

## Effects of Temperature and Light on the Locomotory Activity of Captive Pocket Gophers

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Geomyids are polyphasic with movement in simulated burrows recorded for all hours of a 24 hr cycle; particular troughs or peaks in times of locomotor activity were not evident. Total percentages of locomotory activity per day oscillated at separate levels for the three genera tested (one to ten percent for *Geomys*; 10 to 20 percent for *Thomomys*; and 30—40 percent for *Pappogeomys*). Temperature did not greatly effect the amount of locomotory activity or the length of extended locomotory activity periods. Light did not greatly effect total mean percent of locomotory activity; species or individuals within species were not consistently more active in either dark or lighted conditions, although certain days were skewed up to 50 percent in favour of either light or dark conditions. The multiplicity of factors involved in determining the duration and patterning of locomotory activity may center around metabolic demands, which in turn are influenced by soil porosity, precipitation, availability of preferred foods, inter- and intra-specific interaction (including breeding), and the diameter and length of burrow systems.

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### 1. INTRODUCTION

Geomyids are rodent moles living the majority of their existence subterraneanly. Therefore, although studies on the daily locomotory activity rhythms of extremely elusive fossorial mammals have been conducted (see Hickman, 1980 and references therein), it is not altogether surprising that only scattered notes (Vaughan & Hansen, 1961; Ross, 1980; Kavanau & Havenhill, 1976) were found on the locomotory activity of pocket gophers, one of the most intensively studied fossorial mammals.

Several studies have been conducted on the seasonal burrowing activity of geomyids (Miller, 1948; Miller & Bond, 1960; Hickman & Brown, 1973; and others) but despite some popular misconceptions, "surface mound formation" is not synonymous with "activity", and even burrowing activity may not be visible from the surface when excavated soil is distributed into abandoned tunnelways.

The present study reports on the locomotory activity patterns of representative species of the three genera of North American geomyids (*Thomomys*, *Geomys*, and *Pappogeomys*) under "normal" conditions of moderate temperature and darkness and investigates the effects of experimentally manipulated temperature and light extremes.

## 2. METHODS

Pocket gophers were captured during 1981 with Hickman (1979) live-traps: 13 *Thomomys talpoides* (Richardson, 1828) from Pitkin, Colorado, during October (six cm diameter traps); seven *Geomys bursarius* (Shaw, 1800) from Slaton, Texas, during September (eight cm diameter traps); and nine *Pappogeomys castanops* (Baird, 1852) from Lubbock, Texas, during October (11 cm diameter traps). Animals were acclimatized at 23°C in darkness and housed separately for a period of up to three weeks in 22.5 l plastic buckets containing soil, shredded newspaper, and vegetables before being transferred into the experimental apparatus between 10.00 and 12.00 hrs for the start of day one.

Locomotory activity was monitored with a transparent burrow system of perspex tubing (Hickman, 1978) and photocells positioned on the outside of the burrow so that the light beams intersected tunnelways (Hickman, 1980); red gel paper was positioned in front of the photocells making light beams less conspicuous. Movement through light beams was automatically recorded on an Esterline-Augus event recorder. Twenty-four hour time periods were subdivided into ten minute periods; the animal was considered active for the entire ten minute period, disregarding the number of times locomotory activity was recorded during the ten minutes.

For *Thomomys* and *Geomys*, 520 cms length of six cm diameter perspex tubing was connected to one nine cm<sup>2</sup> T-junction of perspex (Hickman, 1978) which served as a nest, and one 17 cm<sup>2</sup> chamber where food was placed. For *Pappogeomys*, a 60 cm length of 11 cm diameter clear perspex tubing was taped at either end onto 10 cm diameter, 40 cm lengths of opaque PVC plastic tubing. Two separate burrow systems (two concurrent trials, each monitored by two photocells and each housing a single pocket gopher of the same species) were constructed in a three m wide × 2.5 cm deep × 2.5 high environmental chamber where temperatures were maintained at 23, 28 and 13°C in darkness (three consecutive days per trial were run consecutively from moderate, to hot, to cold). Resetting at 23°C, various treatments of light (darkness, 7W red incandescent, and 60W white incandescent) were then applied from 600–1800 hrs, alternating with darkness from 1800 hrs — 1600 hrs (three days per trial in the sequence of dark, red, and white). Attempts at controlling humidity were thwarted by pocket gophers plugging tunnel openings with food and nesting which kept humidity within burrows at a high level throughout the various treatments of temperature and light. All tunnels and chambers were thoroughly cleansed before introducing new animals into tunnel systems, and establishing animals to new treatments of temperature and light.

## 3. RESULTS

Locomotory activity is presented as a percentage of ten-minute periods per 24 hrs that movement was recorded by photocells, facilitating analysis of locomotory activity in terms of circadian rhythms.

### 3.1. General Locomotory Activity

Polyphasic locomotory patterns were characteristic of *Thomomys*, *Geomys*, and *Pappogeomys* (Fig. 1). Movement was recorded for all ten-mi-

nute periods of the 24 hr cycle. Total percentages of locomotory activity per day oscillated at separate levels for each species: (approximate values were: *Geomys*, one to ten percent; *Thomomys*, 10 to 20 percent; and *Pappogeomys*, 30—40 percent. Peaks and troughs of locomotor activity deviated modestly (generally less than ten percent from the mean), and were not characteristic of any particular hour of the day (moderate troughs appear at 400 and 900 hrs). Synchronous locomotor activity was not noted for pocket gophers in separate but concurrent trials.

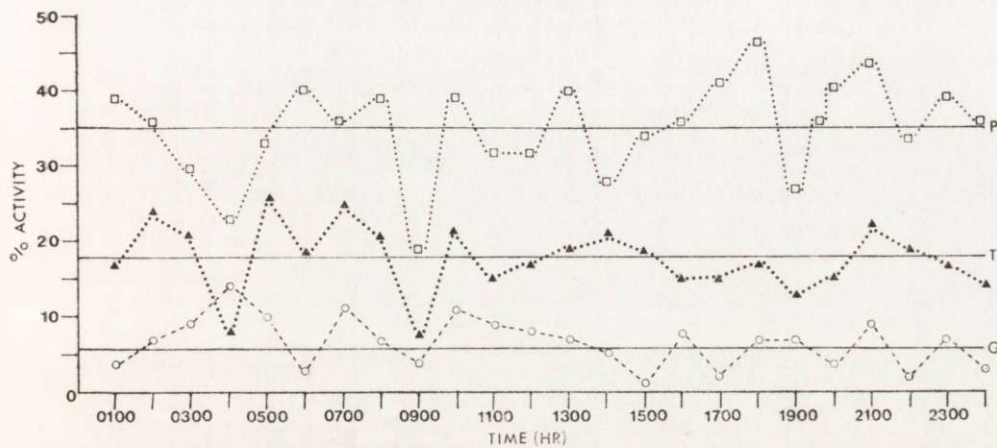


Fig. 1. Percentages of ten minute units per hour that individual *Thomomys talpoides* (12 days total for five animals), *Geomys bursarius* (15 days total for six animals), and *Pappogeomys castanops* (13 days total for five animals) engaged in locomotory activity while housed in plastic burrow systems at 23°C in darkness. Means for total percentages of locomotory activity for each species are indicated by unbroken lines.

Duration and time of locomotory activity periods under "normal" conditions of 23°C and darkness are presented in the following sections with reference to various treatments of light and temperature extremes.

### 3.2. Effects of Temperature

Total mean percent of locomotory activity at 23°C in darkness remained stable (ranges of four percent for *Thomomys*, three percent for *Geomys*, and ten percent for *Pappogeomys*) with an increase and decrease in temperature (Fig. 2). However, considerable individual variation was evident in some cases, and there was a distinct downward trend in total activity with time for approximately 41 percent of the animals tested under various temperature conditions.

Number of locomotory activity periods lasting more than a single ten minute period ("extended locomotory activity periods") were greater at higher temperatures (Fig. 3A), although there were wide fluctuations in number in some cases: 3.5 to 7.3 for *Thomomys* (range 2—8); 2.4 to

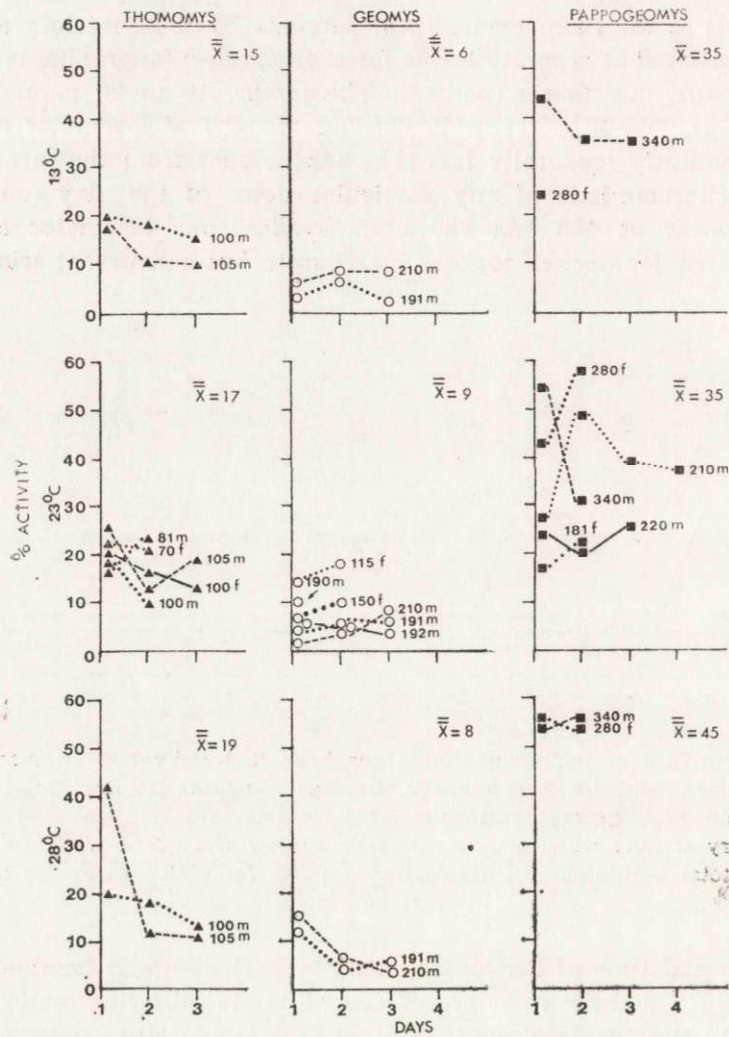


Fig. 2. Total percent of locomotory activity per day at varying degrees of temperature (23, 28, and 13°C) in darkness for individual (weight in grams and sex are indicated) *Thomomys talpoides*, *Geomys bursarius*, and *Pappogeomys castanops* housed in a plastic burrow system. Grand means for total percentage of locomotory activity per temperature treatment per species appears in the corresponding upper right hand corner for each graph.

3.3 for *Geomys* (range 2—6); and 9.0 to 15.0 for *Pappogeomys* (range 6—18).

Average length of extended locomotory periods fluctuated slightly (Fig. 3B), but overall range in length of locomotory periods (two to nine ten minute periods for *Thomomys*, two to seven ten minute periods for *Geomys*, and two to sixteen ten minute periods for *Pappogeomys*) remained almost constant.

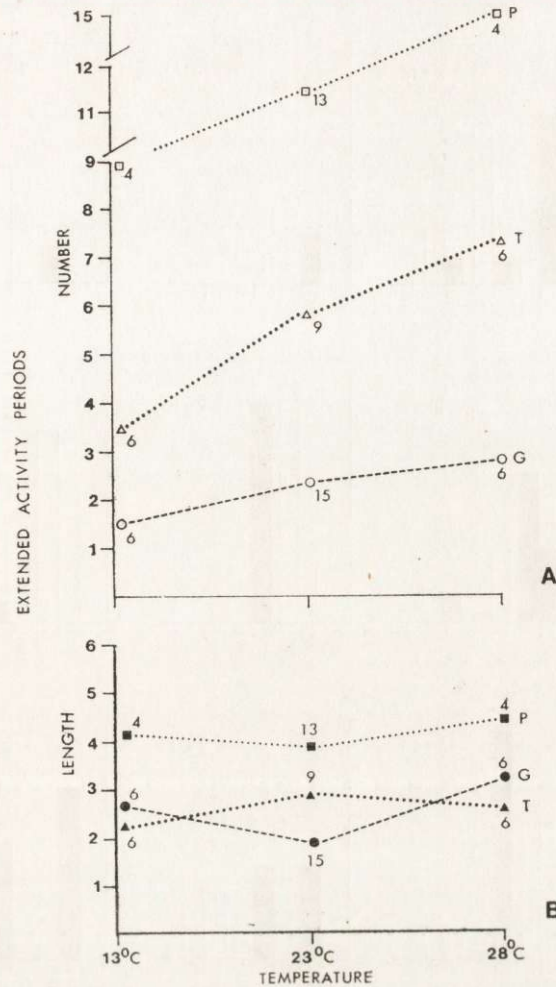


Fig. 3. Locomotory activity periods greater than a single ten-minute period (extended periods) for individual *Thomomys talpoides*, *Geomys bursarius*, and *Pappogeomys castanops* housed in a plastic burrow system at varying temperatures 13, 23, and 28°C under constant darkness. (Number of daily trials are indicated for each temperature treatment). A, above: total mean number; B, below: total mean length (number of consecutive ten minute periods).

### 3.3. Effects of Light

Total mean percent of locomotory activity at a constant temperature of 23°C in darkness between 1800 and 600 hrs remained generally unaffected (a change of five percent for *Thomomys*, one percent for *Geomys*, and eight percent for *Pappogeomys*) with different light intensities (7W red incandescent or 60W white incandescent light, Fig. 4). Species or individuals within species did not favour either dark or lighted conditions for locomotory activity although certain days were skewed up to 50 percent in favour of either dark or light conditions.

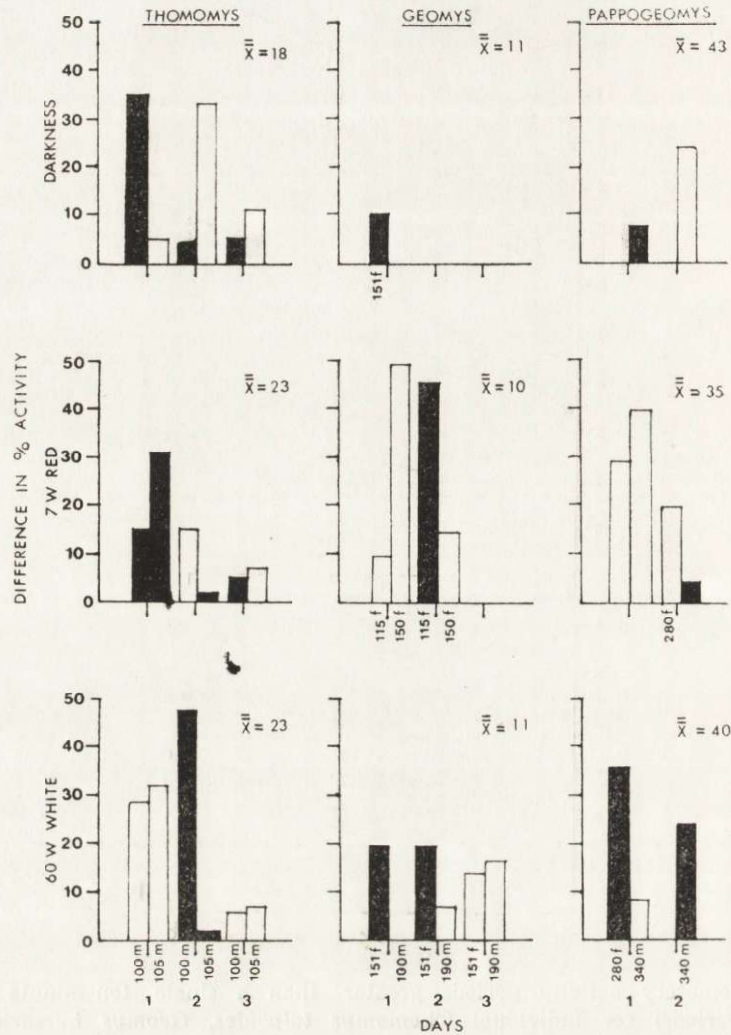


Fig. 4. Differences in total percent of locomotory activity of individual captive *Thomomys talpoides*, *Geomys bursarius*, and *Pappogeomys castanops* (weights in grams and sexes are indicated at the bottom axis unless a change in animals is indicated) alternating between periods of darkness from 1800—600 hrs (shaded bars), and periods of either: darkness, 7W red incandescent light, and 60W white incandescent light from 600—4800 hrs (unshaded bars) at a constant temperature of 23°C. Grand means for total percentage of locomotory activity per light treatment per species appear in the upper right hand corner of corresponding histograms.

Number of extended locomotory periods increased slightly for *Thomomys* at the more intense light treatments, but not for *Geomys* or *Pappogeomys* (Fig. 5A). The number of extended locomotory periods for dark rather than lighted conditions was less than one percent higher

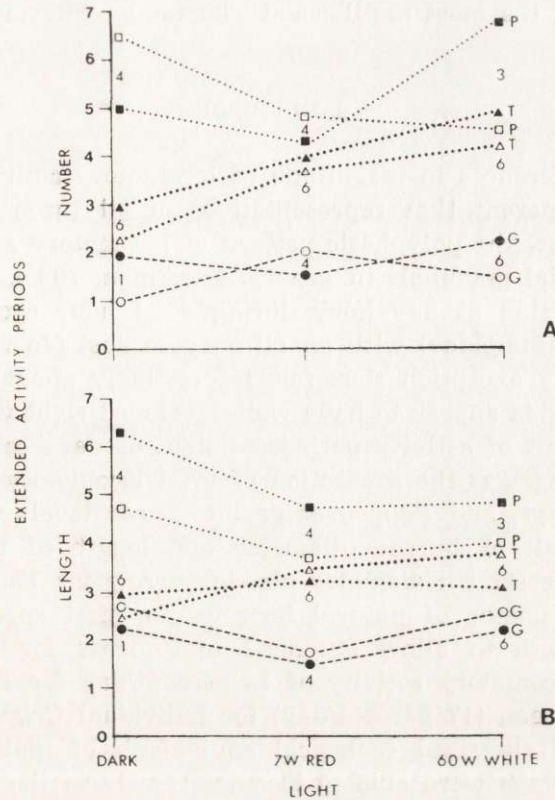


Fig. 5. Locomotory activity periods greater than a single ten-minute period (extended periods) for individual *Thomomys talpoides*, *Geomys bursarius*, and *Pappogeomys castanops* housed in a plastic burrow system during alternating conditions of darkness (1800—600 hrs, shaded points), and varying light treatments (600—1800 hrs, unshaded points) of total darkness, seven W incandescent, and 60W clear incandescent light at a constant temperature of 23°C. (Number of daily trials are indicated for each light treatment). A, above: total mean number; B, below: total mean length (number of consecutive ten minute periods).

for *Thomomys*; otherwise, the number of extended locomotory periods was not greater for either dark or light treatments.

Average length of extended locomotory periods also fluctuated slightly (Fig. 5B), with little difference in overall range for light and dark conditions (*Thomomys*, range two to seven ten minute periods for both light and dark; *Geomys*, range two to four ten minute periods for light, two to five ten minute periods for dark; and *Pappogeomys*, range two to nine ten minute periods for light, two to 12 ten minute periods for dark).

The three-tiered separation of number and length of extended locomotory periods under various treatments of temperature (Fig. 3) and light (Fig. 5) initially indicated for total percent of locomotory activity at 23°C (Fig. 1) was maintained, with *Geomys* being least motile;

*Pappogeomys*, the most motile; and *Thomomys*, intermediate in amount of motility.

#### 4. DISCUSSION

Despite differences in magnitude of locomotory activity between species, it is apparent that representatives of all three North American geomyids follow the polyphasic pattern of locomotory activity characteristic of fossorial mammals in general (Hickman, 1980), with locomotory activity occurring at any hour during a 24 hour cycle. *Tachyoryctes* (*Rodentia*, *Rhizomyidae*) with an all-purpose nest (Jarvis, 1973) appears to be the only exception thus far; interestingly enough, rhizomyids as well as geomyids appear to have well-developed sight which would enable entrainment of activity periods to light or dark conditions.

Most striking was the separation of total locomotory activity of *Thomomys*, *Geomys*, and *Pappogeomys* into three levels which may have been the result of burrow diameter and length of the experimental apparatus. The six cm diameter plastic burrow for *Thomomys* approximated the diameter of natural burrows for that species and was of sufficient length to allow extended movements for exploration. The mean total locomotory activity of 18 percent/day for *Thomomys* approximates the mean (17 percent/day) for individual *Cryptomys* (Hickman, 1980), a similarly sized ecological equivalent of mole-rat in Africa. Although *Geomys* were able to locomote freely in the six cm diameter plastic burrow and length of burrow permitted extended movements, normal burrow diameter approximated eight cms in the field so that the plastic burrows might have been inhibitive to movement. Ross (1980) felt that the activity periods of *Geomys pinetis* in his study (23 percent at 20°C) were probably underestimates of field activity due to the limited opportunity for foraging in terrariums. Vaughan & Hansen (1961) also noted a higher percentage of locomotory activity than the present study for *Geomys bursarius* housed in a wire cage (34 percent, range 25.9 to 47.3), compared to only six percent locomotory activity in the present study. *Pappogeomys* had the reverse problem of *Geomys*, with ten cm diameter plastic tunnels approximating the diameter of their natural burrows, but length of burrow was restrictive; movement was likely to have been exaggerated in such a confined area with extended efforts to escape. Although locomotory activity patterns of fossorial mammals in the laboratory may closely approximate conditions in the field (refer to the discussion in Hickman, 1980), it is apparent that care should be taken to simulate burrow diameter and allow adequate length of burrow when studying the locomotory activity of fossorial mammals in captivity.

Should the separation of locomotory activity into three distinct levels reflect an actual distinction in levels of locomotory activity between spe-



cies, it is difficult to suggest the cause. No correlation of locomotory activity was found with body size; *Geomys* is intermediate in size but was least active of the three species. Also, temperature and habitat were similar for *Geomys* and *Pappogeomys* which were trapped within fifty kilometers of one another in flat and dry areas of Texas grossly different from the cooler mountain habitat of Colorado, yet *Thomomys* was intermediate in mean locomotory activity. Similarities in anatomy and burrow structure (Hickman, 1977a) might be expected to neutralize some of the causes of differences in locomotory activity which do exist between the three species, although a wide range of even individual variation was found for all species tested.

The effects of certain variables such as temperature and light might be expected to exert a relative influence (positive, negative or neutral) similar in effect, if not in degree (keeping in mind the influence of captive conditions mentioned previously), to that of natural conditions.

#### 4.1. Effects of Temperature

Mean locomotory activity for all three species was not much different for each three day trial at 13, 23, and 28°C. Nonetheless, level of locomotory activity did decrease in some cases after an initial first day of high locomotory activity, perhaps reflecting an escape response triggered by unfavourable conditions (particularly for *Thomomys* and *Geomys* at 28°C; *Pappogeomys* was monitored for only two days, perhaps insufficient time to progress beyond heightened initial exploration. Ross (1980) studying *Geomys pinetis* found an eight percent decrease in locomotory activity with an eight degree centigrade increase in temperature for March caught animals. Activity may be inhibited to a small degree by moderate temperature fluctuation, but all species of pocket gopher in the present study remained active. *Thomomys* may even be found at times on the surface (Howell, 1922) and will often burrow in snow (Marshall, 1941). Moreover, it is unlikely that the very low percentages of locomotory activity recorded for *Geomys* would have permitted sufficient gathering of food for survival in the wild; however, food caches are a regular feature of the burrows of some species of pocket gophers (Hickman, 1977a).

The number of locomotory activity periods increased at higher temperatures, while the length of extended locomotory activity periods remained stable. *Spalax* (Rodentia, Spalacidae) in Israel was found to have a smaller number of locomotory activity patterns in cooler climes, and was more active during the day when temperatures might be expected to be higher (Nevo *et al.*, 1982). Increasing the number of extended locomotory periods would generate metabolic heat, particularly when

excavating (Vleck, 1979); however, pocket gophers have a low metabolic rate (McNab, 1966) and may be conditioned to seeking deeper and cooler portions of burrow as a response to temperature increase. In any event, the relatively stable length of extended locomotory periods suggests that the energy available for bouts of locomotory activity and associated activities is closely circumscribed.

#### 4.2. Effects of Light

Setting traps for *Thomomys bottae* in closed as opposed to open burrow systems may make little difference to trapping success (Gamboa, 1975); however, light and air may be effective attractants stimulating locomotory activity (measurement must be taken of how quickly the traps are responded to) rather than providing conditions more conducive for actual capture.

Kavanau & Havenhill (1976) noted that captive *Thomomys bottae* monitored in non-burrow conditions preferred darkness for locomotory activity when given the choice, but were not inhibited by high levels of light. Pocket gopher individuals and species in the present study which were monitored in plastic burrows but only given the choice of light conditions in 12 hr intervals did not consistently favour light over darkness, or red over white incandescent lighting; thigmotaxis may have had an overriding effect on any inhibition towards locomotory activity in lighted conditions. It could in fact be argued that animals were stimulated to locomotory activity by not only the cover provided by darkness, but also prompted by light to locomotory activity as part of a digging response (geomyids plug all entrances to the surface with soil). Even pocket gophers released on the surface during daytime are not inhibited in exploring surroundings (Hickman, 1984). The most important trigger to locomotory activity may be the changing of light to dark or vice versa, and the type of activities immediately preceding the time of change in light conditions (an animal just completing an exploratory period may be less motivated to respond to light stimuli by moving than an animal which has been resting for an hour or so beforehand). With dawn and dusk periods removed by experimental conditions, pocket gophers had no warning for adjusting the timing of locomotory activity by delay of movement or shortening of rest time which might have skewed activity towards light or dark conditions (Kavanau, 1969); however, most light changes for geomyids are likely to be abrupt as the animal excavates an opening to the surface.

The number of mean extended periods of locomotory activity did not consistently increase or decrease to any great degree with changes in light for the periods of 600—1800 or 1800—600 hrs, except for *Thomomys* which is considered by some to wander on the surface (Fassler

& Leavitt, 1975), perhaps more so than *Geomys* or *Pappogeomys*. The mountain habitat certainly offers greater cover and more lush vegetation, so that *Thomomys* may be more responsive to changes in light conditions in terms of surface activity. Length of locomotory activity periods were stable, so that periods of locomotory activity (as found with temperature treatments), may be limited to a fairly narrow range by available energy.

#### 4.3. Other Considerations

Vaughan & Hansen (1961) found that natural light had little effect on the locomotory activity of captive *Geomys bursarius*, and suggested that the major effect of temperature is likely the effect temperature has on seasonal rates of metabolism (seasonal metabolic changes were noted by *Geomys pinetis* in Florida by Ross, 1980), and that diel activity may be considered directly dependent on metabolic demands. In addition to temperature, metabolism may also be influenced by the level of various gases in the confined space of burrows, despite, for example, specific physiological adaptation to high levels of CO<sub>2</sub> (Darden, 1972; Chapman & Bennett, 1975), which in turn would be influenced by permeability of the soil under both wet and dry conditions (Arieli, 1979). Bandoni (1981) noted that the burrowing activity of *Thomomys bottae* in Arizona was not directly influenced by precipitation, but rather by the availability of preferred foods and the seeking of mates, while Hickman (1975) noted that *Pappogeomys* may spend little time outside of the nest when caring for young. Frequent inter- or intra specific incursion into burrows (Hickman, 1977b), may, in turn, promote frequent movement via checking of the tunnels.

Further field and laboratory studies are needed to unravel the multiplicity of factors responsible for the large range in total locomotory activity for individuals and species of fossorial mammals. Since neither light nor dark conditions were consistently favoured by pocket gophers, behavioural observations should be generally unhindered by moderate light sources. Refinement of field techniques (Virchow, 1977, Gettinger, 1984) are needed to clarify the ratio of useage of deep to surface tunnels (Hickman, 1977a), and the effect of other microenvironmental conditions (Kennerly, 1964) on the locomotory patterns of geomyids. By comparing animals from different areas (Bradley, *et al.*, 1974; Nevo, 1982), it should be possible to determine if shifts are made in the pattern of locomotory activity for certain habitats, and then perhaps determine more precisely for certain habitats the selective pressures influencing times and duration of locomotory activity.

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#### WPŁYW TEMPERATURY I ŚWIATŁA NA AKTYWNOŚĆ RUCHOWĄ GOFFERÓW TRZYMANÝCH W NIEWOLI

##### Streszczenie

Badania nad aktywnością ruchową u *Thomomys talpoides*, *Geomys bursarius* i *Pappogeomys castanops* prowadzono w warunkach doświadczalnych przy użyciu sztucznych nor o różnej wielkości. Przejawy aktywności ruchowej notowano w cyklach 24 godzinnych (Ryc. 1). Poszczególne szczyty i spadki aktywności nie były wyraźne. Ogólny procent aktywności ruchowej w ciągu doby był różny dla tych trzech testowanych gatunków i wynosił: 1—10% dla *Geomys*, 10—20% dla *Thomomys* i 30—40% dla *Pappogeomys*. Temperatura nie ma większego wpływu na poziom aktywności ruchowej lub długość okresu jej trwania (Ryc. 2). Światło nie ma większego wpływu na ogólny średni procent tej aktywności. Długość fazy świetlnej czy też ciemnej nie wpływa istotnie na aktywność zarówno u badanych gatunków jak i u osobników w obrębie gatunku. Zdarzały się jednak dni odbiegające nawet o 50% na korzyść jednej z faz (Ryc. 3, 4, 5).

Różnorodność czynników odpowiedzialnych za określenie czasu trwania i wzorca aktywności ruchowej można tłumaczyć zapotrzebowaniem metabolicznym. Te zaś z kolei są uzależnione od: struktury gleby, opadów, dostępności ulubionego pokarmu, między- i wewnątrzgatunkowych interakcji (włączając rozród) oraz wielkości systemu nor.