

REGULATION OF THE BREEDING SEASON IN MAMMALS

(Invited Paper)

H. M. RADFORD*

Summary

The nature of seasonal breeding in both domestic and wild mammals has been known for centuries but only recently have we gained some insight into the mechanisms involved. Environment, encompassing climatic, nutritional, and biotic factors, plays a major role in synchronizing reproductive rhythms. Examples of the effect of environmental factors upon reproductive activity are discussed within the conceptual framework of central nervous control of pituitary secretion.

I. INTRODUCTION

Reproductive activity in the non-pregnant female mammal is manifest in periodic changes in the reproductive tract with associated times of sexual receptivity — the period of such changes being known as the oestrous cycle. Those species that experience only one cycle each year are monoestrous, those experiencing two or more each year are polyoestrous, and those in which the cycle(s) occupies a regular seasonal position are known as seasonal breeders. Seasonal breeding is apparent in many mammals, and seems to be an accompaniment of genetic selection whereby only those animals that produce young during a particular period are able to perpetuate themselves. Domestication, which involves artificial selection and provides comparatively uniform nutrition and housing, has removed the necessity for seasonal breeding and some domestic breeds have apparently freed themselves from the influence of seasonal changes upon their reproductive activity. None the less, seasonal breeding persists to a varying degree in some domesticated species and places limits upon the extent to which man can manipulate their breeding.

Seasonal breeding in domestic and wild mammals has been recognized for centuries, but it is only during the past 30 years that man has gained some understanding of the underlying mechanisms. This has come in some measure from the results of numerous studies on the net effect of certain environmental variables upon reproductive function, but owes much to the concept of central nervous control of anterior pituitary function — a concept largely due to Marshall (1937) and developed by Harris (1955). While this concept was in part a result of studies of seasonal breeding in mammals, seasonal breeders have been little used in the numerous investigations undertaken over recent years into

*Division of Animal Physiology, C.S.I.R.O., Ian Clunies Ross Animal Research Laboratory, Prospect, N.S.W.

the nervous control of reproductive phenomena (see reviews by Sawyer 1964; Everett 1964).

In this review no attempt is made to consider more than a few examples of environmental control of reproductive performance. These are then discussed within the framework of central nervous regulation of pituitary secretion.

II. ENVIRONMENT AND SEASONAL BREEDING

Environment encompasses the full range of conditions to which an organism is exposed, and is a complex of climatic, nutritional and biotic factors. Within each of these classes there are variables that play a role in regulation of reproduction in some species.

(a) *Climatic factors*

(i) *Light*

There is a vast literature, reviewed by Yeates (1954), Hammond (1954), Amoroso and Marshall (1960), Clegg and Ganong (1959), and Ortavant, Mauleon and Thibault (1964), on the effects of light on reproduction in both birds and mammals; there can be no doubt that light plays an important role in determining reproductive periodicity. In some mammals, light determines only macroperiodicity, i.e., the timing of the breeding season, while in others, events of the oestrous cycle are also regulated by light (Everett and Sawyer 1950).

Many species commence breeding when days lengthen in the spring, and in these so called "long-day" breeders, the experimental provision of increased lighting promotes the onset of reproductive activity. In others the onset of the breeding season is consequent upon decreasing daylength.

Of the "long-day" breeders, ferret and mink have been the most widely investigated, and the evidence is incontrovertible that the provision of increased lighting during winter months hastens the onset of oestrus (Bissonnette 1932; Hammond 1951). A similar situation exists also for the fieldmouse, *Microtus agrestis*, (Baker and Ranson 1932), raccoon (Bissonnette and Csech 1937), domestic cat (Dawson 1941) and the horse (Burkhardt 1947). There is presumptive evidence from statistical studies in cattle (Mercier and Salisbury 1947) that increased fertility is associated with increasing daily photoperiod, but equally as much evidence to relate maximum fertility with decreasing daily photoperiod (Courot and Ortavant 1963).

There is presumptive evidence from the time of occurrence of births that decreasing or low daily amounts of light stimulate the onset of the breeding season in the badger (Neale and Harrison 1958), the grey seal (Amoroso and Matthews 1952) and in a number of other species (reindeer, yak, warthog, bushbaby) kept in zoos (Zuckerman 1953; Brand 1963). However, the sheep and goat are the most widely known "short-day" breeders and the sheep certainly the most widely studied. Yeates (1949), Hart (1950), and Hafez (1952) provided evidence that in many English breeds of sheep the breeding season starts after a change from increasing to decreasing hours of daylight, and Yeates (1956) demonstrated similar photosensitivity in Merino ewes. Subsequently Radford (1961) showed that continuous light did inhibit but not completely suppress the development of normal sexual activity in Merino ewes and that

the response of mature Merino ewes to equatorial light was variable, some ewes exhibiting continuous sexual activity, others remaining seasonal. In Merino ewes subjected to equatorial light and reversed temperature seasons, Wodzicka-Tomaszewska, Hutchinson and Bennett (personal communication) observed individual variation in occurrence of oestrus, but generally shorter and earlier breeding seasons; under the same conditions Southdown ewes exhibited seasons of oestrous activity shorter than those of controls. Thwaites (1965) has shown that Southdown ewes subjected to equatorial light exhibit some degree of seasonal oestrous activity for a year at least, although activity never exceeded 50% of control **values** and eventually became very low.

The extent to which a photoperiodic mechanism operates to regulate seasonal breeding in sheep is obviously variable. In Australia there are many examples of the breeding season commencing while days are still increasing in length (Watson and Radford 1955). Results obtained from photoperiodic studies on sheep have been interpreted by most workers as consistent with the thesis that decreasing daily photoperiods stimulate and increasing daily photoperiods inhibit reproductive activity. An alternative, proposed by Ortavant, Mauleon and Thibault (1964) is that there is an optimal photoperiod for reproduction, and values above or below this are inhibitory. A further possibility is that increasing light per day inhibits reproductive activity which, after a period of rest, recurs without further stimulus provided that the current light regime does not provide more than a maximum number of hours of light per day. This last explanation has the advantage that it can account adequately for the onset of the breeding season in Merino ewes before the longest day. Despite considerable experimentation, no one hypothesis based solely on photoperiodism serves to explain all of the observed facts on seasonal breeding in sheep.

In photoperiodic studies many different light treatments have been used, ranging from reversed seasonal lighting, exaggerated seasons, sudden increases or decreases in light per day, and pulse type light : dark ratios. It is not possible here to summarize the results of such experimentation except to say that contrast detecting mechanisms seem to operate in all species studied. The experimental finding that a regime of 2 hours light 10 hours dark (i.e., only 4 hours light in any 24 hours) will bring ferrets into oestrus almost as effectively as days of 14 hours light : 10 hours dark suggests that the photosensitive mechanism takes account of only one light : dark ratio per 24 hours. Hammond (1954) believes that the 2L : 10D : 2L : 1 OD regime is in essence a 14 hour day, the ferret taking no account of one 10 hour dark period.

(ii) Temperature and rainfall

The evidence implicating temperature as a factor regulating the onset of breeding seasons in mammals is sketchy. It appears that prolonged cool weather rather than light is the stimulus for gonadal development in the ground squirrel (Wells and Zalesky 1940) and low environmental temperature can modify reproductive behaviour in the rat (Lee 1926). Further, Dutt and Bush (1955) involved temperature as a modulator of reproductive function in sheep when they showed that a lowered environmental temperature (40-45°F) induced oestrus some 50 days earlier than in controls at a temperature of approximately 90°F.

Marshall (1937) believed that low temperature is a factor in inducing full autumn rut in red deer.

There is no evidence that rainfall **per se** exerts reproductive effects in mammals.

(b) Nutritional factors

Only in recent years has nutrition definitely been shown to regulate breeding seasons in mammals, some of the evidence coming from studies on wild rabbits and sheep. Myers and Poole (1962) have observed a correlation between availability of feed and breeding activity in wild rabbits — activity commencing very shortly after rains had promoted growth of feed. Suijendorp (1959) has also noted an association between occurrence of oestrus and feed availability in Merino ewes in Western Australia. Hunter (1961) too has shown an effect of nutrition upon occurrence of oestrus in ewes, and Smith (1962, 1966) has demonstrated that both current and previous nutritional status have an influence upon occurrence of oestrus in Merino ewes.

While there is no doubt that malnutrition can interfere with reproductive function (Leatham 1961), the extent to which nutrition actively contributes to regulation of the breeding season has not been investigated in any animal other than the sheep.

(c) Biotic factors

The presence of the male can profoundly modify reproductive activity in females of some mammals. There is little point in detailing here the well known effect of introduction of rams in synchronization of ovulation and oestrus in Merino ewes in the spring (Schinckel 1954; Watson and Radford 1960), or the effect of discontinuous association of the sexes in extending the breeding season in Merino ewes (Riches and Watson 1954; Lamond, Wells and Miller 1963). It is perhaps less well known that in Angora goats also the male can synchronize ovulation shortly before the normal time of onset of the breeding season (Shelton 1960). Signoret, du Mesnil du Buisson and Busnel (1960) have shown that recorded boar sounds influence the intensity of oestrus in sows.

Reproductive phenomena related to the presence of the male are not confined to domestic species. This is evident in the effects of male rodents in synchronizing oestrus and interrupting pregnancy (Whitten 1956; Bruce 1960; Lamond 1959; Hughes 1964).

Other social factors also can operate to modulate reproductive function. Changes in population structure and density have been invoked as explanation for change in breeding activity in wild rabbits (Myers and Poole 1962), and in mice (Whitten 1959). The existence of hierarchies in many species automatically introduces a social factor in breeding activity; this has been observed in sheep recently by Mattner, Braden and Turnbull (1966).

It should be emphasized that as yet little is known of the complexities of interaction both "within and between sexes in the regulation of reproductive performance in mammals.

III. MECHANISM OF ACTION OF ENVIRONMENTAL FACTORS

(a) *Relation between pituitary and hypothalamus*

Thirty years ago it was considered that control of mammalian gonadal function rested with the adenohypophysis, and that cyclic regulation of gonadal activity was a function of a closed loop involving interactions between gonad and adenohypophysis (Moore and Price 1932). The feedback of gonadal steroids is still an integral part of hypotheses on control of the oestrous cycle, but it is now believed that the site of feedback is within the hypothalamus (Szentogathai *et al.* 1962). The hypothalamus has now essentially assumed the role originally accorded the adenohypophysis.

Owing largely to detailed studies by Green (1951) there is no doubt that there are but few, and then only vasomotor, nerve fibres from the hypothalamus to the adenohypophysis. Hypothalamic control of anterior lobe secretion is exerted by the secretion of neurohumoural mediators — the so-called releasing factors — from hypothalamic nerve endings. These nerve endings lie near the primary capillary plexus of a system of blood vessels (the hypophyseal portal system) which provides the major if not the sole blood supply to the adenohypophysis. A representation of this system is shown in Figure 1. The precise site of the perikarya of the neurons that produce the releasing factors is not known. However, cells of the arcuate nucleus and other areas that contribute axons ending in apposition to the primary capillary plexus of the hypophyseal portal

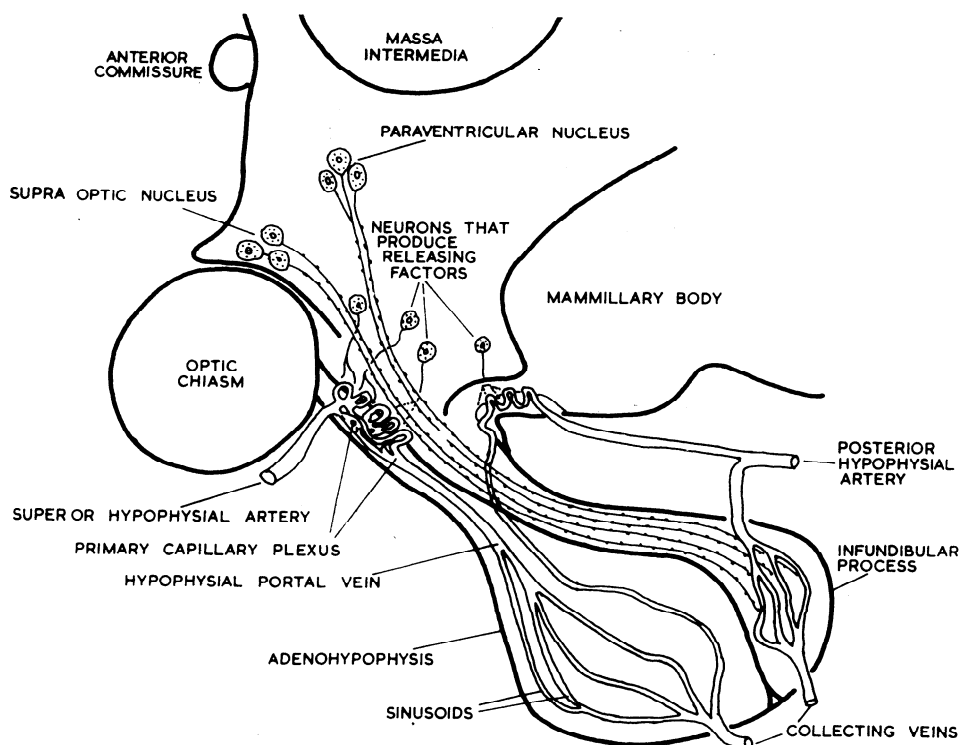


Fig. 1.—Neural and vascular connections from hypothalamus to pituitary.

system are probably involved. The releasing factors are apparently concentrated within the median eminence of the hypothalamus from which they may be extracted chemically (Nikitovitch-Winer 1962; Guillemin and Schally 1963). With this transfer of endocrine control from a non-nervous to a nervous structure it is now possible to visualize the means whereby environmental sensory input can modify reproductive function, and the next part of this discussion refers very briefly to the relationship between the hypothalamus and other parts of the central nervous system.

(b) Nervous pathways to hypothalamus

This relationship has recently been reviewed in detail by Nauta (1963) and Gloor (1956). The hypothalamus receives much of its sensory influx from the brain stem or midbrain reticular formation. This is a highly complex multisynaptic system intimately concerned with consciousness in its broadest sense. Some correlates between release of gonadotrophin and electrical activity within the reticular formation have been observed and studied by Sawyer and Kawakami (1959).

Another system in close functional and anatomical relationship to the hypothalamus in the rhinencephalon, including the olfactory bulbs and tubercle, septum, hippocampus and amygdala. This system is certainly involved in reproductive

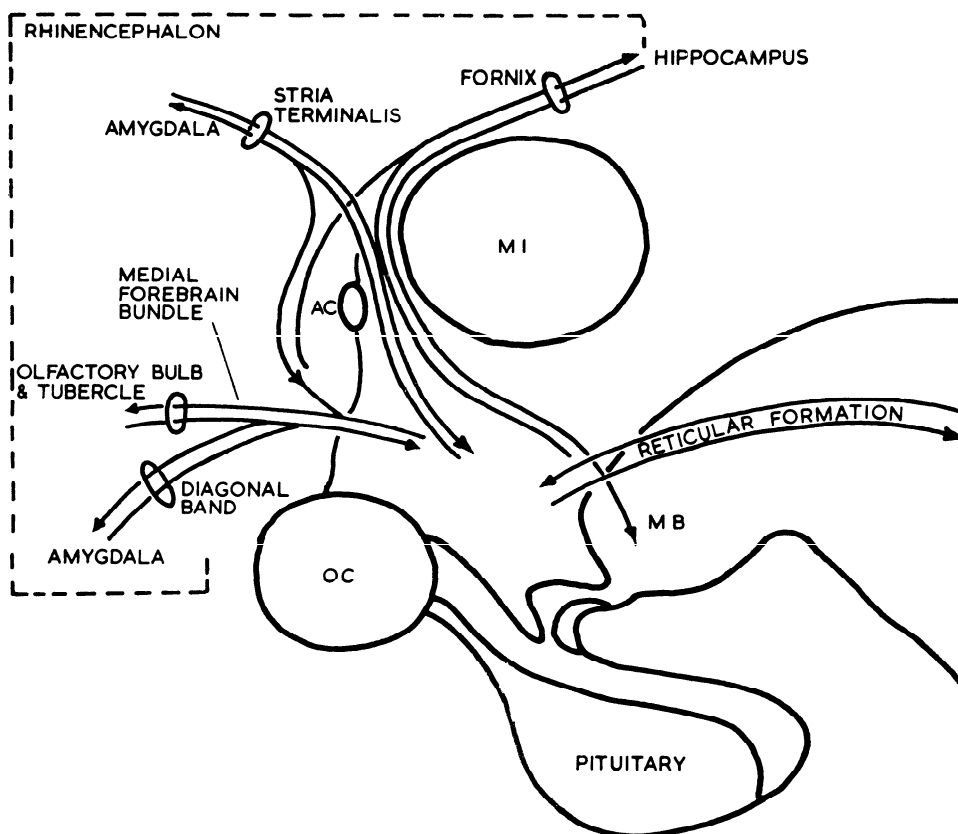


Fig. 2—Neural connections to hypothalamus.

control. Lesions in certain parts lead to hypersexualism (Critchlow 1961) and stimulation of other parts can induce release of gonadotrophin (Koikegami, Yamada and Usei 1954). There is evidence, too, that fibre paths between this system and the reticular formation relay extensively within the lateral hypothalamus and preoptic region (Nauta 1963).

There is little evidence for direct cortico-hypothalamic projections, but every reason to believe that much of the cortical outflow is at various points both proximal to and parallel with both the reticular formation and rhinencephalon. Cortical control of hypothalamic neurons therefore remains a possibility. A representation of hypothalamic afferents is shown in Figure 2.

(c) Mediation of environmental stimuli

(i) Light

It has been well established that the integrity of the eye is not essential for mediation of light effects, the hypothalamus itself being light sensitive (Benoit 1964; Lisk and Kannwischer 1964). However, an intact retinal ganglion layer has been shown to be essential in the ferret for light to influence reproductive activity (Thomson 1951), and it seems likely that a similar situation would exist in other mammals. However, experiments on blinded mammals have been confined to ferrets, and, since Ganong *et al.* (1963) have shown that light can penetrate to the brain in the sheep, dog, rabbit, and rat (Table 1), some direct effect of illumination upon central nervous activity remains a possibility. If the eye is the receptor, the pathway from eye to hypothalamus still remains a mystery. There have been claims for the existence of direct retino-hypothalamic tracts (Critchlow 1963) but such findings are doubted by Nauta (1963) and Hayhow, Webb and Jervie (1960). An alternative is that the light input is channelled by accessory optic tracts from where it could be processed by the midbrain reticular formation and/or the rhinencephalic system. Visual projections related to endocrine function are considered in some detail by Marg (1964), Feldman (1964) and Gergen and MacLean (1964). Another possibility is that the hypothalamus, being so close to the optic tract, is sensitive to overall field effects arising in the optic tract itself as a result of incident illumination. Certainly, in sheep, electrical activity recorded from the hypothalamus close to the optic tract

TABLE 1
Amount of light reaching photovoltaic cell in brain when head of animal exposed to daylight (from Ganong et al. 1963)

Animal	Lumens of Light Hypothalamus	Measured in Temporal Lobe	Weather
Sheep 1	0	5 x 10 ⁻⁹	Sunny
Sheep 2	0	2 x 10 ⁻⁶	Sunny
Sheep 3	2 x 10 ⁻⁹		Cloudy
Dog 1	1 x 10 ⁻⁸		Sunny
Dog 2	2 x 10 ⁻⁸		Cloudy
Dog 3	2 x 10 ⁻⁹		Cloudy
Rabbit	3 x 10 ⁻⁶		Cloudy
Rat	>1 x 10 ⁻³		Sunny

does vary with intensity of optic stimulation (Radford, unpublished data). The effects of illumination upon reproductive activity take place gradually, implying some storage of energy arising from stimulation. No attempt has been made to determine just how such storage occurs.

There has been a recent upsurge of interest in the **pineal** body as a possible mediator of light induced reproductive changes in the rat (Cohen *et al.* 1964) but there is no unequivocal evidence for the involvement of the **pineal** in the regulation of seasonal breeding.

(ii) Temperature

It is perhaps surprising that temperature has not been implicated more in the control of reproductive function. Temperature sensing mechanisms exist in the hypothalamus (Barbour 1921; Andersson and Larsson 1961; Hardy 1961) which is supposed to function as a computer in thermoregulation. These mechanisms lie in anatomical proximity to the **preoptic** area which can play a role in the release of pituitary gonadotrophin in the rat (Everett 1961). Environmental temperature also has a marked centrally mediated effect on thyrotrophic hormone release (Von Euler and Holmgren 1956) and a similar mechanism for gonadotrophins is equally possible. The fact that environmental temperature can alter both thyroid and adrenal activity presents another possibility, namely that of altered thyroid and/or adrenal activity indirectly providing a stimulus for change in gonadotrophin secretion (Young 1961).

(iii) Nutrition

The mechanisms whereby nutrition can modulate ovarian activity are perhaps as conjectural as those already considered for light and temperature. The facts that undernutrition results in changed pituitary gonadotrophin content (Casida 1963; Srebnik and Nelson 1963) and that exogenous gonadotrophin can restore gonadal function in undernourished animals (Meites 1953) suggests strongly that nutritionally induced variation in gonadal activity is not due to gonadal change *per se*. However, there is no evidence to indicate whether the effect is directly upon the adenohypophysis or the central nervous system. The delayed effect of earlier nutrition upon oestrous activity in ewes (Smith 1962, 1966) suggests a storage mechanism, perhaps implicating the central nervous system, a system well adapted for storage, and certainly the hypothalamus has a function in regulation and recognition of food intake. On the other hand the effects of current nutrition upon oestrous activity (Smith 1966) or ovulation rate (Allen and Lamming 1961) may imply a more direct metabolic effect within the pituitary.

(iv) Biotic factors

There is no question that reproductive effects initiated by association with the opposite sex are mediated by the central nervous system, and that the specialized sense organs for sight, sound and smell are to some extent involved. There would seem little doubt that the olfactory input is processed by rhinencephalic networks before influencing the hypothalamus (Green 1956), and indeed, electrical activity in olfactory structures has been related to release of pituitary gonadotrophin in rabbits by Sawyer (1955) and Radford and Sawyer (1960). The manner **in**

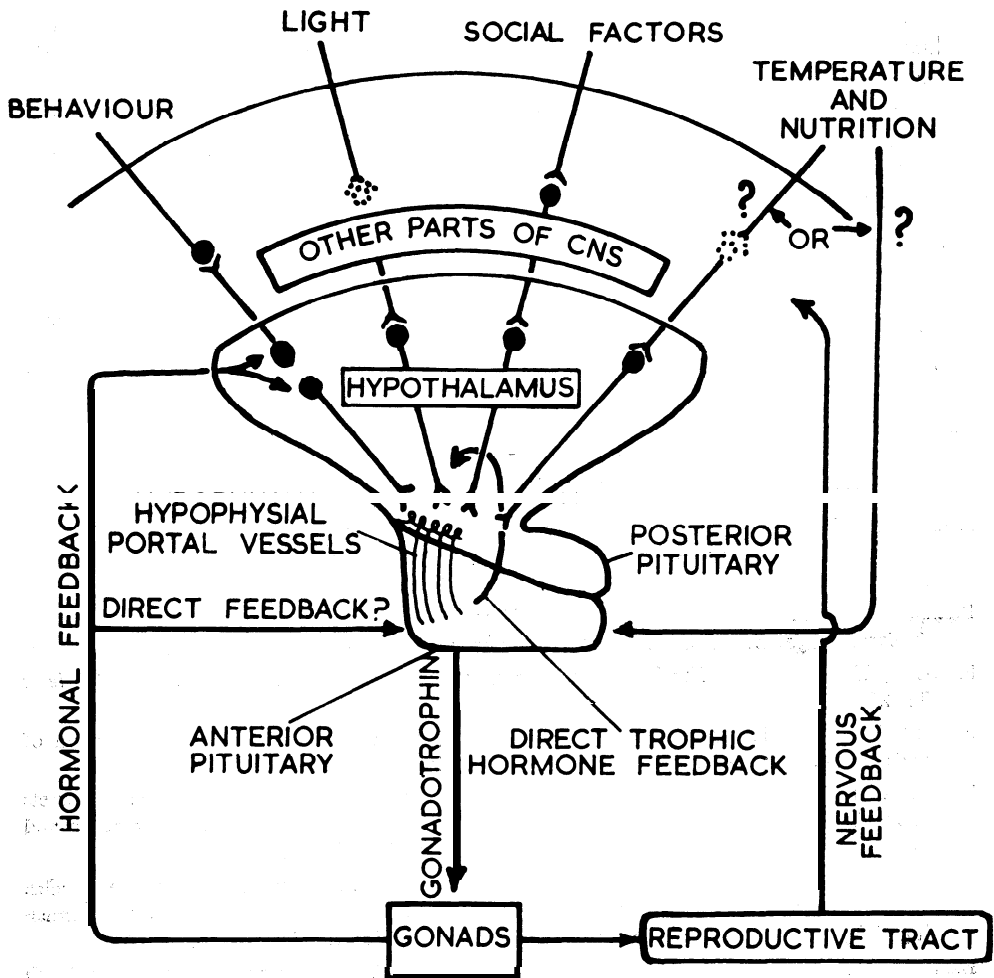


Fig. 3.—Brain-pituitary-gonad interrelationships.

which auditory stimulation operates to modify reproductive activity is completely unknown.

IV. CONCLUDING REMARKS

Within the preceding discussion it has been assumed that rhythmicity in breeding is largely controlled by external factors. This is not to say that such rhythmicity in all species and breeds is necessarily dependent upon environmental change. There is no *a priori* reason why rhythmic breeding should not be endogenous, becoming seasonal only upon being synchronized by external environmental rhythms.

Of necessity the foregoing has been but a brief discussion of seasonal breeding. An attempt has been made to fit known facts relating environment and seasonal breeding to an anatomical and physiological framework, (Figure. 3), and from this the following conclusion would seem justified.

Within mammals there exist appropriate mechanisms for the integration of a host of environmental variables. Within any species the final timing of the breeding season is almost certainly not controlled by one environmental factor but by a combination of environmental stimuli. These stimuli operate through exteroceptors, the central nervous system and the pituitary gland, to regulate reproductive activity. The response to the stimuli varies between species and between breeds. In no case do we understand in detail how these factors operate.

V. REFERENCES

- ALLEN, D. M., and LAMMING, G. E. (1961) . Nutrition and reproduction in the ewe. *Journal of Agricultural Science* **56**: 69.
- AMOROSO, E. C., and MATTHEWS, L. H. (1952). Reproduction and lactation in the seal. *Report II International Congress of Animal Reproduction, Copenhagen* **11**:193.
- AMOROSO, E. C., and MARSHALL, F. H. A. (1960). External factors in sexual periodicity. "Marshall's Physiology of Reproduction". Vol. 1, part II, p. 797. (Ed. A. S. Parkes.) (Longmans, Green and Co.: London).
- ANDERSSON, B., and LARSSON, B. (1961) . Influence of local temperature changes in the preoptic area and rostral hypothalamus on the regulation of food and water intake. *Acta Physiologica Scandinavica* **52**: 75.
- BAKER, J. R., and RANSON, R. M. (1932). Factors affecting the breeding of the fieldmouse (*Microtus agrestis*). Part 1, Light. *Proceedings of the Royal Society Series B* **110**: 3 13.
- BARBOUR, H. G. (1921). The heat-regulating mechanism of the body. *Physiological Reviews* **1**: 295.
- BENOIT, J. (1964). The role of the eye and of the hypothalamus in the photostimulation of gonads in the duck. *Annals of the New York Academy of Sciences* **117**/1: 204.
- BISSONNETTE, T. H. (1932). Modification of mammalian sexual cycles: Reactions of ferrets (*Putorius vulgaris*) of both sexes to electric light added after dark in November and December. *Proceedings of the Royal Society Series B* **110**: 322.
- BISSONNETTE, T. H., and CSECH, A. G. (1937). Modification of mammalian sexual cycles. VII. Fertile matings of raccoons in December instead of February induced by increasing daily periods of light. *Proceedings of the Royal Society Series B* **122**: 246.
- BRAND, D. J. (1963). Records of mammals bred in the National Zoological Gardens of South Africa during the period 1908 to 1960. *Proceedings of the Zoological Society London* **140**: 617.
- BRUCE, H. M. (1960). A block to pregnancy in the mouse caused by proximity of strange males. *Journal of Reproduction and Fertility* **1**: 96.
- BURKHARDT, J. (1947). Transition from anoestrus in the mare and effects of artificial lighting. *Journal of Agricultural Science* **37**: 64.
- CASIDA, L. E. (1963). The level of fertility in the female as influenced by feed level and energy intake. *Proceedings of the Sixth International Congress of Nutrition*, p. 366.
- CLEGG, M. T., and GANONG, W. F. (1959). Environmental factors other than nutrition, affecting reproduction. "Reproduction in Domestic Animals." Vol. 2, p. 225. (Eds. H. H. Cole and P. T. Cupps.) (Academic Press: New York and London).
- COHEN, R. A., WURTMAN, R. J., AXELROD, J., and SNYDER, S. H. (1964). Some clinical, biochemical, and physiological actions of the pineal gland. *Annals of Internal Medicine* **61**: 1144.
- COUROT, M., and ORTAVANT, R. (1963). Cited by Ortavant, Mauleon and Thibault (1964).
- CRITCHLOW, V. (1961). "Control of Ovulation" p. 75. (Ed. C. A. Villee.) (Pergamon Press: New York).
- CRITCHLOW, V. (1963). The role of light in the neuroendocrine system. "Advances in Neuroendocrinology." p. 377. (Ed. A. V. Nalbandov.) (University of Illinois Press).

- DAWSON, A. B. (1941) . Early oestrus in the cat following increased illumination. *Endocrinology* 28: 907.
- DUTT, R. H., and BUSH, L. F. (1955). The effect of low environmental temperature on initiation of the breeding season and fertility in sheep. *Journal of Animal Science* 14: 885.
- EVERETT, J. W. (1961). The preoptic region of the brain and its relation to ovulation. "Control of Ovulation." p. 101. (Ed. C. A. Villee.) (Pergamon Press: New York).
- EVERETT, J. W. (1964). Central nervous control of reproductive functions of the adeno-hypophysis. *Physiological Reviews* 44: 373.
- EVERETT, J. W., and SAWYER, C. H. (1950). A 24-hour periodicity in the "LH-release apparatus" of female rats, disclosed by barbiturate sedation. *Endocrinology* 47: 198.
- FELDMAN, S. (1964). Visual projections to the hypothalamus and preoptic area. *Annals of the New York Academy of Sciences* 117/1: 53.
- GANONG, W. F., SHEPHERD, M. D., WALL, J. R., VAN BRUNT, E. E. and CLEGG, M. (1963). Penetration of light into the brain of mammals. *Endocrinology* 72: 962.
- GERGEN, J. A., and MACLEAN, P. D. (1964). The limbic system: photic activation of limbic cortical areas in the squirrel monkey. *Annals of the New York Academy of Sciences* 117/1: 69.
- GLOOR, P. (1956). Telencephalic influences upon the hypothalamus. "Hypothalamic-hypophyseal interrelationships." p. 74. (Ed. W. S. Fields *et al.*) (Charles C. Thomas: Springfield, Illinois).
- GREEN, J. D. (1951). The comparative anatomy of the hypophysis, with special reference to its blood supply and innervation. *American Journal of Anatomy* 88: 225.
- GREEN, J. D. (1956). Neural pathways to the hypophysis. "Hypothalamic-hypophyseal Interrelationships." p. 3. (Ed. W. S. Fields *et al.*) (Charles C. Thomas: Springfield, Illinois).
- GUILLEMIN, R., and SCHALLY, A. V. (1963). Recent advances in the chemistry of neuro-endocrine mediators originating in the central nervous system. "Advances in Neuroendocrinology." p. 3 14. (Ed. A. V. Nalbandov.) (University of Illinois Press).
- HAFEZ, E. S. E. (1952). Studies on the breeding season and reproduction of the ewe. *Journal of Agricultural Science* 42: 189.
- HAMMOND, J. Jr. (195 1). Control by light of reproduction in ferrets and mink. *Nature*, London, 167: 150.
- HAMMOND, J. Jr. (1954). Light regulation of hormone secretion. *Vitamins and Hormones* XII: 157.
- HARDY, J. D. (1961). Physiology of temperature regulation. *Physiological Reviews* 41: 521.
- HARRIS, G. W. (1955). "Neural control of the pituitary gland". (Edward Arnold Ltd.: London).
- HART, D. S. (1950). Photoperiodicity in Suffolk sheep. *Journal of Agricultural Science* 40: 143.
- HAYHOW, W. R., WEBB, C., and JERVIE, A. (1960). The accessory optic fibre system in the rat. *Journal of Comparative Neurology* 115: 187.
- HUGHES, R. L. (1964). Effect of changing cages, introduction of the male, and other procedures on the oestrous cycle of the rat. *C.S.Z.R.O. Wildlife Research* 9: 115.
- HUNTER, G. L. (196 1) . Some effects of plane of nutrition on the occurrence of oestrus in Merino ewes. *Proceedings of the Fourth International Congress of Animal Reproduction* II: 197.
- KOIKEGAMI, H., YAMADA, T., and USEI, K. (1954). Stimulation of the amygdaloid nuclei and periamygdaloid cortex with special reference to its effects on uterine movements and ovulation. *Folia Psychiatrica et Neurologica Japonica* 8: 343.
- LAMOND, D. R. (1959). Effect of stimulation derived from other animals of the same species on oestrous cycles in mice. *Journal of Endocrinology* 18: 343.

- LAMOND, D. R., WELLS, K. E., and MILLER, S. J. (1963). Study of a breeding problem in Merino ewes in central Queensland. *Australian Veterinary Journal* **39**: 295.
- LEATHEM, J. H. (1961). Nutritional effects on endocrine secretion. "Sex and Internal Secretions." 3rd Ed. Vol. 1. p. 666. (Ed. William C. Young.) (Williams and Wilkins: Baltimore).
- LEE, M. O. (1926). Studies on the oestrous cycle of the rat. The effect of low environment, mental temperature. *American Journal of Physiology* **78**: 246.
- LISK, R. D., and KANNWISCHER, L. R. (1964). Light: Evidence for its direct effect on hypothalamic neurons. *Science* **146**: 272.
- MATTNER, P. E., BRADEN, A. W. H., and TURNBULL, K. E. (1966). Studies of mating in sheep under field conditions. I. Mating behaviour. *Australian Journal of Experimental Agriculture and Animal Husbandry*. (In press).
- MARG, E. (1964). The accessory optic system. *Annals of the New York Academy of Sciences* **117**/1: 35.
- MARSHALL, F. H. A. (1937). On the changeover in the oestrous cycle in animals after transference across the equator, with further observations on the incidence of the breeding seasons and the factors controlling sexual periodicity. *Proceedings of the Royal Society Series B* **122**: 4 13.
- MEITES, J. (1953). Relation of nutrition to endocrine-reproductive functions. *Iowa State College Journal of Science* **28**: 19.
- MERCIER, E., and SALISBURY, G. N. (1947). Fertility level in artificial breeding associated with season, hours of daylight and the age of cattle. *Journal of Dairy Science* **30**: 747.
- MOORE, C. R., and PRICE, D. (1932). Gonad hormone functions, and the reciprocal influence between gonads and hypophysis with its bearing on the problem of sex hormone antagonism. *American Journal of Anatomy* **50**: 13.
- MYERS, K., and POOLE, W. E. (1962). A study of the biology of the wild rabbit, *Oryctolagus cuniculus* (L) in confined populations. *Australian Journal of Zoology* **10**: 225.
- NAUTA, W. J. H. (1963). Central nervous organization and the endocrine motor system. "Advances in Neuroendocrinology." p. 5. (Ed. A. V. Nalbandov.) (University of Illinois Press).
- NEALE, E. G., and HARRISON, R. J. (1958). Reproduction in the European badger (*Meles meles*, L.). *Transactions of the Zoological Society of London* **29**: 67.
- NIKITOVITCH-WINER, M. B. (1962). Induction of ovulation in rats by direct intrapituitary infusion of median eminence extracts. *Endocrinology* **70**: 350.
- ORTAVANT, R., MAULEON, P., and THIBAUT, C. (1964). Photoperiodic control of gonadal and hypophysal activity in domestic mammals. *Annals of the New York Academy of Sciences* **117**/1: 157.
- RADFORD, H. M. (1961). Photoperiodism and sexual activity in Merino ewes. *Australian Journal of Agricultural Research* **12**: 139.
- RADFORD, H. M. and SAWYER, C. H. (1960). E.E.G. changes in the rabbit rhinencephalon related to pituitary activation by intra-ventricular norepinephrine. *Anatomical Record* **138**: 378.
- RICHES, J. H., and WATSON, R. H. (1954). The influence of the introduction of rams on the incidence of oestrus in Merino ewes. *Australian Journal of Agricultural Research* **5**: 141.
- SAWYER, C. H. (1955). Rhinencephalic involvement in pituitary activation by intraventricular histamine in the rabbit under Nembutal anesthesia. *American Journal of Physiology* **180**: 37.
- SAWYER, C. H. (1964). Control of secretion of gonadotropins. "Gonadotropins, Their Chemical and Biological Properties and Secretory Control." p. 113. (Ed. H. H. Cole.) W. H. Freeman & Co.: San Francisco and London).

- SAWYER, C. H., and KAWAKAMI, M. (1959). Characteristics of behavioral and electroencephalographic after-reactions to copulation and vaginal stimulation in the female rabbit. *Endocrinology* **65**: 622.
- SCHINCKEL, P. G. (1954). The effect of the presence of the ram on the ovarian activity of the ewe. *Australian Journal of Agricultural Research* **5**: 465.
- SHELTON, M. (1960). Influence of the presence of a male goat on the initiation of estrus cycling and ovulation in Angora does. *Journal of Animal Science* **19**: 368.
- SIGNORET, J. P., du MESNIL du BUISSON, F., and BUSNEL, R. G. (1960). Rôle d'un signal acoustique de verrat dans le comportement réactionnel de la truie en oestrus. *Comptes Rendus des Seances de l'Academie des Sciences, Paris* **250**: 1355.
- SMITH, I. D. (1962). The effect of plane of nutrition upon the incidence of oestrus in the Merino ewe in Queensland., *Australian Veterinary Journal* **38**: 338.
- SMITH, I. D. (1966). The influence of level of nutrition during winter and spring upon oestrus activity in the ewe. *World Review of Animal Production*. (In press).
- SREBNIK, H. H., and NELSON, M. M. (1963). The influence of diet on the gonadotrophins of the anterior pituitary gland. *Proceedings of VIth International Congress of Nutrition* p. 375.
- SULJENDORP, H. (1959). Observations on the breeding performance of Merinos at Abydos Station. *Journal of Department of Agriculture, Western Australia* (Series 3) **8**: 711.
- SZENTOGATHAI, J., FLERKO, B., MESS, B., and HALASZ, B. (1962). "Hypothalamic control of the anterior pituitary gland." (Academic Press: Budapest).
- THOMSON, A. P. D. (1951). Relation of retinal stimulation to oestrus in the ferret. *Journal of Physiology (London)* **113**: 425.
- THWAITES, C. J. (1965). Photoperiodic control of breeding activity in the Southdown ewe with particular reference to the effects of an equatorial light regime. *Journal of Agricultural Science* **65**: 57.
- VON EULER, C., and HOLMGREN, C. (1956). The role of hypothalamo-hypophysial connexions in thyroid secretion. *Journal of Physiology (London)* **131**: 137.
- WATSON, R. H., and RADFORD, H. M. (1955). A note on the hours of daylight associated with the seasonal increase in sexual activity in Merino ewes. *Australian Veterinary Journal* **31**: 31.
- WATSON, R. H., and RADFORD, H. I. M. (1960). The influence of rams on onset of oestrus in Merino ewes in the spring. *Australian Journal of Agricultural Research* **11**: 65.
- WELLS, L. J., and ZALESKY, M. (1940). Effects of low environmental temperature on the reproductive organs of male mammals with annual aspermia. *American Journal of Anatomy* **66**: 429.
- WHITTEN, W. K. (1956). Modification of the oestrous cycle of the mouse by external stimuli associated with the male. *Journal of Endocrinology* **13**: 399.
- WHITTEN, W. K. (1959). Occurrence of anoestrus in mice caged in groups. *Journal of Endocrinology* **18**: 102.
- YEATES, N. T. M. (1949). The breeding season of the sheep with particular reference to its modification by artificial means using light. *Journal of Agricultural Science* **39**: 1.
- YEATES, N. T. M. (1954). Daylight changes. "Progress in the Physiology of Farm Animals". Vol. 1, p. 363. (Ed. John Hammond.) (Butterworths Scientific Publications: London).
- YEATES, N. T. M. (1956). The effect of light on the breeding season, gestation, and birth-weight of Merino sheep. *Australian Journal of Agricultural Research* **7**: 440.
- YOUNG, W. C. (1961). The mammalian ovary. "Sex and Internal Secretions." 3rd Ed. Vol. 1, p. 449. (Ed. William C. Young.) (Williams and Wilkins, Baltimore).
- ZUCKERMAN, S. (1953). The breeding season of animals in captivity. *Proceedings of Zoological Society, London* **122**: 827.