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Population Dynamics of *Oryzomys palustris* and *Microtus pennsylvanicus* on the Eastern Shore of Virginia

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POPULATION DYNAMICS OF *Oryzomys palustris* AND *Microtus pennsylvanicus* ON THE EASTERN SHORE OF VIRGINIA

by

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ABSTRACT

POPULATION DYNAMICS OF *Oryzomys palustris* AND *Microtus pennsylvanicus* ON THE EASTERN SHORE OF VIRGINIA

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Old Dominion University, 1993

Director: Dr. Robert K. Rose

The population dynamics of *Oryzomys palustris*, the marsh rice rat, and of *Microtus pennsylvanicus*, the meadow vole, were determined during a year-long mark-and-recapture study on the Eastern Shore of Virginia. Three nights of trapping per month were conducted on two live trap grids totaling 5456 total trap nights. The grids were located on Nature Conservancy land, one in Oyster, and the second at Steelman's Landing, which is east of Townsend in Northampton County Virginia. Trapped animals were evaluated using established criteria. Reproductive activity, age and sex composition, and density of the population, capture probability, survival rate, and recruitment were determined.

Analysis of variance showed no significant effect between grids, seasons, species, or the set of interactions. *O. palustris* had a maximum density of 109/ha in May 1994 on Grid 1 and 92/ha on Grid 2 during August 1994. Monthly densities of *M. pennsylvanicus* increased sharply on

1 of 20/ha (April 1995), and Grid 2 of 104/ha (May 1995). Survival rates were predictably significantly higher during the summer than the winter for both species on both grids. Meadow voles on Grid 1 had a high survival rate (80.6%) compared to other populations in the study. Both species were highly vagile on both grids, with *M. pennsylvanicus* having the greatest number of individuals seen only once (91.17%) on Grid 1. Maximum residence time was five months for both species. Adult *M. pennsylvanicus* made up the majority of the meadow vole population on both grids. Males of both species were more abundant on both grids and reached a level of statistical difference on Grid 2.

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INTRODUCTION

When the Eastern Shore of Virginia was settled more than 300 years ago, the majority of colonists looked to agriculture or the sea for their main sources of income. Today, the Eastern Shore is still much the same as it was then, and the lack of urbanization has left expanses of tidal marsh communities virtually undisturbed. Since the 1970s, the Nature Conservancy has been purchasing some wetland areas to further ensure their preservation. The tidal marshes of the Eastern Shore are of unique importance because of their preserved and undisturbed natural beauty and the small mammal populations they support. These small mammal communities are of prime interest to mammalogists, because the marshes are undisturbed it is possible to get a clearer picture of the dynamic structure of the community and the factors that influence these small mammal populations.

Two species of small mammal, the marsh rice rat, *Oryzomys palustris* and the meadow vole, *Microtus pennsylvanicus,* are dominant in the coastal tidal marshes of the Eastern Shore of Virginia and on the nearby barrier islands. These species have held the interests of many researchers and have been frequently studied, but seldom in tidal marshes and rarely together. Goldman (1918) was the first to study these populations on the Eastern Shore of Virginia. He reported the presence of *O. palustris* on Wreck and Smith islands, two Eastern Shore barrier islands. Farther northward up the coast, Bailey (1946) conducted a survey of the small mammal fauna of Wallops Island and also noted the presence of the marsh rice rat. Paradiso and Handley (1965) surveyed the mammal fauna on Assateague Island, which is located farther north than Wallops Island, and is the northernmost Virginia barrier island. This survey listed numerous species and of course included *Oryzomys palustris*. Dueser et al. (1979), who conducted the most comprehensive study of the barrier islands by trapping small mammals on 11 different islands, used these studies to examine the biogeography of barrier island mammals rather than their populations. Carter and Merritt (1981), interested in the ability of certain small mammals to invade islands in the Back Bay National Wildlife Refuge studied the swimming ability of *Oryzomys palustris, Microtus pennsylvanicus, Peromyscus leucopus,* and *Sigmodon hispidus* on the islands on the western side of the Eastern Shore. Cranford and Maly (1990) were also interested in the small mammal communities of the Eastern Shore and reported on the population densities and habitat associations of the populations on Assateague Island. Although not conducted on the Eastern Shore of Virginia, the longest and most comprehensive study of *Oryzomys palustris* was conducted by

Negus et al. (1961) on Breton Island, Louisiana, in the Gulf of Mexico. This study has served as the template for many other studies and has been frequently used for comparisons of other populations. Other demographic studies on the marsh rice rat have been seasonal, or else monitored over shorter periods of two to three months, whereas this year-long study is the most comprehensive study since Negus et al. (1961).

Previously, studies on the Eastern Shore have focused on populations that inhabit the barrier islands. This study focused on two populations that were located on the mainland in coastal tidal marshes. Mark-and-recapture studies were conducted on two live-trap grids, one in Oyster, and the second at Steelman's Landing. The data collected from the live-trapping were used to determine reproductive cycles, age and sex composition of the population, density of the population, and information on the spatial overlap of *Oryzomys palustris* and *Microtus pennsylvanicus* with other species of small mammals. This study began with survey trapping in March, 1994 and continued through May, 1995.

Mainland populations are important to understand because they are responsible for feeding the often studied barrier island populations and may aid the work of these researchers. Also, it is important to look at the interaction of these two small mammals as there have been few comparative studies conducted on microtine and non-microtine, rodent populations (Rose and Birney 1985).

Purpose of the Study

One objective was to determine the population dynamics of two populations of *Oryzomys palustris* on the Eastern Shore of Virginia. This information was important in analyzing the dynamic structure of *O. palustris* populations and in interpreting their interactions with other small mammals that also occupy the marsh habitat, particularly, *Microtus pennsylvanicus*, the meadow vole. These data will be useful for further comparisons of geographically different populations, and for studies of the barrier islands of the Eastern Shore. A second objective was to evaluate seasonal changes in reproductive activity in marked and released animals. By comparing the reproductive activity of different months I have gained insight into the cycle of reproduction in these small mammal populations, and compared these results to those of earlier studies, such as Negus et al. (1961) and Wolfe (1985).

Although *Oryzomys palustris* was the focus of this study, *Microtus pennsylvanicus*, the meadow vole, occupied the same study areas as the marsh rice rat. Rose and Birney (1985) noted the necessity of comparisons between microtine rodents and non-microtines because few investigations have made such comparisons. Hence, the demographies of the meadow vole populations were also evaluated and compared to those of the rice rat.

BACKGROUND AND REVIEW

General Characteristics

The marsh rice rat is a long-tailed, medium-sized muroid rodent with a grayish-brown dorsum and whitish belly and feet (Wolfe 1982). However, pelage color has been found to be highly variable among different age classes and sexes (Humphrey and Setzer 1989). Weight has been used as a surrogate of age, with juveniles defined as (0-30 g), subadults (31-50 g), and adults (>50 g) (Wolfe, 1985). The range of total lengths of adult *Oryzomys palustris* is reported to be 225-305 mm (Wolfe 1982). However, Hamilton and Whitaker (1979) report average total length measurements for Virginia and Florida marsh rice rats to be 252 mm and 227 mm, respectively.

Oryzomys palustris has an omnivorous, seasonally shifting diet (Negus et al. 1961); in fact, it is second only to the grasshopper mouse (*Onychomys*) as the most carnivorous small mammal in North America (Wolfe 1982). Sharp (1967) reports that in Georgia the rice rat eats vegetation and other food sources seasonally. He noted that the main diet of the rice rat consists of insects and small crabs of the genera *Uca* or *Sesarma* during the summer. Crabs constitute the majority of their diets in September, but in October a grass, *Spartina*, was determined to be the main source of food. Hamilton and Whitaker (1979), Lowery (1974), and Svhila (1931) concur that the diet of the rice rat is predominantly that of an herbivore with some seasonal feeding on insects and small crabs. Other sources of food such as the eggs and young of the marsh wren (*Telmatodytes palustris*) and baby turtles (*Graptemys sp.*) have also been reported (Kale 1965, Goodpaster and Hoffmeister 1952, Wolfe 1982).

The high metabolic rate of the rice rat is maintained by the high resource availability in the marsh. Higher metabolic rates allow an animal to produce more offspring than would an animal with lower metabolic rate (McNab 1980); however, not all animals with high metabolic rates reproduce throughout the year. The opportunistic feeding strategy of the rice rat and the plentiful food supply of productive tidal marshes may be the reasons that it has the ability to reproduce throughout the year. One of the attributes of the rice rat is its capacity to swim allowing it to inhabit commonly flooded areas and to colonize islands. The ability of *Oryzomys palustris* to swim and dive has been previously well documented (Hamilton 1946, Svhila 1931, Esher et al. 1978, and Carter and Merritt 1981). Esher et al. (1978) reported the rice rat to be able to swim and dive underwater for approximately 10m and to enter the water more readily than *Sigmodon hispidus,* the cotton rat. Forys and Dueser (1993) reported *O. palustris* to cross 50-m gaps of water frequently and to be able to cross a 300-m channel.

The most common predator of the marsh rice rat is the barn owl, *Tyto alba* (Blem and Pagels 1973). Upon studying the diet of barn owls in Louisiana, Jemison and Chabreck (1962) noted that *O. palustris* comprised 97.5% of 1008 vertebrate remains from pellets. Harris (1953) found the rice rat to be present in twice as many barn owl pellets as in the fecal pellets of its next greatest predator, the marsh hawk, *Circus cyaneus*. He attributed this to increased encounters between the species due to the nocturnal habits of both the rice rat and the barn owl. The raccoon, *Procyon lotor* and the red fox, *Vulpes vulpes* are also predators of the rice rat but to a much lesser extent (Harris 1953).

Biogeography and Habitat

Oryzomys palustris, the marsh rice rat, inhabits wetlands ranging from the southernmost tip of peninsular Florida to southern New Jersey and southeastern Pennsylvania (Edmonds and Stetson 1993). It has been reported as far west as southern Texas, specifically near Corpus Christi (Wolfe 1982). The distribution of the rice rat in the north is sporadic, with populations from southern Oklahoma, southwestern Missouri, southern Illinois, and southern Kentucky (Wolfe 1982).

Although the marsh is its preferred habitat, *Oryzomys palustris* is also found in swamps, meadows, and hydric hammocks (Wolfe 1982). *O. palustris* is often found in nests placed in tall grasses or vacant wren nests during the day (Sharp 1967). Harris (1953), Stone (1898), and Rhoads (1902) all found the rice rat to frequently use both occupied and vacant nests of the muskrat, *Ondatra zibethicus*.

The marsh is a difficult area to inhabit due to twice daily tidal fluctuations, storm surges, and changes in salinity that cause problems for most terrestrial mammals; however, these pose few problems for *Oryzomys palustris* because it is one of the true semi-aquatic mammals (Wolfe 1990). The semi-aquatic nature of the rice rat allows it to inhabit the open coastal tidal marsh, an area that is difficult for most other species of small mammals to occupy. Cranford and Maly (1990) concur with Wolfe (1982) that the rice rat is more abundant in wetter areas; Wolfe (1990) reported that the presence of rice rats increases as one moves from the marsh-forest ecotone toward the shoreline (Wolfe 1990).

Oryzomys palustris and *Microtus pennsylvanicus* are both known to inhabit the Eastern Shore of Virginia and many of its barrier islands. Dueser et al. (1979) found *O. palustris* to inhabit nine of the 11 Virginia barrier islands, some of which were separated by 50-300 m gaps of water from each other and often by several kilometers from the mainland (Forys and Dueser 1993). In studies of South Carolina barrier islands, Andre (1981) examined the abundance of small mammals in a number of different habitats, such as fore and rear dunes, saltspray forest, maritime live oak forest, freshwater marsh, salt marsh, old field, and residential area. *O. palustris* was most abundant in five out of the seven habitats, and was the most abundant species overall. The rice rat was present in the latter two areas but not in great abundance.

There has been some debate as to the true home ranges of *Oryzomys palustris*. Birkenholz (1963) used the inclusive boundary zone method to estimate the home range of a Florida population, and estimated home range for males to be 0.25 ha (0.56 acres) and 0.33 ha (0.72 acres) for females. Negus et al. (1961) reported a home range for males of 0.37 ha (0.81 acres) and a smaller range for females 0.23 ha (0.51 acres). Pournelle (1950) reported average range lengths to be 67.7 m to 82.3 m, whereas Negus et al. (1961) observed the greatest range length reported in the literature from an adult male to be 610 m.

Systematics

Fossil evidence of *Oryzomys palustris* dates back to the early Rancholabrean, one of the warm interglacial periods of the Pleistocene, or about 500,000 years ago (Wolfe 1982). John Bachman Harlan is given credit for the discovery of the genus, but it was later revised by Bangs in 1898, Merriam in 1901, and Goldman in 1918 (Humphrey and Setzer 1989). In the past, up to six subspecies of *O. palustris* were recognized. However, Humphrey and Setzer (1989), who revised the group using multivariate analyses of 12 skull measurements, currently recognize two groups, *O. p. palustris* from the continental United States and *O. p. nator* from peninsular Florida.

Breeding

Oryzomys palustris is reproductively active throughout the year. Park and Nowosielski-Slepowron (1972) noted that the breeding season of the Dundee, Scotland rice rat colony had a bimodal peak. By contrast, Negus et al. (1961) reported a single peak, with increased breeding between January and March and a decrease during the warmer summer months. Goldman (1918) and Cranford and Maly (1990) agree that increased production begins in March, but Goldman (1918) believes breeding ends in May whereas Cranford and Maly (1990) report breeding to continue through November. However, Wolfe (1982) found reproduction to peak between late spring and autumn in Mississippi.

Oryzomys palustris has a gestation period of 25 days (Svihla 1931), and an average litter size of 5 individuals (Conway 1954). The average litter size of 5 is interesting because the female possesses eight mammae, four pectoral and four inguinal, more than appear to be necessary (Svihla, 1931). Negus et al. (1961) noted that when subjected to adverse conditions, such as food shortages, inclement weather, and high density, females produce fewer litters per season and smaller litter sizes than under normal conditions. Svihla (1931) reports that juveniles are weaned between 11 to 13 days and reach puberty in 50 to 60 days. The age of puberty has been estimated to be the same for both males and females (Negus et al. 1961). The rice rat is in estrus from between six and nine days, and undergoes a post-partum estrous cycle (Conway 1954 and Svihla 1931).

General Characteristics

Microtus pennsylvanicus, the meadow vole, is also common in wetland habitats and is known to coexist with *Oryzomys palustris* (Harris 1953). Unlike the rice rat, the meadow vole has a short tail, short ears, and an overall shorter total body length (140-195 mm). The shortness of the tail and ears, and the denseness of the pelage, allow the meadow vole to conserve heat very well (Rose and Birney 1985). The pelage is a blackish color and fades as the animal becomes older (Starrett 1958). Dale (1940) reports the pelage color to become lighter and body size to increase as one moves northward. The meadow vole of eastern Virginia, *M.p. nigrans,* is the darkest of the subspecies recognized by Hall (1981). The meadow vole is primarily diurnal, especially in areas of dense ground cover (Graham 1968). The dense ground cover serves as protection from the Northern Harrier and the barn owl, which are also predators of the meadow vole as well as the rice rat. Harris (1953) reports all predators present in his study to prey more heavily on *Microtus pennsylvanicus* than on *Oryzomys palustris*. Eadie (1952) noted that *Blarina brevicauda*, the short-tailed shrew, may also prey on the young of the meadow vole.

Carter and Merritt (1981) report on the swimming ability of *Microtus pennsylvanicus* and *Peromyscus leucopus,* the white-footed mouse, as a means of island invasion in the Back Bay National Wildlife Refuge, Virginia Beach, Virginia. The meadow vole was a much better swimmer than the white-footed mouse and exhibited the capability to dive underwater for short distances (Carter and Merritt 1981). The pelage of *M. pennsylvanicus* is known to insulate better than that of *P. leucopus*; however, the fur of *Oryzomys palustris* is still denser and a better insulator than that of *M. pennsylvanicus* (Esher et al. 1978, and Carter and Merritt 1981). The rice rat is also able to withstand cold water temperatures for longer periods of time than the meadow vole (Esher et al. 1978, Carter and Merritt 1981).

Biogeography and Habitat

Microtus pennsylvanicus inhabits graminoid habitats extending its range northward throughout Canada and much of the northern and eastern United States (Reich 1980). The most southerly populations are from Mexico (Bradley and Cockrum 1968). The meadow vole typically is found in moist grassland areas with abundant ground cover. Getz (1966) noted that it may be the inefficiency of the kidneys that keeps *Microtus pennsylvanicus* restricted to wet areas, such as wet meadows and tidal marshes. However, Reich (1981) notes their presence in woodland areas also. Meadow voles are known to inhabit muskrat houses, as are rice rats, and to build nests of grass inside these houses (Harris 1953). The meadow vole may rely on these houses to avoid flood conditions in the marsh. *Microtus pennsylvanicus* is reproductively active throughout the year with peak reproduction occurring during the summer (Cranford and Maly 1980; Keller and Krebs 1970). The gestation period is 21 days, and the average litter size is 3.8 (Dieterich and Preston 1977; Lee and Horvath 1969; Nadeau 1985). Keller and Krebs (1970) reported an overall decrease in litter size during the winter, spring, and autumn. Hamilton (1941) reports young to be weaned between 12 to 14 days and to reach maturity between 25 to 30 g. Myers and Krebs (1971) found the sex ratios of the meadow vole to be significantly different and to favor males. They linked this occurrence to transferrin genotypes. When *Microtus pennsylvanicus* is present in a small mammal community it tends to be the dominant small mammal and to influence the other populations through its fluctuations in density, increased diurnal activity, alteration of plant communities, and year-round activity (Rose and Birney 1985). However, Harris (1953) speculated there to be no competition apparent between the meadow vole and the rice rat.

METHODS

Description of the Study Area

The study sites were located on Nature Conservancy property on the Eastern Shore of Virginia. Grid 1, located 4.4 km east of U.S. Route 13 in the village of Oyster, measured 0.5 ha and was 100m x 50 m. The vegetation here was representative of a common salt grass community and contained a combination of *Spartina alterniflora, Iva fructescens, Spartina patens, Phragmities australis,* and *Juncus roemerianus*. Low-lying areas were subject to more frequent flooding as the tidal levels changed; however, most of Grid 1 was on higher ground and remained relatively dry. A thick ground cover of *Spartina patens* blanketed most of Grid 1, and *Phragmities australis* covered the northwest corner of this grid.

The second site was located at Steelman's Landing, which is east of Townsend, also in Northampton County. Grid 2 measured 130 m x 100 m or 1.3 ha, had 128 trap stations, and was primarily covered with *Spartina alterniflora, Iva fructescens*, and *Phragmities australis*. The three trap stations closest to the water in each transect were in areas of least ground cover and were more subject to frequent tidal flooding than other trap stations on this grid. In general, Grid 2 flooded less often than did Grid 1 because it was farther away from the water, but it was on lower ground, flooded more evenly, and was usually wetter than Grid 1.

Trapping Procedures

Trapping began with survey trapping in March 1994 and continued through May 1995. Each grid was trapped three days per month. A total of 1872 trap nights were conducted on Grid 1 and 3584 trap nights on Grid 2. Since the grids were located in a coastal tidal marsh it was necessary to account for tidal water levels so that the traps would not become inundated. Dr. Robert K. Rose devised a floating trap using foam insulation styrofoam and the Fitch trap. The 1.58 cm thick styrofoam was cut into 31 cm x 21 cm rectangles, and the Fitch traps were then fastened to the styrofoam rectangles using strips of inner tube cut from an old tire tube. Each floating trap was then tied to a four-foot numbered stake using monofilament line in order to keep the trap in the same location on the numbered grid. The monofilament line was tied to two "wire ties" which were placed near the corners at one end of the styrofoam rectangle.

Trap stations were located 10 m apart from each other, and each transect was located 10 m apart from each adjacent transect. Each Fitch trap was baited with birdseed, and in the winter polyester fiberfill was added to provide insulation for the animals. Newly captured animals were marked by attaching a numbered fingerling ear tag to the ear of the animal. All captured animals were examined in the field using established criteria. These criteria included location on the grid, species, fate, weight, sex, position of the testes if male, and nipple size, pubic symphysis open or closed, and vagina perforate or not for females. This information was collected on both newly captured and recaptured animals. Following this examination, each animal was released at the point of capture.

Statistical Analysis

The software package JOLLYAGE was used in order to calculate the density, time-specific survival rate of both adults and young, capture probability, and recruitment for both species (Pollock et al. 1990). The Lincoln-Peterson Index was also used to estimate density of the populations (Chapman 1951; Seber 1982). This method was chosen as the primary estimator because it works well with smaller sample sizes. The above population parameters were also analyzed using a Model II, 3-factor analysis of variance. The factors of grid, season, species, and interactions of the three were tested for effects on each parameter using a Ryan-Einot-Gabriel-Welsch Multiple Range Test. Chi-square analyses were used to compare the sex ratios of both species on both grids independently.

RESULTS

During the 13 - month study period, a total of 185 animals of five different species were captured in 1872 trap nights on Grid 1, and a total of 535 animals of five different species were captured in 3584 trap nights on Grid 2. On Grid 1, *Oryzomys palustris* accounted for 83 (44.86%) of the total captures, while *Microtus pennsylvanicus* comprised 68 (36.75%) (Table 1). *Peromyscus leucopus, Mus musculus,* and *Blarina* sp. were also represented on Grid 1 but to a much lesser extent, (12.97%, 3.78%, and <1.00%, respectively). Grid 2 yielded 306 (57.19%) captures of *O. palustris* and 216 (40.22%) of *M. pennsylvanicus* (Table 2). *M. musculus, P. leucopus,* and *Blarina* sp. were also represented on Grid 2 but to a lesser extent (1.3%, 1.1%, and <1.0%, respectively). The software program JOLLYAGE was used to determine the population density estimates, survival rates, capture probabilities, and recruitment for *Oryzomys palustris* and *Microtus pennsylvanicus* on both grids. In order to fit the data to two age classes, subadult was added into the adult age class. Juvenile animals formed the second class. A Model II, 3-factor analysis of variance was performed on all of the above population parameters using grid, season, species, and

Table 1. Number of individuals of each species and the number of individuals of each sex of each species captured on Grid 1. Numbers in parentheses indicate the number of captures in each group.

Species	Total	Male	Female	Unk.
Oryzomys palustris	65 (83)	34 (40)	28 (40)	3
Microtus pennsylvanicus	62 (68)	34 (35)	24 (29)	4
Peromyscus leucopus	16 (24)	6 (11)	6 (9)	4
Mus Musculus	6 (7)	6 (7)	0	0
Blarina sp.	1 (1)	0	1 (1)	0
Total	150 (183)	80 (95)	59 (75)	11

Table 2. Number of individuals of each species and the number of individuals of each sex of each species captured on Grid 2. Numbers in parentheses indicate the number of captures in each group.

Species	Total	Male	Female	Unk
Oryzomys palustris	218 (306)	118 (173)	72 (105)	28
Microtus pennsylvanicus	180 (216)	94 (115)	67 (83)	19
Blarina sp.	7 (7)	6 (11)	1 (1)	5
Mus Musculus	5 (5)	2 (2)	0	3
Peromyscus leucopus	1 (1)	2 (1)	1 (1)	0
Total	411 (535)	222 (302)	141 (190)	55

all interactions of the three factors. The factor "season" was broken into four seasons, consisting of Summer (June-August), Autumn (September-November), Winter (December-February), and Spring (March-May). A Ryan-Eniot-Gabriel-Welsch Multiple Range Test was performed for all variables following the analysis of variance.

Population Density

Population density estimates were calculated using JOLLYAGE (J-A) and the Lincoln-Peterson (L-P) Indices. The Lincoln-Peterson Index was chosen as the primary estimator because it yields more precise values for small populations, and it calculates values for the first and last month of study, whereas JOLLYAGE does not. However, the JOLLYAGE calculations are useful for comparing data trends that are concurrent between the methods. No data were collected on Grid 1 during January due to a human disturbance (vandalism) on the grid. Analysis of variance showed no significant effect on the population density between grids ($F=0.68$ $DF=1$, $p=>0.05$), seasons ($F=0.20$ $DF=1$, $p>0.05$), and species ($F=0.67$ $DF=1$, $p>0.05$). The interactions also showed no significant effects on the population density.

The estimates of density for the *O. palustris* population on Grid 1 were greatest in May 1994 (the first month of trapping) (109/ha), and after an intervening decline subsequent increases in density followed in September 1994,December 1994, and March 1995, (10/ha, 11/ha, and 29/ha, respectively) (Figure 1). The lowest density levels were seen during July 1994 (1/ha) and February 1995 (2/ha). JOLLYAGE also estimated low densities in February 1995 (3/ha) and during April 1995 (3/ha) (Figure 1). The mean density over the entire year for *O. palustris* on Grid 1 was 15.67/ha.

On Grid 2 the population density of *Oryzomys palustris* peaked during August (92/ha) and December 1994 and January 1995 (91/ha and 88/ha, respectively); peaks also evident using JOLLYAGE (Figure 2). Overall low densities were seen on Grid 2 during March 1995 (2/ha L-P, 3/ha J-A) (Figure 2). The mean density of *O. palustris* for the entire year on Grid 2 was 38.08/ha.

The estimates of density for the *Microtus pennsylvanicus* population on Grid 1 were highest (20/ha) during April 1995 (Figure 3). Population densities were at their lowest levels during October 1994, December 1994, and February 1995 (3/ha, 3/ha, and 1/ha, respectively) (Figure 3). The mean density of *M. pennsylvanicus* on Grid 1 over the entire year was 8.00/ha.

By contrast, densities of *Microtus pennsylvanicus* on Grid 2 were nearly five times higher than Grid 1, with a mean density for the entire study of 38.66/ha. The lowest population density was also observed in October 1994 (2/ha) (Figure 4). The peak density occurred in May 1995 (104/ha). Densities on both grids increased sharply in spring 1995.

Figure 1. A comparison of the monthly population density estimates for *Oryzomys palustris* on Grid 1 using JOLLYAGE and The Lincoln-Peterson Index. No data were collected in January due to vandalism.

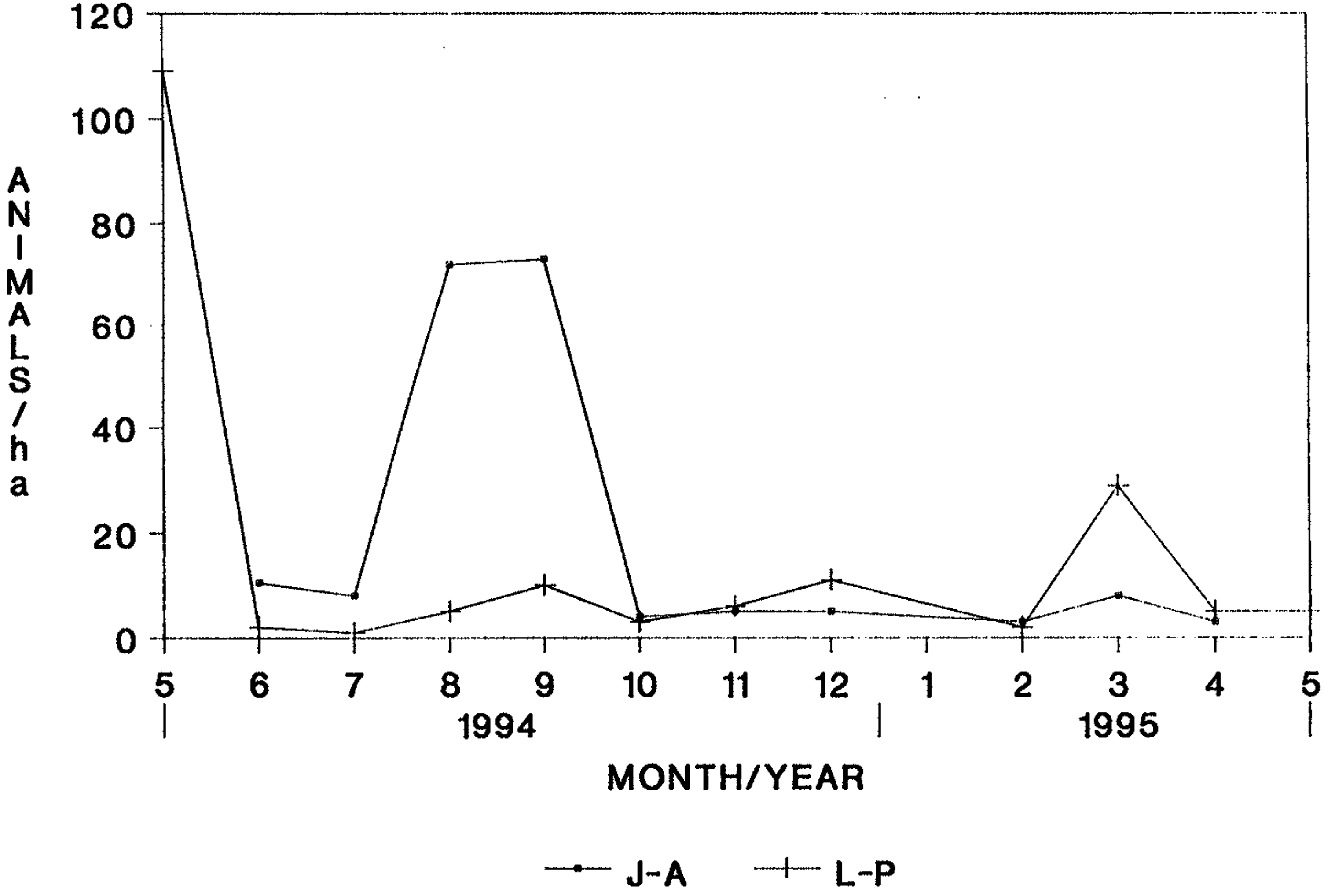
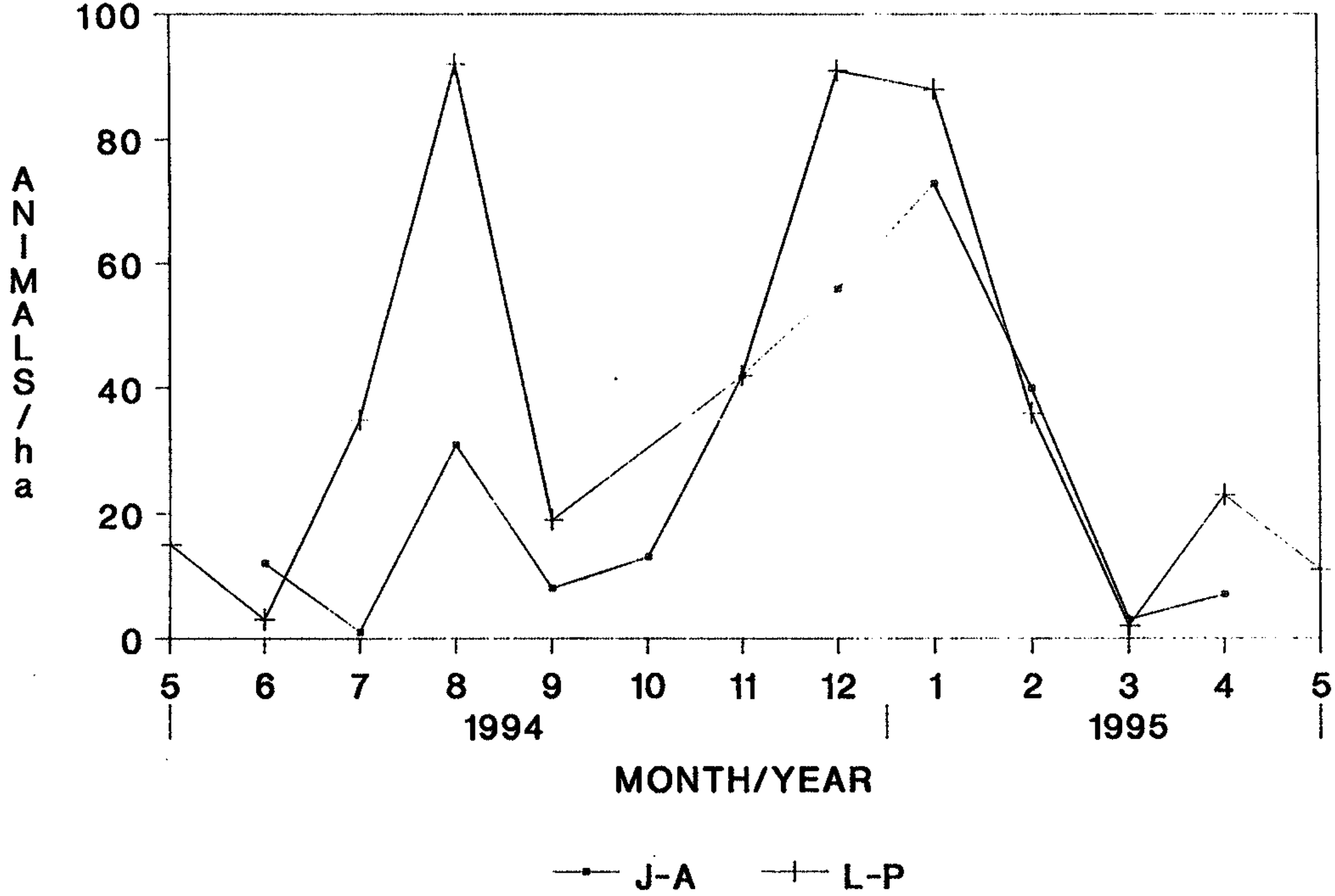

120
100
80
60
40
20
0
ANIMALS/ha
5
6
7
8
9
10
11
12
1
2
3
4
5
1994
1995
MONTH/YEAR
J-A
L-P

Figure 2. A comparison of the monthly population density estimates for *Oryzomys palustris* on Grid 2 using JOLLYAGE and The Lincoln-Peterson Index.


100
80
60
40
20
0
ANIMALS/ha
5
6
7
8
9
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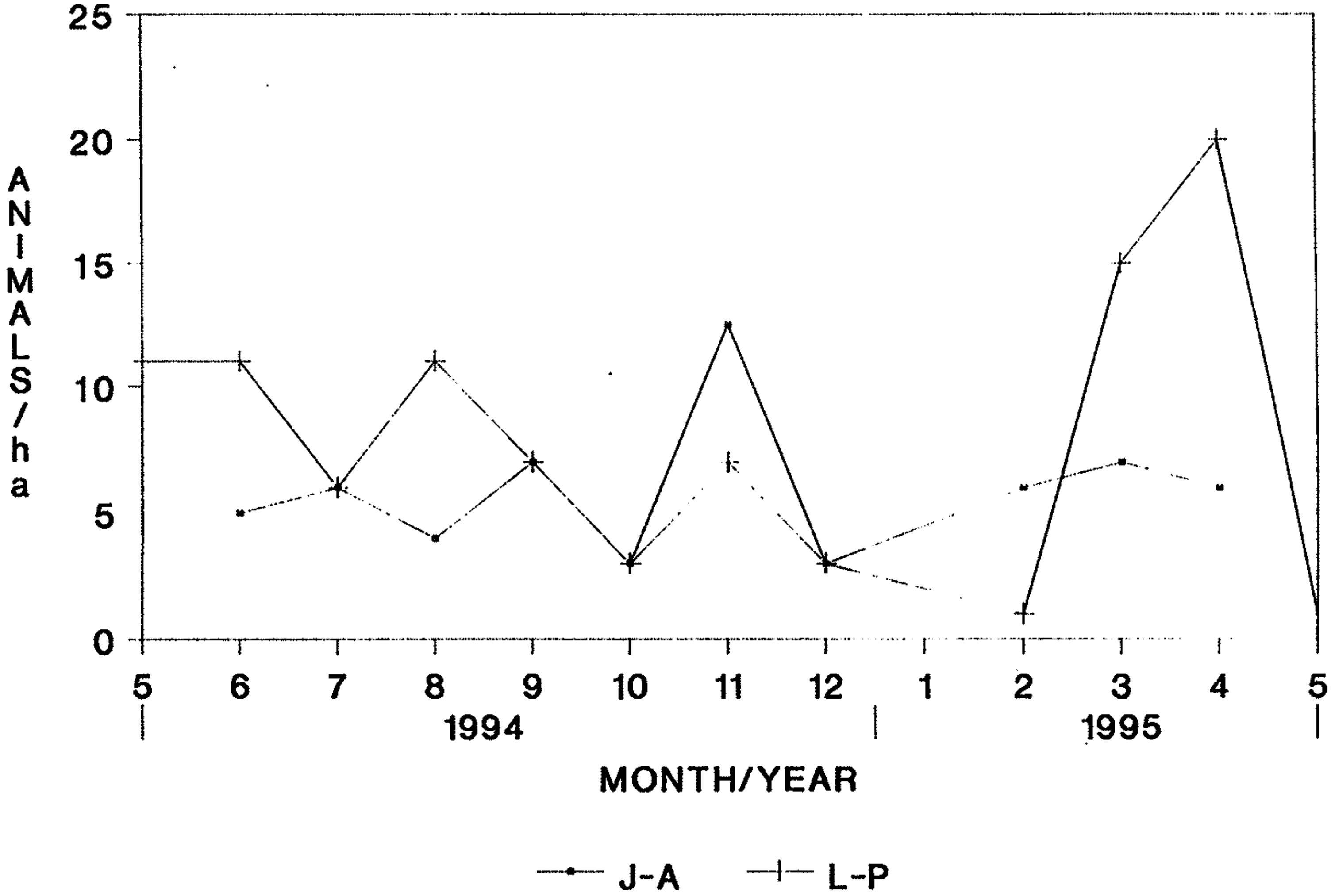
11
12
1
2
3
4
5
1994
1995
MONTH/YEAR
J-A
L-P

Figure 3. A comparison of the monthly population density estimates for *Microtus pennsylvanicus* on Grid 1 using JOLLYAGE and The Lincoln-Peterson Index. No data were collected in January due to vandalism.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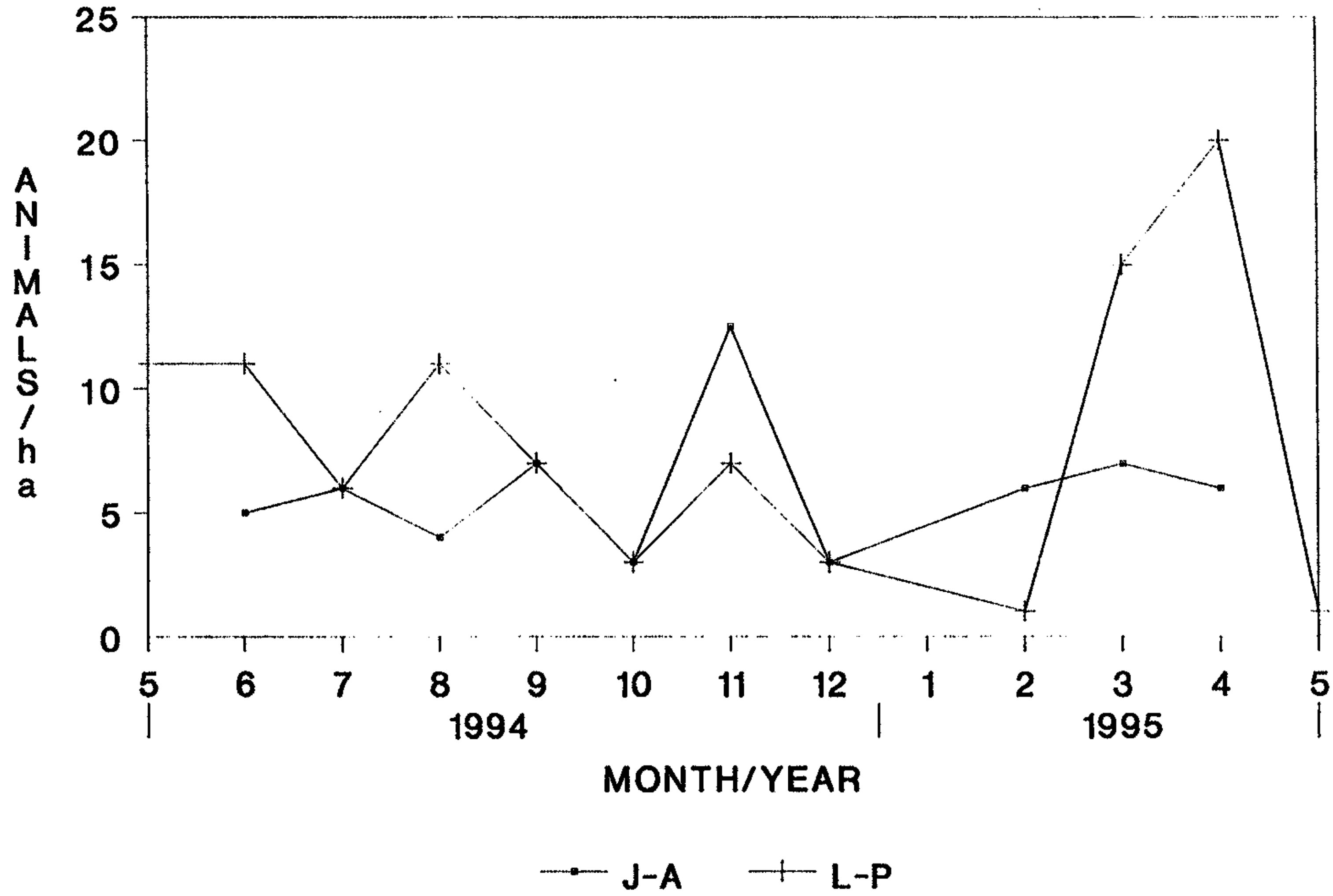
MONTH/YEAR
J-A
L-P

Figure 4. A comparison of the monthly population density estimates for *Microtus pennsylvanicus* on Grid 2 using JOLLYAGE and The Lincoln-Peterson Index.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Survival Rates

Time-specific survival rates were calculated for both juveniles and adults of *Oryzomys palustris* and *Microtus pennsylvanicus* on both grids. Grid ($F=17.01$ $DF=1$, $p<0.05$), species ($F=2.94$ $DF=1$, $p<0.05$) and the interaction of grid with species ($F=39.62$ $DF=1$, $p<0.05$) all had significant effects on the time-specific adult survival rates. Summer survival rates (0.535 per month) were significantly higher than winter rates (0.372 per month, $p<0.05$); however, no other seasons differed significantly. A significant difference also existed between the species in the time-specific survival rates for adults (*O.p.* $x=0.397$; *M.p.* $x=0.524$, $p<0.05$). The interaction of Grid and species also showed levels of statistical significance (Grid 1: *O.p.*, $x=0.351$; *M.p.*, $x=0.753$: Grid 2: *O.p.*, $x=0.438$; *M.p.*, $x=0.316$, $p<0.05$).

The survival rate for young *Oryzomys palustris* on Grid 1 was not calculated due to a small sample size. However, the mean time-specific survival rate for juvenile *O. palustris* on Grid 2 was 0.164 per month. The time-specific survival rates of adult *O. palustris* were calculated for both grids. *O. palustris* had survival rates ranging between 0.125-0.500 per month on Grid 1, with a mean value of 0.335 per month. This means that 33.5% of tagged animals survived from one month to the next. On Grid 2, a broader range of survival rates was observed, 0.321-0.923 with a slightly larger mean value of 0.3831 per month.

The mean time-specific survival rate of juvenile *Microtus pennsylvanicus* also could not be calculated on Grid 1 due to a small sample size. However, on Grid 2 *M. pennsylvanicus* juveniles had a mean time-specific survival rate of 0.309 per month. The monthly survival rates of adult *M. pennsylvanicus* on Grid 1 ranged between 0.250-0.833, with a mean of 0.806 per month. Grid 2 had a smaller range, 0.083-0.533, and a much smaller mean 0.316 per month than Grid 1. Thus, except for meadow voles on Grid 1, mean monthly survival on the grids was substantially less than 50 % per month.

Capture Probabilities

JOLLYAGE was also used to calculate the capture probabilities for the entire year. The overall recapture probability of tagged animals was significantly different (Grid 1, 0.350, Grid 2, 0.465, $p<0.05$). There was also a significant difference between winter (0.475) and summer (0.316). The recapture probability for *Oryzomys palustris* on Grid 1 ($x=0.614$) was much greater than that of *Microtus pennsylvanicus* on Grid 1 ($x=0.225$); these values were statistical different ($p<0.05$). However, capture probabilities of *O. palustris* and *M. pennsylvanicus* on Grid 2 ($x=0.426$ and $X=0.476$, respectively) did not differ statistically ($p>0.05$). When comparing just the factor of species, the capture probabilities of *O. palustris* ($x=0.474$) and *M. pennsylvanicus* ($x=0.347$) were significantly different ($p<0.05$). Significant differences existed in the set of interactions.

The number of times an animal was recaptured was calculated as a percent for both species and grids (Table 3). *M. pennsylvanicus* had the greatest percentages of animals that were seen only once, with 91.17% (62 individuals) on Grid 1 and 86.57% (180 individuals) on Grid 2. The comparable values for *O. palustris* were 84.33% (65 individuals) that were seen only once on Grid 1 and 83.98% (218 individuals). On Grid 2, *O. palustris* was the only species with an individual to be captured five times during the study period.

Longevity (Residence Time)

The residence time for individuals of *Oryzomys palustris* and *Microtus pennsylvanicus* was longer on Grid 1 than on Grid 2, with both species having individuals present on the grid for a span of six months (Table 4). The majority of both species stayed on Grid 2 for 2 months. However, both species had individuals present for a maximum of five months on the grid.

Age Structure

The age structure was determined for each species on each grid. Age classes of *Oryzomys palustris* were based on weights originally proposed by Negus et al. (1961); however, the modified version proposed by Wolfe (1985) were used here (juvenile, 0-30g, subadult, 31-50g, and adult,>50g). The age classes of *M. pennsylvanicus* were defined using a scale

Table 3. Percentages of captures/individuals of *Oryzomys palustris (O.p.)* and *Microtus pennsylvanicus (M.p.)*

Recaptures/ Individual	*O.p.* 1	*M.p.* 1	*O.p.* 2	*M.p.*2
1	84.33	91.17	83.98	86.57
2	10.84	5.88	12.09	10.19
3	2.4	2.94	2.28	2.7
4	2.4	0.0	1.3	<1.0
5	0.0	0.0	<1.0	0.0

Table 4. Number of individuals of *Oryzomys palustris (O.p.)* and *Microtus pennsylvanicus* (*M.p.*) and the length of time each remained on the grids.

Months of Presence	*O.p.* 1	*M.p.* 1	*O.p.* 2	*M.p.*2
2	2	0	13	5
3	1	0	7	3
4	0	1	2	3
5	2	0	2	1
6	2	1	0	0

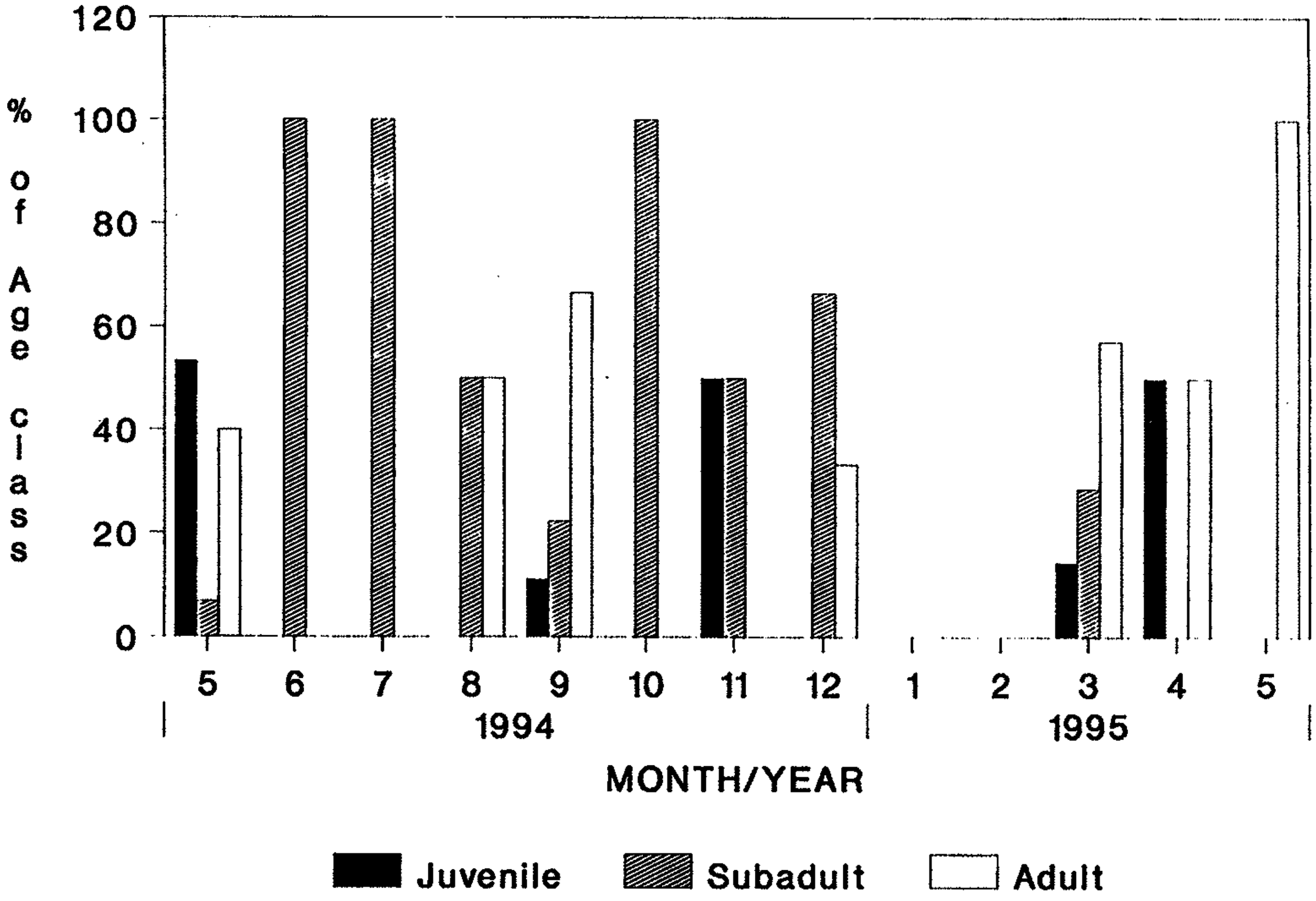
adapted from Krebs et al. (1969) (juvenile: <22g, subadults: 22-29g, adults: ≥ 30g). Recaptures are defined within a trapping period as well as between trapping periods.

Juvenile *Oryzomys palustris* were present in greatest number in May 1994 on Grid 1 (Figure 5). However, they were absent from June through August 1994, and also absent during the winter months. Subadults were absent from the population in April and May 1995. The subadult population increased from July to August 1994 and remained high through November 1994 (Figure 5). The adult population declined greatly from its maximum in May 1994 to being absent during June and July. Levels predictably increased from August to September 1994 following the recruitment of the earlier subadult population (Figure 5). Numbers of juvenile *Oryzomys palustris* on Grid 2 declined from July and August 1994 until none were found in October 1994 (Figure 6). The subadult population increased in late summer following a large recruitment of juveniles. A peak in the population also was seen from November 1994 through January 1995, but adults declined through February 1995 and March 1995.

There was considerable variation in the composition of age classes between the grids. The distribution of age classes was most similar between the grids during May and June 1994 and also between April and May 1995 (Figure 6).

Juvenile *Microtus pennsylvanicus* were very limited in their presence on Grid 1, but were on the grid during May 1994

Figure 5. The population age structure of *Oryzomys palustris* on Grid 1. Age classes are defined as Juvenile (0-30g), Subadult (31-50g), and Adult (>51g).



120
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% of Age class
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1994
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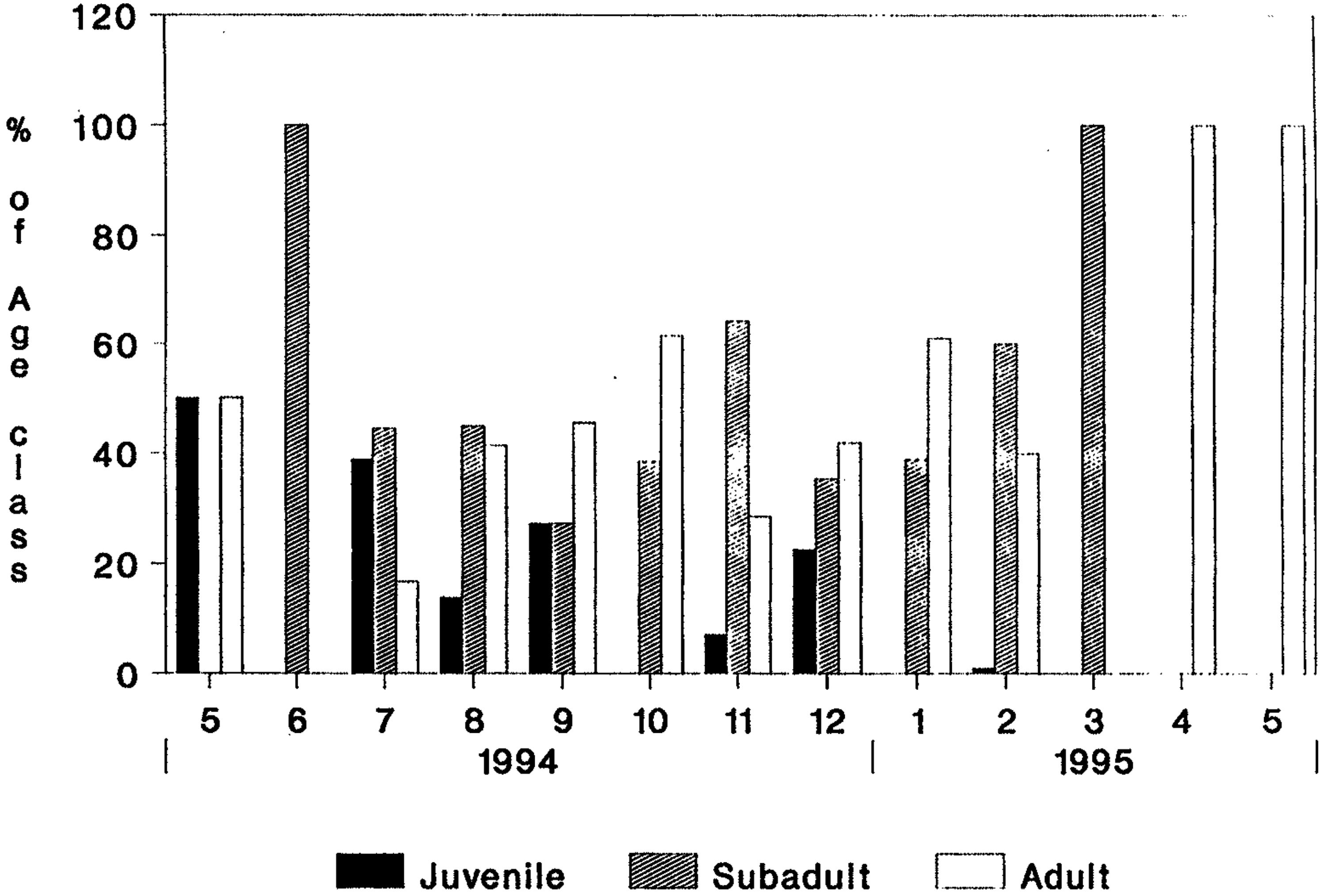
MONTH/YEAR
Juvenile
Subadult
Adult

Figure 6. The population age structure of *Oryzomys palustris* on Grid 2. Age classes are the same as defined in Figure 5.


% of Age class
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1994
1995
Juvenile
Subadult
Adult

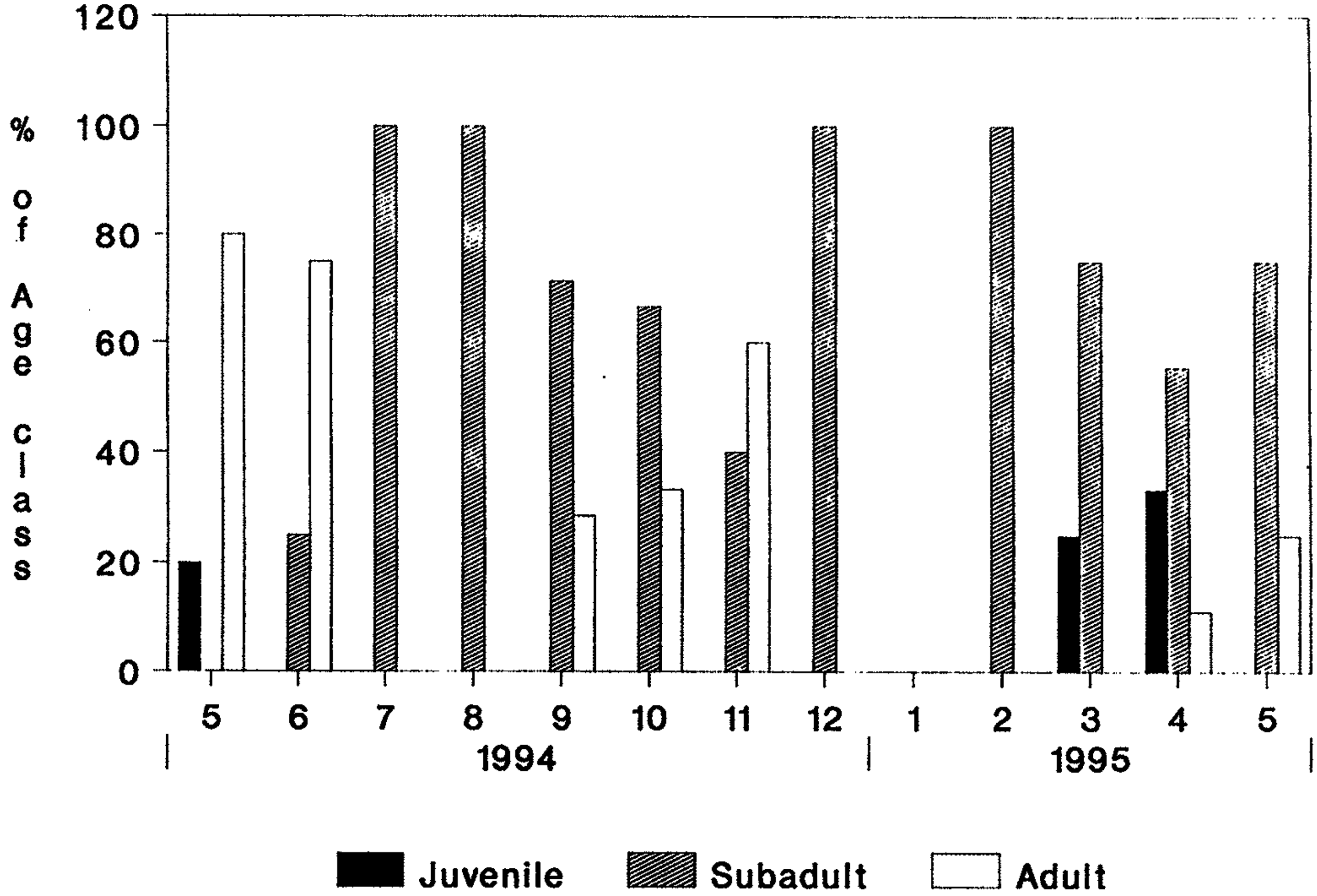
and April 1995 (Figure 7). The recruitment of juveniles lead to the steady increase in the subadult population through the spring. However, the subadults decline during the winter. Overall, across the study, adults made up the majority of the population on Grid 1. Adult populations were prominent from June 1994 through February 1995 (Figure 7).

Juvenile *Microtus pennsylvanicus* were present on Grid 2 only during May 1995 (Figure 8). However, juveniles help swell the numbers of subadult meadow voles during April 1995 and July 1994. Adult *M. pennsylvanicus* populations were at maximums from late summer through the autumn. Adults were the only age class present in every month. Adult population size moves inversely with an increase in any other age class. No more than two age classes were captured during any month.

Sex Ratios

The sex ratios of *Oryzomys palustris* and *Microtus pennsylvanicus* were calculated for both grids and checked for levels of significance using Chi-square analysis. On Grid 1 *O. palustris* had a sex ratio of 1♂:1♀ with 34♂ and 28♀ present (X^2=0.2903, p>0.05). *M. pennsylvanicus* also had a sex ratio of 1♂:1♀ with 34♂ and 24♀ (X^2=0.862, p>0.05). For *O. palustris* on Grid 2, significantly more males were present, with 118♂ and 72♀ (X^2=5.568, p<0.05). The sex ratio of *M. pennsylvanicus* on grid 2 also differed from unity, with 94♂ and 67♀ (X^2=2.263, p<0.05).

Figure 7. The population age structure of *Microtus pennsylvanicus* on Grid 1. Age classes are defined as Juvenile (<22g),Subadult (22-29g), and Adult (>29g).



% of Age class
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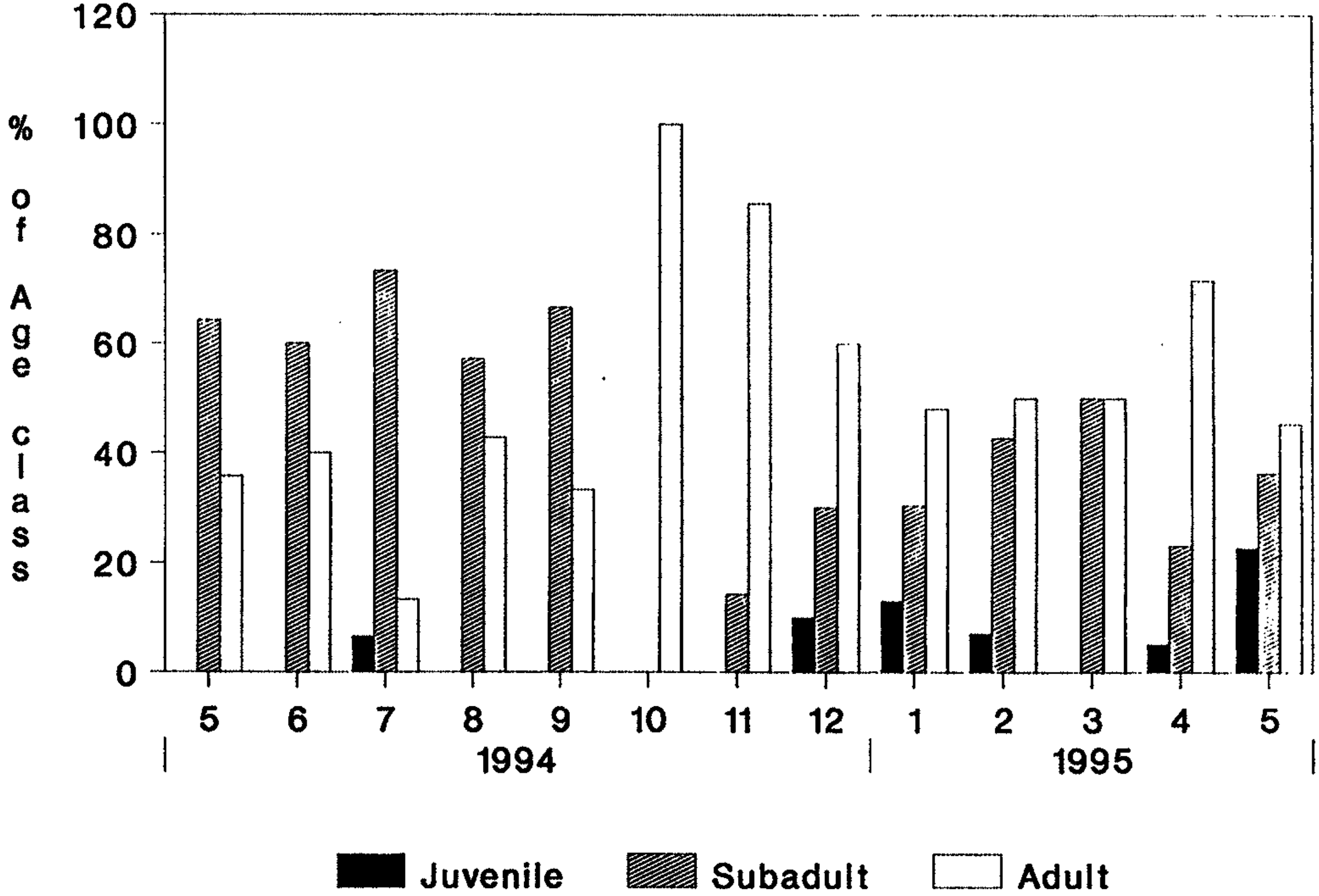
1994
1995
Juvenile
Subadult
Adult

Figure 8. The population age structure of *Microtus pennsylvanicus* on Grid 2. Age classes are the same as defined in Figure 7.


% of Age class
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1994
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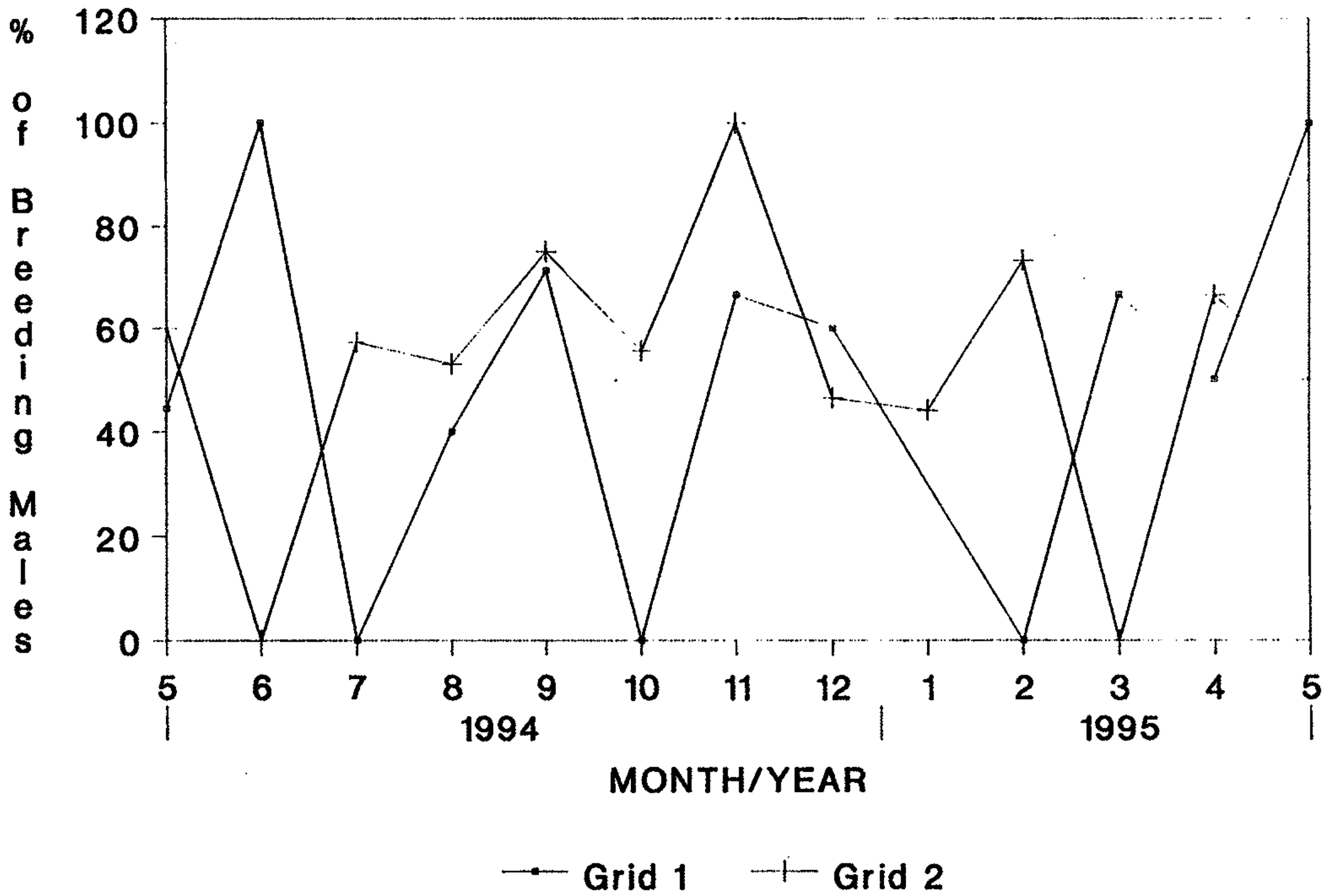
Juvenile
Subadult
Adult

Reproduction

Monthly changes in reproduction were analyzed using the position of the testes in males and the nipple size in females as estimators for reproductive activity of the sexes. McCravy and Rose (1992), who analyzed the use of external features as predictors of reproductive status in small mammals, reported that testis position was a fairly good predictor of reproductive status in males (87-94%). The ability to predict female reproductive status was not as good as males; however, nipple size was found to be the best estimator of reproductive status (71.7%) in females. Reproduction in male *Oryzomys palustris* had two peaks, the first in June 1994 (x=100%) and the second in May 1995 (x=100%) on Grid 1 (Figure 9). However, breeding activity on Grid 1 was lowest during the late summer (x=45.5%) and late winter (x=0.0%). The most distinct peak on Grid 2 occurred during November when reproduction was at 100%. After this peak, reproductive activity decreased drastically into March 1995 with the exception of a late winter spurt in activity (x=73.33 %). Both grids showed increases from early to late summer and from mid-autumn to early winter.

On Grid 1 peaks of breeding activity in male *Microtus pennsylvanicus*were seen from late summer through autumn on both grids (x=100%). Percentages of reproductively active males were greatly reduced on both grids during the early summer and December 1994, after which they began to increase

Figure 9. Proportion of adult male *Oryzomys palustris* in breeding condition using the criterion of descended testes to define breeding.


% of Breeding Males
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MONTH/YEAR
Grid 1
Grid 2

again from February 1995 to March 1985 (x=83.33%) (Figure 10). The reproductive activity on Grid 2 showed similar trends; however, reproductive activity was still high during June 1994 (x=90%), but it had peaked a month previously on Grid 1, May 1194 (x=100%).

Female reproductive activity of *Oryzomys palustris* was very low during the summer and winter months on Grid 1 (Figure 11). However, peak levels occurred during April 1995 (x=75%) and continued into May 1995 (x=100%). Reproductive activity was greatest on Grid 2 during November 1994 (x=72.72 %) and January 1995 (x=41%). Numbers decreased on both grids during December 1994. Both populations showed increases during November 1994.

The reproductive status of female *Microtus pennsylvanicus* peaked during November 1994 (x=100%) and February 1995 (x=50%) on Grid 1 (Figure 12). No females were found to be reproductively active during the summer on Grid 1; however, they were breeding during July (x=33%) and August 1994 (x=50%) on Grid 2. Female reproductive activity was at its maximum on Grid 2 in October 1994 and was also high during May 1995 (x=80%). Lows were seen on both grids during June 1994 (x=0%).

Recruitment

The software JOLLYAGE was used to determine the recruitment values for *Oryzomys palustris* and *Microtus pennsylvanicus* on both Grids 1 and 2. Recruitment was

Figure 10. Proportion of adult male *Microtus pennsylvanicus* in breeding condition using the criterion of descended testes to define breeding.

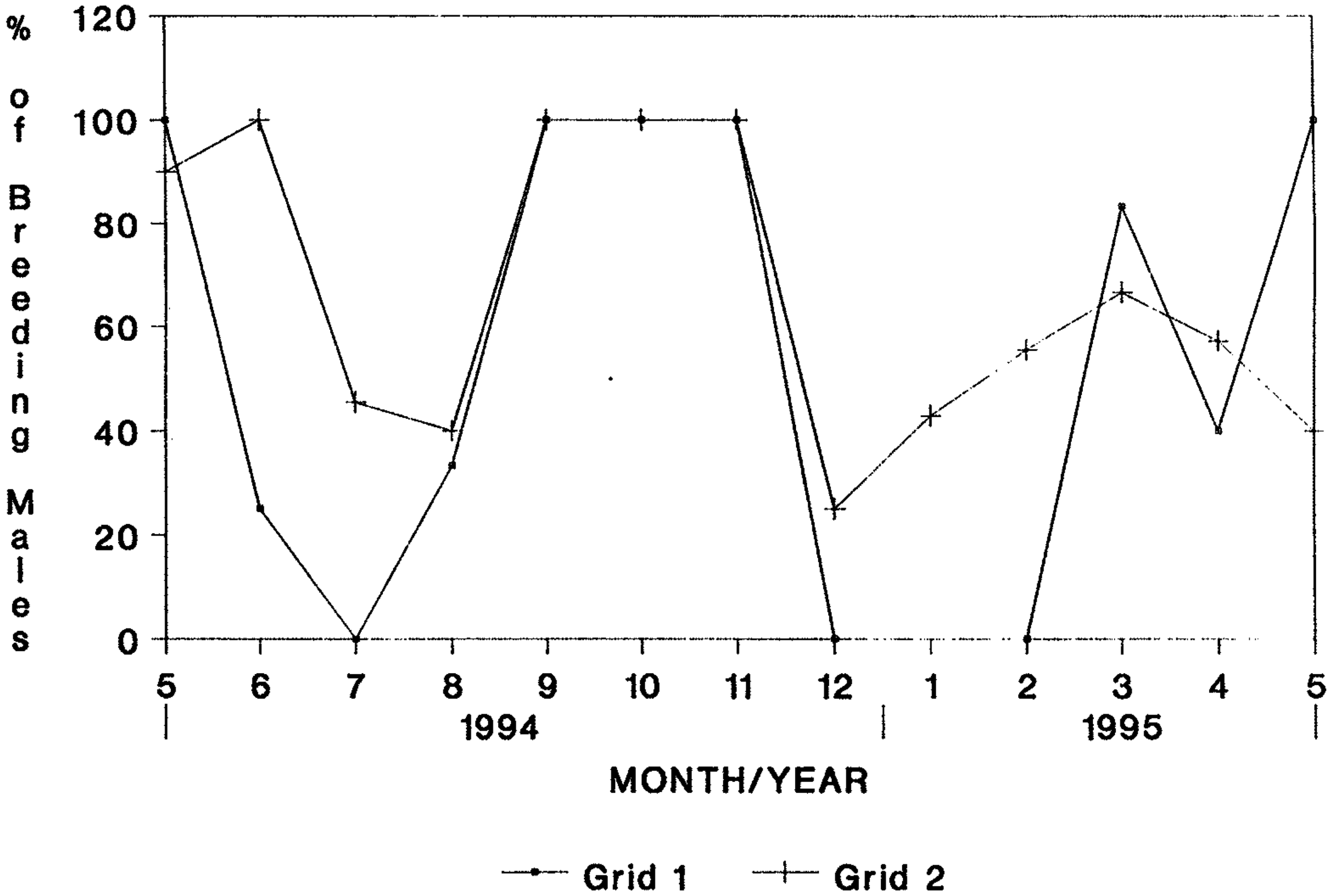
% of Breeding Males
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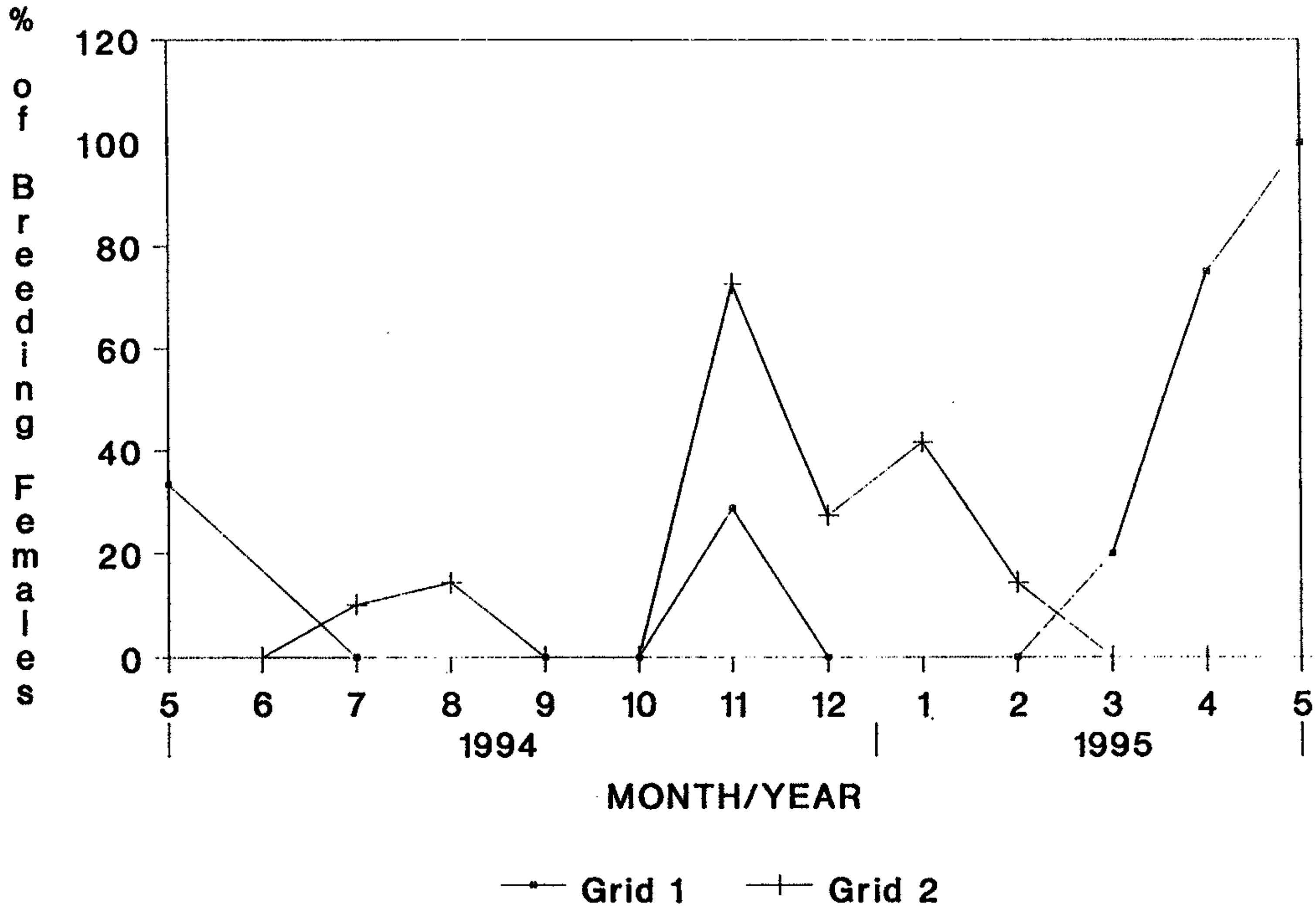
Figure 11. Proportion of adult female *Oryzomys palustris* in breeding condition using medium to large nipple size to define breeding.



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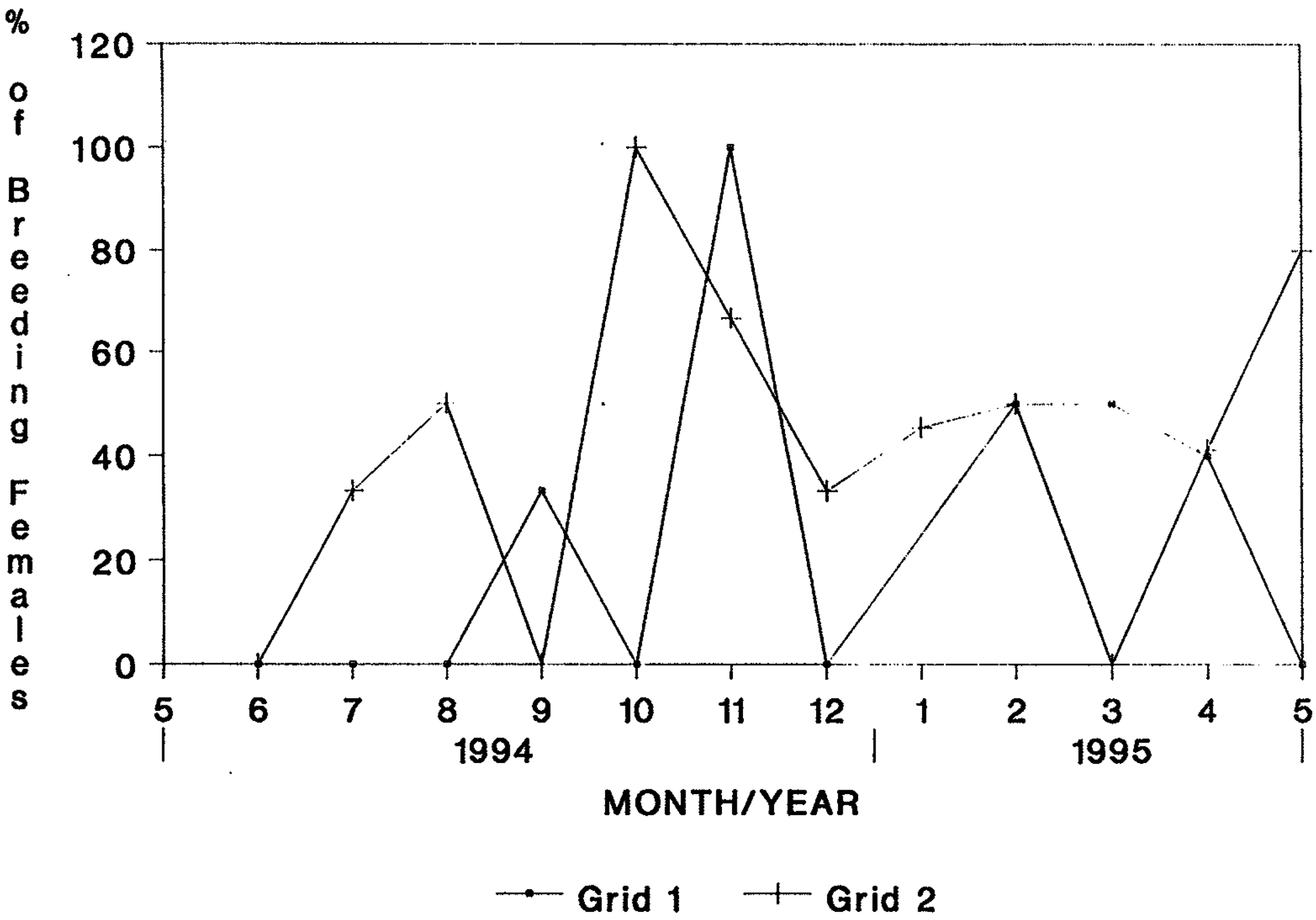
MONTH/YEAR
Grid 1
Grid 2

Figure 12. Proportion of adult female *Microtus pennsylvanicus* in breeding condition using medium to large nipple size to define breeding.


% of Breeding Females
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Grid 1
Grid 2

defined as individuals which either immigrated or were recently born into the population.

In this study no attempt is made to distinguish between these sources of new individuals to the population. In effect, the recruits were the newly tagged animals for the month.

On Grid 1, between 2-10 *Oryzomys palustris* were recruited each month, with a mean recruitment of 3.96 per month. That value was slightly larger than for *Microtus pennsylvanicus*, which had a range from 2-7 meadow voles and a mean of 3.40 recruited per month. The recruitment values were larger for both species on Grid 2 due to the larger population size and grid area. *O. palustris* had a range from 16-45 recruits with a mean value of 21.54. *M. pennsylvanicus* had a broader range of 9-56 meadow voles and had a larger mean value (30.61 recruited per month) than *O. palustris*.

DISCUSSION

Most demographic studies of *Oryzomys palustris* have been seasonal, or of shorter periods of two to three months. However, Negus et al. (1961) conducted a year-long mark-and-recapture study on Breton Island, a Louisiana island in the Gulf of Mexico. My study is the longest mark-and-recapture study conducted since Negus et al. (1961). Secondly, this study examined the population dynamics of two coastal species in a tidal marsh on the Eastern Shore of Virginia. Previous studies of the small mammal fauna on the Eastern Shore have focused on the biogeography of the species or the species composition on the barrier islands (Goldman 1918; Bailey 1946; Pardiso and Handley 1965; Dueser et al. 1979; and Cranford and Maly 1990).

Although *Microtus pennsylvanicus* has been well studied from a population standpoint, Rose and Birney (1985) noted that little investigation has been conducted in comparisons of microtine rodents and non-microtine populations. Therefore, this study compared the population biology of *M. pennsylvanicus* as well as *Oryzomys palustris*.

Population Density

Oryzomys palustris was present at its greatest density during May 1994 on Grid 1 (109/ha) (Figure 1). This was almost four times greater than the next largest peak, and contradicts Wolfe (1985) and Negus et al. (1961), who reported lows in early spring. Increases in density were also seen in September, December, and March. High densities were observed during December and January on Grid 2. These highs were comparable to high densities reported by Negus et al. (1961), Wolfe (1985), and Smith and Vrieze (1979) who also note densities as increasing in autumn and also report early winter highs. Cranford and Maly (1990) contradict the finding of low densities during August on Grid 2 as their populations on Assateague Island, Virgina exhibited low densities during the winter. Wolfe (1985) and Smith and Vrieze (1979) concur that densities are low in early spring, which was also the case on Grid 2. The mean densities for the entire year in Smith and Vrieze (1979) and this current study were very similar (31/ha and 38/ha, respectively).

Microtus pennsylvanicus showed population density peaks during the late spring on both grids (Figures 3 and 4). However, Tamarin (1977) reports highs to occur during the winter months in coastal Massachusetts. *M. pennsylvanicus* was at its lowest densities during the month of October and was also low throughout the winter on both grids.

As *Oryzomys palustris* decreased from its peak in March on Grid 2, *M. pennsylvanicus* reacted by increasing in density. Both species had late summer and late winter peaks on Grid 2, and the overall mean densities were quite similar (*O.p.* 38.08/ha and *M.p.* 38.66/ha). However, *M. pennsylvanicus* increases readily when density levels of *O. palustris* were low. It appeared that the two species can coexist with no effect on the density of the other, but in the absence of one species the other will show density compensation. Of, course replicate grids would be needed to substantiate a pattern of density compensation when one species is removed. Smith and Vrieze (1979) reported the absence of *O. palustris* during dry periods on the island hammocks in the Florida Everglades, and their subsequent recolonization once the grids became wet again. This disappearance in the dry season may account for the low population densities during the spring (Wolfe 1985).

Survival Rates

The time-specific survival rates of adults were significantly ($p<0.05$) greater on Grid 1 for *Microtus pennsylvanicus* and for *Oryzomys palustris* on Grid 2. Because survival rate is calculated using recapture data, the moisture conditions on these grids may be the reason for these differences. Grid 1 was drier than Grid 2 in the areas with sufficient ground cover where animals were usually captured. Grid 2 was usually more uniformly covered with water which was a more suitable condition for *O. palustris*. Wolfe (1985) reported a survival rate of only 24% after the initial capture. Survival rates of *O. palustris* on both grids were higher in this study (Grid 1, 33.5% and Grid 2, 31.6%). Both species had increased survival rates during the summer months, most likely due to the increased food supply and percent of cover on the grids. The latter was substantiated by A. Sowell's thesis research during the same study period.

Capture Probabilities

The capture probability of tagged animals was significantly greater on Grid 2, in part due to the larger size of the grid. A difference between summer and spring capture probabilities also existed on both grids. This difference was most likely due to a general decrease in activity during the warmer summer months (Negus et al. 1961). The higher capture probability of *Oryzomys palustris* on Grid 1 ($x=0.6143$, $p<0.05$) was most likely the reason that the capture probabilities of the two species combining the grids differ.

Negus et al. (1961) reported a larger percentage of *Oryzomys palustris* seen more than once (30.46%) than was observed on either Grid 1 (16.46%) or 2 (16.47%) (Figure 3). Even so, *O. palustris* had a larger percentage of recaptures on both grids when compared to *Microtus pennsylvanicus*. The higher percentage of recaptures in Negus et al. (1961) may be due to the fact that their study was conducted on an island. Rodents on islands face larger barriers to dispersal than do the same rodents living in coastal habitats.

Longevity

Wolfe (1985) reported the maximum longevity of one individual *Oryzomys palustris* to be 24 months, whereas Negus et al. (1961) reported one individual to survive for 20 months. Although my study was only 13 months long, the longest trap-revealed lifespan for any animal was six months. Two *O. palustris* and one *Microtus pennsylvanicus* remained on Grid 1 for six months, the maximum length of stay in this study (Figure 4). The short residency times on the grids correspond with the vagility of the rice rat in Florida that were not frequently recaptured (Smith and Vrieze, 1979). Longevity estimates require information on animals that are captured more than once in order to determine the amount of time the individual has remained on the grid. The high percentage of animals seen only once contributed to the difficulty in determining longevity for both species. Although trap aversion is one explanation for this pattern of brief residency on the grid, a more likely explanation relates to the high vagility in these dynamic tidal marshes, where twice daily flooding and occasional heavy and long flooding impose additional demands and selective pressures on small mammals.

Age Structure

Juvenile *Oryzomys palustris* were most numerous during the late spring and then decreased during the late summer. Negus et al. (1961) reported juveniles to be present between January and March, which corresponds to this study, in which juveniles were also present then (Figures 5 and 6). Wolfe (1985) reported juveniles to be present in greatest abundance between May and September, and subadults to increase in late autumn and early winter. Subadults were observed to be at lower levels during May and June. This same pattern was recurrent in *O. palustris* populations on both grids in this study (Figures 5 and 6). Levels of adult rice rats were at lower levels during the summer months (Wolfe 1985 and Negus et al. 1961). Higher levels are seen during the late winter, spring, and late autumn.

Tamarin (1977) reported increased juvenile meadow voles to be most numerous during the summer months; however, peak levels were seen during the spring in this study. Subadult populations were large during the late spring and summer due to the high recruitment of juveniles during the early spring. Many adults also were present on the grid in the spring. It is interesting that a spring with a high level of adults would not yield large numbers of juveniles, as suggested by Tamarin (1977).

Sex Ratios

Individual male *Oryzomys palustris* outnumbered the number of females, significantly so on Grid 2 (Tables 1 and 2). Smith and Vrieze (1979), Wolfe (1985), and Birkenholz (1963) also report male captures to be greater than females, but none reports a sex ratio different from unity. The differing ratio of male and female *O. palustris* on Grid 2 may be due to females not moving as much on the grid because of reproductive condition (Wolfe, 1985).

Males of *Microtus pennsylvanicus* also outnumbered females on both grids; however, as with the rice rats the differences are statistical significant only on Grid 2 (Tables 1 and 2). Myers and Krebs (1971), who report a significant sex ratio which favors males, credit the difference to greater trappability and to the more rapid growth of males. This may be the reason the ratio of males to female on Grid 2 was significant. Myers and Krebs (1971) also noted that increased male recruitment lowered the rate of population growth, and that because of this the population tended to maintain equal numbers of males and females.

Reproduction

Male *Oryzomys palustris* were found to be most reproductively active in August and September and from late fall to mid-winter (Figure 9). Wolfe (1985) found maximum breeding from late spring to late autumn, whereas Smith and Vrieze (1979)report a summer peak. Negus et al. (1961) observed modest summer reproduction and Wolfe (1985) concurs that his Mississippi populations experienced a mid-summer lull. This was also the case with the populations on both grids in this study.

The male *Microtus pennsylvanicus* are most reproductively active during the spring (Harris 1953 and the present study). However, Tamarin (1977) reports peak breeding to occur during the summer months. In this study, males were also reproductively active during the winter on Grid 2. Keller and Krebs (1970) and Getz et al. (1979) reported winter breeding to occur in their populations of meadow voles in Indiana and Illinois, respectively.

No seasonal pattern emerged when comparing reproductively active female *Oryzomys palustris* on the two grids (Figure 11). On Grid 1, females were most reproductively active during the spring. Harris (1953), Edmonds and Stetson (1990), and Wolfe (1985) concur with this finding by also reporting spring highs. In contrast, Smith and Vrieze (1979) report low reproductive activity during April and May in their studies in southern Florida.

Reproductive activity in female *Microtus pennsylvanicus* differed between the two grids. Grid 2 exhibited peaks and depressions one month before they would occur on Grid 2 until the depressions both occurred in December. Females were reproductively active during November and April on both grids (Figure 12). Breeding was observed during all of the seasons; however, the populations in this study seem to conform to those of Harris (1953), who observed females to breed during the spring. Tamarin (1977) reported breeding peaks to occur during the summer months, which is in contrast to my results. This study also supported the results of Getz et al. (1979) and Keller and Krebs (1970), who also reported breeding to occur throughout the winter.

Recruitment

High population turnover in *Oryzomys palustris* populations seemingly is related to a high rate of dispersal

(Smith and Vrieze 1979). Both grid populations in this study showed that the populations in the tidal marshes of the Eastern Shore of Virginia also were highly vagile. The large proportion of animals caught only once means that they were highly mobile, with only a small fraction of either species showing a pattern of sustained residency.

More *Microtus pennsylvanicus* than *O. palustris* were recruited onto Grid 2. Meadow voles typically were less vagile, especially during the winter months (Grid 1, $\bar{x}$= 2.0 recruits). During the winter meadow voles may form huddling groups, and therefore may not disperse as much (Madison et al. 1984).

CONCLUSION

Oryzomys palustris population density appears to increase during late autumn and early winter. These increases may be due to increased survival during begnin weather conditions, to improved food supply then, or to increased breeding. Trap success will directly affect estimated densities; therefore, it may be a good idea to trap for more consecutive days than were done in this study. *O. palustris* was very vagile and six of seven (85%) of rice rats were never recaptured. The fact that this study was conducted on a coastline rather than an island may also have led to the high rates of dispersal. *Microtus pennsylvanicus* also demonstrated unusually high levels of vagility and few were recaptured.

Both *Oryzomys palustris* and *Microtus pennsylvanicus* seemed to coexist with little competition occurring. However, in the regression of one species the other seems to increase and return to normal when the other population reaches a higher level.

Reproduction in *Oryzomys palustris* during the late fall and early winter showed more pronounced effects in males than females. A general lull in reproductive activity in both species occurred during the summer months. As a result the population had more juveniles in autumn than during any other season.

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