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Reproductive Phase Dependent Photosensitivity of Gonad and Pineal Gland of a Short-Nosed Fruit Bat, *Cynopterus sphinx*

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ABSTRACT—Photoperiodic sensitivity of gonad in relation to pineal gland activity was noted during two important reproductive phases i.e. reproductively active (February- March) and inactive (July- August) phases of nocturnal flying mammal, *Cynopterus sphinx* of Indian tropical origin. They were exposed to experimental long (Light: Dark in hours; 16L: 8D) and short (8L: 16D) photoperiods for 30 days during both the reproductive phases. Exposure to the long photoperiod (LP) during reproductively active phase had no significant effect on pineal gland, gonad and its hormonal concentration. However, exposure to short photoperiod (SP) induced a decrease in gonadal activity and increase in pineal activity (as judged by the gland weight, histology, low level of estradiol / testosterone and high level of melatonin in plasma). Increased melatonin and decreased estrogen levels following the short photoperiod exposure caused abortion in females, which were undergoing delayed embryonic development during reproductive inactive phase. Exposure to LP during reproductively inactive phase reactivated the gonadal axis and inhibited the pineal activity (as judged by the gland weight, histology, high level of estradiol / testosterone and low level of melatonin in plasma), while exposure to SP had no significant effect on pineal and gonad during this phase.

From these observations, it is suggested that depending upon the reproductive status, short and long photoperiod affected differently the gonadal and pineal gland activity of this bat. SP induced gonadal regression during reproductive active phase and LP reactivated the gonadal axis during reproductive inactive phase. Under experimental condition the inverse relationship between pineal and gonadal activity was maintained as observed in nature.

INTRODUCTION

The nocturnal flying mammal bats constitute almost 25% of all species of mammals. Most of them live in the tropics and many breed seasonally (Fleming *et al*, 1972; Bonaccorso, 1979; Heideman, 1988). The effect of photoperiod alone on seasonal reproduction was examined in few species of bats of Temperate Zone. Beasely and Zucker (1984) reported that the photoperiod influences the reproductive physiology of the male pallid bat, *Antrozous pallidus* while, Racey (1978) presented evidences for increased day length regulation of testicular development of *P. pipistvellus* suggesting that it might be sensitive to particular photoperiods only. However, there is a lack of detailed study explaining the effect of long photoperiod and short photoperiod on the specific reproductive phases of these nocturnal mammals in relation to the pineal gland. Hence, the present experiment was planned to assess the potential role of photoperiod (LP and SP) on the gonad and pineal gland function during reproductively active (February-March) and inactive phases (July-August) of Indian short-nosed fruit bat, *C. sphinx*.

This nocturnal mammal presents two peaks of annual gonadal cycle (one in October and second in February-March; bimodal breeder; Krishna and Dominic, 1983, 1984; Alipreeta, 1998). Interestingly, the photoperiod in nature during both the peak gonadal activity were approximately same i.e. 11 hr and 30 min (October; decreasing day length) and 11 hr 15 min to 11 hr 45 min (February- March; Increasing day length). It could be that, bats if exposed to less than the above mentioned photoperiod may present gonadal inactivity as observed in nature (Alipreeta, 1998) was experimentally assessed in our present investigation.

Till date, no report exists to explain whether this bat is photoperiodic or not, therefore, we exposed them to LP of 16L:8D length. It is also not known for this bat the length of photoperiod which may cause gonadal inhibition, hence, we

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exposed them SP of 8L: 16D length, which is commonly used for tropical animals as effective inhibitory photoperiod (Haldar and Srivastava, 1987).

MATERIALS AND METHODS

The adult bats, *Cynopterus sphinx* (Body weight; female, 45–50g and male 50–55g) were collected locally from the vicinity of Varanasi (Lat. 25° 18'N; long 83° 1'E). They were kept in wire net cages (25″ × 25″ × 30″ in size) for fortnight in an out door enclosure and fed with fleshy fruits like guava, banana, papaya, melons etc. and water *ad libitum*. After acclimatization to the above condition they were placed in photoperiodic chambers with light/dark schedule of 16L: 8D and 8L: 16D adjusted with the help of photoperiodic automatic clock (VEB, Zeitschaltelektronik, Frauenstein, Germany), in the same out door enclosure so that other ecofactors (temperature and humidity) are same as noted in nature.

The experiments were performed twice during reproductively active phase (February-March; temperature: max. 26.4°–28.6°C, min. 12.0°–13.7°C; humidity: max. 85.8%–69.7%, min 50.7%–35.2%; photoperiod: 11 hr 5 min 11hr 45 min) and reproductively inactive phase (July-August; temperature: max. 36.0°–32.7°C, min. 27.7°– 25.9°C; humidity: max. 85%–83%, min. 74%–65%; photoperiod: 13 hr–13 hr 30 min). Bats of both sexes were divided into three groups (i.e. each group consisted of 10 male and 10 female bats). Group - I (Control): Bats exposed to natural day length. Group- II: Bats exposed to long photoperiod (16L: 8D). Group-III: Bats exposed to short photoperiod (8L: 16D). The female bats of reproductive inactive phase were pregnant (90%) and under delayed embryonic development condition.

After 30 days of experimentation, all the bats were weighed and bled from sub-clavian vein during nighttime at ~ 11 p.m. (collection was made under very dim red light). Blood was centrifuged at 5000 r.p.m. and kept at –20°C till the RIA of melatonin following the method of Rollag and Niswender (1976) and reported earlier (Bishnupuri and Haldar, 2000). Following decapitation (next day at 11 a.m.) the trunk blood was collected, plasma was separated and stored at –20°C till the RIA of steroid (testosterone/estradiol) hormones. Gonads (testes / ovary), accessory sex organs (vas deferens / oviduct and uterus) and pineal gland were dissected out carefully, weighed and processed for histological examinations. RIA of steroid was performed with the help of estradiol kit (Leeco Diagnostic Inc. Miss, USA). The validation data of above hormonal assays were given in Table. 1.

Table 1. Hormonal validation data

Hormones	Precision		Sensitivity
	Intra-assay	Inter-assay	
Estradiol	5.97	8.13	0.817 pg/ml
Testosterone	4.2	5.1	0.006 ng/ml
Melatonin	9.0	15.0	10 pg/ml

Statistical analysis

Organ weights were presented as relative values. All values were presented as means +/– SEM (M+/– SE). The level of significance between different groups was analyzed using student's t-test. The data obtained from the weight of all the collected organs (Table 2) and hormonal assays were subjected to two-way analysis of variance (ANOVA, Bruning and Knitz 1977).

RESULT

Photosensitivity during reproductively active phase

Control Group I:

All the animals of both sexes of group I under natural condition showed high gonadal, accessory sex organ's weight (Figs. 1a,b) and high plasma testosterone/estradiol levels (Table 3) when compared with bats of reproductive inactive phase. Histological observation showed complete spermatogenic activity, large seminiferous tubules and lumen filled with numerous spermatozoa. The Leydig cells were also hypertrophied (Fig. 3-1). In females, active oogenesis was noted with large number of primordial, and secondary follicles (Fig. 4-1), with high plasma estradiol level (Table 3). Pineal gland weight (Fig1a, b) and plasma melatonin level (Table 3) of the bat of reproductive active phase showed low values in comparison to that of reproductive inactive phase.

Group II Exposed to LP:

Exposure of bats to long photoperiod, had no significant effect on gonad and accessory sex organ weight (Figs. 1a,b). Histologically, similar gametogenic activity was noted in control group I (Figs. 3-2, 4-2). Plasma steroid level also showed no significant difference as compared to group I (Table 3). The pineal gland weight (Figs.1a,b) along with the plasma melatonin level (Table 3) showed no significant difference as compared to group I.

Group III Exposed to SP:

Exposure of bats to short photoperiod caused significant decrease in gonad and accessory sex organ weight (Figs. 1a,b) along with plasma steroid level (Table 3). Histological observation showed a complete arrest of spermatogenesis hence, atrophy of seminiferous tubule's diameter (by obser-

Table 2. Summary of two way analysis of variance (ANOVA) of data on the effect of LP (16L: 8D) and SP (8L:16D) on gonad (testicular/ovarian), accessory sex organs (vas deference/oviduct + uterus) and pineal gland weight during reproductively active and inactive phases of *C. sphinx*.

Parameters	Treatment	Phase	Interaction treatment phase
Male			
Testes	27.94, P<0.001	53.20, P<0.001	8.14, P<0.05
Vas def.	8.19, P<0.05	16.65, P<0.001	3.76, NS
Pineal	45.19, P<0.001	14.56, P<0.001	9.28, P<0.05
Female			
Ovary	3.21, NS	22.81, P<0.001	0.35, NS
Oviduct + Uterus	20.47, P<0.001	7.60, P<0.025	3.18, NS
Pineal	34.77, P<0.001	22.55, P<0.001	19.32, P<0.001

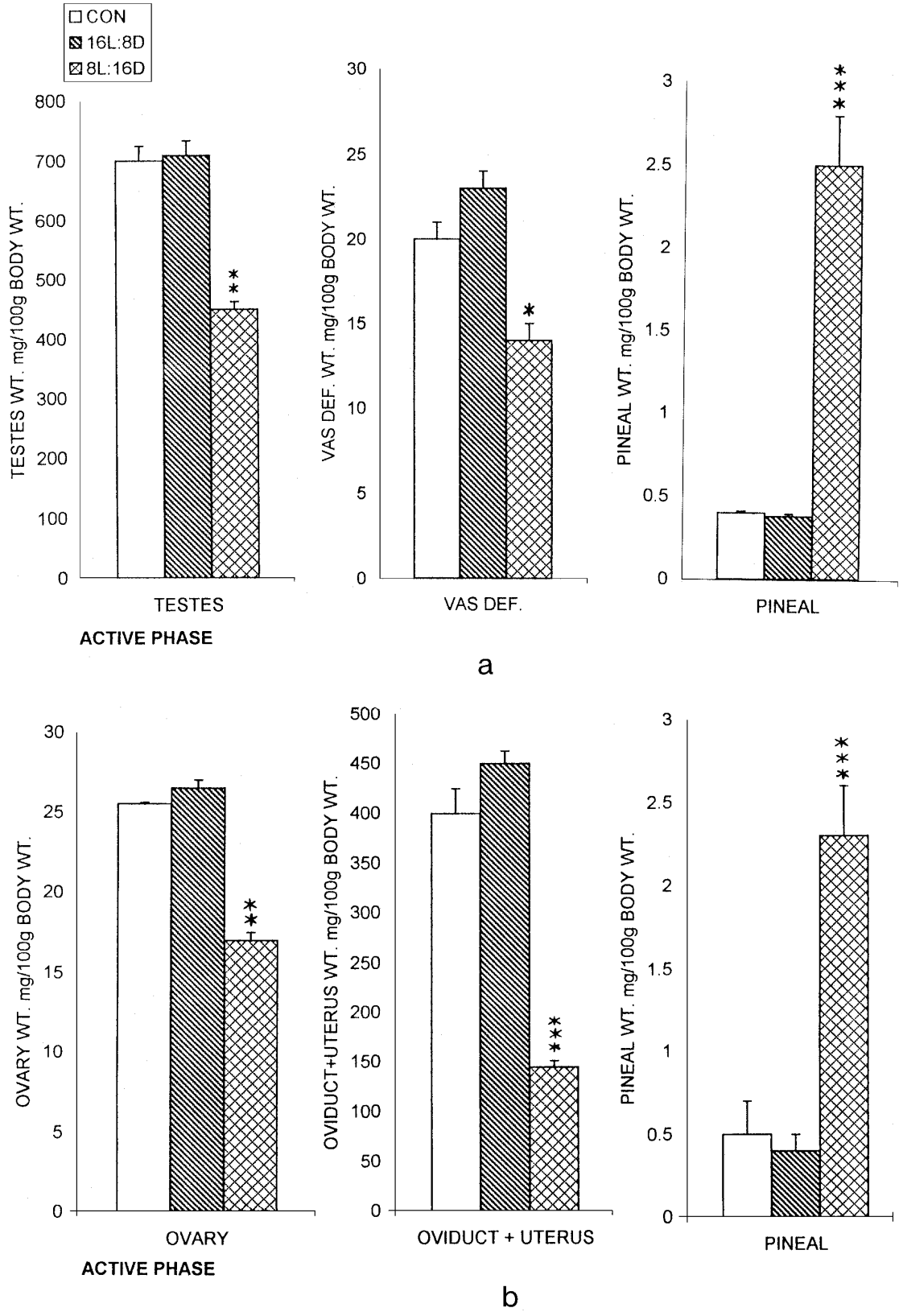

Fig. 1. **a**, Effect of long (16L:8D) and short photoperiod (8L:16D) on the testes, vas deferens and pineal gland weight of *C. sphinx* during reproductively active phase. Significance of difference from control group I * P<0.05; ** P<0.01; *** P<0.001 **b**, Effect of long (16L:8D) and short ohotoperiod (8L:16D) on the ovary, oviduct + uterus and pineal gland weight of *C. sphinx* during reproductively active phase. Significance of difference from control group I ** P<0.01; *** P>0.001

Table 3. Variation in plasma steroids (estradiol/testosterone) and melatonin level in control and experimental group (LP, 16L:8D; SP, 8L:16D) during reproductively active and inactive phases of *C. sphinx*.

Reproductive phases	Testosterone ng/ml (Male)	Estradiol pg/ml (Female)	Melatonin Male	Melatonin Female
Active phase				
Control	3.13 ± 0.07	830 ± 100	183 ± 25	180 ± 27
Long Photoperiod	3.23 ± 0.06	800 ± 100*	175 ± 14	170 ± 11**
Short photoperiod	1.24 ± 0.05**	210 ± 32**	406 ± 34**	410 ± 33
Inactive phase				
Control	1.52 ± 0.16	290 ± 32	420 ± 34	450 ± 20
Long photoperiod	3.02 ± 0.07**	820 ± 110**	180 ± 22**	200 ± 22**
Short Photoperiod	1.40 ± 0.12	210 ± 32**	424 ± 27	500 ± 16*

Significance of difference from control group of active and inactive phase * $p<0.01$; ** $p<0.001$

vation) was noted. Leydig cells showed complete inactivity (Fig. 3-3).

Histological observation of the ovary presented single large corpus luteum, which is the characteristic of this species of bat (Fig. 4-3). No pregnant female bat was noted during this phase. Pineal gland weight and activity of both the sexes showed a significant increase (Figs. 1a, b), with high plasma melatonin level (Table 3) as compared to group I of reproductively active phase.

Photosensitivity during reproductive inactive phase

Control Group I:

All the bats of control group I showed low ovary / testes weight (Figs. 2a, b) with low plasma estradiol / testosterone level (Table 3) when compared with reproductive active phase. Vas deferens also showed less weight (Fig. 2a) but oviduct and uterus weight was high as the 90% females were pregnant and undergoing delayed embryonic development (Fig. 2b). Hence, the uterus weight was higher than the control group of active phase. Histologically inactive gonads were observed (Figs. 3-4, 4-4). Few inactive Leydig cells were also noted. Pineal gland weight of the both sexes showed high value (females have high pineal weight than males during this phase; (Figs. 2a, b) and plasma melatonin level was also high (Table 3).

Group II:

Exposures of bats to long photoperiod presented significant increase in testicular weight (Fig. 2a), with no significant difference in ovarian weight (Fig. 2b) and vas difference weight (Figs. 2a, b). Histologically active testes was noted with lumen full of spermatozoa and enlarged Leydig cells (Fig. 3-5), along with significant increase in plasma testosterone level (Table 3) when compared to group I. Though there was no significant difference in ovarian weight females presented hisotologically high ovarian activity with Graafian follicle and large number of well developed secondary follicles (Fig. 4-5) along with a significantly increased plasma estradiol level (Table 3). Oviduct weight increases significantly when compared with the active phase suggesting advanced growth in the uterus (fig 2b). Pineal gland weight and plasma melatonin level of both sexes showed a significant decrease (Figs. 2a, b; Table 3).

Group III:

Exposure of bats of both the sexes to short photoperiod, had no significant effect on gonad, vas deferens and pineal gland weight (Figs. 2a,b) since the organs were already in inactive conditions. Oviduct and uterus weight decreased significantly when compared with group I(figs 2a,b) because the pregnant females aborted within a week of short photoperiodic treatment. The aborted embryos were noted in the cages. No significant changes in plasma steroid and melatonin level (Table 3) were observed as compared to the group I.

DISCUSSION

The presence of large and morphologically active pineal gland in many tropical bats, including *C. sphinx* (Bhatnagar *et al*, 1990) suggest that elements of pineal mediated photoperiodic transduction pathway could be functional as noted for rodents from the tropics (Haldar and Srivastava, 1987).

The tropical fruit bat has two peaks of reproductive activity, phase I in February - March, and phase II in October. The bat seems to be reproductively active when the photoperiod in nature is 11.30 to 12.45 hr during both the phases. Interestingly, day length is increasing during the reproductively active phase I, while it is decreasing during reproductively active phase II. Therefore, photoperiod of approximately 12L:12D or more than 12 hrs appears to be stimulatory for gonadal activity for this bat irrespective of the increasing or decreasing trend of day length.

In the present investigation, potential role and sensitivity of gonad and pineal gland to different photoperiodic condition was studied for the first time in a tropical zone nocturnal flying mammal, *C. sphinx.* Exposure of bats to SP (8L: 16D) during reproductively active phase I significantly decreased the gonadal weight and plasma steroidal /testosterone level with

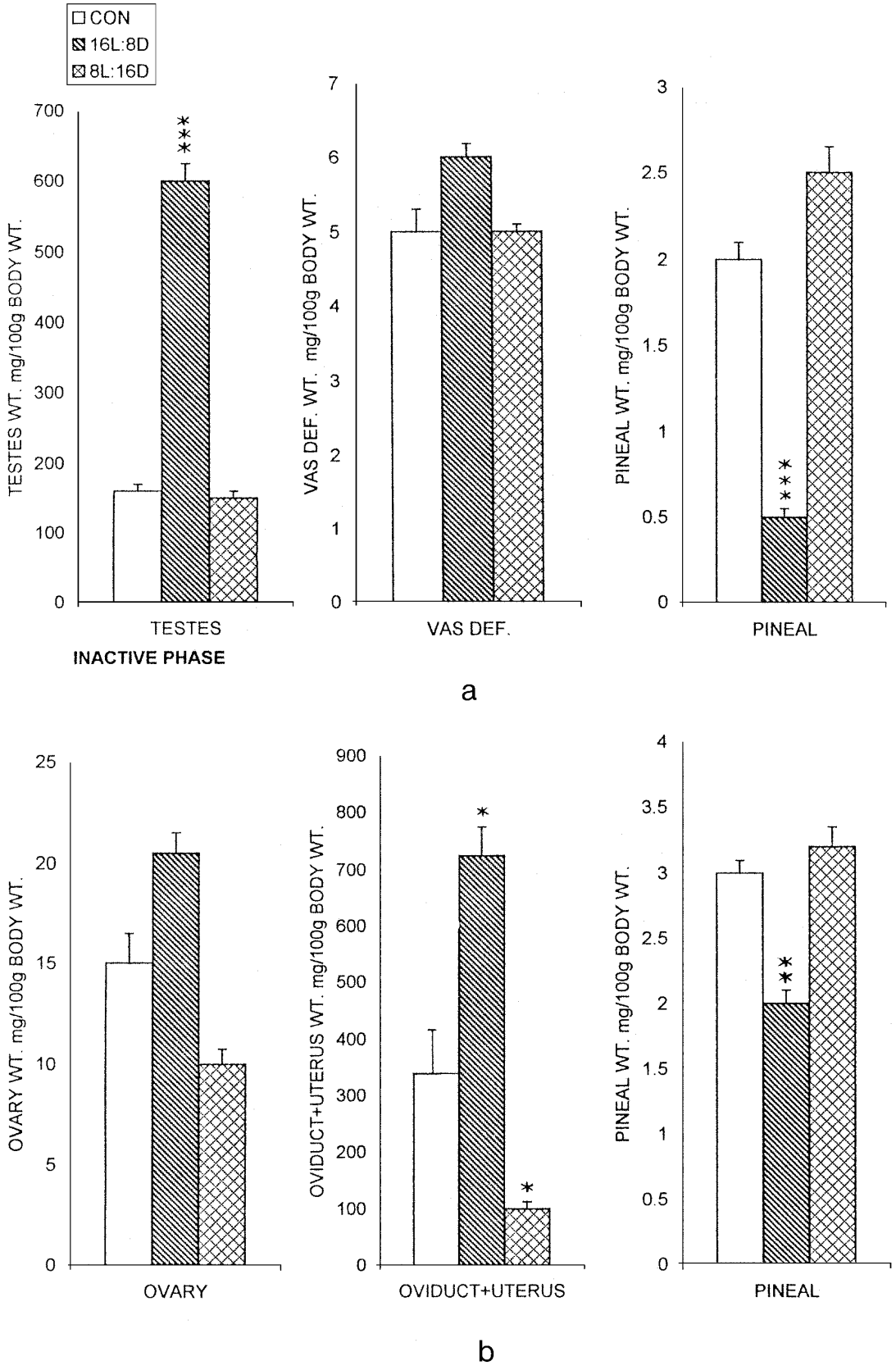

Fig. 2. **a**, Effect of long (16L:8D) and short photoperiod (8L:16D) on the testes, vas deferens and pineal gland weight of *C. sphinx* during reproductively inactive phase. Significance of difference from control group I *** P<0.001 **b**, Effect of long (16L:8D) and short ohotoperiod (8L:16D) on the ovary, oviduct + uterus and pineal gland weight of *C. sphinx* during reproductively inactive phase. Significance of difference from control group I * P<0.05; ** P>0.01.

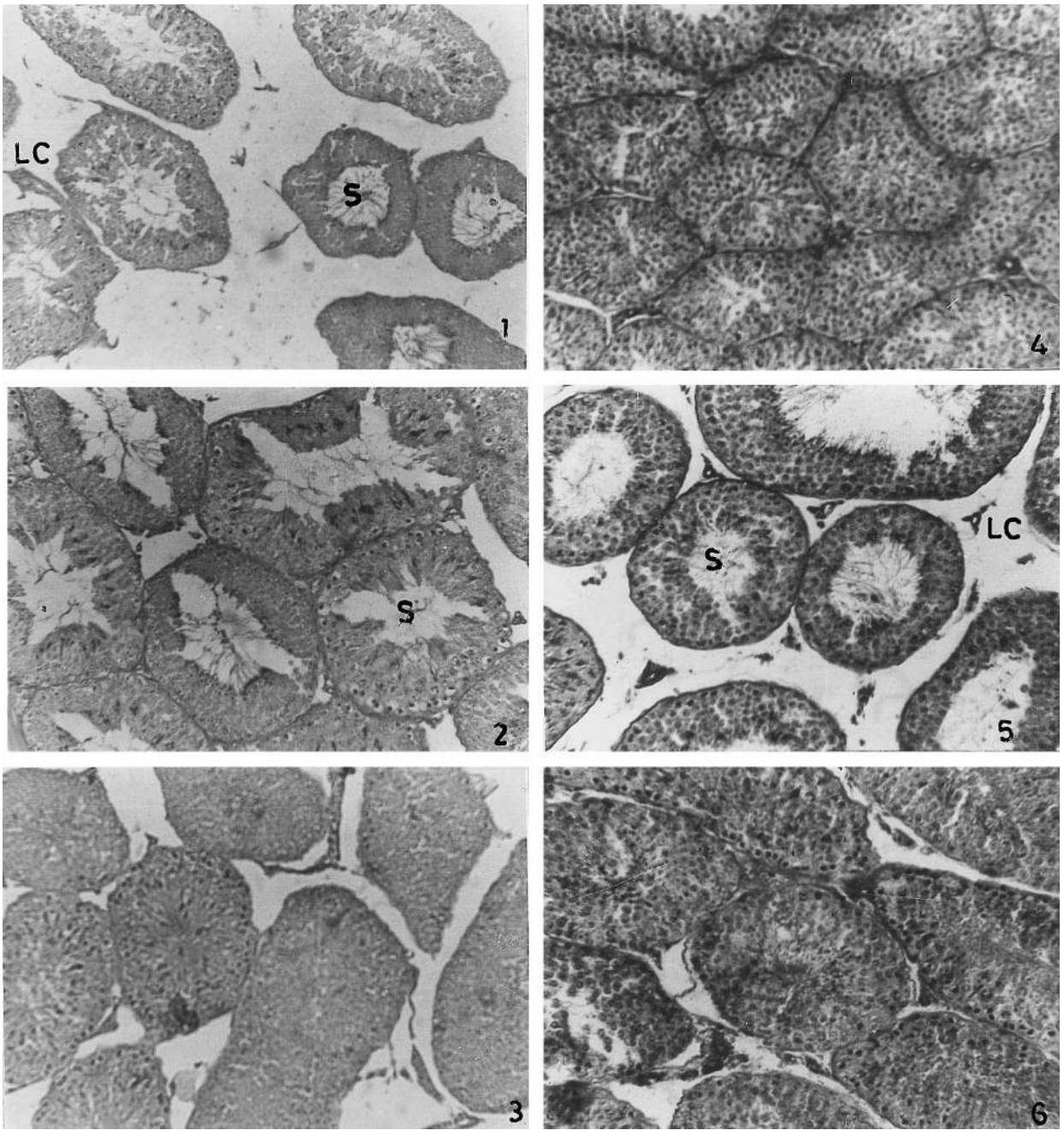

Fig. 3. **1**, Photomicrograph of testes of control bats of reproductively active phase, kept under natural condition. Note the active spermatogenesis along with bunch of spermatozoa (S), Leydig Cell (LC). ×150. **2**, Photomicrograph of testes of bats of reproductively active phase, exposed to long photoperiod (16L:8D).Note acceleration of spermatogenesis with increase in tubular size, lumen filled with full of spermatozoa (S). ×150. **3**, Photomicrograph of testes of bats of reproductively active phase, exposed to short photoperiod (8L:16D). Note the complete arrest of spermatogenesis. ×150. **4**, Photomicrograph of testes of control bats of reproductively inactive phase, kept under natural condition showing complete inactivity with complete arrest of spermatogenesis. ×150. **5**, Photomicrograph of testes of bats of reproductively inactive phase, exposed to long photoperiod (16L:8D). Note the active spermatogenesis with bunch of spermatozoa in lumen (S) and well developed Leydig Cells (LC). ×150. **6**, Photomicrograph of testes of bats of reproductively inactive phase, exposed to short photoperiod (8L:16D). Note no effect. ×150.

complete arrest of gametogenesis. It increased the pineal gland activity with significantly high plasma melatonin level. This condition was also noted in other tropical mammals (rodents) in response to SP (in nature/ or under experimental condition; Haldar and Srivastava 1987, Haldar and Saxena ,1990). When the animals were exposed to LP (16L : 8D i.e. a period longer than 11.45 to 13.00 hrs in nature) during reproductively inactive phase (July-August), the gonadal activity increased (in term of weight; histology and hormonal concentration) and pineal gland weight and plasma melatonin level decreased significantly, suggesting that LP is stimulatory for gonadal function and inhibitory for pineal function for this spe-

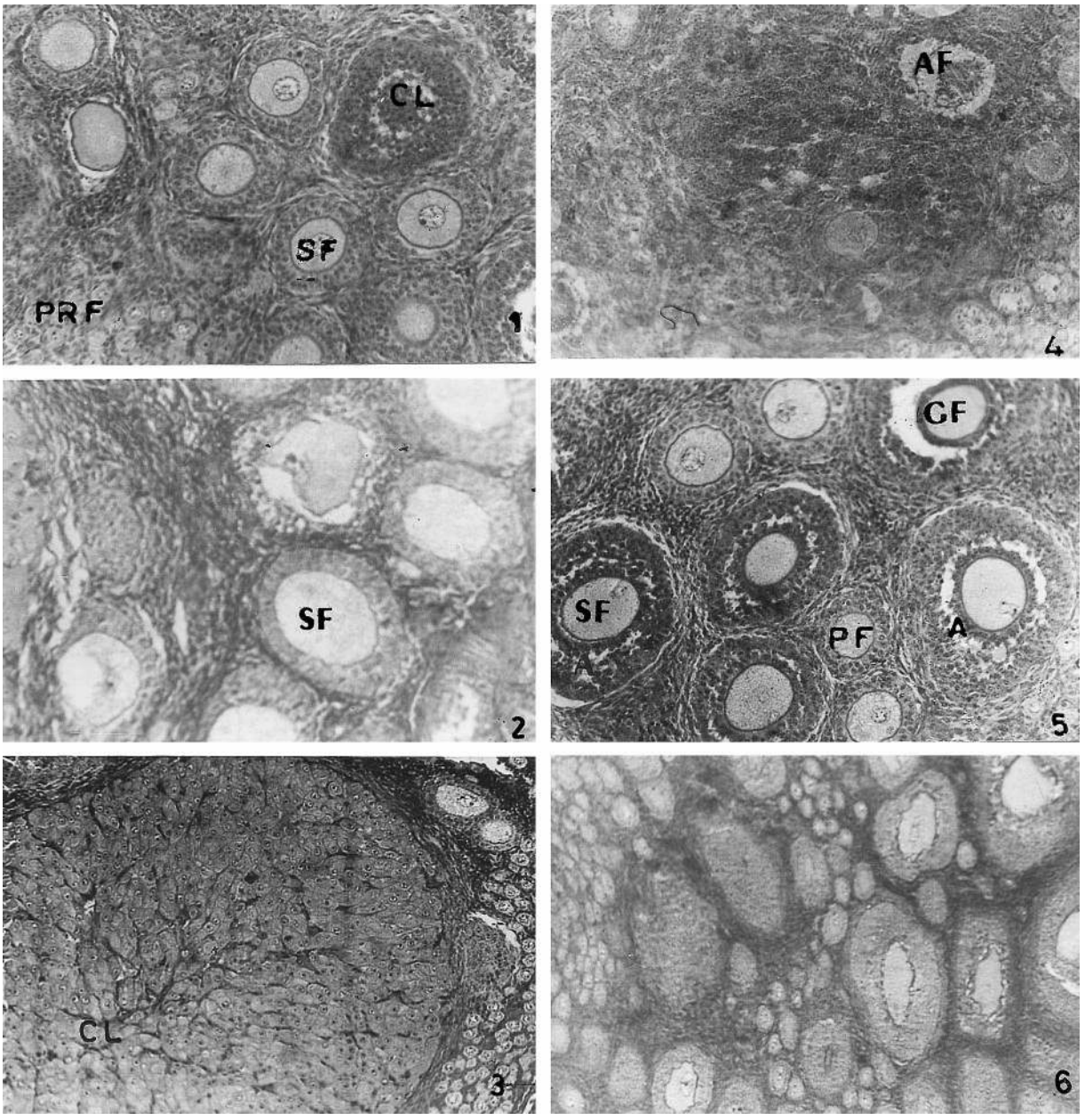

Fig. 4. **1**, Photomicrograph of ovary of control bats of reproductively active phase, kept under natural condition showing active oogenesis along with secondary follicle (SF), corpus luteum (CL), primordial follicles (PRF). ×150. **2**, Photomicrograph of ovary of bats of reproductively active phase, exposed to long photoperiod (16L:8D). Note the advancement of oogenesis with number of well developed secondary follicles (SF). ×150. **3**, Photomicrograph of ovary of bats of reproductively active phase, exposed to short photoperiod (8L:16D). Note the regression in oogenesis along single large corpus luteum (CL) which is a characteristic of the *C. sphinx*. ×150. **4**, Photomicrograph of ovary of control bats of reproductively inactive phase, kept under natural condition. Note the complete inactivity; Atretic follicle (AF). ×150. **5**, Photomicrograph of ovary of bats of reproductively inactive phase, exposed to long photoperiod (16L:8D) showing acceleration of oogenesis with initiation of Antrum (A) formation (Folliculogenesis) in the secondary follicles (SF). Graafian follicle (GF), primary follicle (PF). ×140. **6**, Photomicrograph of ovary of bats of reproductively inactive phase, exposed to short photoperiod (8L:16D) showing arrest of oogenesis. ×140.

cies of bat . Similar reports came from the studies of the male pallid bat, *A. pallidus* of temperate zone (Beasly and Zucker, 1984) favoring our results. Further, we found that under each experimental (photoperiodic) condition the pineal gland of this fruit bat presented an inverse relationship with gonadal function as noted in nature during annual cycle study (Alipreeta,1998).

The gonad under experimental condition were responsive to LP of 16L:8D (photosensitive) during reproductively inactive phase (July-August) and also to SP of 8L:16D (scotosensitive) during reproductively active phase (February-March).These results indicate that bats are photosensitive and not photorefractory to experimental conditions of LP /SP when exposed during different reproductive phase. Hence, photoperiodic response of this bat is a reproductive phase-dependent phenomenon.

The seasonal chronology of the events of the reproductive cycle of the tropical rodents reveals that the ecofactors (temperature, rainfall and humidity) other than lights are equally important (Haldar and Saxena 1988 ; Haldar and Srivastava 1992) in influencing both pineal and gonadal function. If the photoperiod during both the reproductive phases are same then question arises "is their any role of temperature (i.e. high of summer and low of winter) in controlling reproduction and pineal function of this species ? Unlike the similar length of photoperiod in nature during both the reproductive phases, the temperature was relatively different during both the phases. Therefore, temperature could be a cofactor for high /low gonadal activity as temperature is known to effect melatonin secretion (Stokkan *et al*.1991) and in turn gonadal activity.

The bat increased the gonadal weight under LP condition only during reproductive inactive phase when temperature was same as reproductive active condition and directs the question to other ecofactors in nature that could be responsible for gonadal regression. The metrological data around Varanasi suggest that there is a drastic change in % humidity in nature during the reproductive inactive condition (Alipreeta, 1998). In July-August a very high humidity in nature occurs due to monsoon rainfall, which is quite stressful for these bats. Heavy rainfall disturbs the shelters of the bats and there is also seasonal decrease in the variety of fleshy fruit in the nature which might have decreased the gonadal activity and increased the pineal function.

Therefore, it may be suggested that relative increase in day length (13L-16L in summer) along with temperature and humidity (as cofactor) is stimulatory for gonad and inhibitory for pineal gland (pineal off and gonad on), while relative decrease in day length (11.5 L – 8 L in early spring) is inhibitory for gonadal function and stimulatory for pineal gland (pineal on gonads off). This phenomenon of adjustment of gonadal activity with ecofactor appears to be dependent on inter hormonal (i.e. gonadal steroids and melatonin) mechanism and it could be suggested that pineal plays an important adaptive role for reproduction in this bat.

It has been reported that the reproductive inactive period of female bats present a peculiar phenomenon of delayed embryonic development (Krishna and Dominic, 1983). When we exposed the bats to SP during reproductively inactive phase the vas deferens weight showed no significant change while the female bats which were pregnant (90%) and under delayed embryonic development condition showed a significant decrease in oviduct and uterus weight when compared to control group I of reproductive inactive phase. Actually, SP treatment terminated pregnancy (100%) by abortion in pregnant female bats within few days of exposure to SP hence, a low uterus weight was observed. There was no abortion at all following LP treatment to other group of pregnant females during this phase of delayed embryonic development suggesting that LP was favorable for maintaining embryos and result suggest that it accelerated the embryonic growth since uterus weight increase significantly (Fig.2b). From the present study as well as the study performed in order to note the reproductive pattern of this bat (Alipreeta, 1998) we may suggest that the delayed embryonic developmental phenomenon noted in bats perhaps requires a photoperiod longer than 8L. The moderately high level of melatonin (melatonin 450 pg/ml due to natural and experimental short day) was enough to suppress endogenous progesterone level. Further, during reproductive inactive phase under LP condition the level of melatonin decreased significantly while the estradiol level increased in plasma of the female bats but the delayed embryonic development continued. It seems that a high level of melatonin and estradiol in plasma are required for this delayed embryonic development. The supports comes from our data following SP exposure during this phase, the high level of melatonin was maintained but estradiol level reduced hence abortion was noted.

Earlier reports suggest that the level of progesterone becomes relatively low during delayed developmental period, as judged by steroidogenic orgenelles in luteal cytoplasm and low plasma progesterone (Kimura *et al*., 1987). Insufficient prolactin and gonadotrophins may be responsible for suboptimal luteal cell development and consequently failure of luteal cells to secret sufficient hormone during delayed developmental period (Crichton et. al. 1990). We observed histologically that the ovary of *C. sphinx* showed increase in folliculogenesis following LP treatment (Fig. 4-5), but the luteal cell activity increased following SP treatment (Fig. 4-6) and might have increased endogenous progesterone. It could be that this high level of progesterone in pregnant female bats following SP exposure consequently led to abortion. Normally in most of the mammals, high progesterone level is known to be responsible for termination of pregnancy and parturition. However, it is clear from the present study that the slow rate of embryonic development is due to high melatonin and high estradiol level in plasma of the bats.

It is still not known how melatonin act at cellular level and what are the site of action in the brain or elsewhere of these bats for delayed embryonic development but some data on the others mammals suggest that, to express its inhibitory effect, melatonin may act directly, as melatonin receptors are present on the pars tuberalis and the pars distalis of pituitary gland (Weaver and Reppert, 1990, Ayre *et al*, 1994) as well as on the gonads. The inverse relationship between the steroid hormone and melatonin as noted in this bat under experimental conditions partially supports the above suggestion of adaptive role for melatonin in reproduction.

Therefore, it could be suggested that like other nocturnal rodent (Reiter, 1980; Zucker *et al*, 1980), *C. sphinx* is photosensitive (as judged by the gonadal and pineal function). The pineal gland in *C. sphinx* certainly has an important adaptive role not only in the regulation of gonadal function, but also in maintenance of the delayed embryonic development.

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