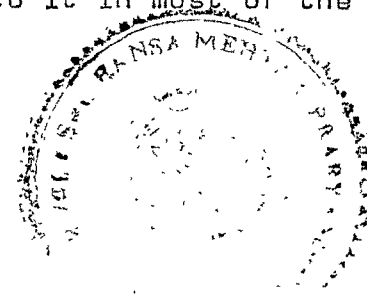


"That there is a small gland in the brain, the pineal in which the soul exercises its functions more particularly than in any other part" (Rene Descartes 1646). Hats off to Rene Descartes, the philosopher physiologist for his prophetic notion that the pineal housed the seat of the rational soul and his farsighted formulation that the eyes perceived the events of the external world and transmitted what they saw to the pineal by way of "strings" in the brain and in response to which the pineal allowed "humors" to pass down "hollow tubes" to the muscle where they produced the appropriate responses. Substitute "nerves" in place of "strings", "hormones" in place of "humors" and "blood vessels" in place of "hollow tubes" and we have the modern concept of the prophetic formulation of Rene Descartes. The above philosophical concept of the functional role of pineal rendered as early as in 1646, when endocrinology, circulation and muscle physiology were still in a premature stage of understanding, bespeaks of the admirable visionary zeal of this philosopher physiologist. It is really astonishing that Rene Descartes could conceive of a status for pineal which we now with over 300 years of scientific hindsight has come to recognize as a neuro-endocrine transducer. Pineal is an organ whose discovery predates that of the pituitary and adrenal as its anatomical descriptions can be found in the writings of Claudius Galen (130-201 AD) who is accredited with the christening of the name pineal. However, the function of this midline

azygous structure remained a total mystery till the 20th century. Many of the experimental studies in the last three decades or so have succeeded in establishing quite a bit of physiology, morphology, cytology, chemistry and pharmacology of the pineal organ. The pineal body or "epiphysis cerebri" is an evagination of the roof of the diencephalon in a site that becomes in the adult the parietal region. During the process of brain morphogenesis, a number of structures originated around the third ventricle, collectively termed as circumventricular organs (Kelly, 1968) of which pineal is one. In certain vertebrates rostral to the pineal another primordium might differentiate, the forerunner of the parapineal organ. In some, the parapineal anlage might fuse with the pineal primordium to form a single structure while in yet others the parapineal might develop as an altogether separate entity. The parietal eye of some species is the parapineal derivative. Phylogenetically pineal is represented in almost all vertebrate groups except for in the myxinoidea, crocodylians, armadillo, edentates and perhaps dugongs (Kelly, 1968). The wider occurrence of the pineal amongst vertebrates is suggestive of a constancy like that of pituitary and it may be rather fallacious to consider it as an evolutionarily vestigial structure. Despite this constancy in occurrence, a constancy in function in vertebrates as a whole is not ascribable. Another feature of the pineal is its structural variation met with amongst the vertebrates. Whereas both the pineal and the

parapineal organs are photoreceptors as in the case of lampreys, great structural diversity is noted in elasmobranchs and teleosts with some members of both groups lacking the parapineal organs but possessing a well developed pineal organ with photoreceptor cells. In gymnophians and amphibians the only parietal organ is the epiphysis. A vesicular distal portion of the pineal primordium migrates prior to ossification of the skull to form an eye (frontal organ) lying below the skin on top of the skull as in some anurans (Ralph, 1975b). The frontal organ with the intra-cranial pineal structure are together designated as the pineal complex. Reptiles as a group show remarkable variation in the nature of their parietal organs. *Sphenodon* and some lacertilians have both pineal organ and parietal eye (Gundy and Wurst, 1976). Whereas a sac like pineal organ is found in turtles, a solid glandular pineal is the feature in snakes (Kelly, 1968; Collin and Oksche, 1981). The aves have pineal varying in structure from sac like as in lizards to nearly solid ones as in mammals (Ralph, 1970). Though it is assumed that the pineal body in general is secretory in nature, this aspect of function may be subsidiary in those forms where it is highly developed for photoreception. The non-committal term, pineal organ or pineal body may in this context be more preferable while referring to it in most of the lower vertebrates.



The earliest light microscopic observations of Holmgren (1918) on the pineals of frog and dogfish revealed the presence of sensory cells in effective contact with nerve cells bearing resemblance to the retinal cone cells, based on which he suggested that the pineal might function as a photoreceptor or "third eye" in poikilotherms. Within the next few years Ebenhardt Dodt and his German colleagues hinted that the pineal in frog could be a wave length discriminator which can convert light energy of certain wave lengths into nervous impulses. This was followed by the observation of the skin blanching effect of cattle pineal extracts on tadpoles (McCord and Allen, 1927). This was the state of knowledge about the pineal in the first half of the 20th century; it appears to be a photoreceptor in the frog, had something to do with sexual functions in mammals and contained a factor that blanched the pigment cells of the tadpoles. The second half of this century witnessed a flurry of experimental excavations on pineal structure and functions which led to some sort of crystallisation of ideas and thoughts about pineal function in vertebrates. Accordingly functions such as circadian pace maker, gonadotrophic activity, patterns of integumentary colouration, thermoregulation, photoreception and heat loss regulation have all come to be associated with pineal.

Information on pinealⁱⁿ reproductive functioning is a better documented one. Most of the seasonally breeding animals

especially mammals and aves are known to regulate their reproductive activities by a subtle interaction between a variety^{of} external cues with internal cues of which photoperiod, temperature, humidity, annual rainfall, availability of food etc. are some of the important ones. It is only within the last three decades has it been unequivocally established that the biochemical and secretory activities of the pineal are intimately linked to photic information conveyed by the lateral eyes, a tenet which is nothing but the three centuries old prophetic formulation of Rene Descartes come true. The relationship between pineal and reproductive physiology is being increasingly elucidated^d in the modern era of pineal research. There are more evidences at present to indicate a general influence of inhibition on reproduction by this gland. The relationship between photoperiod and pineal is of a dual nature, with long photoperiod inhibiting pineal function and short photoperiod stimulating its function. It is now recognized that reducing day light length or darkness exerts a favourable influence on pineal activity leading to elaboration and release of pineal principles (melatonin and arginine vasotocin) which have an antigonadal influence. Apparently short photoperiod induced gonadal regression in mammals is mediated via the pineal. Since pinealectomy during periods of long daily photoperiods does not affect the gonadal function while its removal during the shorter day length periods leads to positive stimulation of gonadal functions, it can be easily surmised that

shorter photoperiods activates the pineal which in turn through its secretion(s) inhibits the hypothalamo-hypophysis-gonadal axis and thereby induces gonadal involution. Removal of the pineal during shorter daylength periods leads to removal of its inhibiting influence and thereby preventing gonadal regression. This pattern of regulation of seasonal reproductive rhythms is more clearly established for mammals. In lower vertebrates like fishes, amphibians and reptiles the function of photoreception is more implicated. The thermoregulating role of pineal is also gaining increasing evidence in recent times, a function which is being demonstrated in many vertebrate species. The extent of its involvement in the varied functions mentioned remains yet to be defined with clarity, more so with the avian pineal. It is quite likely that the avian pineal represents a conglomerate of all the above functions as scattered evidences are available for each. Good evidence has been accumulated for the involvement of avian pineal in circadian rhythmicity (Gaston and Menaker, 1968; Binkley et al., 1971; McMillan, 1972; McBride and Ralph, 1972; Cogburn et al., 1976; Rutledge and Angle, 1977; Gwinner, 1978). A general scan of the relevant literature of the possible role of pineal in reproduction among the aves fails to yield a common case. In fact a progonadal, an anti-gonadal and even no relation with the gonads whatsoever have all been suggested in various species of birds. Quite likely, negative results might occur due to the fact that appropriate experimental designs have not

been made or proper challenges have not been presented especially with regard to temporal features (Ralph et al., 1979).

It is this temporal aspect which gains credence, as seasonal cycling of the state of reproductive structures is of greater significance in avian than in mammalian species. Besides, the occurrence of pineal in almost all vertebrates also implies the possibility of pineal participating in subtle modifications and regulations of various physiological processes, if not directly albeit indirectly. Speculations on these lines have been sounded by other workers also. "There is now considerable documentation that the mammalian pineal participates in the affairs of gonads, the thyroid, the brain and several other organs and organ systems. One can also find evidence to support the argument that sub-mammalian pineal organs influence pigmentation and behaviour. However, it has not yet been demonstrated that any physiological process in the body is controlled primarily by pineal organs. And presently, no one knows what pineal organs, be they photoreceptive or secretory, are for. This situation is not unique to the pineal and certainly should not lead potential students of pineal physiology to conclude that the pineal has no function. An alternative explanation is that the appropriate questions about pineal functions remain to be asked" (Wurtman et al., 1968). Recently, Ralph et al. (1979) have stated "There has been much well founded speculation about physiological roles of pineal organs in a few species,

but it has proven difficult to formulate a pan vertebrate role for pineal organs. This situation may indicate that either pineal bodies do not have identical functions in different kinds of animals or that they participate in some central, fundamental, regulatory mechanism that underlines the operation of several different organ systems. If the latter is true, one might expect to discover subtle relationships between pineal organs and a number of physiological functions. Such appear to be the case, especially with regard to endocrine organs". Wurtman and Tay (1969) have conjectured pineal gland to be a neuroendocrine device, receiving exogenous and endogenous input and having outputs to several peripheral systems. Further, Quay (1969) thought that pineal organs are primarily concerned with the environment.

As an offshoot to the facts and speculations about the pineal functions, studies were initiated in this laboratory to understand the possible relationship if any between pineal and gonads together with other endocrines and also between pineal and metabolic physiology on a temporal basis in relation to seasonal reproductive cyclicity of wild feral blue rock pigeon, Columba livia (Patel, 1982). These studies revealed certain definite relationships between pineal and reproductive physiology on one hand and between pineal and other endocrine and nonendocrine organs and metabolic physiology on the other hand. Accordingly, a progonadal role for the pineal was

suggested whereby presence of an intact pineal was shown to be essential for maintaining gonadal function during the breeding season. With reference to its relationship with thyroid and adrenals, antagonistic and synergistic interactions respectively were recorded. Probable interaction of pineal with other organs like pancreas, spleen and uropygium was also highlighted. Apart from these, definite alterations in the metabolic physiology in the form of hypoglycemia and reduced hepatic glycogen content together with suppressed mobilization of lipids from liver and muscle were also noted. Based on these observations Patel (1982) had hinted at the possibility of the pineal in wild pigeons having an anti-insulinic and anti avian pancreatic polypeptide role. Deviations from the normal adaptive modulations in the activity of various enzymes like SDH, G₆Pase, ATPase and the nonspecific phosphatases were also shown to occur due to pinealectomy. Further, pinealectomy in the wild pigeons also brought about alterations in ascorbic acid content and ions such as Na⁺, K⁺ and Ca⁺⁺. The evaluation of various parameters in the above study indicated that there are definite alterations in body physiology and total body economy in relation to reproductive cyclicity. Pinealectomy tended to interfere with the adaptive modulations in metabolic physiology associated with breeding thereby suggesting a possible indirect cause for the observed gonadal regression in pinealectomised wild pigeons.

It is known that some of the domestic varieties of avian species have an antigonadal action of pineal and that domestication can totally modify or eliminate the influence of environment on reproduction. It was thought pertinent in this context to study the seasonal metabolic physiology of tropical domestic pigeons in relation to reproduction and the possible role of pineal in the same and compare the results that accrue with those outlined for wild pigeons previously.

The results obtained from the present study have again proved interesting in the sense the involvement of pineal in reproduction and associated metabolic physiology though very much in evidence, did nevertheless show some differences when compared with those observed for wild pigeons. The most significant outcome of the study is the realisation that the pineal in domestic pigeons is both progonadal as well as antigonadal unlike being only progonadal in the case of wild pigeons. Inferably pineal in domestic pigeons might be elaborating two different principles having season specific influence on the hypothalamo-hypophysis-gonadal axis. Such a conclusion can be drawn from the observed gonadal regression (in both sexes) after pineal ablation in the breeding season and gonadal enlargement and activation post-pinealectomy during the non-breeding season in the present study. Similar dual action of pineal i.e. progonadotropic during the breeding season and antigonad~~o~~tropic during the non-breeding season has been

reported by Saxena et al., (1979) on Indian Weaver birds. It is rather enigmatic as to how the same organ (pineal) can bring about diametrically opposite responses or even both within the same group of animals. In most of the temperate species of aves and mammals, long and short photoperiods are known to act through the pineal to induce gonadal recrudescence and regression respectively. The action of pineal on the hypothalamo-hypophysis-gonadal axis is essentially one of suppression exerted during short photoperiods. Predictably, the hypothalamo-hypophysis-gonadal axis is refractive to the action of pineal during long photoperiods. Moreover the pineal can also be considered to be functioning with reduced efficiency in this context. Though similar mechanisms can be considered to be operative in aves as well, it is however difficult to explain the progonadal role in some species, antigonadal actions in some and both in yet others. Both, the indolamine, melatonin and the polypeptide, arginine vasotocin (AVT) have been shown to possess gonad inhibiting capability in mammals (Tamarkin et al., 1977; Reiter, 1977; Reiter and Vaughan, 1977; Ebels and Benson, 1978). Speculations that the release of AVT from the pineal gland may be under the control of melatonin are also strife (Pavel, 1973; Reiter et al., 1976a). This speculative concept that an amine (melatonin) can bring about the release of a peptide (AVT) within the pineal is attractive as the hypothalamic releasing hormone polypeptides are also released in response to monoamines (Fuxe et al., 1976). AVT, interestingly has also been shown to suppress the release or action of pituitary gonadotrophins in

rats (Pavel, et al., 1973) while stimulating prolactin release (Blask et al., 1976). Unidentified presumptive pineal polypeptides structurally distinct from AVT have also been shown to depress circulating levels of LH (Benson et al., 1972). Moreover counter antigonadotrophic actions of continuously available melatonin have also generated considerable interest (Hoffman, 1974; Reiter et al., 1974). Another possible site of action of pineal principles which has not yet been considered is on the gonads themselves directly, modulating the synthesis release or action of GnRH like substances, which in recent times have been increasingly realised as possible modulators of gonadal functioning. In the midst of these observations and speculations, the possible modes and sites of action of pineal principles in controlling gonadal physiology are multiple, and exact mechanism(s) involved in the progonadal, antigonadal or even both pro as well as antigonadal actions of avian pineal is anybody's guess. Only further searching studies on avian pineal and its relationship with gonads can solve the puzzles plaguing the pineal-gonad axis in birds.

Seasonal reproductive activities involve simultaneous activation and expression of many metabolic and other physiological and biochemical changes either as a cause or effect. Though a few of the physiological and metabolic changes may be the effect of gonadal activation, majority of them are however preparative causal alterations heralding gonadal recrudescence.

Such alterations are bound to affect not only the gonads themselves but even other organ systems of the body. Accordingly changes affecting carbohydrate metabolism of the body in general, quantitative and qualitative alteration in lipid distribution in the gonads, tissue ascorbic acid contents, ionic composition of the gonads, gonadal protein content and activity of phosphomonoesterases and steroid dehydrogenases have all been shown to occur in the course of present study on breeding biology of tropical Indian domestic pigeons. Some of the features associated with breeding worth recalling are 1) increased carbohydrate utilization 2) increased AA accumulation coupled with utilization in the gonads 3) reduction in Na^+ ion content coupled with increase in K^+ ion content in the gonads 4) reduced protein content and increased activity of acid and alkaline phosphatases and 5) reduction in histochemically demonstrable cholesterol positive lipids coupled with increased activity levels of steroid dehydrogenases. These observed changes occurring during the breeding season of domestic pigeons could at best be considered to set up a favourable "internal climate" for reproduction. It is obvious that most of these changes were also reported to occur as a package physiological deal even in the wild pigeons (Patel, 1982) and hence could be considered representative of adaptive breeding physiology characteristic of tropical pigeons. No doubt such widespread physiological changes cannot be thought to occur *de novo*, but should in no uncertain terms involve the

participation of many extrinsic and intrinsic factors acting in sequence as a train of events which might in turn affect the functioning of the neuroendocrine orchestra and attune it in a favourable fashion to meet the needs of breeding activities. The favourable disposition of the neuroendocrine axis might alter the quantitative and qualitative functioning of the various endocrines of the body and contribute to the heralding of the adaptive metabolic physiology associated with breeding. The endocrine pancreas, thyroid and adrenals are the important members of the vertebrate endocrine conglomerate having definite influence on metabolism and physiology of various organs. Justifiably, these three endocrines have been noted to undergo seasonal histomorphological alterations in the course of the present study in the form of decreased pancreas weight and parallel thyroid and adrenocortical activity in conjunction with gonadal activation during the breeding season. Apparently, increased thyroid hormone and increased adreno-cortico-medullary ratio together with the pancreatic hormones contribute significantly to the adaptive breeding physiology.

In the above discussed sequence of events purported to induce alterations in the neuroendocrine axis, pineal might be an essential link and could thereby play an important role in the evocation and expression of adaptive systemic changes. It is this hunch which had been followed up on the present

study whereby pinealectomy during both breeding and non-breeding phases have been used ^{as} a tool. Interestingly pinealectomy successfully inhibited most of the changes ordained to occur during the breeding season and thereby contributed effectively to gonadal regression. This undeniably indicates the progonadal role of pineal in this species of bird. Surprisingly, pinealectomy performed during the non-breeding months led to a physiological stimulation characteristic of intact birds during the breeding season. This when viewed along with the gonadal activation noted to occur concomitantly, prophesies an antigonadal action too of the pineal of tropical domestic pigeons. This is in contradiction to an earlier observation on wild pigeons, where pinealectomy during the non-breeding season was not capable of reversing the gonadal regression occurring at this period. Obviously the pineal has differential season specific interactions with the neuroendocrine axis in the wild and domestic varieties of tropical Indian pigeons. This is well borne out by the herein observed reverse set of changes affecting the various endocrine glands post-pinealectomy in the two seasons. Whereas pinealectomy induced increase in weight of pancreas during both the seasons (a little curious change), the thyroid and adrenal cortex showed decreased functional status during the breeding period with a concomitant increase in adreno-medullary activity. In contrast, birds pinealectomised during the non-breeding phase depicted increased thyroid activity as well as increased cortico-medullary

ratio, a status characteristic of these glands ⁱⁿ intact birds during the breeding season. When viewed with the corresponding functional status of the gonads, these changes tend to indicate a parallel adrenal-thyroid-gonadal axis in domestic pigeons. Since an intact pineal has a favourable influence on the parallel functioning of the above triad of endocrine conglomerate, as denoted by the functional suppression of them by pineal ablation during the breeding period, a pineal-thyroid-adrenal-gonad tetrad axis can be considered to be active in the breeding physiology of domestic pigeons. This axis can then be considered to be sensitive to the suppressive action of some pineal principles during the non-breeding period as could be visualised by the secondary activation that could be induced in thyroid, adrenal and gonads during the non-breeding ^{Season} by pineal ablation.

As has been discussed earlier the breeding activities and gonadal activation are associated with many other favourable causative modulations in general body physiology which are under the purview of the endocrines such as pancreas, thyroid and adrenal. It has become apparent from the present studies that the presence of pineal during the breeding season and its absence during the non-breeding season of Indian domestic pigeons can both elicit similar physiological and metabolic modulations favourable for gonadal functioning. This is well illustrated by the observed suppression of

breeding specific metabolic alterations noted in pinealectomised birds during the breeding season (which are more comparable with the physiological status of intact birds in the regression phase) and vice versa during the non-breeding season. The various threads of the present investigation when knitted together yields a fabric of realisation that the pineal in domestic pigeons secrete at least two if not more active principles having a definite say in the reproductive physiology of this species. The possible nature of these principles is at present far from clear and it may be hoped that in the coming years they would become amenable to experimental analysis and thus reveal themselves. The possibility ^{exists} ~~is~~ that the same or even different pineal substance may influence the hypothalamo-hypophysio-gonadal axis on one hand and the thyroid-adrenal-gonadal axis ~~on~~ the other, and as such needs to be ascertained. It may also be hypothesised that whereas the pineal-hypothalamo-hypophysial interactions may have a direct bearing on gonadal functioning, the pineal-thyroid-adrenal interactions may have an indirect influence on gonadal structure and function by inducing the necessary favourable "physiological climate" for breeding.

An added dimension to the above interactions is the possible pineal-pancreas relationship which was well exemplified in wild pigeons (Patel, 1982). In the domestic pigeons too such a relationship can be inferred from the observed

alterations in carbohydrate metabolism in pinealectomised pigeons. Based on the alterations in hepatic glycogen content and blood glucose noted to occur in pinealectomised wild pigeons on a season specific fashion, a tentative anti-insulinic and anti-avian pancreatic polypeptide action of pineal during the breeding season was suggested (Patel, 1982). This tentative concept has been more critically evaluated in the present study by glucose tolerance test (GTT), insulin response test (IRT), glucagon response test (GRT) and adrenalin response test (ART) in both intact and pinealectomised pigeons during breeding as well as non-breeding periods. The results obtained by these tests have amply demonstrated increased insulin sensitivity and adrenalin sensitivity in pigeon pinealectomised during the breeding phase. Obviously the intact pineal by its antagonistic influence on insulin release or insulin action might be favouring the maintenance of elevated blood glucose level and hepatic glycogenolysis, factors of probable crucial significance in meeting the energy demands associated with gonadal functioning. Significantly this anti-insulinic action of the pineal appears to be exerted only during the breeding season as pinealectomy or even the presence of it during the non-breeding period did not show any variation either in GTT, or IRT responses. The in vitro slice experiments conducted herein have also revealed pinealectomy induced inhibition of glucose uptake and glycogen deposition by liver slices with no alteration in either glucose release or glycogen

depletion. Interestingly, the muscle slices of pinealectomised birds were observed to possess potentially increased ability for glucose uptake in response to insulin thus suggesting an increased insulin sensitivity leading to increased peripheral utilization, a concept which was hinted previously based on the observation of decreased blood glucose level and decreased hepatic glycogen content in pinealectomised wild pigeons (Patel, 1982). The pineal-pancreas axis thus gains definite credence and similar studies need to be extended to domestic pigeons too so as to get a comparative idea of the relative importance and extent of involvement of pineal-pancreas axis in the two species of pigeons. It may be also worthwhile to design more experiments on this line so that a general consensus regarding the pineal-pancreas interaction in aves in general could be aimed at. The present studies have opened up possible new vistas and avenues of investigations on pinealology and it can be hoped that the future will reveal more and more of the hidden mysteries of this once considered enigmatic vestigeal organ.'

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