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Environmental and Endogenous Control of Reproductive Function in the Great Basin Pocket Mouse Perognathus parvus

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ABSTRACT

Pocket mice captured in the field at various times of year were introduced into laboratory experiments to examine the short-term sensitivity of reproductive function to environmental factors, principally day length, and the tendency of the reproductive system to become active spontaneously over longer durations. Spontaneous enlargement and partial activation of the gonads occurred over the course of 4–5 mo in continuous darkness during the hibernation season. Males held for 13 mo in 12L:12D showed patterns of testicular enlargement, but with only partial regression; the degree of endogeneity in the reproductive control system of *P. parvus* is therefore considerably below that of the pronounced and persistent "endogenous circannual rhythms" shown by certain rodents of the squirrel family. Responses to day length varied seasonally. The partially activated reproductive system of mice that emerged from hibernation in spring was further stimulated by long days (16L:8D); in summer gonadal growth was insensitive to differences in day length, and in autumn the gonads remained undeveloped in short days (8L:16D) but were sensitive to stimulation by long days. This "photoperiodic" response of *P. parvus* is based on an endogenous circadian rhythm of photosensitivity as proposed by Bünning (1936). We also found that reproductive function of *P. parvus* is somewhat retarded by low temperature and reduced availability of water. We discuss the general nature of environmental sensitivity of reproductive function and the ways in which the photoperiodic response and spontaneous pattern of winter gonadal development in *P. parvus* are likely to interact with environmental factors that lead to fine-tuning the final reproductive response.

INTRODUCTION

Seasonally breeding mammals possess physiological mechanisms that ensure the coordination of reproductive efforts with times when environmental conditions are generally most favorable for reproduction (Sadleir, 1969). At the gross level of control these mechanisms may involve action of predictive environmental cues upon the endogenous condition of the animal to initiate preparation of the reproductive system for the anticipated breeding season.

Predominant among these cues are seasonal changes in day length, which have been observed to activate and deactivate reproductive function under experimental conditions (Farner et al., 1973; Hoffmann, 1981). However, it is also clear that some of the rodent species that show such a "photoperiodic" response are also capable of spontaneous gonadal activation following the inhibition that occurs during prolonged exposure to short days in winter (Johnston and Zucker, 1980; Reiter, 1980; Zucker et al., 1980; Bartke and Parkening, 1981). In addition, certain rodents in the squirrel family show persistent, endogenous annual cycles of gonadal development and regression in the total absence of seasonal changes in day length or other environmental cues (Kenagy, 1980; 1981a,b). Potentially breeding animals that are initially stimulated by predictive cues should also show further sensitivity—at a level beyond that of gross-level control—to prevailing nutritional, energetic, social, spatial, thermal and other factors. Recent studies have emphasized the importance of the interactions within this complex of factors that are involved in the final adjustments of the natural reproductive response (Bronson, 1979; Wingfield, 1980; Pryor and Bronson, 1981).

We report here experiments with a hibernating and seasonally breeding desert rodent, the Great Basin pocket mouse, *Perognathus parvus*, of the family Heteromyidae. We address primarily the issue of gross-level seasonal regulation of reproduction and then discuss the fine-tuning of the final response. Whereas inbred lab-

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oratory species are useful models for examining a regulatory phenomenon such as the response of reproductive function to a single factor like day length, animals taken from a natural population offer the potential advantage of a full spectrum of sensitivities and responses to natural factors. All our experiments examine reproductive function in the laboratory in mice that we caught in the field.

Perognathus parvus is a common rodent of semiarid sagebrush steppe in interior western North America (Hall, 1981). These pocket mice, which mostly consume seeds but also eat green vegetation when available, hibernate for about 4 mo in winter and begin to reproduce in early spring (O'Farrell et al., 1975). Laboratory data on three other species of *Perognathus* suggest that some kind of "photoperiodic" element is involved in control of the reproductive cycle (Hayden et al., 1965; Ostwald et al., 1972; Kenagy and Bartholomew, 1981). These studies also suggest enhancement of reproductive condition by succulent green food, low temperatures (associated with torpor) in winter, and contact with potential mates. Our studies with *P. parvus* provide an examination of the response to day length, including a test of the Bünning hypothesis, which states that the photoperiodic reaction operates through an endogenous daily rhythm in sensitivity to light (Bünning, 1936; Elliott and Goldman, 1981). We also test for endogenous programming of gonadal growth.

MATERIALS AND METHODS

General Procedures

Adult mice were captured in the field, divided into groups and exposed to various experimentally controlled conditions in the laboratory. Reproductive condition was evaluated by autopsy. Animals were trapped between September 1976 and September 1980 in sagebrush-scrub habitat at three localities (near to 47°N Lat., 120°W Long.) in the eastern Washington counties of Kittitas, Benton and Walla Walla. For each experiment, animals were captured from the same area within a maximum of 3 days and transported to the University of Washington for study. A control sample was autopsied at the beginning of experiments; a terminal control sample was obtained from the field near the end of some experiments. In some experiments, mass of both testes was estimated in live animals from measurements of length and width of a single testis that was exposed by a surgical procedure as described elsewhere; the equation used to estimate testes mass, in mg, with an accuracy that we have determined to lie within 5% of the true mass, is $M=1.180\ (l \times w^2) - 1.263$ (Kenagy, 1979). Smears of the cauda epididymidis were examined under a microscope for motile spermatozoa. We found the appearance of epididymal sperm to coincide generally with the attainment of a mass of both testes between 80 and 100 mg. Masses of tissues were compared statistically by the Mann-Whitney *U* test (Siegel, 1956).

Except as noted below, each pocket mouse was individually housed in a 28 × 17 × 13-cm plastic cage containing a bedding of wood shavings and sand, and a wooden nest box measuring 11 × 11 × 8 cm. The staple food, provided ad libitum, was a commercial seed mix ("parakeet seed") consisting of 65% millet, 25% canary grass, and 10% oat groats. Except as noted, fresh Romaine lettuce was provided three times a week, and no animals were provided with water bottles. Mice were held in animal rooms with temperatures of 23 ± 2°C, except for two experimental groups that were held at 10 ± 0.5°C in walk-in controlled-environment chambers. Photoperiodic regimens of 8L:16D, 12L:12D and 16L:8D were produced with clocks that controlled the overhead fluorescent lighting. Light intensity beneath the wire cage tops ranged 100–400 lx. Some groups were held in continuous darkness (DD) in light-sealed chambers; maintenance of these animals was facilitated with a dim red light. The seasonal differences in effect of photoperiod (Fig. 1) were investigated over a period of 2 yr; spring experiments were conducted in 1977, early summer in 1979, later summer in 1977, and fall in 1978.

Test for Endogenous Annual Rhythmicity in 12L:12D

Thirteen pocket mice were held in a photoregimen of 12L:12D and at 23 ± 2°C for up to 13 mo from September 1977 to October 1978, with a diet of seeds and lettuce. Four of these animals (Numbers 7–10) had been captured on May 1, 1977 and held in 8L:16D until September 24, and the rest were captured on September 23. Ten of the mice were individually housed in small cages (26 × 9 × 10 cm) and had access to a running wheel of 30 cm diameter, from which the daily rhythm of locomotor activity was recorded with an Esterline-Angus event recorder. During the photophase, light intensity was 10–200 lx in the running wheel cages. The other mice were housed in simple cages as described above. Length and width of a surgically exposed testis were measured to the nearest 0.1 mm on about the 4th day of each month beginning in October 1977.

Test of the Bünning Hypothesis

In early summer 1979 groups of newly captured animals were exposed to the following six photoperiods: 6L:6D, 6L:18D, 6L:30D, 6L:42D 6L:54D and 6L:66D, to test the Bünning hypothesis of the role of circadian rhythms in photoperiodic seasonal responses. For further details of this experimental paradigm see Nanda and Hamner (1958). One group each of 8 adult males was placed in each of 6 chambers (123 × 91 × 93 cm). Four individuals in each group had access to running wheels as described above; all the other animals were individually housed in 3.8-l glass jars. During photophase each chamber was illuminated by 6 clear 7-watt lamps (GE 7C7) attached along a single lamp cord hanging from the center of the chamber. This arrangement delivered an intensity of 60–200 lx in the jars, 20–27 lx in the running wheel cages, and 2–3 lx in the running wheels. The

four longer light:dark cycles were timed with Industrial Timer model CM-12 recycling timers; power in parallel to the lights operated a relay that closed an event recorder circuit in order to verify the light:dark cycles graphically. Each chamber was closed with a light-tight seal, and air circulation was maintained through baffles with a 15 CFM ventilator. These chambers were opened for maintenance only during their respective photophases.

RESULTS

Effects of Day Length in Spring, Summer and Fall

The season at which pocket mice were captured in the field influenced the responsiveness of reproductive function in the laboratory to differences in photoperiod (Fig. 1). In early spring, following emergence from hibernation, male pocket mice had well-developed testes (about 2/3 maximal mass) but undeveloped seminal vesicles. Males captured in spring and exposed for 50 days to 16L:8D had significantly larger testes (P=0.041) and seminal vesicles (P=0.004) than those exposed to 8L:16D (Fig. 1). The seminal vesicles of animals in 8L:16D remained essentially inactive despite the presence of spermatogenic testes, whereas seminal vesicles of spring animals in 16L:8D showed the greatest size of any experimental group in the entire study. Males captured in early summer did not maintain reproductive function when brought into the laboratory, whether in long or short day lengths (Fig. 1). Animals captured in August were reproductively quiescent, but initiated testicular growth within 60 days in both long and short photoperiods (Fig. 1). Two additional groups captured in August also showed the same level of initial testicular development after 60 days, in DD (continuous darkness; 66 ± 9 mg, n=7) and in LL (continuous light; 70 ± 5 mg, n=7).

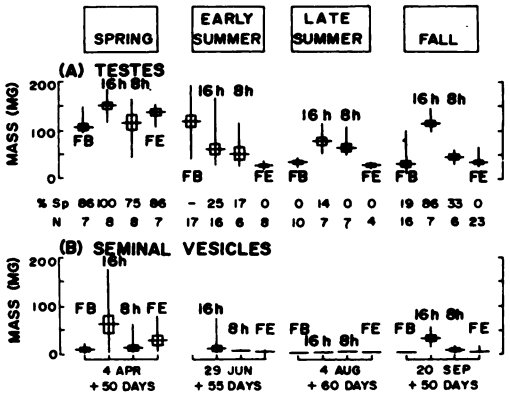

FIG. 1. The effects of day length on (*A*) mass of both testes and (*B*) mass of seminal vesicles at four seasons. Experimental animals were freshly captured in the field, held at 23°C, and exposed to either 16 h light daily (16L:8D) or 8 h light (8L:16D) for about 50 days. *FB* represents a field sample obtained at the beginning of the experiment, and *FE* represents a sample obtained from the field near the end of the experiment. Proportion of animals with epididymal spermatozoa (*% Sp*) and sample size (*N*) are given beneath panel *A*. For the early summer FB sample, testis mass is estimated from measurements of length and width on 17 randomly selected live males, as described in *Materials and Methods*. *Horizontal lines* are means, *vertical lines* are ranges, and *rectangles* represent ± 1 SEM.

Whereas testes and seminal vesicles remained essentially undeveloped in 8L:16D and in the field, the growth of these organs in 16L:8D was substantial, and all but one of the animals showed spermatogenesis.

Spontaneous Development in Winter Darkness and Subsequent Environmental Sensitivity

To investigate the course of testicular development during the wintertime, when *P. parvus* usually hibernate in their dark subterranean nests, we captured mice in early September, held them for as long as 164 days in continuous darkness (DD) at 23°C, and killed groups at intervals to monitor reproductive condition. Mass of testes increased in DD from 25 mg to nearly 100 mg, and spermatogenesis was initiated over the course of 136 days, but both had declined by 164 days (Fig. 2). Testes at 136 days were as large as those of animals captured in the field in spring soon after emergence from hibernation (cf., Fig. 1).

Early transfer, on December 6, of some of the mice from DD to 16L:8D and 8L:16D for 56 days led to no increase in mass of testes (or seminal vesicles) over that of animals that remained in DD (Fig. 2). In fact, the mice exposed to 8L:16D showed a reduction of seminal vesicles to a size (5.3 ± 1.8 mg, n=6) that was significantly smaller than that of mice in 16L:8D (28.9 ± 10.6 mg, n=9; P=0.022).

Test for Endogenous Annual Rhythmicity

The long-term course of testis size in

12L:12D, as measured monthly in individual *P. parvus*, showed an initial increase during fall (Fig. 3) like that of mice held in continuous darkness (Fig. 2). Thereafter, individual trends differed and testes generally remained within an intermediate, but spermatogenic size range; however, there were conspicuous excursions above and below the 80- to 100-mg threshold for spermatogenesis within the group throughout the year (Fig. 3). There was no conspicuous seasonal cycle in body mass, which remained within a 2- to 3-g range in most individuals throughout the experiment. Similarly, there were neither systematic nor consistent changes in duration of daily wheel-running activity; no fluctuations in daily duration of activity could be correlated with the seasonal fluctuations of testis size. Although the data are suggestive of a crude endogenous periodicity of testis size, it is clear from the irregularities in these patterns and the lack of full regression that *P. parvus* does not have a marked, high-amplitude annual rhythm of testis size.

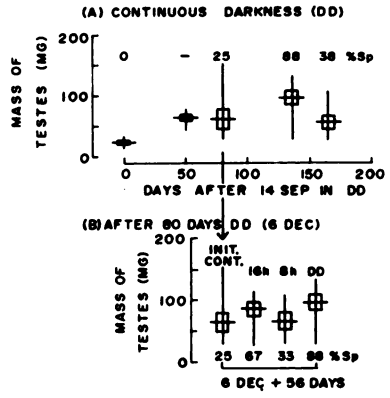

FIG. 2. Spontaneous testicular development of *P. parvus* in fall and winter, 1979–1980. *A*) Development of testes in continuous darkness at 23°C over the course of 164 days, beginning September 16. Each sample=8 mice. *B*) Development of testes in animals held initially for 80 days in DD (until December 6) and then exposed to either 16L:8D (n=9) or 8L:16D (n=6) for 56 days; initial and final controls in *B* are repeated from Days 80 and 136, respectively in *A* above. All data were obtained by autopsy of randomly selected individuals except for data of November 6 (50 days in DD), which are estimates of mass based on measurements of length and width of testes in 8 live animals examined surgically, as described in *Materials and Methods*.

Test of the Circadian Rhythmic Basis of the Photoperiodic Response

P. parvus exposed to six different ahemeral light:dark cycles showed that testicular responsiveness to change in photoperiod depends upon the relationship between the light:dark cycle and an endogenous circadian rhythm (Fig. 4). When the experimental animals were captured in the field in June, testes of adult males had not yet regressed, and thus our experiment was

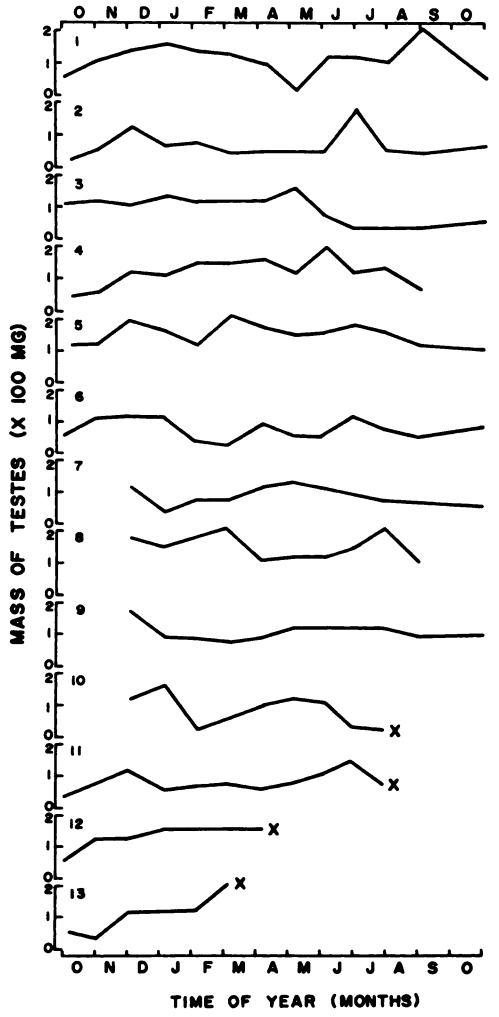

FIG. 3. Seasonal course of testis size in individual *P. parvus* held continuously for as long as 13 mo in 12L:12D at 23°C. Monthly values for mass of both testes are estimated from measurements of length and width (in mm) of surgically exposed testes, according to the relationship $M=1.180\ (1 \times w^2) - 1.263$ (see *Materials and Methods*). X=Death of animal.

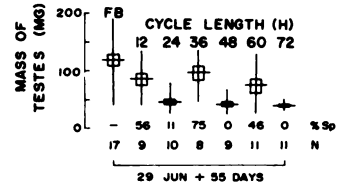

FIG. 4. Response of testes of adults to photocycles of 12, 24, 36, 48, 60 and 72 h duration, each containing 6 h light per cycle. Experiment began on June 29, 1979 and continued for 55 days. The initial mass of testes (*FB*) is estimated from measurements of length and width on 17 live males, as described in *Materials and Methods*. Durations of the six experimental cycles are indicated above final values for mass of testes.

performed on the role of long day length in maintaining reproductive condition versus short day length in allowing or promoting regression of reproductive function. After 55 days of exposure to six different ahemeral photocyles, animals in three of the cycles (12, 36 and 60 h, each with 6 h light) had maintained significantly larger testes and epididymides ($P<0.05$) than animals in the other three cycles (24, 48 and 72 h, each with 6 h light). Of 30 animals in the three inhibitory cycles (24, 48, 72 h), only one, in 24 h, still had epididymal sperm, whereas 16 or 27 animals in the stimulatory cycles (12, 36, 60 h) maintained sperm production (Fig. 4).

We also measured the entrainment of the daily rhythm of wheel-running activity to each of the six photocycles in 4 individuals each. Locomotion in 92% of these cases (22 of 24 individuals) showed at least some degree of circadian (ca. 24-h) periodicity, with entrainment to the photocycles. In the three stimulatory cycles (12, 36, 60 h) activity generally began 6–7 h before 24-h multiples of lights on, whereas in the three nonstimulatory cycles (24, 48, 72 h) activity began 9–11 h before 24-h multiples of lights on.

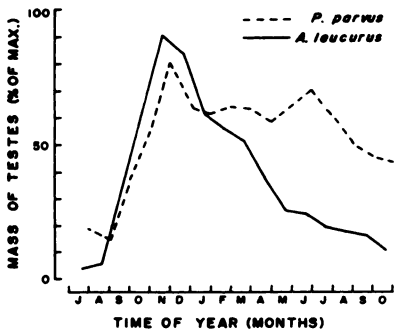

FIG. 5. Comparison of the long-term course of testis size in *P. parvus* and the antelope ground squirrel, *Ammospermophilus leucurus* under identical conditions of 12L:12D and 23°C. Data for *P. parvus* are the average for Animals 1–9 in Fig. 3 plus values for the initial 2 mo taken from the field (Kenagy, unpublished data); data for *A. leucurus* are for 12 animals, redrawn after Fig. 5 in Kenagy (1981b). Mass of both testes is normalized in both species as a percent of the maximum annual mean shown by a field population: *P. parvus* 0.171 g and *A. leucurus* 2.136 g (Kenagy, unpublished data).

Effects of Other Factors—Temperature and Green Food

The response of male reproductive function was sensitive to temperature at the level of seminal vesicles but not testes. A group of 7 mice exposed in fall to 16L:8D at 10°C did not differ significantly ($P=0.203$) in mean mass of testes (92 ± 14 mg) from the 23°C group that underwent testicular development (Fig. 1); however the seminal vesicles of the cold-exposed group (13 ± 5 mg) were significantly smaller ($P=0.006$) than those of the 23°C group (Fig. 1, *FALL*).

Male *P. parvus* were clearly capable of reproductive development on an exclusive diet of seeds with neither lettuce nor drinking water available. Testing groups of 9 mice in fall 1980, we found that although the mean masses of testes and epididymides were smaller in the lettuce-deprived group (66 ± 8 mg; 6 ± 2 mg) than in a group fed with seeds and lettuce in 16L:8D (83 ± 13 mg; 15 ± 6 mg), that these differences were not significant ($P>0.05$). Females in 16L:8D showed a response to the availability of lettuce with their seed diet in a 30-day test in fall 1976, that consisted of significantly larger ovaries ($P=0.041$) in those receiving lettuce with their seeds (2.6 ± 0.2 mg, n=8) than in those with seeds only (2.1 ± 0.2 mg, n=6). These responses to a diet with lettuce, like those of a previous study with *P. formosus* (Kenagy and Bartholomew, 1981) are more likely related to the water value of lettuce than to some other nutritional factor.

DISCUSSION

Annual Cycle and Its Control in Nature

Reproductive function in *P. parvus* is con-

trolled by interactions between seasonally dependent responsiveness to the environment and spontaneous (endogenous) gonadal growth. Under natural conditions the mice cease aboveground activity in autumn and begin to hibernate, during which the reproductive system begins to develop in continuous darkness. This pattern of spontaneous recrudescence is expressed experimentally (actually accelerated ahead of the normal schedule) in long days but retarded in short days. Animals emerge from hibernation in spring having already undergone partial gonadal development. Long days at this time stimulate the completion of reproductive activation, especially the accessory tissues. The influence of soil temperatures on termination of hibernation and onset of reproduction has been shown under natural conditions in pocket mice (Kenagy and Bartholomew, submitted for publication); low temperatures extend hibernation and higher temperatures allow emergence from hibernation and onset of reproduction.

By summer *P. parvus* is generally insensitive to stimulation by long days, suggesting a "refractory" phase in the control system; short days in summer experimentally accelerate gonadal regression. This clearly is not an obligate response, however, because in nature *P. parvus* has a prolonged reproductive season in years of great environmental productivity; in such cases the usual mode of reproductive control is apparently overridden. Adults may remain reproductively active until fall, and juveniles are able to come into breeding condition in the year of birth (Speth et al., 1968; O'Farrell et al., 1975; Kenagy, unpublished observations). We have not been able to produce these effects by experimental enhancement of diet and social contact in the laboratory (Kenagy and Barnes, unpublished observations).

Gross-Level Control and Fine-Tuning of Reproduction

In *P. parvus* the spontaneous development of the gonads during winter is a major component of a gross-level mechanism of control that initiates preparation for reproduction. A consistent yearly scheme for control of the initial preparation for reproduction is advantageous because this preparation requires a lead time prior to the time when the animals can finally assess prevailing springtime conditions. The eventual springtime environmental conditions elicit final adjustments ("fine-tuning") and completion of the reproductive response. A second component of the gross-level control of reproduction consists of the interaction of the process of spontaneous gonadal growth with the general environmental conditions (probably in the previous summer or fall and probably consisting of some combination of day length and temperature) that serve to initiate and synchronize the program of gonadal growth in the first place.

The fine-tuning of initial reproductive development involves completion of gonadal maturation and development of accessory structures such as the seminal vesicles and patterns of behavior associated with mating. Fine-tuning of reproduction in *P. parvus* should consist of responses to weather, environmental productivity including quantity and quality of food, and the accessibility of mates. We have, so far, only superficially investigated some of these effects.

Influence of Day Length on Reproduction

The control of reproduction in *P. parvus* can be characterized as "photoperiodic," with an endogenous circadian rhythm of photosensitivity as its basis, and with an additional component of crude endogenous programming associated with recrudescence of gonads during winter. Photoperiodic responsiveness has previously been reported for *P. formosus* (Kenagy and Bartholomew, 1981). Suggestions of endogenous annual rhythmicity are apparent in data on two other species of *Perognathus* (Hayden et al., 1966; Ostwald et al., 1972). However, no previous study has included an evaluation of the several kinds of observations that we present here: manipulations of day length, a test for the role of circadian rhythmicity in the photoperiodic response (Nanda and Hamner, 1958), and long-term exposure of animals to continuous darkness and to constant photoperiodic conditions. This series of observations shows a pattern of "photoperiodism" that is complex and apparently less pervasive, but nonetheless consistent with that of other photoperiodic rodent species (Zucker et al., 1980; Hoffmann, 1981).

Because seasonal change in photoperiod is a reliable predictive cue to seasonal change in environmental conditions in general and because so many vertebrates and mammals in particular have been shown to exhibit responses of reproductive function to change in day length

(Farner et al., 1973; Hoffmann, 1981), it is often considered that such a reaction is a wide-spread and fairly simple stimulus-response phenomenon. The seasonal change in the control scheme and response of *P. parvus* to light and dark is somewhat more complex than this. The summer insensitivity of *P. parvus* to differences in photoperiod appears similar to the stage of photorefractoriness that characterizes some photoperiodic rodents (Stetson et al., 1976; Turek and Losee, 1979; Bittman and Zucker, 1981), as originally described in birds (for review see Farner and Follett, 1979). This refractory period is followed in *P. parvus* by activation of the gonads in winter; however photoperiodic sensitivity is clearly reestablished by autumn and one can interpret these results either as an acceleration of spontaneous recrudescence by long days or a suppression by short days. This result is the opposite to the effect of photoperiod on chipmunks (*Eutamias* spp.), in which spontaneous testicular recrudescence in winter in inhibited or even abolished by 16L:8D but is permitted by 8L:16D (Kenagy, 1981a).

The growth of the gonads during constant darkness in winter and the variable gonadal growth and partial regression during 13 mo in 12L:12D demonstrate a spontaneous component in the gross-level control system of *P. parvus*. This is similar to the spontaneous recrudescence following exposure to short photoperiods in a variety of rodent species of the family Cricetidae (Reiter, 1975; Johnston and Zucker, 1980; Zucker et al., 1980; Bartke and Parkening, 1981; Hoffmann, 1981). However, the lack of full amplitude and annual precision in the increases in gonadal size in both experiments with *P. parvus* and the lack of full regression in the 13-mo experiment demonstrate that the expression of gonadal growth and perhaps the endogenous mechanism itself are neither as exact nor as persistent as those observed in ground squirrels, chipmunks and related species of the family Sciuridae (Fig. 5) (Kenagy 1980, 1981a,b). Such "endogenous circannual rhythms" in squirrels are self-sustaining and repetitive, whereas we have not yet obtained evidence of such a condition in *P. parvus*. The role in photoperiodic species of "spontaneous processes" like those found in the annual reproductive rhythm of *P. parvus* has until recently received little attention (Reiter, 1975; Farner and Gwinner, 1980; Hoffmann, 1981) and remains poorly understood.

It is interesting that the removal of pocket mice from continuous darkness and exposure to long and short days in early winter resulted in no significant enhancement of gonadal activation above the rising level in DD. That there were some differences between the groups exposed to long and short days (seminal vesicle development) illustrates that differential photoperiodic sensitivity was being maintained or developed further at that time. It has been suggested that photosensitivity of golden hamsters develops during prolonged exposure to nonstimulatory conditions (Turek et al., 1975). In this context it is remarkable that our *P. parvus* exposed in winter to light:dark cycles showed no greater gonadal development than did the animals that remained in DD, despite their renewed photosensitivity (Fig. 2B).

That the photoperiodic response of *P. parvus* is based on a circadian rhythm of photosensitivity reconfirms the phenomenon generally designated by the Bünning hypothesis. This states that reproductive responsiveness to change in photoperiod depends upon the relationship between daily time of exposure to light and an endogenous circadian rhythm that is entrained by the light:dark cycle (Elliott and Goldman, 1981; Pittendrigh, 1981). Although the now well-known hypothesis of Bünning (1936) is suspected to be of widespread importance in organisms as diverse as mammals and plants, it has still only been confirmed in about half a dozen mammalian species, now including *P. parvus* (Elliott and Goldman, 1981; Almeida and Lincoln, 1982; Nelson et al., 1982; Whitsett et al., 1983). Because of this observation in *P. parvus*, it is expected (Pittendrigh, 1972) that the role of the light:dark cycle is both to entrain the circadian rhythm of sensitivity to light and to induce the reproductive response, depending on the duration of coincidence of light with a critical segment of the circadian rhythm of photosensitivity. In addition to these roles of light in the basic photoperiodic response, the light:dark cycle almost certainly must play some role in setting or entraining the winter program of gonadal growth in *P. parvus*. For some of the few species known to possess strong, endogenous annual rhythms, it has been shown that the annual cycle of day length is the principal Zeitgeber of the annual rhythm (Gwinner, 1981).

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