VULNERABILITY OF MEADOW VOLES
MICROTUS PENNSYLVANICUS TO
PREDATION BY DOMESTIC CATS

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VULNERABILITY OF MEADOW VOLES *MICROTUS PENNSYLVANICUS* TO PREDATION BY DOMESTIC CATS

By

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TABLE OF CONTENTS

INTRODUCTION

RESULTS

SMALL RODENT POPULATION

LIST OF TABLES

LIST OF FIGURES

ABSTRACT

To investigate differential vulnerability to predation among sex and age segments of a population of *Microtus pennsylvanicus*, and between *Microtus* and other small rodents, the small mammal population of a 0.8 hectare old field in southern Michigan was live-trapped, ear-tagged, and released during the summer and fall, 1972. Fecal matter of domestic cats (*Felis catus*) was collected and analyzed for the presence of ear tags. It was found that among the rodents preyed upon, the observed numbers of species, sexes, and ages taken were not significantly different than those expected on the basis of abundance. A significant seasonal change occurred in the numbers of subadult and adult voles taken by cats, and corresponded to changes in the age structure of the *Microtus* population. The data indicate that different sex and age segments of meadow voles are taken in proportion to their abundance in the population.

INTRODUCTION

The Problem

It has generally been recognized that predation is, at least in part, a density-dependent phenomenon, and many studies have dealt with its quantitative aspects. For example, Holling (1965, 1966) investigated the responses of predators to changes in prey density; Pearson (1964, 1966, 1971) was concerned with the numbers of California voles (*Microtus californicus*) taken by carnivores at different points in the population cycle. These and other studies have illustrated that numbers of predators and prey are important determinants of any predatory outcome. Holling (1959) notes several other factors which are essential to an assessment of predation, among which he included the characteristics of the prey.

The kinds of prey variables which might influence vulnerability to predation cover a wide range of morphological and behavioral topics. Anatomical characteristics such as body size (see Ashmole, 1968; Brooks, 1968; Estes and Goddard, 1967) and coloration (Dice, 1947) may certainly have an effect on predation. Baker (1971) has suggested possible differences in risk between grass-eating and seed-eating myomorph rodents -- the former may take less risk by remaining under cover when gathering food, whereas seed-eaters must cover greater areas and may expose themselves more in search of seed-bearing plants. Seed-eaters, however, are largely nocturnal, and thus may be less conspicuous than the generally diurnal or crepuscular grass-eating rodents.

The responses of a prey animal to a predator should also be considered. Mech (1966) found that wolves on Isle Royale "tested" the reactions of moose, and rarely killed prime moose that stood their ground. Errington (1967) relates similar responses of mink to adult muskrats that did not attempt escaping after being detected. Schoener (1971) discusses this potential risk of injury to a predator as a frequently ignored handling cost.

While these prey characteristics may remain fairly constant for any one species, or the differences among species in a multi-species system may do likewise, the social and demographic attributes of a population of prey animals may vary through time. Paul Errington (1943), in his analysis of predation by mink upon muskrats, was perhaps the first to consider the operation of these factors in populations of mammalian prey. He found a relationship between changes in population density, with their concurrent changes in intraspecific friction, and the vulnerability of certain segments of a muskrat population to predation. A similar situation might exist in other microtine rodents: recent research into the population processes of voles of the genus _Microtus_ has pointed out that demographic and socio-behavioral attributes may vary among segments of a population and may change dramatically with the population cycle (Krebs, 1966; Myers and Krebs, 1971). The question is raised as to whether or not these or other differences might affect the vulnerability of different sex or age segments of a _Microtus_ population to predation by a carnivore. The research reported herein was designed to test an hypothesis about differential vulnerability to predation among segments of a population of meadow voles (*Microtus pennsylvanicus*). An hypothesis of secondary interest was that of differential vulnerability to predation between *Microtus pennsylvanicus* and other small rodents, notably deermice (*Peromyscus maniculatus*), jumping mice (*Zapus hudsonius*), and house mice (*Mus musculus*). This was intriguing because of the preponderance of *Microtus* over these other rodents in carnivore diets as reported by several food habits studies (Bradt, 1949; Korschgen, 1957).

The Prey

The prey species of primary interest in this study, *Microtus pennsylvanicus* (Family Cricetidae, Subfamily Microtinae), is widely distributed over North America (Hall and Kelson, 1959). The subspecies represented in Michigan, *M. p. pennsylvanicus* Ord, measures 120-188 mm in total length, and weighs between 20 and 69 grams (Burt, 1946). These voles are uniformly dark brown above with paler sides and silver-tipped ventral hair. Their food consists primarily of grasses and sedges, and they are generally found in moist low areas and in old field situations. They are primarily crepuscular, although they are active throughout the day and night (Burt, 1946).

Meadow voles, like many other microtine rodents, are subject to periodic fluctuations in numbers, and it is through the study of the demographic changes accompanying these fluctuations that they have received considerable attention in recent years. These studies have furthered the "interpretation of animal populations as a composite of qualitatively different individuals" (Myers and Krebs, 1971), and it is upon this interpretation that the present study is based. Data supporting the existence of differences in quality among individuals of a *Microtus pennsylvanicus* population have been reported in several studies.

Several papers have discussed differences in aggressive behavior between sexes of meadow voles. Significant antagonism between females, but not among males or between males and females has been reported by Getz (1972). Some of this behavior may be associated with reproductive activity -- Clarke (1956) noted high aggression by female *Microtus agrestis* during the last stages of pregnancy and with subsequent nursing of litters. Changes in aggressive behavior seem also to accompany the population cycle in both *Microtus pennsylvanicus* and *M. ochrogaster* (Krebs, 1970).

Research into the role of dispersal in the regulation of vole populations has yielded considerable evidence of qualitative differences between dispersing and resident animals. Dispersing males are generally more aggressive than residents during peak population density (Myers and Krebs, 1971). These "intolerant" animals tend to move into less densely populated areas as population density increases. Dispersing males show less exploratory behavior in a maze than do males from control populations.

These authors did not find, as is often thought, that young males are more apt to disperse than are adult males or young females. Body weights of dispersing males were not different from controls. They did, however, find a greater tendency for juvenile females (≤ 22 g) to disperse than juvenile males. Differences in reproductive condition were found between dispersing animals and controls. The proportion of subadult males with testes in a scrotal position, and of female subadults with perforate vaginae (each indicating attainment of breeding condition) were greater in dispersing animals than in residents.

Differences between male and female meadow voles in size of and restriction to a home range have been observed. Getz (1961) found male voles to have larger home ranges than females in two southern Michigan habitats. He suggests that this may be due to one or two factors: the restriction of female activity while caring for young, and/or the wide ranging search by males for mates. Getz also observed that a greater percentage of females than males had exclusive home ranges, and that females with established home ranges outnumbered established males during most of his study.

That some of these sex- or age-related behaviors might influence mortality is suggested by the rates of survival reported by Krebs *et al*. (1969). They found female survival rates to be high and relatively constant (until the population they were studying declined), while survival rates of males were highly variable. Male and female rates of survival were not highly correlated, and they concluded that "the loss process must be sex selective." Age differences in survival were also noted. Subadult males and females exhibited lower survival rates than did adults, especially during the summer breeding season when densities were high. It should be noted that in live-trapping studies of the type conducted by Krebs *et al*. (1969), survival refers to disappearance from the grid due to any factor (*e*. *g*., death, dispersal).

Hypotheses

Which, if any, of these sex- or age-related behaviors might affect vulnerability to predation? Several hypotheses would appear justified. Adult males, because of their greater tendency to roam, might expose themselves more to predators. Subadult males and females in breeding condition, through an inclination to disperse, could be more liable to predation than other age segments. Neonates may also be highly vulnerable. Due to the heterogeneity of existing evidence, hypotheses of no difference due to sex or age were postulated. The only hypothesized differences would be due to abundance. The null hypothesis for *Microtus* sex and age segments was phrased as follows:

> Each sex and age segment of a *Microtus* population will be captured and consumed by a carnivore in proportion to that segment's abundance in the environment.

The hypothesis of differential vulnerability between *Microtus pennsylvanicus* and other rodent species parallels that for vole sexes and ages, *i. e.*, the only differences among species in vulnerability would be due to differences in abundance.

Basis of the Method for Testing the Hypotheses

In order to test these hypotheses, it would be necessary to 1) monitor the changes in abundance of *Microtus* sex and age classes, and of the other rodent species; and, 2) identify animals eaten by carnivores. The first could be accomplished by live-trapping and marking the rodent population, as was done in the previously-mentioned demographic studies. In order to determine the identity of animals preyed upon, some marker was needed. Several studies (*e. g.*, Pearson,

1966) have analyzed fecal matter for mandibles to identify rodent species eaten by a carnivore. This technique cannot, however, be used to identify the sex and age of small rodent prey. Thus, it was necessary to devise some marker, to be placed on a prey animal, that would be ingested and passed by a carnivore consuming that prey. The small, numbered monel fingerling gill tags which have been used to identify rodents in demographic studies, seemed well-suited to the purpose. These tags, which are attached to the ear and measure 2 mm by 8 mm when applied, would allow rapid identification of animals both in the field during live-trapping and in carnivore droppings. It was first necessary to test whether a carnivore would ingest a tagged rodent. Several *Microtus* and *Peromyscus* were fed to each of 2 pet domestic cats, this species having been selected as the carnivore for this study. All rodents were eaten without hesitation by the cats, which showed no reaction to the tags. Thus, it was considered feasible to tag live-trapped animals in the field, and to collect carnivore droppings and analyze them for tags.

The Predator

Domestic cats (*Felis catus*) were selected as predators for this study for several reasons:

1. *Microtus* form a major part of the diet of field-roaming domestic cats (Bradt, 1949; Hubbs, 1951).
2. Domestic cats are abundant and reasonably easy to study.
3. There is growing concern among wildlife biologists, pest control operators, and others about the increasing numbers

of field-roaming and free-living domestic cats and their effect on populations of small birds and mammals (Kuroda, 1968; McKee, 1967; Troy, 1951). The ecology of the domestic cat is not well understood.

Domestic cat food habits, studied by Eberhard (1954), Hubbs (1951), McMurray and Sperry (1941), and others, have shown that these cats generally prey upon whatever small mammal or bird is most available or abundant. They occasionally take such larger animals as rabbits, pheasants, and ducks. Bradt (1949) found that one cat killed 1600 rodents in an 18 month period, of which about 75% were meadow voles. Insects occupy a considerable part of the diet during spring and summer.

While several studies (Kuo, 1930; Leyhausen, 1960) have dealt with the development of the domestic cat's response to prey animals and with its killing technique, little work on field-roaming domestic cats, other than the above mentioned food habits studies, has been done. In the only published work on field behavior found by this author, Leyhausen (1965) discussed social organization and found that domestic cats frequently shared common hunting grounds, but usually did not hunt together, generally avoiding close contact in the field.

THE STUDY AREA

This study was carried out in farmland near Williamston, Michigan (section 17, T 3N, R 1E, Ingham County). The small rodent population of an approximately 0.8 hectare (2 acre) old field was sampled by live-trapping. An adjacent farm, directly across a paved county road from the trapping grid, was occupied by approximately 10 domestic cats, the number varying with the movements of wandering toms. The resident cats were fed dry food and table scraps, but supplemented their diet by hunting mice, primarily on the trapping grid. The grid had been fallow for about 5 years, having last been sown in "Sudex" (DeKalb trade name for an annual hybrid forage plant). Three general vegetational types were found on the area (see Figure 1): a central area, consisting primarily of blue-grass (*Poa sp.*); a brushy strip along the south and east consisting of burdock (*Arcticum sp.*), stinging nettles (*Urtica sp.*), and scrub willows (*Salix sp.*); and an area of brome-grass (*Bromus sp.*) and mixed herbaceous plants along the north and west borders. The grid was bordered on the north by the county road, on the west by an alfalfa field, and on the east and south by a small creek. Beyond the creek was a pasture to the east and a fallow field to the south.

A wide variety of vertebrates and invertebrates existed on the study area. Several predators in addition to domestic cats were present. One weasel (*Mustela frenata*) was captured. Although not observed, the presence of raccoons (*Procyon lotor*) and domestic dogs was evidenced by their droppings. A red-tailed hawk (*Buteo jamaicensis*) was observed once in the adjacent alfalfa field, but was not seen on or over the trapping grid.

Potential prey animals, in addition to the small rodents of particular interest in this study, included pheasant (*Phasianus colchicus*), which were abundant on the trapping grid. Crickets (Gryllidae) and grasshoppers (Acrididae and Tettigoniidae), which are common prey of domestic cats during the summer months (Hubbs, 1951; McMurray and Sperry, 1941), were present in large numbers. Sparrows (Fringillidae) and frogs (*Rana pipiens* and *R. sylvatica*) were occasionally captured in traps. Shrews (*Blarina brevicauda* and *Sorex cinereus*) were common on the study area. These are often captured and killed by cats, but infrequently eaten (Nader and Martin, 1962).

Other mammalian species on the study area included muskrat (*Ondatra zibethicus*), whitetail deer (*Odocoileus virginianus*), and opossum (*Didelphis marsupialis*).

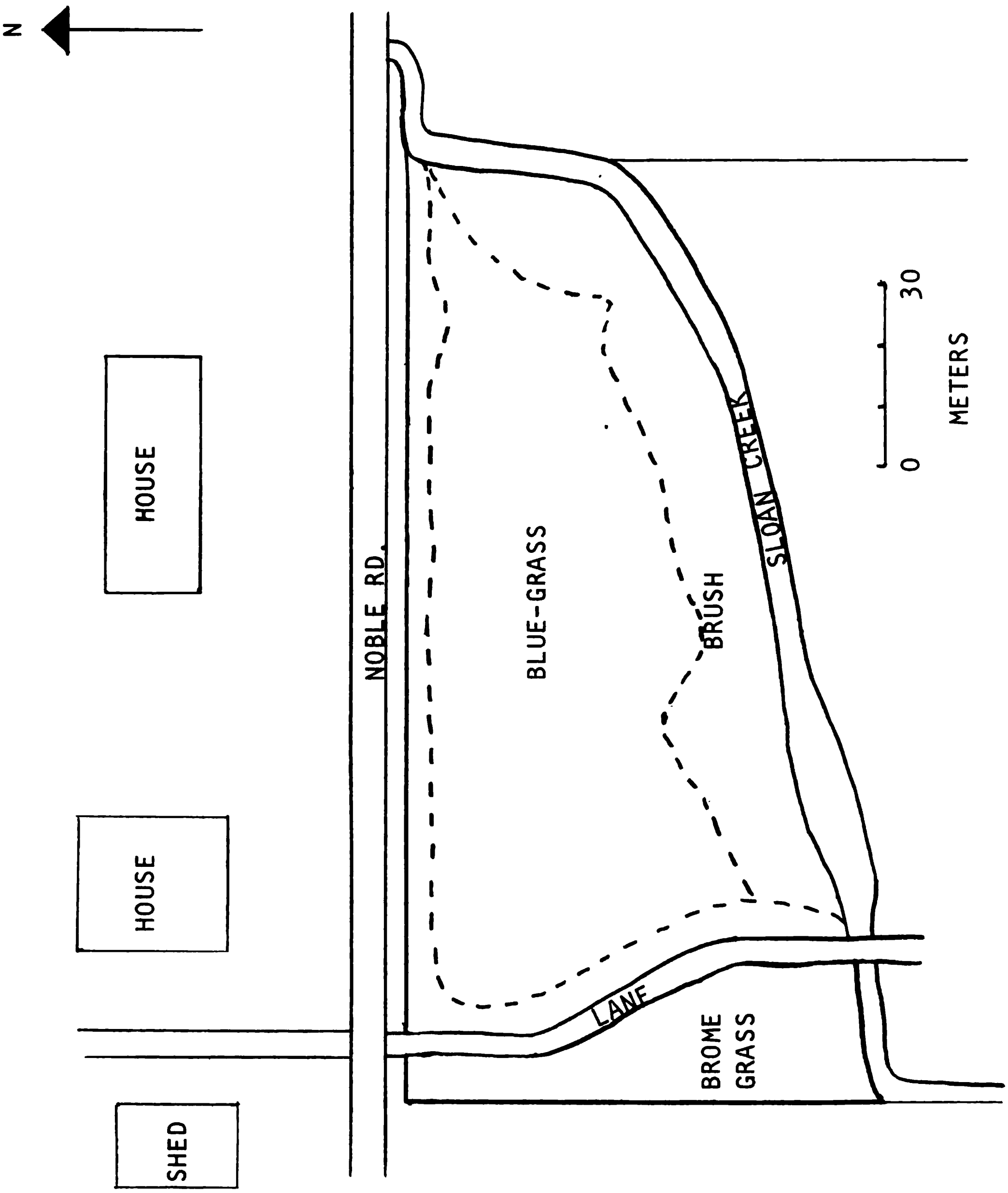

Figure 1. Map of the study area.

METHODS

Data on the independent variable, _i. e._, the relative abundances of sex and age segments of _Microtus_ and of the several other small mammals, were collected by an intensive live-trapping and marking program which took place between 19 July and 1 November, 1972. Box traps with a trip mechanism of the type described by Fitch (1950) were used on a permanent grid of 8 meter spacing, 118 traps being used to cover the area. Traps were placed 4 meters from the north and west borders; border traps on the other sides fell between 0 and 6 meters from the boundaries.

The traps were placed in 9 rows, numbered from north to south, each containing the following number of traps: rows 1 through 4, 18 traps each; row 5, 16; row 6, 13; row 7, 8 traps; row 8, 6; and row 9, 3 traps. Each trap location was assigned a number based on its row and location within a row. Traps were baited with rolled oats, small amounts of which were placed both at the mouth of the trap and behind the trip.

Each of the 16 trap periods was three nights long. Traps were baited in late afternoon or early evening, inspected and closed the following morning, and baited and re-set that evening. Each trap period ended when the traps were closed on the third morning. The traps were left set during the day when temperatures were low enough to present little danger of overexposure to animals in traps. The first day of each trap period was spaced one week from the others with the following exceptions: trap periods 1 through 3 were on 9 successive days, and periods 4 and 5 occurred 1 week later on 6 successive days. These trap periods were compressed to allow rapid tagging of as many animals as possible at the beginning of the study. Trap periods 9 and 10 were spaced 2 weeks apart.

Nine additional traps were placed in areas of highest _Microtus_ density during trap periods 8 through 12. These were then removed when they failed to increase capture success.

Individual mice and voles were identified by attaching the previously mentioned fingerling tags (Salt Lake Stamp Co.) on the ear at first capture. Voles were occasionally captured with torn ears, indicating that they had likely lost previously-applied tags. This loss, however, was minimal: only 15 individuals were captured in this condition.

Several kinds of data were recorded upon trapping an animal: species, location on the grid, sex, weight, tag number (if recaptured), and, in the case of _Microtus_, reproductive condition. Weights were obtained to the nearest gram using a Hanson diet scale. Reproductive condition was assessed in the manner described by Krebs (1966). For males, the position of the testes, whether scrotal or abdominal, was noted. Several reproductive measures were used for females. The condition of the vagina, whether perforate or not, was used as a general indicator of breeding condition. However, as mentioned by Myers and Krebs (1971), this indicator seems to be most reliable for subadults, since its use with adults is complicated by the occurrence of pregnancy. The size of the nipples was used as an indicator of lactation. The condition of the pubic symphysis, whether closed, slightly open, or open, gives some idea of past parturitions (see Hall and Newton, 1946). In addition, females with bulging abdomens were noted as being "likely pregnant".

Age classes were established on the basis of body weight, as described by Chitty (1952). Voles weighing 22 grams or less were classified as juveniles; those greater than 22 g but less than or equal to 32 g as subadults; and those weighing more than 32 grams were classified as adults.

Data on the dependent variable, the number of animals of each sex and age segment of *Microtus* and of each species that was preyed upon by cats, were obtained by collecting and analyzing cat droppings for ear tags. These scats were collected in various locations, primarily on the trapping grid and in flower beds in the farmhouse yard. Droppings were analyzed by x-ray on sheets of Plexiglas. The scats containing ear tags were then easily segregated from the others and the tags removed.

The use of this method is based on several assumptions. First, it is assumed that tagging will have no effect, or that any effect will be systematic among groups, on survivorship of mice and voles, on vulnerability to predation, or on ingestion of mice by carnivores. It is assumed that no bias will be introduced by locations of scats, *i. e.*, that individual carnivores do not select prey differently than others, and that each cat does not use a specific scatorium. The assumption is made that trappability is random and does not change with time among the marked segments of the population.

RESULTS

The results will be presented in 2 sections, one dealing with the characteristics of the small rodent population during the course of the study; the other, with the analysis of predation upon these animals. Since the numbers of Peromyscus, Zapus, and Mus captured were small, no attempt was made to evaluate changes in numbers and other demographic parameters for these species.

SMALL RODENT POPULATION

A total of 5640 trap-nights were logged, during which 576 total captures were made on 261 Microtus, 18 Peromyscus maniculatus, 10 Mus musculus, and 1 Zapus hudsonius. Capture success was consistently low throughout the study, varying between 5 and 20% between trap periods. Trap mortality was minimal: 3 Microtus were found dead in traps. One of these was an adult female which was known to be alive on the grid for 4 weeks previously. The other 2 animals dying were 1 male and 1 female subadult that apparently drowned or chilled during a heavy rainstorm.

Numbers and Age Classes

Numbers of Microtus alive during the study were estimated by the direct enumeration technique described by Krebs (1966). In this technique, the minimum number of mice alive at time t is obtained by summing two counts: 1) the number caught at time t; and 2) the number of previously tagged animals caught after time t, but not at that time. Use of this method avoids making the assumption inherent in capture-recapture methods of random sampling between marked and unmarked segments of the population.

The minimum number of <u>Microtus</u> alive fluctuated widely between trap periods, so minimum numbers were calculated for 2 trap period intervals (except that trap periods 1-3 were combined). These data, illustrated in Figure 2, page 17, show a decrease in total numbers during trap periods 6 and 7, perhaps due to decreased trappability, accounted for in part by the very hot humid weather at these times. This dip was followed by an increase during trap periods 8 and 9, another decrease through trap period 13, and a slight increase through period 15. When minimum numbers are calculated for longer periods of time, as shown in Figure 3, page 18, deviations from a smooth curve are lessened, and the general trend of decreasing numbers of <u>Microtus</u> emerges.

Figures 2 and 3 also illustrate minimum numbers of <u>Microtus</u> alive in each age class throughout the study. The minimum number of juveniles alive decreased slightly throughout the study, while the number of subadults, after a decrease during trap periods 6 and 7, increased. The number of adult voles decreased steadily.

Since the relative abundances of the different age classes were also of interest, the proportions of the total minimum number alive in each age class were calculated, and are shown in Figure 4, page 19. Juveniles represented between 12 and 20 % of the total population

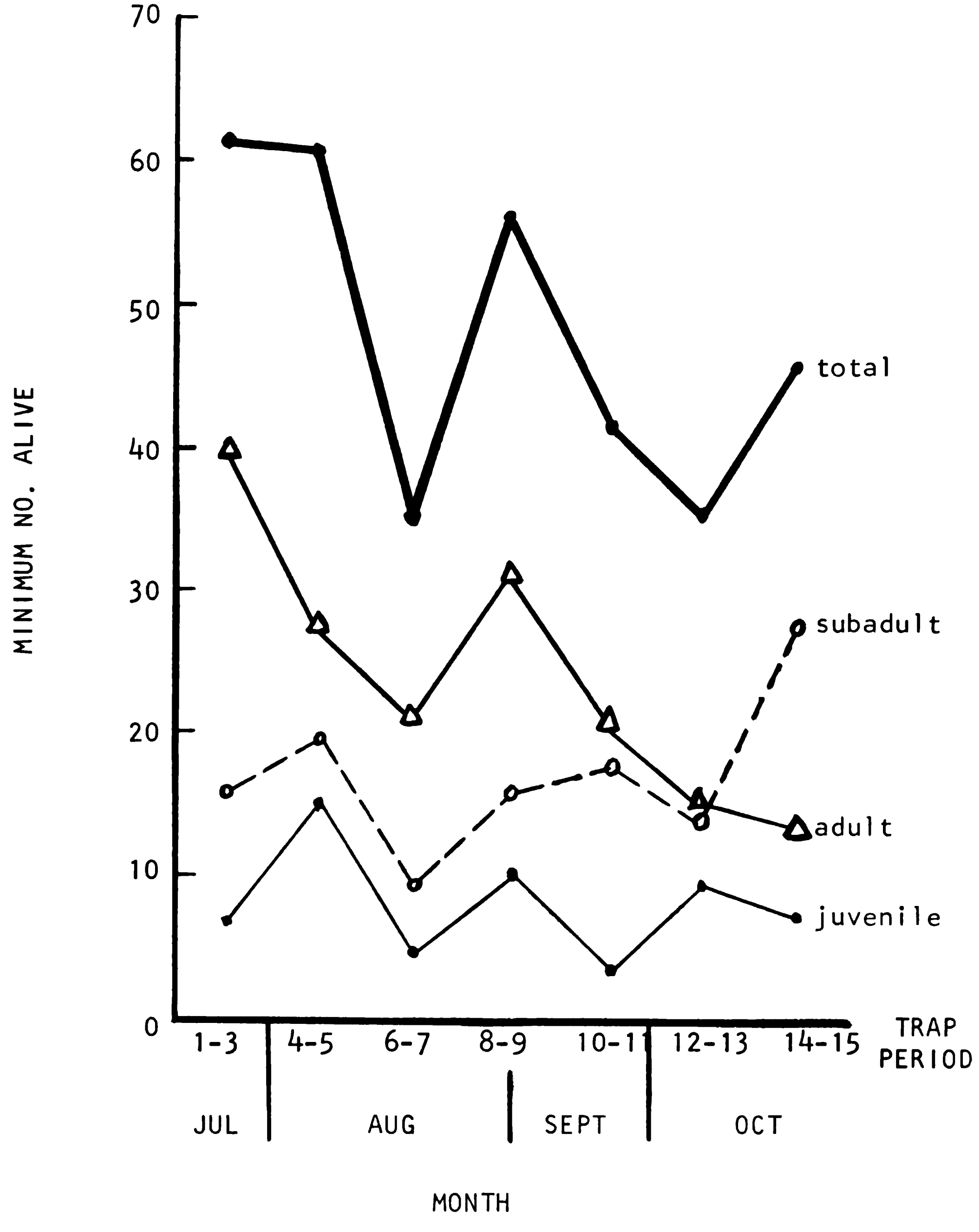

Figure 2. Minimum numbers of *Microtus* alive.

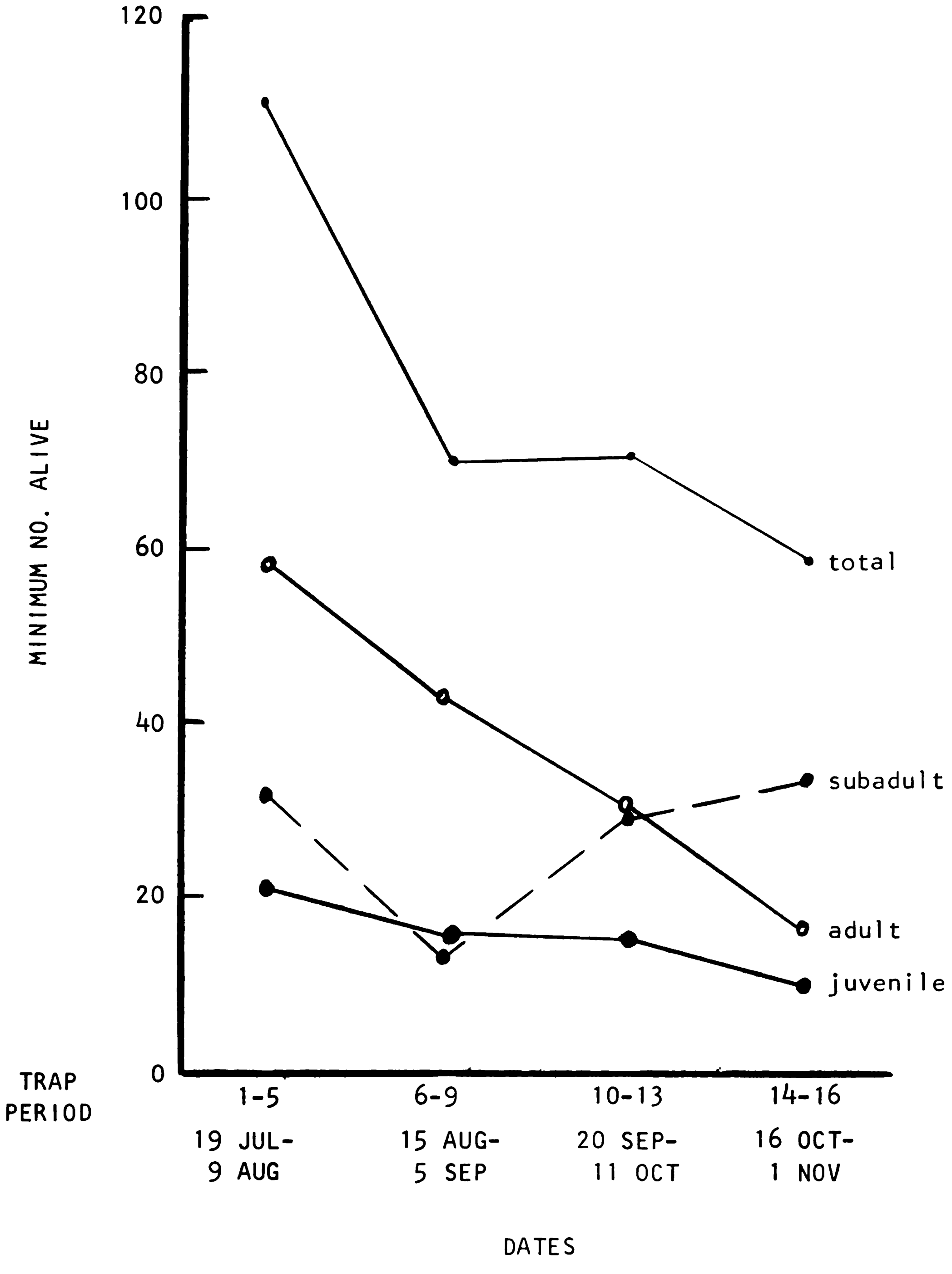

Figure 3. Minimum numbers of *Microtus* alive.

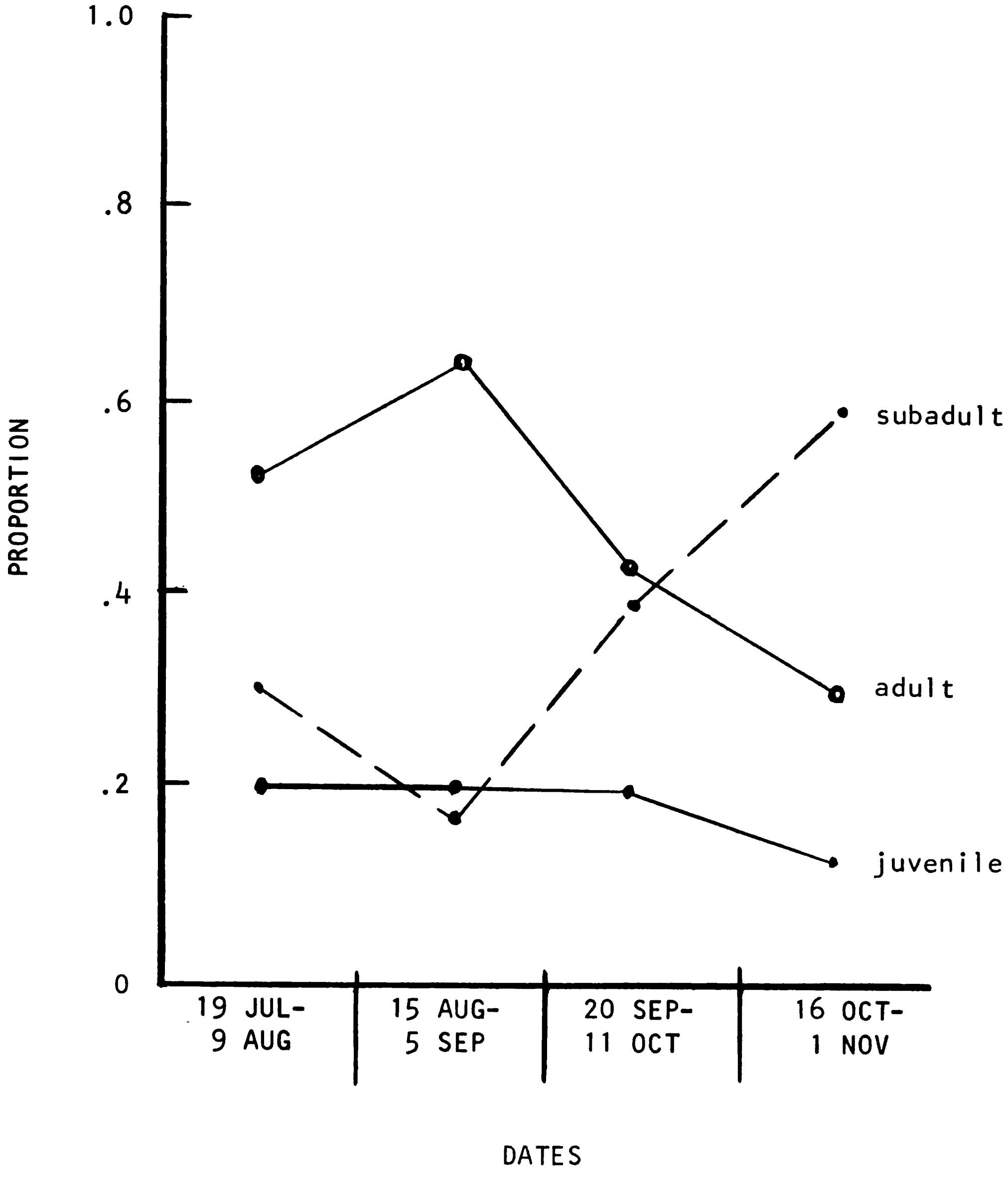

Figure 4. Proportion of the minimum number of *Microtus* alive represented by each age class.

throughout. A Chi-square goodness-of-fit test was used to test for significant changes in the proportion represented by each age segment. The changes in the juvenile proportion were not significant (each $X^2 < 1.45$, $P > .20$). The decrease in the subadult proportion during the second time interval (15 August to 5 September) was not significant ($X^2 = 2.58$, $P > .10$), but the increases in proportion during the following 2 time intervals were significant ($X^2 = 21.33$, $P < .001$; $X^2 = 5.26$, $P < .05$). The increase in the adult proportion from the first to the second time interval was not significant ($X^2 = .97$, $P > .30$); a significant decrease ($X^2 = 5.00$, $P < .05$) occurred between the second and third intervals. The decrease observed in the fourth interval adult proportion was not significant ($X^2 = 1.96$, $P > .10$).

Sex Ratios

Sex ratios (proportion of males of the minimum number of _Microtus_ alive are shown in Figure 5, page 21. None of these ratios is significantly different from 1:1 ($P > .20$).

Reproduction

As stated in the Methods section, reproductive activity was assessed by examining the external sexual characteristics of voles. While these measures are not as accurate as autopsies, they provide a crude measure of changes in reproduction (Krebs _et al._, 1969).

Probably the best measure of a population's breeding activity is the percentage of females with enlarged nipples, _i. e._, lactating (Krebs _et al._, 1969). These percentages are illustrated in Figure 6, page 22. The percentage of adult females that were lactating increased

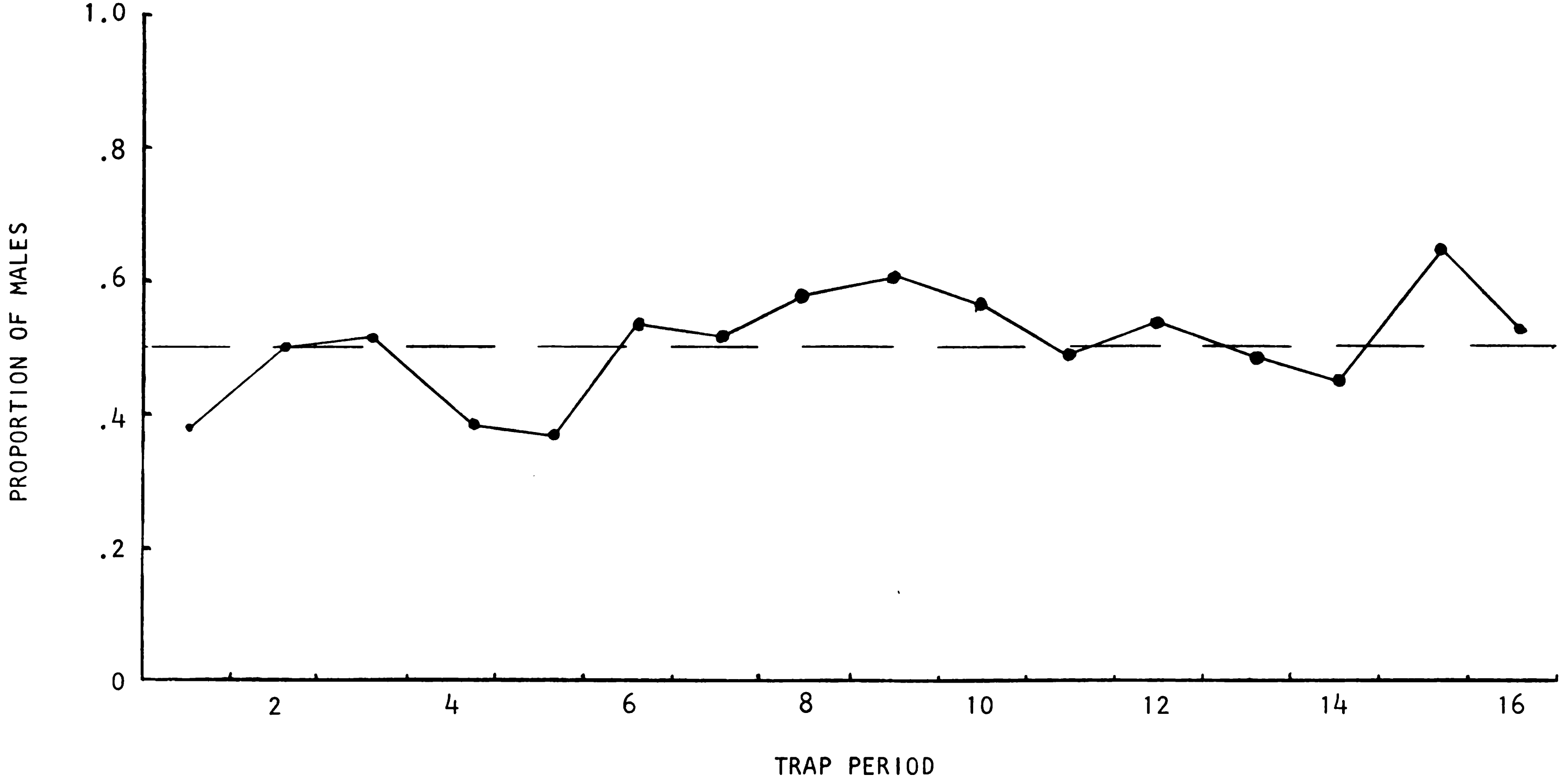

Figure 5. Proportion of male voles in the minimum number alive during each trap period.

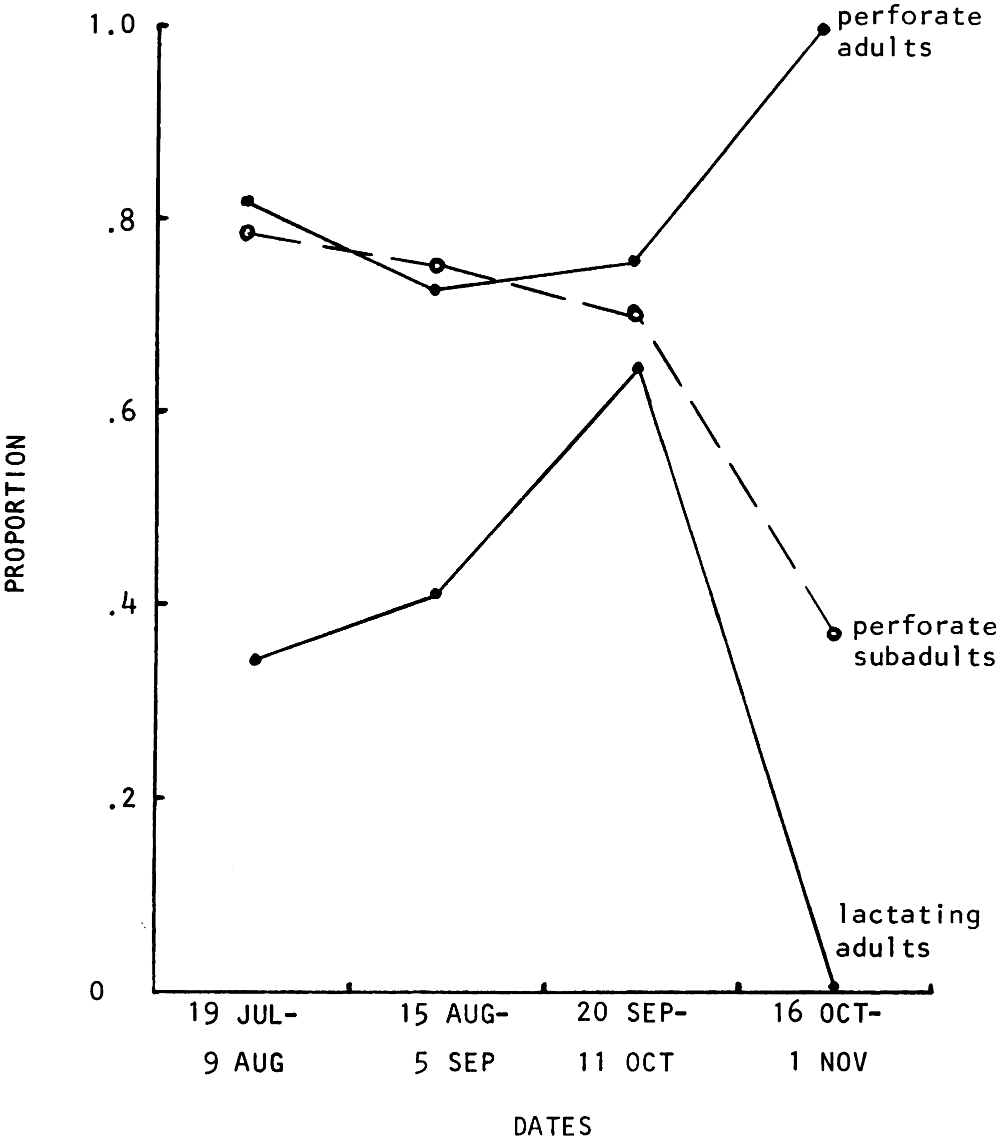

Figure 6. Changes in female vole reproductive measures.

through the first part of October, and then dropped to zero during the last 2 weeks of the study, indicating a decline in breeding. This interpretation is made with no little reservation, since samples were small (*e. g.*, a minimum number of only 5 adult females were alive during the closing 2 weeks of the study).

The proportions of subadult and adult females with perforate vaginae are also shown in Figure 6. This percentage for adult females increased throughout the study, but, as previously stated, the use of this measure for mature females may be invalid. The proportion of subadult females in breeding condition decreased throughout the study.

The proportion of adult females judged pregnant on the basis of bulging abdomen remained between .46 and .60, and showed no increasing or decreasing trend during the study. These proportions are considerably higher than those reported by Krebs, Keller, and Tamarin (1969), and seem to contradict other measures of female reproduction. These factors have led the author to seriously question his lack of bias in using this technique, and for this reason, these data on pregnancy have not been used in assessing reproductive activity.

Breeding condition of males was judged by the position of the testes. The proportion of males with testes in a scrotal position is shown in Figure 7, page 24, for adults, subadults, and both ages combined.

Mortality

Mortality in a live-trapping study is defined as disappearance from the grid, and thus includes dispersal off of the trapping area.

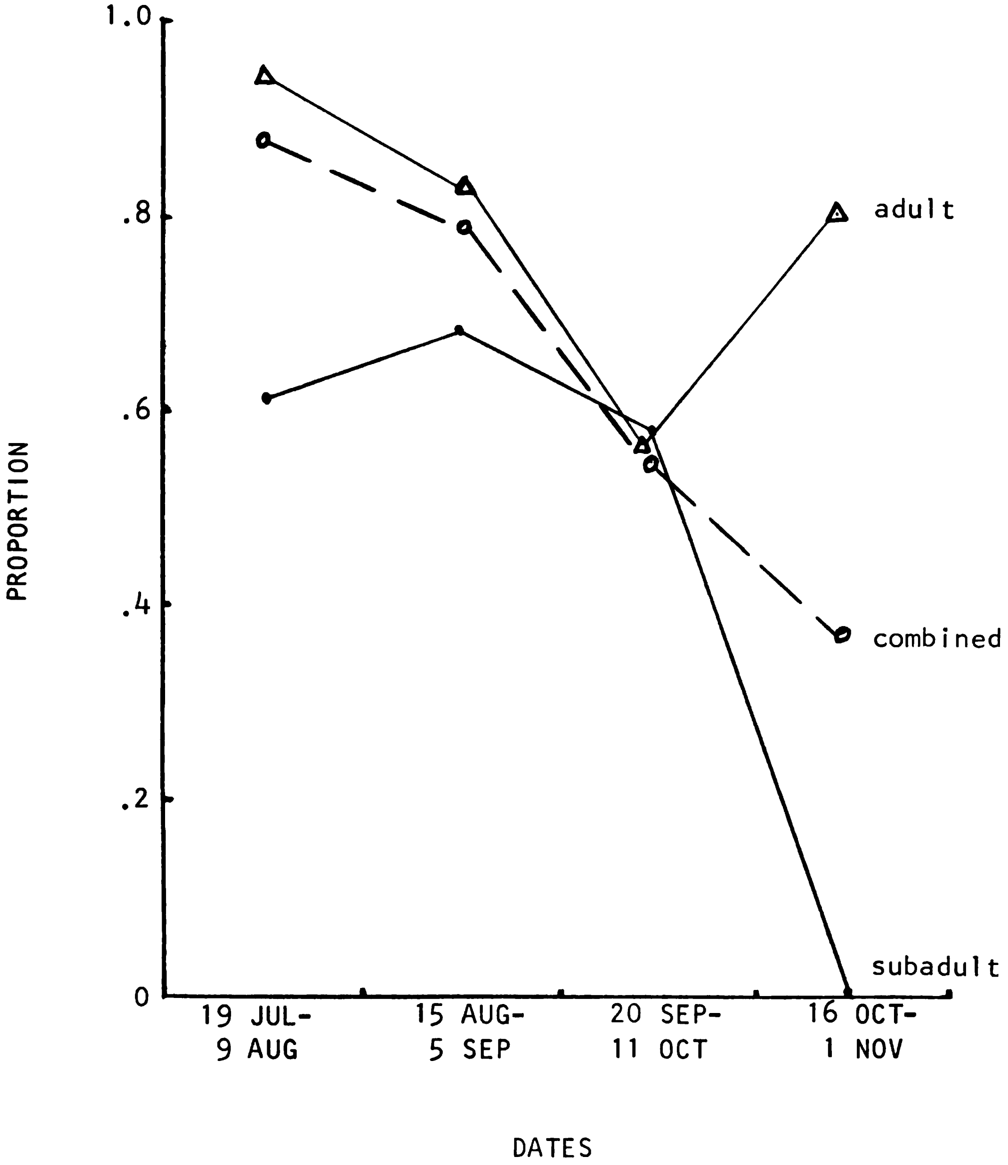

Figure 7. Proportion of male voles (subadult, adult, and combined) with testes in a scrotal position.

Survivorship curves, such as that shown in Figure 8, page 26, were calculated in the following manner. The week in which each vole was first captured was designated week zero. Thus, at week zero, 100 % of the animals were alive on the grid. The proportion remaining at each following week is lower than the previous week by the proportion that was captured for the last time during that week. These curves were constructed for all voles captured for the first time in trap periods 1 through 13. Trap period 13 was the last in which animals first captured were not still being re-captured at the end of the study.

These curves were linearized by plotting on semi-logarithmic graph paper to facilitate comparisons between sexes and ages. The points conformed closely to a straight line, with the exception of the period from week zero to week one, which was excluded from the semi-log plots. Figure 9, page 27, shows survival for males and females. After the first week, both sexes survived at approximately the same rate.

Survivorship of the different ages is illustrated in Figure 10, page 28. After differential survival in the first week, all ages survived at approximately the same rate.

Since it was of interest to examine changes in survivorship over time, the survivorship of voles alive during trap periods 1-10 (n=182) was compared with that of those alive during periods 11-13 (n=60). These data, shown in Figure 11, page 29, illustrate that survival was lower in the latter time period; a t-test of mean survivorship showed this difference not to be significant.

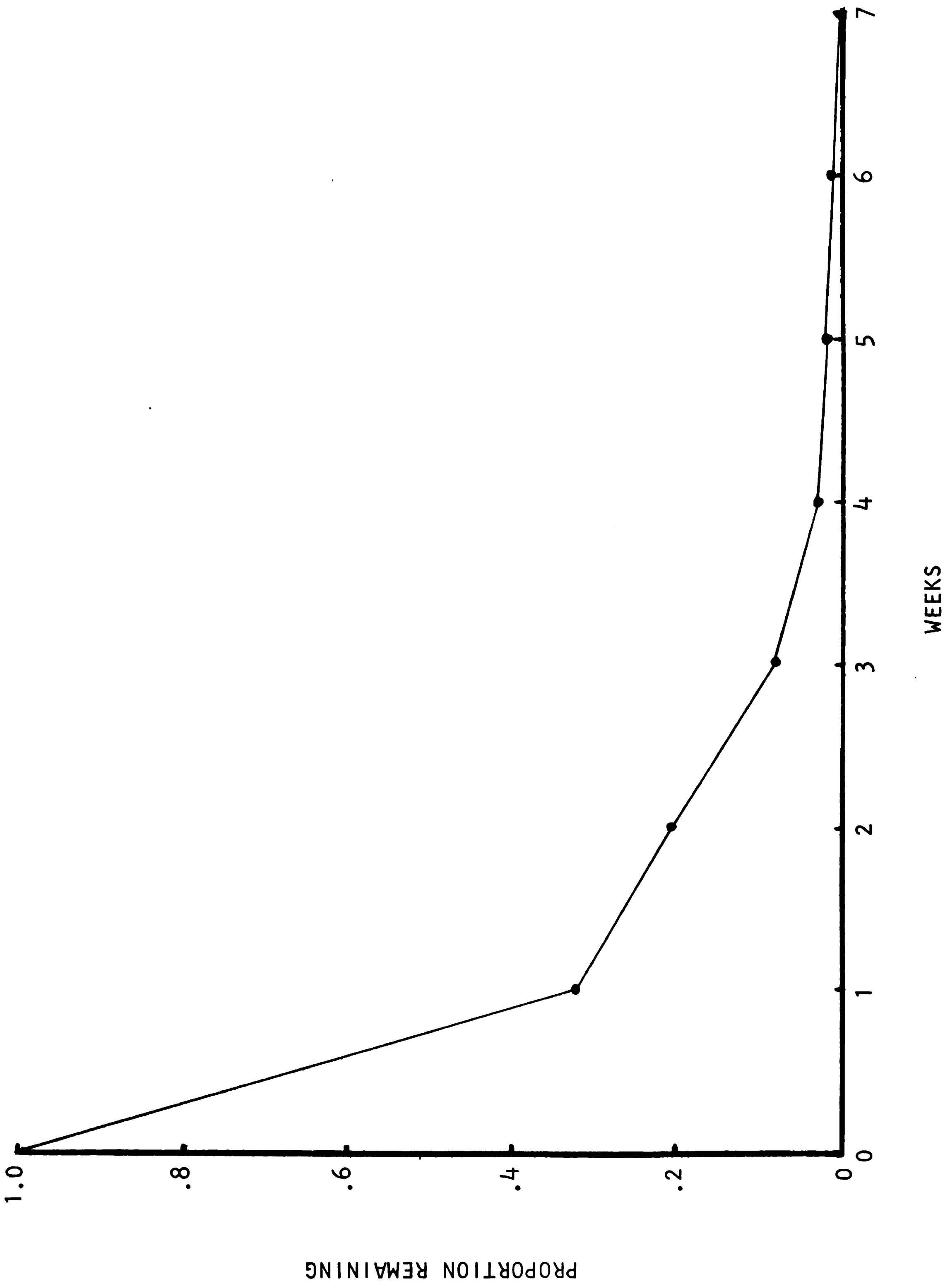

Figure 8. Survivorship of all *Microtus*, trap periods 1-13.

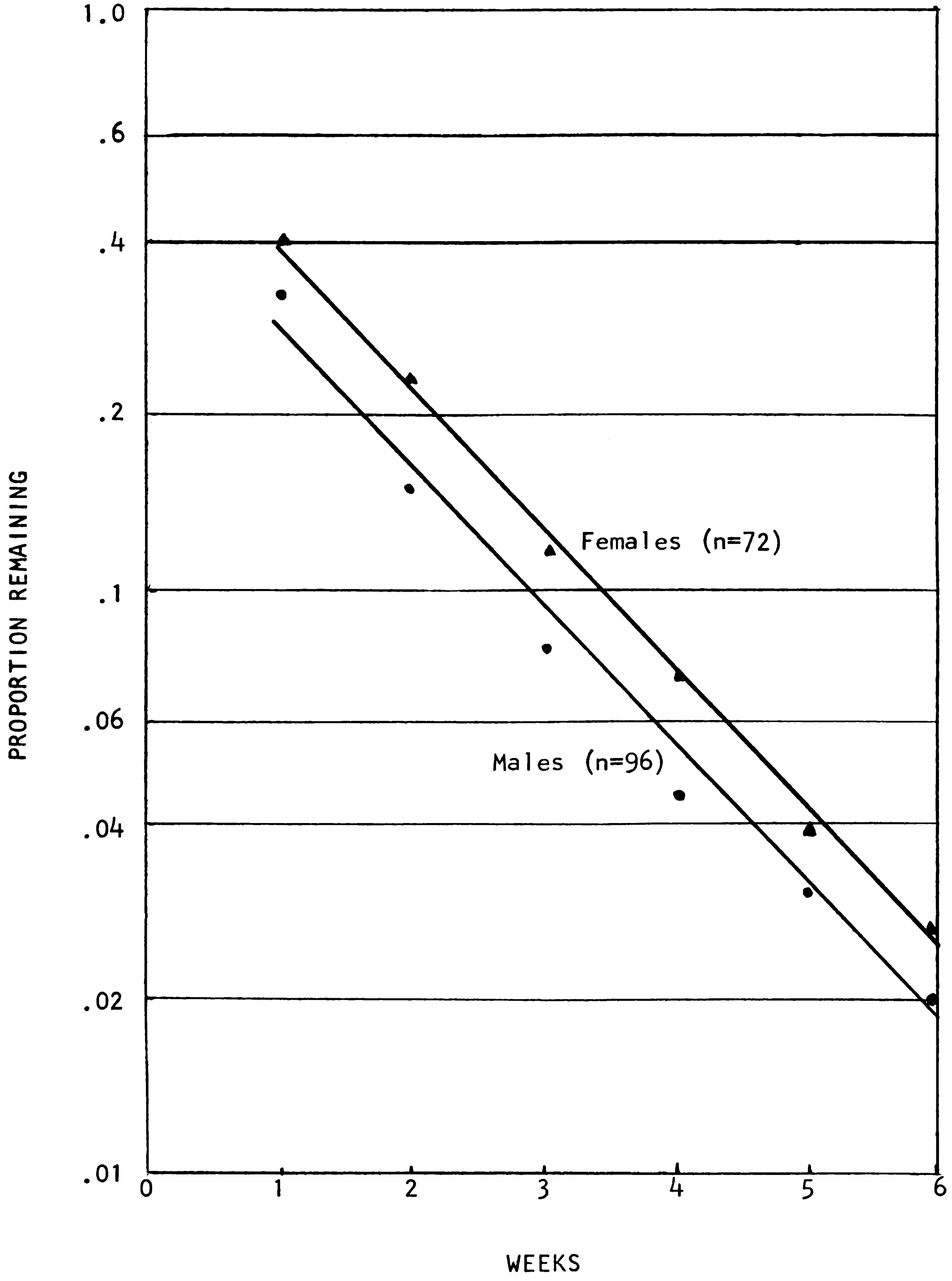

Figure 9. Survivorship by sex, trap periods 1-13.

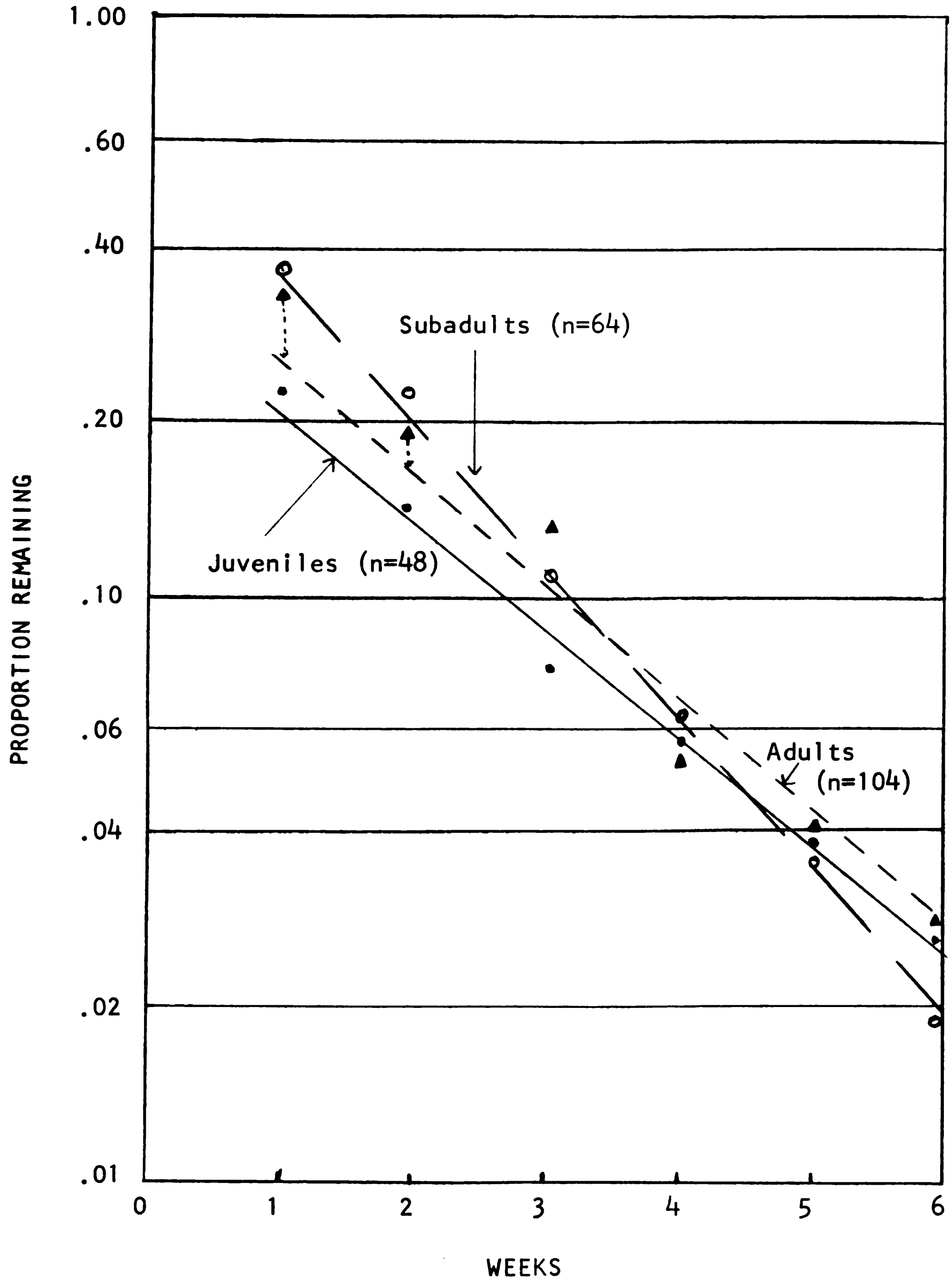

Figure 10. Survivorship by age at first capture, trap periods 1-13.

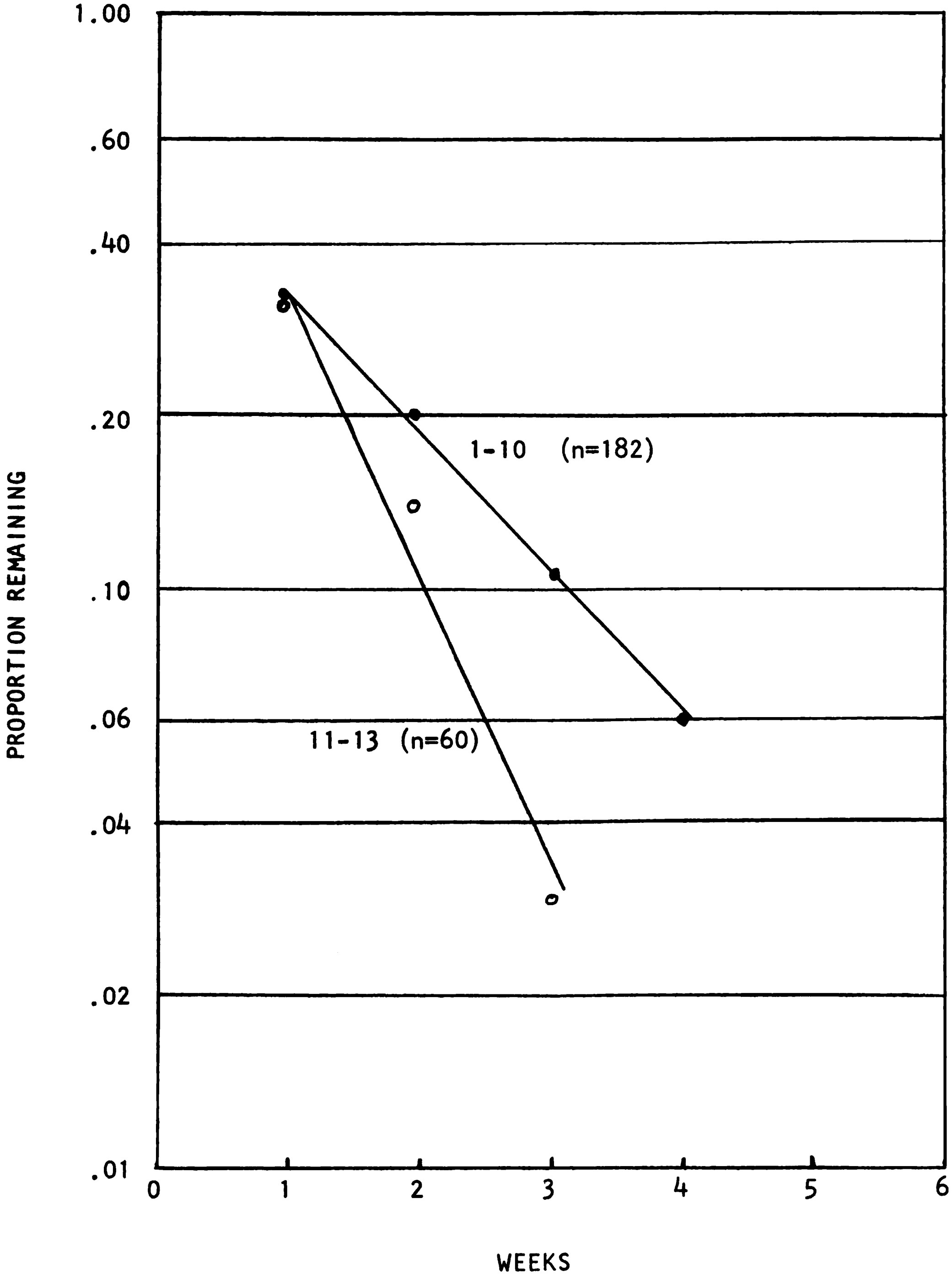

Figure 11. Survivorship of voles alive during trap periods 1-10 and periods 11-13.

No data are available on survival of those very young animals which have not yet reached trappable age, about 4-6 weeks, at which time they weigh 20-25 grams. The index relating recruitment of young into the population to lactating females employed by Krebs (1966) could not be used because of the small number of lactating females captured in this study.

ANALYSIS OF PREDATION

A total of 40 ear tags was recovered from approximately 160 scats. All of the tags were from *Microtus*. The sexes and ages of voles whose tags appeared in scats, along with expected numbers (based on 261 total voles of which 133 were males, 128 females, 45 juveniles, 90 subadults, and 126 adults), X^2, and P values, are shown in Table 1, page 31. The X^2 tests show no differences between observed and expected numbers for sex or age classes or for ages within sex. A conspicuous, although not significant, difference is seen between males and females -- the former being taken less often than expected, the latter more often. These data indicate that sex and age segments of voles are preyed upon in proportion to their abundance.

Since the relative abundances of adults and subadults changed throughout the study, it was of interest to compare changes in the amount of predation suffered by each age class at different times. To accomplish this, the first 20 tags (Group I) recovered were compared with the second 20 (Group II). The age structure of the population during the times tagged animals in each group were known to be available to predators (Group I -- 19 July to 22 September; Group II -- 25 Sep-

Table 1. Sexes and ages of tagged *Microtus* recovered from cat fecal matter during the entire study.

CLASS		OBSERVED	EXPECTED*	X^2	P
Male	Juvenile	4	2	1.26	$.70 < .80$
	Subadult	4	5		
	Adult	8	9		
Female	Juvenile	4	5	0.31	$> .95$
	Subadult	10	10		
	Adult	10	9		
Males		16	20	1.60	$.30 < .50$
Females		24	20		
Juveniles		8	7	0.26	$> .95$
Subadults		14	15		
Adults		18	19		
		n=40			

* Based on the proportion of total captured in each class over the entire study.

tember to 1 November) was computed to derive expected values on the basis of abundance. The expected, observed, X^2, and P values illustrated in Table 2, page 33, show that, <u>within</u> each of these time periods, each age and sex class was preyed upon in proportion to its abundance.

A X^2 test was used to test for differences <u>between</u> Group I and Group II tags. The proportion of Group I tags represented by each class was used to establish expected values for that class in Group II tags. The observed and expected numbers, along with X^2 and P values, are shown in Table 3, page 34. The significant difference between Group I and Group II tags in the amount of predation suffered by each age class may be attributed almost entirely to the deviations between observed and expected values for subadults and adults. These differences correspond to the changes in relative abundances of each of these age classes, and further indicate that age classes of meadow voles in this study were preyed upon in proportion to their abundance.

The minimum number of voles alive during the time when Group I animals were in the population was 169, while 110 were alive when Group II animals were available to predators. Thus, the <u>known</u> percentages of predation were 11 % (20/169) for Group I animals and 18 % (20/110) for Group II animals. This represents a significant increase over time in the proportion of animals alive that were caught by predators (X^2=5.33, $.02<P<.05$). The cause(s) of this increase are not known, but several conjectures may be made. Since no change in vulnerability, beyond changes in abundance, was observed for any one sex or age class, it would appear that, whatever the cause, it affected

Table 2. Sexes and ages of tagged *Microtus* recovered from cat fecal matter within Groups I and II.

Group I

CLASS	OBSERVED	EXPECTED	X^2	P
Males	8	11		
Females	12	9	1.82	$.30 < .50$
Juveniles	4	3		
Subadults	4	5	0.28	$> .95$
Adults	12	12		
	n=20			

Group II

CLASS	OBSERVED	EXPECTED	X^2	P
Males	7	10	1.80	$.30 < .50$
Females	13	10		
Juveniles	5	3		
Subadults	9	9	1.25	$.70 < .80$
Adults	6	8		
	n=20			

Table 3. Comparison between Group I and Group II tags in the amount of predation suffered by each sex and age segment.

Group I

CLASS	OBSERVED	% OF TOTAL
Males	8	40
Females	12	60
Juveniles	4	20
Subadults	4	20
Adults	12	60

Group II

CLASS	OBSERVED	EXPECTED*	X^2	P
Males	8	8	0.00	>.99
Females	12	12		
Juveniles	5	4	8.12	.02<.05
Subadults	9	4		
Adults	6	12		

*Based on % of total represented by each class in Group I tags.

each age and sex segment equally. No data is available on the number of predators hunting on the area, but a larger number might account for an increase in percent predation. Vegetative cover began deteriorating with the first frost in late September, which may have influenced vulnerability.

It was of interest to examine the effects upon vulnerability of the attainment of breeding condition and behaviors associated with reproduction. Seventy percent of all subadult and adult females had perforate vaginae (from the summation of capture data for all trap periods), compared with 85 % of those which were known to be preyed upon. This does not represent a significant difference (X^2=0.64, P>.30). Likewise, no association was found between pregnancy or lactation and the liability to predation.

For males, 69 % of all subadults and adults had testes in a scrotal position (again, from the summation of capture data for all trap periods), compared with 75 % of those males recovered in scats. This represents no difference. Thus, these data indicate that reproductive activity has no effect on vulnerability to predation.

As previously stated, no tagged Mus, Zapus, or Peromyscus were recovered in scats. This difference is striking, but not significant. Individuals of these species represented 10 % (29/290) of all rodents captured. The number expected in scats would thus have been 4, which is not significantly different from the observed zero (X^2=3.06, P>.05). Thus, these data indicate that each rodent species on the area was taken in proportion to its abundance.

DISCUSSION

The data gathered in this study indicate that domestic cats captured small mammal prey in proportion to abundance. Different segments of the *Microtus* population were preyed upon in proportion to their abundance overall, and changes in abundance of age classes were directly reflected in changes in the amount of predation suffered by each class. The various rodent species on the trapping grid were apparently also captured in relation to their relative abundance.

This apparent lack of differential predation among segments of the *Microtus* population may be explained in at least two ways: 1) all voles, regardless of sex or age, are equally liable to predation, or 2) individual voles may differ in vulnerability, but the distribution of vulnerability is the same within each segment of the population. That is, there may be some highly vulnerable voles, but these animals comprise an equal proportion of all segments. Given the existence of behavioral differences within a vole population, this latter hypothesis would seem more tenable.

The lack of differential predation among sexes or ages may be in part a function of the hunting strategy of domestic cats. Hornocker (1970) has hypothesized that canids (*e. g.*, wolves, *Canis lupus*), which run their prey down, are more apt to take sick, weak, or aged animals, while felids, such as the mountain lions (*Felis concolor*) he was studying, which either approach slowly to within attacking distance or wait in ambush, are apt to take any animal, regardless of condition, that is in a vulnerable position. House cats often employ a sit-and-wait strategy, and thus may take any animal that approaches within pouncing distance. It would seem that if differences existed among prey animals in experience, activity, range, and so on, these differences would affect liability to predation by domestic cats. However, unless these differences were distributed unequally among segments of a population, results such as those obtained in this study might be expected.

The decreasing numbers and low survival (see Krebs *et al*., 1969) would indicate that this vole population was in a decline phase; a different distribution of vulnerability among sexes and ages might be expected during another phase in the microtine cycle. Thus, the conclusions of this study should be limited to this population at this point in time.

In summary, it appears that, at least for this study, no differential vulnerability exists among segments of a vole population to predation by domestic cats. Also, there appears to be no difference in vulnerability to predation between *Microtus* and the other rodent species studied.

SUGGESTIONS

The author would like to suggest solutions to some of the problems encountered in this study. One of the limitations on the interpretation of these data stems from the lack of knowledge about the number of cats hunting on the area. Cats were occasionally observed during morning and afternoon, but never more than 2 at a time. The number hunting on the area at night was not determined. The use of an enclosure which would allow maintaining a constant and known number of predators would have been helpful. But since dispersal has been found to be an important part of microtine rodent population biology, it would be necessary for such an enclosure to prevent movement of cats and yet allow free dispersal of voles into and out of the area. An enclosure would also facilitate scat collection, which was one of the major problems in this study.

Trap predation was somewhat of a problem, so it would be advantageous to devise some method of securing traps that would not be a serious hindrance to checking, baiting, and setting.

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APPENDIX: A MODEL OF PREDATOR FEEDING BEHAVIOR

Several authors (Holling 1965; Schoener, 1971) have derived mathematical models describing predation, but these equations often assume control of predator and prey variables. Thus it was difficult to classify the types of prey variables of interest in this study. A schematic model for the behavior of a feeding predator, shown in Figure 12, page 43, was devised for this organizational purpose. This model includes not only prey characteristics, but also predator and environmental variables.

The feeding behavior of a predator has been segmented into several steps. These are depicted in the model as "decisions" with "yes" or "no" alternatives. A "yes" alternative to a step indicates that the predator has completed that "decision" and thus moves on to the next. For example, a "yes" alternative to "search for prey" signifies that the predator is searching for prey, and the next step in the sequence is to detect prey. The model begins with the assumption of an active predator, and proceeds through the several steps, each of which will be explained in turn. A "no" alternative to "search" indicates that the predator will undertake some other activity. After a "no" alternative to any other step, the predator returns to searching.

When the predator has begun searching, its next task is to detect prey, which is dependent on his capabilities and on various

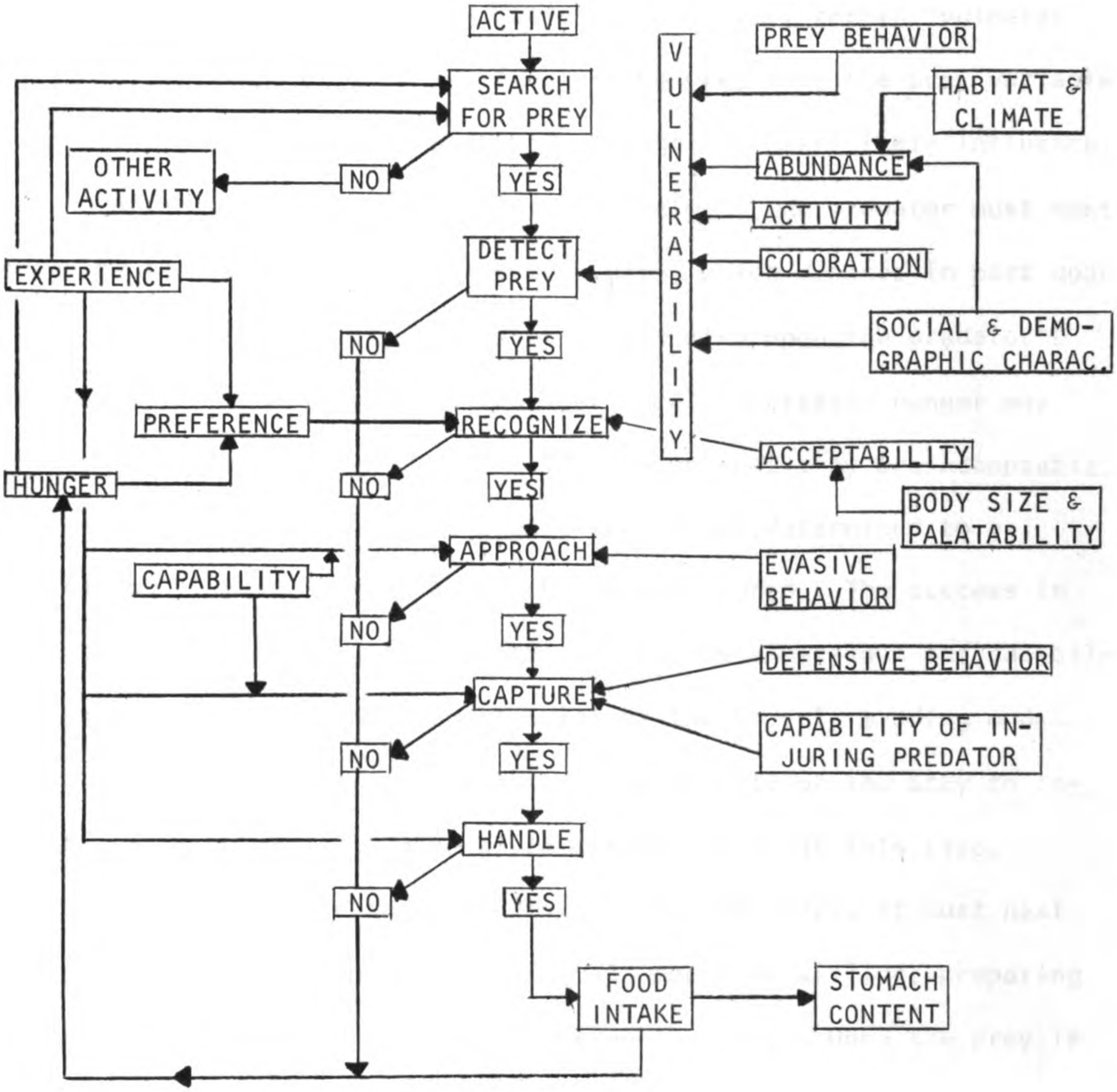

Figure 12. A schematic model for predator feeding behavior. Prey variables on right, predator variables on left.

prey and environmental characteristics collectively termed "vulnerability". It is upon this task of detecting prey that the prey variables of primary interest in this study are thought to exert their influence.

After detecting a potential prey animal, the predator must next recognize that animal as an acceptable prey, which depends in part upon body size and palatability of the prey, and also upon the predator's preference, which may change with experience. Increased hunger may cause a predator to relax its restrictions on what prey are acceptable.

When a prey animal has been detected and determined to be acceptable, it must next be approached and captured. The success in these tasks may be a function of the predator's experience and capability, and of the experience and behavior of the prey in evading and defending itself against the predator. Capability of the prey to injure the predator must also be given consideration at this step.

Once a predator has made contact with the prey, it must next handle it, which has been defined in this model as killing, preparing (plucking, skinning, etc.), and ingesting the prey. Once the prey is eaten, a summation index labeled "stomach content" is increased, and the predator assesses its hunger level and whether or not it will continue to search for prey.

In summary, this model provides a different view of feeding behavior than that suggested by mathematical models. It allows depiction of the effects of various prey, predator, and environmental variables upon specific behaviors of a feeding predator.