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SEASONAL VARIATIONS IN THE FOOD CONSUMPTION OF WOODCHUCKS (MARMOTA MONAX)

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SEASONAL VARIATIONS IN THE FOOD CONSUMPTION OF WOODCHUCKS (*MARMOTA MONAX*)

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ABSTRACT.—Food consumption of 155 woodchucks (*Marmota monax*) was measured immediately after capture to determine whether a seasonal rhythm obtained in feeding of a natural population. Food intake of adults was lowest in March. It reached a maximum in May, then declined through the summer; some individuals increased food intake temporarily in late autumn. Comparative data from a laboratory colony showed that a similar rhythm occurred under conditions of constant temperature and photoperiod. Variability in food consumption maxima associated with different age groups, considered in the context of available life history information, suggested that the rhythm had a period somewhat less than 1 year.

Seasonal variations in the behavioral and physiological processes of hibernators have received considerable attention from physiologists and ecologists, resulting in a rather extensive literature. Considerable information has been collected, mostly from laboratory studies, but there is no satisfactory explanation of the control and interdependence of these seasonal flunctuations. Recent papers summarizing previous research and reporting additional data were presented by Davis (1967*a;* 1967*b*), by Pengelley and Kelley (1966), and by Mrosovsky (1968). The basic pattern emerging from experiments on woodchucks (*Marmota monax*) by Davis and his associates suggests that an endogenous circannian rhythm, apparently independent of both external factors and internal feedbacks, exerts an important influence on all aspects of the ecology and physiology of these sciurid hibernators.

Simpson (1912) first reported that penned woodchucks failed to enter torpor in the autumn when supplied with abundant food. Davis (1966; 1967*b*) reported that woodchucks held under conditions of constant photoperiod and temperature, and supplied with food and water *ad libitum*, did not enter torpor, but showed a pronounced reduction of food intake during the calendar winter. In Davis' earliest observations (1966), woodchucks that ate about 35 grams per day in December and January increased food intake to 170 grams per day in the summer; food consumption decreased again in the autumn. Rhythmic variations in food consumption were reported also by Pengelley and Fisher (1963) for another sciurid hibernator, *Spermophilus lateralis*. Unlike *Marmota*, *S. lateralis* hibernated in the presence of abundant food; direct comparison of these two species is, therefore, of questionable value.

This paper presents data on the monthly food consumption of a naturally occurring population of woodchucks on a 10,000-acre tract of old fields and woodland at the Letterkenny Ordnance Depot in south-central Pennsylvania. Comparative data from a group of woodchucks confined in the laboratory

under constant temperature and photoperiod during the sampling period are presented also.

Detailed studies of woodchuck populations on the Depot during a 12-year period have provided information on the annual cycle in this region. Woodchucks emerge from hibernation in February and March—adult males first, females and yearlings a few weeks later (Snyder and Christian, 1960). Considerable fat is present at the time of emergence, but the fat depots are nearly depleted by May (Davis, 1967*b*). Breeding takes place in March; most young are born between 1 and 21 April (Snyder and Christian, 1960). In June, the young begin to leave their home dens and at this time become susceptible to live-trapping. Woodchucks exhibit more sociability and social interaction (of all types) during the spring than at other seasons; the allelomimetic component of their feeding behavior is highest during this season (Bailey, 1965*b*). Weight changes of adult woodchucks reflect changes in the amount of body fat. In late summer and early autumn, as much as 50 per cent of the body weight may be due to fat (Davis, 1967*b*). The metabolic activity of woodchucks increases in the spring and declines in the autumn; a maximum occurs in May (Bailey, 1965*a*).

The feeding patterns of free-living woodchucks in the Letterkenny populations were summarized by Davis (1967*b*). Woodchucks in the wild ate only green food; caged woodchucks supplied with mixed green and dry grass carefully picked out the green blades. Even starving chucks refused to eat dry grass. Stomachs collected from woodchucks in February by Shyder *et al.* (1961) were essentially devoid of food. In March, woodchucks fed on wild onions (*Allium* sp.) and later bluegrass (*Poa* sp.). The summer diet consisted of a variety of grasses, leaves and buds. In Pennsylvania, woodchucks retire to their winter dens in October or early November when green food is still abundant.

METHODS

During the period June 1966 to September 1967, all available woodchucks from an intensive live-trapping program were immediately confined for 5 to 7 days in single cages placed in an unheated barn. During the period of confinement, they were supplied *ad libitum* with pelletized lab chow and water. Two days were allowed for cage adjustment by animals before food intake figures were recorded. Food consumption was measured daily by counting spillage and weighing the food remaining in the pan, then subtracting this total from the amount of food given the previous day. Although this method was not highly accurate, a reasonable measure of actual food intake was obtained. A mean daily consumption based on 3 to 5 days was calculated. Following the period of confinement, woodchucks were released at the site of capture or were used in other experiments.

Food consumption records were separated for woodchucks of two age groups—young-of-the-year and adults. Because of possible influences of age on the annual feeding cycle, division of animals into several age categories would have been desirable. Unfortunately, available aging techniques (Davis, 1964) are inadequate for separating woodchucks older than 1 year. No differences in food consumption associated with sex have been reported in pervious studies and no major differences were apparent in the animals used in this study. Because some months were represented by small samples, data for males and females were combined for further consideration.

During 1967, the food consumption of one male and eight females was measured in the laboratory. Space limitations and availability of specimens dictated the number and sex of those measured. The group consisted of four 1-year-old animals, two that were 2 years old, and three that were 3 years old or older as of June 1967. These animals were held in individual cages in a windowless, air-conditioned room. Temperature was maintained at abuot 20°C; the photoperiod was maintained at 16 hours, the dark period at 8 hours. Laboratory chow and water were supplied daily *ad libitum;* food consumption was measured during the midmonth week for each woodchuck. Data were explessed both as a weekly total and as a mean in grams per day (only five of the nine woodchucks were available for the November sample). Prior to the time the data were recorded, these woodchucks had been maintained under the same constant conditions in the same laboratory for periods of at least 6 months and had never become torpid in captivity (woodchucks were usually brought to the laboratory colony a few days after they were trapped at the Ordnance Depot).

Results and Discussion

Measurements of the consumption of food (Fig. 1) of recently-trapped woodchucks revealed pronounced seasonal variation. The mean consumption of two March-trapped adults was 106 grams per day. In May, 15 adults had a mean consumption of 254 grams per day. By October, the mean consumption of a sample of 15 adults had declined to 146 grams per day. A similar pattern was found among the monthly samples of juveniles. In June, 15 young woodchucks had a mean consumption of 107 grams per days; this increased to 260 grams per day in July (four specimens) and declined in October to 122 grams per day (13 specimens).

Similar seasonal changes (Fig. 2) were found also in the nine woodchucks maintained under constant conditions in the laboratory, corroborating Davis' (1966) previous report. The woodchucks maintained in the laboratory consistently ate less food and gained more weight than those recently trapped, reflecting the low energy demands of cage-adapted animals.

The major difference apparent between the adults and juveniles in Fig. 1 is the time at which maximum consumption was reached. In the juveniles, maximum food consumption was reached in July; a May maximum was found for the adults. The timing of the juvenile group was predictable, because most young woodchucks are not weaned until late May and undergo their greatest period of growth in June and July.

The maximum food consumption of the laboratory group (Fig. 2) occurred in June—intermediate to the adults juveniles from the natural population. Assuming these maxima are real (an assumption with some difficulties considering the large standard errors of the monthly means), a possible explanation for this pattern of divergence lies in the length of the circannian rhythm. Although no longterm studies of individual woodchucks are presently available, preliminary observations on several woodchucks held under laboratory conditions for three seasons indicate that maximum weight (and presumably maximum food consumption) occurred about 2 weeks earlier each year. If such a shift occurs in all the rhythms to which woodchucks are apparently

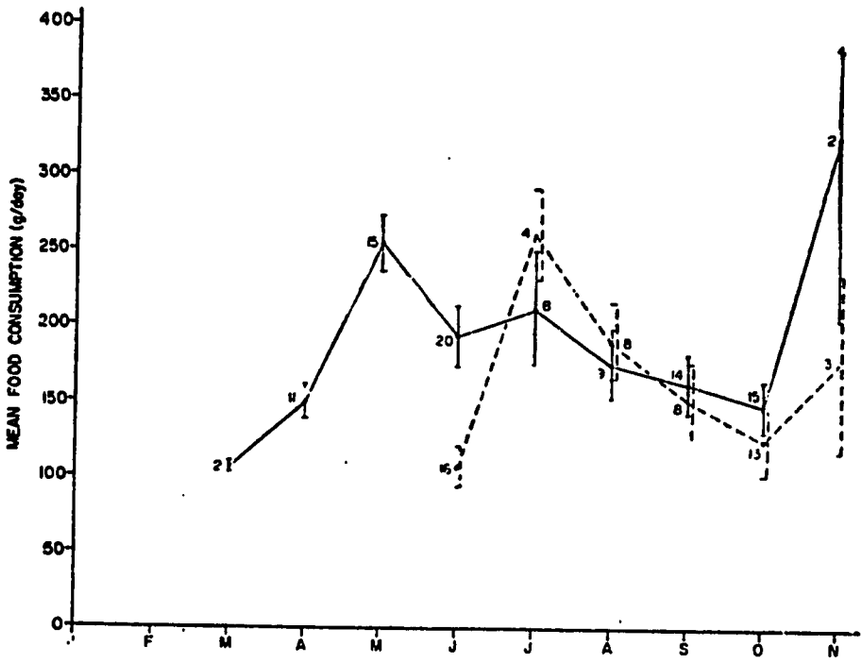

FIG. 1.—Changes in the food consumption of adult and juvenile woodchucks obtained from natural populations in south-central Pennsylvania and caged for 5 to 7 days for measurement. The number tested is indicated at each point. The standard error is given by bars around each point. The data for juveniles are shown by the dashed line.

subject, it could also explain the earlier emergence of older adults in the spring (Snyder and Christian, 1960) and the tendency of juvenile woodchucks to be the last afield in late autumn (Hamilton, 1934). The woodchucks in the laboratory group (mean age about 1.9 years) probably averaged much younger than the adults taken from the natural populations. The order of the maxima of food consumption in the three groups (juvenile, July; lab groups, June; adults, May) thus appeared consistent with the hypothesis that the period of this seasonal rhythm in woodchucks is somewhat less than 1 year.

The significance of the November increase in the food intake of the trapped adults and juveniles is difficult to evaluate. In November, most woodchucks have retired to their winter dens; few test animals could be obtained in that month, despite intensive trapping. The possibility exists that animals trapped in late autumn are diseased or are in some other way abnormal in comparison with the remaining population. The test animals, however, appeared healthy and normal except in respect to their higher food intake. In the laboratory group, six of the nine test animals also exhibited a temporary autumnal increase in food consumption. These observations taken together with Bailey's

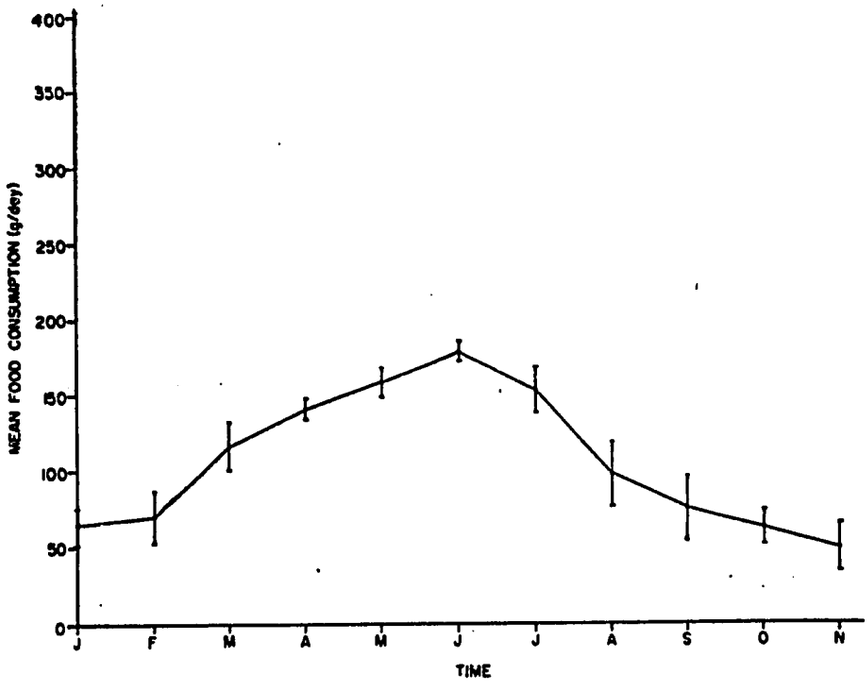

FIG. 2.—Changes in food consumption determined during midmonth weeks for nine woodchucks caged under conditions of constant photoperiod (16 hours light, 8 hours darkness) and temperature (20°C). The standard error is given by the bars around each point. Only five of the nine woodchucks were available for the November sample.

(1965*a*) report of an autumn increase in the metabolic activity of woodchucks, suggest that a true change in feeding behavior of this species occurs in autumn, prior to the onset of hibernation.

Because of wide variation between individuals in the magnitude of food intake and the apparent lack of environmental synchronization of the rhythms of woodchucks (Davis, 1967*a*), a damping effect was introduced by grouping data taken simultaneously from several specimens. More meaningful information can probably be gained by studying the progression of rhythms in the same individual over a period of years under controlled conditions. The consistency of the circannian rhythms of food consumption from laboratory and field groups, when synchronization differences are accounted for, support this approach.

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