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THE LIFE-HISTORY TACTICS OF THE VOLES, CLETHRIONOMYS GAPPERI AND MICROTUS PENNSYLVANICUS, AT TWO ELEVATIONS

by
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Submitted in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy

Faculty of Graduate Studies
The University of Western Ontario
London, Ontario

July, 1984

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ABSTRACT

The life-history tactics of Clethrionomys gapperi and Microtus pennsylvanicus were examined at two elevations (1450m; 2240m) in southwestern Alberta (Kananaskis Country) to test the hypothesis that females in environments with shorter breeding seasons should produce fewer but larger litters and survive less well than those in environments with longer breeding seasons (Spencer and Steinhoff 1968). Other life-history traits such as body weights and the energetics of reproduction were also compared between elevations.

Life-history data were collected by mark-recapture techniques, kill-trapping and from laboratory colonies.

The high elevation was colder, had fewer frost-free days and more precipitation than the low elevation. The length of the breeding season of C. gapperi averaged two days longer at the low elevation than at the high elevation. The length of the breeding season of M. pennsylvanicus averaged 27 days longer at the low elevation than at the high elevation. The shorter breeding season of M. pennsylvanicus at the high elevation may have been related to spring flooding and colder temperatures compared to the low elevation.

As predicted, the lack of a difference in the lengths of the breeding seasons of C. gapperi between elevations was not associated with any differences in the number of litters, litter size or female survival. Contrary to the hypothesis, the differences in the lengths of the breeding seasons of _M_. _pennsylvanicus_ did not limit the number of opportunities for breeding for the average female, yet litter size was greater at the high elevation than at the low elevation and there was no difference in female survival between elevations. The average number of litters per season was slightly less than two in all populations; the average female did not survive long enough to produce young over the entire length of the season. Data from the literature also suggested that the length of the breeding season is not associated with litter size and the maximum number of litters per season within these species.

Few traits showed differences between elevations and these were not necessarily the same ones in both species. The maximum weights of over-wintered males, the age when young opened their eyes and one index of reproductive effort showed differences in _C_. _gapperi_ between elevations. Litter size, nestling survival, maximum weights of over-wintered males, mean weights of mature, young-of-the-year males and the relative fat content of males showed differences in _M_. _pennsylvanicus_ between elevations. These differences are probably phenotypic responses to environmental conditions such as food quality. Alternatively, some differences may have been fixed at random by genetic drift.

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CHAPTER 1

INTRODUCTION

Life-history tactics may be defined as sets of traits (e.g. offspring size and number) which solve certain ecological problems (Stearns 1976). They are considered to be genotypic in nature, although differences in life-history traits may reflect genotypic or phenotypic responses to environmental conditions (Stearns 1980).

Two major theories have been put forward to explain the evolution of life-history tactics: r- and K-selection, and bet-hedging. Both theories have been reviewed by Stearns (1976). Both theories require an assessment of environmental conditions (e.g. stable vs. fluctuating; harsh vs. benign), but the major difference between them is that r- and K-selection bases its predictions on the degree of density-independent or density-dependent mortality, while bet-hedging bases its predictions on the effects of age-specific mortality. These theories have been criticized on many grounds (e.g. Parry 1981; Stearns 1977; Wilbur _et al._ 1974). For example, both theories assume that life-history traits are free to coevolve under any set of environmental conditions. Yet, recent studies show that, among reptiles and mammals (Stearns 1983; 1984, respectively), phylogenetic and design constraints limit the evolution of many traits. These conclusions may also apply to other major taxa.

Within many mammalian taxa, strong correlations between body size and other life-history traits have been documented (e.g. Blueweiss et al. 1978; Eisenberg 1981; Millar 1981). These studies have examined traits among major taxonomic groups. The importance of environmental conditions and design constraints in shaping life-histories at the intra-specific level are not well known. If environmental conditions are important in determining life-history tactics among populations, differences in traits may be particularly evident in montane areas where environmental conditions are diverse. Temperature and length of the snow-free period decrease ~~with~~ increasing elevation (Trewartha and Horn 1980; Billings and Mooney 1968) and annual plant productivity in mountain ecosystems is generally much lower than in other ecosystems (Billings and Mooney 1968). Mountain ecosystems also have a high degree of habitat diversity because of the interaction of elevational, meso- and microtopographical gradients (Billings 1979).

Several studies of small mammals suggest that conditions at high elevations are harsh. For example, Ehrlich et al. (1972) reported that a late June snowfall at 2900m in Colorado was associated with high mortality in several species of small mammals. At 3100m in Colorado, Merritt and Merritt (1978; 1980) found that autumn freezes that occurred before snow accumulated and spring thaws that produced extensive flooding were associated with considerable mortality in populations of the red-backed vole, Clethrionomys gapperi and the deer mouse, Peromyscus maniculatus. At 2900m in Colorado, Stinson (1977) found that the autumn freeze and the vernal overturn were associated with local extinctions of two Microtus spp. At 3000m in Colorado, Vaughan (1969) found that most small mammals were influenced to some degree by the short growing season, low temperatures and a short frost-free period. Again, extensive spring flooding and cold temperatures in autumn with no snow cover were suggested as critical periods for small mammals. At 3000m in Colorado, Sleeper et al. (1976) examined the relationship between densities of several species of small mammals and varying snow conditions. Three species of microtines were unaffected, but P. maniculatus and chipmunks (Eutamius spp.) showed marked declines in numbers after winters of heavy snowfall. In most species, the mean conception date in the spring was correlated with the timing of snowmelt. Negus et al. (1977) also found a close agreement between the onset of breeding in the montane vole, M. montanus and the timing of snowmelt at different elevations in Utah. At low elevations, environmental conditions are likely to be less severe than at high elevations.

Small mammal studies that have examined life-history traits over elevational gradients show many inconsistencies (Table 1). For example, litter size shows no change with elevation in most studies, but has occasionally been found to increase or decrease with elevation. Also, many traits have not been documented. The age at weaning, survival of young, growth rates and reproductive effort have been measured at different elevations in only one study (Halfpenny 1980). Generalizations from this survey are difficult to make, perhaps because these studies were limited in scope. Sample sizes used to determine litter size were often small and none were partitioned to examine the data for possible biases due to differences among years, months, or age or parity groups (Innes 1978; Millar, 1978). Growth rates and indices of reproductive effort were not corrected for possible biases arising from different mean litter sizes among populations (Innes and Millar 1979; 1981). Estimates of the number of litters produced per season were based on the maximum number of sets of placental scars or the proportion of pregnant females in a sample. Placental scars are often poor indicators of breeding history (Martin et al. 1976) and pregnant females are often undetected because embryos are usually not visible until seven days post-conceptus (Greenwald 1957). Better estimates of the number of litters produced can be obtained

Table 1. Literature review showing how life-history traits vary with elevation in small mammals.

Traits are shown to increase, decrease or remain the same with increasing elevation.

Authority	Species	Elevational gradient	Litter size	Maximum number of litters		Adult Weight	Adult Survival	Age at sexual maturity	Age at weaning	Young survival	Growth rates	Reproductive effort
				Adult	Young							
Claude 1970	Clethrionomys glareolus	400-1700m	decrease	no change	decrease	increase	increase	--	--	--	--	--
Dunmire 1960	Peromyscus maniculatus	1400-3800m	increase	decrease		--	increase	no change	--	--	--	--
Hartlinger 1970	C. glareolus	400-1350m	--	--		increase	--	--	--	--	--	--
Halfpenny 1980	P. maniculatus	1500-4300m	increase*	decrease		increase*	no change	--	increase	increase	decrease*	increase*
Hock 1962*	P. maniculatus	1300-4300m	--	--		increase	--	--	--	--	--	--
Innes 1978	Microtus californicus	10-300m	no change*	--		--	-	--	--	--	--	--
Innes 1978	M. montanus	2000-3000m	no change*	--		[illegible]	--	--	--	--	--	--
Innes 1978	M. ochrogaster	100-300m	no change*	--		--		--	--	--	--	--
Innes 1978	M. pennsylvanicus	10-400m	no change*	--		--	--	--	--	--	--	--
Innes 1978	C. gapperi	10-3000m	no change*	--		--	-	--	--	--	--	--
O'Farrell 1975	P. maniculatus	100-1000m	--	--		no change	--	--	--	--	--	--
Otto 1978	C. glareolus	0-750m	--	--		no change*	--	--	--	--	--	--
Robertson 1975	Peromyscus spp.	0-3000m	no change*	--		--	--	--	--	--	--	--
Sloan 1967	P. maniculatus	1500-2300m	no change*	decrease		--	--	decrease	--	--	--	--
Smith and McGinnis 1968	P. maniculatus	--	no change*	--		no change*	--	--	--	--	--	--

Table 1. continued

Authority	Species	Elevational gradient	Litter size	Maximum number of litters		Adult Weight	Adult Survival	Age at sexual maturity	Age at weaning	Young survival	Growth rates	Reproductive effort
				Adult	Young							
Smith and McGinnis 1968	P. leucopus	--	no change*	--		no change*	--	--	—	—	—	—
Spencer and Steinhoff 1968	P. maniculatus	—	increase*	--		--	--	--	—	—	—	—
Zejda 1966	C. glareolus	<1000m;>1000m	decrease*	--		increase*	--	--	—	—	—	—

*Denotes the data were tested statistically.

by following the breeding histories of individual females over the course of a season. In general, many of the inconsistencies among elevational studies may be attributed to small samples and imprecise estimates.

Six studies (Claude 1970; Dunmire 1960; Halfpenny 1980; Sloan 1967; Spencer and Steinhoff 1968; Zejda 1966) suggested or documented that the length of the breeding season decreased with elevation. Spencer and Steinhoff (1968) considered this environmental condition to be important in determining three life-history traits (number of litters, litter size and survival). They hypothesized, for mammals, that females in areas with short breeding seasons (such as high elevations) would have few opportunities to reproduce. Under such conditions, selection should favour those females producing large litters. Females with large litters would incur a greater risk (e.g. increased mortality from predation, related to increased foraging activity) than females with small litters. This risk is unimportant because females are unlikely to survive to the next breeding season. Females in areas with long breeding seasons (such as low elevations) would have several opportunities to reproduce and selection should favour those females producing small litters. Small litters would incur less of a risk to the female than large litters. Risk should be minimized when repeat breeding is possible because repeat breeding results in more potential offspring than one large litter.

In their study, Spencer and Steinhoff (1968) found that litter size in P. maniculatus increased with elevation and inferred that the length of the breeding season was much shorter at high elevations than at low elevations because the growing season on the plains was twice as long as in subalpine areas. However, they had no estimates of female survival or the number of litters females were producing.

The general approach of this study was to document the life-histories of Clethrionomys gapperi (the red-backed vole) and Microtus pennsylvanicus (the meadow vole) at two elevations in the Rocky Mountains and to determine if Spencer and Steinhoff's hypothesis is applicable to these microtines. If the length of the breeding season is short at a high elevation, females of both species should produce a few, large litters and (assuming a cost to reproduction) have poor survival. If the length of the breeding season is long at a low elevation, females of both species should produce many small litters, but have good survival.

Alternatively, given fewer opportunities to reproduce at a high elevation than at a low elevation, reproduction could be enhanced by producing larger offspring with better survival at a high elevation than at a low elevation, while litter size does not change with elevation. To support larger offspring, [illegible] female at a high elevation would have to feed her offspring more and/or deplete her own energy reserves compared to a female at a low elevation. Given that time for breeding is shorter at a high elevation than at a low elevation, offspring at a high elevation could also be weaned earlier (and subsequently mature earlier) than those at a low elevation.

The specific objectives of this study were to:

1) test Spencer and Steinhoff's hypothesis by examining litter sizes, the number of litters and female survival of C. gapperi and M. pennsylvanicus at two elevations 800 vertical metres apart.
2) examine meteorological data at the two elevations and their relationship to the lengths of the breeding seasons.
3) examine other life-history traits such as survival of males, adult weights, growth and development of young, reproductive energetics, including body fat, the amount of food required to raise a litter and three indices of physiological reproductive effort.
4) improve on previous studies which examined traits at different elevations by correcting (whenever possible) for biases on traits which occur because of yearly, monthly or litter size effects.

The general characteristics, reproduction, ecology, behaviour and demography of C. gapperi and M. pennsylvanicus have been summarized by Merritt (1981) and Reich (1981), respectively. Generally, C. gapperi occupies woodlands while

M. pennsylvanicus occupies grasslands. Both species are basically herbivores, although C. gapperi tends to be more omnivorous than M. pennsylvanicus. Both species are active year-round and throughout the day and night. Both species are of similar size. Both species have short gestation periods (18 to 21 days) and give birth to highly altricial young. Young are weaned as early as two weeks and may be sexually mature as early as one month. These reproductive characteristics, as well as the ability to conceive during a post-partum estrus, give both species a potentially high reproductive rate.

CHAPTER 2

METHODS

2.1 Study areas and trapping schedule.

This study was conducted in Kananaskis Country, approximately 80km west of Calgary, Alberta (50°55´N, 115°07´W). Specific study areas included the Kananaskis Valley (1450m (range = 1433-1473m) in areas adjacent to the Kananaskis Highway between Porcupine and Flat Creeks) and a glacial cirque and surrounding areas (2240m (range = 2156-2323m) south and southeast of Mt. Allan in the Marmot Basin Experimental Watershed). Henceforth, 1450m and 2240m will be referred to as the low and high elevations, respectively. (Vegetation types at both elevations are described in Appendix 1).

Trapping was carried out from 1978-1981, although the 1978 data were excluded from most analyses because of small samples. Trapping commenced in mid-May and finished in late September or early October each year, except in 1981 when it ended in mid-August. In each year, trapping started earlier at the low elevation than at the high elevation, but usually finished within the same week at both elevations. The general approach was to alternatively live- and snap-trap each elevation for three or four consecutive nights throughout the trapping season.

2.2 Meteorological data.

Data on temperatures and precipitation were recorded at permanent weather stations within the Marmot Basin Experimental Watershed. The two weather stations used for this study were approximately 300m and 50m above the mean trapping elevations at the low and high elevations, respectively (M.D. Drews, in litt.). Long-term (>10 yrs.) records were examined between elevations and among months. Minor yearly variation in meteorological conditions was expected, but the data were pooled among years because monthly differences far exceeded yearly differences. The data were collected by the Atmospheric Environment Service, Environment Canada.

Daily minimum and maximum temperatures were taken by thermometers housed in Stevenson screens approximately 1.5m above ground. These data were subsampled every second day to give 15 or 16 readings per month per elevation. Midpoint temperatures were calculated by summing daily minimum and maximum temperatures and dividing by two.

Subnivean small mammals experience air temperatures that are warmer and less variable than those recorded by supranivean meteorological stations (Pruitt 1957; 1978). For this reason, only temperatures recorded during the main snow-free period at both elevations (May to September, personal observations) were considered. Days when the minimum temperature was above 0.0°C were considered as frost-free.

Rainfall was measured using Sacramento storage gauges each month from June to September.

Snowfall was calculated from snow density and its water content. Samples were collected from ten standard locations, using a Mount Rose snow sampler, each month from January to June. Therefore, each snow value represents a ten point mean. Snow depth was calculated from:

$$Y = (X\ (100)) \div Z \qquad (1)$$

where Y = snow depth(cm), X = water content(cm) and Z = snow density(%) (L. Meeres, *in litt*.).

2.3 Field studies.

Animals were live-trapped with Longworth traps (one trap per station) provided with carrots, whole oats and cotton mattress stuffing for bait and insulation. Different trapping routines were used for *M. pennsylvanicus* and *C. gapperi* because *M. pennsylvanicus* were more diurnal and less trap hardy than *C. gapperi*. Traps set in *C. gapperi* habitat were opened in late afternoon or early evening and checked the following morning. Traps set in *M. pennsylvanicus* habitat were opened at mid-day, checked in late afternoon or early evening and then rechecked the following morning.

Mark-recapture grids were used to assess densities, trappabilities, survival, the number of litters per season, body weights and growth. Each grid was trapped approximately every six days with this interval being greater during inclement weather. Traps were locked open when not in use, except in areas where human or bear activity necessitated their removal. Four grids were monitored in 1979 (two per elevation), while in 1980 and 1981 a total of nine grids (five and four at the low and high elevations, respectively) were monitored. Although the distance between trap stations was constant (20m), the number and sizes of grids differed between elevations because of the differential availability of suitable habitat. (Sizes and vegetation characteristics of these grids are given in Appendix 1 while population numbers on these grids are presented in Appendix 2).

At each capture, grid animals were identified to species, toe-clipped (if unmarked), weighed to the nearest 0.5g with a Pesola® spring balance, and age and reproductive condition noted. Individuals were classified as either over-wintered or young-of-the-year based on weight, reproductive condition and the time of the year they were caught. For males, testes position was noted as scrotal, abdominal or intermediate. For females, reproductive condition was based on examination of the vagina-(perforate or imperforate), copulation plug-(present or absent), nipples-(extended indicating lactation or flat indicating no lactation) and abdomen-(swollen indicating pregnancy).

The length of the breeding season can be calculated in several ways. In many microtine studies the commencement of the breeding season is considered to be the time when 50% of females are pregnant while the end occurs when less than 50% of the females are pregnant (e.g. Keller and Krebs 1970). Other studies have based the length of the breeding season on the percentage of lactating females in a population (e.g. Tamarin 1977a) or as the length of time between the first and last births in a population (e.g. Millar _et_ _al_. 1979). The first two methods are inaccurate because exact dates of parturition are not determined and the last method does not take into account the possibility of an atypical female producing a litter long before or long after most females are parturient in a population. For these reasons, the length of the breeding season was defined here as the average length of time between the earliest and latest births in a population using five criteria.

The first criterion used the mean embryo weights of dead-trapped females to predict the date of birth of a litter, following Huggett and Widdas (1951). The second criterion was based on females on mark-recapture grids. Females which gained weight rapidly, then lost a large amount of weight (> 5.0g), and were lactating on subsequent trapping days were considered to have given birth. The median date between two trapping sessions was used for these females, except when they gave birth in a trap, in which case the trapping date was used. The third criterion used the date of birth in the laboratory, for females that had conceived in the wild. The fourth criterion used young ($\leq$ 15.0g) caught on the mark-recapture grids for the first time. All of these young were assumed to have been born 18 days prior to capture. The fifth criterion used the dried eye lens weights of dead-trapped young to estimate their date of birth. Since this aging technique may contain considerable error, only those young determined to be 30 days of age or less were considered (Appendix 3). In each year, one date from each criterion was used to calculate a mean initiation date and a mean cessation date and the difference between the two dates was considered to be the length of the breeding season. Realistic estimates were not always available for all five criteria and in some cases a mean was based on only three criteria (Appendix 4).

The number of litters, as well as the time taken to produce those litters, were calculated from females on the mark-recapture grids, based on their reproductive condition, weight changes and births in live-traps. Females that were caught less than three times, or if they were not caught in four consecutive weeks were excluded.

Trappability (the probability of capturing a marked animal on a given trap-night) was calculated following the minimum unweighted method of Sullivan (1979). This method excludes animals caught less than three times and therefore, deals with animals that have long trapping histories. Trappability was calculated as: the number actually caught at time i ÷ the number known to be present at time i. Maximum trappability (Krebs et al. 1976) includes all captures and upwardly biases estimates because it includes individuals that are caught only once; they have a trappability of 1.0.

Two-week survival rates were determined for individuals caught at least three times as: the number known to be alive at time t + 2 weeks ÷ the number caught at time t. The inclusion of only those caught at least three times increases the chances that disappearance was due to death rather than emmigration. Two-week survival rates were calculated throughout the trapping season and were based on six to eight two-week periods per population per year. Since trapping intervals were less than two weeks, all data collected within a two-week period were considered for that period.

Live-trap removal lines were used to capture animals for a laboratory colony. These lines, consisting of 20-125 traps (10-20m spacing), were checked daily for three days and then removed. Animals not used for the colony were killed, frozen and autopsied at a later date. Snap-trap lines (Museum Special traps baited with peanut butter and rolled oats) were operated in the same manner as the live-trap removal lines. Snap-trapped animals were used to obtain additional data on body weight, reproductive condition and fat content. All animals were frozen and autopsied at a later date.

2.4 Laboratory methods.

Captive animals were used to document litter size, growth and development of the young, and the energetics of reproduction. They were maintained in a basement room at the Kananaskis Centre for Environmental Research (The University of Calgary). Temperature was approximately 20°C and a constant photoperiod of 16h light: 8h dark was provided. Humidity was not controlled. Animals were housed in cages (28.5 x 16.5 x 11.5cm) with Beta-Chip® Laboratory Hardwood Bedding, tissue paper, Purina Laboratory Chow® (No. 5001) and water provided ad libitum. For the first two or three days after capture, all animals were also supplied with carrots. All animals were weighed (to the nearest 0.1g) when captured, after a maximum three day acclimation period, and then every second day until they were no longer needed. The acclimation period was shorter if a female gave birth less than three days after capture. Food consumption was measured every second day by subtracting the food remaining from an initial amount provided. Weights and food consumption of males and non-pregnant females were recorded for one month. The cummulative amount of food eaten by females with litters represents both the food required to maintain the female and the food required to raise young (total ingestion). To calculate the amount of food required to raise young, the maintenance cost of each mother was subtracted from her total ingestion. Maintenance costs of lactating females were assumed to be the same as those of non-pregnant, non-lactating females (controls) of a given body weight. Weight and food consumption of lactating females (and young) were usually recorded beyond the time the young were weaned.

Near-term females (> 28.0g) were checked daily and their post-partum weight, litter size and litter weight were recorded on the first day young were present. These females and their litters were assigned to one of two groups. In one group, growth of young was determined by weighing each littermate every second day from birth to 30 days. Individuals within litters were not marked. Mothers were kept with their young throughout this period. Sex ratios of most litters were recorded at 30 days. The second group was used to estimate the age at weaning. Weaning is a period of transition between maternal dependence and independence of the young; it may occur over a period of days in these species. However, it may be quantified for laboratory raised young by defining it as the age when, on average, young do not lose or gain weight upon isolation from their mother and littermates for 24 hours (King et al. 1963). Young were isolated from their mother and littermates between 11 and 16 days, following Innes and Millar (1979). Initially, young were isolated alone for 24 hours, but this method proved inadequate because less than 30% of the variation in weight change could be explained by age. Few young gained large amounts of weight and many lost a considerable amount (> 1.0g) irrespective of age. In order to decrease the variability between weight change and age, young were isolated from their mothers and littermates in pairs or groups of three. This method proved more successful than individual isolation however, samples for M. pennsylvanicus were not large enough to determine the age at weaning by isolating littermates in pairs or groups of three and data from individual isolates were also included. Isolation of young in pairs or groups of three likely resulted in less weight loss than individual isolation, because young would adjust better behaviourally to a new environment with a littermate, than they would alone.

All litters were checked daily to determine when all young of a litter opened their eyes. Many litters were raised beyond weaning or 30 days of age to provide known age eye lens weights that could be used as an aging technique for young-of-the-year (Millar and Iverson 1976).

Common autopsy procedures were applied to all kill-trapped samples. Frozen carcasses were thawed and weighed. Stomach and caecum contents were then removed and the carcass was reweighed to give an adjusted weight. For males, mean testes length and position were recorded. Male C. gapperi and male M. pennsylvanicus were considered to be sexually mature if their testes were scrotal, and $\geq$ 6mm and $\geq$ 7mm in length, respectively. This is the condition when 50% or more of all males have positive epididymal smears

(Iverson and Turner 1976). For females, external reproductive condition was noted, along with the number, length and weight of healthy and regressing embryos. If not recorded, the mean embryo weight was calculated from the mean embryo length by:

$$LN(Y) = LN(-5.72) + 1.93LN(X) \qquad (2)$$

($r = 0.94$, $p<0.01$, $n = 54$) for C. gapperi and

$$LN(Y) = LN(-5.87) + 2.00LN(X) \qquad (3)$$

($r = 0.96$, $p<0.01$, $n = 58$) for M. pennsylvanicus, where Y = mean embryo weight (g) and X = mean embryo length (mm).

To determine the age of wild caught animals, their eye balls were removed and fixed in a 10% solution of formalin buffered with $CaCO_3$ (Millar and Iverson 1976). The eye balls were fixed for at least three weeks, after which the eye lenses were removed and oven dried at 95°C for three days. Eye lenses of known-aged young from the laboratory colony were treated in the same manner as the wild caught animals. Age of the wild caught animals was determined by comparing their eye lens weights with those from the laboratory colony. However, eye lenses from the wild and laboratory populations may not grow at the same rate and this technique may not provide accurate age estimates in these species (Appendix 3).

Carcasses were then refrozen and their fat content was measured at a later date. Carcasses were oven dried at 95°C for three days and the water content was recorded. Each carcass was then ground in a Wiley Mill and the fat content of a 1.5-2.0g sample was determined by petroleum ether extraction in a Goldfisch extractor over a 12h period. Lean dry weight represents body weight less fat, water and gut contents.

2.5 Statistical analysis.

Most data were analyzed by computer using SPSS (Statistical Package for the Social Sciences) or Minitab. Where samples sizes permitted, field data were analyzed for differences among years. If there was a significant year-elevation interaction, the data were tested between elevations within years. To reduce the probability of a Type 1 error (the rejection of a true null hypothesis) in a series of tests on the same data set, the 0.05 level of significance was increased by dividing it by the number of tests (Snedecor and Cochran 1980). An increase in the probability level will be shown as: p_x. 0.05, where x = the number of tests. Laboratory data were not analyzed for differences among years, because laboratory conditions were the same each year.

Yate's correction was not applied on 2 x 2 contingency tests because it tends to be unduly conservative even with very low sample sizes (Grizzle 1967).

Throughout the text, tables and figures, means are presented ± 1 standard error (S.E.) and n refers to sample size. Standard errors are not reported on ratio variables and all ratios were arcsine transformed before statistical analyses were applied (Sokal and Rohlf 1969). ANOVA and ANCOVA represent analysis of variance and analysis of covariance, respectively.

CHAPTER 3

RESULTS

3.1 Meteorological conditions.

Minimum and maximum temperatures were highly correlated with one another (low elevation: $r = 0.65$, $p<0.01$, $n = 954$; high elevation: $r = 0.87$, $p<0.01$, $n = 933$), and daily midpoints were used to test for differences between elevations. The daily midpoint temperature at the low elevation exceeded that at the high elevation by approximately 2°C and this difference occurred in each month (Table 2). A two-way ANOVA indicated that the temperatures were significantly different between elevations ($F = 118.72$, $p<0.01$) and among months ($F = 224.45$, $p<0.01$).

Midpoint temperatures, however, may not be as important as minimum temperatures for these (herbivorous) small mammals, because the latter temperatures can limit the length of the growing season (Watson 1963; Sutcliffe 1977) and may cause thermal stress. The percentage of frost-free days from May to September was 62.8% and 59.8% at the low and high elevations, respectively. The proportion of days with frost to days without frost were significantly different

Table 2. Average midpoint temperatures (°C), at the low and high elevations, from May to September (1969-1981). Ranges are presented in parentheses.

	Elevation				
	Low	n	High	n	Difference
Month					
May	4.5(-3.1/15.0)	192	2.1(-7.8/11.7)	190	2.4
June	8.7(1.1/16.7)	191	6.3(-1.7/17.2)	183	2.4
July	11.5(4.4/19.2)	193	9.6(1.1/19.4)	184	1.9
August	11.1(0.6/20.3)	189	9.3(-1.1/19.4)	191	1.8
September	6.3(-8.6/16.4)	189	4.6(-10.0/16.4)	185	1.7

between elevations ($X^2 = 63.61$, $p<0.01$, $n = 1893$). On average, the low elevation was frost-free seven days longer than the high elevation (Table 3). On a monthly basis, the number of frost-free days was not consistently greater at the low elevation than at the high elevation. In May the high elevation had more frost-free days than the low elevation while in September there was no difference between elevations.

Mean rainfall was greater at the high elevation than at the low elevation (Table 4). A two-way ANOVA indicated that the monthly rainfall pattern was significantly different between elevations ($F = 6.69$, $p<0.01$). This month-elevation interaction reflected a very high rainfall in June at the high elevation, while rainfall during other months was similar at both elevations. Even though the mean rainfall during June is based on only two points at the high elevation, the difference between elevations is likely real; Ferguson and Storr (1969) reported that rainfall increased 5.1cm per 305m of elevation within the Marmot Basin Experimental Watershed.

Snow depth and water content of the snow were related by:

$$\mathrm{LN}(Y) = \mathrm{LN}(2.26) + 1.02\mathrm{LN}(X) \tag{4}$$

($r = 0.98$, $p<0.01$, $n = 52$) and

$$\mathrm{LN}(Y) = \mathrm{LN}(2.45) + 0.93\mathrm{LN}(X) \tag{5}$$

($r = 0.92$, $p<0.01$, $n = 66$) at the low and high elevations, respectively, where Y = snow depth(cm) and X = water content

Table 3. Mean number of frost-free days (days minimum temperature >0.0°C), at the low and high elevations, from May to September (1969-1981).

	Elevation		
	Low	High	Difference
Month			
May	5.6	6.8	1.2
June	22.2	18.8	3.4
July	30.3	27.0	3.3
August	28.0	26.2	1.8
September	14.3	14.5	0.2
Total days/5 months	100.4	93.3	7.1

Table 4. Mean monthly rainfall (cm), at the low and high elevations, from June to September (1969-1980) (n represents the number of times a month was sampled).

	Elevation				
Month	Low	n	High	n	Difference
June	8.6 ± 1.3	12	20.4 ± 2.1	2	11.8
July	5.2 ± 0.6	12	6.5 ± 0.8	10	1.3
August	6.8 ± 1.1	12	7.3 ± 1.3	12	0.5
September	4.9 ± 1.2	5	--	0	--

(cm). ANCOVA (with water content as the covariate) indicated that the slopes and intercepts of these lines were not significantly different (F = 2.12, p>0.05; F = 1.60, p>0.05, respectively). Therefore, snow density was the same for any given snow depth, at each elevation. However, snow depth was much greater at the high elevation than at the low elevation (Table 5). A two-way ANOVA showed that the monthly pattern of snow depth was significantly different between elevations (F = 3.46, p<0.01). This interaction was the result of snow gradually disappearing at the low elevation after January , whereas the snow remained deep at the high elevation until June. It then melted rapidly. Therefore, relative to the low elevation, the high elevation accumulated more snow which remained longer. In some years snow patches remain at the high elevation throughout the summer in unexposed areas (Z. Fisera, personal communication).

3.2 Reproduction and survival.

3.2.1 Length of the breeding season.

It was expected that the length of the breeding season would be shorter at the high elevation than at the low elevation. This was not always the case. In 1980 the length of the breeding season of C. gapperi was one day longer at the high elevation than at the low elevation

Table 5. Mean monthly snow depth (cm) and snow density (%), at the low and high elevations, from January to June (1966-1981).

	Elevation							
	Low			High			Difference	
Month	Snow depth	Snow density	n	Snow depth	Snow density	n	Snow depth	Snow density
January	141.3	21.0	1	286.9 ± 88.2	28.5	2	145.6	27.5
February	119.8 ± 14.0	24.7	13	210.3 ± 16.2	23.5	14	90.5	1.2
March	127.7 ± 12.0	25.1	16	249.4 ± 15.2	24.9	16	121.7	0.2
April	80.3 ± 14.8	29.4	16	285.1 ± 19.7	26.9	15	204.8	2.5
May	43.6 ± 16.8	25.3	6	226.6 ± 23.3	33.5	13	183.0	8.2
June	--	--	0	104.0 ± 34.7	38.8	6	--	--

(Table 6). The breeding season of C. gapperi in 1979 was five days longer at the low elevation than at the high elevation. The breeding seasons of M. pennsylvanicus were much longer at the low elevation than at the high elevation, in 1979 and 1980 (Table 6).

All dates used to estimate the lengths of the breeding seasons (Appendix 4) were converted to days of the year. A two-way ANOVA indicated that the initiation of breeding in C. gapperi was significantly earlier at the low elevation than at the high elevation ($F = 6.05$, $p<0.05$) and there were significant differences among years ($F = 5.84$, $p<0.01$). The initiation of breeding in M. pennsylvanicus was significantly earlier at the low elevation than at the high elevation ($F = 54.50$, $p<0.01$) and there were significant differences among years ($F = 9.35$, $p<0.01$). The cessation of breeding showed no significant differences between elevations in either C. gapperi ($F = 1.57$, $p>0.05$) or M. pennsylvanicus ($F = 1.50$, $p>0.05$). There was a significant difference in the cessation of breeding between years only in C. gapperi ($F = 12.00$, $p<0.01$). These data show that both species started breeding earlier at the low elevation than at the high elevation, but within each species, breeding finished at approximately the same time at each elevation.

The average breeding season of C. gapperi (1979 and 1980) was two days longer at the low elevation than at the high elevation. This difference between elevations is much shorter than the length of gestation of this species

Table 6. Lengths of the breeding seasons of *C. gapperi* and *M. pennsylvanicus*, at the low and high elevations, in different years, based on the average dates of the first and last births from aged embryos, births on live-trap grids, births of wild conceived litters in the laboratory, the appearance of young on live-trap grids and the appearance of young in kill-traps.

Year	Species	Elevation	Initiation of breeding	Gessation of breeding	Total days	Difference between elevations (days)
1979	*C. gapperi*	low	June 4	Sept. 13	101	5
		high	June 16	Sept. 20	96	
1980		low	May 29	Sept. 3	97	1[2]
		high	June 1	Sept. 7	98	
1981		low	June 10	--	--	10[1]
		high	June 20	--	--	
1979	*M. pennsylvanicus*	low	May 26	Sept. 6	103	30
		high	June 20	Sept. 1	73	
1980		low	May 17	Sept. 14	120	24
		high	May 31	Sept. 3	96	
1981		low	May 26	--	--	34[1]
		high	June 29	--	--	

---

[1] In 1981 the trapping season ended before the end of the breeding season. Initiation dates at each elevation and the difference between them are given for each species.

[2] The length of the breeding season was longer at the high elevation than the low elevation.

(19 days; this study), and therefore, females surviving the entire breeding season at the high elevation could not produce more litters than those at the low elevation. The breeding season of M. pennsylvanicus averaged 27 days longer at the low elevation than at the high elevation. Since the length of gestation is 21 days in this species (Dieterich and Preston 1977), a female surviving the entire breeding season at the low elevation could produce one more litter than a female at the high elevation.

3.2.2 Number of litters per season.

Data on the number of litters were pooled among years, because samples were small.

Accurate estimates of the number of litters require females to have high trappabilities. The trappabilities of C. gapperi females used to determine the number of litters (low elevation: 83%; high elevation: 80%; $X^2 = 1.80$, $p>0.05$) and M. pennsylvanicus females (low elevation: 64%; high elevation: 63%; $X^2 = 0.15$; $p>0.05$) were not significantly different between elevations. Therefore, biases due to trappability should be the same within each species at both elevations.

The number of litters produced in different populations may be biased by differential contributions by over-wintered and young-of-the-year females, resulting from differences in the rates at which litters are produced and the proportion of the breeding season that a female was actually present on a grid. Therefore, the frequency of reproduction and the time spent on a grid was compared between age groups.

Among C. gapperi females producing more than one litter, a two-way ANOVA indicated that the time between successive litters was not significantly different between elevations (F = 1.84, p>0.05) or between over-wintered and young-of-the-year females (F = 0.17, p>0.05) (Table 7). Among C. gapperi females the mean length of stay on a grid was not significantly different between elevations (F = 2.69, p>0.05) or between over-wintered and young-of-the-year females (F = 2.51, p>0.05) (Table 7).

Among M. pennsylvanicus females producing more than one litter, the time between successive litters was not significantly different between elevations (F = 1.21, p>0.05) or between over-wintered and young-of-the-year females (F = 0.25, p>0.05) (Table 7). Among M. pennsylvanicus females the mean length of stay on a grid was significantly different between elevations (F = 4.54, p<0.05), but not between over-wintered and young-of-the-year females (F = 0.46, p>0.05). The difference in the mean length of stay on a grid was only eight days. This would not permit an average female at the low elevation from producing more litters than a female at the high elevation.

Since the rate at which litters were produced was not

Table 7. Time between successive litters and length of time spent on a grid by over-wintered and young-of-the-year *C. gapperi* and *M. pennsylvanicus* females, at the low and high elevations.

Species	Elevation	Age	Time between litters (days)	n	Length of time on grid (days)	n
C. gapperi	low	over-wintered	20.8 ± 0.80	35	50.0 ± 6.16	23
		young	18.9 ± 0.72	11	38.2 ± 3.91	18
	high	over-wintered	22.0 ± 0.75	102	55.8 ± 3.40	73
		young	22.1 ± 1.50	18	50.2 ± 3.69	25
M. pennsylvanicus	low	over-wintered	21.5 ± 0.67	39	40.1 ± 4.02	39
		young	21.8 ± 0.67	38	46.4 ± 2.85	47
	high	over-wintered	22.5 ± 1.32	29	37.1 ± 2.88	35
		young	23.5 ± 2.28	10	32.8 ± 3.53	20

different between elevations in either species, and the time a female was present on a grid was not different in C. gapperi, nor sufficiently different to bias the results in M. pennsylvanicus, the distribution of the number of litters (Figures 1 and 2) can be compared. The number of litters produced was independent of both elevation and age class (over-wintered versus young-of-the-year) in C. gapperi (G = 17.86, $p>0.05$) and in M. pennsylvanicus (G = 7.98, $p>0.05$).

3.2.3 Litter size.

Although litter size is the most widely reported reproductive trait of small mammals, few studies have examined it in detail. Sample sizes must be large enough to look for differences among collecting methods (e.g. embryo counts, laboratory births or placental scars), among years and among months. Litter size has also been reported to vary with age, parity and size (weight) of a female. The number of regressing embryos and the number of stillborns can also influence realized litter size. However, many of these variables are interrelated. For example, in spring a population would be composed of old, heavy females carrying their first or second litters. Their numbers would decrease over the course of the season, being replaced by young, light females carrying their first litters. If all possible variables influencing litter size were analyzed together,

FIGURE 1

The number of litters produced by over-wintered and young-of-the-year *C. gapperi* females, at the low and high elevations (n represent the number of individuals).

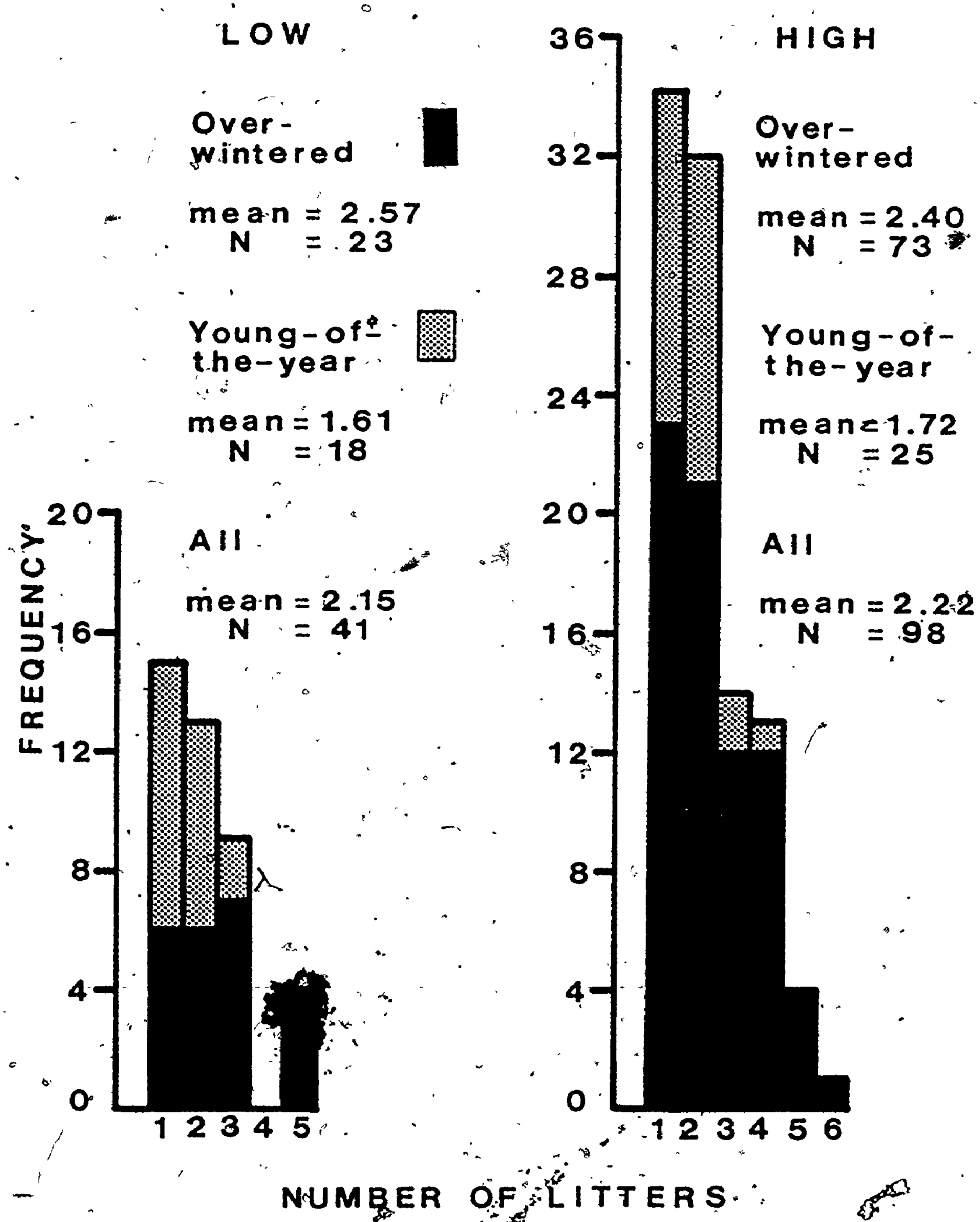
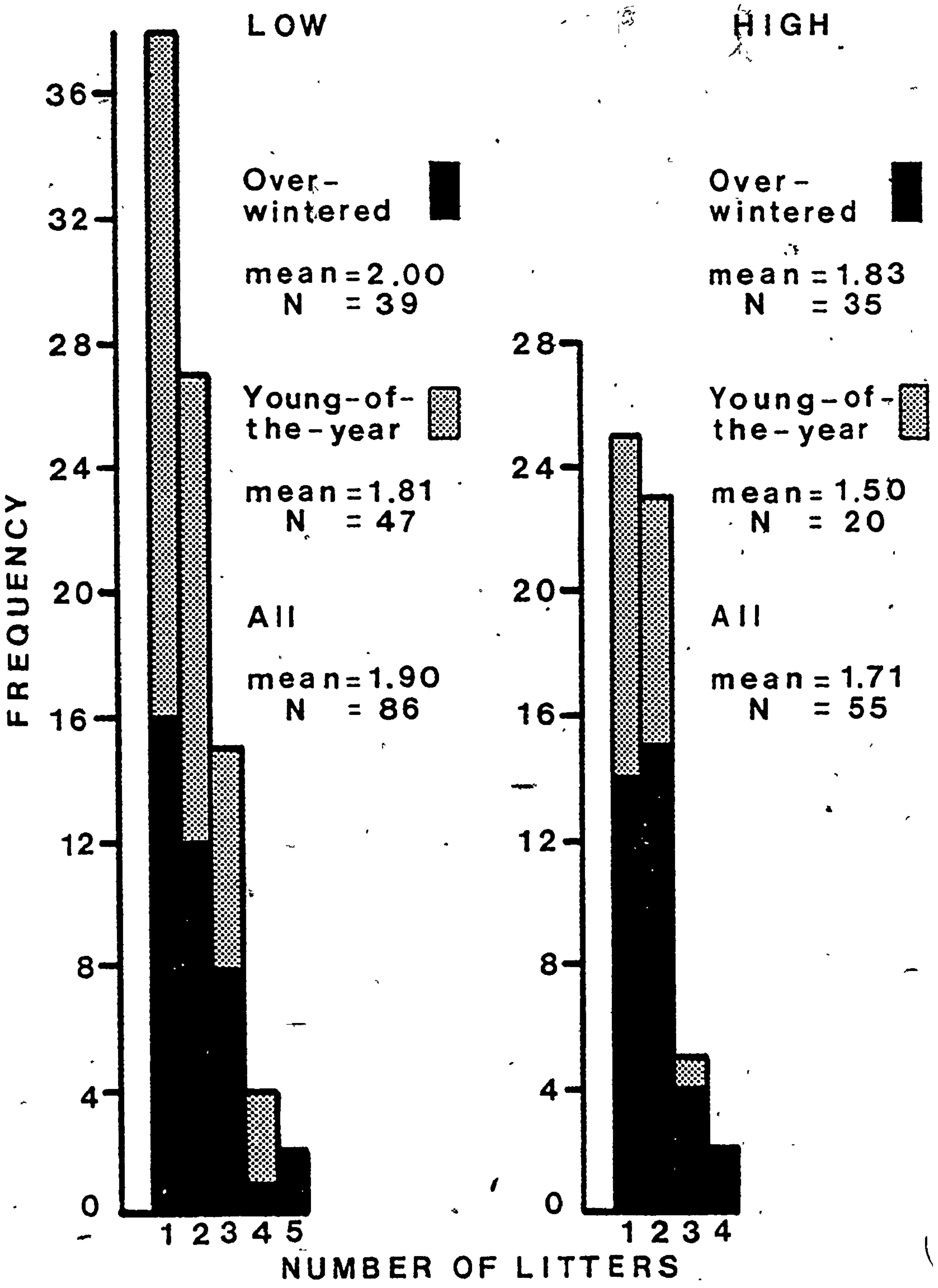

LOW
Over-wintered
mean = 2.57
N = 23
Young-of-the-year
mean = 1.61
N = 18
All
mean = 2.15
N = 41
HIGH
Over-wintered
mean = 2.40
N = 73
Young-of-the-year
mean = 1.72
N = 25
All
mean = 2.22
N = 98
FREQUENCY
0
4
8
12
16
20
24
28
32
36
1 2 3 4 5
1 2 3 4 5 6
NUMBER OF LITTERS

FIGURE 2

The number of litters produced by over-wintered and young-of-the-year *M. pennsylvanicus* females, at the low and high elevations (n represent the number of individuals).


LOW
HIGH
Over-wintered
mean = 2.00
N = 39
Young-of-the-year
mean = 1.81
N = 47
All
mean = 1.90
N = 86
Over-wintered
mean = 1.83
N = 35
Young-of-the-year
mean = 1.50
N = 20
All
mean = 1.71
N = 55
FREQUENCY
0
4
8
12
16
20
24
28
32
36
1 2 3 4 5
1 2 3 4
NUMBER OF LITTERS

interpretation would be difficult. Therefore, each variable was first considered separately and then the ones showing the greatest differences between elevations were considered together in one analysis.

No significant differences in litter size were found between kill-trapped females (embryo counts) and those born in the laboratory (but conceived in the wild) (Table 8). The number of regressing embryos was very low (<1% per population) and the proportion of litters with stillborns to intact litters was not significantly different between elevations in either species (C. gapperi: $X^2 = 0.12$, $p<0.05$, $n = 125$ (litters); M. pennsylvanicus: $X^2 = 0.07$, $p<0.05$, $n = 83$). Therefore, all data for each species were pooled, including the few estimates of litter size from births on the mark-recapture grids.

In all populations, there were no significant differences in litter size among years (Tables 9 and 10). Litter size was then examined in relation to the month a female gave birth (laboratory colony) or the month she would have given birth (determined from embryo weights). A large amount of variation in litter size was found among months in all populations (Figures 3 and 4). Litter size of C. gapperi was small in May and June, but was much larger later in the season at both elevations. The monthly pattern of litter size in M. pennsylvanicus was different at each elevation. Litter size was small in May and September with

Table 8. Estimates of litter size of *C. gapperi* and *M. pennsylvanicus* based on embryo counts from kill-trapped females and litters born to captive females, at the low and high elevations.

Species	Elevation	Source of estimates	Litter size	n	Significance
C. gapperi	low	embryo counts	5.58 ± 0.24	26	t = 1.68[1]
		laboratory births	5.00 ± 0.22	58	
	high	embryo counts	5.65 ± 0.22	43	t = 0.21[1]
		laboratory births	5.60 ± 0.15	67	
M. pennsylvanicus	low	embryo counts	5.10 ± 0.19	52	t = 0.59[1]
		laboratory births	5.95 ± 0.16	60	
	high	embryo counts	6.39 ± 0.27	23	t = 1.54[1]
		laboratory births	5.77 ± 0.33	22	

---

[1] No t-values were significant ($p_2 > 0.05$).

Table 9. Litter size of *C. gapperi*, from all sources, among years, at the low and high elevations.

Elevation	Year	Litter size	mode	Range	n	Significance
low	1978	5.25 ± 0.75	5	3 - 10	8	
	1979	4.75 ± 0.28	4,5,6	2 - 7	24	
	1980	5.44 ± 0.22	5	1 - 7	36	$F = 0.97$[1]
	1981	5.17 ± 0.45	5	1 - 8	18	
	Grand mean	5.17 ± 0.17	5	1 - 10	86	
high	1978	6.40 ± 0.75	5	5 - 9	5	
	1979	5.56 ± 0.23	6	3 - 9	36	
	1980	5.51 ± 0.18	6	2 - 8	43	$F = 0.90$[1]
	1981	5.76 ± 0.20	5,6	2 - 8	37	
	Grand mean	5.64 ± 0.12	6	2 - 9	121	

---

[1] There were no significant differences among years ($p_2 > 0.05$).

Table 10. Litter size of M. pennsylvanicus, from all sources, among years, at the low and high elevations.

Elevation	Year	Litter size	mode	Range	n	Significance
low	1978	4.00 ± 1.16	-	2 - 6	3	
	1979	5.03 ± 0.15	5	2 - 8	62	
	1980	4.90 ± 0.24	5	2 - 7	39	F = 1.07[1]
	1981	5.39 ± 0.35	4,6	4 - 8	13	
	Grand mean	5.00 ± 0.12	5	2 - 8	117	
high	1978	-	-	-	0	
	1979	5.38 ± 0.50	5,6,7	3 - 7	8	
	1980	6.10 ± 0.28	6	4 - 9	20	F = 1.11[1]
	1981	6.20 ± 0.32	7	3 - 9	20	
	Grand mean	6.02 ± 0.20	6	3 - 9	48	

---

[1] There were no significant differences among years ($p_2 > 0.05$).

FIGURE 3

Mean litter size of low and high elevation C. gapperi in relation to the month of actual or predicted birth. One S.E. is given below and above the mean for the low and high elevations, respectively. Numbers refer to sample sizes.

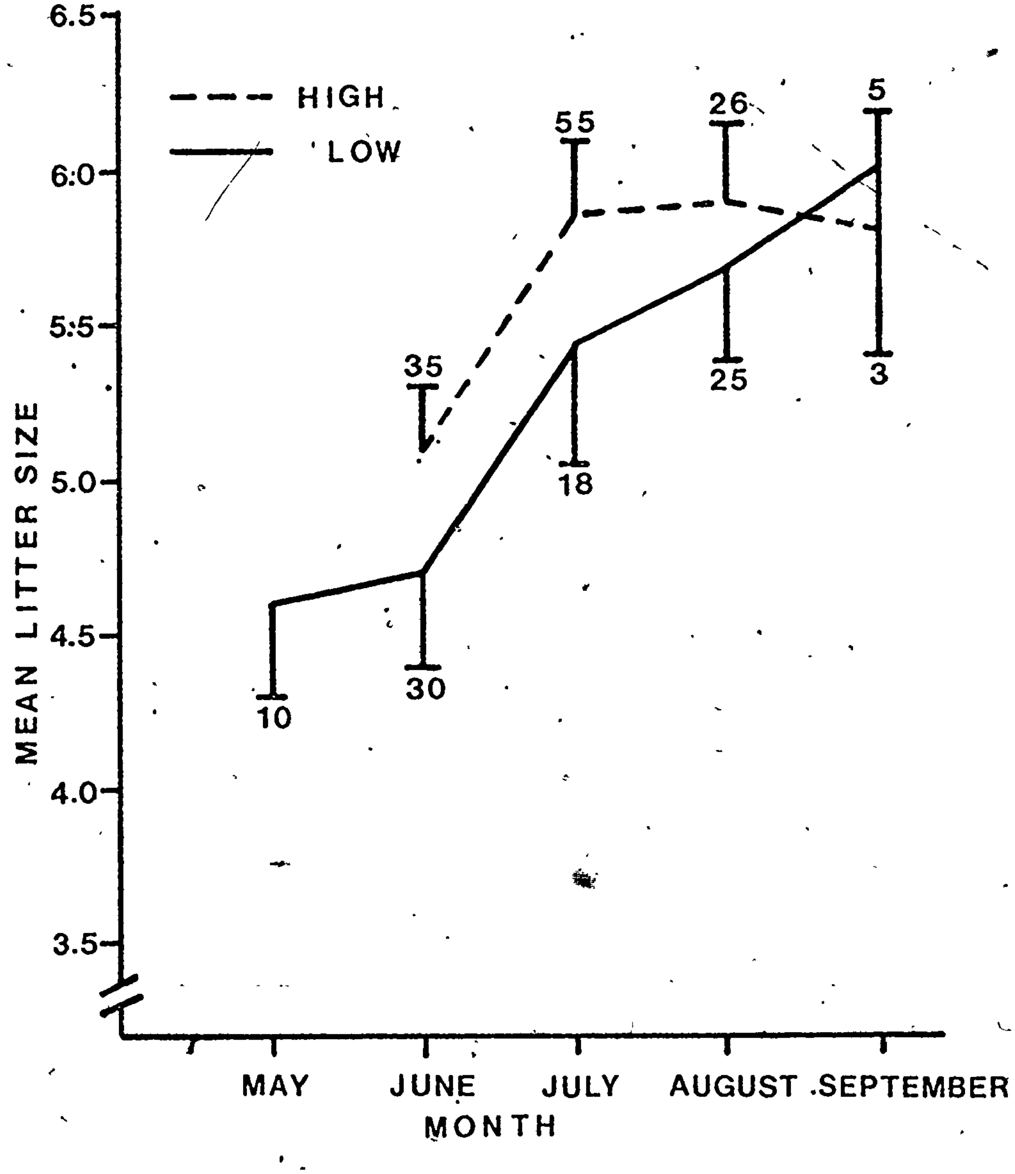
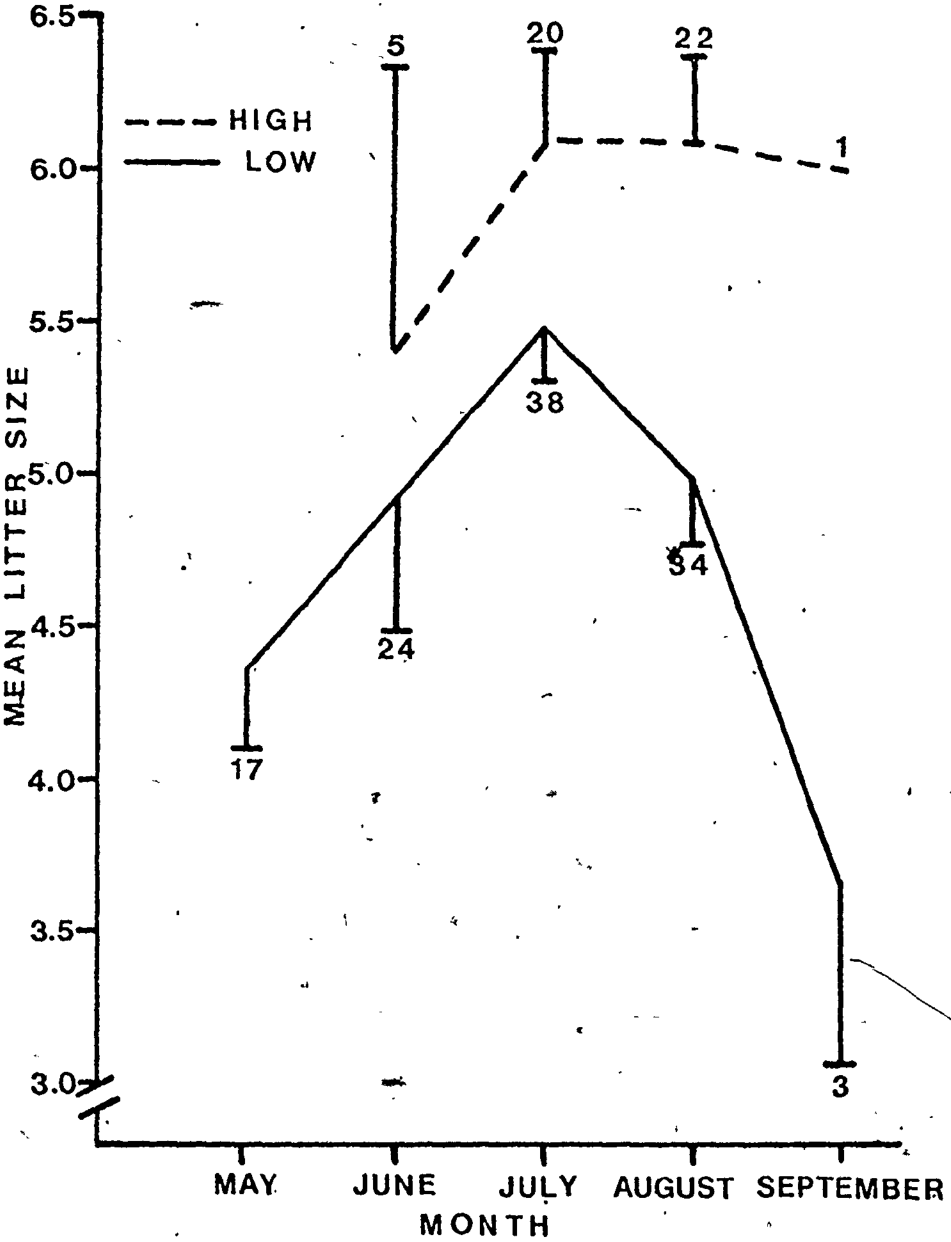

HIGH
LOW
MEAN LITTER SIZE
6.5
6.0
5.5
5.0
4.5
4.0
3.5
MONTH
MAY
JUNE
JULY
AUGUST
SEPTEMBER
35
55
26
5
10
30
18
25
3

FIGURE 4

Mean litter size of low and high elevation _M_. _pennsylvanicus_ in relation to the month of actual or predicted birth. One S.E. is given below and above the mean for the low and high elevations, respectively. Numbers refer to sample sizes.


6.5
6.0
5.5
5.0
4.5
4.0
3.5
3.0
MEAN LITTER SIZE
HIGH
LOW
5
20
22
1
38
24
34
17
3
MAY
JUNE
JULY
AUGUST
SEPTEMBER
MONTH

a peak in July at the low elevation. Litter size was small in June, increased in July and remained large in August at the high elevation.

No significant differences in litter size were found between over-wintered and young-of-the-year females (Table 11).

Litter size was also examined in relation to parity, with primiparous females defined as those with their first litters and multiparous females defined as those with at least their second litter. In all populations, litter size of multiparous females exceeded those of primiparous females (Table 12). Differences between parity groups were generally greater in C. gapperi than in M. pennsylvanicus.

The relationship between litter size and weight of a female was examined in two ways: First, litter size was regressed against the post-partum weights of captive females. The only significant relationship found between these variables was in M. pennsylvanicus from the low elevation (Table 13). Second, litter size was regressed against the body weight (less the litter weight) of kill-trapped females. The only significant relationship found between these variables was in C. gapperi from the low elevation (Table 14).

Month influenced litter size in a substantial manner and parity influenced litter size in a consistent manner, in all populations. These two variables were used in a three-way ANOVA to test for differences between elevations. There

Table 11. Litter size of C. gapperi and M. pennsylvanicus in relation to age, at the low and and high elevations.

Species	Elevation	Age[1]	Litter size	n	Range	Significance
C. gapperi	low	over-wintered	4.97 ± 0.19	65	1 - 8	t = 2.36[2]
		young	6.00 ± 0.37	15	4 - 10	
	high	over-wintered	5.51 ± 0.13	90	2 - 8	t = 1.40[2]
		young	5.91 ± 0.27	23	4 - 9	
M. pennsylvanicus	low	over-wintered	4.94 ± 0.20	52	2 - 8	t = 0.22[2]
		young	5.00 ± 0.17	52	2 - 8	
	high	over-wintered	6.31 ± 0.29	26	3 - 9	t = 1.74[2]
		young	5.61 ± 0.23	18	4 - 7	

---

[1] Females which could not be aged were excluded.

[2] No t-values were significant ($p_2 > 0.05$).

Table 12. Litter size of *C. gapperi* and *M. pennsylvanicus* in relation to parity, at the low and high elevations.

Species	Elevation	Parity	Litter size	n	Range
C. gapperi	low	primiparous	4.77 ± 0.23	48	1 - 10
		multiparous	5.68 ± 0.22	38	2 - 8
	high	primparous	5.25 ± 0.15	57	2 - 7
		multiparous	5.98 ± 0.16	64	2 - 9
M. pennsylvanicus	low	primparous	4.72 ± 0.16	61	2 - 8
		multiparous	5.30 ± 0.17	56	2 - 8
	high	primparous	5.70 ± 0.31	23	3 - 9
		multiparous	6.32 ± 0.24	25	4 - 8

See page 54 for statistical treatment of these data.

Table 13. The relationship between litter size and post-partum weights of *C. gapperi* and *M. pennsylvanicus* laboratory females, at the low and high elevations. Y = weight(g) and X = litter size.

Species	Elevation	$Y = a + bX$	n	Significance
C. gapperi	low	$Y = 25.58 + 0.33X$	58	$r = 0.13^1$
	high	$Y = 24.85 + 0.04X$	67	$r = 0.19^1$
M. pennsylvanicus	low	$Y = 20.55 + 1.23X$	58	$r = 0.41^2$
	high	$Y = 21.07 + 1.19X$	22	$r = 0.39^1$

---

[1] r was not significant ($p_2 > 0.05$).

[2] r was significant ($p_2 < 0.01$).

Table 14. The relationship between litter size and body weight (minus litter weight) of kill-trapped _C_. gapperi and _M_. pennsylvanicus females, at the low and high elevations. Y = weight(g) and X = litter size.

Species	Elevation	Y = a + bX	n	Significance
_C_. gapperi	low	Y = 14.82 + 1.61X	21	r = 0.59[1]
	high	Y = 22.62 + 0.66X	31	r = 0.20[2]
_M_. pennsylvanicus	low	Y = 17.73 + 1.34X	41	r = 0.28[2]
	high	Y = 20.21 + 1.23X	13	r = 0.27[2]

---

[1] r was significant ($p_2 < 0.01$).

[2] r was not significant ($p_2 > 0.05$).

were no significant differences in litter size of C. gapperi between elevations ($F = 2.96$, $p>0.05$) or among months ($F = 1.83$, $p>0.05$). No interaction terms were significant, although there was a highly significant difference between parity groups ($F = 7.25$, $p<0.01$). Litter size was significantly greater at the high elevation than at the low elevation in M. pennsylvanicus ($F = 16.43$, $p<0.01$). A significant interaction term indicated that litter size differed between parity groups depending on the month a female gave birth ($F = 4.36$, $p<0.01$).

3.2.4 Survival.

Nestling survival, two-week summer survival and winter survival were determined from mark-recapture data. Nestling survival was calculated as the proportion of young expected to enter the trappable population (number of litters produced x mean litter size of each population) that were actually caught on all mark-recapture grids in each year. The pattern of nestling survival between elevations was different in both C. gapperi and M. pennsylvanicus, depending on the year ($G = 34.18$, $p<0.01$; $G = 21.52$, $p<0.01$, respectively). Nestling survival of C. gapperi was not significantly different between elevations in 1979 ($X^2 = 3.07$, $p_3>0.05$), but was significantly greater at the low elevation than the high elevation in 1980 ($X^2 = 26.81$, $p_3<0.05$) and significantly greater at the high elevation than the low elevation in 1981 ($X^2 = 10.07$, $p_3 < 0.05$) (Table 15). Nestling survival of M. pennsylvanicus was not significantly different between elevations in 1980 ($X^2 = 2.77$, $p_3 > 0.05$), but was significantly greater at the low elevation than at the high elevation in the other two years (1979: $X^2 = 38.78$, $p_3 < 0.05$; 1981: $X^2 = 17.12$, $p_3 < 0.05$) (Table 16). If these data reflect long-term trends, and years are pooled, the nestling survival of C. gapperi was similar at each elevation (31%), while M. pennsylvanicus at the low elevation had double the nestling survival of those at the high elevation (40% versus 20%, respectively).

Two-week survival rates were examined among years and between sexes, but ages were pooled because significant differences between age groups were found only among females of both species at the low elevation (Tables 17 and 18). Among C. gapperi females, the pattern of survival was different among years ($G = 9.46$, $p < 0.01$). This interaction resulted from high survival at the high elevation in 1979 and 1981, but low survival in 1980, relative to the low elevation (Table 17). Chisquare analysis indicated no significant differences between elevations, within years ($p_3 > 0.05$). Among C. gapperi males, two-week survival rates did not differ between elevations ($G = 0.05$, $p > 0.05$). Among M. pennsylvanicus females and males, there were no significant differences in two-week survival rates between elevations ($G = 2.13$, $p > 0.05$; $G = 0.002$, $p > 0.05$, respectively) (Table 17).

Table 15. Nestling survival of C. *gapperi*, in each year at the low and high elevations.

Elevation	Year	Number of litters produced	Number of young expected[1]	Number of young caught	% nestling survival[2]
low	1979	8	41	17	41.5
	1980	48	248	100	40.3
	1981	32	165	19	11.5
	mean				31.1
high	1979	35	211	94	44.5
	1980	132	745	174	23.4
	1981	46	259	62	23.9
	mean				30.6

---

[1] Calculated by: No. of litters x mean litter size.

[2] Calculated by: (No. of young caught ÷ No. of young expected) x 100.

Table 16. Nestling survival of *M. pennsylvanicus*, in each year at the low and high elevations.

Elevation	Year	Number of litters produced	Number of young expected[1]	Number of young caught	% nestling survival[2]
low	1979	25	125	61	48.8
	1980	110	550	158	28.7
	1981	28	140	70	50.0
	mean				42.5
high	1979	40	241	43	17.8
	1980	43	259	58	22.4
	1981	11	66	13	19.7
	mean				20.0

---

[1] As in Table 14.

[2] As in Table 14.

Table 17. Two-week survival rates of _C. gapperi_, in relation to sex, age and year at the low and high elevations. The number of individuals are presented in parentheses.

Elevation	Sex	Age	Year 1979	 1980	 1981	Mean
low	female	over-wintered	0.60(5)	0.92(36)	0.86(69)	0.86
		young	0.90(10)	0.98(50)	-- (0)	0.97
	male	over-wintered	0.73(11)	0.96(28)	0.88(40)	0.89
		young	0.75(8)	0.87(55)	0.67(3)	0.85
Grand means			0.77	0.93	0.86	0.89
high	female	over-wintered	0.90(52)	0.91(162)	0.97(74)	0.92
		young	0.95(22)	0.93(99)	1.00(5)	0.94
	male	over-wintered	0.88(25)	0.84(98)	0.89(37)	0.86
		young	0.93(28)	0.89(56)	1.00(1)	0.91
Grand means			0.91	0.89	0.95	0.91

Table 18. Two-week survival rates of M. pennsylvanicus, in relation to sex, age and year at the low and high elevations. The number of individuals are presented in parentheses.

Elevation	Sex	Age	Year			Mean
			1979	1980	1981	
low	female	over-wintered	0.81(37)	0.81(87)	0.81(37)	0.81
		young	0.87(37)	0.91(180)	0.80(35)	0.89
	male	over-wintered	0.75(36)	0.83(81)	0.68(22)	0.78
		young	0.76(41)	0.83(63)	0.58(12)	0.78
Grand means			0.79	0.86	0.76	0.82
high	female	over-wintered	0.76(34)	0.80(60)	0.83(18)	0.79
		young	0.78(37)	0.89(26)	-- (0)	0.82
	male	over-wintered	0.88(16)	0.83(73)	0.71(7)	0.83
		young	0.63(8)	0.74(19)	-- (0)	0.70
Grand means			0.78	0.80	0.80	0.79

Winter survival was estimated for 1979-1980 and 1980-1981. Only two animals initially caught as over-wintered individuals survived into a second breeding season: one of 26 (3.8%) over-wintered *C. gapperi* marked during 1979 and 1980 at the low elevation, and one of 102 (1.0%) over-wintered *C. gapperi* marked during 1979 and 1980 at the high elevation. For this reason, winter survival was calculated for young-of-the-year entering their first winter. The pattern of winter survival of *C. gapperi* was different at each elevation depending on the year ($G = 5.13$, $p<0.05$). The interaction resulted from opposite patterns of survival in each year at each elevation (Table 19). Within each year, there were no significant differences between elevations (1979-80: $X^2 = 2.00$, $p_2>0.05$; 1980-81: $X^2 = 2.73$, $p_2>0.05$). Winter survival of *M. pennsylvanicus* was independent of elevation ($G = 0.82$, $p>0.05$) (Table 19). With the exception of *C. gapperi* at the low elevation, winter survival was greater in 1979-1980 than in 1980-1981.

3.3 Reproductive energetics.

3.3.1 Fat content of females.

Fat plays a prominent role in mammalian life-history tactics as a general source of energy (Young 1976).

Fat content of females was compared between elevations, as well as among the following reproductive groups:

Table 19. Winter survival of young-of-the-year C. gapperi and M. pennsylvanicus, over two years, at the low and high elevations.

Species	Elevation	Year	Number marked	Number present the the following year	% present
C. gapperi	low	1979-1980	17	1	5.9
		1980-1981	100	12	12.0
	high	1979-1980	94	19	20.2
		1980-1981	108[1]	6	5.6
M. pennsylvanicus	low	1979-1980	61	5	8.2
		1980-1981	158	3	1.9
	high	1979-1980	43	5	11.6
		1980-1981	58	1	1.7

---

[1] Large forest grid # 1 was excluded because of high trap mortality in September 1980.

1) immature 2) pregnant 3) lactating and, 4) pregnant and lactating. If fat is used to support offspring one might expect that the relative amounts of fat would occur in the following order: immature > pregnant > lactating > pregnant and lactating. The relative amount of fat is expressed as fat (g) ÷ lean dry weight (g).

Small samples precluded a comparison of the relative amounts of fat among months of the breeding season. However samples from May, June and July could be compared with those from August and September (Tables 20 to 23). Only three of 16 comparisons showed significant differences in relative fat content between the first three and last two months of the breeding season, so monthly samples were pooled. Yearly differences in the relative amounts of fat were pronounced in M. pennsylvanicus from the high elevation, being generally greater in 1981 than in other years (Tables 24 to 27). A three-way ANOVA (elevation, year and reproductive group) indicated that there were no significant differences in the relative amounts of fat of C. gapperi between elevations ($F = 0.01$, $p>0.05$) or among reproductive groups ($F = 2.54$, $p>0.05$). However, there was a significant year effect ($F = 3.60$, $p<0.05$). Tables 24 and 25 suggest that all groups had more relative fat in 1981 than in the other years.

Microtus pennsylvanicus showed no difference in relative fat between elevations ($F = 3.14$, $p>0.05$), but a significant two-way interaction among years and reproductive

Table 20. Fat, lean dry weight and percent fat among *C. gapperi* females, in relation to reproductive status and season, from the low elevation. Percent fat = (fat(g) ÷ lean dry weight (g)) x 100.

Reproductive Group	Months	Fat(g)	Lean dry weight(g)	Percent fat	n	Significance[1]
Immature	May, June and July	0.40 ± 0.06	3.90 ± 1.28	10.4	11	ns.
	August and September	0.38 ± 0.03	3.18 ± 0.52	12.3	23	
Pregnant	May, June and July	0.58 ± 0.12	4.77 ± 0.28	11.8	7	ns.
	August and September	0.64 ± 0.00	4.61 ± 0.00	13.9	1	
Lactating	May, June and July	0.45 ± 0.06	5.08 ± 0.16	9.0	6	$t = 2.76$ $p<0.05$
	August and September	0.83 ± 0.08	5.49 ± 0.41	15.5	5	
Pregnant and lactating	May, June and July	0.74 ± 0.08	5.59 ± 0.07	13.3	2	ns.
	August and September	0.87 ± 0.20	5.48 ± 0.33	15.3	6	

---

[1] ns. = not significant.

Table 21. Fat, lean dry weight and percent fat among C. gapperi females, in relation to reproductive status and season, from the high elevation. Percent fat = (fat(g) ÷ lean dry weight (g)) x 100.

Reproductive Group	Months	Fat(g)	Lean dry weight(g)	Percent fat	n	Significance[1]
Immature	May, June and July	0.37 ± 0.03	3.24 ± 0.19	11.3	40	ns.
	August and September	0.42 ± 0.04	3.40 ± 0.11	12.8	33	
Pregnant	May, Ju and July	0.81 ± 0.07	5.76 ± 0.26	14.3	13	ns.
	August and September	0.56 ± 0.11	4.48 ± 0[illegible]2	12.3	4	
Lactating	May, June and July	0.57 ± 0.05	5.90 ± 0.15	9.6	15	ns.
	August and September	0.53 ± 0.07	5.22 ± 0.20	9.8	17	
Pregnant and lactating	May, June and July	0.78 ± 0.17	6.44 ± 0.19	12.0	4	ns.
	August and September	0.98 ± 0.10	6.73 ± 0.30	14.6	8	

---

[1] ns. = not significant.

Table 22. Fat, lean dry weight and percent fat among M. pennsylvanicus females, in relation to reproductive status and season, from the low elevation. Percent fat = (Fat(g) ÷ lean dry weight (g)) x 100.

Reproductive Group	Months	Fat(g)	Lean dry weight(g)	Percent fat	n	Significance[1]
Immature	May, June and July	0.30 ± 0.03	2.78 ± 0.20	11.2	22	ns.
	August and September	0.33 ± 0.04	3.09 ± 0.18	10.9	30	
Pregnant	May, June and July	0.67 ± 0.42	4.87 ± 0.25	13.1	20	ns.
	August and September	0.33 ± 0.00	3.51 ± 0.00	9.4	1	
Lactating	May, June and July	0.63 ± 0.07	5.51 ± 0.26	11.3	6	ns.
	August and September	0.54 ± 0.10	6.09 ± 0.29	8.8	7	
Pregnant and lactating	May, June and July	1.05 ± 0.20	6.00 ± 0.30	16.7	14	ns.
	August and September	1.04 ± 0.26	6.16 ± 0.08	17.1	6	

---

[1] ns. = not significant.

Table 23. Fat, lean dry weight and percent fat among M. pennsylvanicus females, in relation to reproductive status and season, from the high elevation. Percent fat = (fat(g) ÷ lean dry weight (g)) x 100.

Reproductive Group	Months	Fat(g)	Lean dry weight(g)	Percent fat	n	Significance[1]
Immature	May, June and July	0.34 ± 0.04	3.10 ± 0.31	11.8	15	ns
	August and September	0.36 ± 0.13	3.78 ± 0.85	10.4	3	
Pregnant	May, June and July	2.09 ± 0.00	6.58 ± 0.00	31.8	1	ns.
	August and September	1.00 ± 0.26	4.28 ± 0.81	23.3	3	
Lactating	May, June and July	0.39 ± 0.00	5.63 ± 0.00	6.9	1	t = 5.22, $p<0.05$
	August and September	1.47 ± 0.19	6.13 ± 0.63	24.0	4	
Pregnant and lactating	May, June and July	0.70 ± 0.16	7.63 ± 1.15	10.3	3	t = 2.65, $p<0.05$
	August and September	1.56 ± 0.23	7.17 ± 0.63	21.7	5	

[1] ns. = not significant.

Table 24. Fat, lean dry weight and percent fat among C. gapperi females, in relation to reproductive status and year, from the low elevation. Percent fat = (fat(g) ÷ lean dry weight (g)) x 100.

Reproductive Group	Year	Fat(g)	Lean dry weight(g)	Percent fat	n
Immature	1979	0.37 ± 0.06	3.10 ± 0.20	12.4	8
	1980	0.37 ± 0.03	3.51 ± 0.21	11.0	20
	1981	0.47 ± 0.09	3.50 ± 0.47	13.0	6
Pregnant	1979	0.61 ± 0.19	5.00 ± 0.20	12.1	4
	1980	0.56 ± 0.11	4.53 ± 0.44	12.0	4
	1981	--	--	--	0
Lactating	1979	0.36 ± 0.12	5.30 ± 0.15	6.6	2
	1980	0.66 ± 0.09	5.20 ± 0.28	12.9	8
	1981	0.84 ± 0.00	5.75 ± 0.00	14.6	1
Pregnant and lactating	1979	--	--	--	0
	1980	0.59 ± 0.12	5.01 ± 0.26	11.6	3
	1981	0.99 ± 0.21	5.80 ± 0.30	16.7	5

Table 25. Fat, lean dry weight and percent fat among C. gapperi females, in relation to reproductive status and year, from the high elevation. Percent fat = (fat(g) ÷ lean dry weight (g)) x 100.

Reproductive Group	Year	Fat(g)	Lean dry weight(g)	Percent fat	n
Immature	1979	0.34 ± 0.04	2.91 ± 0.17	11.9	25
	1980	0.41 ± 0.03	3.54 ± 0.15	11.6	45
	1981	0.57 ± 0.11	3.19 ± 0.21	18.4	3
Pregnant	1979	0.79 ± 0.19	5.54 ± 0.74	13.8	4
	1980	0.77 ± 0.09	5.69 ± 0.28	13.7	9
	1981	0.66 ± 0.06	4.86 ± 0.52	14.2	4
Lactating	1979	0.50 ± 0.06	5.10 ± 0.21	9.8	11
	1980	0.54 ± 0.05	6.02 ± 0.16	9.0	15
	1981	0.63 ± 0.16	5.19 ± 0.28	11.7	6
Pregnant and lactating	1979	1.00 ± 0.00	7.30 ± 0.00	13.7	1
	1980	0.77 ± 0.18	6.70 ± 0.17	11.5	4
	1981	0.98 ± 0.11	6.49 ± 0.33	15.0	7

Table 26. Fat, lean dry weight and percent fat among *M. pennsylvanicus* females, in relation to reproductive status and year, from the low elevation. Percent fat = (fat(g) ÷ lean dry weight (g)) x 100.

Reproductive Group	Year	Fat(g)	Lean dry weight(g)	Percent fat	n
Immature	1979	0.34 ± 0.04	2.93 ± 0.18	12.0	30
	1980	0.26 ± 0.30	2.98 ± 0.25	9.3	17
	1981	0.34 ± 0.19	3.09 ± 0.32	10.8	5
Pregnant	1979	0.53 ± 0.08	4.78 ± 0.25	10.7	12
	1980	1.11 ± 0.16	5.68 ± 0.41	19.9	6
	1981	0.27 ± 0.10	3.15 ± 0.30	8.6	3
Lactating	1979	0.53 ± 0.08	6.03 ± 0.30	8.9	7
	1980	0.52 ± 0.10	5.21 ± 0.15	9.9	4
	1981	0.88 ± 0.60	6.33 ± 0.23	14.0	2
Pregnant and lactating	1979	1.05 ± 0.22	6.19 ± 0.31	16.3	13
	1980	1.11 ± 0.39	5.79 ± 0.36	18.6	4
	1981	0.94 ± 0.18	5.78 ± 0.16	16.5	3

Table 27. Fat, lean dry weight and percent fat among M. pennsylvanicus females, in relation to reproductive status and year, from the high elevation. Percent fat = (fat(g) ÷ lean dry weight (g)) x 100.

Reproductive Group	Year	Fat(g)	Lean dry weight(g)	Percent fat	n
Immature	1979	--	--	--	0
	1980	0.33 ± 0.04	3.20 ± 0.29	10.8	17
	1981	0.54 ± 0.00	2.34 ± 0.00	23.1	1
Pregnant	1979	--	--	--	0
	1980	--	--	--	0
	1981	1.28 ± 0.33	4.86 ± 0.81	25.4	4
Lactating	1979	0.39 ± 0.00	5.63 ± 0.00	6.9	1
	1980	--	--	--	0
	1981	1.47 ± 0.19	6.13 ± 0.63	24.0	4
Pregnant and lactating	1979	0.75 ± 0.00	6.80 ± 0.00	11.0	1
	1980	0.85 ± 0.25	7.15 ± 1.39	14.0	3
	1981	1.65 ± 0.27	7.62 ± 0.56	21.5	4

groups ($F = 2.61$, $p<0.05$). This interaction resulted from no differences among reproductive groups in 1979 and 1981 ($F = 2.55$, $p_3>0.05$; $F = 1.37$, $p_3>0.05$, respectively), but a significant difference among groups in 1980 ($F = 5.13$, $p_3<0.05$). In 1980 immature females had significantly less fat than pregnant females, while the other two reproductive groups were intermediate between these (Student-Newman-Keuls range test). These data do not follow a logical pattern and, in general, fat content did not vary in a consistent manner with reproductive status.

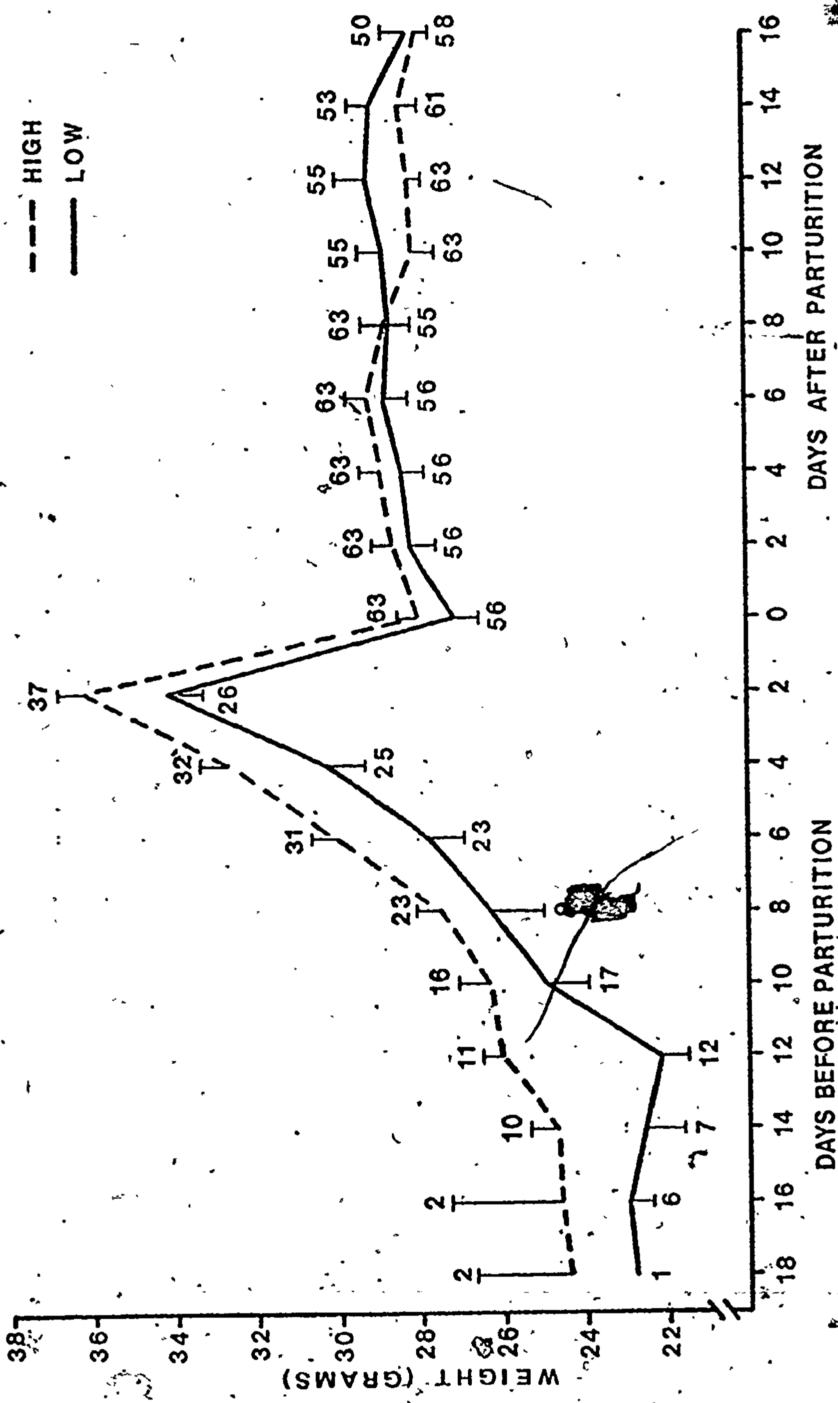
Fat content of males is examined in Appendix 5. There was no significant difference in the amount of relative fat content of C. gapperi males between elevations, but M. pennsylvanicus at the high elevation had significantly more relative fat than those at the low elevation.

3.3.2 Weight changes during pregnancy and lactation.

Weight changes during pregnancy and lactation were examined among laboratory females. In general, all females increased in weight during pregnancy and maintained a relatively constant weight during lactation (Figures 5 and 6). In both species, post-partum weights were not significantly different between elevations (Table 28); overlapping standard errors on other days indicated no differences between elevations in either species.

FIGURE 5

Changes in weight during pregnancy and lactation in _C. gapperi_, at the low and high elevations. One S.E. is given above and below the mean, and numbers refer to sample sizes.


HIGH
LOW
WEIGHT (GRAMS)
38
36
34
32
30
28
26
24
22
DAYS BEFORE PARTURITION
18
16
14
12
10
8
6
4
2
0
DAYS AFTER PARTURITION
2
4
6
8
10
12
14
16
2
2
10
11
16
23
31
32
37
1
6
7
12
17
23
25
26
63
63
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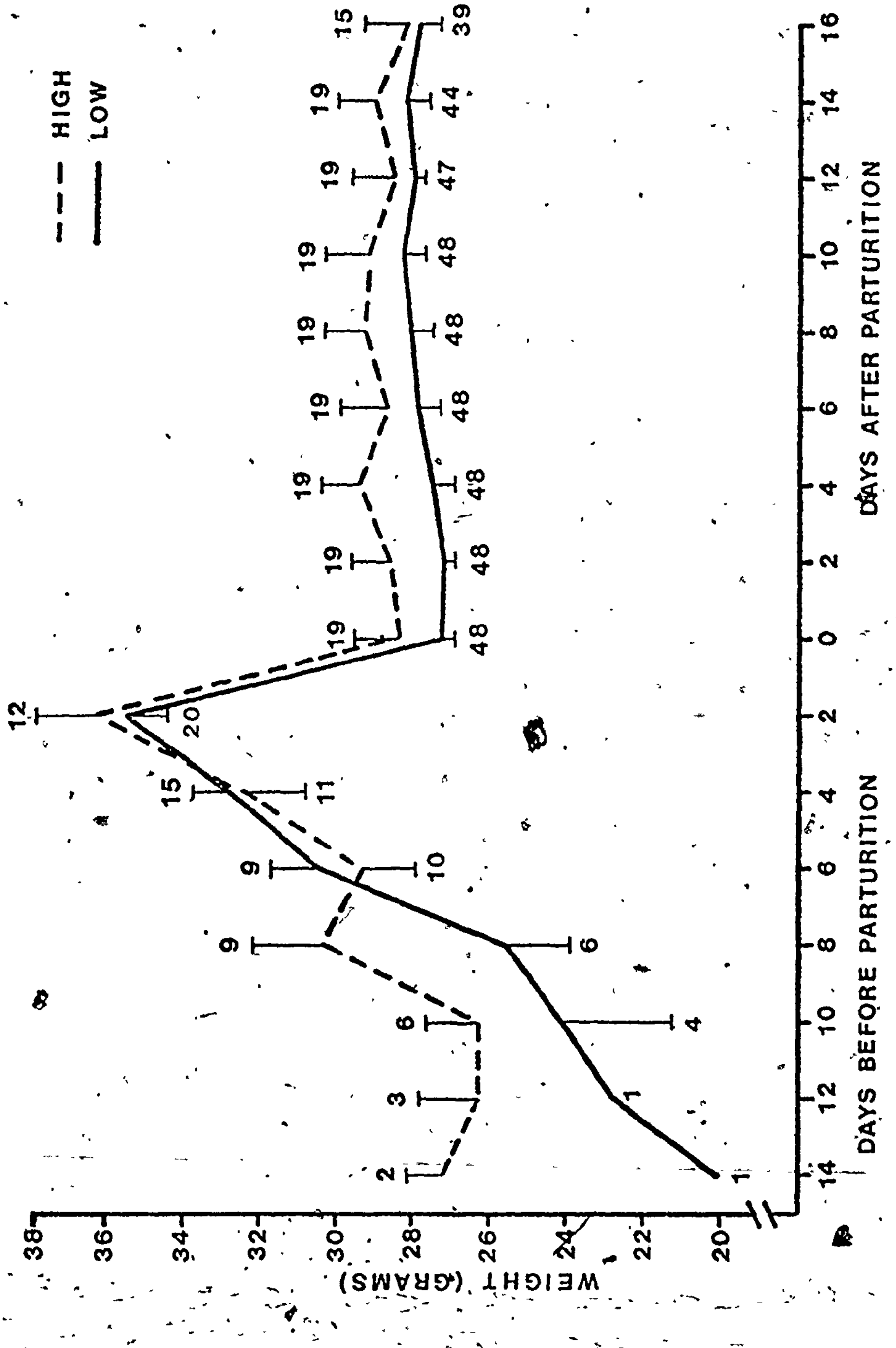
63
63
55
55
53
50
56
56
56
56
55
63
63
61
58

FIGURE 6

Changes in weight during pregnancy and lactation in _M. pennsylvanicus_, at the low and high elevations. One S.E. is given above and below the mean, and numbers refer to sample sizes.


HIGH
LOW
WEIGHT (GRAMS)
38
36
34
32
30
28
26
24
22
20
14
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8
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4
2
0
2
4
6
8
10
12
14
16
DAYS BEFORE PARTURITION
DAYS AFTER PARTURITION
2
3
6
9
9
15
12
19
19
19
19
19
19
19
19
15
1
1
4
6
10
11
20
48
48
48
48
48
48
47
44
39

Table 28. Post-partum weights of *C. gapperi* and *M. pennsylvanicus* laboratory females from the low and high elevations.

Species	Elevation	Weight	n	Significance
C. gapperi	low	27.2 ± 0.57	58	$t = 1.23^1$
	high	28.1 ± 0.46	67	
M. pennsylvanicus	low	26.6 ± 0.50	59	$t = 1.31^1$
	high	27.9 ± 0.92	22	

---

[1] t - values were not significant ($p>0.05$).

3.3.3 Amount of food required to raise a litter.

The energy required to raise young to weaning was examined in the laboratory by measuring food intake of pregnant and subsequently lactating females. The amount eaten per day by pregnant C. gapperi females from both elevations averaged approximately six grams per day (Figure 7). Food consumption declined sharply the day before parturition and the day of parturition. Food intake by C. gapperi females from both elevations increased rapidly during early lactation, after which it gradually increased to day 15 of lactation (the age at weaning). A similar pattern of food intake was found for M. pennsylvanicus females from both elevations (Figure 8).

Food intake by C. gapperi controls (non-pregnant, non-lactating) in relation to body weight was described by:

$$Y = -0.18 + 0.36X \qquad (6)$$

($r = 0.80$, $p<0.01$, $n = 44$) and

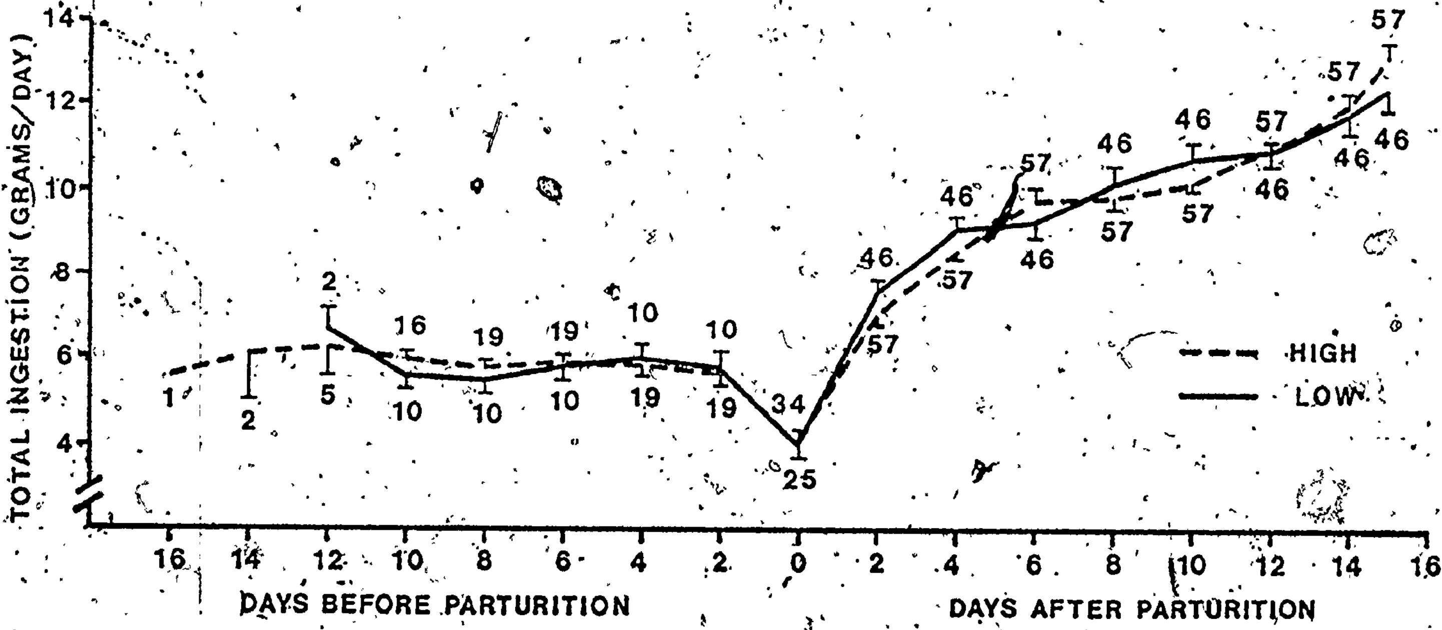
$$Y = 1.41 + 0.38X \qquad (7)$$

($r = 0.78$, $p<0.01$, $n = 41$) for females from the low and high elevations, respectively, where Y = mean food intake(g/2 days) and X = mean body weight(g). ANCOVA showed no significant differences in food intake between elevations, after adjusting for body weight ($F = 1.04$, $p>0.05$).

Food intake by M. pennsylvanicus controls in relation to body weight was described by:

FIGURE 7

Total ingestion (grams/day) by C. gapperi during pregnancy and lactation, at the low and high elevations. One S.E. is given above and below the mean, and numbers refer to sample sizes.


TOTAL INGESTION (GRAMS/DAY)
14
12
10
8
6
4
16
14
12
10
8
6
4
2
0
2
4
6
8
10
12
14
16
DAYS BEFORE PARTURITION
DAYS AFTER PARTURITION
HIGH
LOW
1
2
2
5
16
10
19
10
19
10
10
19
10
19
34
25
46
57
46
57
57
46
46
57
46
57
57
46
57
46
57
46

2

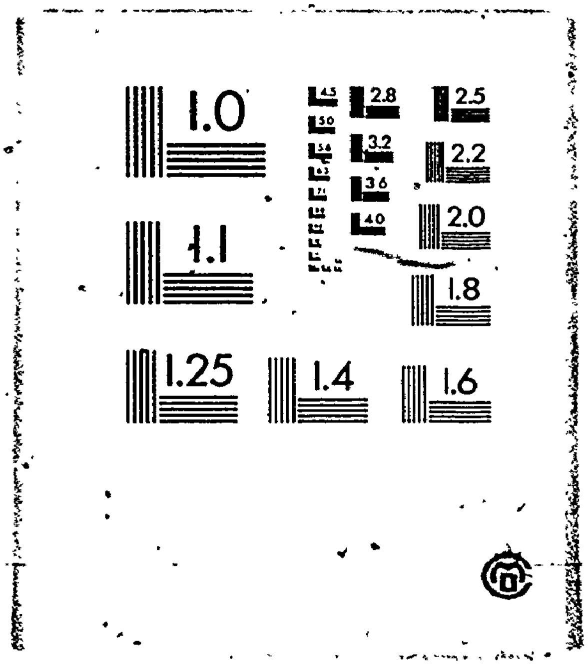
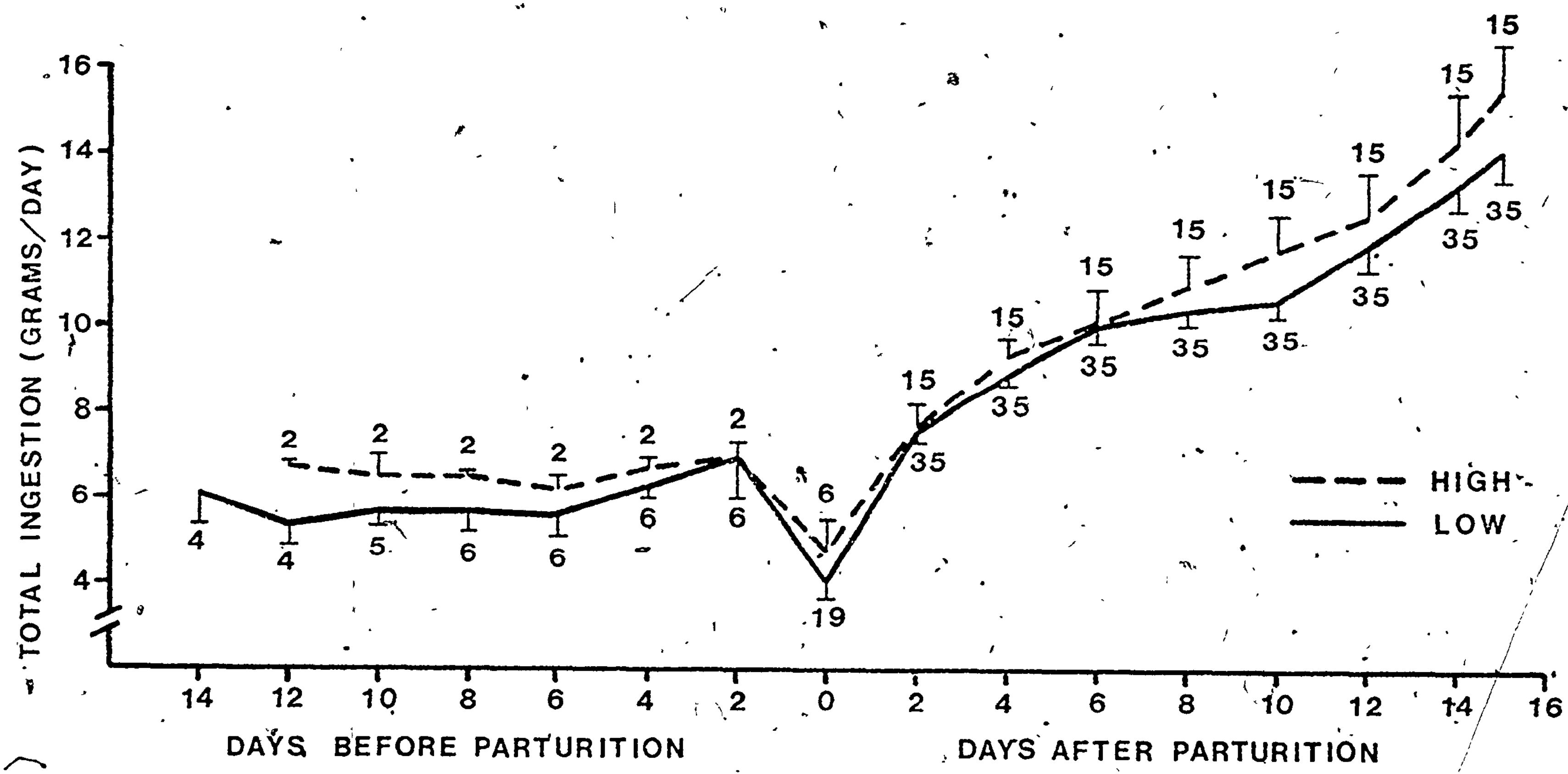


FIGURE 8

Total ingestion (grams/day) by M. pennsylvanicus during pregnancy and lactation, at the low and high elevations. One S.E. is given above and below the mean, and numbers refer to sample sizes.


TOTAL INGESTION (GRAMS/DAY)
16
14
12
10
8
6
4
14
12
10
8
6
4
2
0
2
4
6
8
10
12
14
16
DAYS BEFORE PARTURITION
DAYS AFTER PARTURITION
HIGH
LOW
2
2
2
2
2
2
6
15
15
15
15
15
15
15
15
4
4
5
6
6
6
6
19
35
35
35
35
35
35
35
35

$$Y = 2.85 + 0.25X \tag{8}$$

($r = 0.73$, $p<0.01$, $n = 64$) and

$$Y = 4.34 + 0.25X \tag{9}$$

($r = 0.64$, $p<0.01$, $n = 29$) for females from the low and high elevations, respectively. ANCOVA showed no significant difference in food intake, between elevations, after adjusting for body weight ($F = 1.36$, $p>0.05$).

Total food ingestion and maintenance costs during gesta- tion were not determined because of small samples and incomplete data (Figures 7 and 8). The maintenance costs of lactating females were calculated using the food intake of controls of an equivalent weight (Equations 6 to 9). The weights of lactating females represented an average of nine weighings taken during lactation. Weights of _C. gapperi_ females averaged 28.8 ± 0.64g and 28.3 ± 0.47g during lactation, at the low and high elevations, respectively. Weights of _M. pennsylvanicus_ females averaged 27.7 ± 0.59g and 28.7 ± 1.22g during lactation, at the low and high elevations, respectively.

Food ingestion during lactation was examined in relation to litter size (Tables 29 and 30). Since the amount of food ingested for offspring was significantly correlated with litter size in both _C. gapperi_ populations (low elevation: $r = 0.75$, $p<0.01$, $n = 46$; high elevation: $r = 0.51$, $p<0.01$, $n = 57$), ANCOVA was used to test for differences between elevations. No significant differences were found

Table 29. Ingestion during lactation by *C. gapperi*, in relation to litter size, at the low and high elevations. Ingestion for offspring = total ingestion minus maintenance costs. To convert grams to kilojoules, multiply by 17.8.

Litter[1] size	n		Total ingestion(g)		Maintenance costs(g)		Ingestion for offspring(g)	
	Low	High	Low	High	Low	High	Low	High
1	2	0	84.4 ± 10.7	--	67.9 ± 4.5	--	16.5 ± 6.2	--
2	1	0	122.0	--	87.1	--	34.9	--
3	5	2	118.0 ± 4.5	130.0 ± 4.3	70.4 ± 4.1	65.5 ± 0.1	47.6 ± 4.2	64.4 ± 4.2
4	8	12	142.4 ± 6.9	130.4 ± 2.7	74.1 ± 4.5	67.3 ± 1.7	68.3 ± 4.5	63.1 ± 2.6
5	16	12	150.5 ± 6.2	147.6 ± 5.3	72.2 ± 2.2	70.2 ± 2.4	78.3 ± 5.8	77.5 ± 4.8
6	7	24	150.8 ± 8.5	152.5 ± 4.2	72.5 ± 3.3	69.0 ± 1.6	78.3 ± 6.0	83.5 ± 3.5
7	7	6	192.8 ± 4.3	168.8 ± 7.1	89.2 ± 3.3	74.6 ± 2.6	103.6 ± 4.2	94.2 ± 5.6
8	0	1	--	143.8	--	68.7	--	75.1
Grand Means	46	57	148.5 ± 4.6	147.6 ± 2.7	75.1 ± 1.6	69.3 ± 1.0	73.4 ± 3.8	78.2 ± 2.3

---

[1] The mean litter size was 4.8 ± 0.2 and 5.4 ± 0.1 for the low and high elevations, respectively.

Table 30. Ingestion during lactation by M. pennsylvanicus, in relation to litter size, at the low and high elevations.

See Table 29 for further explanation.

Litter size[1]	n		Total ingestion(g)		Maintenance costs(g)		Ingestion for offspring(g)	
	Low	High	Low	High	Low	High	Low	High
2	1	0	105.6	--	71.4	--	34.2	--
3	5	2	123.6 ± 14.2	166.9 ± 20.2	69.6 ± 5.1	70.2 ± 1.3	54.0 ± 11.2	96.6 ± 21.5
4	8	1	134.8 ± 7.1	170.5	69.2 ± 2.0	63.8	65.5 ± 6.6	106.7
5	9	4	159.5 ± 4.9	162.0 ± 12.2	74.8 ± 1.3	76.5 ± 3.4	84.7 ± 5.2	85.5 ± 9.4
6	9	4	191.1 ± 10.2	183.7 ± 32.1	76.0 ± 1.8	73.0 ± 3.1	115.1 ± 9.6	110.7 ± 29.1
7	2	3	160.7 ± 17.0	154.5 ± 9.6	77.0 ± 1.7	73.2 ± 1.5	83.7 ± 15.3	81.3 ± 8.3
8	1	1	157.6	221.9	74.6	88.8	83.0	133.1
Grand means	35	15	155.3 ± 5.7	171.5 ± 9.7	73.1 ± 1.1	74.0 ± 1.8	82.2 ± 5.2	97.5 ± 8.7

---

[1] The mean litter size was 4.9 ± 0.2 and 5.5 ± 0.4 for the low and high elevations, respectively.

in the amount of food invested in offspring between elevations, after adjusting for litter size. ($F = 0.22$, $p > 0.05$).

Ingestion of food for M. pennsylvanicus offspring was significantly correlated with litter size only at the low elevation ($r = 0.61$, $p < 0.01$, $n = 35$). A two-way ANOVA indicated there were no significant differences in the amount of food ingested for young between elevations ($F = 0.03$, $p > 0.05$), but there were significant differences among litters of five, six and seven young ($F = 3.91$, $p < 0.05$).

3.3.4 Indices of physiological reproductive effort.

Indices of reproductive effort can show how the basic energy requirements are partitioned during reproduction and this may reflect future maternal and offspring survival. Since these indices are measured under specified laboratory conditions, the term physiological reproductive effort is used (Randolph et al. 1977).

Three indices were examined and all three increased with increasing litter size (Tables 31 and 32), so that litter size was used as a covariate along with the denominator of each index.

In C. gapperi, the ratio of litter weight at birth to female body weight (Williams 1966) averaged 0.33 ($n = 58$) and 0.35 ($n = 65$) for females from the low and high elevations, respectively. Post-partum weight and litter weight at birth were significantly correlated at both

Table 31. Comparison of three indices of physiological reproductive effort in *C. gapperi*, in relation to litter size, at the low and high elevations.

	Litter weight at birth/ female weight				Litter metabolism at weaning/ female metabolism				Food invested in offspring/ total ingestion during lactation			
	Low	n	High	n	Low	n	High	n	Low	n	High	n
Litter size												
1	0.09	2	--	0	0.58	2	--	0	0.19	2	--	0
2	0.13	2	--	0	1.02	1	--	0	0.29	1	--	0
3	0.28	6	0.12	6	1.44	5	1.60	2	0.40	2	0.50	2
4	0.28	10	0.29	10	1.82	8	1.81	12	0.48	8	0.48	12
5	0.35	18	0.32	21	2.20	16	2.12	12	0.51	16	0.52	12
6	0.40	9	0.37	28	2.27	7	2.47	24	0.52	7	0.54	24
7	0.40	10	0.41	6	2.60	7	2.64	6	0.53	7	0.56	6
8	—	0	0.44	2	--	0	2.80	1	--	0	0.52	1
9	--	0	0.48	2	—	0	--	0	--	0	--	0
10	0.58	1	--	0								
Grand means	0.33		0.35		2.0		2.3		0.49		0.53	

Table 32. Comparison of three indices of physiological reproductive effort in *M. pennsylvanicus*, in relation to litter size, at the low and high elevations.

	Litter weight at birth/ female weight				Litter metabolism at weaning/ female metabolism				Food invested in offspring/ total ingestion during lactation			
	Low	n	High	n	Low	n	High	n	Low	n	High	n
Litter size												
1	--	0	--	0	--	0	--	0	--	0	--	0
2	--	0	--	0	0.89	1	--	0	0.32	1	--	0
3	0.27	6	0.22	1	1.48	5	1.44	2	0.42	5	0.57	2
4	0.34	10	0.32	3	2.00	8	2.60	1	0.48	8	0.63	1
5	0.38	20	0.35	5	2.24	9	2.20	4	0.53	9	0.52	4
6	0.43	11	0.46	6	2.71	9	2.69	4	0.60	9	0.57	4
7	0.45	4	0.48	4	2.82	2	2.60	3	0.52	2	0.52	3
8	0.57	1	0.46	1	3.03	1	3.45	1	0.53	1	0.60	1
9	--	0	0.73	1	--	0	--	0	--	0	--	0
Grand means	0.38		0.42		2.2		2.4		0.53		0.57	

elevations (low elevation: $r = 0.46$, $p<0.05$; high elevation: $r = 0.32$, $p<0.01$). ANCOVA showed no differences in litter weight between elevations ($F = 0.03$, $p>0.05$) after adjusting for female weight and litter size.

In M. pennsylvanicus, the ratio of litter weight at birth to female weight averaged 0.38 ($n = 52$) and 0.42 ($n = 21$) for females from the low and high elevations, respectively. Post-partum weight and litter weight at birth were significantly correlated in both populations (low elevation: $r = 0.46$, $p<0.01$; high elevation: $r = 0.38$, $p<0.05$). Again, ANCOVA showed no differences in litter weight between elevations ($F = 0.02$, $p<0.05$) after adjusting for female weight and litter size.

Another index, based on the ratio of litter metabolism at weaning to female metabolism, was calculated from:

$$N\ Ww^{0.75}(m^{0.75})^{-1} \qquad (10)$$

where N = litter size, Ww = mean weight of young at weaning(g) and m = mean female weight during lactation (Millar 1977). This index gave means of 2.0 ($n = 46$) and 2.3 ($n = 57$) for the low and high C. gapperi populations, respectively. Female weight during lactation and weight of young at weaning were significantly correlated in both populations (low elevation: $r = 0.53$, $p<0.01$; high elevation: $r = 0.46$, $p<0.01$). ANCOVA showed no differences in the metabolism index between elevations ($F = 0.22$, $p>0.05$) after adjusting for female metabolism and litter size.

In M. pennsylvanicus, the mean ratio of litter metabolism at weaning to female metabolism was 2.2 (n = 35) and 2.4 (n = 15) for females from the low and high elevations, respectively. Female weight during lactation and weight of young at weaning were significantly correlated in both populations (low elevation: $r = 0.56$, $p<0.01$; high elevation: $r = 0.76$, $p<0.01$). ANCOVA showed no differences in the metabolism index between elevations ($F = 0.01$, $p>0.05$) after adjusting for female metabolism and litter size.

A third index, based on the amount of food ingested during reproduction, was calculated from:

$$IR(TI)^{-1} \tag{11}$$

where IR = ingestion for offspring(g) (= total ingestion - maintenance costs) and TI = total ingestion(g) (Innes and Millar 1981). Calculated for lactation only, this index gave mean ratios of 0.49 (n = 46) and 0.53 (n = 57) for the low and high C. gapperi populations, respectively. IR was significantly correlated with TI in both populations (low elevation: $r = 0.94$, $p<0.01$; high elevation: $r = 0.94$, $p<0.01$). ANCOVA showed that females from the low elevation ingested significantly less for their offspring than those from the high elevation, after adjusting for the total amount eaten and litter size ($F = 9.86$, $p<0.01$).

In M. pennsylvanicus, the mean ratio for this index was 0.53 (n = 35) and 0.57 (n = 15) for the low and high elevations, respectively. IR was significantly correlated with TI in both populations (low elevation: $r = 0.99$, $p<0.01$; high elevation: $r = 0.99$, $p<0.01$). ANCOVA showed no difference in the amount of food ingested for offspring between elevations ($F = 0.44$; $p>0.05$), after adjusting for total ingestion and litter size.

3.4 Growth and development.

3.4.1 Growth.

Growth of microtines in the laboratory may differ among litter sizes and between sexes (Innes and Millar 1979). Differences in these variables could bias comparison of growth between elevations. Weight was negatively correlated with litter size (at various ages) in both species and mean litter size of families used for growth was greater at the high elevation than at the low elevation (Appendix 6). To compare growth of young between elevations, only litters of six were used, in both species, because samples were not large enough to compare growth of other litter sizes.

Individual growth within litters was not documented and therefore, possible differential growth of the sexes could not be determined. Sex ratios of C. gapperi young used for growth estimates from litters of six (with no mortality within a litter) were 75.0% and 50.0% males for the low and high elevation populations, respectively. These ratios were not significantly different ($X^2 = 2.24$, $p>0.05$, $n = 60$).

Sex ratios of M. pennsylvanicus young used for growth estimates from litters of six (with no mortality) were 58.3% and 25.0% males for the low and high elevation populations, respectively. These ratios were not significantly different ($X^2 = 2.74$, $p>0.05$, $n = 24$). Therefore, differences in growth between the sexes was unlikely to bias growth rate comparisons between elevations, in either species.

The average growth rate of C. gapperi young from litters of six, from birth to 30 days, was 0.54g/day and 0.56g/day from the low and high elevations, respectively. Growth was described by:

$$LN(Y) = LN(0.34) + 0.68LN(X) \qquad (12)$$

($r = 0.97$, $p<0.01$, $n = 342$) and

$$LN(Y) = LN(0.32) + 0.72LN(X) \qquad (13)$$

($r = 0.97$, $p<0.01$, $n = 1056$) for young from the low and high elevations, respectively. Overlapping standard errors at most ages indicated no differences in weights between elevations (Figure 9). The average growth rate of M. pennsylvanicus young from litters of six, from birth to 30 days, was 0.59g/day and 0.52 g/day from the low and high elevations, respectively. Growth was described by:

$$LN(Y) = LN(0.55) + 0.67LN(X) \qquad (14)$$

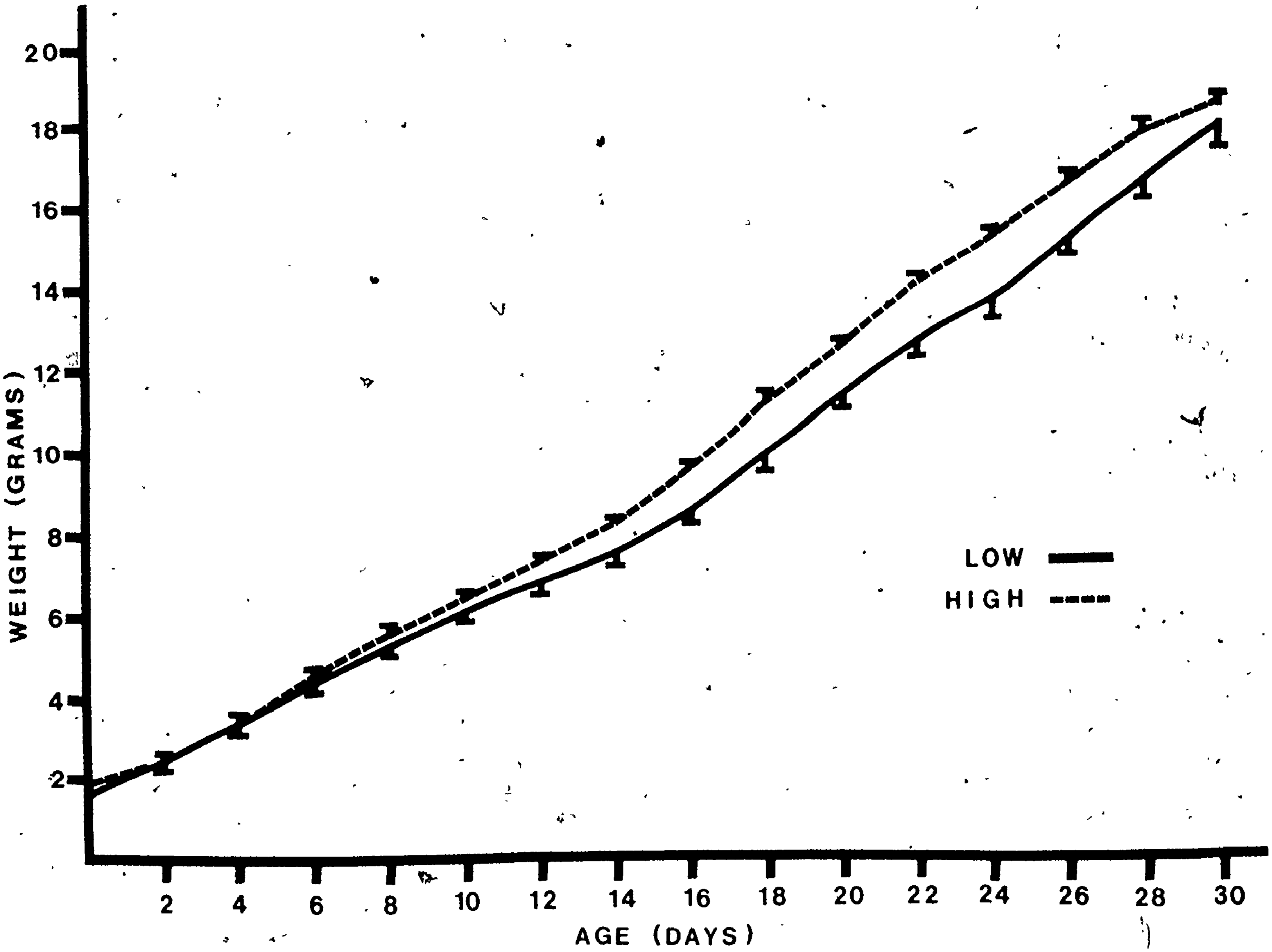
($r = 0.95$, $p<0.01$, $n = 528$) and

$$LN(Y) = LN(0.59) + 0.66LN(X) \qquad (15)$$

($r = 0.96$, $p<0.01$, $n = 203$) for young from the low and high elevations, respectively. Overlapping standard errors at most ages indicated no differences between elevations

FIGURE 9

Growth of C. *gapperi*, from birth to 30 days, in the laboratory; litters of six only. One S.E. is given below and above the mean for the low and high elevations, respectively. Samples ranged from 24 to 12 individuals for the low elevation and were 66 individuals at all ages for the high elevation.



WEIGHT (GRAMS)
20
18
16
14
12
10
8
6
4
2
AGE (DAYS)
2
4
6
8
10
12
14
16
18
20
22
24
26
28
30
LOW
HIGH

(Figure 10).

Growth of wild young-of-the-year was examined from data collected on the mark-recapture grids. Growth rates were determined for young shortly after they entered the trappable population by selecting individuals weighing 15.0g or less at first capture, and that were reweighed within the next two weeks. Although growth may have varied among years, sample sizes were too small to partition the data in this manner. Seasonal differences in growth were examined by comparing samples from June and July with those from August and September (Table 33). Weight gain was significantly correlated with the number of days between captures only in M. pennsylvanicus young from the low elevation ($r = 0.67$, $p<0.01$, $n = 39$), and ANCOVA could not be used. A two-way ANOVA showed a significant difference in growth rates of C. gapperi young between monthly intervals ($F = 4.15$, $p<0.05$), but no difference between elevations ($F = 0.02$, $p>0.05$). The growth rates of M. pennsylvanicus young were significantly different between monthly intervals ($F = 16.51$, $p<0.01$), but not different between elevations ($F = 0.68$, $p>0.05$).

Weight of adults in the wild was examined between elevations by comparing the maximum weight obtained by over-wintered males on the mark-recapture grids. (Weight of adult females in the wild was not considered because weight varied with reproductive status.) Adult males were classified as non-residents if they were caught three times

FIGURE 10

Growth of M. pennsylvanicus from birth to 30 days in the laboratory; litters of six only. One S.E. is given below and above the mean for the low and high elevations, respectively. Samples ranged from 36 to 24 individuals and 18 to 12 individuals for the low and high elevations, respectively.

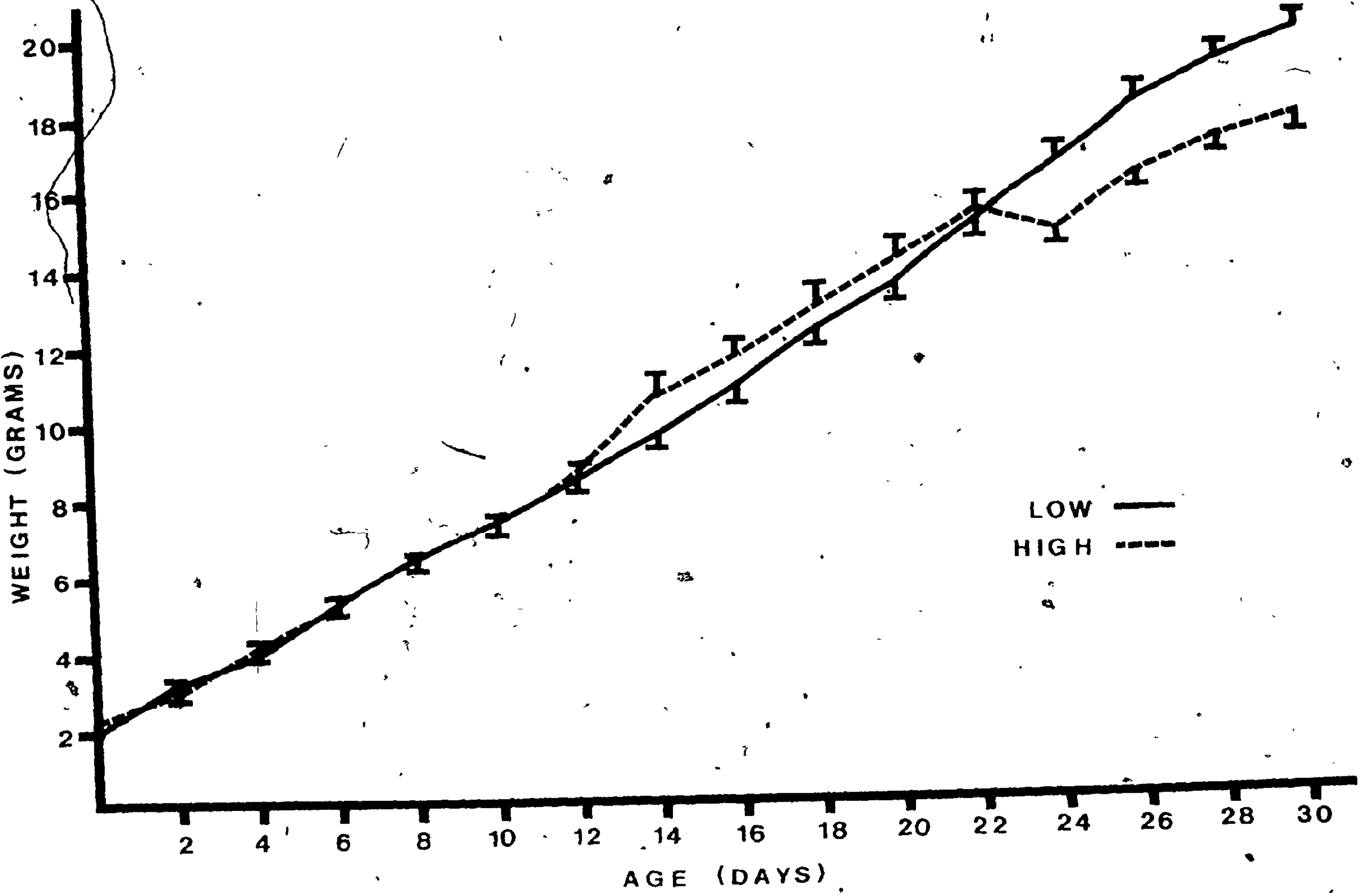

WEIGHT (GRAMS)
2
4
6
8
10
12
14
16
18
20
AGE (DAYS)
2
4
6
8
10
12
14
16
18
20
22
24
26
28
30
LOW
HIGH

Table 33. Growth rates of wild *C. gapperi* and *M. pennsylvanicus* young, in relation to season, at the low and high elevations.

Species	Elevation	Months	Growth rate (g/da)	n
C. gapperi	low	June and July	0.54	11
		August and September	0.34	17
		Mean	0.42	28
	high	June and July	0.49	13
		August and September	0.39	36
		Mean	0.42	49
M. pennsylvanicus	low	June and July	0.72	28
		August and September	0.39	11
		Mean	0.63	39
	high	June and July	0.86	12
		August and September	0.32	2
		Mean	0.78	14

or less and residents if they were caught more than three times. In all populations, the maximum weight of resident males significantly exceeded those of non-residents by at least two grams (C. gapperi: $F = 11.07$, $p<0.01$; M. pennsylvanicus: $F = 10.60$, $p<0.01$) (Table 34). Furthermore, males from the low elevation weighed significantly less than those from the high elevation (C. gapperi: $F = 13.62$, $p<0.01$; M. pennsylvanicus: $F = 12.12$, $p<0.01$).

3.4.2 Development.

Feotal growth rates were not estimated, but a minimum gestation period was established, based on the time between the capture of a pregnant female and the birth of her litter in the laboratory. Minimum gestation in C. gapperi was 19 days at both elevations. These estimates of gestation agree very closely with those previously reported (Langford 1980 - 18.5 days; Innes and Millar 1981 - 18.0 days). The minimum gestation lengths of M. pennsylvanicus were too short to be considered realistic.

Litters were checked when young were approximately seven days of age and daily thereafter, to determine when the young opened their eyes. In most cases littermates opened their eyes over a three day period, so the age at which all littermates had their eyes open was compared between elevations. The mean age when all C. gapperi littermates had their eyes open was 12.8 ± 0.14 days (n = 56

Table 34. Maximum weights of resident and non-resident over-wintered *C. gapperi* and *M. pennsylvanicus* males on mark-recapture grids, at the low and high elevations.

Species	Elevation	Weight of residents(g)	n	Weight of non-residents(g)	n
C. gapperi	low	25.1 ± 0.51	19	22.2 ± 1.10	12
	high	26.9 ± 0.53	34	25.3 ± 0.46	40
M. pennsylvanicus	low	32.9 ± 0.85	29	29.9 ± 0.74	51
	high	37.0 ± 1.35	10	33.5 ± 0.87	15

litters) and 13.4 ± 0.14 days (n = 64), for the low and high elevation populations, respectively. The mean age when all *M. pennsylvanicus* littermates had their eyes open was 10.1 ± 0.14 days (n = 49) and 10.8 ± 0.30 days (n = 19) for the low and high elevation populations, respectively. The age when all littermates had their eyes open was significantly correlated with litter size only in the low elevation populations (*C. gapperi*: $r = 0.42$, $p<0.01$; *M. pennsylvanicus*: $r = 0.39$, $p<0.01$). A two-way ANOVA indicated that there was no significant difference in the age at which *C. gapperi* young opened their eyes among litter sizes ($F = 1.42$, $p>0.05$), but there was a significant difference between elevations ($F = 5.74$, $p<0.05$). The equivalent analysis for *M. pennsylvanicus* young indicated a significant difference among litter sizes ($F = 3.84$, $p<0.01$), but no difference between elevations ($F = 3.70$, $p>0.05$).

The age at weaning was quantified following King *et al.* (1963). The relationship between weight change and age with isolation among *C. gapperi* young was described by:

$$Y = -6.15 + 0.41X \qquad (16)$$

($r = 0.62$, $p<0.01$, $n = 45$) and

$$Y = -6.13 + 0.42X \qquad (17)$$

($r = 0.65$, $p<0.01$, $n = 56$) for the low and high elevations, respectively, where Y = weight change(g) and X = age(days). ANCOVA (with age as the covariate) indicated that there were no significant differences between elevations in either the slopes ($F = 0.10$, $p>0.05$) or the intercepts ($F = 0.62$, $p>0.05$). Therefore, the ages at weaning (or the age at which young did not lose or gain weight); 15.1 days for young from the low elevation and 14.8 days for young from the high elevation, were not significantly different. Fifteen day old young averaged 9.2g and 8.9g at the low and high elevations, respectively (interpolated from Figure 24).

The relationship between weight change and age with isolation among M. pennsylvanicus young was described by:

$$Y = -3.27 + 0.21X \tag{18}$$

($r = 0.52$, $p<0.01$, $n = 52$) and

$$Y = -4.29 + 0.28X \tag{19}$$

($r = 0.52$, $p<0.01$, $n = 28$) for the low and high elevations, respectively. ANCOVA indicated that there were no significant differences in the slopes ($F = 0.56$, $p>0.05$) or intercepts ($F = 0.07$, $p>0.05$), and the age of weaning was 15.8 days and 15.3 days for young from the low and high elevations, respectively. Fifteen day old young averaged 10.0g and 9.9g at the low and high elevations, respectively (interpolated from Figure 25).

Age at weaning in the wild could not be estimated from eye lens age estimates (Appendix 3), however, weight distributions of live- and snap-tapped young ($\leq$ 20.0g) could be used to estimate the median weight at weaning. This method assumes that the most abundant weight class represents the weight at which all the young had entered the trappable population, before mortality had any significant effect on abundance (Millar et al. 1979).

The most abundant weight category (at 2.0g intervals) of C. gapperi young was 15.5g at both elevations (Figure 11). Taking each lower weight class as a percentage of the most abundant weight class and using probit analysis (Caughley and Caughley 1974; Finney 1952), the median weight at weaning of C. gapperi young was 12.7g and 12.1g from the low and high elevations, respectively.

The most abundant weight class of M. pennsylvanicus young was 13.5g at both elevations (Figure 12). The median weight at weaning of M. pennsylvanicus young was 9.2g and 10.4g from the low and high elevations, respectively. The median weights at weaning could not be tested directly for differences between elevations, but a comparison of the frequency distributions of weights (up to and including the most frequent weight class) showed no significant differences between elevations in either species (C. gapperi: X^2 = 7.24, $p>0.05$; M. pennsylvanicus: X^2 = 5.22, $p>0.05$).

Age at maturity can have a great impact on the rate of increase of a population (Cole 1954). Young-of-the-year could not be aged. However, growth rates of both laboratory and wild young were not different between elevations in either species, so that weight was used as an index of the age at maturity. Samples were too small to permit probit analysis, but mean and minimum weights of all kill-trapped pregnant, young-of-the-year females (minus embryo weight)

FIGURE 11

Weight distributions of C. gapperi young-of-the-year ($\leq$20.0g), at the low and high elevations (n represents the sample size).

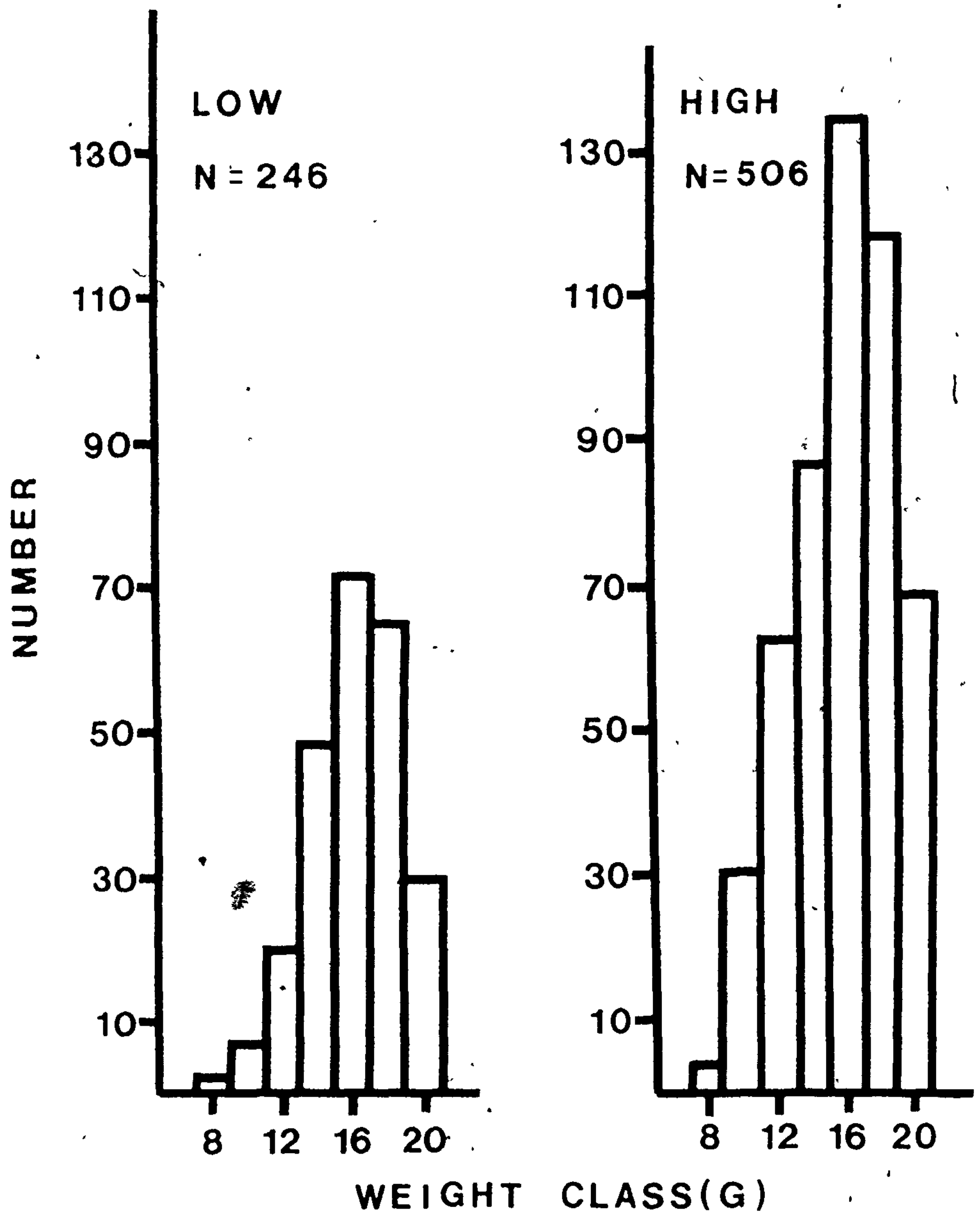
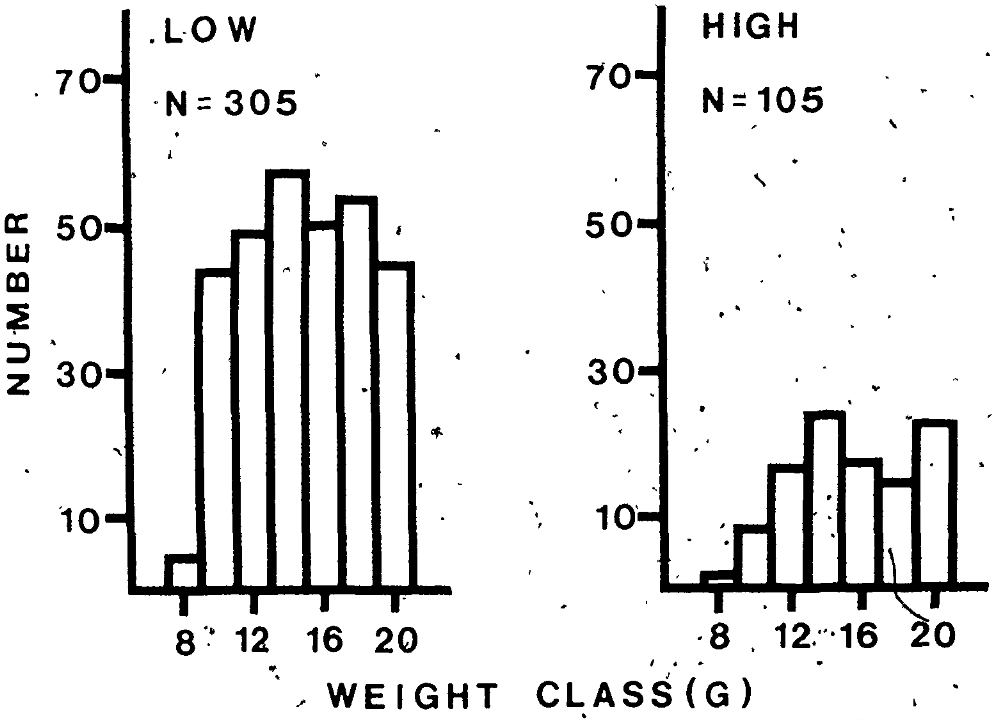

LOW
N = 246
HIGH
N=506
130
110
90
70
50
30
10
NUMBER
8
12
16
20
WEIGHT CLASS(G)

FIGURE 12

Weight distributions of M. pennsylvanicus young-of-the-year ($\leq$20.0g), at the low and high elevations (n represents the sample size).


LOW
N = 305
HIGH
N = 105
NUMBER
70
50
30
10
8
12
16
20
WEIGHT CLASS (G)

and mature, young-of-the-year males were compared (Tables 35 and 36). There were no significant differences in the mean weights of mature, young-of-the-year females between elevations, in either species (*C. gapperi*: t = 0.51; p>0.05; *M. pennsylvanicus*: t = 0.34, p>0.05). A comparison of minimum weights showed that some females matured at a very light weight, and likely at a very early age, in all populations (Table 35).

There was no significant difference in the mean weight of mature, young-of-the-year *C. gapperi* males between elevations (t = 1.20, p>0.05), although mature, young-of-the-year *M. pennsylvanicus* males at the low elevation were significantly heavier than those at the high elevation (t = 2.72, p<0.01). A comparison of minimum weights showed that some males, like females, matured at a very light weight, and likely at a very early age, in all populations (Table 36).

Table 35. Mean and minimum weights of mature, young-of-the-year *C. gapperi* and *M. pennsylvanicus* females, at the low and high elevations.

Species	Elevation	Mean weight(g)	Minimum weight(g)	n
C. gapperi	low	21.8 ± 1.45	16.0	6
	high	23.3 ± 2.47	14.6	8
M. pennsylvanicus	low	23.3 ± 1.20	11.1	25
	high	24.0 ± 2.06	14.1	7

Table 36. Mean and minimum weights of mature, young-of-the-year *C*, *gapperi* and *M*. *pennsylvanicus* males, at the low and high elevations.

Species	Elevation	Mean weight(g)	Minimum weight(g)	n
C. *gapperi*	low	16.7 ± 0.53	10.8	28
	high	17.4 ± 0.29	10.6	78
M. *pennsylvanicus*	low	21.9 ± 0.92	10.8	39
	high	18.0 ± 0.98	11.0	23

CHAPTER 4

DISCUSSION

4.1 Summary of the results.

The length of the breeding season of *C. gapperi* averaged only two days longer at the low elevation than at the high elevation, over two years. The length of the breeding season of *M. pennsylvanicus* averaged 27 days longer at the low elevation than at the high elevation. *Microtus pennsylvanicus* females, unlike *C. gapperi* females, had time to produce one more litter than those at the high elevation, if they survived the entire breeding season at the low elevation. However, the potential to produce as many litters as the length of the breeding season could accommodate was rarely realized. The average number of litters produced was slightly less than two in all populations.

When parity and month effects were controlled there was no significant difference in the mean litter size of *C. gapperi* between elevations, but the mean litter size of *M. pennsylvanicus* was significantly greater (by 1.02 offspring) at the high elevation than at the low elevation.

Taken alone, neither litter size nor the number of litters, provides a complete picture of total reproductive output. The mean reproductive capacity (mean litter size x mean number of litters) estimates the potential fitness of an average female. The mean reproductive capacity of C. gapperi was 11.1 offspring/female at the low elevation and 12.5 offspring/female at the high elevation. Mean reproductive capacity of M. pennsylvanicus was 9.5 offspring/female at the low elevation and 10.3 offspring/female at the high elevation. Thus, mean reproductive capacities were similar between elevations, in both species.

Nestling survival differed significantly between elevations in two of the three years, in both species. Nestling survival of C. gapperi followed no consistent pattern, being greatest at the high elevation in 1980 and greatest at the low elevation in 1981, and not different when all years were combined (low elevation: 31.1%; high elevation: 30.6%). Nestling survival of M. pennsylvanicus was greater at the low elevation than the high elevation in 1979 and 1981, and when all years were combined (low elevation: 42.5%; high elevation: 20.0%). Two-week survival rates during the summer were not different between elevations in either sex, in both species. Winter survival was variable among years, but generally low (<20.0%) in both species. There were no significant differences in winter survival between elevations.

There were no significant differences in the relative fat content of females between elevations, in both species. Females also did not appear to deposit energy (fat) that was subsequently used to support offspring. The relative fat contents of C. gapperi males were not different between elevations, but M. pennsylvanicus males at the high elevation had relatively more fat than those at the low elevation.

Under laboratory conditions, the weights of pregnant and subsequently lactating females showed no differences between elevations in either species. Also, the amount of food ingested by females during lactation was not different between elevations in either species. One index of physiological reproductive effort (amount of food ingested for young ÷ total amount of food ingested during lactation) was greater for C. gapperi females from the high elevation than from the low elevation. No index of physiological reproductive effort of M. pennsylvanicus showed a difference between elevations.

Growth of laboratory young from birth to 30 days of age (from litters of six), and growth rates of young in the wild, were not different between elevations, in either species. The maximum weight attained by over-wintered males on mark-recapture grids was greater at the high elevation than the low elevation, in both species. This difference applied to both short-term and long-term residents.

Minimum gestation length in C. gapperi was not different between elevations; realistic estimates for M. pennsylvanicus were not recorded. The age when all littermates opened their eyes was approximately 1.5 days later in C.

gapperi at the high elevation than at the low elevation, while in M. pennsylvanicus there was no difference between elevations. The laboratory estimates of the age at weaning were not different between elevations in either species. There were no differences in the weights at which young entered the trappable population between elevations in either species.

The mean weights of mature, young-of-the-year females were not different between elevations in either species and minimum weights indicated that females from all populations could breed at a very light weight. Mean weights of mature, young-of-the-year C. gapperi males were not different between elevations. Mean weights of mature, young-of-the-year M. pennsylvanicus males were greater at the low elevation than the high elevation. Males could also breed at a very light weight in all populations.

4.2 Evaluation of the hypothesis.

A combination of colder temperatures, fewer frost-free days and a delay in the onset of the snowmelt should shorten the growing season and decrease the time that food is plentiful for these species, thus shortening the length of the breeding season at the high elevation compared to the low elevation. However, the length of the breeding season was shorter at the high elevation than at the low elevation only for M. pennsylvanicus. The length of the breeding season of

C. gapperi showed no real difference between elevations.

Since the general climatic conditions were the same for both species, at each elevation, differences in the lengths of the breeding seasons may be related to the different habitats they occupy. Greater snow accumulation, resulting in more runoff could limit the length of the breeding season of M. pennsylvanicus at the high elevation relative to the low elevation. Most M. pennsylvanicus at the high elevation were caught in a meadow which was extensively flooded for most of June in all years (personal observations). Flooding or a combination of flooding and colder temperatures could delay breeding at the high elevation, whereas M. pennsylvanicus at the low elevation experienced no flooding and warmer temperatures. The length of the breeding season of C. gapperi at both elevations would not be influenced by flooding because runoff did not accumulate in their forest habitats (personal observations).

The length of the breeding season of C. gapperi was similar at both elevations. According to Spencer and Steinhoff (1968) no differences in litter size, the number of litters or female survival should have been found between elevations. This was the case. The length of the breeding season of M. pennsylvanicus was shorter at the high elevation than at the low elevation. According to Spencer and Steinhoff (1968) there should be fewer opportunities to breed, but larger litters and poorer female survival at the high elevation than at the low elevation. However, the shorter breeding season at the high elevation did not result in fewer opportunities to breed than at the low elevation. The mean number of litters produced was slightly less than two, at both elevations. Most females had ample time to produce more litters at both elevations, but did not survive long enough to do so. A long breeding season could only be taken advantage of by long-lived females and there were very few of these at either elevation. The litter size of *M. pennsylvanicus* was significantly greater at the high elevation than at the low elevation, even though the number of litters produced was the same at both elevations. This is contrary to Spencer and Steinhoff's hypothesis. A large litter size at the high elevation did not seem to incur a greater risk to those females, as assumed by Spencer and Steinhoff; survival of females during [illegible] summer did not differ between elevations. However, nestling survival of *M. pennsylvanicus* was significantly greater at the low elevation than at the high elevation.

If females in most populations average only two litters, as indicated in this study, then Spencer and Steinhoff's hypothesis may only be applicable to populations where the length of the breeding season limits the average female to producing much less than two litters. However, snap-trapping data suggests that females (both adult and young) in very time restricted environments (i.e. at very high latitudes) all appear to be able to produce at least two litters per season: *C. gapperi*-60°N (Fuller 1969);

M. pennsylvanicus - 69°N (Martell and Pearson 1978). If average females produce approximately two litters irrespective of the length of the breeding season, then Spencer and Steinhoff's hypothesis cannot explain variation in litter size or survival among populations in these species. Data from populations where the average number of litters per season is only one, or greatly exceeds two, are needed.

To examine Spencer and Steinhoff's hypothesis more generally, I searched the literature for estimates of litter size, the number of litters, female survival and lengths of the breeding season (Appendix 7). Litter sizes were primarily embryo counts taken from at least six females within a population, following Innes (1978). Estimates of the maximum number of litters per season were used because the average number was rarely reported. Survival estimates were too few to be included in the analyses. The length of the breeding season was defined as the number of months in which pregnant females were caught.

Litter size was significantly and positively correlated with the length of breeding season in C. gapperi ($r = 0.58$, $p<0.05$, $n = 14$), but the maximum number of litters per season showed no significant relationship ($r = 0.00$, $p>0.05$, $n = 6$). Litter size was significantly and negatively correlated with the length of the breeding season in M. pennsylvanicus ($r = -0.51$, $p<0.05$, $n = 12$) but the maximum number of litters per season showed no significant relationship ($r = 0.34$, $p>0.05$, $n = 5$). If Spencer and Steinhoff's hypothesis is correct, litter size should be negatively correlated with the length of the breeding season, while the maximum number of litters should be positively correlated with the length of the breeding season. Only the relationship between litter size and the length of the breeding season in M. pennsylvanicus agreed with the predictions, indicating that the relationship among length of the breeding season, litter size and number of litters is weak.

Fleming and Rausher (1978) and Millar (1978) suggested that negative correlations between litter size and the length of the breeding season may be biased, reflecting difference in age structure, with a higher proportion of older, more experienced females carrying larger litters being caught in areas with short breeding seasons than in areas with long breeding seasons. This study shows, however, that significant differences in litter size do occur between areas with different lengths of the breeding season even when month and parity were taken into account.

4.3 Evaluation of the life-history traits differing between elevations.

If life-history traits differ between elevations and cannot be related to the length of the breeding season, then they must be explained in other ways. The following traits of C. gapperi showed differences between elevations: maximum weights of over-wintered males, the age when the young opened their eyes and the food ingestion index of physiological reproductive effort. The following traits of M. pennsylvanicus showed differences between elevations: litter size, nestling survival, maximum weights of over-wintered males, the mean weights of mature, young-of-the-year males and the relative fat content of males. Many of these differences are probably phenotypic responses to environmental conditions. Krohne (1981) found that litter size in M. californicus had low heritability and this may be the case for many other microtine life-history traits. Therefore, selection may operate only very slowly on microtine life-history traits. Genetic differences in life-history traits have not been demonstrated, but phenotypic responses to differences in forage quality have been documented (e.g. Cengel et al. 1978; Cole and Batzli 1979; Krohne 1980). For example, the prairie vole, M. ochrogaster was heavier, fatter and had a greater litter size in an alfalfa habitat than in a bluegrass habitat (Cole and Batzli 1979). This was correlated with the nutritive value of the plants in each habitat; alfalfa contained more digestible energy and more crude protein than did bluegrass.

In this study, food quality may have been greater at the high elevation that at the low elevation. I have no direct measure of this, but subalpine and alpine plants are known to have high caloric values (Anderson and Armitage 1976). Potential food items are likely different between elevations (Appendix 1) and, if the growing season is shorter at the high elevations, more synchronous growth of young plants may influence life-history traits to a greater degree than at the low elevation, where a longer growing season would make plant growth less synchronous. Young plants have more protein and are easier to digest than mature plants (Bezeau and Johnston 1962; Campbell and Cassady 1954).

Diet is not likely the only factor determining variation in litter size, body weight and relative fat content because for example, C. gapperi should have shown differences in litter size and the relative fat content of males between elevations, but they did not. The relationship between life-history traits and food quality has not been investigated in Clethrionomys spp. It is possible that their omnivorous diets are similar in quality in different areas.

Poorer nestling survival of M. pennsylvanicus at the high elevation than at the low elevation may be closely related to topography. Vaughan (1969) suggested that dead adult M. montanus, found during snowmelt at a high elevation, were unable to find dry sites and were drowned or died of exposure. If adult voles are detrimentally affected by cold temperatures and flooding, then it is likely that young would be affected to a greater extent. Nestling survival of M. pennsylvanicus may have been low at the high elevation because of colder temperatures and the flooding of nests, whereas young at the low elevation would experience warmer temperatures and no flooding.

The age at which C. gapperi young opened their eyes was earlier at the low elevation than at the high elevation. There is no logical explanation for this because it was not due to differences in litter size or growth between elevations.

The difference in the food ingestion index of reproductive effort of C. gapperi was not related to the amount eaten for young, but appeared to be due to differences in maintenance costs of the females. Females from the high elevation had lower maintenance costs than those from the low elevation, resulting in a greater index of physiological reproductive effort at the high elevation than at the low elevation. The difference in maintenance costs can not be explained on the basis of metabolic efficiency, because females from both elevations maintained the same weights during lactation and for any given body weight, non-breeding controls from the low elevation ate the same amount as those from the high elevation. The assumption that maintenance costs of non-breeding and breeding females is the same for a given body weight may not be valid.

The differences in the mean weight of mature, young-of-the-year M. pennsylvanicus males may be related to the length of the breeding season. At the high elevation with a shorter season, a lighter weight (and probably an earlier age) at maturity might permit breeding in a limited time period, despite the disadvantages of small size. An advantage to being larger at maturity at the low elevation might be important if there is competition for nest-sites. Why this difference in weight between elevations was not found in females is unknown.

4.4 Summary and conclusions.

These intraspecific comparisons showed that most life-history traits could not be directly related to general meteorological conditions or to the lengths of the breeding seasons. Spencer and Steinhoff's hypothesis could not adequately explain variation in the number of litters, litter size or female survival. Also, fewer opportunities to breed at the high elevation, compared to the low elevation, in M. pennsylvanicus was not associated with more rapid growth or development to weaning.

Some traits did differ between elevations, but they were not the same ones in both species. This may explain some of the conflicting results found by others who have examined small mammals at different elevations; different species react differently to environmental conditions at different elevations. Even within species, traits do not differ consistently with elevation (Table 1). Local conditions such as food quality may permit litter size of a species to be large at a high elevation in one area, while in another area it may permit litter size to be large at intermediate or low elevations. Flooding may cause differences in some traits between elevations. Winter survival showed no differences between elevations in this study. In other montane situations there might be differences in this trait because of greater differences in snowfall or temperatures between elevations. In this study, the temperature at the high elevation averaged 2°C less than at the low elevation. Sutcliffe (1977) suggested that temperature should decrease 1°C for every 160m increase in elevation. This translates into a predicted 5°C difference between elevations in this study. Local topography in the study area may allow frequent temperature inversions, making temperatures more similar between elevations than would be expected, resulting in no differences in some life-history traits of voles between elevations.

Clearly, in both species, life-history traits did not form discrete packages as outlined by the life-history theories of r- and K-selection, or bet-hedging (Stearns 1976). As suggested by Millar (1981), Stearns (1980) and others, environmental conditions may not cause a coevolved complex of traits and traits may vary independently of one another to some degree. Those traits that did differ between elevations were likely phenotypic responses. Species which occur in highly variable environments should have a high capacity for nongenetic modification (Mayr 1983). Microtines should be very flexible phenotypically because of the uncertainty of their environments, especially in terms of their food resources (Negus et al. 1977).

Alternatively, differences in traits between elevations may be the result of stochastic (chance) events such as genetic drift (Mayr 1983). Many unpredictable environmental factors make selection less than perfect resulting in stochastic events which result in some traits being different between elevations. Studies on P. maniculatus subspecies (Millar 1982; Millar and Innes 1983) also show that patterns among life-history traits are weak and that individual traits are not clearly related to environmental conditions.

Future studies on the life-history tactics of small mammals should focus on a number of areas. Studies should examine populations where the average number of litters differs greatly. More studies should examine the effects of varying food quality on life-history traits. Studies should examine within population variation in life-history traits. Data on heritabilities of litter size and other traits are badly needed for many species,

APPENDIX 1

Grid sizes, and vegetation characteristics of the grids and other trapping areas.

Four mark-recapture grids were operated in 1979 (two per elevation). At the low elevation, the Roadside 1 grid (20m spacing; 2 x 20) was located on a section of the highway right-of-way with moderate grass cover. The other grid, low Forest 1 (20m spacing; 10 x 10) was located in a mixed deciduous-coniferous forest approximately 30m from the highway. At the high elevation, the Meadow grid (20m spacing; 3 x 16) was located in a glacial cirque containing grasses and shrubs interspersed with clumps of trees. The high Forest 1 grid (20m spacing; 10 x 10) was located on the forested south-facing slope of the cirque where tree cover was broken up by several shallow ravines.

Five additional grids (three at the low elevation and two at the high elevation) were used in 1980 and 1981. The low Forest 1 grid was reduced to a 5 x 10 arrangement after two consecutive trapping sessions in 1980 because only half the grid yielded any <u>C</u>. <u>gapperi</u>. The low Roadside 2 grid (20m spacing; 2 x 20) was located along another section of the highway right-of-way with relatively thick grass cover. The low Roadside 3 grid (20m spacing; 1 x 20) was located on the other side of the highway from low Roadside 1 and had relatively sparse grass cover. The low Forest 2 grid (20m spacing; 10 x 10) was located in an almost pure stand of conifers with considerable deadfall. At the high elevation, the Stream grid (20m spacing; 2 x 10) was placed along a stream with surrounding low grass cover and some deadfall. The high Forest 2 grid (20m spacing; 5 x 10) was placed on a south-facing slope outside the cirque.

All roadside grids were dominated by grasses such as *Bromus* and *Elymus*. The low Forest 1 grid had a mixture of aspens (*Populus tremuloides*), spruce (*Picea* spp.) and lodgepole pine (*Pinus contorta*). Bearberry (*Arctostaphylos*) and juniper (*Juniperus*) were found throughout the grid. The low Forest 2 grid was in a stand of lodgepole pine, although one corner had a few aspens. Understory plants were scarce, but bearberry was found occassionally.

The high Meadow grid had a good cover of grasses (e.g. *Bromus*) and shrubs (e.g. *Salix*). Between this understory were clumps of subalpine fir (*Abies lasiocarpa*). The high Stream grid was dominated by grasses. The high Forest 1 grid was dominated by fir and spruce, but larch were common at the bottom of the grid. The high Forest 2 grid was dominated by spruce and larch and was much more open than the high Forest 1 grid. Shrubs such as *Vaccinium* spp. were present on both of these grids.

Removal trapping was carried out in habitats similar to those described above. Removal trapping at the low elevation was also carried out in areas dominated by aspens and grasses, and in areas where there was a mixture of shrubs, grasses and aspens. Both of these habitats yielded M. pennsylvanicus. Rocky areas were also trapped at the high elevation, but no C. gapperi or M. pennsylvanicus were caught.

More detailed accounts of the vegetation in the Kananaskis Valley and the Marmot Creek Experimental Watershed can be found in Carroll (1978), Sloan (1967) and Stevenson (1967).

APPENDIX 2

Population numbers of C. gapperi and M. pennsylvanicus on the mark-recapture grids.

Rarely are all individuals in a population caught by standard mark-recapture techniques because some segments of the population will not enter live-traps (Boonstra and Krebs 1978). However, frequent and consistent trapping schemes at both elevations provide a reasonable comparison of relative population numbers between elevations.

The use of the minimum number known alive technique (enumeration) to assess population sizes assumes that individuals are trapped frequently (Hilborn et al. 1976). They found that if the trappability was greater than 50%, the minimum number known alive is a reasonable estimate of actual population number. Below 50% this technique becomes unreliable.

In this study, trappability was heterogeneous with respect to year, age and sex (Tables 37 and 38). Trappabilities of C. gapperi at the low elevation were above 69% in all groups, except young males in 1979 and young females in 1981. Trappabilities of C. gapperi from the high elevation were above 64% in all year, sex and age groups.

Trappabilities of both M. pennsylvanicus populations were generally lower than those of C. gapperi. Only 67% of all year, sex and age groups of M. pennsylvanicus from the

Table 37. Trappabilities of *C. gapperi*, in relation to age, sex and year, at the low and high elevations.

Elevation	Age	Sex	1979	n	1980	n	1981	n
			Year					
low	over-wintered	female	0.87	2	0.85	8	0.84	17
		male	0.67	3	0.78	10	0.77	11
	young	female	0.77	5	0.76	27	0.00	1
		male	0.41	4	0.69	34	1.00	2
Means			0.69	14	0.77	79	0.81	30
high	over-wintered	female	0.95	13	0.74	38	0.86	28
		male	0.70	6	0.68	25	0.87	11
	young	female	0.73	21	0.64	34	1.00	6
		male	0.85	32	0.67	26	1.00	1
Means			0.84	72	0.70	123	0.87	46

Table 38. Trappabilities of *M. pennsylvanicus*, in relation to age, sex and year, at the low and high elevations.

Elevation	Age	Sex	Year 1979	n	1980	n	1981	n
low	over-wintered	female	0.77	10	0.50	26	0.49	10
		male	0.70	10	0.37	24	0.57	10
	young	female	0.56	15	0.53	99	0.60	13
		male	0.46	19	0.55	20	0.33	11
Means			0.72	54	0.49	169	0.53	44
high	over-wintered	female	0.74	12	0.50	19	0.83	7
		male	0.52	3	0.40	7	0.50	3
	young	female	0.67	14	0.49	14	--	0
		male	0.63	5	0.30	9	--	0
Means			0.68	34	0.45	49	0.75	10

low elevation had trappabilities 50% or greater, while at the high elevation only 60% of the groups had trappabilities above 50%. Grand means also indicated that the trappabilities of C. gapperi (low elevation: 76.7%; high elevation: 74.9%) were much greater than those of M. pennsylvanicus (low elevation: 54.9%; high elevation: 55.6%). Therefore, comparisons of the minimum number known alive between elevations are valid for C. gapperi, but may be considered unreliable or less reliable for M. pennsylvanicus.

The minimum number of C. gapperi known alive varied widely over time as well as among grids at the same elevation (Figures 13 to 18). (Numbers of M. pennsylvanicus are presented for interest only (Figures 19 to 23)). Much of the variation in numbers can be explained by different grid sizes, but not always. For example, peak numbers of C. gapperi at the high elevation in 1980 were greater on a smaller grid (2ha) than on a larger grid (4ha) (Figures 15 and 16). To examine population sizes (no./ha) of C. gapperi between elevations, the two largest forest grids (Figures 14 and 15) were chosen because they were equal in size (4ha). With these grids, densities were similar at both elevations and within each grid mean densities were also relatively constant from year to year (Table 39).

Therefore, population densities of C. gapperi were similar at both elevations when similar sized grids were compared. Conclusions regarding the densities of M. pennsylvanicus could not be made because trappabilities were too low.

FIGURE 13

Minimum number of C. gapperi known alive on the low Forest 1 grid (2ha).

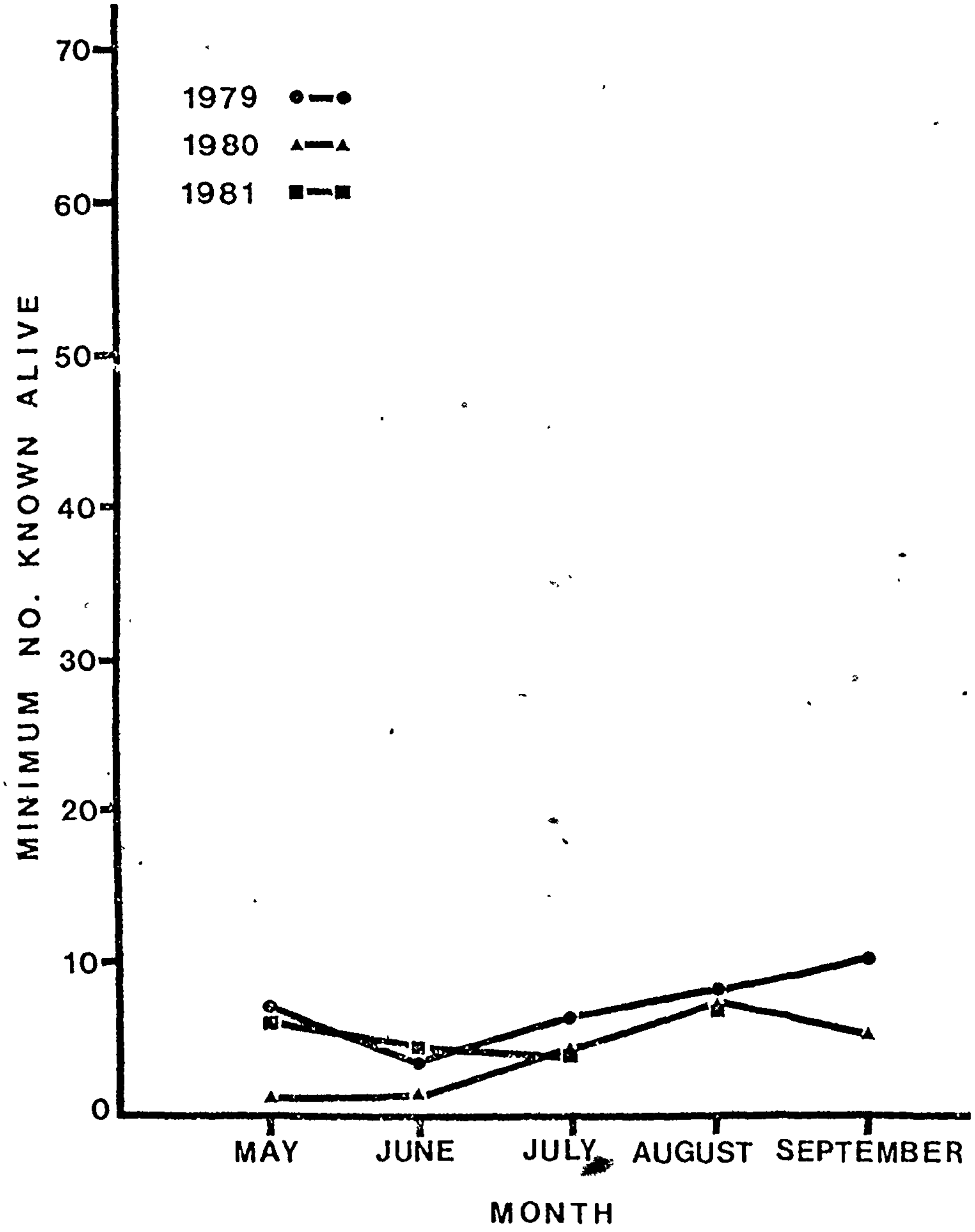

70
60
50
40
30
20
10
0
1979
1980
1981
MINIMUM NO. KNOWN ALIVE
MAY
JUNE
JULY
AUGUST
SEPTEMBER
MONTH

FIGURE 14

Minimum number of C. gapperi known alive on the low Forest 2 grid (4ha).

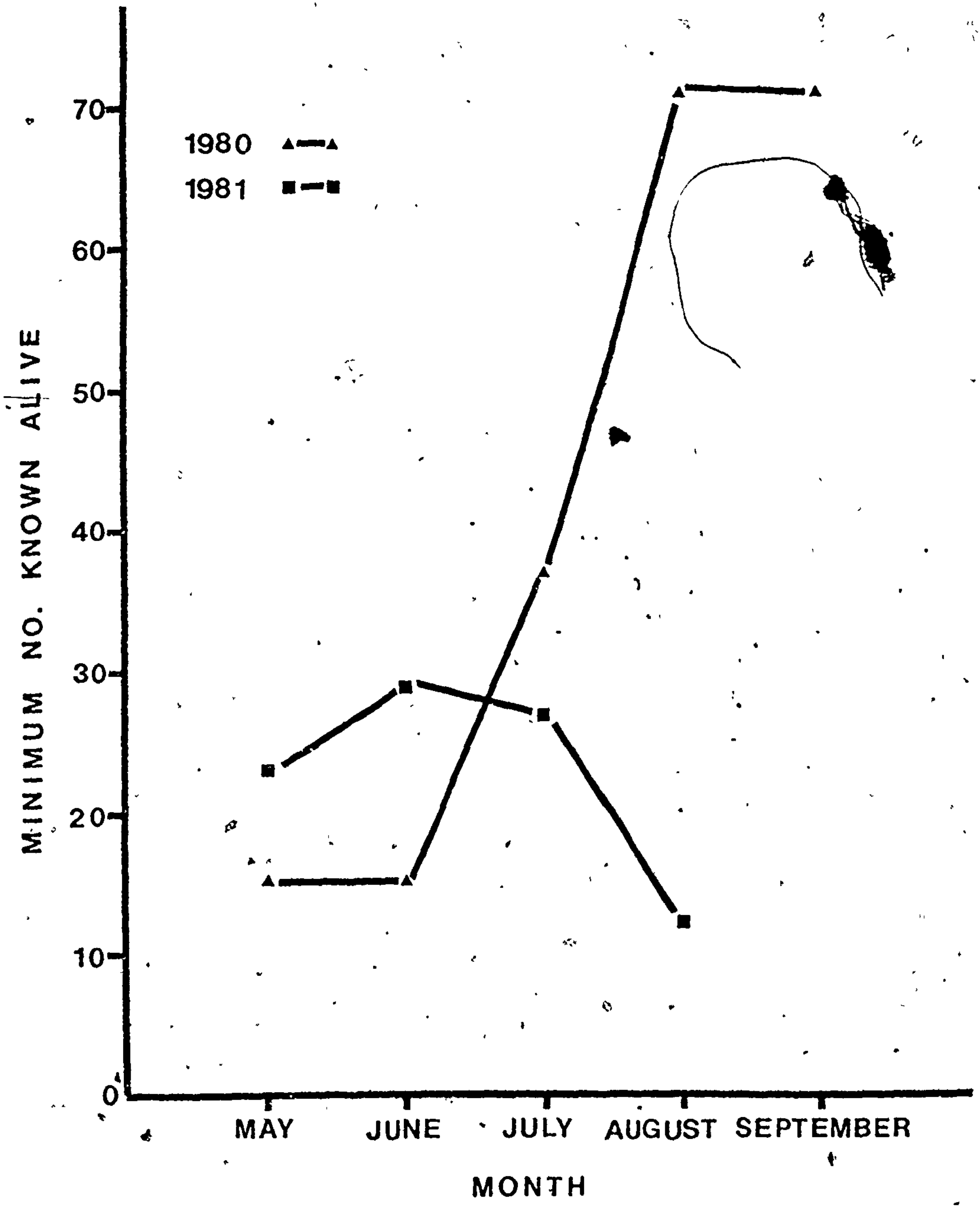
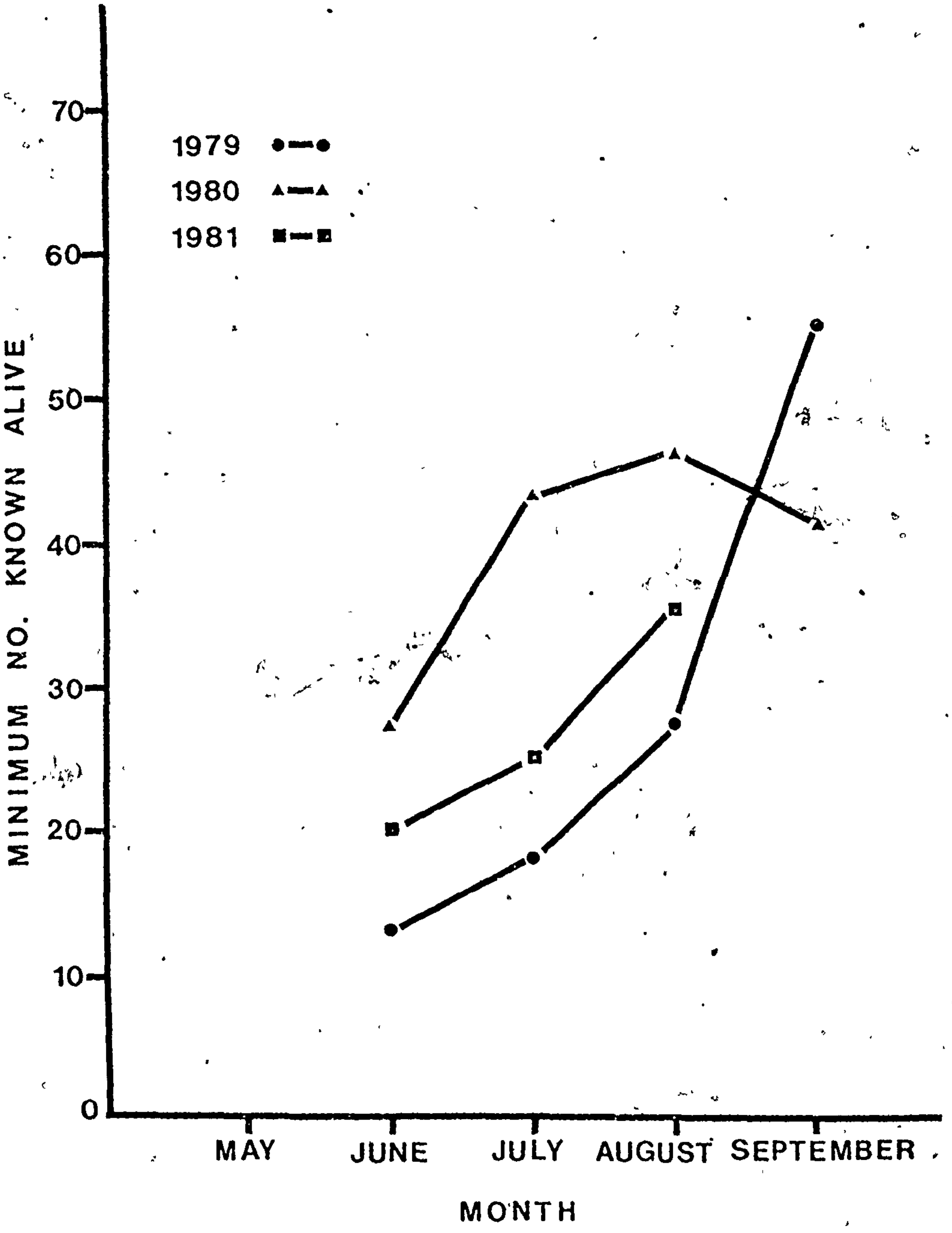

1980 ▲—▲
1981 ■—■
MINIMUM NO. KNOWN ALIVE
70
60
50
40
30
20
10
0
MAY
JUNE
JULY
AUGUST
SEPTEMBER
MONTH

FIGURE 15

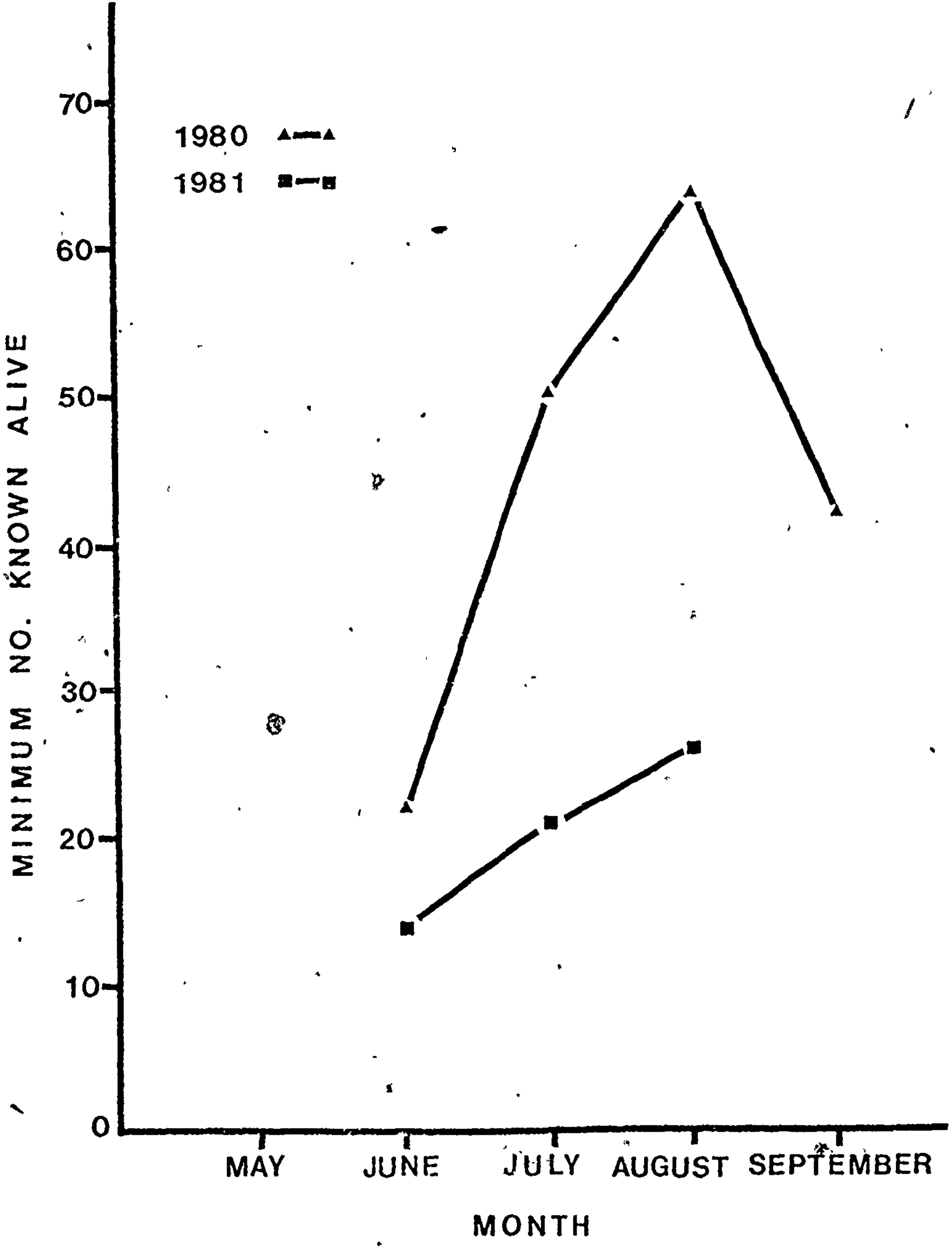
Minimum number of C. gapperi known alive on the high Forest 1 grid (4ha).



1979 ●—●
1980 ▲—▲
1981 ■—■
MINIMUM NO. KNOWN ALIVE
70
60
50
40
30
20
10
0
MAY
JUNE
JULY
AUGUST
SEPTEMBER
MONTH

FIGURE 16

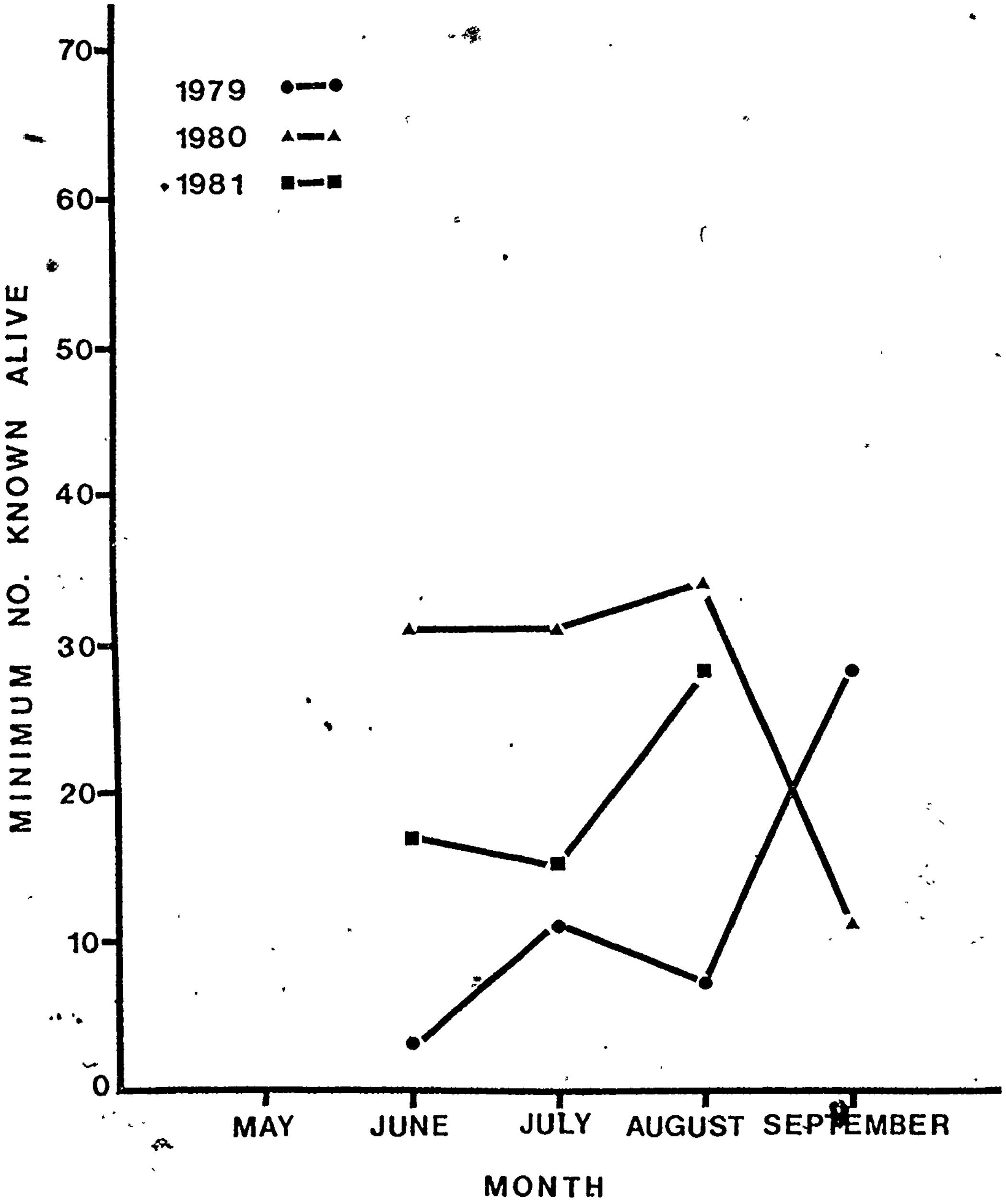
Minimum number of *C. gapperi* known alive on the high Forest 2 grid (2ha).



1980
1981
MINIMUM NO. KNOWN ALIVE
0
10
20
30
40
50
60
70
MAY
JUNE
JULY
AUGUST
SEPTEMBER
MONTH

FIGURE 17

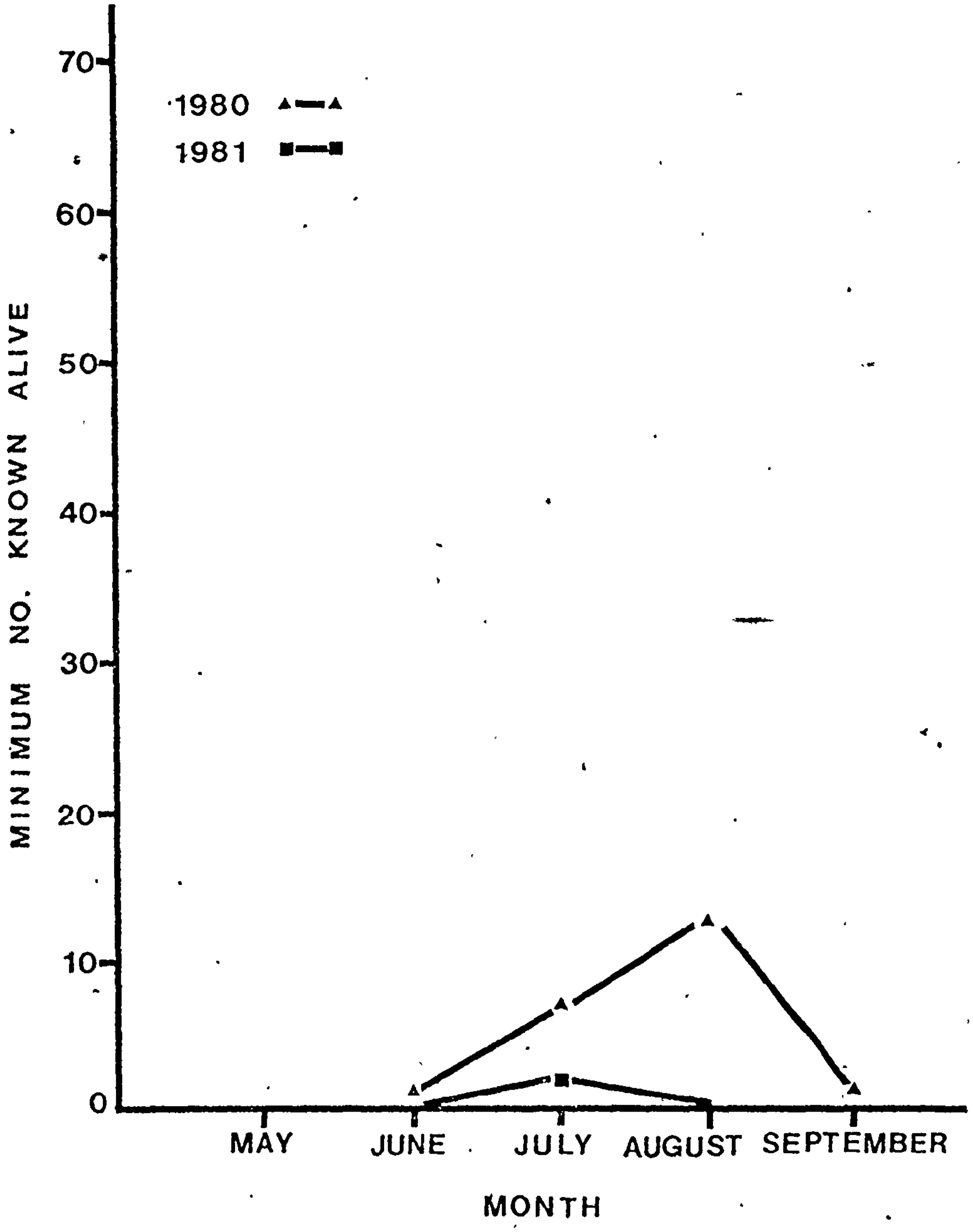
Minimum number of C. gapperi known alive on the high Meadow grid (1.7ha).



70
60
50
40
30
20
10
0
MINIMUM NO. KNOWN ALIVE
1979 ●—●
1980 ▲—▲
1981 ■—■
MAY
JUNE
JULY
AUGUST
SEPTEMBER
MONTH

FIGURE 18

Minimum number of C. gapperi known alive on the high Stream grid (0.42ha).



70
60
50
40
30
20
10
0
MINIMUM NO. KNOWN ALIVE
1980 ▲—▲
1981 ■—■
MAY
JUNE
JULY
AUGUST
SEPTEMBER
MONTH

FIGURE 19

Minimum number of _M_. _pennsylvanicus_ known alive on the low Roadside 1 grid (0.42ha).

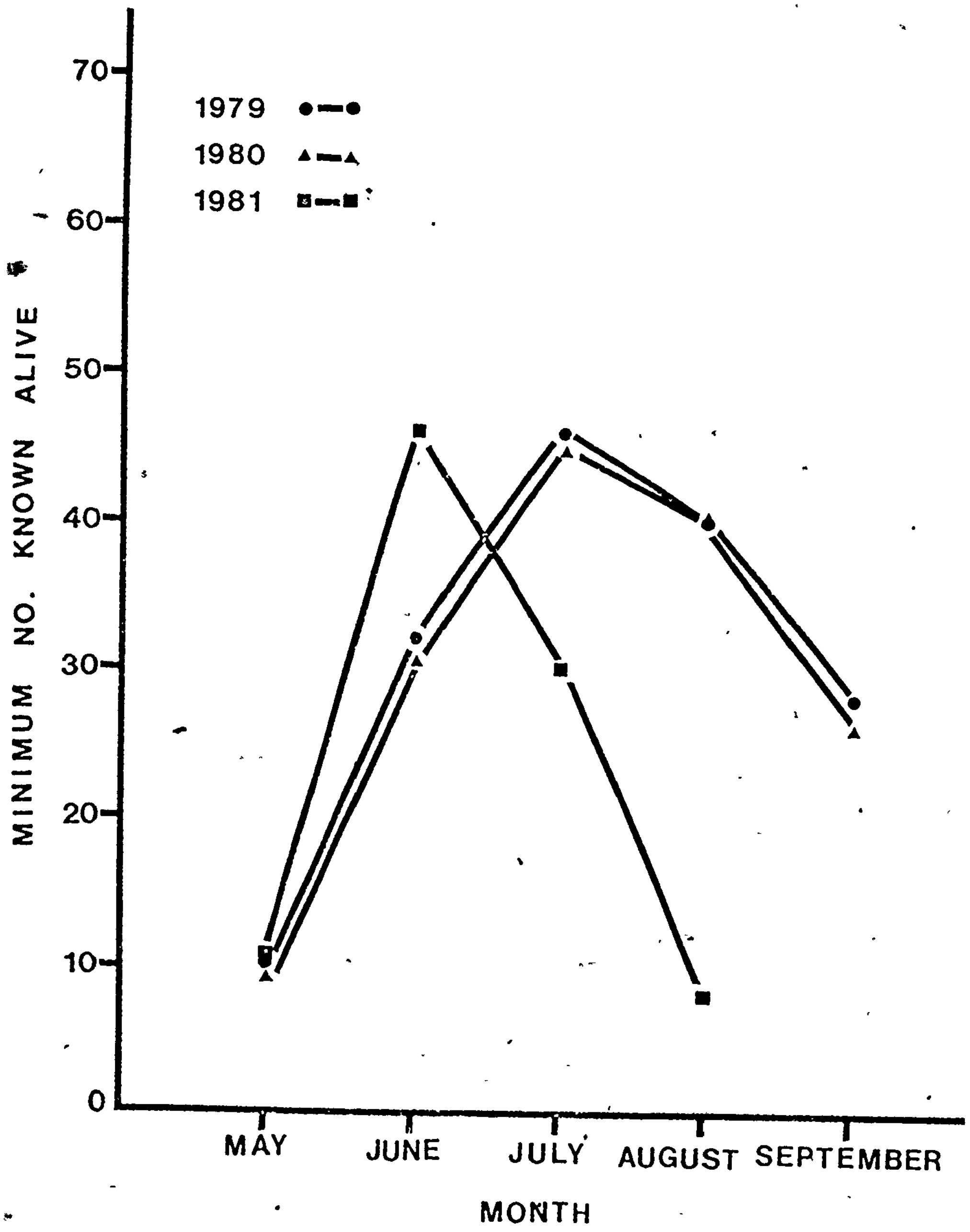

1979 ●—●
1980 ▲—▲
1981 ■—■
MINIMUM NO. KNOWN ALIVE
70
60
50
40
30
20
10
0
MAY
JUNE
JULY
AUGUST
SEPTEMBER
MONTH

FIGURE 20

Minimum number of M. pennsylvanicus known alive on the low Roadside 2 grid (0.42ha).

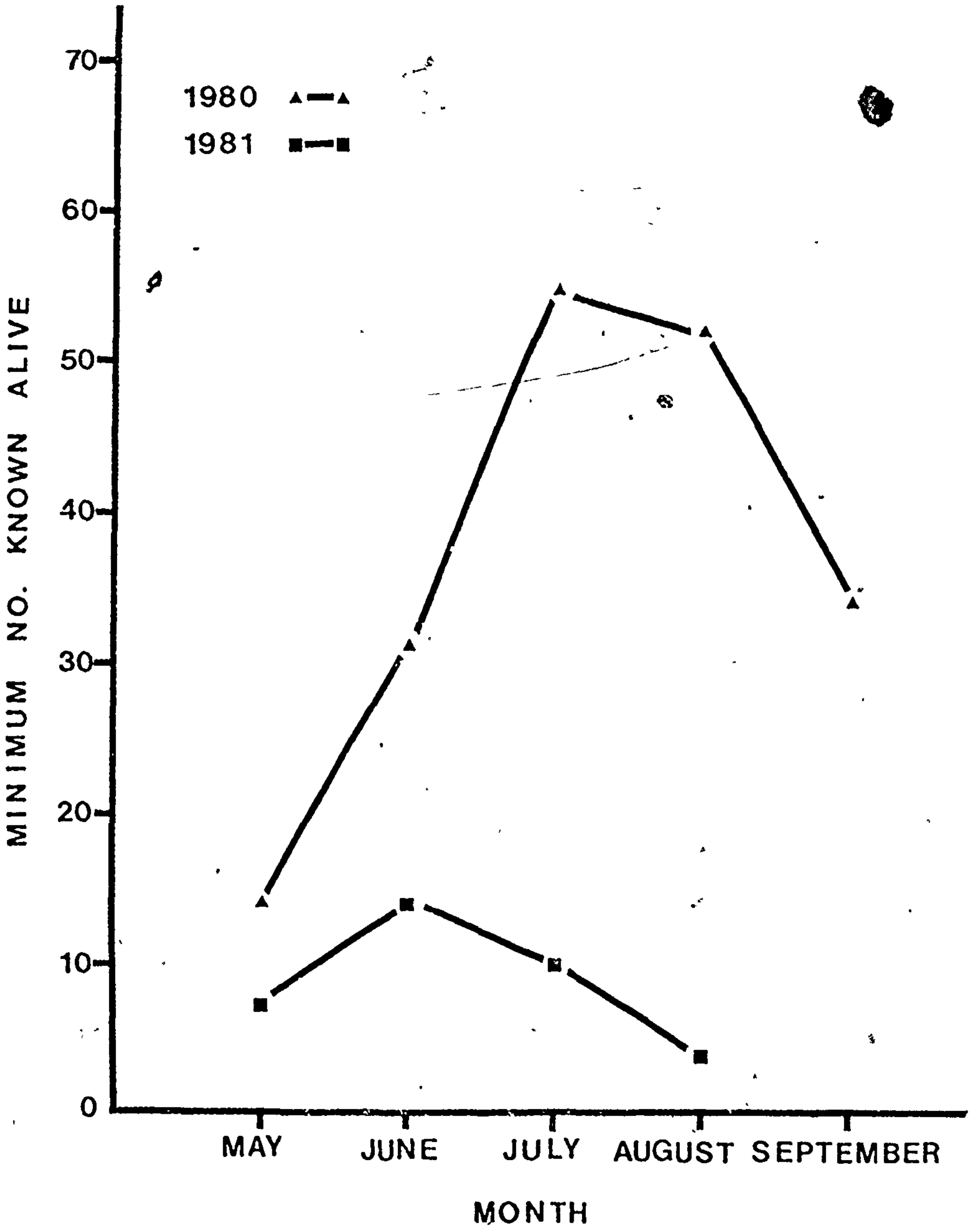

1980 ▲—▲
1981 ■—■
MINIMUM NO. KNOWN ALIVE
70
60
50
40
30
20
10
0
MAY
JUNE
JULY
AUGUST
SEPTEMBER
MONTH

FIGURE 21

Minimum number of M. pennsylvanicus known alive on the low Roadside 3 grid (0.42ha).

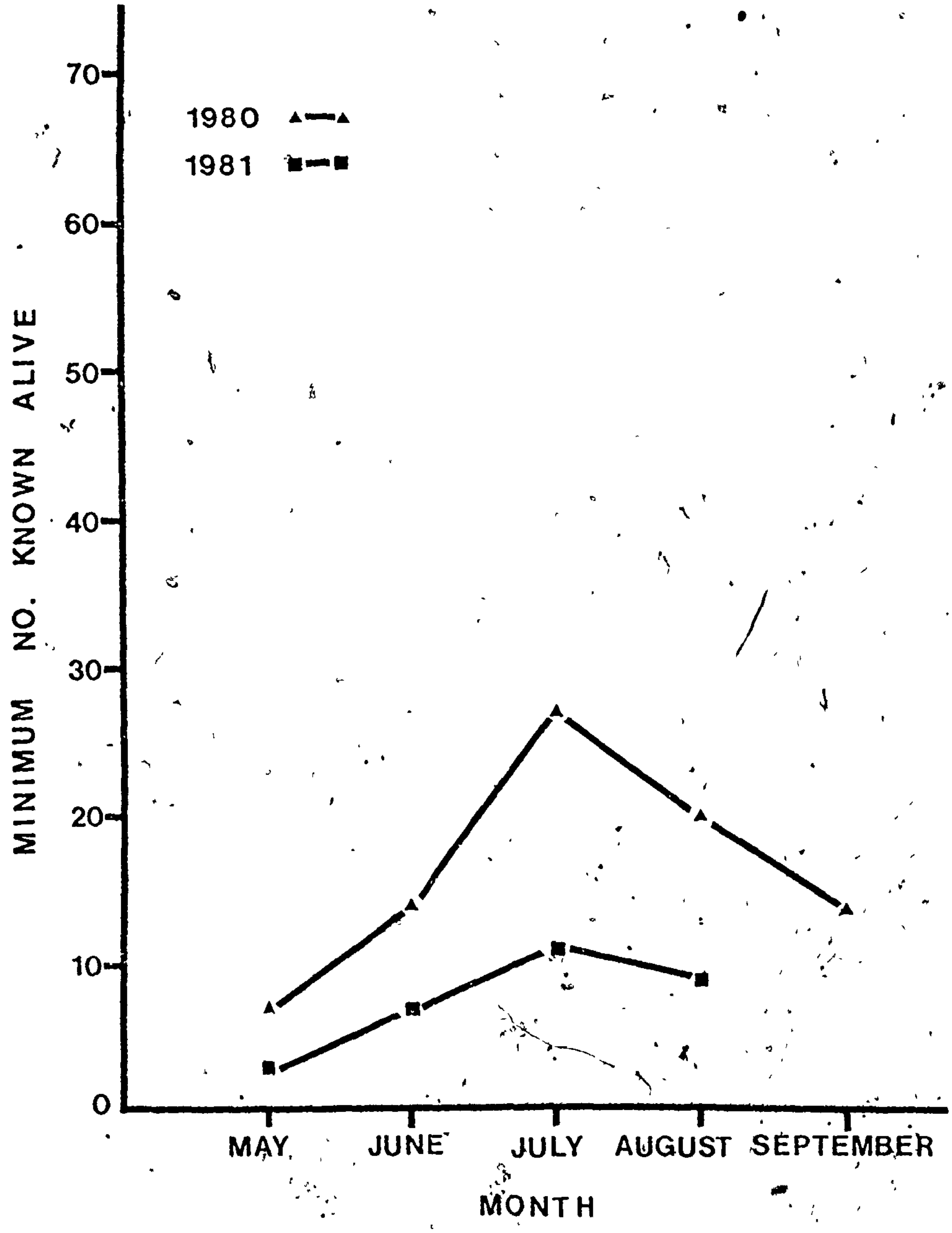

70
60
50
40
30
20
10
0
MINIMUM NO. KNOWN ALIVE
1980 ▲—▲
1981 ■—■
MAY
JUNE
JULY
AUGUST
SEPTEMBER
MONTH

FIGURE 22

Minimum number of M. pennsylvanicus known alive on the high Meadow grid (1.7ha).

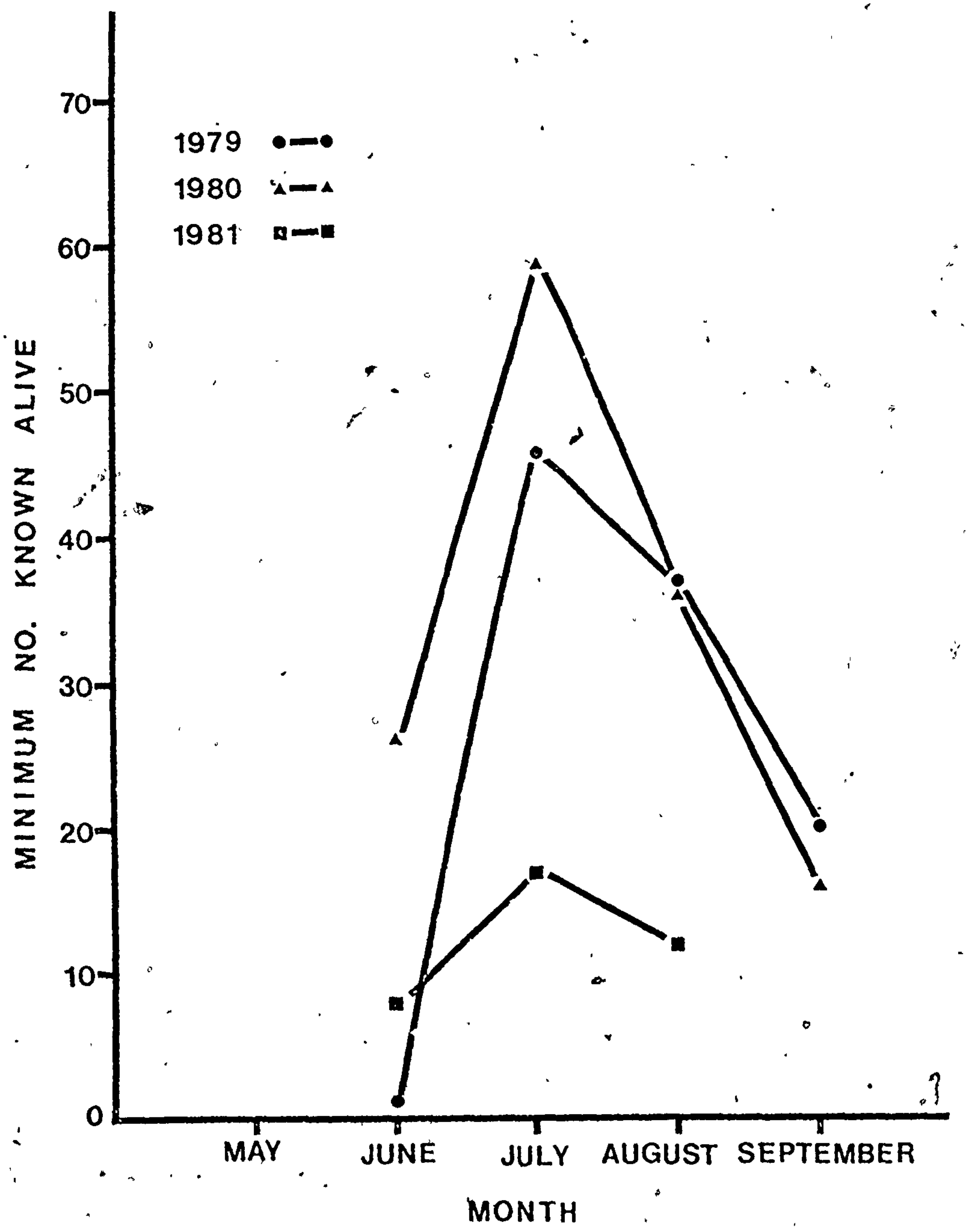

1979 ●—●
1980 ▲—▲
1981 ■—■
MINIMUM NO. KNOWN ALIVE
0
10
20
30
40
50
60
70
MAY
JUNE
JULY
AUGUST
SEPTEMBER
MONTH

FIGURE 23

Minimum number of M. pennsylvanicus known alive on the high Stream grid (0.42ha).

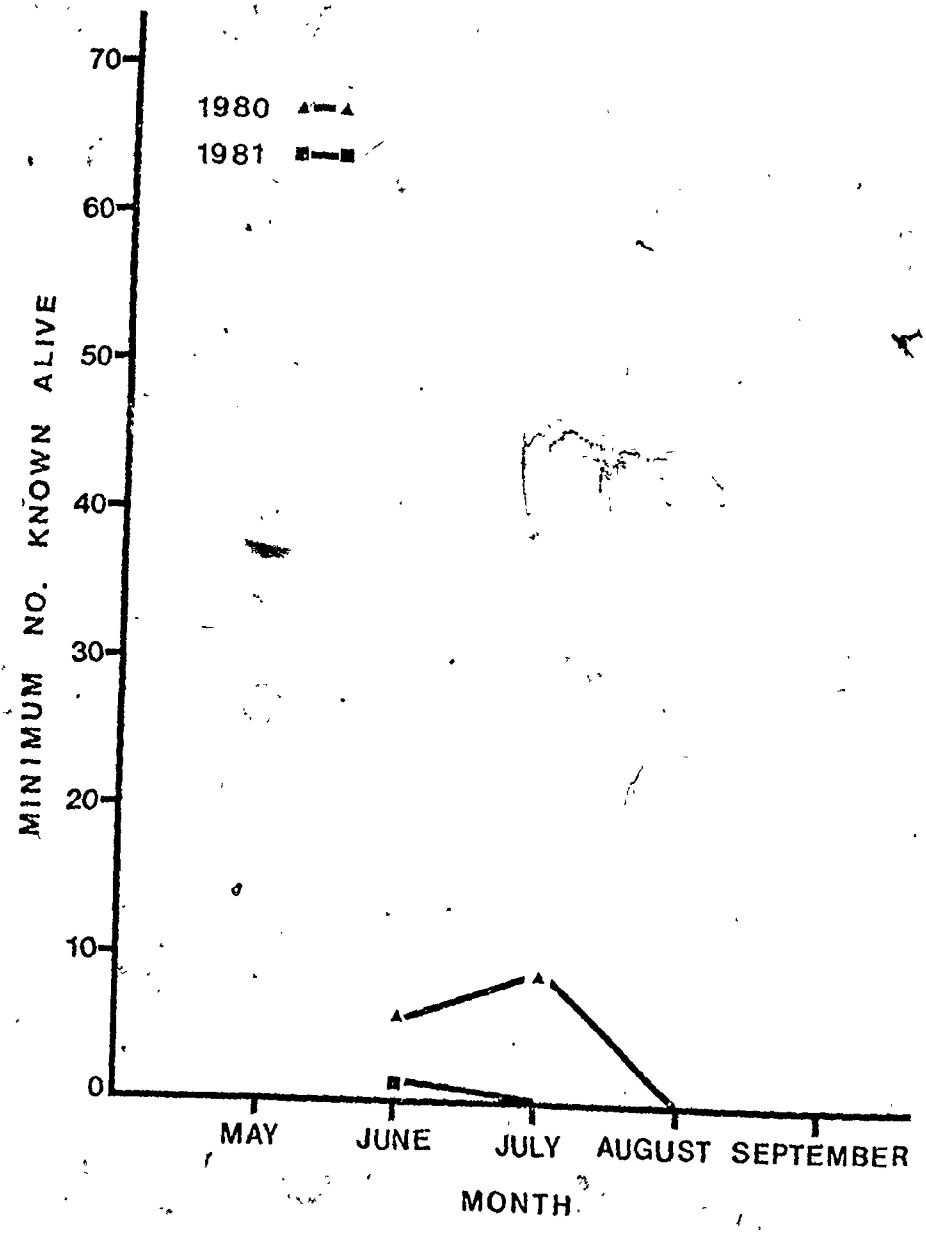

70
60
50
40
30
20
10
0
1980 ▲—▲
1981 ■—■
MINIMUM NO. KNOWN ALIVE
MAY
JUNE
JULY
AUGUST
SEPTEMBER
MONTH

Table 39. Densities (no./ha) of *C. gapperi* on the low Forest 2 grid (see Figure 14 also) and on the high Forest 1 grid (see Figure 15 also). Means are based on monthly values.

Year	Elevation	Mean	Minimum	Maximum
1979	low	--	--	--
	high	7.1	3.3	13.8
1980	low	10.5	3.8	17.8
	high	9.8	6.8	11.5
1981	low	5.7	3.0	7.3
	high	6.7	5.0	8.8
Grand means	low	8.3	3.8	17.8
	high	8.0	3.3	13.8

APPENDIX 3

The use of dried eye lens weights as an aging technique in C. gapperi and M. pennsylvanicus.

A number of studies have used dried eye lens weights as indicators of age in small mammals (e.g. M. ochrogaster - Hoffmeister and Getz 1968; M. montanus and M. pinetorum - Gourley and Jannett 1975; M. pennsylvanicus - Thomas and Bellis 1980; P. leucopus and P. maniculatus - Millar and Iverson 1976). These authors found this technique to be accurate and superior to other techniques such as pelage characteristics or body weight.

In this study, two major problems were encountered using this technique. First, the minimum eye lens weights of over-wintered animals correponded to the eye lens weights of known aged laboratory young that were approximately 55 and 50 days in C. gapperi and M. pennsylvanicus, respectively. Since wild young would not be caught until they were at least 15 days of age, this limited the applicability of the technique to animals 15 to 55 days of age. Secondly, the eye lenses of laboratory young appeared to grow more rapidly than those of wild young. Some of the eye lenses of wild caught animals did not fix properly and had the appearance of decomposition described by Montgomery (1963); such lenses were discarded.

In C. gapperi, logarithmic transformation did not substantially improve the relationship between mean eye lens weight and age, and the relationship was described by:

$$Y = 0.00069 + 0.00004X \tag{20}$$

($r = 0.97$, $p<0.01$, $n = 55$) and

$$Y = 0.00077 + 0.00003X \tag{21}$$

($r = 0.96$, $p<0.01$, $n = 68$) where Y = mean eye lens weight (g) and X = age (days) for young from the low and high elevations, respectively.

In M. pennsylvanicus, the relationship between mean eye lens weight and age was best described by transforming the independent variable (age) and was given by:

$$Y = -0.0009 + 0.00059LN(X) \tag{22}$$

($r = 0.97$, $p<0.01$, $n = 80$) and

$$Y = 0.0011 + 0.00065LN(X) \tag{23}$$

($r = 0.95$, $p<0.01$, $n = 50$) for young from the low and high elevations, respectively.

To check the accuracy of the above equations the age of the young-of-the-year that died in live-traps on mark-recapture grids were examined by two methods. (All of these young were C. gapperi and most were from the high elevation). First, the length of time that these young were present on a grid plus 15 days to weaning was calculated. The average age of these young at death was calculated to be 70.2 ± 3.45 days (n = 12). Second, the age of these young were estimated by weighing their eye lenses and using equations 20 and 21. The mean age of the young calculated in this manner was 59.3 ± 2.93 days. Therefore, the eye lens technique underestimated their true age by at least 11 days. These young may represent a biased sample because they all died in live-traps and their eye lens weights may have been lower than usual because of the way they died. Alternatively, the difference in ages may indicate that the eye lenses of laboratory young grew faster than those in the wild, reflecting differences in nutrition. Further data suggested that the latter, rather than the former explanation may be the case. A number of _M_. _pennsylvanicus_ females (all from the low elevation) brought in for the laboratory colony were etherized because they were considered too small ($\leq$15.0g) to be pregnant. At autopsy, ten were found to be pregnant and of these 50% would have conceived at ages 15 days or younger (range = 8 - 25 days; equations 3 and 22). Most of these ages at maturity are too early to be considered realistic, supporting the view that the eye lenses of laboratory young grow more rapidly than those of wild young.

Dried eye lens weights may not be a very useful technique in microtines because it can only be applied over a short range of ages and with limited accuracy. In seasonal environments, eye lens weights of microtines may be most useful in separating over-wintered from young-of-the-year.

APPENDIX 4

Raw data used to calculate the lengths of the breeding seasons.

Table 40. Raw data used to calculate the lengths of the breeding seasons of C. gapperi, from the low elevation. Initiation and cessation dates of breeding were based on five criteria: 1) pregnant females that were snap-trapped, 2) births on mark-recapture grids, 3) births in the laboratory, 4) appearance of young-of-the-year on mark-recapture grids and 5) aged kill-trapped young. For further detail see the Methods section.

Year	Criterion number	Initiation date	Cessation date
1979	1	May 16	--
	2	June 5	September 16
	3	May 23	--
	4	June 25	September 21
	5	June 12	September 1
	Mean	June 4	September 13
1980	1	June 1	--
	2	May 27	September 6
	3	May 28	August 27
	4	May 28	September 7
	5	--	September 2
	Mean	May 29	September 3
1981	1	June 19	--
	2	June 5	--
	3	June 7	--
	4	June 12	--
	5	June 5	--
	Mean	June 10	--

Table 41. Raw data used to calculate the lengths of the breeding seasons of C. gapperi, from the high elevation. See Table 40 for further explanation.

Year	Criterion number	Initiation date	Cessation date
1979	1	June 25	--
	2	June 19	September 25
	3	June 12	September 24
	4	June 15	September 24
	5	June 10	September 7
	Mean	June 16	September 20
1980	1	June 8	September 10
	2	June 9	September 19
	3	June 13	August 29
	4	May 21	September 8
	5	May 17	September 1
	Mean	June 1	September 7
1981	1	June 25	--
	2	June 13	--
	3	June 8	--
	4	July 1	--
	5	June 21	--
	Mean	June 20	--

Table 42. Raw data used to calculate the lengths of the breeding seasons of _M. pennsylvanicus_, from the low elevation. See Table 40 for further explanation.

Year	Criterion number	Initiation date	Cessation date
1979	1	May 20	--
	2	May 19	September 12
	3	May 17	September 6
	4	June 8	September 1
	5	June 4	--
	Mean	May 26	September 6
1980	1	May 19	September 16
	2	May 11	September 26
	3	May 14	August 30
	4	May 18	September 15
	5	May 24	--
	Mean	May 17	September 14
1981	1	May 30	--
	2	June 3	--
	3	June 3	--
	4	May 17	--
	5	May 17	--
	Mean	May 26	--

Table 43. Raw data used to calculate the lengths of the breeding seasons of M. pennsylvanicus, from the high elevation. See Table 40 for further explanation.

Year	Criterion number	Initiation date	Cessation date
1979	1	--	--
	2	July 6	September 14
	3	June 12	August 20
	4	June 17	August 31
	5	June 16	--
	Mean	June 20	September 1
1980	1	--	August 31
	2	June 12	September 7
	3	--	August 31
	4	May 30	September 9
	5	May 20	September 1
	Mean	May 31	September 3
1981	1	June 22	--
	2	June 24	--
	3	July 8	--
	4	July 1	--
	5	June 28	--
	Mean	June 29	--

APPENDIX 5

Fat content of males.

Fat content of males was compared to determine if there were differences between elevations, and between immature and mature animals. In most groups fat was not correlated with lean dry weight, and ANOVAs on the relative amounts of fat were used. The relative amount of fat is expressed as fat (g) ÷ lean dry weight.

Small samples precluded the analysis of the relative amounts of fat in each month of the breeding season. However, samples from May, June and July were compared with those from August and September (Tables 44 to 47). There were no significant differences in the relative amounts of fat between monthly groups, so monthly samples were pooled. A three-way ANOVA (elevation, year and reproductive group) indicated that the relative amounts of fat of C. gapperi males were significantly different among years ($F = 4.02$, $p<0.05$) (Tables 48 and 49). There was also a significant elevation-reproductive group interaction ($F = 5.41$, $p<0.05$) indicating that the relative amounts of fat of either immatures or matures were different at each elevation. T-tests within each reproductive group indicated there were no significant differences in the relative amounts of fat between elevations (immatures: $t = 1.08$, $p_2>0.05$; matures: $t = 2.04$, $p_2>0.05$). A three-way ANOVA indicated

Table 44. Fat, lean dry weight and percent fat among C. *gapperi* males, in relation to reproductive status and season, from the low elevation. Percent fat = (fat(g) ÷ lean dry weight (g)) x 100.

Reproductive Group	Months	Fat(g)	Lean dry weight(g)	Percent fat	n
Immature	May, June and July	0.49 ± 0.10	4.34 ± 0.63	11.1	4
	August and September	0.35 ± 0.03	3.52 ± 0.10	9.9	30
Mature	May, June and July	0.53 ± 0.03	4.70 ± 0.09	11.6	92
	August and September	0.44 ± 0.03	4.09 ± 0.34	11.3	9

Table 45. Fat, lean dry weight and percent fat among C. gapperi males, in relation to reproductive status and season, from the high elevation. Percent fat = (fat(g) ÷ lean dry weight (g)) x 100.

Reproductive Group	Months	Fat(g)	Lean dry weight(g)	Percent fat	n
Immature	May, June and July	0.30 ± 0.10	2.55 ± 0.39	11.9	3
	August and September	0.45 ± 0.04	3.71 ± 0.80	12.9	16
Mature	May, June and July	0.54 ± 0.03	5.13 ± 0.15	10.8	70
	August and September	0.43 ± 0.06	4.44 ± 0.32	10.3	13

Table 46. Fat, lean dry weight and percent fat among *M. pennsylvanicus* males, in relation to reproductive status and season, from the low elevation. Percent fat = (fat(g) ÷ lean dry weight (g)) x 100.

Reproductive Group	Months	Fat(g)	Lean dry weight(g)	Percent fat	n
Immature	May, June and July	0.47 ± 0.14	4.21 ± 0.58	10.6	10
	August and September	0.32 ± 0.03	3.27 ± 0.19	9.5	31
Mature	May, June and July	0.54 ± 0.02	5.77 ± 0.12	9.5	104
	August and September	0.65 ± 0.10	6.98 ± 0.49	10.1	7

Table 47. Fat, lean dry weight and percent fat among M. pennsylvanicus males, in relation to reproductive status and season, from the high elevation. Percent fat = (fat(g) ÷ lean dry weight (g)) x 100.

Reproductive Group	Months	Fat(g)	Lean dry weight(g)	Percent fat	n
Immature	May, June and July	0.18 ± 0.0	1.74 ± 0.0	10.3	1
	August and September	0.50 ± 0.06	3.92 ± 0.19	12.8	6
Mature	May, June and July	0.71 ± 0.12	4.31 ± 0.39	15.5	21
	August and September	0.76 ± 0.11	5.05 ± 0.45	14.9	15

Table 48. Fat, lean dry weight and percent fat among _C. gapperi_ males, in relation to reproductive status and year, from the low elevation. Percent fat = (fat(g) ÷ lean dry weight (g)) x 100.

Reproductive Group	Year	Fat(g)	Lean dry weight(g)	Percent fat	n
Immature	1979	0.37 ± 0.04	3.63 ± 0.20	10.1	14
	1980	0.37 ± 0.04	3.61 ± 0.15	10.0	20
	1981	--	--	--	0
Mature	1979	0.55 ± 0.04	4.89 ± 0.10	11.6	55
	1980	0.51 ± 0.03	4.54 ± 0.13	11.3	40
	1981	0.40 ± 0.04	3.13 ± 0.42	13.2	6

Table 49. Fat, lean dry weight and percent fat among *C. gapperi* males, in relation to reproductive status and year, from the high elevation. Percent fat = (fat(g) ÷ lean dry weight (g)) x 100.

Reproductive Group	Year	Fat(g)	Lean dry weight(g)	Percent fat	n
Immature	1979	0.35 ± 0.07	3.50 ± 0.39	10.0	6
	1980	0.47 ± 0.04	3.54 ± 0.24	14.0	13
	1981	--	--	--	0
Mature	1979	0.47 ± 0.04	5.12 ± 0.24	9.4	24
	1980	0.52 ± 0.03	5.04 ± 0.19	10.5	50
	1981	0.66 ± 0.09	4.65 ± 0.37	15.0	9

that the relative amounts of fat of M. pennsylvanicus males were significantly greater at the high elevation than at the low elevation ($F = 15.25$, $p<0.01$) (Tables 50 and 51). There were no differences among years ($F = 1.59$, $p>0.05$) or between reproductive groups ($F = 0.04$, $p>0.05$). However, no three-way interaction term could be calculated because there were too few degrees of freedom. The significant difference between elevations should be valid because of the large F-value and also no two-way interaction terms were significant (R. Green, personal communication).

Table 50. Fat, lean dry weight and percent fat among *M. pennsylvanicus* males, in relation to reproductive status and year, from the low elevation. Percent fat = (fat(g) ÷ lean dry weight (g)) x 100.

Reproductive Group	Year	Fat(g)	Lean dry weight(g)	Percent fat	n
Immature	1979	0.40 ± 0.08	4.02 ± 0.36	9.4	18
	1980	0.32 ± 0.04	3.14 ± 0.21	10.0	22
	1981	0.24 ± 0.00	1.90 ± 0.00	12.6	1
Mature	1979	0.52 ± 0.03	5.93 ± 0.15	9.1	61
	1980	0.58 ± 0.03	5.81 ± 0.18	10.1	45
	1981	0.52 ± 0.15	5.19 ± 1.07	9.3	5

2

Table 51. Fat, lean dry weight and percent fat among *M. pennsylvanicus* males, in relation to reproductive status and year, from the high elevation. Percent fat = (fat(g) ÷ lean dry weight (g)) x 100.

Reproductive Group	Year	Fat(g)	Lean dry weight(g)	Percent fat	n
Immature	1979	0.18 ± 0.00	1.74 ± 0.00	10.3	1
	1980	0.50 ± 0.06	3.92 ± 0.19	12.8	6
	1981	--	--	--	0
Mature	1979	--	--	--	0
	1980	0.68 ± 0.10	4.43 ± 0.38	14.8	21
	1981	0.80 ± 0.15	4.88 ± 0.47	16.0	15

APPENDIX 6

Growth of laboratory young from all litter sizes.

Growth of young from all families, from birth to 30 days, was examined for potential biases due to sex and litter size as well as differences between elevations.

Sex ratios of all C. gapperi young used to measure growth were 44.4% males and 44.6% males for the low and high elevation populations, respectively and they were not significantly different ($X^2 = 0.00$, $p>0.05$). Sex ratios of all M. pennsylvanicus used to measure growth were 52.4% and 38.5% males for the low and high elevation populations, respectively and they were not significantly different ($X^2 = 1.43$, $p>0.05$). Therefore, differences in growth between the sexes was unlikely to bias growth rate comparisons between elevations, in either species.

The relationship between weight and litter size was examined at birth, 16 days (approximately the age at weaning) and 30 days of age, following Innes and Millar (1979). Weight of C. gapperi young was negatively correlated with litter size at birth and 16 days of age, at both elevations (Table 52). Weight at 30 days of age was negatively correlated with litter size only among young from the low elevation. At all three ages the mean litter size of the litters measured for growth were greater from the high elevation than from the low elevation. Weight of M.

Table 52. The relationship between weight and litter size in C. gapperi young at three ages, where Y = weight(g) and X = litter size, at the low and high elevations.

Age	Elevation	Y = a + bX	r	n	Mean litter size
Birth	low	Y = 2.33 - 0.10X	-0.51[1]	84	4.42
	high	Y = 1.97 - 0.03X	-0.18[1]	123	5.55
16 days	low	Y = 14.84 - 1.05X	-0.54[1]	82	4.56
	high	Y = 11.14 - 0.28X	-0.24[1]	123	5.55
30 days	low	Y = 25.57 - 1.36X	-0.45[1]	57	4.09
	high	Y = 19.69 - 0.17X	-0.08[2]	118	5.58

---

[1] r was significant ($p_3 < 0.01$).

[2] r was not significant ($p_3 > 0.05$).

pennsylvanicus young was negatively correlated with litter size at 16 days of age, at both elevations (Table 53). Weight at 30 days of age was negatively correlated with litter size only among young from the high elevation. At all three ages, the mean litter size of the litters measured for growth were greater from the high elevation than from the low elevation.

Given that the relationship between weight and litter size were not always consistent between elevations and that litter size was greater at the high elevation than the low elevation in both species, a comparison of the growth curves using young for all litter sizes may not be valid; they are presented for interest (Figures 24 and 25).

Table 53. The relationship between weight and litter size in *M. pennsylvanicus* young at three ages, where Y = weight(g) and X = litter size, at the low and high elevations.

Age	Elevation	Y = a + bX	r	n	Mean litter size
Birth	low	Y = 2.29 - 0.04X	-0.15^2	106	4.82
	high	Y = 2.30 - 0.03X	-0.16^2	39	5.57
16 days	low	Y = 12.35 - 0.33X	-0.24^1	106	4.82
	high	Y = 17.34 - 1.19X	-0.56^1	39	5.57
30 days	low	Y = 19.01 - 0.17X	-0.07^2	87	4.83
	high	Y = 21.87 - 0.99X	-0.50^1	22	5.50

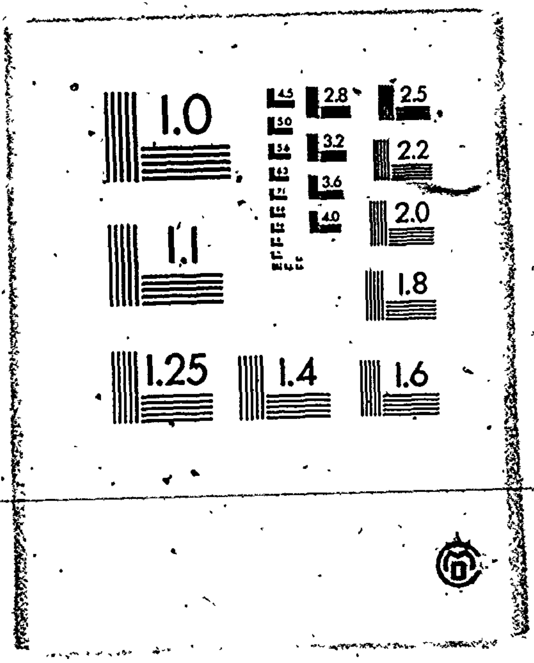
[1] r was significant ($p_3<0.01$).

[2] r was not significant ($p_3>0.05$).

FIGURE 24

Growth of all C. gapperi litters, from birth to 30 days of age, in the laboratory, at the low and high elevations. One S.E. is given above and below the mean for the low and high elevations, respectively. Sample sizes ranged from 84 to 57 individuals, and 123 and 118 individuals at the low and high elevations, respectively.

3 OF/DE 3



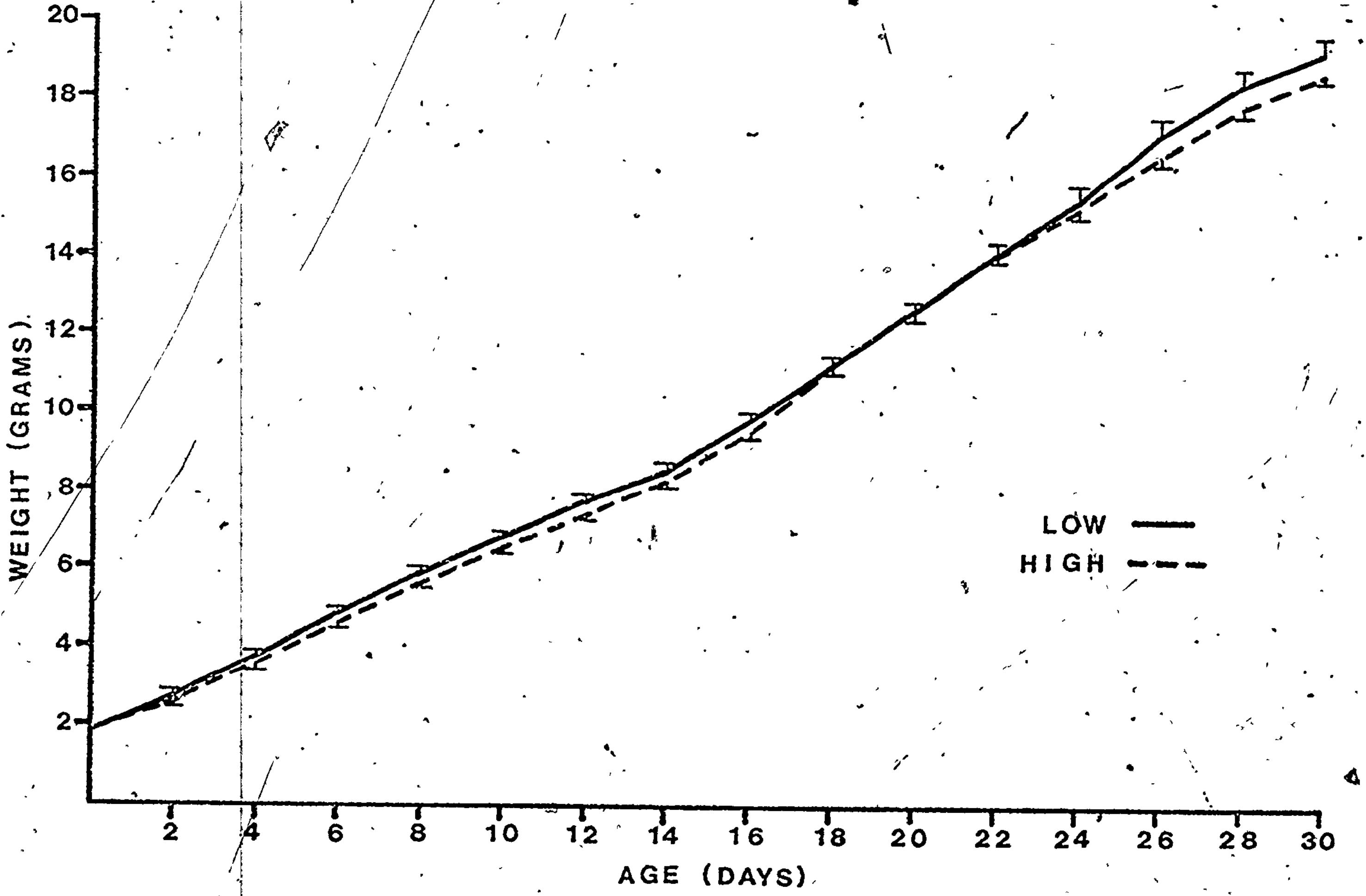
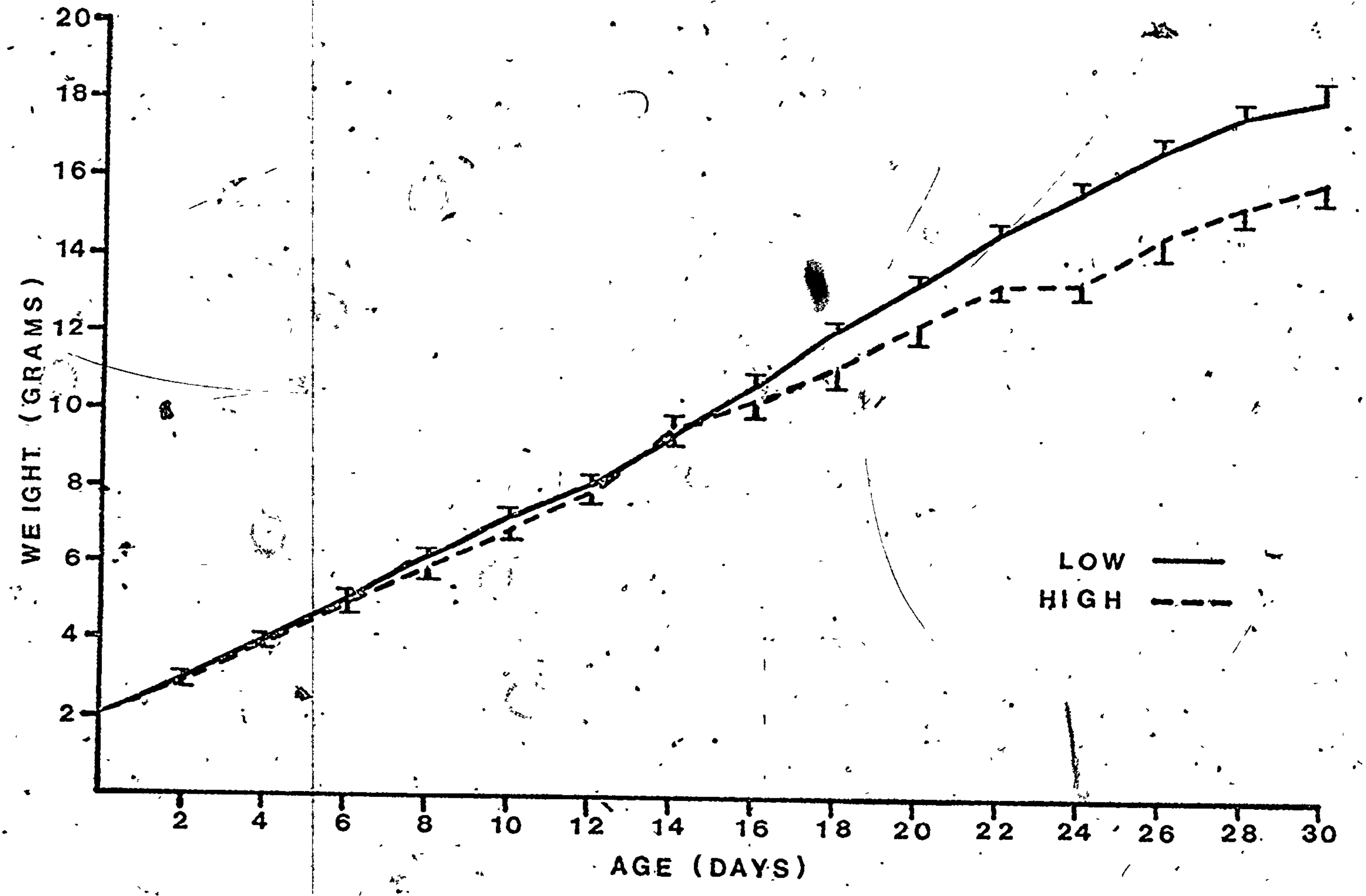

WEIGHT (GRAMS)
20
18
16
14
12
10
8
6
4
2
AGE (DAYS)
2
4
6
8
10
12
14
16
18
20
22
24
26
28
30
LOW
HIGH

FIGURE 25

Growth of all M. pennsylvanicus litters, from birth to 30 days of age, at the low and high elevations. One S.E. is given above and below the mean for the low and high elevations, respectively. Sample sizes ranged from 106 to 87 individuals, and 39 and 27 individuals at the low and high elevations, respectively.


WEIGHT (GRAMS)
20
18
16
14
12
10
8
6
4
2
AGE (DAYS)
2
4
6
8
10
12
14
16
18
20
22
24
26
28
30
LOW
HIGH

APPENDIX 7

Length of the breeding season, litter size and the maximum number of litters of C. gapperi and M. pennsylvanicus, from the literature.

Table 54. Length of the breeding season, litter size and maximum number of litters of *C. gapperi*, from the literature.

Length of the breeding season (mons)	Litter size	Maximum number of litters	Source
4	5.70	3	Fuller 1969
4	5.21	–	Sleeper *et al*. 1976
5	5.75	–	Perrin 1979
4	6.10	–	Campbell and Clark 1980
8	6.50	–	Merritt and Merritt 1978
7	6.10	–	Vaughan 1969
7	6.10	–	Beer *et al*. 1957
8	6.90	3	Elliot 1969
5	5.68	–	Iverson and Turner 1976
6	4.60	–	Wrigley 1969
6	6.50	4	Stinson 1977
5	5.17	6	This study
5	5.64	5	This study
3	5.45	3	Mihok 1979

Table 55. Length of the breeding season, litter size and maximum number of litters of *M. pennsylvanicus*, from the literature.

Length of the breeding season (mons)	Litter size	Maximum number of litters	Source
3	5.11	2	Martell and Pearson 1978
3	7.75	2	Martell and Pearson 1978
10	4.50	-	Tamarin 1977b, 1978
12	5.70	-	Beer and MacLeod 1961
11	4.46	4	Corthum 1967
12	4.54	-	Keller and Krebs 1970
5	4.93	-	Iverson and Turner 1976
5	6.90	-	Smith and Foster 1957
8	5.83	-	Coventry 1937
4	5.00	5	This study
3	6.02	4	This study
6	5.80	-	Wrigley 1969

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