Temporal Phase Relation of Serotonergic and Dopaminergic Oscillations Alters Seasonal Reproduction and Adrenal Function in Jungle Bush Quail and Rain Quail

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Abstract: Present study investigates the role of temporal phase relation of serotonergic and dopaminergic oscillations in the regulation of seasonal reproduction in summer breeding Jungle bush quail, *Perdicula asiatica* and autumn breeding rain quail, *Coturnix coturnix coromandelica.* Two sets of experiments were performed in month of August, in reproductively quiescent (RQ) bush quail and reproductively active (RA) rain quail. In experiment I, both quails received the serotonin precursor, 5-HTP and the dopamine precursor, L-DOPA (5 mg/100 gm body weight/day for 13 days) at the interval of 8-hr or 12-hr. At the termination of the study (30 days post treatment), 8-hr suppressed and 12-hr increased body weight and testicular development compared to their respective controls in both the species of quail. However, in RA rain quail, testicular development in 12-hr group was similar to control. Further, in RQ bush quail, while adrenal activity of 8-hr group was more or less similar to control, 12-hr relation stimulated the activity of steroidogenic cords. On the other hand, in RA rain quail, control and 12-hr quail adrenal activity was similar while that of 8-hr showed suppression. In experiment II (quails receiving total dose of experiment I, i.e. 32.5 mg/100 gm body weight/ day for 2 days only, and sacrificed 30 days thereafter), response of the birds were similar to that of the experiment I. These findings indicate that, 8-hr and 12-hr relation of the 5-HTP and L-DOPA administration induced suppression and stimulation of the gonadal and adrenal function respectively, irrespective of the phase of the annual gonadal cycle of the two species of quail. It is concluded that specific relation of serotonergic and dopaminergic oscillation induces reproductively quiescent or active condition out of the season as a function of their time relation. These findings also suggest that, circadian organization may regulate reproductive and metabolic seasonality irrespective of the phase of the annual gonadal cycle.

Keywords: 5-Hydroxytryptophan (5-HTP), L-Dihydroxyphenylalanine (L-DOPA), testis, adrenal, Bush quail, Rain quail, seasonal reproduction.

1. INTRODUCTION

Reproduction in a majority of the birds occurs at a specific time of the year that is most favourable to the survival of the young and their parents. The environmental components used in timing the reproductive functions include photoperiod, rainfall, humidity, temperature and food in addition to other intrinsic mechanism(s) which may be hormonal or neural. In temperate zones, seasonal day length variation serves as the primary means of timing reproductive periodicity [1,2]. However, in most of the tropical and sub-tropical species environmental information (annual photoperiod) is not the primary regulator of annual gonadal cycle and initiation and termination of breeding varies according to the species. Studies on different species of birds have indicated the possibility of involvement of more than one environmental factor while direct influence of photoperiod in the process of regulation of annual reproductive cycle is also reported in some species similar to the photoperiodic species of temperate zones [3,4]. Although the proximate factor(s) in the tropics are not known, all the birds irrespective of their distribution and domestication respond to artificial illumination [5-12]. This indicates an ancestral capacity or the light may have a role in the stimulation or maintenance of the reproductive system even though it may not act as a synchronizer. Obviously most of the non-temperate zone birds if not all, although do not use daylength to time their seasonal reproduction but still respond to the artificial photoperiod.

In vertebrates, existence of circadian variation in endocrine secretions, hypothalamic factors and neurotransmitters is well reported [13]. The pattern of daily variation appears to change with physiological condition (viz. breeding, migration, molting, hibernation etc.), and with different seasons in seasonally breeding species. It is also reported that seasonal change in reproduction and other metabolic conditions (fattening etc.) may result from a temporal interaction of circadian neural oscillations that changes seasonally in their phase relations with one another. Meier and his group reported that daily phase relationship of two hormones i.e. corticosterone and prolactin may influence seasonal condition of migratory bird white throated sparrow, *Zonotrichia albicolis* [14]. This view was further supported when the effects of corticosterone and prolactin administered at different time intervals on a circadian basis could be duplicated by the administration of serotonergic and dopaminergic drugs given on the same ground [15-17]. Administration of these precursor drugs at 12 hour interval stimulated but at the 8 hour interval suppressed testicular function in many wild

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1874-3366/09 2009 Bentham Open

avian species including Japanese quail [18-26]. Moreover, daily injections of these two neurotransmitter precursors probably induced a diurnal rhythm in the hypothalamic serotonergic and dopaminergic functions in Japanese quail [27].

Jungle bush quail (*Perdicula asiatica*), a small wild species of quail (weighing 25 to 40 gm) breeds during May-June [28] followed by sharp regression and quiescent phase which extends during later half of the year. On the other hand, rain quail (*Coturnix coturnix coromandelica*) breeds during August-September [29] followed by slow regressive phase and long quiescent (preparatory) phase during early part of the year. Obviously in nature, gonadal cycle of bush and rain quail follows the annual cycle of day length and rain fall respectively at Varanasi (Lat. 25^o 18' N; Long. 83^o 01' E) and hence appear to utilize different environmental factors to time their seasonal reproduction (Fig. **1**). Hence, present study was undertaken for the first time in these two wild species of quail (in the month of August, when bush quail was in quiescent phase and rain quail in early breeding phase) to test the hypothesis that temporal phase relation of serotonergic and dopaminergic oscillations is the basis of seasonality. Since in all the earlier studies, treatment was given for 11 or 13 days, another objective was to compare and test the effect of long (13 days) and short (2 days) duration of treatment.

2. MATERIALS AND METHODS

Seasonally breeding Bush quail locally known as Lawa (body weight in nature 25 to 40 gms, breeding phase, May - June) and Rain quail (order: Galliformes; family: Phasianidae), locally known as Chinik Bater (body weight in nature 50 to 65 gms, breeding phase, August- September) obtained from a local bird supplier in the month of August were acclimatized to laboratory conditions, under natural day length for about one week. Both the species of birds were then randomly distributed into two sets of three groups (n=5). They were maintained in individual wire net cages and housed in a photoperiodic room, fitted with fluorescent light (300 lux at cage level) and automatic timer. Birds were fed with millet seeds. Food and water was available *ad libitum*. Further, for both the experiments, all birds were acclimatized to continuous conditions of light (LL) for four days, treated with the neurotransmitter precursor drugs (13 or 2 days) in LL and shifted to long day length (LD 16:8; lights on at 6:00 A.M. and off at 10:00 P.M.) until the termination of the study. All the experiments were conducted in accordance with institutional practice and within the framework of revised animals (Scientific Procedures) Act of 2002 of Govt. of India on Animal Welfare. Birds were treated as described previously [27].

2.1. Experiment 1

Group I (Control): Birds received two normal saline injections daily for 13 days in LL and then shifted to LD 16:8 until the termination of the study. (Since two normal saline injections either at 8-hr or 12-hr interval had similar effect, only one control was taken into account).

Group II (8-hr): Birds in this group were administered with the serotonin precursor, 5-HTP (5-hydroxytryptophan) at 8:00 A.M. followed by administration of the dopamine precursor, L-DOPA (L-dihydroxyphenylalanine) at 4:00 P.M. establishing 8-hr relationship between two injections.

Group III (12-hr): The treatment schedule was similar to group II, however, L-DOPA was administered at 8:00 P.M. establishing 12-hr relationship.

To induce specific phase relationship between serotonergic and dopaminergic oscillations, the serotonin precursor, 5-HTP and the dopamine precursor, L-DOPA were used because these neurotransmitters cannot cross the blood brain barrier where as their precursors do cross [30]. Both the precursor drugs were administered daily at a dose of 5

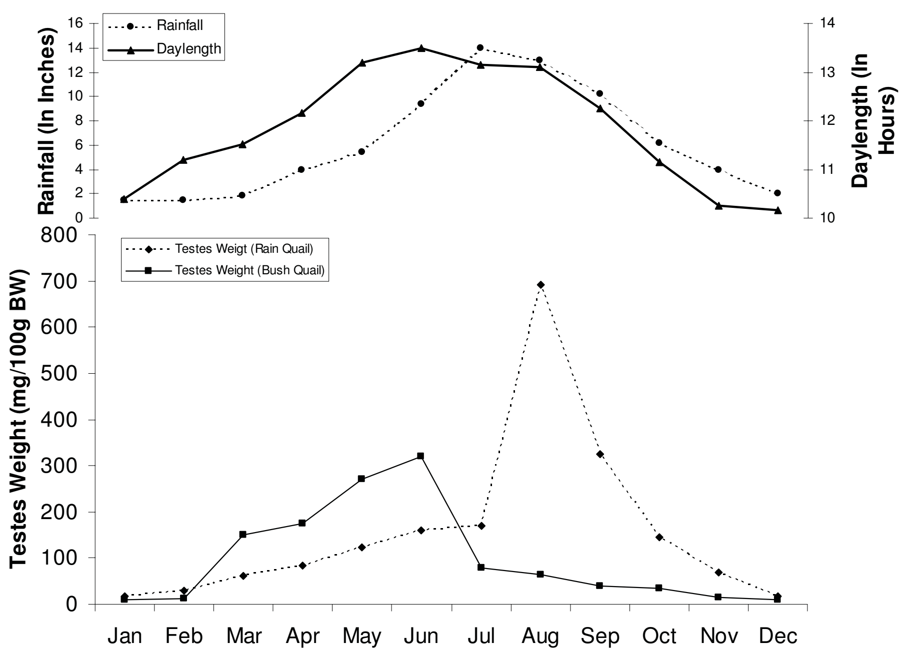

Fig. (1). Annual variation in the body weight and testicular weight of bush quail (*Perdicula asiatica*) (Haldar and Ghosh, 1990) and rain quail (*Coturnix coturnix coromandelica*) (Chaturvedi and Thapliyal, 1976). Upper panel shows variation in annual day length and rainfall at Varanasi.

mg/100g body weight / day for 13 days (total dose received 65mg/bird). Moreover, these precursor drugs were administered in LL to avoid possible photoperiodic interference of light:dark cycle with drug injections during treatment period and then shifted to light:dark cycle (LD 16:8) [27] until the termination of the study (30^{th} day post treatment).

2.2. Experiment II

In experiment II, both the species of quail were again randomly divided into three groups each and treated as in experiment I but with a dose of 32.5 mg/ 100 gm body weight/ day (total dose 65mg/bird) for two days only in LL and then shifted to LD 16:8 until the termination of the study (30^{th} day post-treatment period).

In each experiment, birds were weighed every week until sacrificed. Testes and adrenals were removed quickly, weighed and fixed in Bouins' fluid for routine histology. Cortico-medullary ratio (area occupied by steroidogenic cords - homologous to mammalian adrenal cortex and patches of chromaffin cells - homologous to mammalian adrenal medulla) was measured to determine the relative amount of steroidogenic cords and patches of chromaffin cells using image analyzer software (Motic Images 2000 v1.3). The cortico-medullary ratio was calculated as variation in steroidogenic cord areas per unit of chromaffin cell patches and presented as n:1 (Cortico:Medullary ratio). This cytometric method has been used widely as significant indicator of adreno-cortical or steroidogenic activity [31]. Cortico-medullary ratio i.e. surface area occupied by steroidogenic cords and chromaffin patches were measured using Motic Images Software (Version1.3, 2000)

2.3. Statistical Analysis

All the data were calculated as Mean ± Standard error. TWO-WAY ANOVA followed by multiple range test (Duncan Test) was used to analyze the data. Significance was calculated at the level of $p<0.05$.

3. RESULTS

3.1. Experiment I

Thirteen daily injections of 5-HTP and L-DOPA given 12 hours apart (12-hr) increased body weight of reproductively quiescent (RQ) bush quail (from 2^{nd} week onwards) compared to control, but when given 8 hours apart (8-hr) had no effect (Fig. **2A**). Further, testicular weight of 8-hr RQ bush quail was not different from control while 12-hr quail had enlarged testes ($p<0.001$) (Fig. **3A**). Histologically, testes of control bush quail (Fig. **4a**) showed inactive/non-breeding condition with thick tunica albugenia and smaller seminiferous tubules containing spermatogonial cells only. 8-hr quail (Fig. **4b**) testes were more or less in similar condition. However, 12-hr quail (Fig. **4c**) testes showed full breed-

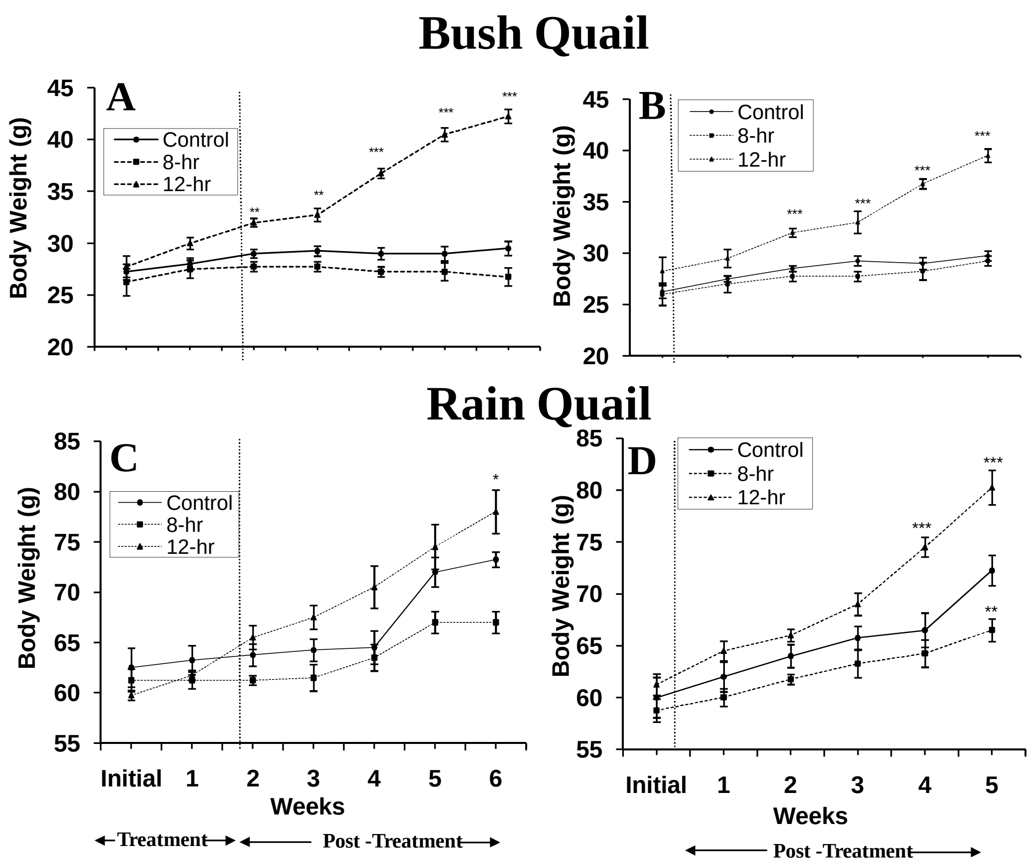

Fig. (2). Body weight responses of non-breeding bush quail (**A,B**) and breeding rain quail (**C, D**) administered with 5-HTP and L-DOPA at 8 hour and 12 hour interval for 13 days (left Panels) and 2 days (right Panels) in continuous light condition and then shifted to long daylength (LD 16:8). Dotted lines represent end of the treatment.

Values are Mean ± Standard Error.

Significance of difference from control (NS) *p<0.05, ** p<0.01, *** p<0.001.

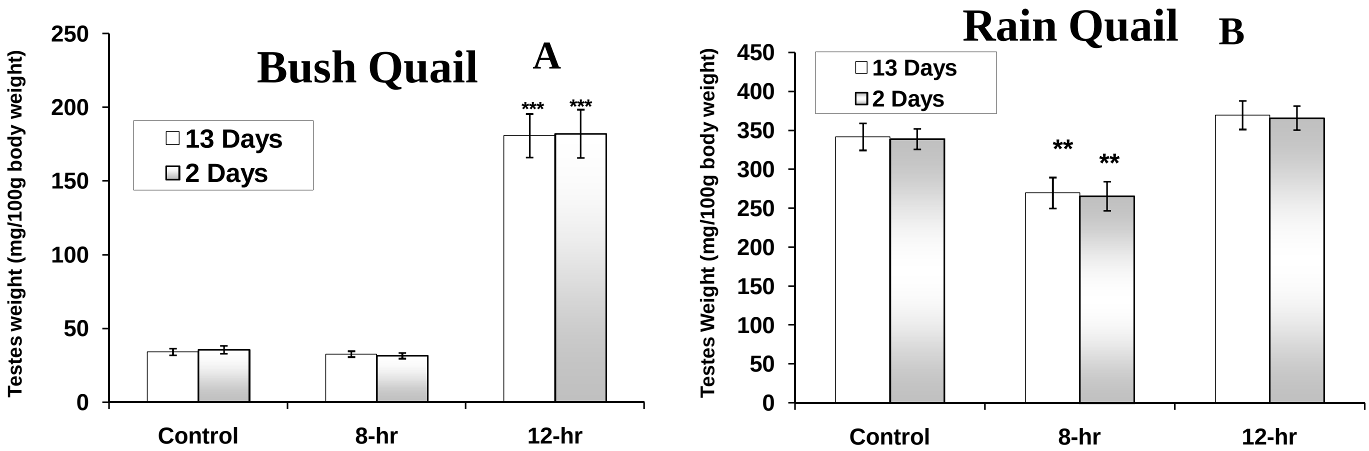

Fig. (3). Testicular Response of bush quail (**A**) and breeding rain quail (**B**) administered with 5-HTP and L-DOPA (for 13 days or 2 days) at the interval of 8 hours (8-hr) and 12 hours (12-hr).

Values are Mean $\pm$ Standard Error.

Significance of difference from control (NS) ** p<0.01, *** p<0.001.

ing condition. Enlarged seminiferous tubules had all the stages of spermatogenesis along with spermatozoa. Transverse sections of adrenal showed typical avian pattern having steroidogenic/cortical cords intermingled with the patches of chromaffin/medullary cells. In majority of the lightly stained cords, the cells and prominent nuclei were arranged in double rows while darkly stained chromaffin cells formed irregular patches (Figs. **6** & **7**). In the 12-hr Bush quail, the steroidogenic cords of the adrenal showed hypertrophy with the nuclei containing prominent nucleolus. Compared to control, cortico-medullary ratio i.e. relative surface area of the steroidogenic cords in relation to the chromaffin patches (n:1) also increased in 12-hr quail, while that of 8-hr was not different (Figs. **6a**, **b**, **c**; **8a**, **b** & **c**, Table **1**).

In the reproductively active (RA) rain quail, the thirteen days treatment had no effect on the body weight except at the termination of the study when compared to the control, 12-hr bird had increased and 8-hr bird had lower body weight (Fig. **2C**). Further, compared to fully developed testes of control rain quail, 8-hr quail had smaller testes while that of 12-hr was not different from control (Fig. **3B**). Histologically, control (Fig. **5a**) rain quail testes showed breed-

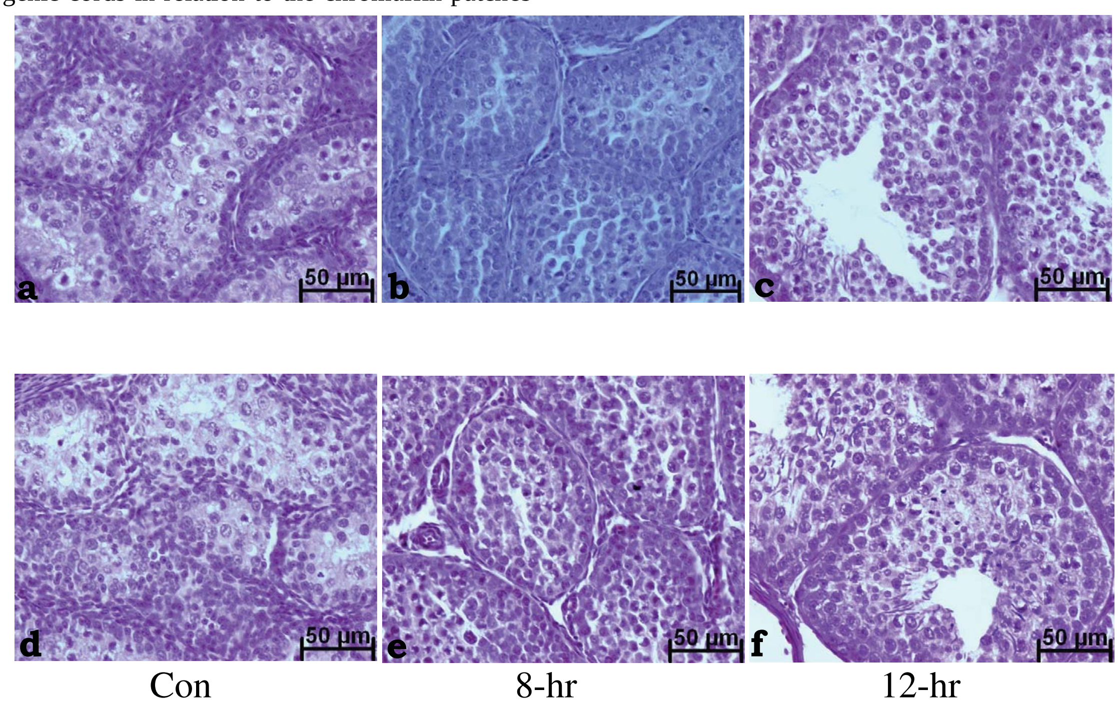

Fig. (4). Transverse section of testis of bush quail administered with 5-HTP and L-DOPA at the interval of 8 hours and 12 hours for 13 days (**a, b, c**) and 2 days (**d, e, f**). Note inactive testes in control (**a** & **d**) and 8-hr (**b** & **e**) quail having smaller seminiferous tubules containing spermatogonial cells only. Testes of 12-hr (**c** & **f**) birds with enlarged seminiferous tubules are showing full breeding condition with spermatozoa. Scale bar = 50 µm.

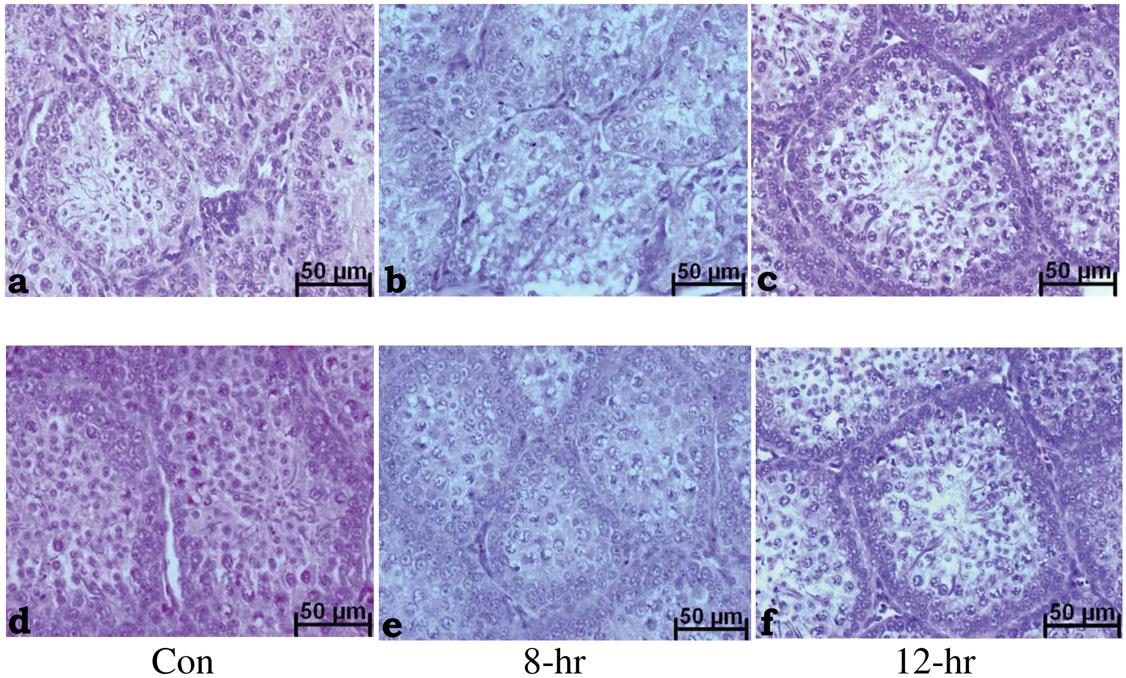

Fig. (5). Transverse section of testis of rain quail administered with 5-HTP and L-DOPA at 8 hour and 12 hour interval for 13 days (**a, b, c**) and 2 days (**d, e, f**). Compared to developed testis of control (**a** & **d**), 8-hr (**b** & **e**) quail testis shows atrophy, while degree of development is more in 12-hr (**c** & **f**) testis having bunches of spermatozoa. Scale bar = 50 µm.

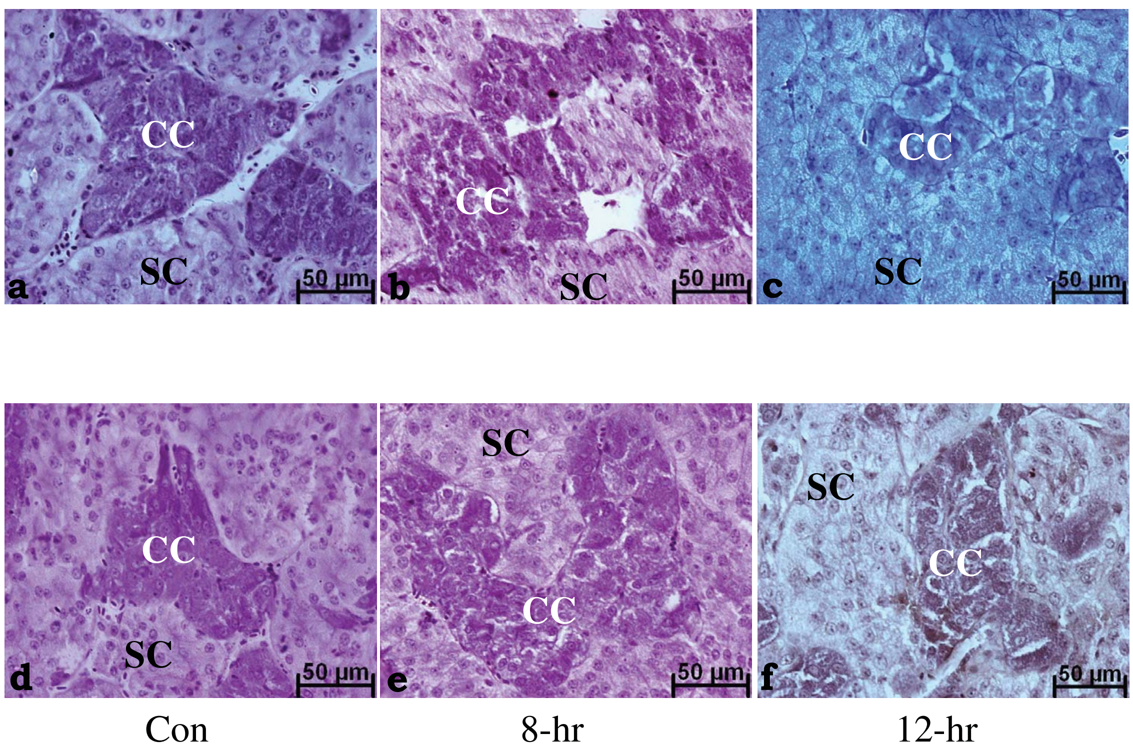

Fig. (6). Transverse section of adrenal of bush quail administered with 5-HTP and L-DOPA at 8 hour and 12 hour interval for 13 days (**a, b, c**) and 2 days (**d, e, f**). Compared to control (**a** & **d**) and 8-hr quail (**b** & **e**), cortico-medullary ratio has increased in 12-hr (**c** & **f**) quail along with hypertrophied cords. Scale bar = 50 µm.

ing condition with seminiferous tubules containing all the stages of spermatogenesis and spermatozoa. But, 8-hr (Fig. **5b**) rain quail testes showed suppressed condition with smaller seminiferous tubules and had no advanced stages of spermatogenesis except few layers of spermatogonial cells. However, testes of 12-hr (Fig. **5c**) rain quail showed full breeding condition as in control but appear to be more developed with enlarged seminiferous tubules containing increased number of spermatozoa in bunches and prominent Leydig cells in the interstitial spaces (Figs. **5a**, **b** & **c**). Transverse section of control rain quail adrenal (Fig. **7a**) showed active/hypertrophied condition. Prominent cords

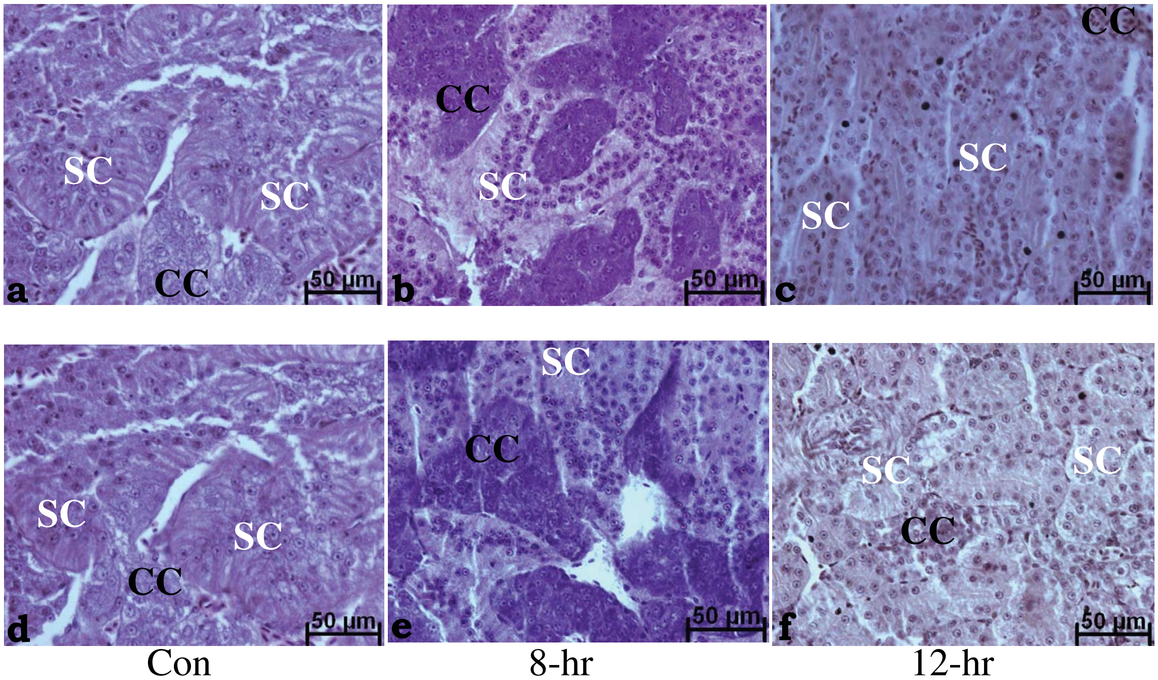

Fig. (7). Transverse section of adrenal of rain quail administered with 5-HTP and L-DOPA at 8 hour and 12 hour interval for 13 days (**a**, **b**, **c**) and 2 days (**d**, **e**, **f**). 8-hr (**b** & **e**) quail adrenal shows narrow steroidogenic cords (SC) and less cortico-medullary ratio compared to that of control (**a** & **d**). Although cords size is reduced in 12-hr quail (**c** & **f**) but overall surface area occupied by streoidogenic cords has increased and patches of medullary/ chromaffin cells (CC) are reduced significantly compared to control. Scale bar = 50 µm.

appeared as bigger mass due to folded condition and had clear nuclei and nucleoli. Adrenal of 8-hr quail (Fig. **7b**) had relatively narrow cords with somewhat smaller nuclei. In 12-hr quail (Fig. **7c**) as in control, highly vasculorized active adrenal had hypertrophied cords with prominent nuclei and nucleolus and relatively less number and area of patches of chromaffin cells. However, unlike folded cords of control, in 12-hr quail the cords were straight. In RA rain quail, cortico-medullary ratio was more in 12-hr and less in 8-hr compared to control (Fig. **8d**, **e** & **f**, Table **1**).

3.2. Experiment II

In experiment II, effects of 2 days of the injections of neurotransmitter precursor drugs on the body weight (Fig. **2B** & **2D**), testes weight (Fig. **3A** & **B**), testis (Fig. **4d**, **e** & **f** and Fig. **5d**, **e** & **f**) and adrenal (Fig. **6d**, **e** & **f** and Fig. **7d**, **e** & **f**) histology in both the species of quail were more or less similar to that of experiment I

4. DISCUSSION

Present study confirms that daily administration of serotonergic and dopaminergic precursors for either 13 days or 2 days, suppresses and stimulates gonadal development if given 8 hours or 12 hours apart respectively. It is interesting to note that both the species of the quail respond similarly to specific phase relation of serotonergic and dopaminergic oscillations irrespective of their annual gonadal condition [28,29]. 8-hr relation did not allow gonadal growth in bush quail similar to its control while 12-hr bush quail attained full breeding condition out of the season, which coincides with the peak reproductive condition of this species observed in the month of June. In rain quail also, 8-hr relation of the two precursor injections suppressed the gonadal development compared to the control which showed breeding condition, while the testes of 12-hr quail were in more advanced stage (Figs. **3-5**). Further this is the first report that indicates similar effectiveness of the total dose of the two precursor drugs, administered either in 13 or 2 days irrespective of the species and phase of their gonadal cycle.

It is obvious that present effect is not the pharmacological effect of serotonin and/or dopamine alone but is actually the effect of circadian phase relation of the two neurotransmitters on the neuroendocrine-gonadal axis which varies according to the interval between the two injections. Although we did not test in these species but in all our previous studies performed in males of different avian species including Japanese quail, out of six relations (0, 4, 8, 12, 16 and 20-hr), only 2 relations were found to be effective (8-hr gonado-inhibitory and 12-hr gonado-stimulatory) and rest of the relations were ineffective [22,25,26].

Although in the present study adrenal response also varied depending on the specific phase relation of serotonergic and dopaminergic oscillations / activities, it is yet to be tested if serotonin / dopamine alone can induce any effect on adrenal. However it is quite reasonable to suggest that it is the combined effect of the two drugs given at specific time interval hence producing the opposite effects in 8- and 12-hr quail adrenal. If this would have been the pharmacological or direct effect of serotonin and/or dopamine, response should be similar in both 8 and 12-hr birds. Reports are also there that serotonin induces glucocorticoid secretion from the adrenal cortex by stimulating the hypothalamo – hypophyseal axis and also by direct adrenocortical tissue stimulation [32, 33], although direct effect of dopamine on adrenal function is not known. Further, it is yet to be investigated

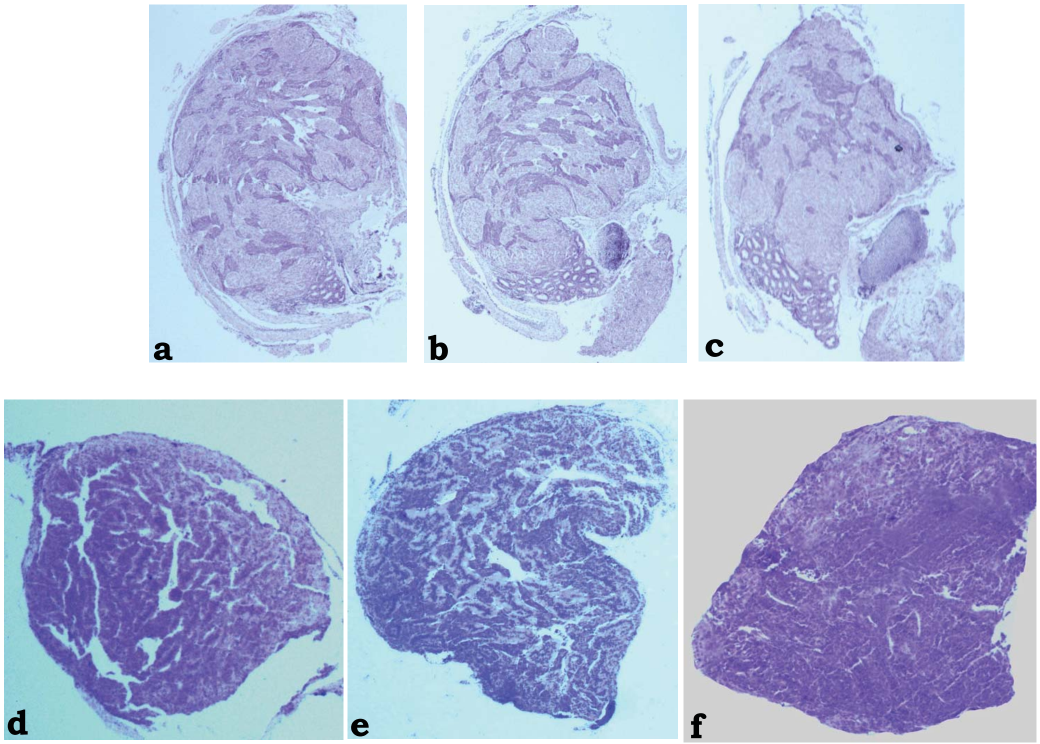

Fig. (8). Photomontage of adrenal of bush quail (**a**, **b** & **c**) and rain quail (**d, e** & **f**). Note increased amount of steroidogenic cords/corticomedullary ratio in 12-hr (**c**) Bush quail compared to control (**a**) and 8-hr (**b**) which are not significantly different from each other. In Rain quail, 8-hr (**e**) has decreased and 12-hr (**f**) adrenal has increased amount/area of steroidogenic cords and cortico-medullary ratio compared to control (**d**).

Table 1. Cortico-Medullary Ratio

Species	Treatment Period	Control	8-hr	12-hr
Bush Quail	3 Days	1.73:1	1.8:1	2.18:1
	2 Days	1.79:1	1.76:1	2.28:1
Rain Quail	13 Days	1.83:1	1.31:1	2.71:1
	2 Days	1.92:1	1.25:1	2.68:1

whether temporal synergism of serotonin and dopamine influences adrenal function directly or indirectly. Indirect evidence suggests that reproductive system by such treatments is influenced *via* higher brain center and/or altering hypothalamic/GnRH activity. But mechanism of temporal phase relation of serotonin and dopamine induced changes in metabolic responses (body weight and fat deposition) is yet to be explained. Since 8-hr is always gonado-inhibitory and 12- hr is gonado- stimulatory and body weight/ fat deposition if influenced, is suppressed and increased respectively, it is possible that adrenal activity / function runs parallel to metabolic/gonadal activity suggesting parallel gonad - body weight – adrenal relationship in these species.

It is interesting to note that not only the treatment of thirteen days but even two days of treatment could produce similar effect. This may be an interesting and applied way of reproductive regulation. It is worth mentioning that noticeable response occurs from 5th day onwards (2 days treatment + 3 days post-treatment) or on 5th day of ongoing 13 day treatment [34, 35]. Since, except 8- and 12-hr relation all other treatments were ineffective, it is reasonable to suggest that these are the effects of specific circadian phase/time relation between two drugs but not the individual/independent effect of either serotonergic or dopaminergic drug. It also can not be the combined effect of two drugs otherwise effects should have been similar in all the relationships. Most important point is that the two effective relations are having opposite effects.

Apart from gonadal response which is the major focus of the present as well as number of earlier studies, responses were seen in the body weight and fat deposition as well. In migratory bird red headed bunting, *Emberiza bruniceps*, which winters in India from Afghanistan and eastern Europe, enormous amount of migratory fat observed during spring migration may be abolished completely in 8-hr birds along with gonadal suppression, while 12-hr relation, may induce both fat deposition as well as gonadal stimulation out of the season [22]. Similar treatment when given in day old chicks of Japanese quail as well as three weeks old sexually immature quail, rate of growth (body weight gain) is significantly slow/less in 8-hr bird compared to control and 12-hr birds were significantly heavier. However, once attained the adult size/weight, there was no difference among the control and experimental groups, neither of the treatment induced any effect in the body weight response if given in adult Japanese quail [25].

This study also reveals that the adrenal cortical activity varies distinctly with the seasonal gonadal cycle of birds both in natural and experimental condition. Adrenal responses always maintained direct relationship with gonad in experimental conditions, confirming parallel gonad-adrenal relationship in these quail, under natural condition.

It is concluded that serotonergic and dopaminergic drugs when given 8 hours apart suppressed but when given 12 hours apart stimulated neuroendocrine-gonadal axis irrespective of the season, gonadal condition and the species. Further these effects appear to be the physiological effects since same drugs and doses produced different effects depending on the time interval of their administration. Moreover, not only the gonadal axis, but general metabolism (body weight) and adrenal function was also altered as a function of the time/ phase relation between the two circadian neural oscillations. These findings further strengthen the hypothesis that temporal synergism of serotonergic and dopaminergic oscillations may be the basis of seasonality.

ACKNOWLEDGEMENTS

The authors wish to thank University Grants Commission, New Delhi, India for the major research project (F-3-201/2001 (SR-II) to CMC and Project Fellowship to PK.

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Received: January 06, 2009 Revised: January 20, 2009 Accepted: February 02, 2009