Pineal, Photoperiod and Gonadal Function in the Indian Palm Squirrel, Funambulus pennanti

Authors: Saxena, N., and Sinha, M. P.

Source: Zoological Science, 17(1) : 69-74

Published By: Zoological Society of Japan

URL: https://doi.org/10.2108/zsj.17.69

ZOOLOGICAL SCIENCE **17**: 69–74 (2000)

Pineal, Photoperiod and Gonadal Function in the Indian Palm Squirrel, *Funambulus pennanti*

N. Saxena[1]* and M. P. Sinha[2]

[1]*Department of Zoology Marwari College, Ranchi University Ranchi India and*
[2]*Post Graduate Department of Zoology, Ranchi University, Ranchi India*

ABSTRACT—Effects of morning and evening injections of pineal 5-methoxyindoles (MI), melatonin (aMT) and 5-methoxytryptamine (MT), for 60 continuous days, were observed on the testes of sham-operated (SO) and pinealectomized (Px) Indian palm squirrel, *Funambulus pennanti* maintained under different photoperiods during the gonad active phase. Long photoperiod (LP) of 14L:10D appeared stimulatory to the testes and caused a significant increase in the weight and seminiferous tubule diameter of both SO and Px animals, as compared to the animals under natural day-length (NDL). Short photoperiod (SP) of 10L:14D had an inhibitory influence and reduced the testes weight and its tubule diameter. aMT and MT injections during evening hours significantly reduced testes weight and tubule diameter of SO and Px animals under NDL, LP and SP. However morning injections, under all conditions, were without any significant effect. The results suggest an inhibitory effect of aMT and MT, under above photoperiodic conditions, on the testes of this tropical mammal. The time of administration of the MI is important in the expression of the effect.

INTRODUCTION

Almost all animals inhabiting natural environments are exposed to changes in important climatic factors like temperature, rainfall, humidity and photoperiod. It is these factors on which they rely to cue changes in their sexual status, and an interaction between them and the sexual activity has been reported (Pevet, 1985a, b; Pevet *et al*., 1987; Vivien-Roles and Pevet, 1983). The pineal gland has been shown to be involved in the long term adaptation of animal to seasonal reproduction (Pevet, 1985b; Reiter, 1985). The MI synthesized by the pineal gland act on the hypothalamo-hypophyseal-gonadal axis and may exert a stimulatory, inhibitory or no effect on the gonads depending on their mode and time of administration (Berndtson *et al*., 1974; Ebels *et al*., 1965; Hoffmann, 1981a; Peat *et al*., 1971; Turek *et al*., 1975). The pineal gland of *F. pennanti*, a tropical seasonal breeder, is sensitive to environmental daylength, temperature and humidity (Haldar *et al*., 1988; Haldar *et al*., 1990). Evening injections of MI inhibit testicular activity of this rodent (Saxena *et al*., 1992; Saxena, 1997). Day-night variations in plasma aMT suggest the existence of a diurnal rhythmi- city in pineal activity of this mammal (Saxena *et al*., 1993).

There is, however, no report relating the time of MI administration to photoperiodic regulation of testicular activity in tropical species. Therefore, the present study was aimed at observing the effects of morning and evening administration of aMT and MT in an Indian tropical mammal, *F. pennanti*, under different photoperiodic conditions.

* Corresponding author: c/o P. Saxena, c/47 CMPDI Colony, Kanke Road,
RANCHI-834 008, India

MATERIALS AND METHODS

The study was performed during the testicular active phase (Apr-June) of the annual testicular cycle of the animal (Haldar *et al*., 1990). Adult males (100–120 g body weight) of *F. pennanti* were obtained in the äfirst week of April and acclimatized, for two weeks, in a room fully exposed to natural environmental conditions. They were housed in wire net cages and provided with food (soaked gram seeds) and water *ad libitum*. They were divided into different groups of eight animals each, in accordance with the protocol in Table 1. Pinealectomy (Px) was performed following the technique of Haldar-Misra (Haldar, 1986). Besides NDL animals were exposed to LP of 14L:10D and SP of 10L:14D. The environmental temperature during the period of experimentation was recorded as a maximum of 37.02°C and a minimum of 28.11°C. The animals exposed to experimental LP and SP were maintained at 37°C. Two such sets of animals were maintained. One set. received injections in the morning at 7 hr. and another during evening at 16.30 hr. Animals under LP received morning injections 2 hr after lights on and evening injections 2 1/2 hr before light off. Animals exposed to SP received morning injections 15 min after lights on and 15 min before lights off. Solutions of aMT and MT (Sigma Chemical Co., USA) were made following the method of Pevet and Haldar-Misra (Pevet *et al*., 1982a). The animals were injected subcutaneously with 10µg MI/animal/day. Control animals were injected with vehicle (normal saline, 0.90% aqueous NaCl)/animal/day. After completion of 60 days the animals were sacrificed by cervical dislocation and their body weights noted. Testes were removed, weighed on a microelectrical balance and fixed in Bouin's fluid. They were processed by the routine paraffin method for histological observations. Seminiferous tubule diameter of testes was measured by an ocular micrometer. The data was statistically analysed with the help of Student's 't' test and analysis of variance, ANOVA (Bruning *et al*.,

Table 1. Details of the experimental protocol. The experiment was performed during April-June (gonad active phase)

	NDL	14L:10D (LP)	10L:14D (SP)
SO+saline (control)	G1	G7	G13
Px+saline (control)	G2	G8	G14
SO + a MT	G3	G9	G15
Px + a MT	G4	G10	G16
SO + MT	G5	G11	G17
Px + MT	G6	G12	G18

SO, sham operated; Px, Pinealectomized; aMT, Melatonin
MT, 5-methoxytryptamine; G,group; NDL, natural day length
LP, long photoperiod; SP, short photoperiod.

1977).

RESULTS

Results are presented in Figs. 1 and 2 and Tables 2 and 3. It is evident that in both morning and evening sets exposure to a LP of 14L:10D caused a significant increase in the testes weight (morning, P<0.001;. evening, P<0.001), and seminiferous tubule. diameter (morning, P<0.001; evening, P<0.001) of SO-sal, animals as compared to the saline treated animals under NDL. Exposure to a SP of 10L:14D showed a significant reduction in the testes weight (morning, P<0.001; evening,P<0.001) and seminiferous tubule diameter (morning, P<0.001, evening, P<0.001) of SO saline treated animals as compared to SO-saline animals under NDL. However, Px animals maintained under LP as well as SP and injected with saline indicated no significant effect on their testes weight and seminiferous tubule diameter when compared with the Px animals under NDL.

Evening injections of aMT and MT significantly reduced testes weight and tubule diameter of SO and Px animals maintained under NDL, LP and SP (Fig 1, Table 2). Morning injections, under all conditions, were without any significan effect on the testes (Fig. 2, Table 3).

Results of ANOVA showed a significant variation in. the testicular weight, in relation to pineal removal (F=26.14, P<0.001), time of MI administration (F=241.05, P<0.005) and different photoperiodic condition (F=10.12, P<0.001).

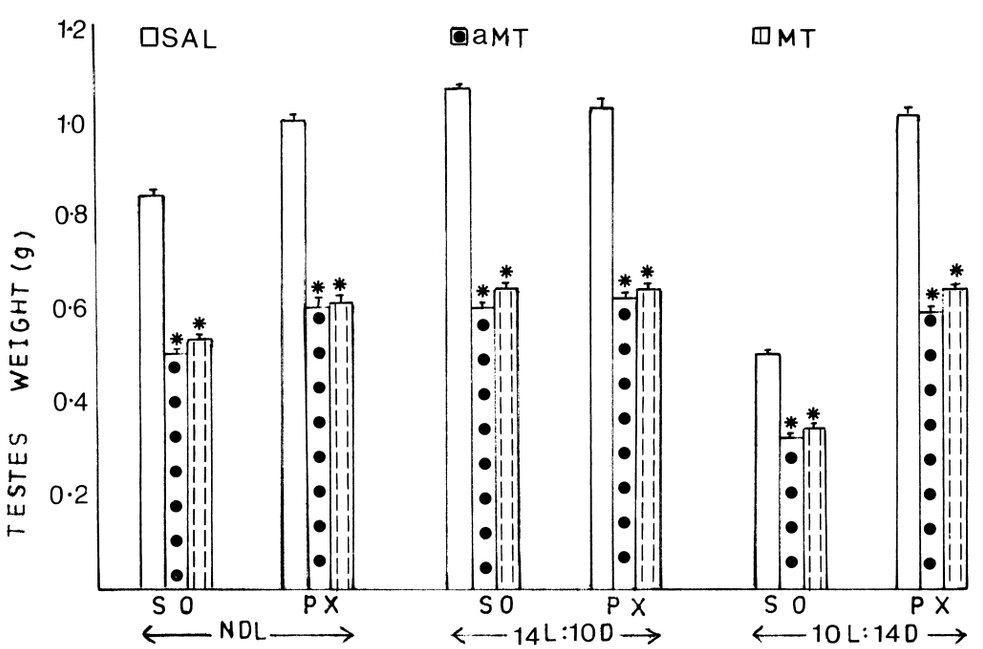

Fig. 1. Effect of evening injections of melatonin (aMT), 5- methoxytryptamine (MT) and saline (Sal) on the testes weight (g/100g body weight) of shamoperated (S0) and pinealectomized (Px) *F. pennanti* exposed to. natural daylength (NDL), long photoperiod (14L:10D) and short photoperiod (10L:14D) during the gonad active phase. Significance of difference from control: *, P<0.001.

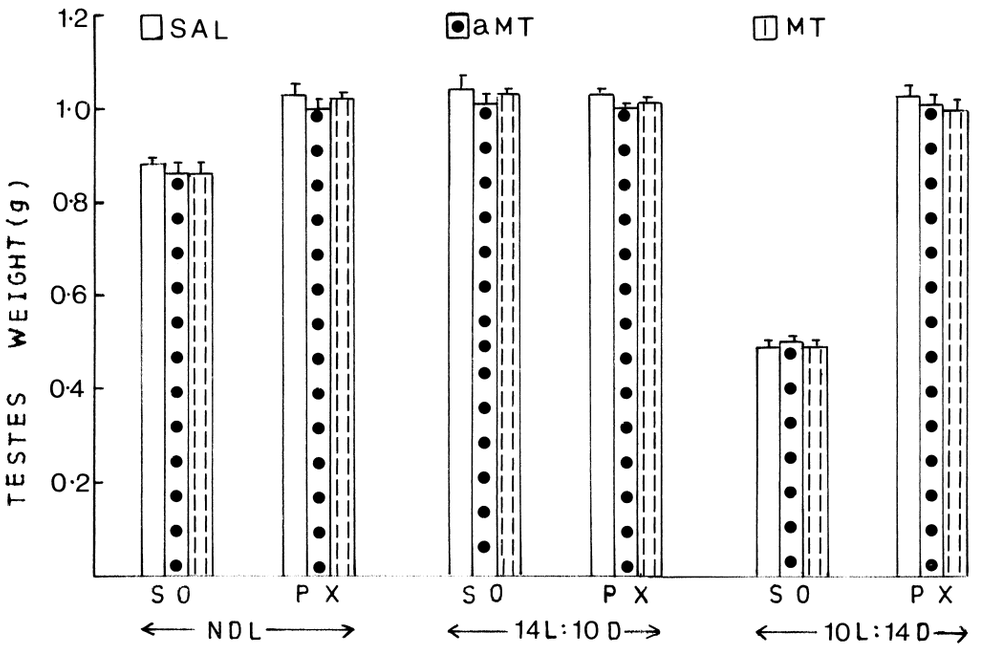

Fig. 2. Effect of morning injections of melatonin (aMT), 5- methoxytryptamine (MT) and saline (Sal) on the testes weight (g/100g body weight) of sham-operated (SO) and pinealectomized (Px) F. pennanti exposed to. natural daylength (NDL), long photoperiod (14L:10D) and short photoperiod (10L:14D) during the gonad active phase.

Table 2. Effect of evening injections of melatonin (aMT) and 5- methoxytryptamine (MT), for 60 continuous days, on the seminiferous tubule diameter (μm) of testis in sham-operated (S0) and pinealectomized (Px) F. pennanti exposed to natural daylength (NDL), long photoperiod (14L:10D) and short photoperiod (10L:14D) during the gonad active phase.

	NDL	14L:10D (LP)	10L:14D (SP)
SO+saline (control)	260.37 + 1.28	293.25 + 0.84	122.00 + 2.13
SO + aMT	238.50 + 1.38*	237.25 + 1.96*	89.63 + 2.14*
SO + MT	235.50 + 1.51*	238.37 + 2.53*	94.25 + 2.85*
Px + saline (control)	295.50 + 1.25	301.87 + 1.88	289.37 + 2.49
Px + aMT	245.75 + 1.65*	238.62 + 1.99*	226.75 + 2.33*
Px + MT	244.87 + 2.13*	232.39 + 1.20*	226.87 + 2.78*

Significance of difference from control : *, P<0.001

Table 3. Effect of morning injections of melatonin (aMT)) and 5-methoxytryptamine (MT), for 60 continuous days, on the seminiferous tubule diameter (μm) of testis in sham-operated (S0) and pinealectomized (Px) F.Pennanti exposed to natural daylength (NDL), long photoperiod (14L:10D) and short photoperiod (10L:14D) during the gonad active phase.

	NDL	14L:10D (LP)	10L:14D (SP)
SO+saline (control)	259.38 + 2.33	294.25 + 2.73	122.88 + 1.91
SO + aMT	259.88 + 1.35	297.12 + 3.64	121.50 + 1.20
SO + MT	258.50 + 1.63	296.00 + 2.61	122.12 + 1.98
Px + saline (control)	296.00 + 1.17	300.37 + 2.01	290.12 + 3.31
Px + aMT	294.88 + 1.57	298.38 + 2.75	288.12 + 2.53
Px + MT	294.50 + 1.75	296.37 + 3.22	289.38 + 3.74

DISCUSSION

Although a large number of seasonally breeding rodent species are known, most studies have centred on the elucidation of pineal function in the control of reproduction in case of temperate zone animals (Pevet *et al*., 1987; Hoffmann, 1981b; Pevet *et al*., 1986).

This study shows that both aMT and MT are physiologically active compounds inhibiting the testicular activity of this tropical mammal. The present results indicate a sensitivity of the animal to change in lighting condition. This result further confirms the previous finding that the pineal and testes of *F.pennanti* are sensitive to daylength (Haldar *et al*., 1990). The results also demonstrate, for the first time, that the animal can distinguish between the time of the day when MI are administered. In other words, the inhibitory effects of aMT and MT are dependent on the period of the day when they are administered. While evening injections led to inhibition of testicular activity under both long and short photoperiods, MI administration during morning hours failed to produce any significant effect on the testes of *F. pennanti* under short or long photoperiod. LP was stimulatory to the testes whereas SP was inhibitory to the testes of the squirrel. Our results are similar to those on adult golden hamsters (*Mesocricetus auratus*) in which daily aMT injections in morning, under long days result in gonadal maintenance (Reiter *et al*., 1976; Stetson *et al*., 1983; Tamarkin *et al*., 1976; Tamarkin *et al*., 1977). Other studies indicate that morning injections of aMT under long to short days retards gonadal regression in the same animal (Pevet *et al*., 1982b; Turek *et al*., 1980).

The present results can be explained on the basis of the "hourglass mechanism" (Skopik *et al*., 1976; Underwood, 1981; Underwood *et al*., 1982) according to which photoperiodic discrimination is achieved by comparison of the environmental photoperiod to an internal rhythm of sensitivity consisting of a light-sensitive. and a light-insensitive phase. The. external coincidence model of Bunning (Bunning, 1936) explains that light coincident with the insensitive phase of the rhythm is translated as a short day, while light coincident with the photosensitive phase of the rhythm as a long day. In the external coincidence. model the environmental light cycle has two roles. It acts as a zeitgeber (entraining agent) for the circadian system and it has an inductive effect producing the long day or short day response (Pittendrigh, 1965). The resonance experiments by Nanda and Hamner (Nanda *et al*., 1958) for daylength discrimination consist of exposing the animals to different cycle lengths with a light phase of constant duration and dark phase of variable durations. Resonance experiments with golden hamsters indicated that the animals can discriminate daylength in different cycles with a constant light phase (Elliott *et al*., 1972; Stetson *et al*., 1975). A circadian basis for the photoperiodic reproductive response has been demonstrated with the help of resonance experiments in the case of vole, *Microtus agrestis* (Grocock *et al*., 1974) and in deer mouse, *Peromyscus maniculatus* (Whitsett *et al*., 1983). It may be opined that in *F. pennanti* MI injections only during evening hours are able to cause gonadal suppression as during morning hours the animals lose sensitivity to exogenous MI administration. This inhibitory effect of MI injection is evident under artificial long and short as well as natural photoperiod. Exogenous administration of aMT and MT have been found to exert a season dependent inhibitory influence on the testes of *F. pennanti* and evening injections of both MI inhibit the testes of the animal under natural long days and short days (Saxena, 1997). The plasma aMT content in this squirrel shows a clear circadian rhythm. This endogenous rhythm is evident during summer (April) as well as winter (December) months (Saxena *et al*., 1993; Saxena, 1988) and injections given 3–4 hr prior to the lights off result in testicular inhibition (Saxena *et al*., 1992; Saxena, 1997). In the present study also the injections given 2 1/2 hr before lights off, in LP, and 15 min before light off, in SP, causes gonadal inhibition. The effects are also found to be independent of the pineal gland since the testes of Px animals showed a similar response as those of SO animals.

It has become clear that the pineal gland is necessary for the regulation of photoperiodic responses and that pineal melatonin may be responsible for transmitting daylength information (Hoffmann, 1981b; Goldman, 1983; Hoffmann, 1985; Masson-Pevet *et al*., 1986).

Studies have shown that exogenous administration of MT (via injections) to golden hamsters exhibits a biphasic sensitivity. A daily injection just prior to lights on or up to 5 hr before lights out induces rapid and complete gonadal regression (Reiter *et al*., 1976; Tamarkin *et al*., 1977; Sackman *et al*., 1977). Injections at other times of the day are ineffective. Also pinealectomized hamster is not responsive to a single daily injection of aMT but requires three daily injections timed 3 hr or 30 min apart (Goldman *et al*., 1979; Tamarkin *et al*., 1977). Our results are different from these as in this tropical animal only a single daily injection during evening hr results in gonad inhibition. Also in *F. pennanti* Px animals, under the tested photoperiodic conditions, are equally responsive to the MI injections. Therefore, it can be suggested that pinealectomy does not block the circadian rhythm of aMT and MT sensitivity in this tropical species.

Pinealectomy always appeared stimulatory to the testes and pinealectomized squirrels exhibited significant increase in testes weight and seminiferous tubule diameter in comparison to SO controls. Under SP pinealectomized animals showed significantly higher testes weight and seminiferous tubule diameter as compared to SO animals as these were unable to perceive environmental information in the absence of pineal gland. Therefore, they maintained an active gonad as evident by higher testes weight and seminiferous tubule diameter.

The present study reveals, for the first time in a tropical mammalian species, that besides aMT there also exists a diurnal rhythm in the sensitivity of the animal to exogenous MT injections. Pinealecomy and constant release of aMT and MT have been reported to cause atrophy of gonad in male European hamsters kept under long photoperiod (Masson-

Pevet *et al*., 1986). aMT implants have been reported to hasten recrudescence in male hamsters on short days (Turek *et al*., 1976). aMT implants cause testicular regression in long-day intact. male *Peromyscus leucopus* (Johnston *et al*., 1980; Lynch *et al*., 1976) but do not retard testicular regression on short days (Petterborg *et al*., 1981). Also varied results have been observed on the effects of photoperiod and melatonin on gonadal function of prepubertal and adult animals of *Microtus* and *Peromyscus* species. Although in the case of *F. pennanti* silastic capsule implants of aMT and MT lead to testicular regression in both intact and Px animals, (Saxena, 1988) the effects of this continuous mode of MI administration under different photoperiods remains to be assessed.

Thus, although MT effects on sexual axis have been studied in different animals (Vivien-Roels *et al*., 1983; Vevien-Roels 1983) the results have been varied (Pevet *et al*., 1986). Reports relating to actions of MT on the gonadal function of tropical mammals, experiencing different climatic conditions than temperate animals, are scarce. Our results of the present study provide evidence. for the role of pineal MT, besides aMT, in the photoperiodic adaptive response to reproduction in a tropical seasonally breeding mammal, *F. pennanti*. The results suggest the possibility of the existence of a rhythm in the gonadal response to exogenous MI administration under different photoperiods but the exact mechanisms involved in this phenomenon remain yet to be identified.

REFERENCES

Berndtson WE, Desjardins C (1974) Circulating LH and FSH levels and testicular function in hamsters during light deprivation and subsequent photoperiodic stimulation Endocrinol 95: 195–199

Bruning JL, Kintz BL (1977) Computational handbook of statistics, Scott Feresman, Co Palo, Alto, California

Bunning E, (1936) Die endogene Tagesrhythmic al Grundlage der photoperiodischen Reaktion. Ber. Deut. Bot. Ges 54: 590–607

Ebels I, Prop N (1965) A study of the effect of melatonin on the gonads, the estrous cycle and the pineal organ of the rat. Acta Endocrinol 49: 567–577.

Elliott J.A, Stetson M.H, Menaker M (1972) Regulation of testis function in golden hamsters: A circadian clock measures photoperiodic time. Science, 171: 1169–1171.

Goldman B D (1983) The physiology of melatonin. In Pineal research reviews. Ed by Reiter R J, Alan R Liss, N Y, 1: 145–182

Goldman B D, Hall V, Hollister C, Roychoudhury P, Tamarkin, L, Westrom W (1979) Effects of melatonin on the reproductive system in intact and pinealectomized male hamsters maintained under various photoperiods. Endocrinol 104: 82–88

Grocock C A, Clark J R (1974) Photoperiodic control of testes activity in the vole, *Microtus agrestis*. J. Reprod. Fertil 39: 337–347

Haldar-Misra C (1986) Method of pinealectomy in some vertebrates. Ind. J. Exptl. Biol. 24: 319–322

Haldar C, Saxena N (1988) Pineal and humidity effect on testicular function of Indian palm squirrel, *Funambulus pennanti*. J. Pineal Res 21: 1–11

Haldar C, Saxena N (1990) Ecofactors and effect of pinealectomy in regulation of seasonal testicular cycle in the Indian palm squirrel, *Funambulus pennanti*. J. Interdiscipl. Cycle Res 21: 1–11

Hoffmann K (1981a) Photoperiodic function of the mammalian pineal organ. In The Pineal Organ-photobiology, biochronometry endocrinology Ed by Oksche A, Pevet P Elsevier, Amsterdam pp 123–128

Hoffmann K (1981b) Pineal involvement in the photoperiodic control of reproduction and other functions in the Djungarian hamster, *Phodopus sungorus*. In The Pineal Gland. Ed by Reiter R J, Boca Raton, CRC Press pp 83–102

Hoffmann K (1985) Interaction between photoperiod pineal and seasonal adaptation in mammals. In The pineal gland: current state of pineal research. Ed by Mess B, C S Ruzsas, L Tima, P Pevet, Akademia Kiado, Budapest, Elseiver Science Publisher, Amsterdam pp 163–186

Johnston P G, Zucker I (1980) Antigonadal effects of melatonin in white-footed mice (*Peromyscus leucopus*). Biol Reprod 23: 1069–1074

Lynch G R, Epstein A L(1976) Melatonin induced changes in gonads, pelage and thermogenic characters in the white-footedmouse, *Peromyscusleucopus*. Comp. Biochem.Physiol 53 C:67–68

Masson-Pevet, M Pevet, P Vivien-Roels B. (1986) Pinealectomy and constant release of melatonin or 5-methoxytryptamine induce testicular atrophy in the European hamster (*Cricetus cricetus* L) J. Pineal Res 4: 79–88

Nanda K K, Hamner KC (1958) Studies on the nature of the endogenous rhythm affecting photoperiodic response of Biloxi soybean. Bot. Gaz. (Chicago) 120: 14–25

Peat F, Kinson G A (1971) Testicular steroidogenesis in vitro in the rat in response to blinding, pinealectomy and to the addition of melatonin. Steroids 17: 251–253

Petterborg L J, Reiter R J (1981) Effects of photoperiod and subcutaneous melatonin implants on the reproductive status of adult white-footed mice, *Peromyscus leucopus*. J Androl 2 : 222–224.

Pevet P, Haldar-Misra C (1982a) Effect of 5-methoxytryptamine on testicular atrophy induced by experimental or natural short photoperiods in the golden hamster. (*Mesocricetus auratus*). J. Neural Transm 55: 69–84

Pevet P, Haldar-Misra C (1982b) Daily 5-methoxytryptamine injections inhibit short-dayinduced testicular atrophy in golden hamster. J. Neural Transm 55: 95–99

Pevet P(1985a) 5-Methoxyindole,pineal and seasonal reproduction. A new approach. In The Pineal Gland: Current State of Pineal Research. Ed by Mess B, Ruszas C S, L Tima, P Pevet, Elsevier, Amsterdam pp 163–186

Pevet P. (1985b) 5-Metoxyindoles, pineal peptides and reproduction In The Pineal Gland Endocrine Aspects. Ed by Brown G. M, Wainwright S. B, Pergamon Press, Oxford pp 8 1–102

Pevet P, Masson-Pevet B, Vivien-Roels B, Bonn B (1986) Photoperiod, temperature, melatonin, 5-methoxytryptamine and seasonal reproduction : some data on the golden hamster. In Advances in pineal research. Ed by Reiter R.J , M Karasek, John Libbey, London 1: 185–196

Pevet P, Buijs R. M, Masson-Pevet M (1987) Effect of pinealectomy and a constant high level of circulating melatonin or of 5-methoxytryptamine on the vasopressinergic innervation in the brain of the European hamster (*Cricetus cricetus L*). J. Neural Transm 70: 287–294

Pittendrigh C S (1965) On the mechanism of the entrainment of a circadian rhythm by light cycles. In Circadian Clocks. Ed by Aschoff J, Elsevier, Amsterdam pp 277–297

Reiter RJ, Blask DE, Johnson LY, Rudeen PK , Vaughan MK, Waring PJ (1976) Melatonin inhibition of reproduction in the male hamster: Its dependency on time of day of administration and on intact and sympathetically innervated pineal gland. Neuroendocrinol 22: 107–116

Reiter RJ (1985) Pineal indoles in reproduction : Retrospect and prospect. In The Pineal Gland : Endocrine Aspects. Ed by Brown G. M, Wainwright SD, Pergamon Press, Toronto pp 163–174

Sackman JW, Little J C , Rudeen P K, Waring P J, Reiter RJ (1977) The effects of pineal indoles given late in the light period on reproductive organs and pituitary prolactin levels in male golden

hamsters. Horm. Res 8: 84–92
Saxena N (1988) Pineal in Indian palm squirrel, *Funambulus pennanti* : 5-methoxyindoles and environmental control of reproduction. Ph. D. Thesis, Banaras Hindu University, Varanasi, India
Saxena N, Mehrotra PN (1992) Dose dependent effects of 5-methoxyindoles on the testicular function of the Indian palm squirrel, *Funambulus pennanti*. Eur. Arch. Biol 103: 121–126
Saxena N, Haldar C, Mehrotra PN (1993) Circadian and circannual variations in plasma melatonin and testosterone in Indian palm squirrel, *Funambulus pennanti*. Proc. Nat. Acad. Sci., India 63(B) III: 325–332
Saxena N (1997) Pineal and 5-methoxyindoles in the regulation of seasonal testicular cycle in Indian palm squirrel, *Funambulus pennanti*. Ind. J. Exptl. Biol 35: 898–902
Skopik SD, Bowen MF (1976) Insect photoperiodism : An hourglass measures photoperiodic time in *Ostrinia nubilalis*. J. Comp. Physiol 111: 249–259
Stetson MH, Elliott JA, Menaker M(1975) Photoperiodic regulation of hamster testis : Circadian sensitivity to the effects of light. Biol Reprod 13, 329–339
Stetson MH, Tay DE (1983) Time-course of sensitivity of golden hamsters to melatonin injections throughout the day. Biol Reprod 29: 432–438
Tamarkin L, Westrom W K, Hamill A I, Goldman B D (1976) Effect of melatonin on the reproductive systems of male and female Syrian hamsters : A diurnal rhythm in sensitivity to melatonin, Endocrinol 99: 1534–1541
Tamarkin L, Lefebvre N G, Holcister C W, Goldman B D (1977) Effect of melatonin administered during the night on reproductive function in the Syrian hamster. Endocrinol 101: 631–634
Tamarkin L, Lefebvre N G, Holbister C W, Goldman B D (1977) Effect of melatonin administered during the night on reproductive function in the Syrian hamster. Endocrinol 101: 631–634
Turek FW, Desjardins C, Menaker M (1975) Melatonin: antigonadal and progonadal effects in male golden hamsters. Science 190: 280–282
Turek FW, Losee SH (1978) Melatonin induced testicular growth in golden hamsters maintained on short days. Biol Reprod 18: 299–305
Turek F W, Pappas P (1980) Daily melatonin injections inhibit short-day induced testicular regression in hamsters. Experientia 36: 1426–1427
Underwood H(1981) Circadian clocks in lizards: Photoreception, physiology an photoperiodic time measurement. In Biol. clocks in Seasonal Repro. Cycles. Ed by B. K. and D. E. Follett, Wright, Bristol, pp 137–151
Underwood H, Hall D (1982) Photoperiodic control of reproduction in the male lizard, *Anolis carolinensis* J. Comp. Physiol 146: 485–492
Vivien–Roels B (1983) The pineal gland and the integration of environmental information: possible role of hydroxy and methoxyindoles. Mol. Physiol 4: 331–345
Vivien–Roels B, Pevet P (1983) The pineal gland and the synchronization of reproductive cycles with variations of the environmental climatic conditions with special reference to temperature. In Pineal Res. Rev. Ed by Reiter RJ, Alan R. Liss Inc., NY, pp 91–143
Whitsett JM, Underwood H, Cherry J (1983) Photoperiodic stimulation of pubertal development in male deer mice: Involvement of the circadian system. Biol Reprod 28: 652–656

(Received March 1, 1999/ Accepted July 14, 1999)