. Sci.* **28**: 739-746.
- Labrie, F. (1993). Mechanism of action and pure antiandrogenic properties of Flutamide. *Cancer*. **72**: 3816-3827.
- Lal, P. (1982). *Role of thyroid in reproduction of migratory redheaded bunting, Embriza bruniceps*. Ph.D. thesis, BHU, Varanasi, India.
- Levin, R.N. and Wingfield, J.C. (1992). The hormonal control of territorial aggression in tropical birds. *Ornis Scand.* **23**: 284-291.
- Lofts, B. (1962). Photoperiod and the refractory period of reproduction in the equatorial bird (*Quelea quelea*). *Ibis*. **104**: 407-414.
- Lofts, B., Murton, R.K. and Thearle, R.J.P. (1973). The effects of testosterone propionate on the bill pigmentation and testis of the house sparrow, *Passer domesticus*. *Gen. Comp. Endocrinol.* **21**: 202-209.
- Lynn, S.E. and Wingfield, J.C. (2008). Dissociation of testosterone and aggressive behavior during the breeding season in male chestnut-collared longspurs, *Calcarius ornatus*. *General and Comparative Endocrinology*. **156**: 181-189.
- Maitra, S.K. and Ghosh, A. (1981). Gonadal responses to testosterone propionate during breeding and Post-breeding phases in the male blossomheaded parakeet, *Psittacula cyanecephala*. *Aust. J. Zool.* **29**: 853-859.
- Moore, C.B., Siopes, T.D., Steele, C.T. and Underwood, H. (2002). Pineal melatonin secretion, but not ocular melatonin secretion, is sufficient to maintain normal immune responses in Japanese quail (*Coturnix coturnix japonica*). *Gen. Comp. Endocrinol.* **126**: 352-358.
- Nelson, R.J. (2000). *An Introduction to Behavioral Endocrinology*. 2nd ed. Sinauer, Sunderland, MA.
- Saxena, R.N. (1964). *Sexual cycle and secondary sex characters of Indian weaver bird, Ploceus philippinus*. Ph. D. Thesis, Banaras Hindu University, Varanasi, India.
- Schleussner, G., Dittami, J.P. and Gwinner, E. (1985). Testosterone implants affect molt in male European starlings, *Sturnus vulgaris*. *Physiol. Zool.* **58**: 597-604.
- Schlinger, B.A. and Arnold, A.P. (1991). Brain is the major site of estrogen synthesis in a male songbird. *Proc. Natl. Acad. Sci. USA* **88**: 4191-4194.
- Schwabl, H. and Kriner, E. (1991). Territorial aggression and song of male European robins (*Erithacus rubecula*) in autumn and spring: Effects of antiandrogen treatment. *Horm. Behav.* **25**: 180-194.
- Singh, S. and Chandola, A. (1981). Photoperiodic control of seasonal reproduction in tropical weaver bird. *J. Exp. Zool.* **216**: 293-298.

- Singh, V.K. (1982). *Role of gonadal steroid hormones in annual gonad development cycle of male birds*. Ph.D. thesis. BHU. Varanasi, India.
- Stetson, M.H. (1972). *Control mechanisms in avian hypothalamo-hypophyseal-gonadal axis*. Ph.D. thesis. University of Washington, Seattle.
- Tewary, P.D., Tripathi, P.M. and Tripathi, B.K. (1985). Effects of exogenous gonadal steroids and castration of photoperiodic responses of the yellow-throated sparrow. *Indian J. Exp. Bio.* **23**: 426-428.
- Thapliyal, J.P. and Gupta, B.B.P. (1989). Reproductive cycle in birds. In: Saidapur SK, editor. *Reproductive cycles of Indian vertebrates*. Allied Publishers Ltd., New Delhi. 273-310.
- Thapliyal, J.P. and Lal, P. (1983). Photorefractoriness in birds: In: *Recent Trends in Life Sciences*. Eds. A. Gopalakrishna, S.B. Singh and A.K. Saxena, 276-286. Manu publication, Kanpur.
- Thapliyal, J.P. and Lal, P. (1984a). Role of thyroid and male hormones in photorefractory state in the migratory redheaded bunting, *Embriza bruniceps*. *Indian J. Exp. Biol.* **22**: 295-297.
- Thapliyal, J.P. and Lal, P. (1984b). Light, thyroid, gonad and photorefractory state in the migratory redheaded bunting, *Embriza bruniceps*. *Gen. Comp. Endocrinol.* **56**: 41-52.
- Thapliyal, J.P., Lal, P., Pati, A.K. and Gupta, B.B.P. (1983). Thyroid and gonad in the oxidative metabolism, erythropoiesis and light responses of migratory redheaded bunting, *Embriza bruniceps* to long photoperiod. *Gen. Comp. Endocrinol.* **51**: 444-453.
- Tsutsui, K., Saigoh, E., Yin, H., Ubuka, T., Chowdhury, V.S., Osugi, T., Ukena, K., Sharp, P.J., Wingfield, J.C. and Bentley, G.E. (2009). A new key neurohormone controlling reproduction, gonadotropin-inhibitory hormone in birds: discovery, progress and prospects. *J. Neuroendocrinol.* **21**: 271-5.
- Turek, F.W., McMillan, J.P. and Menaker, M. (1976). Melatonin: Effects on the circadian locomotor rhythm in sparrows. *Science*. **194**: 1441-1443.
- Turek, F.W., Desjardins, C. and Menaker, M. (1980). Testosterone treatment blocks the termination of the gonadal photorefractory condition in white throated sparrows maintained on short days. *Gen. Comp. Endocrinol.* **41**: 365-371.
- Wada, J., Schlinger, B.A., Hodges, L. and Arnold, A.P. (1994). Fadrozole: A potent and specific inhibitor of aromatase in the Zebra finch brain. *Gen. Comp. Endocrinol.* **94**: 53-61.
- Wikelski, M., Hau, M. and Wingfield, J.C. (1999a). Social instability increases testosterone year-round in a tropical bird. *Proc. R. Soc. Lond. B.* **266**: 1-6.
- Wikelski, M., Hau, M. and Wingfield, J.C. (2000). Rainforest seasonality and reproduction in a neotropical rainforest bird. *Ecology*. **81**: 2458-247.
- Wikelski, M., Hau, M., Robinson, D.W. and Wingfield, J.C. (1999b). Seasonal endocrinology of tropical passerines-A comparative approach. In: *Proceedings 22. International Ornithological Congress*. Eds. N. Adams and R. Slotow, 1224-1241. BirdLife South Africa, Johannesburg.
- Wikelski, M., Lynn, S., Breuner, C., Wingfield, J.C. and Kenagy, G.J. (1999). Energy metabolism, testosterone and corticosterone in white-crowned sparrows. *J. Comp. Physiol. A Neuroethol. Sens. Neural. Behav. Physiol.* **185**: 463-470.
- Wingfield, J.C. (1994a). Control of territorial aggression in a changing environment. *Psychoneuroendocrinol.* **19**: 709-721.
- Wingfield, J.C. and Lewis, D.M. (1993). Hormonal and behavioural responses to simulated territorial intrusions in the cooperatively breeding white-browed sparrow weaver, *Plocepasser mahali*. *Anim. Behav.* **45**: 1-11.
- Wingfield, J.C., Hegner, R.E. and Lewis, D.M. (1992). Hormonal responses to removal of a breeding male in the cooperatively breeding white-browed sparrow weaver, *Plocepasser mahali*. *Horm. Behav.* **26**: 145-155.

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