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QUESTIONS

Flyger: We don't always find upper premolars present in our gray squirrel.

Moore: This does not surprise me because there is frequently some variation in taxonomic characters.

Shorten: What subspecies of gray do we have in Britain? We have some black squirrels introduced in one or two parts of Britain.

Moore: This is certainly a point in favor of the northern subspecies.

Uhlig: Dr. Mosby, what are the weights of the southern subspecies that you have handled?

Mosby: 450-500 grams.

Moore: I would hesitate to accept weights as a taxonomic character. Scheffer has found considerable decrease in weights of fur seals in recent years.

Sharp: Is there a relative of Tamiasciurus in Asia?

Moore: A Chinese rock squirrel and African ground squirrels appear to be the closest relatives.

Clark: Squirrels may have evolved rapidly because a nasal mite found in gray squirrels at Patuxent is similar to a mite found in an African squirrel (Funisciurus).

Moore: I would say, nevertheless, that these two squirrels are about as far apart as any tree squirrels can be.

Johnson: You say that *Sciurus* has many more species here and only one species in Eurasia. Do you therefore say the squirrels went over there or came over here?

Moore: I have a theory that they came over here but it would take me too long to go into this at present. I hope to publish on this soon.

CURRENT KNOWLEDGE OF TREE SQUIRREL REPRODUCTIVE CYCLES AND DEVELOPMENT[1]

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Knowledge of the reproductive behavior and physiology of a particular species is a prerequisite to its successful management. In those wild species which can adapt to life in artificial surroundings (mink, fox) considerable information has accumulated regarding length of estrus, type of estrous cycle, reproductive development, nutritional balance required for successful breeding, etc., all of which aid in the successful propagation and management. In tree squirrels, however, artificial propagation has been generally unsuccessful. Consequently, much of the information on reproductive cycles in tree squirrels has been acquired by empirical means.

A review of the literature reveals almost complete agreement that tree squirrels have two main breeding seasons per year. Each mating period is rather restricted in time although it vvaries somewhat with latitude and perhaps with age, nutrition, climatic conditions and possibly even with population density.

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In the vicinity of Lafayette, Indiana, the first mating takes place primarily in January and February while the second breeding period occurs in late May and June and possibly into July.

Since our work has dealt almost exclusively with the male squirrel, this report summarizes our knowledge regarding this sex.

REVIEW OF PREVIOUS WORK

When we first considered a comprehensive study of male squirrel reproduction, a considerable amount of information had already been accumulated by Allen (1942) in Michigan and Brown and Yeager (1945) in Illinois. These workers, using subjective impressions, body weight, Cowper's gland palpation, scrotal pigmentation, and testis weights or measurements, attempted to age and classify male squirrels according to sexual development. Conveniently descriptive terminology was evolved, e.g., "in breeding condition," "sexually active," "inactive," etc., although it was known that male squirrels develop sexually in the fall and regress in late summer. Hence, this system did not appraise males accurately in intermediate stages of development and regression because it did not make a physiological distinction between function and non-function of reproductive organs. In addition to adults in indeterminable phases of their cycle, the fact that fall populations contained two groups of juvenile males, one becoming sexually active for the first time, indicated that considerable error could be expected from such a classification.

For the purpose of aging and assessing sexual condition, histological studies of male reproductive organs revealed considerable error in gross methods, and histology as a method promised more accuracy. Accordingly, we described the histological anatomy of testes and accessory glands in relation to ages and seasons (Hoffman, 1952; Kirkpatrick, 1955; Mossman *et al.*, 1955). Five distinct classes of sexual development, comprising two major age classes, were recognized: infantile and prepubertal were considered as juveniles, while functional, degenerating, and redeveloping were classed as adults.

In the light of the histological method for assessing sexual development, a reevaluation of gross methods previously used for that purpose revealed that testis weights and sizes overlap within and between classes of sexual development. The same was true of Cowper's glands, which are often palpated or measured, indicating that these measurements are not reliable for determining sexual activity or even age (Hoffman and Kirkpatrick, 1956). When body weights were correlated with histological indications of sexual activity and age, it was obvious that weights were also poor criteria of age even though this is a measurement frequently obtained by field biologists (Kirkpatrick and Hoffman, 1960).

Measurements of long bones and skull dimensions likewise offer little promise for an easy or accurate aging technique. The weight of the baculum, however, does increase with age during the first year and consequently can be used with some confidence in determining age composition, i.e., juveniles and adults (Kirkpatrick and Barnett, 1957).

RECENT INVESTIGATIONS

With an accurate method for aging and classifying sexual activity, we analyzed a male gray squirrel population in terms of sexual development for all months of the year. For this purpose, we had available 259 animals comprising about 20 males per month. A detailed analysis of this material is in press (Kirkpatrick and Hoffman, 1960), but some generalizations will indicate the seasonal fluctuations in age composition and sexual activity.

Peaks in abundance for the sexual development classes suggested that male squirrels attain sexual maturity at 10-11 months of age regardless of whether they were born in spring or summer. Spring males remain sexually active for 6-8 months while summer males are sexually active for about 3 months. Late summer is a period of sexual degeneration in both groups. The data indicated definite and restricted periods of sexual stimulation of adults and juveniles and well-defined periods of degeneration regardless of the length of time the animals remained functional. This suggested environmental factors operating to regulate and control the sequence of reproductive cycles. Further evidence for an environmental influence is the observation that gray squirrels, transported to the southern hemisphere, reverse their breeding periods to coincide with the change in environmental conditions (cited by Shorten, 1951).

The two most obvious environmental factors are light and temperature. If we plot, in a rough way, the monthly changes in light duration and mean temperatures throughout the year (Fig. 1), it is apparent that both periods of estrus in the female occur primarily during the first 6 months of the year. Some exceptional breeding takes place in July and in December, but as a rule most breeding occurs in January-February and again in May-June. The January-February estrus occurs soon after the minimal daily light duration and during minimal temperatures; coversely, the May-June estrus occurs near the time of maximal daily light and high temperatures. It may be an over-simplification to conclude that estrus and mating activity are induced on increasing daily amounts of light and independent of temperature, but little or no mating takes place when light and temperature are both decreasing (August-December). The age of females could also be a factor in the timing of estrous periods since the proportions of parous and nulliparous females comprising the breeding population at either period are unknown.

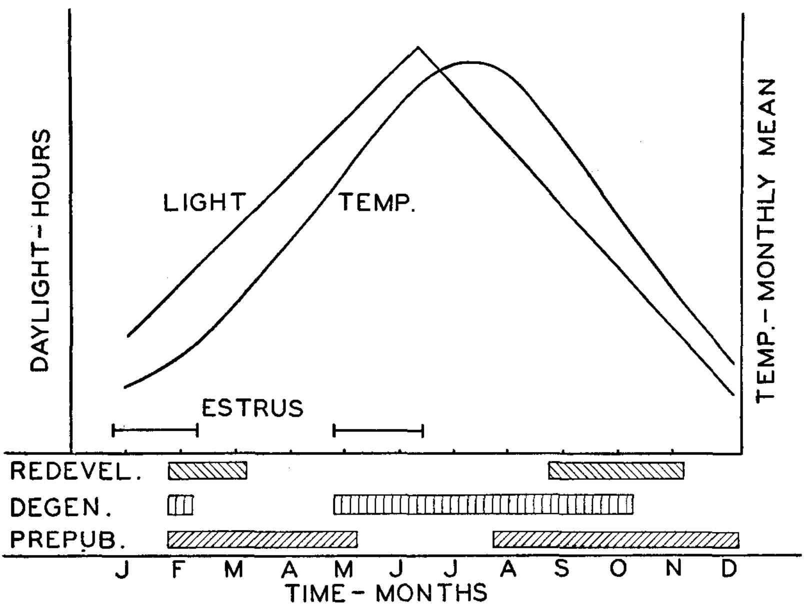

Fig. 1. Reproductive development and regression of gray squirrels correlated with generalized seasonal curves for environmental temperature and light duration.

Different conditions obtain for the male since sexual stimulation of young and adults alike occurs both under decreasing light and temperature and increasing light and temperature. Hence, it does not appear that the environmental factors of light or temperature are solely responsible for sexual stimulation in the male. The major period of degeneration occurs primarily under conditions of a decreasing light and temperature, suggesting that either factor might indirectly suppress sexual activity.

We are considering the possible influence of other endocrine organs on gonad development or suppression. In view of the recognized effect of a hyperthyroid or hypothyroid condition on reproductive vigor in several species of domestic animals, we investigated the thyroid gland (Hoffman and Kirkpatrick, 1960). For this purpose we collected at least 10 males per month, removed and weighed the thyroid glands and assessed thyroid activity by measuring epithelial cell height. In general, an increased thyroid cell height is associated with increased function while a low cell height is indicative of a low level of activity.

When we disregarded seasonal differences, relative thyroid weight and cell height was found to be maximum in the infantile animal (Fig. 2). There was a progressive reduction in values through the prepubertal and functional classes. Hence, signs of reproductive development coincident with somatic development were not correlated with morphological changes indicative of related activity in the thyroid gland. Cell heights exhibited no gross differences among the three classes of adults. Thyroid gland weight in the degenerating and redeveloping classes appeared to be significantly less than that of the functional class but not in those months when all three classes were found in the population. Infantiles and prepubertals showed consistent differences in all months. Thus, once adulthood is reached, thyroid gland activity remains at a certain level regardless of any change in reproductive activity. A high level of activity of the thyroid gland is associated with somatic growth and development but not with reproductive development.

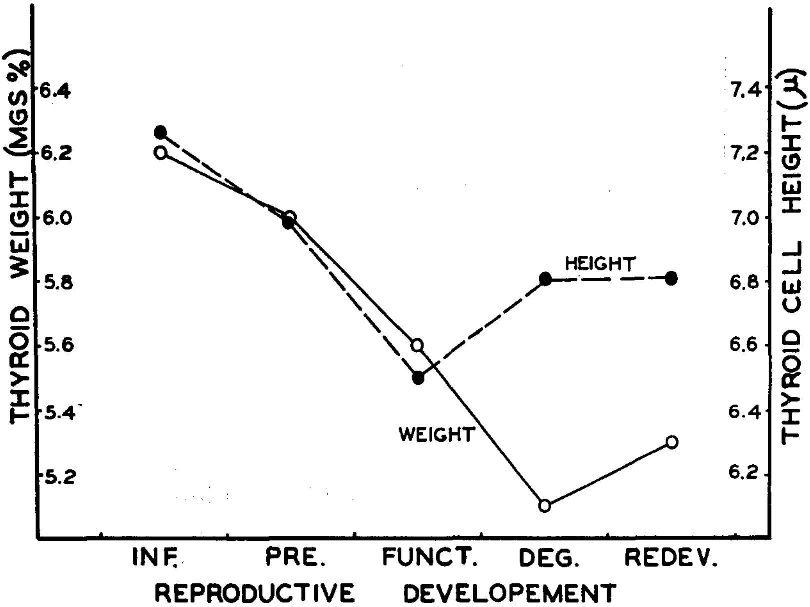

Fig. 2. Mean thyroid gland weight and cell height for all months correlated with reproductive development in male gray squirrels.

To emphasize the effect of season alone and to eliminate the probable influence of somatic and sexual development, thyroid gland cell height was plotted for the functional animals only (Hoffman and Kirkpatrick, 1960). Maximal activity occurred in October-November and the minimum in June-July. Sexual degeneration is first evident in May-June, increasing in July-September. These observations of a low thyroid gland activity associated with a progressive gonad degeneration plus the many references correlating thyroid and gonad function (see review by Maqsood, 1952) suggests that gonad atrophy during the summer is probably due to inadequate support by the thyroid gland secretions. Thus, when certain minimal levels of thyroid activity are reached, reproductive processes cannot be maintained and an irreversible process of sexual degeneration sets in which lasts for approximately 3 months. By this time, environmental factors, i.e., decreasing light and temperature, cause reactivation of the thyroid gland and consequently a redevelopment of reproductive glands.

When the weight of the adrenal gland was plotted throughout the year, two peaks of maximal adrenal weight occurred, one in September-October and one in May-June. However, the relatively heavier weight of glands of juvenile animals was found to bias the curve. When adrenal weights from functional animals only were considered, thus eliminating age and sexual development differences, maximal weight was evident in September-October followed by a dramatic decline to the minimum in November-December. Pituitary weights were found to show a comparable change. Thus we have found no correlation of adrenal or pituitary weight with the male reproductive cycle (Hoffman and Kirkpatrick, Unpubl, ms.).

The available knowledge relative to the sequence of male reproductive development still does not explain the control of the initial stimuli. Both puberty and subsequent redevelopment occur simultaneously and within restricted periods of time, suggesting that a rather precise control mechanism is acting. While environmental factors are probably implicated, according to empirical observations, neither light nor temperature alone appear to be clearly involved with sexual stimulation and as regards the endocrine glands, the relationships are as yet incompletely known.

It is significant that a summer period of inactivity exists when few animals of either sex are capable of breeding. Because the primary breeding periods fall at other seasons, the two littering periods occur only in those seasons when environmental factors of temperature, food supplies, etc., are conducive to successful growth and development of the young. Without a summer period of sexual inactivity, young could be born throughout the year, many at times when their appearance as weanlings would coincide with harsh environmental conditions.

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