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Patterns of Transience, Sex Bias, and Body Mass in Open-Habitat Rodent Populations

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PATTERNS OF TRANSIENCE, SEX BIAS, AND BODY MASS IN OPEN-HABITAT RODENT POPULATIONS

by

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ABSTRACT

PATTERNS OF TRANSIENCE, SEX BIAS, AND BODY MASS IN OPEN-HABITAT RODENT POPULATIONS

Stephen Edward Rice
Old Dominion University, 2011
Director: Dr. Robert K. Rose

Rodents are assumed to live their lives in circumscribed (natal) areas with males being more prone to disperse than females and juveniles more prone to disperse than adults. To test these assumptions we examined the initial captures of geographic populations of hispid cotton rat, meadow vole, prairie vole, and marsh rice rat obtained through capture-mark-recapture methods. Capture records were obtained from Kansas and Illinois from long-term studies, and through live-trapping in Chesapeake, Virginia. I evaluated proportions of residents and transients, adults and juveniles, and males and females for significant differences among seasons, years, and geographic locations. The overall body masses of residents and transients were compared for each species and between populations.

Hispid cotton rats exhibited seasonally significant, density-independent transience, with adults forming the greatest proportions of initial captures, and no difference in body mass between residents and transients. Sex ratios of cotton rats deviated from unity for Kansas but not Virginia populations; both had seasonal variation. Meadow and prairie vole populations had seasonally significant transience, with geographic variation in the density dependence of transience and differences in the body mass between residents and transients. Vole populations also had seasonal differences in sex ratios, and the Illinois population of prairie vole was the only 1 that differed from overall unity. The marsh rice rat from Virginia had seasonal transience and no detectable difference between body mass of residents and transients. The dominant maturity group of the rice rat changed seasonally and was generally juvenile-biased. Sex ratios of marsh rice rats did not differ from unity overall, but were different only for groups of adults and residents. All populations had seasonally significant transience, and 6 populations had a majority (>50%) of initial captures comprised of transients. Three populations, both Illinois voles and Kansas meadow voles, had residents that were heavier than transients, as well as a negatively correlated relationship between population density and proportion of transients.

No population met the expectations of the prominent paradigms, namely that animals are born and live their lives in a circumscribed area, and those that choose to leave a population are prone to biases towards juveniles and males over adults and females. The lack of fit with these paradigms provides support that generalizations of population structure and behavior of open-habitat rodent populations are erroneous and should be used with caution as these paradigms were not useful models of population sub-structure for the examined populations.

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CHAPTER I

INTRODUCTION

The Order Rodentia is the most cosmopolitan, diverse, and abundant in the Class Mammalia. Rodents account for ca 43% of all mammals (Vaughan et al., 2000) with 2277 species (Carleton and Musser, 2005), 174 of which have been described since 1993 (Ceballos and Ehrlich, 2009). Rodents are used extensively in studies of populations, genetics, ecology, demography, and physiology due to their prolific nature, short generation time, and relative ease of maintenance in captivity (Nunes, 2007; Wolff and Sherman, 2007). Based on long-held dogma, rodent populations are believed to exhibit site fidelity (philopatry) and minimal vagility, with the exception being the biased dispersal of juvenile males (Aars and Ims, 1999; Boven and Weissing, 1999; Bush et al., 1977; Collett, 1895; Elton, 1924; Errington, 1954; Greenwood, 1980; Ray et al., 2003; Wakeley, 2001; Wakeley and Takahashi, 2004; Waser et al., 2006; Wright, 1956). However, field observations of rodents have led some investigators to suggest that the perception of philopatry and minimal vagility is inadequate (Brown et al., 2005; Dueser et al., 1981; Gaines and McClenaghan, 1980; Getz et al., 1979; Metzgar, 1979).

Rodents range in size from 5 g to 50 kg, share cranial features, and possess a single pair of continuously growing incisors in both upper and lower jaws (Vaughan et al., 2000). The family Muridae (Old World rodents) accounts for over one-quarter of mammalian species and two-thirds of all rodents (Vaughan et al., 2000). Murids range in size from 10 g to 2 kg; most have a mouse-like form with a long tail, generalized limbs, and full retention of all digits. Morphological features of the skull are used to diagnose the family, with the infraorbital foramen always lying above the zygomatic plate. Murid species display a wide variety of morphological and behavioral specializations that are used to further categorize subfamilies (Vaughan et al., 2000). The subfamilies included in my study are Sigmodontinae and Arvicolinae.

Four murid species are of interest to my study: hispid cotton rat (*Sigmodon hispidus*), marsh rice rat (*Oryzomys palustris*), meadow vole (*Microtus pennsylvanicus*), and prairie vole (*Microtus ochrogaster*). These species share a preference for open habitat, mostly herbivorous diet, little to no known social structure, and broad distribution in North America. Each species can be studied using standard capture-mark-recapture (CMR) techniques with attributes of sex, reproductive maturity, and mass assessed in the same manner. Rodent populations with minimal social structure allow for the assessment of site fidelity without the confounding effects of range or burrow inheritance significantly associated with social or subterranean rodents.

The hispid cotton rat (Sigmodontinae) is active year-round in open, grassy habitats of southeastern and southcentral United States (Cameron and McClure, 1988; Cameron and Spencer, 1981; Linzey et al., 2008). *Sigmodon hispidus* is sexually dimorphic with adult males generally larger in size, 110 to 225 g, than adult females, 100 to 200 g (Cameron and Spencer, 1981). Reproductive activity varies with season and geographic distribution; southern populations breed year-round in some years whereas northern populations tend to breed April through October (Bergstrom and Rose, 2004; Rose and Mitchell, 1990). Sexual maturity is achieved as early as 1 month of age, but generally does not begin for males until 2 to 3 months (Cameron and Spencer, 1981). Rose and Mitchell (1990) found animals in reproductive condition at 50 g. Gestation lasts 27 days with an average litter of 3.4 to 7.3 pups, each weighing ca 6 g; litter size is also subject to geographic variation and generally increases in the north (Cameron and McClure, 1988). Population density peaks in autumn, with a maximum recorded density of >100 individuals/ha in eastern Virginia (Green and Rose, 2009) and minimum densities in summer and winter as low as 8 individuals/ha (Cameron and Spencer, 1981). Hispid cotton rat populations seem to be organized into a relative dominance system with exclusive female home ranges where dominant individuals are most likely to be trapped (Cameron and Spencer, 1981).

Oryzomys palustris (Sigmodontinae) is active year-round in wetlands and occasionally meadows (Wolfe, 1982). The marsh rice rat weighs 45 to 80 g as adults with sexual dimorphism in mass noted for populations in Texas and eastern Virginia (Cameron and Spencer, 1983; Dreelin, 1997). Animals in Virginia tidal marshes were reproductively mature at 30 g (Dreelin, 1997). Cameron and Spencer (1983) found males to be significantly heavier at 45 g than females at 37 g. Dreelin (1997) found the same trend with males at 56 g and females at 48 g. Reproduction can be seasonal, with typical peaks in spring and autumn, but some southern populations breed year-round (Dreelin, 1997; Negus et al., 1961). Reproductive maturity is generally reached at ca 2 months for both sexes. Gestation lasts 25 days, producing litters of 4 to 6 pups, with the newborns weighing 3.2 to 3.7 g and weaned between 11 and 20 days (Svihla, 1931; Wolfe, 1982). Population density ranges geographically with 0.1 to 3.3 individuals/ha reported for Louisiana (Negus et al., 1961), whereas an eastern Virginia study found a maximum density of 109 individuals/ha during the breeding season (March, 1995). No study to date has reported evidence of social structure in the marsh rice rat.

The meadow vole (Arvicolinae) is active year-round in moist, grass-dominated habitats across northern and eastern North America (Reich, 1981). *Microtus pennsylvanicus* weighs 30 to 60 g as adults, with no sexual dimorphism noted (Reich, 1981). Body size increases from northern to southern latitudes and high to low elevations (Reich, 1981). Reproductive maturity is reached at 30 g in Virginia and Illinois (Dueser et al., 1981). Reproduction may occur year-round, with the rate dependent on season and population density (Reich, 1981). Gestation lasts 21 days with litters of 4.0 to 6.2 pups, each weighing 1.6 to 3.0 g and weaned at 12 to 14 days (Reich, 1981). Population densities reach a maximum of 600 individuals/ha in northern prairie wetlands (Fritzell, 1989) and range from 27 to 398 individuals/ha in Virginia old-field sites (Linzey and Cranford, 1984). Intraspecific aggression is noted for both sexes, varying with population density and reproductive activity (Boonstra et al., 1993; Madison, 1980; Reich, 1981). Social structure in *M. pennsylvanicus* is unclear with descriptions ranging from no formal structure (Getz, 1972) to female-dominated territorial structure during reproductive seasons (Madison, 1980).

Microtus ochrogaster (Arvicolinae) is active year-round in prairie and grassland habitats of central North America (Stalling, 1990). The prairie vole is not sexually dimorphic, and adults generally weigh 37 to 48 g, although individuals have been reported at 73 g (Stalling, 1990), and in reproductive condition at 30 g (Rose and Gaines, 1978). Reproduction may occur year-round with peaks from May through October, dependent on available moisture (Rose and Gaines, 1978; Stalling, 1990). Females are sexually mature within 6 weeks. Gestation lasts 20 to 22.8 days with litters of 3.5 pups weighing 3 to 3.5 g each (Stalling, 1990). Population density varies with season and moisture; a maximum of 1,060 individuals/ha has been reported (Stalling, 1990). A loose social structure seems to be formed on the basis of communal groups centered on territorial pairs and relative dominance (Getz et al., 1993; Stalling, 1990).

Sex Bias.—A one-to-one ratio of males to females in a population, referred to as unity, and is expected due to gametic probability. Empirical studies of birds and mammals provide evidence of populations in which strong patterns of sex bias exist, though not consistently (Cockburn et al., 2002). Sex ratios that do not conform to unity suggest differential mortality within a population, but the mechanisms are unclear (Cockburn et al., 2002). Many mammalian populations have biased dispersal of 1 sex, with the opposite sex displaying philopatric tendencies (Boonstra et al., 1987; Greenwood, 1980).

Mechanisms of sex bias in rodents can be classified as nutritive or non-nutritive mechanisms (Cockburn et al., 2002; Rosenfeld and Roberts, 2004). Exploration of nutritive causes of sex bias in laboratory mice has revealed that the composition of maternal diet relative to saturated fats and carbohydrates can skew sex ratios at birth (Rosenfeld and Roberts, 2004). The combination of high saturated fat with low carbohydrate intake caused a male-biased shift, whereas low saturated fat and high carbohydrate created a female-biased shift (Rosenfeld and Roberts, 2004). Non-nutritive mechanisms of shifting sex ratios include intrauterine position, stress, timing of copulation and population parameters (Cockburn et al., 2002; Rosenfeld and Roberts, 2004). Rosenfeld and Roberts (2004) found more sons were produced by a female which had been between 2 males in utero or females which mated at the first post-partum estrus, whereas stressed females produced fewer than expected sons.

The expected pattern of sex distribution in rodent populations is that of dispersal of juvenile males but female philopatry (Boonstra et al., 1987; Greenwood, 1980). Populations in which females compete for resources should display female philopatry and juvenile males should be more prone to emigrate than adults. Thus, the expectation is that emigration should be dominated by males and philopatry dominated by females. Single factor hypotheses regarding sex biases are often confounded by factors such as density, season, reproductive conditions, and habitat fragmentation (Bloch, 1997; Diffendorfer et al., 1995; March, 1995; Reich, 1981; Stalling, 1997; Wolfe, 1982).

Transience.—Transience is the appearance of individuals in a population that are captured during only 1 sampling period and never seen again. Transience is a common concept of demographic studies, occasionally interpreted as being related to dispersal and emigration, in birds, bats, large and small mammals, reptiles, amphibians, and fish, and can represent factors such as nomadic traveling through a study site, temporary appearances of prospective non-breeders, or residents of a neighboring population on an excursion (Bjorndal and Bolton, 2000; Clavel et al., 2008; Karanth et al., 2006; Labonne and Gaudin, 2005; Morales et al., 2010; Perret et al., 2003; Sendor and Simon , 2003; Tannerfeldt and Angerbjörn, 1996). Transience affects the distribution of ectoparasites, such as fleas, through host movements (Krasnov et al., 2006). Multiple studies (Table 1) have noted that transients can account for a significant proportion of individuals captured in CMR studies, especially in populations of herbivorous rodents in open habitats. Population studies of many species of rodent, including those in Table 1, indicate that most animals are not captured and tagged as juveniles, a high proportion is seen only during 1 trapping period, and that marked adults tend to disappear in high proportion with a small percentage returning to the trappable population later.

Transiency can be a confounding effect in demographic studies and statistical models in which survival and age are measured parameters (Pradel et al., 1997; Sendor and Simon, 2003). Statistical models based on capture-recapture survival probabilities allow separation and analysis of transients from residents based on apparent survival. In such models, transients have a survival of 0; they merely travel through a trappable population (Pradel et al., 1997). The identification of transients and residents within a population presents an opportunity to explore the characteristics of each category in a quantitative manner (Perret et al., 2003; Pradel et al., 1997). If populations are truly philopatric with minimal vagility, we would intuitively expect to find the majority of individuals in a population tagged below adult masses with a history of multiple captures across multiple trapping periods, especially for females.

TABLE 1.—Proportions of transients in CMR studies for rodents of open habitats. An asterisk (*) indicates significant transience within populations based on analysis of proportions using the Nemenyi test (Zar, 2010). Multiple values for species indicate separate entries for season, location, or investigator(s).

Species	% Transient	Source
Apodemus sylvaticus	59.5*	Benston et al., 1989
Long-tailed field mouse	61.2*	
Microtus ochrogaster	40.0	Getz et al., 1994
Prairie vole	13.0	

Table 1 Continued

Species	**% Transient**	**Source**
Prairie vole	23.0	Diffendorfer et al., 1995
Microtus pennsylvanicus Meadow vole	51.5	Bell, 2010
	47.5	
	39.0	Dueser et al., 1981
	56.0*	Bloch, 1997
Oryzomys palustris Marsh rice rat	63.7*	Bloch, 1997
	85.0*	March, 1995
Peromyscus californicus California deer mouse	25.0	M'Closkey, 1972
Peromyscus eremicus Cactus deer mouse	54.0	M'Closkey, 1972
Peromyscus maniculatus North American deer mouse	57.0*	M'Closkey, 1972
	29.0	Diffendorfer et al., 1995
	75.0*	Crespin et al., 2008
Reithrodontomys megalotis Western harvest mouse	41.0	M'Closkey, 1972
Reithrodontomys humulis Eastern harvest mouse	46.0	Cameron et al., 2009
Sigmodon hispidus Hispid cotton rat	42.7	Green and Rose, 2009
	51.0	Cameron et al., 2009
	32.0	Diffendorfer et al., 1995

Objectives.—Using data from our long-term CMR field studies and larger data sets sent by cooperating investigators, I have sought to determine how the characteristics of sex, reproductive maturity, and body mass compare between transients and residents, and between geographical populations. CMR studies of herbivorous rodents in open habitats allow me to examine whether geographic populations of *S. hispidus, O. palustris, M. ochrogaster,* and *M. pennsylvanicus* are initially captured and tagged at juvenile or adult masses, and to examine the patterns of transiency for these age and sex groups. These species share common attributes of herbivory, year-round activity, preference for open habitat, and minimal social structure.

I examined initial capture records, and hypothesized that populations of transients would display male-biased sex ratios and residents would be female-biased, based on the expectations of Greenwood (1980), which have become commonly accepted. I also tested whether mean body mass differed between residents and transients, hypothesizing that the majority of residents should be initially captured at juvenile masses as an indication of their natal place and of site fidelity, whereas transients are more likely to be initially captured at adult masses due to an increase in vagility with maturity. The expectation is that animals are initially caught and tagged as juveniles, with a high probability of being born in the study area, and contributing greatly to the population density. Thus, a high proportion of residents would be tagged at juvenile masses. A small proportion would be tagged as adults, and few such adults transition to residency, thus contributing little to population density.

The notion that rodents in open-habitats are born and live their lives in a relatively limited, circumscribed area was the underpinning of the examination of transience. If this notion holds true the expectation is that the majority of individuals tagged in CMR studies would be captured again, thus being classified as residents, and supporting the notion that there is a central area of activity and given range in which the average individual could be found. Those that do depart a population would then be expected to conform to the expectations listed in Greenwood (1980), with males more prone to dispersal than females, and juveniles more prone than adults. Greenwood (1980) bases his belief in sex-biased dispersal and philopatry on the notion that the philopatric sex remains in the population to procure resources needed for successful reproduction. These trends should then be more apparent in those individuals with the potential of breeding, if resource allocation and limitation lead to the expectations of sex biases. Thus, I examined sex ratios within the context of these paradigms and hypothesized that, if useful, we should find patterns of male transiency, female philopatry, and a detectable difference in body mass between residents and transients for adults in reproductive condition. Within the substructure of populations, we should also see, in general, higher proportions of juveniles than adults in the transient groups, and specifically that juvenile male transients should be of greater proportion than juvenile female transients, and adult male transients should contribute a greater proportion of captures than adult female transients.

CHAPTER II

MATERIALS AND METHODS

Live trapping was conducted monthly at 2 1 ha sites in Chesapeake, Virginia. Long-term data sets used for comparison were provided from the studies of Norman Slade (Kansas) and Lowell Getz (Illinois).

Study Areas.—Rodent communities in Chesapeake, Virginia were studied through monthly live trapping at 2 old-field sites based on CMR methodology. The study sites, owned by The Nature Conservancy, are being allowed to progress through successional stages, eventually returning to Dismal Swamp forest. The 11.5 ha Su tract was last used for agriculture in 2000. The study grid on the Su tract was monitored monthly from December 2002 until September 2005, when the site became dominated by loblolly pine (*Pinus taeda*) and no longer suitable as habitat for old-field rodents. The 60 ha Stephens tract was last used for agriculture in 2003. The study grid on the Stephens tract was established in October 2005 and continues to be monitored. Red maple (*Acer rubrum*), sweet gum (*Liquidambar styraciflua*), and blackberries (*Rubus* spp.) are increasing in dominance; however, herbaceous ground cover remains to support old-field rodents. The same 1 ha grid design used on each site consisted of 64 stations with 2 modified Fitch traps (Rose, 1994) at each coordinate. Each grid consisted of 8 rows and 8 columns with each station 12.5 m apart; the row and column of each station was used as part of a Cartesian coordinate system on the grids.

Trapping.—Live trapping and CMR methodology followed American Society of Mammalogists (ASM) guidelines (Gannon et al., 2007) and was approved by the Old Dominion University Institutional Animal Care and Usage Committee (IACUC #10-016).

Trapping was conducted for 3 days each month, generally near the time of the new moon. Traps baited with mixed birdseed and sunflower seed were opened in 1 afternoon and checked for 3 consecutive mornings. During the summer months, traps were locked "open" in the morning and re-set in the late afternoon to prevent the death of animals due to hyperthermia. During the winter months, polyfill was added to traps as insulation.

Each captured animal was identified to species and given a uniquely numbered ear tag in the right ear. If an ear tag was present that number was recorded; if the right ear was torn a new tag was placed on the left ear and the animal was later synonymized with the most likely match from previous months based on its mass, sex, and location on the grid. In addition to species and tag number, the location on the grid (coordinates), sex, mass, and reproductive condition were recorded. Reproductive condition for males was based on the position of testes (abdominal or scrotal) and for females on the vaginal opening (perforate or not perforate), nipple size (small, medium, or large), and pubic symphysis (closed, slightly open, or open). Rodents were released at the point of capture. In the event that a litter was born in the trap, the number of pups was noted, body mass recorded for the mother, and the trap locked open to enable her to retrieve her pups.

Occasional disturbance of Fitch traps required the use of Havahart traps to capture, remove, and relocate nuisance animals such as raccoons (*Procyon lotor*) and opossums (*Didelphis virginianus*). During periods of extreme disturbance, trapping periods were sometimes truncated or suspended until the nuisance animals had been removed, in order to reduce the chances of mortality of small mammals in traps.

Statistical Analyses.—Individuals were coded for residency status (resident, transient), reproductive maturity (juvenile, adult), and season of capture. Residents were defined as individuals captured during at least 2 trapping periods; transients were defined as animals captured during only 1 trapping period (Cameron 1977; Cawthorn and Rose, 1989; Dueser et al., 1981). Reproductive maturity was determined using 2 criteria: mass and reproductive condition. Individuals meeting the minimum mass criterion for reproductive maturity (Table 2) were labeled as adults, indicating their potential for reproduction. Reproductive condition was evaluated separately from mass to identify mature individuals: scrotal for males, and for females with any 2 of the 3 reproductive traits: pubic symphysis slightly open or open, vagina perforate or not, and medium or large nipples (McCravy and Rose, 1992). Seasons were defined in traditional terms of winter (Dec-Feb), spring (Mar-May), summer (Jun-Aug), and autumn (Sept-Nov).

TABLE 2.—Minimum adult masses for the 4 species evaluated in this study. Those meeting these minimum criteria were classified as adults.

Species	Minimum Mass Criterion	Sources
Hispid cotton rat	50 g	Rose and Mitchell, 1990
Marsh rice rat	50 g	Wolfe, 1982; Wootton, 1987
Meadow Vole	30 g	Dueser et al., 1981
Prairie Vole	30 g	Rose and Gaines, 1978

Capture patterns were evaluated on the basis of season, residency, sex, reproductive status, and body mass for each species. Analyses were conducted in IBM SPSS Statistics (Version 19) and Microsoft Excel 2010. The analyses performed in Excel were run by using the equations (Appendix I) for calculation of the two-sample Z-test and Nemenyi test. Assumptions of normality and homoscedasticity were evaluated on original and transformed residuals with Kolmogrov-Smirnov and Lavene's tests. Where assumptions could not be met, data were ranked and analyzed with non-parametric tests. Differences in mean body mass were evaluated with a one-way analysis of variance (ANOVA) or Kruskal-Wallace (K-W) tests. Associations among factors were examined through contingency tables using the Chi-square test of independence. The expected values ($\hat{f}_{ij}$) (Equation 1) for the Chi-square test of independence (χ^2) (Equation 2) were generated intrinsic to the frequency of observations on the basis of 1 fixed margin.

Proportional components ($\hat{p}_i$) that were of binomial distribution, such as resident and transient proportions overall and within seasons, were analyzed with a one-tailed, two-sample Z-test (Z) (Equation 3) that was cast from a 2x2 contingency table with 1 fixed margin. Proportional components compared among groups, such as seasons, were analyzed with contingency table using χ^2 (Equation 4) with pooled proportions ($\overline{p, q}$) (Equation 5).

Significant χ^2 for factors with multiple levels were followed by the post-hoc Nemenyi test (Zar, 2010). The Nemenyi test is a non-parametric equivalent to the Tukey test, and can identify significant differences in the proportions of groups by comparing each group against the others with the null hypothesis that all groups are equal. Significant results of the Nemenyi test identify differences among the groups tested. The Nemenyi test was used as a follow-up test to determine similarity among seasons for proportion of transients and adults, as well as the similarity of groups contributing to the trappable population within each season and overall. Each proportion to be compared was first transformed (Equation 6) and converted into degrees. The standard error of the comparison was calculated (Equation 7) and used to compute the q-statistic of the Nemenyi test (Equation 8).

Proportions of resident to transients, of adults to juveniles, and of other groups were evaluated on seasonal and yearly bases and across the total data set (overall) using Chi-square tests of independence, two-sample Z-tests, and the post-hoc Nemenyi test. To determine density dependence of transience, normality was assessed and correlation used to evaluate seasonal densities and seasonal proportions of transients within each year. Geographically separate populations were compared to identify common trends within a species. Values in Table 1 were analyzed for significance using a two-sample Z-test that compared residents to transients based on the published values in each study.

CHAPTER III

RESULTS

Values from the Literature.—I analyzed published values of transience and residence for rodent species in open habitats to determine whether transience was significant. Transience was significant in populations of *Apodemus sylvaticus*, *Microtus pennsylvanicus*, *Oryzomys palustris*, and *Peromyscus maniculatus* (Table 1). Values for other species included in my study did not display significant transience.

Assumption Testing, Data Transformations, and Analysis of Body Mass.—Assumptions were checked for all parametric tests. The residuals for body mass for all species were non-normal and heteroscedastic, and were analyzed with multiple transformations. No transformation of the data met the assumption of normality for cotton rats, meadow voles, and prairie voles, so values were rank-transformed and analyzed with non-parametric tests. The body mass of marsh rice rats met test assumptions after being log-transformed. For the correlation of density and proportion of transients the values were non-normal for each species, but when log-transformed were normalized.

Body masses for each species were analyzed for differences between adults and residents, as well as differences among other population groups. The body masses of cotton rats, meadow voles, and prairie voles were analyzed with the non-parametric K-W test. The body mass analysis for population groups was followed up with a post-hoc Nemenyi test to determine significant differences among the population groups overall. Body masses of the marsh rice rat were analyzed with a one-way ANOVA, followed by a post-hoc Tukey test to determine significant differences among groups.

The mean ranked body masses of resident and transient groups for Virginia cotton rats and meadow voles, as well as Kansas cotton rats and prairie voles were not significantly different ($P>0.05$). The body masses of resident and transient groups for the Virginia marsh rice rat were also not significantly different. The body mass of adult and juvenile groups was different in all species, because the groups were defined as non-overlapping by the mass criterion applied during coding.

Sigmodon hispidus from Virginia.—Tests of independence for transience with season, sex, and reproductive maturity groups revealed that transience was significantly associated with season ($\chi^2=221.8477$, df=3, $P=8.00\times10^{-48}$) but not sex or reproductive maturity groups. Proportions of transients in the population were significant during spring, summer, and winter. Nemenyi tests of the proportion of transients among seasons (Table 3) revealed spring to be significantly different from other seasons, and summer different from autumn. Proportions of transients were highest in the spring at 72.95%, followed by summer, winter, and autumn. Autumn was the only season with significant residency, with a proportion of 52.94%. Transience for the data set was significant with a proportion of 54.41%. The test of independence of residency status, i.e., the number of individuals coded as residents and transients, from year of study revealed a significant association ($\chi^2=64.9967$, df=8, $P=4.83\times10^{-11}$). One year, 2002, had a significantly higher proportion of residents, whereas 4 years, 2005, 2007, 2009, and 2010, had significantly higher proportions of transients (Fig. 1). Other years were not significant for a difference in proportions of residents and transients. There was no correlation between population density and proportion of transients.

The reproductive maturity (adult or juvenile) of cotton rats at initial capture was significantly associated with season (χ^2=22.996, df=3, P=4.05x10^{-5}). Using two-sample Z-tests for each season, adults formed a significant proportion of the population for each season and overall. The Nemenyi test of adult proportions among seasons (Table 3) placed winter and spring together, and summer and autumn as significantly different from winter.

TABLE 3.—Results of Nemenyi tests of transients and adults for *Sigmodon hispidus* from Chesapeake, Virginia. The proportion of each group in each season is listed above the Nemenyi similarities. Different letters denote significant differences among seasonal proportions. Transients include both sexes and both reproductive maturity groups, and adults include both sexes and both residency status groups. An asterisk (*) denotes a significant proportion of transients in a season.

	Spring*	**Summer***	**Autumn**	**Winter***
Proportion of Transients	72.95%	58.75%	47.06%	54.82%
Nemenyi Similarities	*c*	*b*	*a*	*ab*
Proportion of Adults	76.03%	62.20%	65.25%	89.67%
Nemenyi Similarities	*ab*	*a*	*a*	*b*
Sample Size	122	257	476	301

Proportions of reproductive maturity, sex, and residency status groups (Fig. 2) were significantly associated with season (χ^2=128.1159, df=21, P=2.273x10^{-17}). When seasonal and whole data set comparisons of the proportions for each group were evaluated with the Nemenyi test (Table 4), the proportion of adult male transients in spring was different from all groups except adult female transients. Adult female residents in summer were different from all other resident groups. Adult male residents and adult female transients were different from juvenile transients in autumn. All juvenile groups were different from all adult groups during winter and overall.

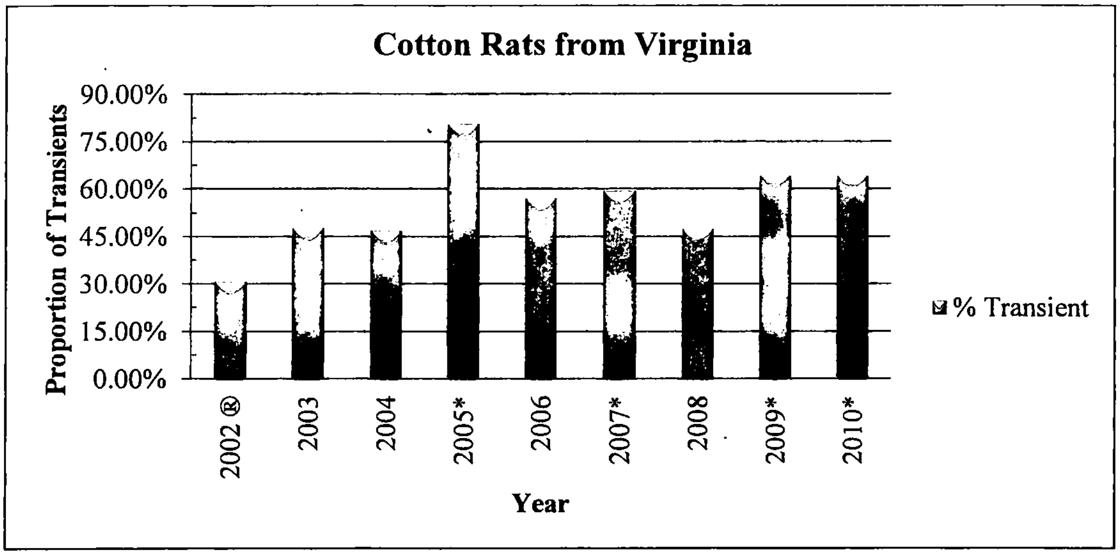
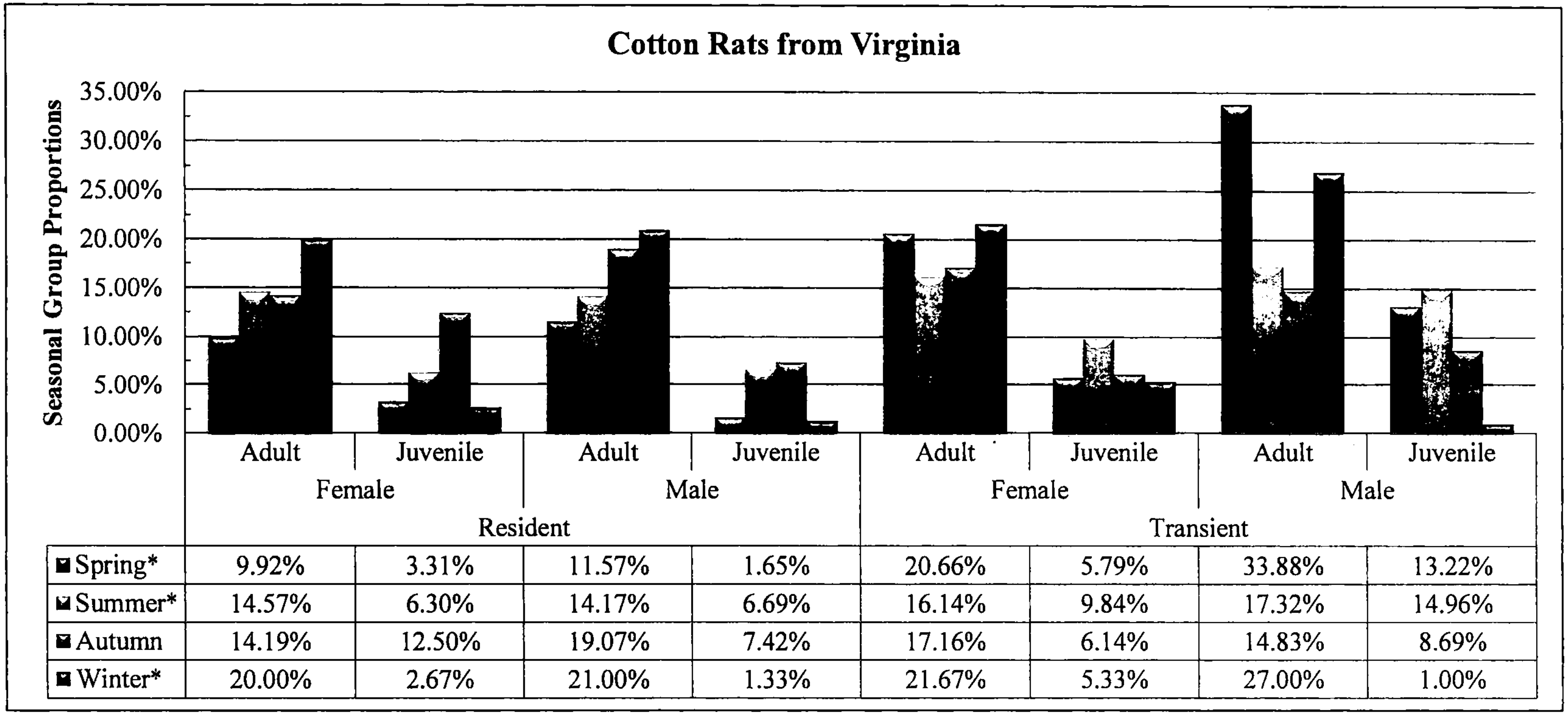


FIG. 1.— Proportion of transients by year of *Sigmodon hispidus* from Chesapeake, Virginia. Asterisks (*) denote significantly greater proportions of transients than residents in a year, ® denotes significantly greater proportions of residents. The overall proportion of transients was significantly greater than that of residents, 54.41%.

Proportions of reproductive maturity, sex, and residency status groups (Fig. 2) were significantly associated with season (χ^2=128.1159, df=21, P=2.273x10^{-17}). When seasonal and whole data set comparisons of the proportions for each group were evaluated with the Nemenyi test (Table 4), the proportion of adult male transients in spring was different from all groups except adult female transients. Adult female residents in summer were different from all other resident groups. Adult male residents and adult female transients were different from juvenile transients in autumn. All juvenile groups were different from all adult groups during winter and overall.



	Resident				Transient			
	Female		Male		Female		Male	
	Adult	Juvenile	Adult	Juvenile	Adult	Juvenile	Adult	Juvenile
■ Spring*	9.92%	3.31%	11.57%	1.65%	20.66%	5.79%	33.88%	13.22%
■ Summer*	14.57%	6.30%	14.17%	6.69%	16.14%	9.84%	17.32%	14.96%
■ Autumn	14.19%	12.50%	19.07%	7.42%	17.16%	6.14%	14.83%	8.69%
■ Winter*	20.00%	2.67%	21.00%	1.33%	21.67%	5.33%	27.00%	1.00%

FIG. 2.—Group proportions by season for *Sigmodon hispidus* from Chesapeake, Virginia. Groups are defined by maturity, sex, and residency status. Asterisks (*) denote significantly greater proportions of transients than residents. The proportion of adults in each season was greater than that of juveniles. The proportion of adults was similar across all seasons (Table 3).

TABLE 4.—Results of Nemenyi tests for *Sigmodon hispidus* groups from Chesapeake, Virginia. Abbreviations for each group are based on reproductive maturity (juvenile, adult), sex (male, female), and residency status (resident, transient). Different lower-case letters denote significant differences in Nemenyi tests. Percentage (%) is the proportion of transients. Mean body masses (g) are listed, although their distribution was not normal. An asterisk (*) denotes a significant proportion of transients in a season. Sample sizes for each season are listed in Table 5.

	JFR	JFT	JMR	JMT	AFR	AFT	AMR	AMT
Spring*	*ab*	*ab*	*a*	*bc*	*abc*	*bcd*	*bc*	*d*
%	3.31	5.79	1.65	13.22	9.92	20.66	11.57	33.88
mass	40.0	30.0	15.5	26.3	97.1	113.0	116.9	114.0
Summer*	*a*	*abc*	*ab*	*bcd*	*d*	*cd*	*abc*	*cd*
%	6.30	9.84	6.69	14.96	26.38	16.14	14.17	17.32
mass	31.4	28.9	30.2	27.9	98.5	101.2	103.7	91.0
Autumn	*bcd*	*a*	*ab*	*abcd*	*bcd*	*cd*	*d*	*bcd*
%	12.50	6.14	7.42	8.69	14.19	17.10	19.07	14.83
mass	33.6	32.4	33.6	32.0	88.2	91.9	88.7	94.4
Winter*	*a*	*a*	*a*	*a*	*b*	*b*	*b*	*b*
%	2.66	5.30	1.33	1.00	19.93	21.59	20.93	26.91
mass	39.1	39.1	44.5	36.7	81.1	86.9	89.9	91.1
Total*	*a*	*a*	*a*	*a*	*b*	*b*	*b*	*b*
%	7.58	6.71	5.05	8.53	17.94	18.47	17.68	20.56
mass	34.0	32.4	32.7	29.6	88.5	94.6	93.7	96.0

The proportion of breeding adults, as evidenced by their reproductive condition, was evaluated for independence from season, residency status, and sex. The proportion of breeding adults was significantly associated with season (χ^2=113.0275, df=3, P=2.447x10^{-24}) and sex (χ^2=11.0486, df=1, P=8.875x10^{-4}), but not residency status. Residency status of breeding animals was not associated with season. Reproductive animals formed a significantly smaller proportion of the population in summer, autumn, and winter, which had the smallest proportion of all, 9.31%. The greatest proportion of breeding adults, 47.93% in spring, was not significantly different from non-reproductive animals.

Breeding animals were male-biased overall (χ^2=12.0370, df=1, P=5.00x10^{-4}) with a 1.45 sex ratio. Seasonal sex biases (Table 5) were detected for breeding adults, breeding residents, and breeding transients. Seasonal sex ratios were male-biased in spring, summer, and autumn, whereas winter was female-biased overall and for the transient group. The mean ranked body masses of breeding residents and transients, examined with the K-W test, were not different.

Overall, the sex ratios in Virginia cotton rats did not differ from unity (Table 5), but seasonal sex biases were detected for the spring (χ^2=5.165, df=1, P=0.023) and for some groups within each season. The overall sex ratio in spring was male-biased at 1.52. Fifteen seasonal sex-biases were identified for groups, 8 of which were female-biased. The sex ratios of groups in winter were female-biased, whereas spring groups were male-biased.

TABLE 5.—Sex ratios and biases of *Sigmodon hispidus* by season and group from Chesapeake, Virginia. An asterisk (*) indicates a significant proportion of transients within a season. NS indicates the result was not significant. Adults were ≥ 50 g and breeding refers to scrotal testes in males and the presence of 2 of 3 reproductive cues in females. Only significant results are presented within seasons; groups not presented were not significant

Season	**Group**	**Ratio (M:F)**	**Sex Bias**	**P Value**	χ^2	**Sample Size**
Overall			*No Bias*			1148
	Adults	NS	No Bias			828
	Juveniles	NS	No Bias			323
	Residents	NS	No Bias			525
	Transients	NS	No Bias			626
	Adult Residents	NS	No Bias			379
	Adult Transients	NS	No Bias			449
	Juvenile Residents	NS	No Bias			146
	Juvenile Transients	NS	No Bias			177
	Breeding Adults	1.45	Male	0.0005	12.037	351
	Breeding Residents	1.50	Male	0.016	5.8000	145
	Breeding Transients	1.42	Male	0.012	6.2913	206
Spring *		1.52	*Male*	0.023	5.165	121
	Transients	1.78	Male	0.008	7.022	89
	Adult Transients	1.64	Male	0.049	3.879	66

Table 5 Continued

Season	**Group**	**Ratio (M:F)**	**Sex Bias**	**P Value**	**χ^2**	**Sample Size**
	Adult Transients	1.64	Male	0.049	3.879	66
	Breeding Adults	2.87	Male	0.0002	13.517	58
	Breeding Transients	3.67	Male	0.0002	13.714	42
*Summer **			*No Bias*			254
	Adult	0.54	Female	0.002	9.330	103
	Residents	0.64	Female	0.010	6.618	136
	Adult Residents	0.54	Female	0.002	9.330	103
	Breeding Adults	1.64	Male	0.0078	7.067	119
	Breeding Transients	1.68	Male	0.0378	4.313	67
Autumn			*No Bias*			472
	Juvenile Residents	0.59	Female	0.013	6.128	94
	Breeding Residents	1.68	Male	0.0378	4.3134	67
*Winter **			*No Bias*			301
	Juvenile	0.29	Female	0.0023	9.323	31
	Juvenile Transients	0.19	Female	0.0029	8.895	19
	Breeding Adults	0.33	Female	0.0082	7.000	28
	Breeding Transients	0.29	Female	0.0184	5.556	18

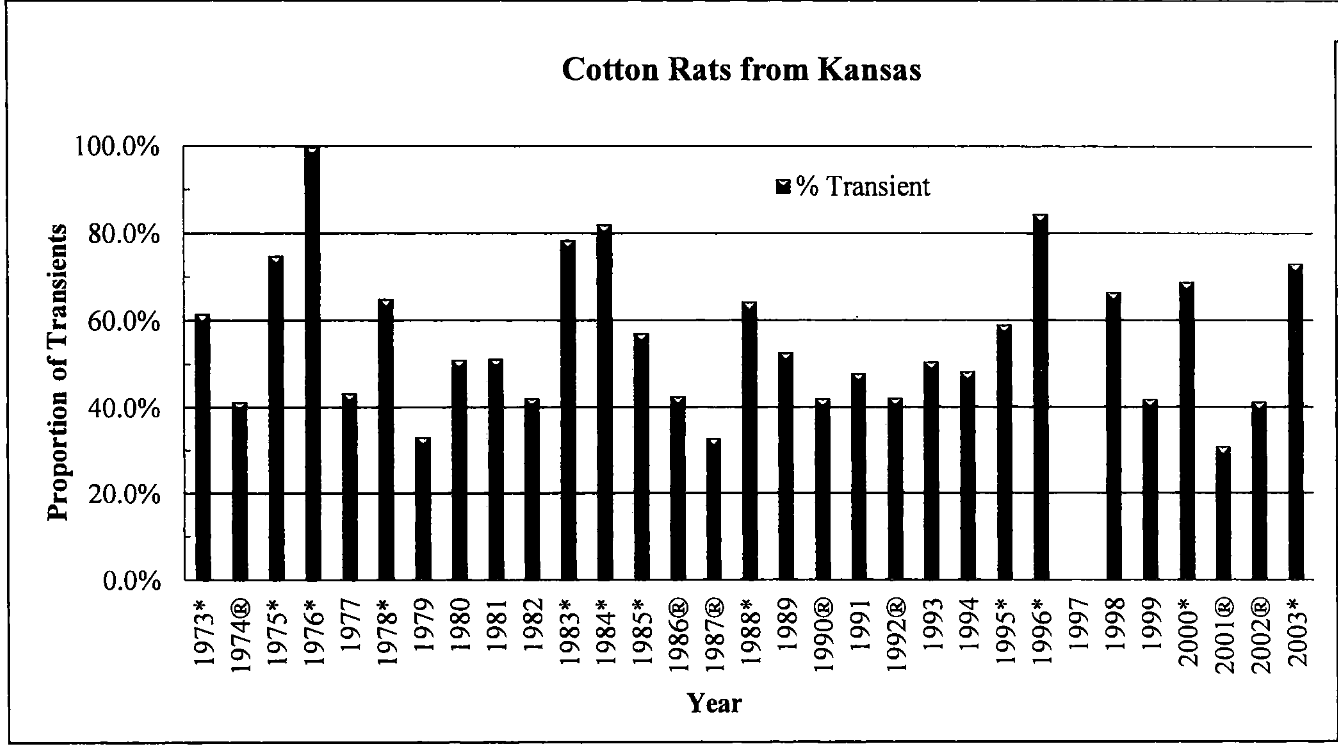
Sigmodon hispidus from Kansas.—The tests of independence of transience with season, sex, and reproductive maturity revealed transiency in Kansas cotton rats was significantly associated with season (χ^2=72.0006, df=3, P=1.59x10^{-15}) and sex (χ^2=4.5530, df=1, P=0.0329), but not reproductive maturity. The proportion of transients was highest in summer, 62.56%, and the Nemenyi test (Table 6) separated summer from all other seasons. The two-sample Z-test for each season indicated that summer was the only season with a significantly greater proportion of transients, whereas autumn had a significantly greater proportion of residents, 54.07%. The overall proportion of transients for all trapping sessions, 51.0%, was not significant. The test of independence for proportion of transients and year of study revealed a significant association (χ^2=224.6314, df=30, P=1.1088x10^{-31}). The proportion of transients was significantly greater than the proportion of residents during 12 years, whereas the proportion of residents was significantly greater during 7 years (Fig. 3). The correlation analysis of proportion of transients and density revealed no association.

For an analysis of the proportion of transients by season for 6 consecutive years, I chose 1981 to 1986 (Fig. 4) due to the consistency of captures for each season; other years had more sporadic or uneven captures from season to season, with most transient captures occurring only in 1 season. The proportion of transients for 1981 to 1986, as graphed in Figure 4, illustrates the variability in seasonal captures; in some seasons transients comprised 100% of the initial captures, but in other seasons no new transients were tagged.

Reproductive maturity of cotton rats was associated with season when tested for independence (χ^2=70.3365, df=3, P=3.616x10^{-15}). Two-sample Z-tests revealed that the proportion of adults was significantly greater than that of juveniles during each season and for the entire data set. The post-hoc Nemenyi test revealed that the proportions of adults were similar during spring, summer, and autumn, and that winter, with the largest proportion of adults, 89.67%, was similar only to spring (Table 6).

TABLE 6.—Results of Nemenyi tests of transients and adults for *Sigmodon hispidus* from Kansas. The proportion of each group in each season is listed above the Nemenyi similarities. Different letters denote significant differences among seasonal proportions. Transients include both sexes and both reproductive maturity groups, and adults include both sexes and both residency status groups. An asterisk (*) denotes a significant proportion of transients in a season.

	Spring	**Summer***	**Autumn**	**Winter**
Proportion of Transients	51.77%	62.56%	45.92%	48.46%
Nemenyi Similarities	*a*	*b*	*a*	*a*
Proportion of Adults	61.50%	53.13%	56.92%	75.77%
Nemenyi Similarities	*ab*	*a*	*a*	*b*
Sample Size	226	975	2073	454



Year	n	Year	n
1973	138	1989	161
1974	162	1990	178
1975	12	1991	146
1976	7	1992	317
1977	53	1993	219
1978	263	1994	153
1979	9	1995	299
1980	47	1996	26
1981	105	1997	1
1982	45	1998	6
1983	42	1999	81
1984	28	2000	151
1985	91	2001	159
1986	96	2002	342
1987	182	2003	108
1988	101		

FIG. 3.—Proportion of transients by year of *Sigmodon hispidus* from Kansas. Years with an asterisk (*) denote significantly greater proportions of transients than residents, ® denotes significantly greater proportions of residents. Annual totals of initial captures (n) are listed in the table. The overall proportion of transients, 51.0%, was not significantly greater than that of residents.

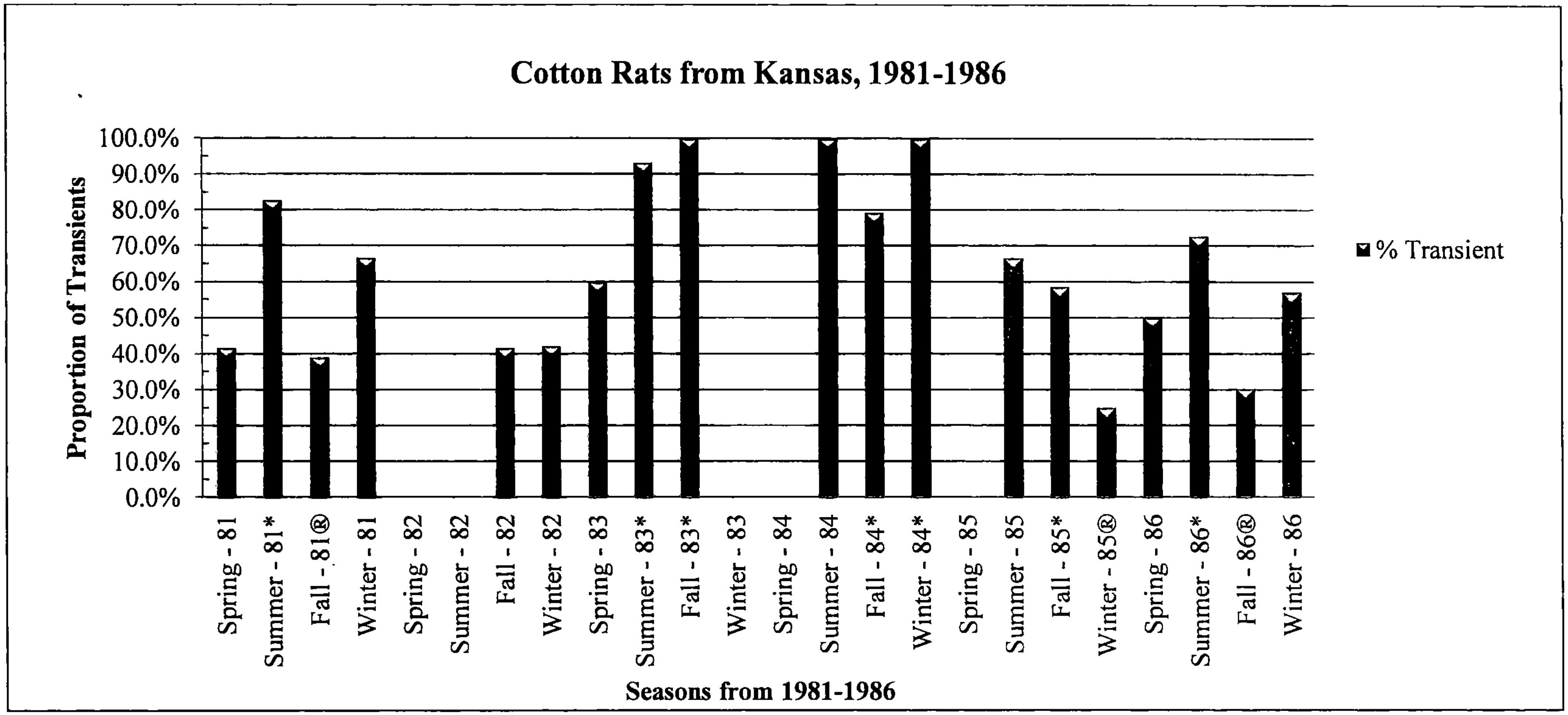
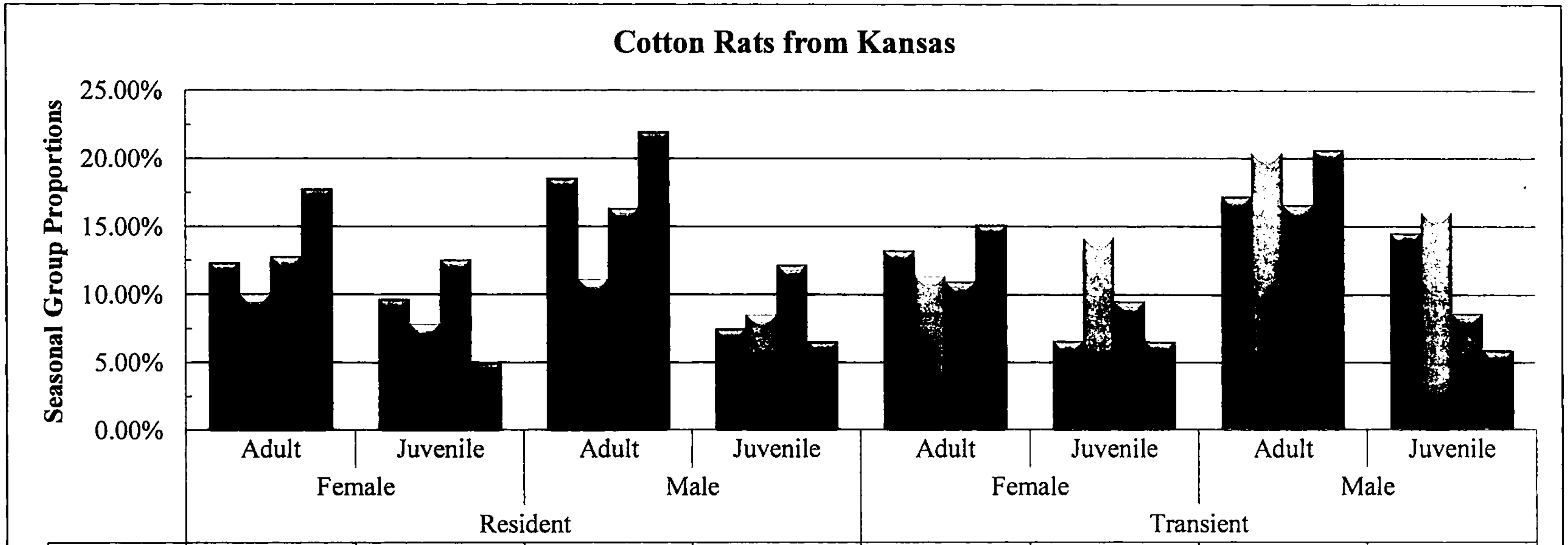


FIG. 4.—Proportion of transients by season (1981-1986) for *Sigmodon hispidus* from Kansas. Seasons with an asterisk (*) denote those with significantly greater proportions of transients, ® denotes significantly greater proportions of residents. Seasons with 0% transients had zero newly tagged animals.

All reproductive maturity, sex, and residency status groups were tested for independence from season (Fig. 5). An association between groups and season was supported (χ^2=726.1394, df=21, P=3.9617x10^{-140}). The Nemenyi tests (Table 7) revealed that proportions of adult males were different from those of juvenile female transients and juvenile male residents during the spring. The group proportions were highly variable during the summer and resulted in the most separations of groups for any season. During the summer, the proportion of adult male transients was different from all resident groups, juvenile transients were separated from juvenile residents, and all resident groups were similar. Adult male groups in autumn were different from adult female and juvenile transients. All adult groups in winter were different from all juvenile groups. Overall, adult male transients and residents were similar, whereas adult male residents were different from all juvenile groups; all other groups were similar.



	Resident				Transient			
	Female		Male		Female		Male	
	Adult	Juvenile	Adult	Juvenile	Adult	Juvenile	Adult	Juvenile
■ Spring	12.39%	9.73%	18.58%	7.52%	13.27%	6.64%	17.26%	14.60%
■ Summer*	10.05%	7.90%	11.18%	8.62%	11.38%	14.26%	20.51%	16.10%
■ Autumn	12.88%	12.59%	16.40%	12.20%	11.00%	9.60%	16.64%	8.68%
■ Winter	17.84%	5.07%	22.03%	6.61%	15.20%	6.61%	20.70%	5.95%

FIG. 5.—Group proportions by season for *Sigmodon hispidus* from Kansas. Groups are defined by maturity, sex, and residency status. Asterisks (*) denote significantly greater proportions of transients than residents. The proportion of adults in each season was greater than that of juveniles. The proportion of adults was similar across all seasons (Table 6).

TABLE 7.—Results of Nemenyi tests for *Sigmodon hispidus* groups from Kansas. Abbreviations for each group are based on reproductive maturity (juvenile, adult), sex (male, female), and residency status (resident, transient). Different lower-case letters denote significant differences in the Nemenyi tests. Percentage (%) is the proportion of transients. Mean body masses (g) are listed, although their distribution was not normal. An asterisk (*) denotes a significant proportion of transients in a season. Sample sizes for each season are listed in Table 8.

	JFR	JFT	JMR	JMT	AFR	AFT	AMR	AMT
Spring	*ab*	*a*	*a*	*ab*	*ab*	*ab*	*b*	*b*
%	9.73	6.64	7.52	14.60	12.39	13.27	18.58	17.26
mass	32.9	34.2	35.0	34.4	81.6	89.2	81.9	84.5
Summer*	*a*	*bcd*	*a*	*bcd*	*ab*	*abc*	*abc*	*cd*
%	7.90	14.26	8.62	16.10	10.05	11.38	11.18	20.51
mass	28.8	26.3	24.5	33.9	100.5	103.6	119.7	107.7
Autumn	*ab*	*a*	*ab*	*a*	*ab*	*a*	*b*	*b*
%	12.59	9.60	12.20	8.68	12.88	11.00	16.40	16.64
mass	31.8	31.5	28.5	33.3	94.5	89.7	112.2	91.2
Winter	*a*	*a*	*a*	*a*	*b*	*b*	*b*	*b*
%	5.07	6.61	6.61	5.95	17.84	15.20	22.03	20.70
mass	36.3	40.1	38.4	38.2	73.9	71.7	80.9	79.3
Total	*a*	*a*	*a*	*a*	*ab*	*ab*	*bc*	*bc*
%	10.27	10.27	10.30	10.65	12.71	12.71	15.85	18.19
mass	32.7	33.4	33.4	34.2	86.4	87.6	90.0	87.1

The proportion of breeding adults was evaluated for independence from season, residency status, and sex. The proportions of breeding adults were significantly associated with season (χ^2=300.3238, df=3, P=8.466x10^{-65}), residency status (χ^2=26.9821, df=1, P=2.054x10^{-7}), and sex (χ^2=29.0031, df=1, P=7.226x10^{-8}). The residency status of breeding adults was independent of season. Reproductively active animals formed a significantly smaller proportion of the population than non-breeding animals in each season and for the entire data set. The proportion of breeding adults in the spring was the highest, 37.61%, whereas the proportion in winter was the lowest, 1.76%. Overall, breeding animals were significantly transient, 59.33%, and male-biased with a sex ratio of 1.75. Seasonal sex biases (Table 8) were detected for breeding adults, breeding residents, and breeding transients. The sex ratios of breeding adults during the spring and summer were male-biased, whereas the sex ratios in autumn and winter did not differ from unity. Breeding residents were male-biased during spring and summer, but female-biased in autumn. The sex ratios of breeding residents did not differ from unity for winter or overall. Breeding transients were male-biased for spring, summer, autumn, and overall. The sex ratio of breeding transients did not differ from unity during the winter.

The sex ratios of hispid cotton rats from Kansas (Table 8) at initial capture differed from unity with a male-biased ratio of 1.22 (χ^2=37.1202, df=1, P=1.11x10^{-9}) overall, and male biases in each season. The seasonal male-biased ratios ranged from 1.17 in the autumn to 1.38 in the spring. In addition to the overall and seasonal biases, 13 biased sex ratios were identified for other groups.

TABLE 8.—Sex ratios of *Sigmodon hispidus* by season and group from Kansas. An asterisk (*) indicates a significant proportion of transients for a season. NS indicates the result was not significant. Adults were ≥ 50 g and breeding refers to scrotal testes in males and the presence of 2 of 3 reproductive cues in females. Only significant results are presented within seasons; groups not presented were not significant. Most sex ratios were male-biased, but the sex ratio of breeding residents in autumn was female-biased.

Season	**Group**	**Ratio (M:F)**	**P Value**	χ^2	**Sample Size**
Overall		1.22	1.11×10^{-9}	37.1202	3728
	Adults	1.39	2.10×10^{-14}	58.4360	2181
	Juveniles	NS			1547
	Residents	1.14	5.80×10^{-3}	7.6004	1832
	Transients	1.31	5.43×10^{-9}	34.0274	1896
	Adult Residents	1.25	3.00×10^{-3}	12.8535	1065
	Adult Transients	1.55	7.00×10^{-13}	51.6129	1116
	Juvenile Residents	NS			767
	Juvenile Transients	NS			780
	Breeding Adults	1.75	5.39×10^{-14}	56.5813	750
	Breeding Residents	NS			305
	Breeding Transients	2.27	2.38×10^{-16}	67.2562	445
Spring		1.38	1.70×10^{-2}	5.7345	226
	Transients	1.60	1.26×10^{-2}	6.2308	117

Table 8 Continued

Season	**Group**	**Ratio (M:F)**	**P Value**	**χ^2**	**Sample Size**
	Juvenile Transients	2.20	9.00×10^{-3}	6.750	48
	Breeding Adults	2.70	2.33×10^{-5}	17.8941	86
	Breeding Residents	3.89	8.87×10^{-5}	15.3636	44
	Breeding Transients	1.93	4.23×10^{-2}	4.1219	41
*Summer**		1.29	6.25×10^{-5}	16.0256	975
	Adult	1.48	1.11×10^{-5}	19.3050	518
	Transient	1.43	1.41×10^{-5}	18.8616	607
	Adult Transient	1.80	4.49×10^{-7}	25.4695	311
	Breeding Adults	2.58	4.10×10^{-16}	66.1765	340
	Breeding Residents	1.63	6.35×10^{-3}	7.4496	129
	Breeding Transients	3.59	2.60×10^{-16}	67.1137	211
Autumn		1.17	3.00×10^{-4}	12.8167	2073
	Adult	1.38	3.18×10^{-8}	30.5932	1180
	Transient	1.23	1.40×10^{-4}	10.0882	952
	Adult Resident	1.27	3.00×10^{-3}	8.7792	607
	Adult Transient	1.51	1.02×10^{-6}	23.8901	573
	Breeding Residents	0.67	2.65×10^{-2}	4.9213	127
	Breeding Transients	1.60	1.41×10^{-3}	10.1895	190
Winter		1.24	2.43×10^{-2}	5.0749	454
	Adult	1.29	1.76×10^{-2}	5.6279	344

The mean ranked body masses for breeding residents and transients examined with a K-W test were significantly different (K=17.883, df=749, P=2.64x10^{-5}), with residents having a greater mean of ranked body masses than transients. The mean ranked body masses of population groups were different (K=2693.112, df=7, P<0.001), with adult male residents significantly different from all adult female groups.

Comparisons of Sigmodon hispidus from Virginia and Kansas.—Tests of independence of geographic location with transience revealed a significant association (χ^2=4.4618, df=2, P=0.035). The proportions of Virginia and Kansas cotton rats were compared using two-sample Z-tests for the factors of reproductive maturity and residency status for each season and for the complete data sets. The 2 populations were different for proportions of adults, sex ratios, and residency status. The proportion of juveniles in winter was similar for each population.

Specifically, the Virginia cotton rat population had significantly greater proportions of transients during spring, autumn, winter, and overall, whereas the Kansas population had a greater proportion of transients, 62.26%, in the summer. The Kansas population was dominated by residents in spring, autumn, winter, and overall, whereas Virginia populations had a significantly greater proportion of residents during the summer. Virginia cotton rats had a greater proportion of adults than the Kansas population for every season and overall, whereas Kansas cotton rats had a significantly greater proportion of juveniles for every season and overall. An analysis of the overall proportions of population groups revealed significant differences across all groups, with the Virginia and Kansas populations separated on the basis of maturity. The mean ranked body mass of breeding animals was not different between Kansas and Virginia.

Oryzomys palustris from Virginia.—When residency status was tested for independence from the factors of season, sex, and reproductive maturity, a significant association was seen between residency status and season (χ^2=7.9316, df=3, P=0.004), but not sex or reproductive maturity. A comparison of the proportion of transients and residents within each season with two-sample Z-tests revealed significantly greater proportions of transients in the summer and overall. The Nemenyi test (Table 9) indicated that the proportion of summer transients was similar to that of spring, but different from proportions in autumn and winter. Transients constituted 83.33% of initial captures in summer and 54.49% overall. Tests of independence revealed that residency status was independent of the year of study (Fig. 6). Correlations analysis found no association between the proportion of transients and population density.

When reproductive maturity and season were tested for independence no association was found; however, two-sample Z-tests revealed significant differences in the proportions of adults to juveniles (Table 9) during spring, autumn, winter, and overall. The proportion of adults was significant only during the spring, 66.67%, whereas the proportions of juveniles were significant in autumn, winter, and overall.

The groups (Fig. 7) of marsh rice rat were significantly associated with season (χ^2=33.151, df=21, P=0.0446). The results of the Nemenyi test (Table 10) revealed that proportions for all groups were similar in spring, whereas juvenile female residents in summer were different from juvenile female transients and adult male transients. The summer proportions of juvenile female transients were also different from adult female residents. During the autumn, juvenile male residents were different from adult female transients. Adult female residents in winter were similar to adult female transients, but separate from all other groups. Overall, juvenile female transients were separated from adult female groups, and adult female residents were separated from adult male groups.

TABLE 9.— Results of Nemenyi tests of transients and adults for *Oryzomys palustris* from Chesapeake, Virginia. The proportion of each group in each season is listed above the Nemenyi similarities. Different letters denote significant differences among seasonal proportions. Transients include both sexes and both reproductive maturity groups, and adults include both sexes and both residency status groups. An asterisk (*) denotes a significant proportion of transients in a season.

	Spring	**Summer***	**Autumn**	**Winter**
Proportion of Transients	57.14%	83.33%	45.90%	53.57%
Nemenyi Similarities	*ab*	*b*	*a*	*a*
Proportion of Adults	66.67%	44.44%	36.67%	35.71%
Nemenyi Similarities	*a*	*b*	*b*	*b*
Sample Size	21	18	61	56

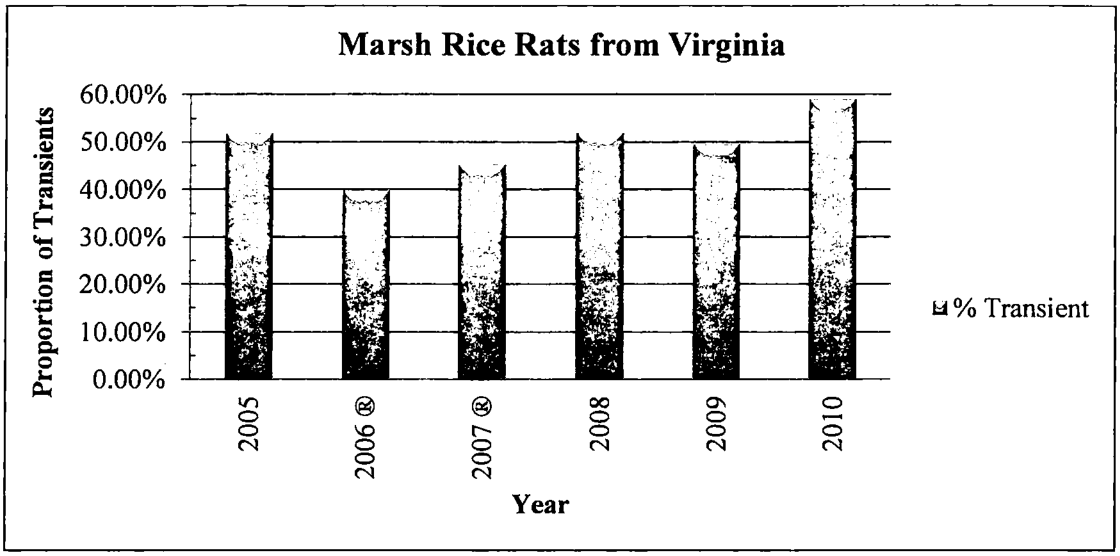
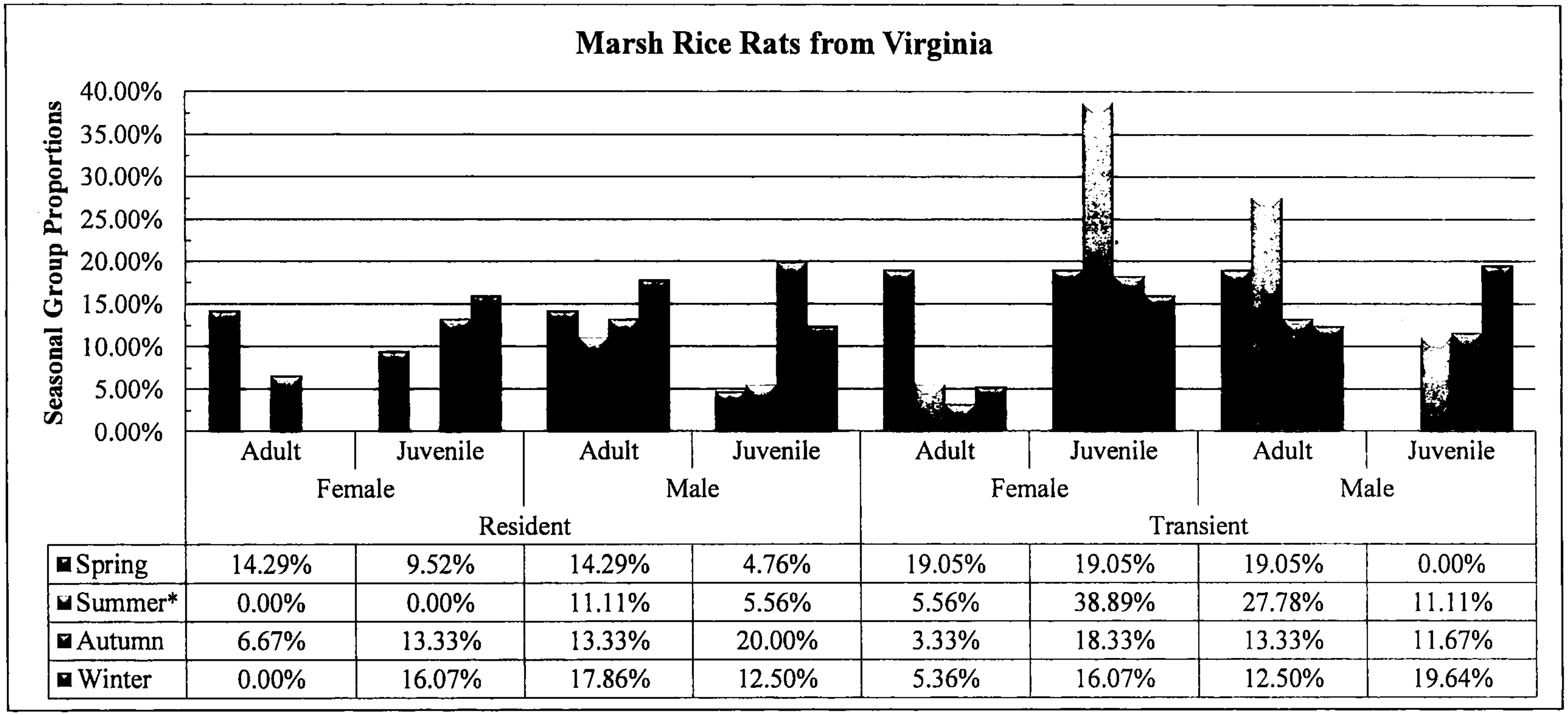


FIG. 6.— Proportion of transients by year for *Oryzomys palustris* from Chesapeake, Virginia. ® denotes significantly greater proportions of residents than transients. Small sample size (n=22) resulted in no significant difference in proportion even at 59.09% transiency in 2010. Overall, the proportion of transients, 54.49%, was significantly greater than that of residents.

The proportion of marsh rice rats in breeding condition was evaluated for independence from season, residency status, and sex. Reproductive condition was independent of residency status, but significantly associated with season (χ^2=18.9471, df=21, P=0.00028) and sex (χ^2=11.5851, df=1, P=6.65x10^{-4}). The residency status of breeding adults was tested for independence from season, and no association was found. The proportion of breeding and non-breeding rice rats was equal during spring and summer, whereas in autumn and winter significantly fewer animals were found in breeding condition. The Nemenyi test results revealed that the proportions of breeding adults during the spring, summer, and autumn were similar but separate from the winter, 10.71%. Breeding animals were male-biased overall with a ratio of 4.88. Seasonal patterns of sex bias (Table 11) were noted for breeding animals in general and for breeding transients. Animals in reproductive condition were male-biased in summer and autumn. Breeding transients were male-biased in summer and overall, whereas breeding residents did not differ from unity during any season but were male-biased overall. The body mass of breeding residents and transients was similar when examined with a one-way ANOVA.

The sex of marsh rice rats was independent of season and did not differ from unity for any season; however, sex ratios (Table 11) were consistently male for groups overall and for adults during the summer, autumn, and winter.



	Resident				Transient			
	Female		Male		Female		Male	
	Adult	Juvenile	Adult	Juvenile	Adult	Juvenile	Adult	Juvenile
■ Spring	14.29%	9.52%	14.29%	4.76%	19.05%	19.05%	19.05%	0.00%
■ Summer*	0.00%	0.00%	11.11%	5.56%	5.56%	38.89%	27.78%	11.11%
■ Autumn	6.67%	13.33%	13.33%	20.00%	3.33%	18.33%	13.33%	11.67%
■ Winter	0.00%	16.07%	17.86%	12.50%	5.36%	16.07%	12.50%	19.64%

FIG. 7.—Group proportions by season for *Oryzomys palustris* from Chesapeake, Virginia. Groups are defined by maturity, sex, and residency status. Asterisks (*) denote significantly greater proportions of transients than residents. Only in spring was the proportion of adults greater than that of juveniles. The proportion of adults was significantly less than that of juveniles, during summer, autumn, and winter (Table 11). Zeroes denote no newly tagged rice rats were captured during the season.

TABLE 10.—Results of Nemenyi tests for *Oryzomys palustris* groups from Chesapeake, Virginia. Abbreviations for each group are based on reproductive maturity (juvenile, adult), sex (male, female), and residency status (resident, transient). Different lower-case letters denote significant differences in the Nemenyi tests. Percentage (%) is the proportion of transients. Mean body masses (g) are listed. An asterisk (*) denotes a significant proportion of transients within a season. Sample sizes for each season are listed in Table 11.

	JFR	**JFT**	**JMR**	**JMT**	**AFR**	**AFT**	**AMR**	**AMT**
Spring	*a*	*a*	*a*	*a*	*a*	*a*	*a*	*a*
%	9.52	19.05	4.76	0.00	14.29	19.05	14.29	19.05
mass	38.0	37.3	45.0	-	71.7	64.5	66.7	65.0
Summer*	*a*	*b*	*abc*	*abc*	*ac*	*abc*	*abc*	*bc*
%	0.00	38.89	5.56	11.11	0.00	5.56	11.11	27.78
mass	-	28.0	30.0	34.0	-	56.0	77.0	77.0
Autumn	*ab*	*ab*	*a*	*ab*	*ab*	*b*	*ab*	*ab*
%	13.33	18.33	60.00	11.67	6.67	3.33	13.33	13.33
mass	37.0	31.4	36.0	39.6	55.5	55.0	60.0	70.0
Winter	*a*	*a*	*a*	*a*	*b*	*ab*	*a*	*a*
%	16.07	16.07	43.75	19.64	0.00	5.36	17.86	12.50
mass	35.6	35.8	42.4	39.4	-	60.0	62.6	59.3
Total	*abc*	*bc*	*abc*	*abc*	*b*	*bc*	*ab*	*ab*
%	12.26	20.00	13.55	12.90	4.52	6.45	14.84	15.48
mass	36.4	32.7	38.3	38.9	62.4	60.4	63.5	67.5

TABLE 11.—Sex ratios of *Oryzomys palustris* by season and group from Chesapeake, Virginia. An asterisk (*) indicates a significant proportion of transients for a season. NS indicates the result was not significant. Adults were ≥ 50 g and breeding refers to scrotal testes in males and the presence of 2 of 3 reproductive cues in females. Only significant results are presented within seasons; groups not presented were not significant. Significant sex ratios for results were all male-biased.

Season	Group	Ratio (M:F)	P Value	χ^2	Sample Size
Overall		NS			156
	Adults	2.76	1.77×10^{-4}	14.0625	64
	Juveniles	NS			91
	Residents	1.69	3.14×10^{-2}	4.6286	70
	Transients	NS			85
	Adult Residents	3.29	3.49×10^{-3}	8.5333	30
	Adult Transients	2.40	1.64×10^{-2}	5.7647	34
	Juvenile Residents	NS			40
	Juvenile Transients	NS			51
	Breeding Adults	4.88	6.13×10^{-6}	20.4468	47
	Breeding Residents	3.60	6.71×10^{-3}	7.3478	23
	Breeding Transients	7.00	2.39×10^{-4}	13.5000	24
Spring		NS			21
*Summer**		NS			18
	Adult	7.00	3.39×10^{-2}	4.5000	10

Table 11 Continued

Season	**Group**	**Ratio (M:F)**	**P Value**	χ^2	**Sample Size**
	Breeding Adults	No ♀	2.00×10^{-3}	9.000	9
Autumn		NS			60
	Adult	2.70	3.30×10^{-2}	4.5454	22
	Breeding Adults	6.00	1.06×10^{-3}	10.714	21
	Breeding Transients	No ♀	2.53×10^{-2}	10.000	10
Winter		NS			56
	Adult	5.67	1.75×10^{-3}	9.8000	20
	Adult Resident	No ♀	1.57×10^{-3}	10.000	10

Microtus pennsylvanicus from Virginia.—Residency status was independent from sex and reproductive maturity, but significantly associated with season (χ^2=10.9129, df=3, P=0.0122). The Nemenyi test results (Table 12) for proportion of transients among seasons identified all seasons as being similar. The two-sample Z-test for the proportions of residents and transients during each season detected significant differences during spring, summer, winter, and overall. Spring was the only season with significantly greater proportions of transients, 55.90%, whereas the summer, winter, and overall had significantly greater proportions of residents. The proportions of residents and transients in autumn were similar. The overall proportion of transients was 47.30%. Residency status and year of study (Fig. 8), when examined for independence, were significantly associated (χ^2=15.588, df=7, P=0.029). The year 2006 was significant for a greater proportion of residents, 59.82%, whereas 2003 and 2005 had significantly greater proportions of transients. Correlation analysis revealed no relationship between density and proportion of transients.

Tests of independence for reproductive maturity and season revealed a significant association (χ^2=21.7809, df=3, P=7.24x10^{-5}). Results of the Nemenyi test (Table 12) identified the summer as different from all other seasons. The two-sample Z-test revealed that all seasons had significantly greater proportions of adults than juveniles. The proportion of adults in summer was the greatest, 95.60%, and lowest, 82.50%, in autumn. The overall proportion of adults, 86.30%, was significant.

TABLE 12.—Results of Nemenyi tests of transients and adults for *Microtus pennsylvanicus* from Chesapeake, Virginia. The proportion of each group in each season is listed above the Nemenyi similarities. Different letters denote significant differences among seasonal proportions. Transients include both sexes and both reproductive maturity groups, and adults include both sexes and both residency status groups. An asterisk (*) denotes a significant proportion of transients in a season.

	Spring*	**Summer**	**Autumn**	**Winter**
Proportion of Transients	55.90%	41.70%	49.30%	43.90%
Nemenyi Similarities	*a*	*a*	*a*	*a*
Proportion of Adults	82.60%	95.60%	82.50%	86.60%
Nemenyi Similarities	*a*	*b*	*a*	*a*
Sample Size	201	206	342	373

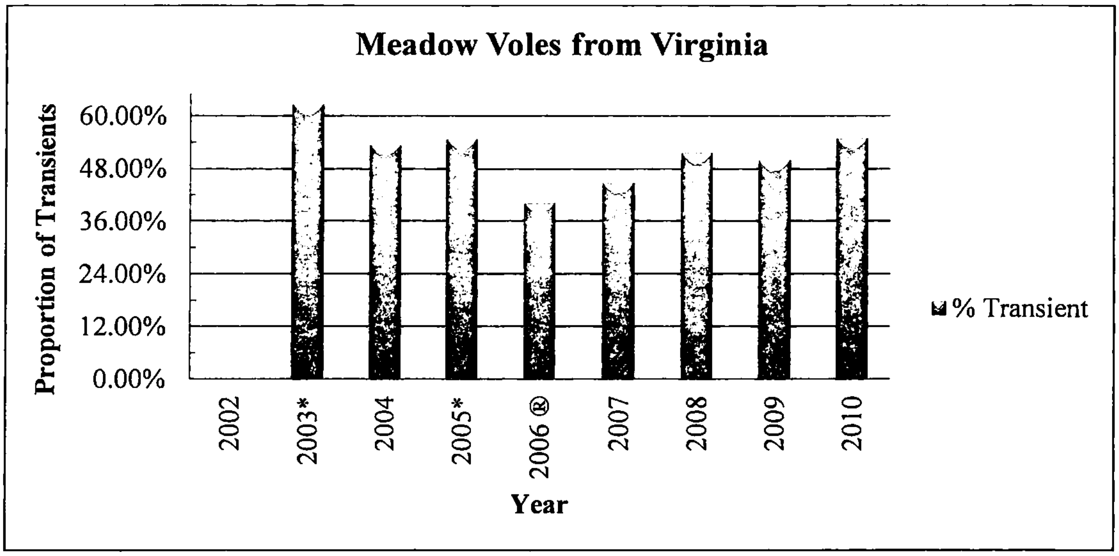
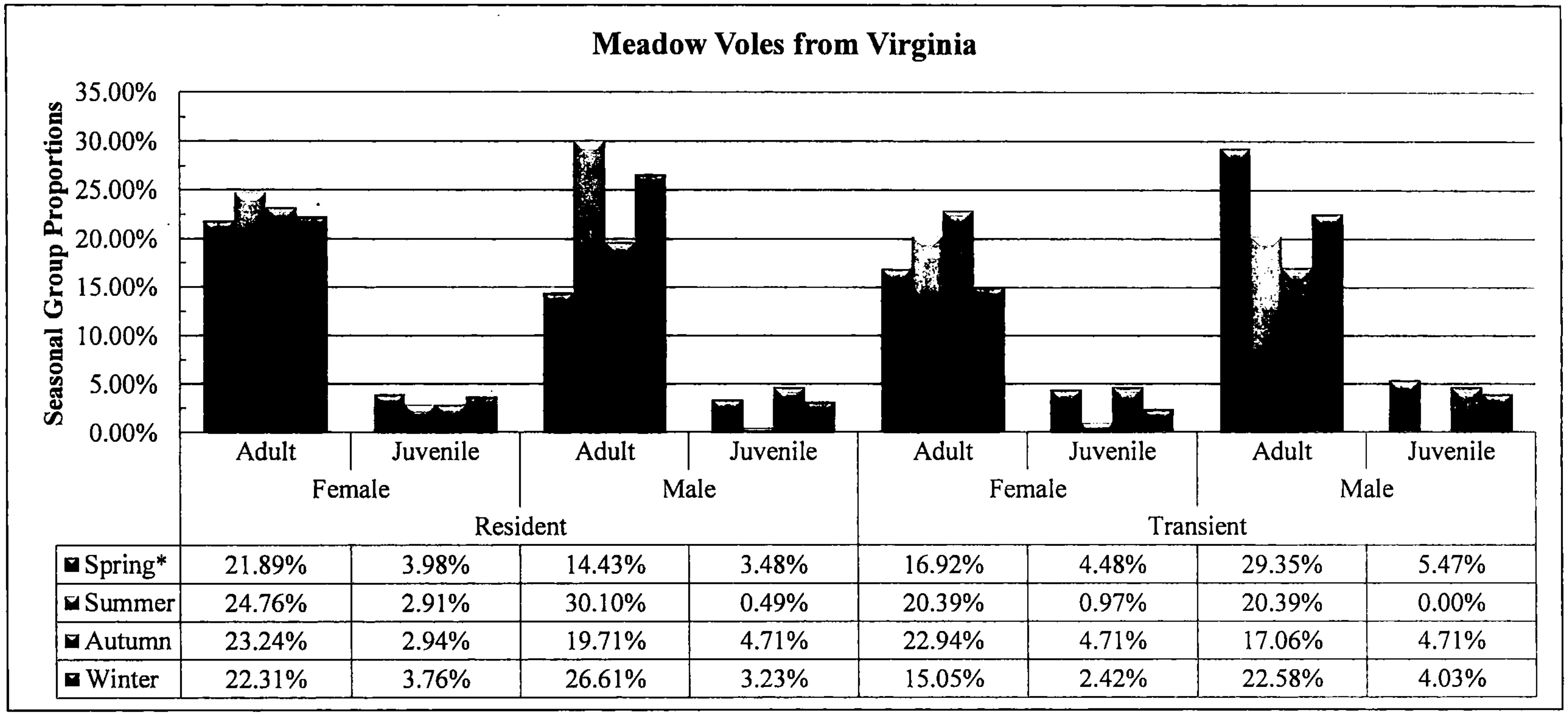


FIG. 8.—Proportion of transients by year for *Microtus pennsylvanicus* from Chesapeake, Virginia. Years with an asterisk (*) denote significantly greater proportions of transients, ® denotes significantly greater proportions of residents. Trapping began in late 2002, but no meadow voles were captured. The overall proportion of transients, 47.30%, was not significantly greater than that of residents.

The reproductive maturity, sex, and residency status groups (Fig. 9) were significantly associated with season (χ^2=56.1522, df=21, P=0.0006). The results of the Nemenyi test (Table 13) revealed differences in the proportions of groups for every season and overall. During the spring, all juvenile groups were different from adult female groups and adult male residents. The proportion of adult male residents in spring was also different from adult male transients. The proportions of all adult groups were similar and separate from all juvenile groups in summer, but juvenile female residents were different from juvenile male transients. The proportions of all adult groups were different from all juvenile groups, but were similar to each other during autumn. In the winter, proportions of juveniles were different from adults, and adult male residents were different from adult female transients. Overall, the proportions of adult and juvenile groups were significantly different from each other, but sex and residency status were similar.

The proportions of meadow voles in breeding condition were independent from season, residency status, and sex. Residency status of breeding adults was also independent of season. Seasonal sex biases were identified (Table 14) for breeding adults, residents, and transients, with breeding adults being male-biased during the summer and winter, breeding residents being female-biased during the spring but male-biased during summer, and breeding transients being male-biased in summer, winter, and overall. The mean ranked body masses of breeding residents and transients were not different when analyzed with the non-parametric K-W test.

When tested for independence, sex was significantly associated with season (χ^2=7.9220, df=3, P=0.0477). The overall sex ratio, and the ratios during spring, summer, and autumn, did not differ from unity. The sex ratio in winter was male-biased, 1.29 (χ^2=5.9223, df=1, P=0.015). Overall, no group had a sex bias, but 6 seasonal biases (Table 14) were detected.



	Resident				Transient			
	Female		Male		Female		Male	
	Adult	Juvenile	Adult	Juvenile	Adult	Juvenile	Adult	Juvenile
■ Spring*	21.89%	3.98%	14.43%	3.48%	16.92%	4.48%	29.35%	5.47%
■ Summer	24.76%	2.91%	30.10%	0.49%	20.39%	0.97%	20.39%	0.00%
■ Autumn	23.24%	2.94%	19.71%	4.71%	22.94%	4.71%	17.06%	4.71%
■ Winter	22.31%	3.76%	26.61%	3.23%	15.05%	2.42%	22.58%	4.03%

FIG. 9.—Group proportions by season for *Microtus pennsylvanicus* from Chesapeake, Virginia. Groups are defined by maturity, sex, and residency status. Asterisks (*) denote significantly greater proportions of transients than residents. The proportion of adults in each season was greater than that of juveniles. The proportion of adults was similar across spring, autumn, and winter, but greatest in summer, 95.60% (Table 12).

TABLE 13.—Results of Nemenyi tests for *Microtus pennsylvanicus* groups from Chesapeake, Virginia. Abbreviations for each group are based on reproductive maturity (juvenile, adult), sex (male, female), and residency status (resident, transient). Different lower-case letters denote significant differences in the Nemenyi tests. Percentage (%) is the proportion of transients. Mean body masses (g) are listed, although their distribution was not normal. An asterisk (*) denotes a significant proportion of transients within a season. Sample sizes for each season are listed in Table 14.

	JFR	JFT	JMR	JMT	AFR	AFT	AMR	AMT
Spring*	*a*	*a*	*a*	*ad*	*bc*	*bc*	*b*	*ce*
%	3.98	4.48	3.48	5.47	21.89	16.92	14.43	29.35
mass	23.9	25.1	22.9	19.6	49.9	51.2	53.0	50.3
Summer	*a*	*ab*	*ab*	*b*	*c*	*c*	*c*	*c*
%	2.91	0.97	0.49	0.00	24.76	20.39	30.10	20.39
mass	27.1	23.0	19.0	-	45.9	42.7	50.7	51.3
Autumn	*a*	*a*	*a*	*a*	*b*	*b*	*b*	*b*
%	2.94	4.71	4.71	4.71	23.24	22.94	19.71	17.06
mass	20.9	20.4	20.6	21.6	53.9	49.1	57.7	56.6
Winter	*a*	*a*	*a*	*a*	*bc*	*b*	*c*	*bc*
%	3.76	2.42	3.23	4.03	22.31	15.05	26.61	22.58
mass	24.0	23.2	20.1	21.7	44.8	47.6	51.9	49.1
Total	*a*	*a*	*a*	*a*	*b*	*b*	*b*	*b*
%	3.40	3.22	3.22	3.75	22.97	18.77	22.97	21.72
mass	23.7	22.4	20.8	21.1	48.7	47.8	53.2	51.6

TABLE 14.—Sex ratios and biases of *Microtus pennsylvanicus* by season and group from Chesapeake, Virginia. An asterisk (*) indicates a significant proportion of transients in a season. NS indicates the result was not significant. Adults were ≥ 30 g and breeding refers to scrotal testes in males and the presence of 2 of 3 reproductive cues in females. Only significant results are presented within seasons; groups not presented were not significant.

Season	**Group**	**Ratio (M:F)**	**Sex Bias**	**P Value**	**χ^2**	**Sample Size**
Overall			*No Bias*			1123
	Adults	1.30	Male	2.31×10^{-2}	5.1613	310
	Juveniles	NS	No Bias			152
	Residents	NS	No Bias			589
	Transients	NS	No Bias			531
	Adult Residents	NS	No Bias			515
	Adult Transients	NS	No Bias			453
	Juvenile Residents	NS	No Bias			74
	Juvenile Transients	NS	No Bias			78
	Breeding Adults	NS	No Bias			668
	Breeding Residents	NS	No Bias			358
	Breeding Transients	NS	No Bias			310
*Spring**			*No Bias*			202
	Transient	1.63	Male	1.11×10^{-2}	6.4513	113
	Adult Transient	1.74	Male	9.53×10^{-3}	6.7204	93
	Breeding Residents	0.55	Female	2.22×10^{-2}	5.2258	62

Table 14 Continued

Season	**Group**	**Ratio (M:F)**	**Sex Bias**	**P Value**	**χ^2**	**Sample Size**
Summer			*No Bias*			206
	Juvenile	0.13	Female	$1.96\text{x}10^{-2}$	5.444	9
	Breeding Adults	1.93	Male	$5.20\text{x}10^{-4}$	12.033	120
	Breeding Residents	1.73	Male	$2.41\text{x}10^{-2}$	5.0841	71
Autumn			*No Bias*			342
	Adults	2.70	Male	$3.30\text{x}10^{-2}$	3.9091	22
Winter		1.29	Male	$1.50\text{x}10^{-2}$	5.9223	373
	Adult	1.32	Male	$1.42\text{x}10^{-2}$	6.0124	322
	Transient	1.52	Male	$7.93\text{x}10^{-3}$	7.0488	164
	Adult Transient	1.50	Male	$1.80\text{x}10^{-2}$	5.6000	140
	Breeding Adults	1.34	Male	$3.40\text{x}10^{-2}$	4.512	213
	Breeding Transients	1.54	Male	$3.50\text{x}10^{-2}$	4.455	99

Microtus pennsylvanicus from Illinois.—Residency status was significantly associated with season (χ^2 =52.3168, df=3, P=$2.56\text{x}10^{-11}$), sex (χ^2 =44.3053, df=1, P=$8.92\text{x}10^{-6}$), and maturity (χ^2 =31.0308, df=1, P=$2.54\text{x}10^{-8}$) when examined for independence. The proportion of transients was significantly greater than that of residents during spring and winter, whereas the proportion of residents was significantly greater during the autumn. Overall, the proportion of transients, 53.55%, was significant. The Nemenyi test results (Table 15) for proportion of transients among seasons indicated that spring, summer, and winter were similar to each other, but separate from autumn.

Residency status was significantly associated with year of study (χ^2 =83.443, df=24, P=1.70x10^{-8}); 14 years had significantly greater proportions of transients than residents, whereas 2 years had significantly greater proportions of residents, and 9 years had no significant difference between the groups (Fig. 10). The proportion of transient meadow voles from Illinois was negatively correlated with population density (r^2 = -0.401, df=97, P=6.127x10^{-5}).

TABLE 15.—Results of Nemenyi tests of transients and adults for *Microtus pennsylvanicus* from Illinois. The proportion of each group in each season is listed above the Nemenyi similarities. Different letters denote significant differences among seasonal proportions. Transients include both sexes and both reproductive maturity groups, and adults include both sexes and both residency status groups. An asterisk (*) denotes a significant proportion of transients in a season.

	Spring*	**Summer**	**Autumn***	**Winter**
Proportion of Transients	52.22%	50.76%	59.79%	50.75%
Nemenyi Similarities	*a*	*a*	*b*	*a*
Proportion of Adults	57.50%	51.39%	58.55%	35.24%
Nemenyi Similarities	*a*	*b*	*a*	*c*
Sample Size	1426	1704	1790	1345

A significant association between reproductive maturity and season was detected when tested for independence (χ^2=147.9777, df=3, P=7.19x10^{-32}). The results of the Nemenyi test (Table 15) for proportions of adults among seasons identified that spring and autumn were similar, but all other pairings were different. The greatest proportion of adults, 58.54%, occurred in the autumn, whereas the smallest, 35.24%, was seen during the winter. Winter was the only season with a significantly greater proportion of juveniles, 64.76%, than of adults. The overall proportion of adults, 51.41%, was significant.

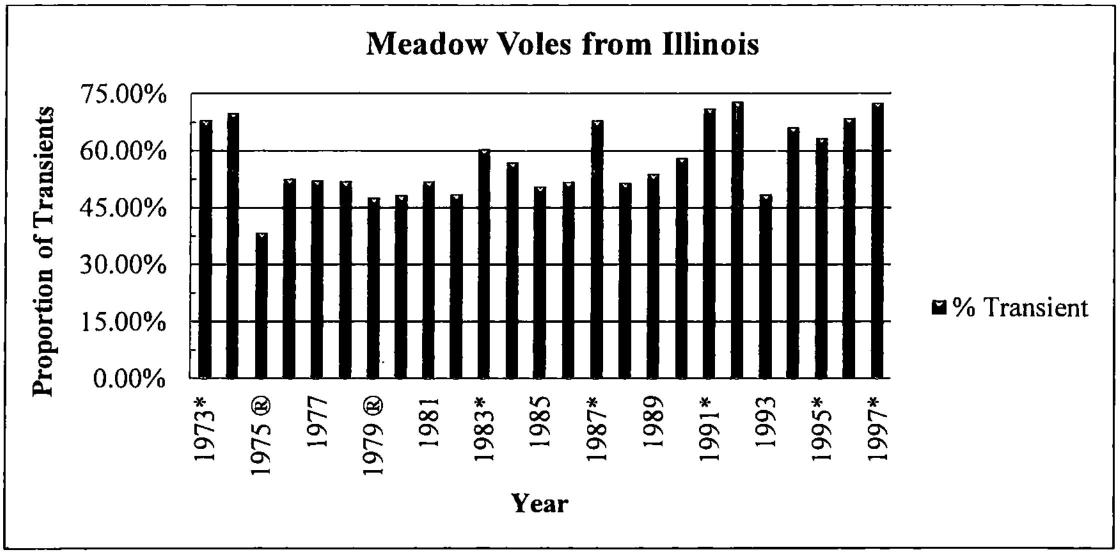
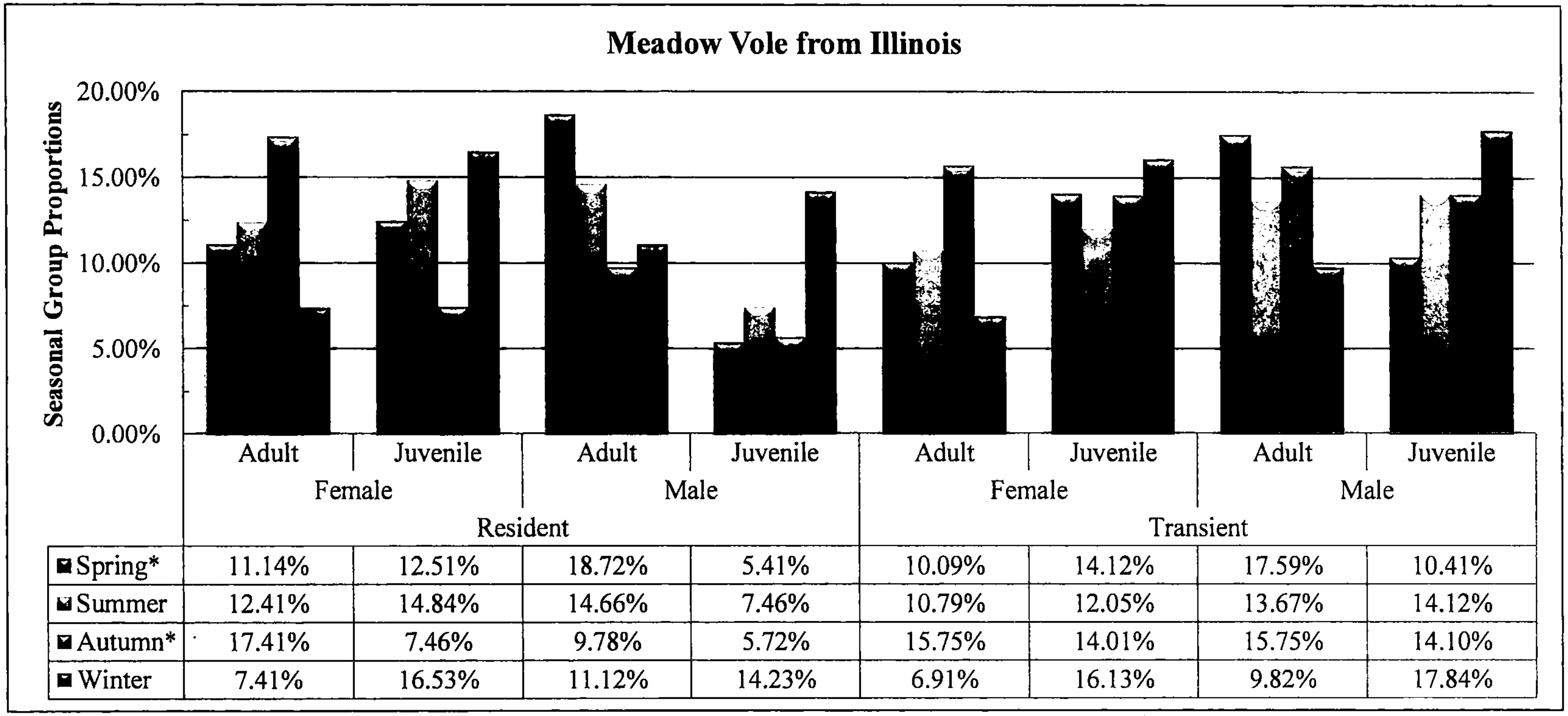


FIG. 10.— Proportion of transients by year for *Microtus pennsylvanicus* from Illinois. Years with an asterisk (*) denote significantly greater proportions of transients, ® denotes significantly greater proportions of residents. Overall, the proportion of transients, 53.55%, was significantly greater than that of residents.

The proportions of meadow vole groups (Fig. 11) were significantly associated with season (χ^2=291.9065, df=21, P=1.41x10^{-49}). The results of the Nemenyi tests (Table 16) revealed that, in spring, the proportion of juvenile male residents was different from all other groups, adult females were different from adult males, and adult males were different from juvenile males. Juvenile male residents in summer were different from all groups except female transients. During autumn, male residents were different from adult females and adult male transients, juvenile male residents were different from juvenile male transients, and juvenile female residents were different from all other female groups and male transients. Adult females were different from all juveniles, and juvenile male transients were different from adult males in winter. Also during the winter, adult male transients were different from all juvenile female groups. Overall, juvenile male residents were different from all groups except adult female transients.

The proportion of Illinois meadow voles in breeding condition was evaluated for independence from season, residency status, and sex; a significant association with season was detected (χ^2 =922.3926, df=3, P=1.20x10^{-199}) but not for residency status or sex. Reproductively active animals had significantly greater proportions than non-breeding individuals during spring, summer, and autumn, but not in winter or overall. The residency status of breeding adults was significantly associated with season (χ^2 =7.916, df=3, P=0.048) with a significant proportion of transients in the autumn, 55.90%, and overall, 51.52%. Sex biases (Table 17) were detected overall and seasonally for breeding adults. Overall, breeding adults were male-biased (χ^2 =52.9346, df=1, P=3.45x10^{-13}) with a ratio of 1.37. Sex ratios in spring and summer were also male-biased, but those in autumn and winter did not differ from unity. The sex ratios of breeding residents were male-biased overall and during spring and summer, but female-biased in autumn. Sex ratios of breeding transients were male-biased overall and during spring and summer.



	Resident				Transient			
	Female		Male		Female		Male	
	Adult	Juvenile	Adult	Juvenile	Adult	Juvenile	Adult	Juvenile
■ Spring*	11.14%	12.51%	18.72%	5.41%	10.09%	14.12%	17.59%	10.41%
■ Summer	12.41%	14.84%	14.66%	7.46%	10.79%	12.05%	13.67%	14.12%
■ Autumn*	17.41%	7.46%	9.78%	5.72%	15.75%	14.01%	15.75%	14.10%
■ Winter	7.41%	16.53%	11.12%	14.23%	6.91%	16.13%	9.82%	17.84%

FIG. 11.—Group proportions by season for *Microtus pennsylvanicus* from Illinois. Groups are defined by maturity, sex, and residency status. Asterisks (*) denote significantly greater proportions of transients than residents. The proportion of adults was significantly greater than that of juveniles in spring and autumn but not summer or winter. The proportion of adults was similar in spring and autumn, and summer and winter were separate from each other and other seasons (Table 15).

TABLE 16.—Results of Nemenyi tests for *Microtus pennsylvanicus* groups from Illinois. Abbreviations for each group are based on reproductive maturity (juvenile, adult), sex (male, female), and residency status (resident, transient). Different lower-case letters denote significant differences in the Nemenyi tests. Percentage (%) is the proportion of transients. Mean body masses (g) are listed, although distribution was not normal. An asterisk (*) denotes a significant proportion of transients in a season. Sample sizes for each season are listed in Table 17.

	JFR	**JFT**	**JMR**	**JMT**	**AFR**	**AFT**	**AMR**	**AMT**
Spring*	*a*	*ab*	*c*	*a*	*a*	*a*	*b*	*b*
%	12.51	14.12	5.41	10.41	11.14	10.09	18.72	17.59
mass	19.3	19.6	17.6	18.6	36.7	36.0	38.0	38.1
Summer	*a*	*ab*	*b*	*a*	*b*	*a*	*b*	*b*
%	14.84	12.05	7.46	14.12	12.41	10.79	14.66	13.67
mass	22.4	21.2	21.2	20.5	36.7	36.0	38.0	38.1
Autumn*	*a*	*b*	*a*	*b*	*b*	*b*	*ab*	*b*
%	7.46	14.01	5.72	14.10	17.41	15.75	9.78	15.75
mass	18.1	17.4	17.1	16.7	38.9	39.1	41.6	42.0
Winter	*a*	*a*	*ab*	*a*	*b*	*b*	*b*	*b*
%	16.53	16.13	14.23	17.84	7.41	6.91	11.12	9.82
mass	22.7	21.8	23.9	22.9	34.6	36.2	35.4	36.6
Total	*a*	*a*	*b*	*a*	*a*	*ab*	*a*	*a*
%	12.62	14.03	7.93	13.92	12.29	11.06	13.70	14.45
mass	21.0	19.9	20.8	19.8	37.5	37.6	38.4	39.1

TABLE 17.—Sex ratios and biases of *Microtus pennsylvanicus* by season and group from Illinois. An asterisk (*) indicates a significant proportion of transients for a season. NS indicates the result was not significant. Adults were ≥ 30 g and breeding refers to scrotal testes in males and the presence of 2 of 3 reproductive cues in females. Only significant results are shown for seasons; groups not presented were not significant.

Season	**Group**	**Ratio (M:F)**	**Sex Bias**	**P Value**	**χ^2**	**Sample Size**
Overall		NS	*No Bias*			4555
	Adults	1.20	Male	6.77×10^{-6}	20.257	2346
	Juveniles	0.82	Female	3.17×10^{-6}	21.712	2209
	Residents	0.87	Female	1.12×10^{-3}	10.613	2120
	Transients	1.13	Male	2.53×10^{-3}	9.117	2435
	Adult Residents	NS	No Bias			1184
	Adult Transients	1.31	Male	6.25×10^{-6}	20.410	1162
	Juvenile Residents	0.63	Female	2.66×10^{-12}	48.927	936
	Juvenile Transients	NS	No Bias			1273
	Breeding Adults	1.37	Male	3.45×10^{-13}	52.933	2171
	Breeding Residents	1.23	Male	7.82×10^{-4}	11.283	1053
	Breeding Transients	1.52	Male	6.04×10^{-12}	47.317	1118
*Spring**			*No Bias*			1239
	Adults	1.71	Male	2.50×10^{-12}	49.043	713
	Juveniles	0.59	Female	5.10×10^{-9}	34.137	526
	Adult Residents	1.68	Male	1.02×10^{-6}	23.881	370
	Adult Transients	1.74	Male	5.13×10^{-7}	25.215	343

Table 17 Continued

Season	**Group**	**Ratio (M:F)**	**Sex Bias**	**P Value**	**χ^2**	**Sample Size**
	Juvenile Residents	0.43	Female	$3.50\text{x}10^{-9}$	34.883	222
	Juvenile Transients	0.74	Female	$8.33\text{x}10^{-3}$	6.961	304
	Breeders	1.70	Male	$4.90\text{x}10^{-12}$	47.734	717
	Breeding Residents	1.62	Male	$6.20\text{x}10^{-6}$	20.431	362
	Breeding Transients	1.77	Male	$1.50\text{x}10^{-7}$	27.609	355
Summer			*No Bias*			1112
	Adults	1.22	Male	$1.72\text{x}10^{-2}$	5.670	573
	Juveniles	0.80	Female	$1.10\text{x}10^{-2}$	6.458	539
	Residents	0.81	Female	$1.50\text{x}10^{-2}$	5.918	549
	Transients	1.22	Male	$2.05\text{x}10^{-2}$	5.373	563
	Juvenile Residents	0.43	Female	$3.50\text{x}10^{-9}$	34.883	222
	Breeding Adults	1.76	Male	$3.70\text{x}10^{-13}$	52.795	691
	Breeding Residents	1.50	Male	$1.90\text{x}10^{-4}$	13.881	343
	Breeding Transients	2.08	Male	$6.20\text{x}10^{-11}$	42.770	348
*Autumn**		0.83	Female	$1.25\text{x}10^{-3}$	10.401	1206
	Adult	0.77	Female	$5.45\text{x}10^{-4}$	11.955	708
	Residents	0.62	Female	$3.05\text{x}10^{-7}$	26.220	487
	Adult Residents	0.56	Female	$3.78\text{x}10^{-7}$	25.805	328
	Breeding Residents	0.68	Female	$1.46\text{x}10^{-3}$	10.125	288

Table 17 Continued

Season	**Group**	**Ratio (M:F)**	**Sex Bias**	**P Value**	χ^2	**Sample Size**
Winter			*No Bias*			998
	Adults	1.46	Male	$4.35\text{x}10^{-4}$	12.375	352
	Transients	1.20	Male	$4.09\text{x}10^{-2}$	4.182	506
	Adult Residents	150	Male	$6.50\text{x}10^{-3}$	7.400	185
	Adult Transients	1.42	Male	$2.48\text{x}10^{-2}$	5.036	167

A significant association between the sex of meadow voles and season was found when tested for independence (χ^2 =18.8046, df=3, P=0.0003). Overall, and for spring, summer, and winter, the sex ratios did not differ from unity. The sex ratio of meadow voles in autumn was female-biased (χ^2 =10.4013, df=1, P=0.00126) with a ratio of 0.83. All groups (Table 17) had seasonal sex biases with the dominant sex varying among seasons and groups. Overall, adults were male-biased (χ^2 =20.2575, df=1, P=$6.77\text{x}10^{-6}$), juveniles were female-biased (χ^2 =21.7116, df=1, P=$3.17\text{x}10^{-6}$), transients were male-biased (χ^2 =9.1175, df=1, P=0.0025), and residents were female-biased (χ^2 =10.6132, df=1, P=0.001).

The mean ranked body masses of residents and transients, when analyzed using the K-W test, differed (K =32.433, df=4564, P=$1.31\text{x}10^{-8}$), with residents having a greater mean ranked body mass; however, the body masses of breeding residents and transients did not differ. The mean ranked body masses of each group were different (K=1978.174, df=4554, P=0.000) with the Nemenyi tests resulting in adult males being shown as different from all other groups, adult females different from all other groups, and juvenile male residents different from juvenile transients.

Comparison of Microtus pennsylvanicus from Virginia and Illinois.—When tested for independence, geographic location and residency status were significantly associated ($\chi^2=771.204$, df=2, $P=1.10\times10^{-169}$). The residency status ($\chi^2=205.831$, df=9, $P=4.77\times10^{-28}$) and reproductive maturity ($\chi^2=240.7583$, df=9, $P=8.53\times10^{-162}$) of the geographic populations of meadow voles were significantly associated with season. When proportions of Virginia and Illinois meadow voles were compared through two-sample Z-tests for the factors of reproductive maturity and residency status for each season and the complete data sets, the populations differed for each seasonal factor and overall. Virginia meadow voles had a greater proportion of transients and juveniles, whereas Illinois meadow voles had greater proportions of residents and adults.

An examination of the overall difference in proportions of groups revealed that Illinois meadow voles had significantly greater proportions of adult residents and transients of both sexes, whereas the Virginia population had significantly greater proportions of juvenile females and juvenile male transients. There was no difference in the proportion of juvenile male residents between geographic populations. The mean ranked body masses between populations were different ($K=605.276$, df=5672, $P=5.57\times10^{-239}$), as was the mean rank body mass of residents and transients ($K=4.49$, df=5672, $P=0.034$), with residents having a greater mean ranked body mass.

Microtus ochrogaster from Kansas.—Tests of independence of residency status from season, sex, and reproductive maturity resulted in a significant association with season ($\chi^2=101.5638$, df=3, $P=7.165\times10^{-22}$) and maturity ($\chi^2=44.3053$, df=1, $P=2.81\times10^{-}$

^{11}), as well as a marginal association (χ^2 =3.6214, df=1, P=0.057) with sex. The results of the Nemenyi test (Table 18) for the proportion of transients among seasons identified autumn and winter as similar but different from spring and summer; spring and summer were also different from each other. The proportions of transients during spring and summer were significantly greater than the proportion of residents, but the proportion of residents was significantly greater during autumn and winter. The overall proportion of transients, 50.23%, was not significant. When tested for independence, residency status was significantly associated with year of study (χ^2 =519.602, df=27, P=1.38x10^{-92}), with 11 years having significantly greater proportions of residents than transients, 11 years had significantly greater proportions of transients, and 6 years had no detectable difference (Fig. 12). There was no correlation between the proportion of transients and density.

Reproductive maturity and season were significantly associated when tested for independence (χ^2 =51.3346, df=3, P=4.15x10^{-11}). The results of the Nemenyi test (Table 18) for proportions of adults indicated that spring and winter were similar and summer and autumn were similar to each other but different from spring and winter. The proportions of adults were significantly greater than that of juveniles in summer and autumn, but proportions of juveniles were significantly greater in spring and winter. Overall, the proportions of adults and juveniles were not significantly different.

The proportions of reproductive maturity, sex, and residency status groups (Fig. 13) of prairie vole were significantly associated with season (χ^2=299.1237, df=21, P=4.80x10^{-51}). The Nemenyi test results (Table 19) indicated that the proportions of juvenile male transients in spring were different from all resident groups and all other male groups. Also during the spring, adult females and female transients were different from male residents. The proportion of juvenile transients in summer was different from that of juvenile residents; adult female residents were different from juvenile and adult male transients. In autumn, the proportion of adult male residents was different from that of juvenile transients. Adult male residents in winter were different from adult females. Also during the winter, adult females were different from juvenile females, and adult female transients were different from other transient groups. Overall, the proportions of each group were similar.

TABLE 18.—Results of Nemenyi tests of transients and adults for *Microtus ochrogaster* from Kansas. The proportion of each group in each season is listed above the Nemenyi similarities. Different letters denote significant differences among seasonal proportions. Transients include both sexes and both reproductive maturity groups, and adults include both sexes and both residency status groups. An asterisk (*) denotes a significant proportion of transients in a season.

	Spring*	**Summer***	**Autumn**	**Winter**
Proportion of Transients	59.61%	53.29%	43.52%	45.35%
Nemenyi Similarities	*a*	*b*	*c*	*c*
Proportion of Adults	46.42%	54.28%	52.96%	43.12%
Nemenyi Similarities	*a*	*b*	*b*	*a*
Sample Size	1426	1704	1790	1345

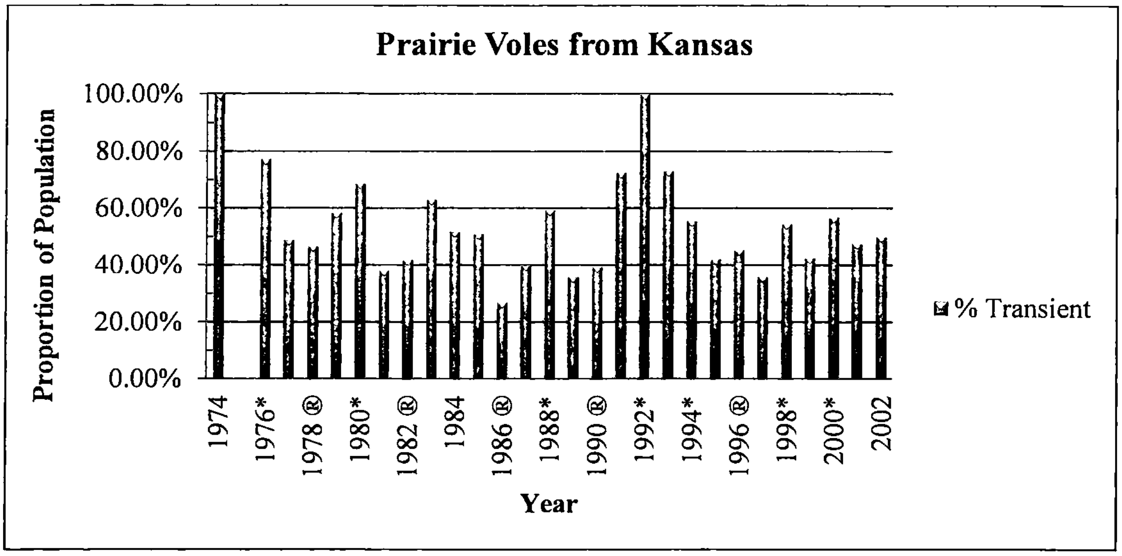
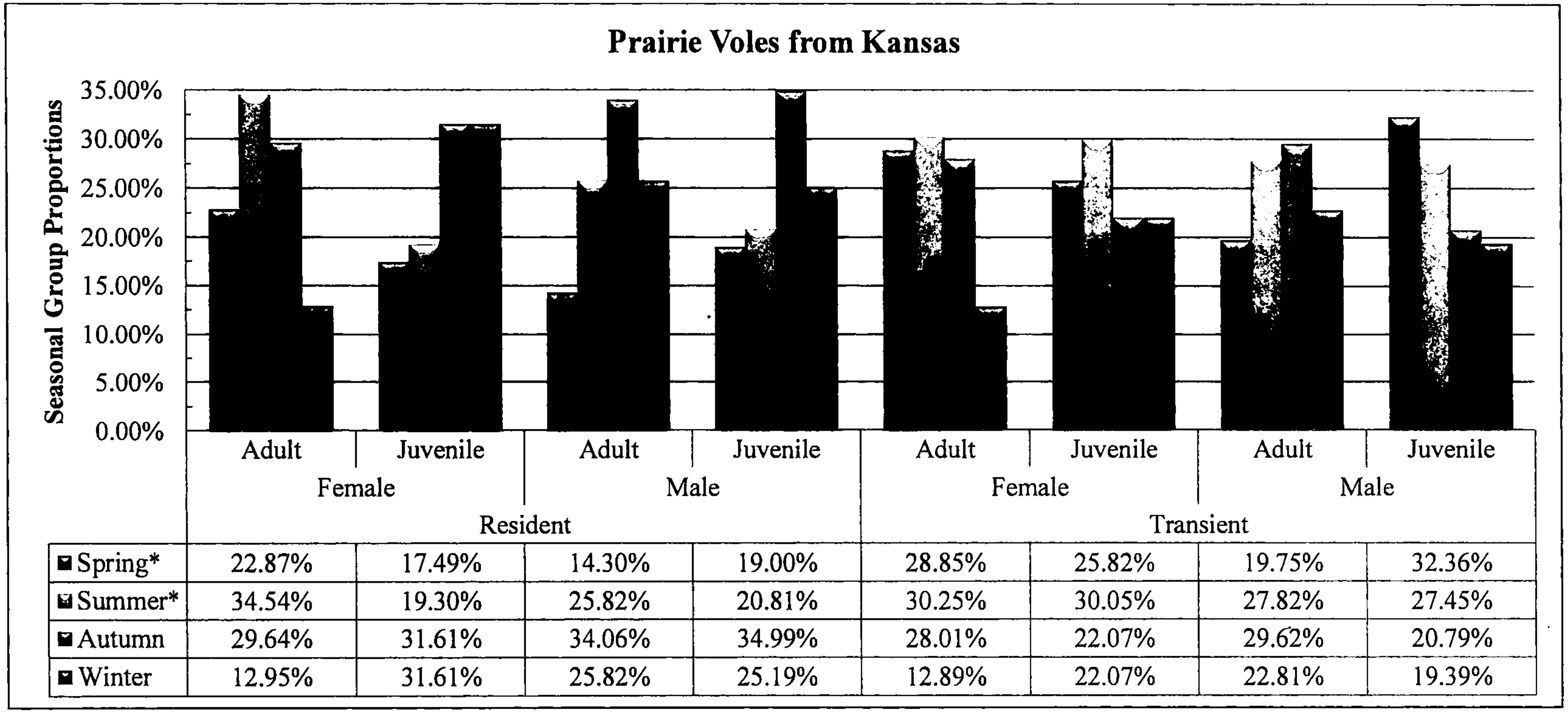


FIG. 12.—Proportion of transients by year for *Microtus ochrogaster* from Kansas. Years with an asterisk (*) denote significantly greater proportions of transients, ® denotes significantly greater proportions of residents. Years with low sample sizes skew the graph: 1974 (n=1), 1975 (n=0). The year 1992 (n=189) had no resident captures. The overall proportion of transients, 50.23%, was not significantly greater than that of residents.

The proportion of Kansas prairie voles in breeding condition was significantly associated with season (χ^2=405.9813, df=3, P=1.12x10^{-87}). The results of the Nemenyi tests indicated that spring was different from all other seasons, whereas winter was different from summer and autumn, which were similar. Breeding adults had significantly greater proportions of residents than transients (χ^2=4.1026, df=1, P=0.0428), 51.52%, and had a male-biased (χ^2=9.7637, df=1, P=0.0018) sex ratio of 1.12. Overall, a male-biased sex ratio (χ^2=13.152, df=1, P=2.87x10^{-4}) of 1.21 was detected for breeding transients. When tested for independence, an association between the residency status of breeding adults and season was detected (χ^2 =16.372, df=3, P=0.001). Comparisons between the proportions of resident and transient groups for each season revealed a significantly greater proportion of transients in spring, 54.54%, whereas the proportion of residents was significantly greater during all other seasons. The proportion of residents was the greatest, 55.49%, in winter.

When tested for independence, sex and season were significantly associated (χ^2=17.8863, df=3, P=0.00046). The sex ratio of the population (Table 20) varied between male and female biases among seasons and groups. Sex ratios in the spring (χ^2=6.2225, df=1, P=0.0126) and summer (χ^2=10.0769, df=1, P=0.0015) were female-biased, but a male-biased (χ^2=4.1822, df=1, P=0.0408) ratio of 1.12 was detected for winter. The sex ratios did not differ from unity for autumn or overall. Overall, residents had female-biased (χ^2=6.3782, df=1, P=0.0116) sex ratio, 0.91, as did juvenile residents (χ^2=8.279, df=1, P=0.0040) with a sex ratio of 0.86.

The mean ranked body mass of residents and transients differed (K=55.493, df=6264, P=1.06x10^{-13}), with residents having a greater mean rank. The mean ranked body mass of breeding residents and transients was significantly different (K =10.888, df=3029, P=0.001), and residents also had a greater mean rank score. The mean ranked body masses of all groups differed (K =2126.498, df=6257, P=0.000). The results of the Nemenyi tests revealed that adult female residents and transients were similar only to each other, adult male residents and transients were similar only to each other, and juvenile male residents were different from juvenile transients (Table 20).



	Resident Female Adult	Resident Female Juvenile	Resident Male Adult	Resident Male Juvenile	Transient Female Adult	Transient Female Juvenile	Transient Male Adult	Transient Male Juvenile
■ Spring*	22.87%	17.49%	14.30%	19.00%	28.85%	25.82%	19.75%	32.36%
■ Summer*	34.54%	19.30%	25.82%	20.81%	30.25%	30.05%	27.82%	27.45%
■ Autumn	29.64%	31.61%	34.06%	34.99%	28.01%	22.07%	29.62%	20.79%
■ Winter	12.95%	31.61%	25.82%	25.19%	12.89%	22.07%	22.81%	19.39%

FIG. 13—Group proportions by season for *Microtus ochrogaster* in Kansas. Groups are defined by maturity, sex, and residency status. Asterisks (*) denote significantly greater proportions of transients than residents. The proportions of adults in summer and autumn were significantly greater than that of juveniles. The proportions of adults were similar for summer and autumn, and for spring and winter, but summer and autumn were different from spring and winter (Table 18).

TABLE 19.—Results of Nemenyi tests for *Microtus ochrogaster* groups from Kansas. Abbreviations for each group are based on reproductive maturity (juvenile, adult), sex (male, female), and residency status (resident, transient). Different lower-case letters denote significant differences in the Nemenyi tests. Percentage (%) is the proportion of transients. Mean body masses (g) are listed, although distribution was not normal. An asterisk (*) denotes a significant proportion of transients in a season. Sample sizes for each season are listed in Table 20.

	JFR	JFT	JMR	JMT	AFR	AFT	AMR	AMT
Spring*	*ab*	*bc*	*a*	*b*	*cde*	*bce*	*a*	*ade*
%	9.51	15.49	8.87	19.51	13.80	14.51	8.31	10.00
mass	27.1	25.0	28.1	23.8	45.4	45.3	43.2	42.8
Summer*	*ab*	*cd*	*a*	*cd*	*c*	*bcd*	*abcd*	*abd*
%	8.75	15.03	8.10	13.80	17.38	12.68	12.51	11.74
mass	28.4	26.4	28.8	26.8	44.7	45.1	43.3	42.9
Autumn	*a*	*a*	*ab*	*ab*	*ab*	*ab*	*ab*	*b*
%	13.63	10.50	12.96	9.94	14.19	11.17	15.70	11.90
mass	24.9	24.8	25.8	25.0	45.4	46.3	43.8	44.6
Winter	*a*	*ab*	*bc*	*bc*	*cd*	*d*	*ab*	*bc*
%	18.14	13.98	12.42	12.34	8.25	6.84	15.84	12.19
mass	27.9	27.5	27.8	27.6	42.1	43.3	43.0	43.1
Total	*a*	*a*	*a*	*a*	*a*	*a*	*a*	*a*
%	12.34	13.61	10.59	13.68	13.69	11.41	13.18	11.49
mass	26.9	25.9	27.4	25.6	44.7	45.2	43.4	43.4

TABLE 20.—Sex ratios and biases of *Microtus ochrogaster* by season and group from Kansas. An asterisk (*) indicates a significant proportion of transients for a season. NS indicates the result was not significant. Adults were ≥ 30 g and breeding refers to scrotal testes in males and the presence of 2 of 3 reproductive cues in females. Only significant results are shown for seasons; groups not presented were not significant.

Season	**Group**	**Ratio (M:F)**	**Sex Bias**	**P Value**	χ^2	**Sample Size**
Overall			*No Bias*			6265
	Adults	NS	No Bias			3115
	Juveniles	NS	No Bias			3150
	Residents	0.91	Female	$1.15x10^{-2}$	6.378	3118
	Transients	NS	No Bias			3147
	Adult Residents	NS	No Bias			1682
	Adult Transients	NS	No Bias			1433
	Juvenile Residents	0.86	Female	$4.01x10^{-3}$	8.279	1436
	Juvenile Transients	NS	No Bias			1714
	Breeding Adults	1.12	Male	$1.78x10^{-3}$	9.764	3030
	Breeding Residents	NS	No Bias			1561
	Breeding Transients	1.21	Male	$2.87x10^{-4}$	13.152	1469
*Spring**		0.88	*Female*	$1.26x10^{-2}$	6.223	1420
	Adult	0.65	Female	$3.41x10^{-8}$	30.459	662
	Residents	0.74	Female	$2.85x10^{-4}$	13.163	575
	Adult Residents	0.60	Female	$1.07x10^{-5}$	19.376	314
	Adult Transients	0.69	Female	$6.01x10^{-4}$	11.770	348

Table 20 Continued

Season	**Group**	**Ratio (M:F)**	**Sex Bias**	**P Value**	**χ^2**	**Sample Size**
	Juvenile Transients	1.25	Male	1.05×10^{-2}	6.537	497
	Breeding Adults	0.85	Female	2.22×10^{-2}	5.229	759
	Breeding Residents	0.78	Female	2.06×10^{-2}	5.359	345
*Summer**		0.86	*Female*	1.50×10^{-3}	10.077	1703
	Adults	0.81	Female	1.13×10^{-3}	10.596	925
	Residents	0.79	Female	8.63×10^{-4}	11.100	796
	Adult Residents	0.72	Female	2.34×10^{-4}	13.534	509
	Breeding Adults	1.15	Male	2.32×10^{-2}	5.147	1064
	Breeding Transients	1.42	Male	9.45×10^{-5}	15.244	508
Autumn			*No Bias*			1790
Winter		1.12	*Male*	4.08×10^{-2}	4.182	1345
	Adults	1.86	Male	5.01×10^{-13}	52.200	580
	Juveniles	0.77	Female	3.44×10^{-4}	12.812	765
	Transients	1.18	Male	4.29×10^{-2}	4.098	610
	Adult Resident	1.92	Male	1.46×10^{-8}	32.111	324
	Adult Transient	1.78	Male	6.80×10^{-6}	20.250	256
	Juvenile Residents	0.68	Female	1.46×10^{-4}	14.426	411
	Breeding Adults	1.89	Male	7.25×10^{-9}	33.468	355
	Breeding Residents	1.90	Male	1.39×10^{-5}	18.888	197
	Breeding Transients	1.87	Male	1.34×10^{-4}	14.582	158

Microtus ochrogaster from Illinois.—The tests of independence for residency status from season, sex, and reproductive maturity revealed an association with season (χ^2 =431.0038, df=3, P=4.26x10^{-93}), sex (χ^2 =14.0070, df=1, P=1.82x10^{-4}), and reproductive maturity (χ^2 =64.5264, df=1, P=9.52x10^{-16}). The Nemenyi test results (Table 21) detected that the proportion of transients in spring and winter were different from each other and from all other seasons, but the proportions in summer and autumn were similar. Comparison between the proportions of residents and transients with the two-sample Z-test revealed that the proportion of transients was significantly greater in every season and overall. The overall proportion of transients, 57.69%, and peaked in winter at 64.98%. When tested for independence, residency status was significantly associated with year of study (χ^2 =439.2360, df=26, P=1.16x10^{-76}). The comparison between proportions of residents and transients for each year of study revealed that the proportion of transients was significantly greater for 21 years, whereas the proportion of residents was significantly greater for 3 years, and no difference in proportions was detected for 4 years (Fig. 14). The proportion of transients and density were negatively correlated (r^2 = -0.468, df=100, P=9.31x10^{-7}).

Reproductive maturity was not significantly associated with season when tested for independence; however, two-sample Z-tests revealed that the proportion of adults was significantly greater during summer, autumn, winter and overall. The overall proportion of adults, 50.77%, was lowest in spring, 49.63%, and greatest in winter, 51.60%.

TABLE 21.—Results of Nemenyi tests of transients and adults for *Microtus ochrogaster* from Illinois. The proportion of each group is listed above the Nemenyi similarities. Different letters denote significant differences among seasonal proportions. Transients include both sexes and both reproductive maturity groups, and adults include both sexes and both residency status groups. An asterisk (*) denotes a significant proportion of transients in a season.

	Spring*	**Summer***	**Autumn***	**Winter***
Proportion of Transients	60.23%	55.48%	53.42%	64.98%
Nemenyi Similarities	*a*	*b*	*b*	*c*
Proportion of Adults	49.63%	51.08%	50.59%	51.60%
Nemenyi Similarities	*a*	*a*	*a*	*a*
Sample Size	2547	3203	6268	3744

The proportions of prairie vole groups from Illinois (Fig. 15) were significantly associated with season (χ^2=314.2026, df=21, P=4.06x10^{-54}). The results of the Nemenyi tests (Table 22) identified all transient groups as similar in spring and different from juvenile male residents. During the spring, proportions of juvenile male transients were different from all resident groups, juvenile female residents were different from juvenile female transients and adult male transients, and adult male transients were different from adult female residents. The proportion of juvenile male residents in summer was different from all groups except juvenile female residents. Also during the summer, juvenile male transients were different from adult transients and juvenile residents, and juvenile female residents were separate from adult residents and juvenile female transients. The proportion of all groups was similar in autumn. The proportion of adult female residents was similar to juvenile residents but different from all other groups in winter. In the winter, proportions of adult female transients were similar only to adult male residents and juvenile transients, adult male residents were different from adult male transients and juvenile female transients, adult male transients were similar only to juvenile female transients, and juvenile residents were different from juvenile transients. Overall, adult female residents were different from male transients, adult female transients were different from juvenile male residents, and juvenile residents were different from juvenile transients.

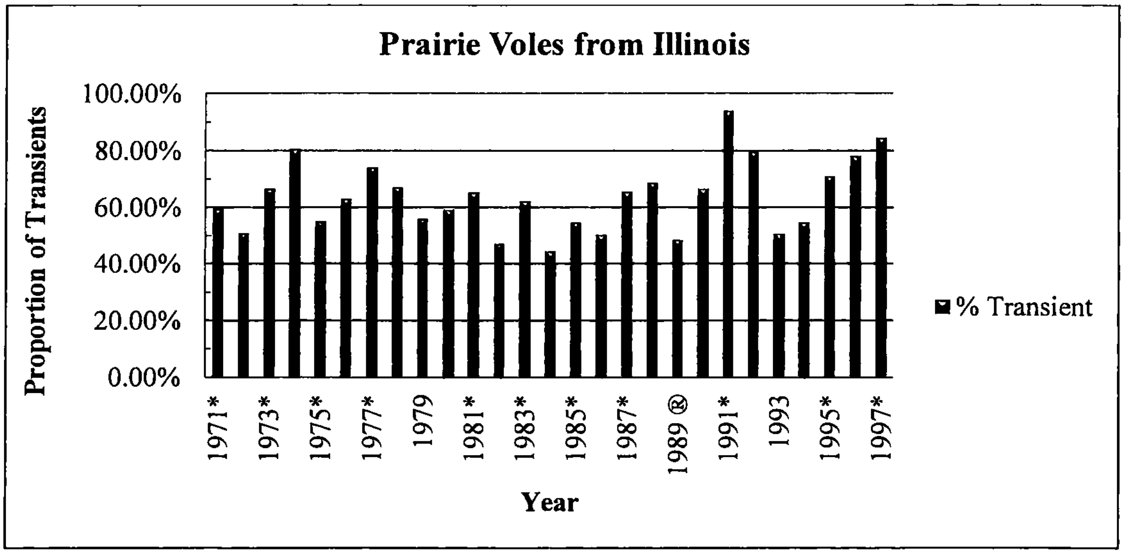
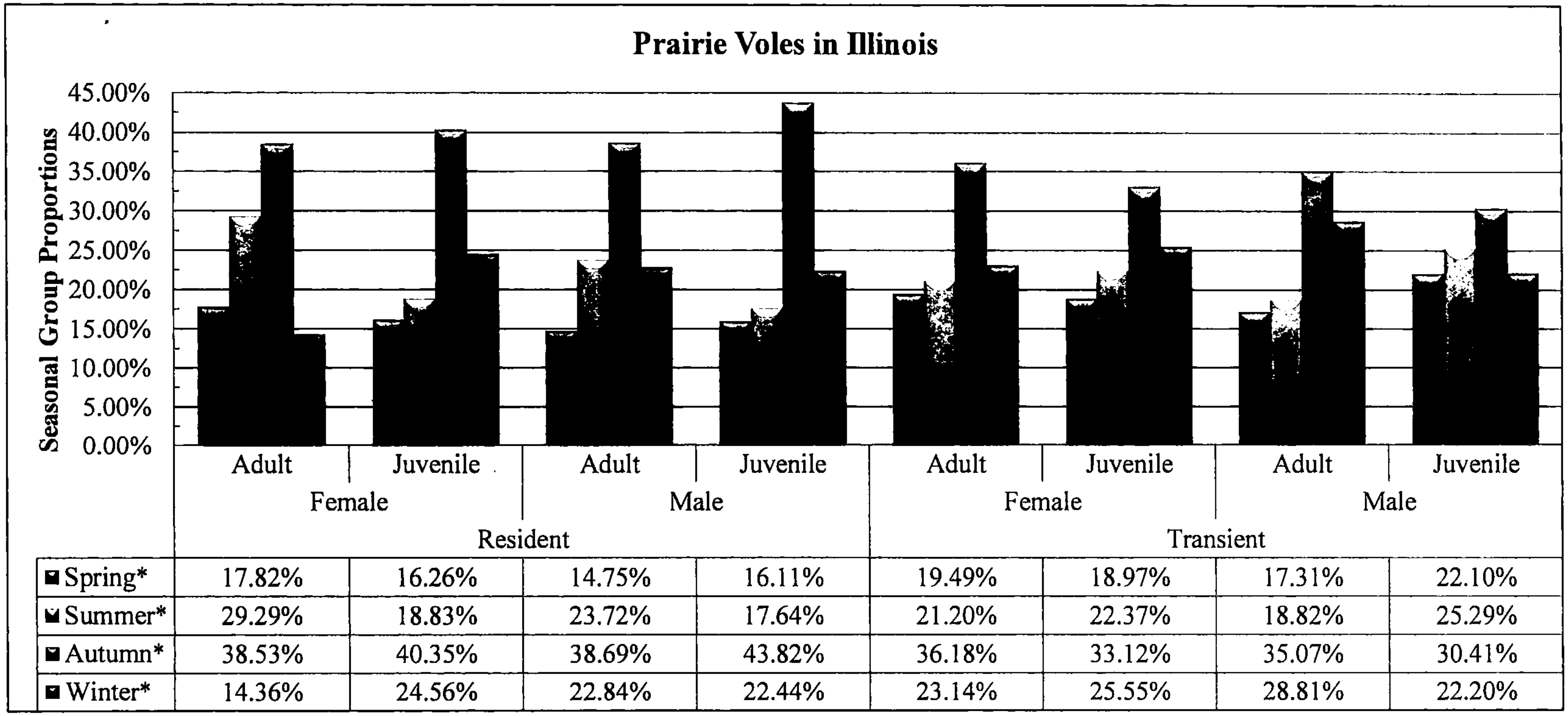


FIG. 14.—Proportion of transients by year for *Microtus ochrogaster* from Illinois. Years with an asterisk (*) denote significantly greater proportions of transients, ® denotes significantly greater proportions of residents. Overall, the proportion of transients, 57.69%, was significantly greater than that of residents.



	Resident				Transient			
	Female		Male		Female		Male	
	Adult	Juvenile	Adult	Juvenile	Adult	Juvenile	Adult	Juvenile
■ Spring*	17.82%	16.26%	14.75%	16.11%	19.49%	18.97%	17.31%	22.10%
■ Summer*	29.29%	18.83%	23.72%	17.64%	21.20%	22.37%	18.82%	25.29%
■ Autumn*	38.53%	40.35%	38.69%	43.82%	36.18%	33.12%	35.07%	30.41%
■ Winter*	14.36%	24.56%	22.84%	22.44%	23.14%	25.55%	28.81%	22.20%

FIG. 15.—Group proportions by season for *Microtus ochrogaster* from Illinois. Groups are defined by maturity, sex, and residency status. Asterisks (*) denote significantly greater proportions of transients than residents. The proportions of adults in summer, autumn, and winter were significantly greater than that of juveniles. The proportion of adults was similar among all seasons (Table 21).

Tests of independence revealed that the proportion of prairie voles in breeding condition was significantly associated with season (χ^2=26.101, df=3, P=9.08x10^{-6}). The results of the Nemenyi test identified summer as different from spring but similar to autumn, autumn as different from winter, and spring as similar to autumn and winter. The proportions of breeding transients and residents were compared for each season and overall. The proportion of transients was significantly greater during the spring, autumn, winter, and overall. There was no detectable difference in the proportion of transients and residents during the summer. Overall, the proportion of transients was 52.51% for breeding adults. All groups of breeding animals had male-biased sex ratios during each season and overall (Table 23).

The sex of prairie voles was significantly associated with season when tested for independence (χ^2=8.8829, df=3, P=0.030), with male-biased sex ratios seasonally and overall (Table 23). Female-biased sex ratios were found for groups of juveniles, residents, and transients within each season.

The mean ranked body mass of residents and transients was different (K=62.528, df=15761, P=2.80x10^{-15}), with residents having a greater mean rank. The mean ranked body mass of breeding residents and transients was also significantly different (K =24.768, df=7964, P=6.54x10^{-7}), and residents had the greater mean rank.

TABLE 22.—Results of Nemenyi tests for *Microtus ochrogaster* groups from Illinois. Abbreviations for each group are based on reproductive maturity (juvenile, adult), sex (male, female), and residency status (resident, transient). Different lower-case letters denote significant differences in the Nemenyi tests. Percentage (%) is the proportion of transients. Mean body masses (g) are listed, although distribution was not normal. An asterisk (*) denotes a significant proportion of transients in a season. Sample sizes for each season are listed in Table 23.

	JFR	**JFT**	**JMR**	**JMT**	**AFR**	**AFT**	**AMR**	**AMT**
Spring*	*ad*	*bce*	*a*	*e*	*acd*	*bcde*	*abcd*	*be*
%	9.93	14.68	8.31	17.06	10.57	12.54	11.20	15.71
mass	17.1	18.0	19.3	17.7	38.5	37.9	37.6	37.7
Summer*	*ab*	*cd*	*a*	*d*	*cd*	*bc*	*c*	*bc*
%	9.37	13.87	7.23	18.08	14.62	11.10	13.58	12.14
mass	18.7	16.7	19.3	17.8	40.8	40.9	37.6	38.2
Autumn*	*a*	*a*	*a*	*a*	*a*	*a*	*a*	*a*
%	11.51	13.60	10.99	12.83	12.04	12.43	12.43	14.17
mass	17.2	17.6	17.2	17.9	40.4	40.2	38.1	38.4
Winter*	*ab*	*cd*	*ab*	*ce*	*a*	*ce*	*be*	*d*
%	9.10	16.32	8.08	14.63	7.03	14.20	10.95	19.68
mass	16.8	19.0	15.4	17.4	36.4	36.8	38.3	38.0
Total*	*ab*	*cd*	*a*	*d*	*abc*	*bcd*	*abc*	*d*
%	10.25	14.48	9.10	15.01	11.13	12.60	12.11	15.32
mass	17.4	17.8	17.5	17.7	39.6	39.0	37.9	38.1

TABLE 23.—Sex ratios and biases of *Microtus ochrogaster* by season and group from Illinois. An asterisk (*) indicates a significant proportion of transients for a season. NS indicates the result was not significant. Adults were ≥ 30 g and breeding refers to scrotal testes in males and the presence of 2 of 3 reproductive cues in females. Only significant results are presented within seasons; groups not presented were not significant.

Season	**Group**	**Ratio (M:F)**	**Sex Bias**	**P Value**	**χ^2**	**Sample Size**
Overall		1.06	*Male*	1.16×10^{-4}	14.858	15762
	Adults	1.16	Male	1.03×10^{-10}	41.761	8003
	Juveniles	NS	No Bias			7759
	Residents	0.95	Female	3.01×10^{-2}	4.702	6669
	Transients	NS	No Bias			9093
	Adult Residents	1.09	Male	1.11×10^{-2}	6.440	3635
	Adult Transients	1.22	Male	1.25×10^{-10}	41.380	4365
	Juvenile Residents	0.89	Female	1.14×10^{-3}	10.592	3025
	Juvenile Transients	NS	No Bias			4725
	Breeding Adults	1.49	Male	9.14×10^{-64}	284.198	7398
	Breeding Residents	1.35	Male	8.17×10^{-19}	78.459	3513
	Breeding Transients	1.63	Male	8.03×10^{-50}	220.238	3885
*Spring**		1.10	*Male*	2.22×10^{-2}	5.233	2527
	Adult	1.16	Male	6.93×10^{-3}	7.291	1264
	Adult Transients	1.25	Male	2.75×10^{-3}	8.964	714
	Juvenile Transients	1.16	Male	3.41×10^{-2}	4.489	802

Table 23 Continued

Season	Group	Ratio (M:F)	Sex Bias	P Value	χ^2	Sample Size
	Breeding Adults	1.59	Male	1.19×10^{-17}	72.150	1384
	Breeding Residents	1.41	Male	2.27×10^{-5}	17.949	626
	Breeding Transients	1.77	Male	2.39×10^{-14}	58.179	758
*Summer**			*No Bias*			3180
	Transients	1.16	Male	1.53×10^{-3}	10.043	1788
	Juvenile Residents	0.77	Female	3.08×10^{-3}	8.758	528
	Juvenile Transients	1.30	Male	2.62×10^{-5}	17.673	1016
	Breeding Adults	1.34	Male	1.54×10^{-10}	40.976	1927
	Breeding Residents	1.14	Male	4.70×10^{-2}	3.947	974
	Breeding Transients	1.60	Male	1.30×10^{-12}	50.326	953
*Autumn**			*No Bias*			6204
	Adults	1.09	Male	1.90×10^{-2}	5.500	3168
	Adult Transients	1.14	Male	7.84×10^{-3}	7.069	1650
	Breeding Adults	1.43	Male	5.71×10^{-23}	97.383	1927
	Breeding Residents	1.33	Male	3.54×10^{-8}	30.388	1493
	Breeding Transients	1.53	Male	4.67×10^{-17}	70.472	1602
*Winter**		1.14	*Male*	4.51×10^{-5}	16.645	3725
	Adults	1.44	Male	1.68×10^{-15}	63.406	1932
	Juveniles	0.89	Female	1.71×10^{-2}	5.689	1793
	Adult Residents	1.55	Male	1.70×10^{-8}	31.815	670
	Adult Transients	1.39	Male	9.33×10^{-9}	32.976	1262

Table 23 Continued

Season	Group	Ratio (M:F)	Sex Bias	P Value	χ^2	Sample Size
	Breeding Adults	1.88	Male	4.82×10^{-22}	93.161	992
	Breeding Residents	2.04	Male	2.12×10^{-12}	49.371	420
	Breeding Transients	1.78	Male	2.23×10^{-11}	44.755	572

Comparison of Microtus ochrogaster from Kansas and Illinois.—When tested for independence, geographic population and residency status were significantly associated (χ^2=100.9182, df=2, P=9.59×10^{-124}). The residency status of geographic populations (χ^2=205.831, df=9, P=4.77×10^{-28}) and maturity (χ^2=843.6955, df=9, P=9.75×10^{-89}) were also significantly associated with season. The proportions of residents and transients and adults and juveniles were compared between geographic populations with two-sample Z-tests. The proportions of transients, residents, adults, and juveniles were different between the populations during each season and overall. Kansas prairie voles had greater proportions of transients in each season and overall, whereas Illinois prairie voles had greater proportions of residents in each season and overall. Reproductive maturity varied with season, with Kansas voles having significantly greater proportions of adults than Illinois during the spring, winter and overall. The Illinois population had significantly greater proportions of adults in summer and autumn. Prairie voles from Illinois had significantly greater proportions of juveniles during spring, winter, and overall, whereas Kansas had greater proportions of juveniles during summer and autumn.

Overall, the mean ranked body masses of Kansas and Illinois populations when compared were not significantly different, and residents had a greater mean ranked body mass than transients ($K=62.528$, $df=15761$, $P=2.80\times10^{-15}$) in both populations.

CHAPTER IV

DISCUSSION

I have evaluated the topics of transience/residency, sex ratios and biases, body mass, and aspects of population structure for patterns among seasons and years for 4 species, 3 of which are compared between geographic populations. These analyses revealed that all populations had high proportions of transients, 47.30% to 57.69%; adults generally constituted the majority of initial captures, 41.29% to 86.28%; sex ratios for most populations did not differ from unity overall, but some populations had a dominant sex in some seasons; and that body mass varied in predictable, yet unexpected, ways.

The patterns will be summarized by comparing species and populations and then setting these results in the context of the dominant paradigms of population structure in order to provide support (or not) for these ideas. The dominant paradigms to be discussed relate to the movement of small mammals as well as sub-structuring of open-habitat rodent populations. Old-field rodents are believed to live their lives in a relatively small circumscribed natal site, with males being more likely to leave than females, and juveniles more likely to leave than adults. To assist in these comparisons I have prepared a table (Table 24) that broadly summarizes these factors. Some of relationships are not concordant among all species and populations.

TABLE 24.—Summary of results for all species and populations evaluated in this study. The overall proportion of transients (% Transient), seasons that the proportion of transients was significant (Season Trans), overall proportion of adults (% Adult) and seasons that the proportion of adults was significant (Season Ad) are listed. Letters next to values listed in % Transient and % Adult indicate the significantly greater proportion if any was detected, R=Resident, T=Transient, A=Adult, J=Juvenile, N=No difference. Any association of proportion of transients and population density (Density) is listed with the direction of association (No, Negative). Body mass comparisons of residents and transients list the group with greater mass, where equal means no difference was detected. Sex ratio is calculated by dividing the total number of males by total number of females. Seasonal detections of dominant sexes are listed in Seasonal Dom. For all seasonal rows Sp=Spring, Su=Summer, Au=Autumn, Wi=Winter.

Species	**Cotton Rats**		**Meadow Voles**		**Prairie Voles**		**Rice Rats**
State	**Virginia**	**Kansas**	**Virginia**	**Illinois**	**Kansas**	**Illinois**	**Virginia**
% Transient	54.41^{T}	51.00^{N}	47.30^{R}	53.55^{T}	50.23^{N}	57.69^{T}	54.49^{T}
Season Trans.	Sp, Su, Wi	Su	Sp	Sp, Au	Sp, Su	Sp, Su, Au, Wi	Su
Density	No	No	No	Negative	No	Negative	No
Body mass	Equal	Equal	Equal	Residents	Residents	Residents	Equal

Table 24 Continued

Species	**Cotton Rats**		**Meadow Voles**		**Prairie Voles**		**Rice Rats**
State	**Virginia**	**Kansas**	**Virginia**	**Illinois**	**Kansas**	**Illinois**	**Virginia**
% Adult	69.14 ^{A}	58.50 ^{A}	86.28 ^{A}	51.41 ^{A}	49.72 ^{N}	50.77 ^{A}	41.29 ^{J}
Season Ad	Sp, Su, Au, Wi	Sp, Su, Au, Wi	Sp, Su, Au, Wi	Sp, Su, Au	Su, Au	Su, Au, Wi	Sp
Sex Ratio Male: Female	1.00	1.22	1.00	1.00	1.00	1.06	1.00
Seasonal Dom	Sp	Sp, Su, Au, Wi	Wi	Au	Sp, Su, Wi	Sp, Wi	-

Transience.—There has been little study of transience in rodent populations. Transience is considered by many investigators to be either an initial phase of dispersal or exploratory excursions into neighboring areas, potentially to scout for resources (Bjorndal and Bolton, 2000; Clavel et al., 2008; Karanth et al., 2006; Labonne and Gaudin, 2005; Morales et al., 2010; Perret et al., 2003; Sendor and Simon, 2003; Tannerfeldt and Angerbjörn, 1996). My study, designed to identify the quality of animals entering and perhaps passing through populations, evaluates transience as a life-history trait. Some immigrants are recruited into a population and become residents but others simply pass through. For 6 of the 7 populations evaluated here, transients formed a majority (>50%) of the initial captures (Table 24). The implications of this are that the majority of the individuals in these populations will not be seen after the trapping session in which they were initially captured, and that some proportion of these individuals is potentially functioning without the commonly held notion of a "home" range. If more than half of rodents within open-habitat populations are not limited to a circumscribed area around a central point of activity, then this concept should be viewed with caution, perhaps re-evaluated, and applied only after assessing the extent to which it may apply for specific geographic populations.

The proportion of transients in each geographic population was significantly associated with season, with spring and summer being the most common seasons in which high proportions of transients were detected (Table 24). Geographically, populations from Kansas had significantly greater proportions of transients in summer, whereas populations from Illinois had significantly greater proportions of transients in spring. Populations from Virginia did not have a season in which the proportion of transients was significantly greater than residents for all species. Cotton rats from Kansas and Virginia, as well as marsh rice rats, had significantly greater proportions of transients than residents in summer but not autumn. All geographic populations of *Microtus* had significantly greater proportions of transients than residents in the spring. The proportion of breeding transients was similar to that of breeding residents for all Virginia populations and for Kansas cotton rats; however, both Illinois populations had a significantly greater proportion of breeding transients than breeding residents.

The notion that small mammals, especially old-field rodents, live their lives in relatively small circumscribed areas is not supported by my study. The high proportions of transient animals entering 7 geographic populations supports the idea that there may be no circumscribed "home" range for a majority of individuals in a population. Undoubtedly some of the animals classified as transients died before recapture; however, I believe mortality alone cannot explain these large proportions of transients. The large proportion of transients supports the notion that small mammals are more vagile than current paradigms allow, even among more social species such as prairie voles.

No association between density and the proportion of transients was found for Kansas or Virginia populations. The lack of a relationship between density and proportion of transients in these populations supports the notion that resource availability is not a limiting factor for individuals entering but not remaining within a trappable population. Furthermore, Illinois populations had a negative relationship between density and transience, indicating that the proportion of transients passing through the populations decreased as density increased. This decrease in proportion of transients could be due to the recruitment of individuals into the resident population upon entry, thereby decreasing the detection of transients. An alternative explanation, presented by Dueser et al. (1981), is that when considering the immigration of animals, a negative correlation with density may indicate an immigrant-resistance effect, implying density-independent dispersal. In context, the populations with negative correlations (Table 24) all had a majority of initial captures comprised of transients, with both Illinois voles being significantly so. The negative correlation would then support the notion that there is a resistance to immigration, and thus an increase in transients, especially among more social rodent species. In corollary, a finding of no relationship between immigration and density supports the notion that there is little immigration-resistance within populations and the influx of immigrants into existing populations supports the notion of higher than assumed vagility. Those populations with no correlation of density and transience were generally comprised of a majority of transients as well, but none as high a proportion as Illinois prairie voles, 57.69%.

Body mass was similar between residents and transients for all populations from Virginia and for cotton rats from Kansas. The similarity of body masses between transients entering and passing through a population, and residents that were either born on, or recruited to, a study site indicates that the motivation for transience may not be food limitation in these populations, or possibly that the costs associated with transience are equivalent to the costs of residence. Voles from Kansas and Illinois had a difference in the mean body mass of residents and transients, with residents being significantly heavier than transients for both species. This implies either a higher proportion of juveniles as transients, which would equate to a lower mean mass on average, or that the costs of a transient lifestyle for voles in this system are greater than those of residents entering or remaining in a study area. The current paradigm would suggest that juveniles are more prone to leave a population, resulting in lighter animals traversing the landscape as transients and heavier animals remaining on the study grids as residents. The populations of Illinois and Kansas voles conform to this expectation as interpreted through body mass, but cotton rats from Kansas and all Virginia populations do not support this notion.

Expectations for the Proportions of Adults and Juveniles.—The proportion of adults for the 7 populations ranged from 41.29% to 86.28%, and varied seasonally with no dominant season common to all populations (Table 24). Populations from Kansas had greater proportions of adults than juveniles during summer and autumn, Illinois voles had greater proportions of adults during spring and autumn but not summer, and all Virginia populations had greater proportions of adults during spring. Geographically, there was variability among species for seasonal dominance; cotton rats from Kansas and Virginia and meadow voles from Virginia had significantly greater proportions of adults in every season, whereas other populations had dominant adult proportions between 1 and 3 seasons.

According to Greenwood (1980), juvenile males should comprise the largest proportion of transients (if transience is related in any way to dispersal), followed by adult males, juvenile females, and lastly adult females. No population or species met the expectation of juvenile males being the dominant transient group (Table 25). The proportions of juvenile male transients and adult male transients were similar for populations from Illinois, whereas proportions of adult male transients in Virginia and Kansas were similar to or greater than those of juvenile male transients in each area.

No geographic population had a biased sex ratio for juvenile transients, except rice rats from Virginia; cotton rats from Virginia and Kansas, and voles from Illinois had male-biased sex ratios for adult transients. These findings do not agree with the expectations of Greenwood (1980) in age or sex bias of transients. The implication of these findings is that differential mortality may occur for transients through selective pressure against reproductive maturity groups or sex. An alternate explanation of the biased sex ratios of adults could be that females recruit more successfully into populations and higher proportions become residents. The design of my study would not detect these animals as transients, but as adult residents; however, the change in proportion of recruited female transients is unlikely due to the absence of biased sex-ratios for adult residents in any geographic population.

TABLE 25.—Proportions of transient groups overall and results of Nemenyi tests for each geographic population. Groups are identified by 3 letter abbreviations on each row for reproductive maturity (juvenile or adult), sex (male or female), and residency status (transient). The proportion for each group is listed above the Nemenyi results, which are displayed as lower case letters. Different lower-case letters denote significant differences in proportions within a geographic population. Groups are listed in descending order of the expected proportions based on Greenwood (1980).

	Cotton Rat Virginia	Cotton Rat Kansas	Rice Rat Virginia	Meadow Vole Virginia	Meadow Vole Illinois	Prairie Vole Kansas	Prairie Vole Illinois
JMT	8.33	10.65	12.90	3.75	13.92	13.68	15.01
Nemenyi	*a*	*a*	*a*	*a*	*a*	*a*	*a*
AMT	20.56	18.19	15.48	21.72	14.45	11.49	15.32
Nemenyi	*b*	*b*	*b*	*b*	*a*	*a*	*a*
JFT	6.71	10.27	20.00	3.22	14.03	13.61	14.48
Nemenyi	*a*	*a*	*a*	*a*	*a*	*a*	*a*
AFT	18.47	12.71	6.45	18.77	11.06	11.41	12.61
Nemenyi	*b*	*ab*	*a*	*b*	*a*	*a*	*a*

Expectations of Sex Ratios.—The overall sex ratios of 5 of the populations did not differ from unity, whereas 2 populations had male-biased ratios (Table 24). All populations, except marsh rice rats, had seasonal biases in sex ratios. Kansas populations had biased ratios in spring and summer and Illinois populations in spring and autumn. Biased sex ratios differed within a geographic location, with 1 population from Kansas and Illinois having a bias but the other not differing from unity.

The sex ratios of groups, namely residents and transients, were expected to display biases on the basis of Greenwood (1980) and Dobson (1982). Overall, transients were expected to have a male-biased sex ratio and residents a female-biased ratio. Transients were male-biased sex ratios for both cotton rat populations and meadow voles from Illinois, and residents were female-biased for vole populations from Illinois and Kansas. The other species and populations did not conform to expectations. If the expectations of Greenwood (1980) and Dobson (1982) are interpreted in terms of reproductive resources, then we would expect transients and residents in active reproductive condition to have similarly biased sex ratios. Breeding transients had male-biased sex ratios for every geographic population, but sex ratios of breeding residents had a female-bias only for Virginia voles and were male-biased for populations in Illinois and the other remaining Virginia populations. Meadow voles from Illinois were the only geographic population to meet the biased sex-ratio expectation overall, or within a season. No other population met the sex-ratio expectation of a male bias for transients and female bias for residents overall or within any season. The lack of support provided by these results implies that there may be more complex mechanisms involved, not only in dispersal and philopatry, but also in differential mortality and selection between sexes.

Sigmodon hispidus.—Transience ranged from 51.0% to 54.49% overall for Virginia and Kansas, and 45.92% to 72.95% seasonally (Table 24). Both populations had a majority proportion of initial captures as transients, but only in Virginia was the proportion significantly greater than that of residents. Seasonally, both populations had a greater proportion of transients than residents in the summer and a greater proportion of residents in autumn. Both populations displayed annual variation in significant differences between residents and transients. The observed variation among seasons and years supports the effect that local climate can have on cotton rat abundance, and perhaps the quality of animals in the population (McClenaghan and Gaines, 1978). Seasonal abundance for cotton rats in Kansas declined in winter and peaked in both spring and autumn (McClenaghan and Gaines, 1978). Proportions of transients in both populations were unrelated to density, so variation between the proportions of residents and transients may be due to habitat quality as a result of climatic differences instead of density-dependent phenomena.

Breeding adults from Virginia did not differ in their proportions of residents and transients, but Kansas animals had a significantly greater proportion of breeding transients, 59.33%, than breeding residents, 40.67%. Breeding adults and transients in both populations were male-biased overall, which supports the notion of males in reproductive condition being transient; however, breeding residents were male-biased in Virginia and did not differ from unity in Kansas. From a reproductive resource perspective, we would expect breeding residents to be female-biased on the expectation of female philopatry and descriptions of female-dominated home ranges (Cameron and Spencer, 1981).

Oryzomys palustris.—For marsh rice rats in Virginia transients comprised a significant majority of the population overall and ranged from 45.90% to 83.33% seasonally, with trends similar to the Virginia populations of cotton rat (Table 24). Overall, the proportion of transients was not associated with density and the proportions of transients were significantly greater in summer and smaller in autumn than in other seasons. Because sample sizes of marsh rice rats captured from 2005 to 2010 were small, some of the proportions that might differ, such as the 57.14% proportion of transients in spring, were not significantly different from residents. Breeding adults and transients, similar to those of cotton rats, were male-biased overall but sex ratios of breeding residents did not differ from unity. These findings, as with the cotton rats, do not support either notion that the majority of individuals are born and live in circumscribed areas for the duration of their lives or the expectation of sex biases due to the life-history choice of transience.

The proportion of adult rice rats peaked in spring, 66.67%, and declined for each progressive season to a low of 35.71% in winter. An interesting note is the persistence of juveniles as the dominant maturity group overall and for 3 seasons of the year. In spite of this dominance, some juvenile groups were unrepresented in initial captures during spring and summer, most likely due to these seasons having the lowest sample sizes. In fact, the expectation of juvenile males as the group most prone to disperse was not supported for any season. The groups captured most often were juvenile female transients followed by adult male transients and adult male resident, and juvenile males last. This could be an artifact of sample size, or a representation of population structure that has not been previously evaluated. Future research into population structure of marsh rice rats should evaluate transience in more established populations, as well as age structure across seasons.

Microtus pennsylvanicus.—The overall proportion of transients was a significant majority in Illinois populations but not in Virginia populations. Both populations had seasonally significant proportions of transients in spring, but differed in other seasons (Table 24). The proportions of transients ranged from 41.70% to 59.79%. Both populations had annual variation in the dominant resident group, but differed in the association between density and proportion of transients. These differences in proportion of transients, their relationship with density, and seasonal fluctuations of proportions indicate that these populations operate under separate selective pressures, most likely attributed to their local climatic conditions. Aars and Ims (2002) found that conditions in winter, defined in their study as November through May, influenced survival as well as the demographic makeup of northern populations of tundra vole, with females being the more likely sex to survive the long Scandinavian winter.

The age structure of meadow voles at initial capture was significantly adult-biased for every season and overall. Furthermore, adults formed 82.50% to 95.60% of the population in Virginia compared to 35.24% to 58.55% in Illinois. Virginia populations had no initial captures of juvenile male transients in the summer, the season in which they were generally the most abundant in Illinois. The Virginia population had very low proportions of each juvenile group, 0% to 5.47%, whereas Illinois had a more uniform distribution overall, with only juvenile male residents being a significantly lower proportion than other groups (Fig. 11). Illinois meadow voles were the only population that conformed to the expectations of the paradigms of sex-biased life-history traits.

However, it was the only meadow vole population with a significant proportion of transients overall, offering further support to the notion that the majority of individuals on a study site will generally not have a central, or at least definable, point of activity.

Microtus ochrogaster.—Overall, the proportion of transients of prairie voles ranged from 50.23% to 57.69%. In Illinois prairie voles the proportion of transients was significantly greater than residents overall, was negatively correlated with density, and transients were significantly lighter than residents. Kansas prairie voles were not significantly resident or transient, but did share the trends of body mass found in Illinois. The seasonal proportion of transients ranged from 43.52% to 64.98%, with significant proportions of transients in the spring and summer in Kansas, but the Illinois populations had significant transience in every season. Both populations conformed to the expectation of female-biased sex ratios of residents, but neither population had a biased sex ratio for transients. The prairie vole is the "most" social of the 4 species evaluated in my study, yet had the highest proportion of transients. Both populations had transients as the majority of initial captures. The implication is that sociality in open-habitat rodent populations may not be a factor associated with transient behavior.

Structuring of prairie vole populations varied between geographic regions as well. Overall, Kansas voles had a more uniform distribution in their proportions of each group; all groups were equally represented (Table 19), which was not noted in any other species. Illinois populations were more complex and less uniform, with male transients having the highest proportions and juvenile residents the least (Table 22). The proportion of adults ranged from 43.12% to 54.28%. The proportions of adults in each season for Illinois were not significantly different, which given the support for seasonal changes in body mass (Aars and Ims, 2002; Iverson and Turner, 1974), is surprising because mass was the criterion for defining reproductive maturity. We would expect, if animals are generally lighter in spring or the end of winter, that there should be a significant difference between the proportions of adults due to the mass criterion; however, this was observed only for Kansas prairie voles.

CHAPTER V

CONCLUSIONS

My study was designed to examine patterns of transience in geographic populations of open-habitat rodent populations, as well as to test the paradigms governing our perceptions on the vagility of rodents and their population structure. No population examined conformed to all expectations listed by these paradigms, specifically that animals are born and live their lives in a circumscribed area with males being more prone to emigrate than females, and juveniles more prone than adults. The majority of animals in Kansas, Illinois, and Virginia had significant proportions of transients overall and seasonally. Similarly, the proportions of transient animals did not meet sex or age biased expectations; no population had a greater proportion of juvenile male transients than adult male transients, and for most of the populations adults were the most transient age group. No paradigm has become apparent that could adequately predict the patterns seen in this study, but existing paradigms should be applied with caution and used only as a starting point until greater analysis provides a framework for more reliable predictions.

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APPENDIX A

EQUATIONS

$$\hat{f}_{ij} = (\frac{R_i + C_j}{n})$$

EQUATION 1: Expected frequencies used in the Chi-square test of independence.

$$x^2 = \frac{(f_{ij} + \hat{f}_{ij})^2}{\hat{f}_{ij}}$$

EQUATION 2: Chi-square test of independence using expected frequencies.

$$Z = \frac{\hat{p}_1 - \hat{p}_2}{\sqrt{\frac{\overline{pq}}{n_1} + \frac{\overline{pq}}{n_2}}}$$

EQUATION 3: Two-sample Z-test (one tailed). Z value was compared to $Z_{crit} = 1.649$.

$$x^2 = \sum_{i=1}^{k} \frac{(X_i - n_i\bar{p})^2}{n_i\bar{p}\bar{q}}$$

EQUATION 4: Contingency table analysis using Chi-square test of independence with pooled proportions.

$$\bar{p} = \frac{\Sigma X_i}{\Sigma n_i} \qquad \bar{q} = 1 - \bar{p}$$

EQUATION 5: Calculation of pooled proportions for use in Equation 4.

$$p_i' = (\arcsin\sqrt{p_i}) \text{ x } 57.29578$$

EQUATION 6: Arcsin transformation of proportions and conversion into degrees.

$$\text{SE} = \sqrt{\frac{410.35}{n_a + 0.5} + \frac{410.35}{n_b + 0.5}}$$

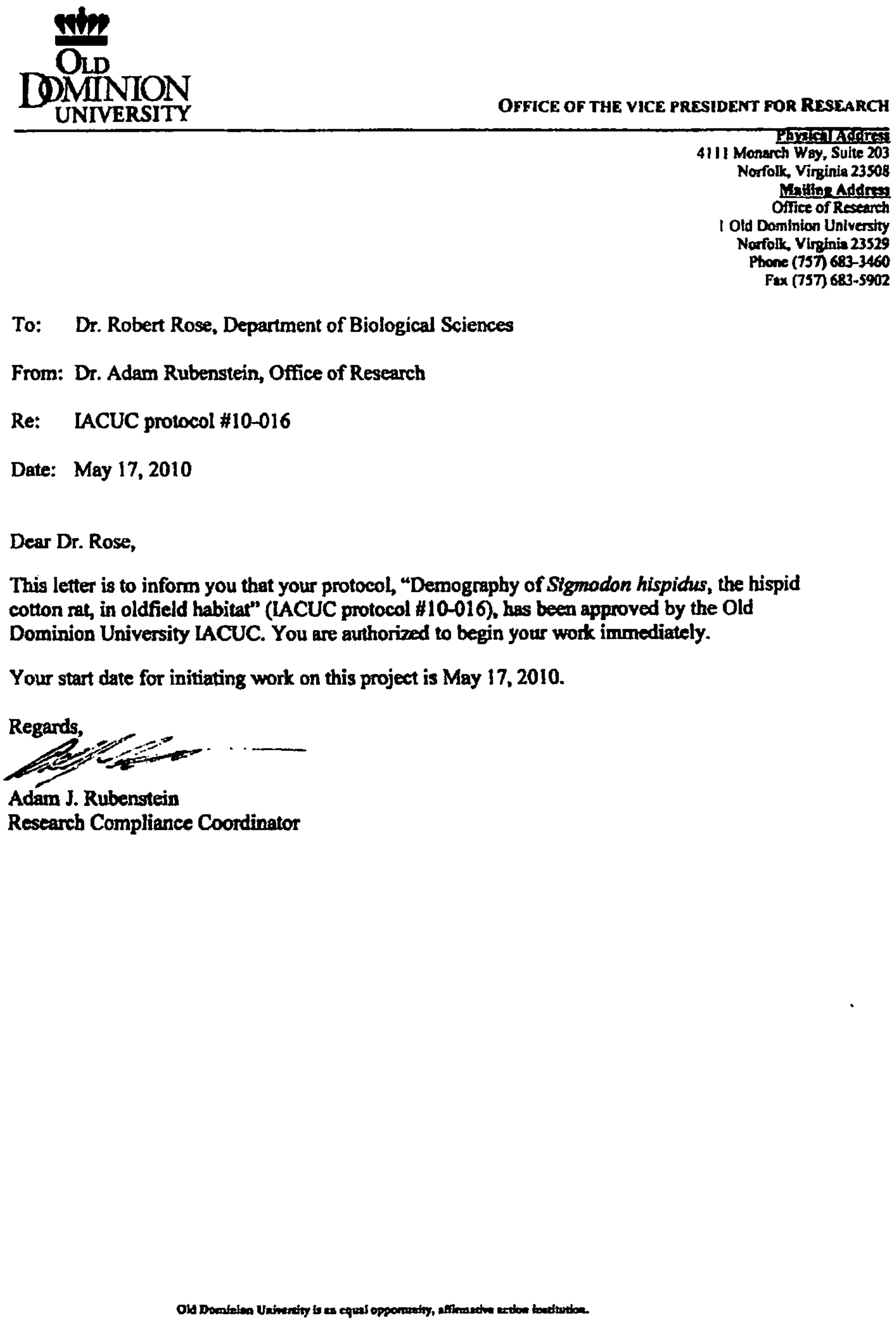
EQUATION 7: Calculation of the standard error of comparison for the Nemenyi test.

$$q = \frac{p'_a - p'_b}{\text{SE}}$$

EQUATION 8: Nemenyi Test for multiple comparisons among proportions.

APPENDIX B

COMPLIANCE INFORMATION



OLD DOMINION UNIVERSITY

OFFICE OF THE VICE PRESIDENT FOR RESEARCH

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Norfolk, Virginia 23508
Mailing Address
Office of Research
1 Old Dominion University
Norfolk, Virginia 23529
Phone (757) 683-3460
Fax (757) 683-5902

To: Dr. Robert Rose, Department of Biological Sciences

From: Dr. Adam Rubenstein, Office of Research

Re: IACUC protocol #10-016

Date: May 17, 2010

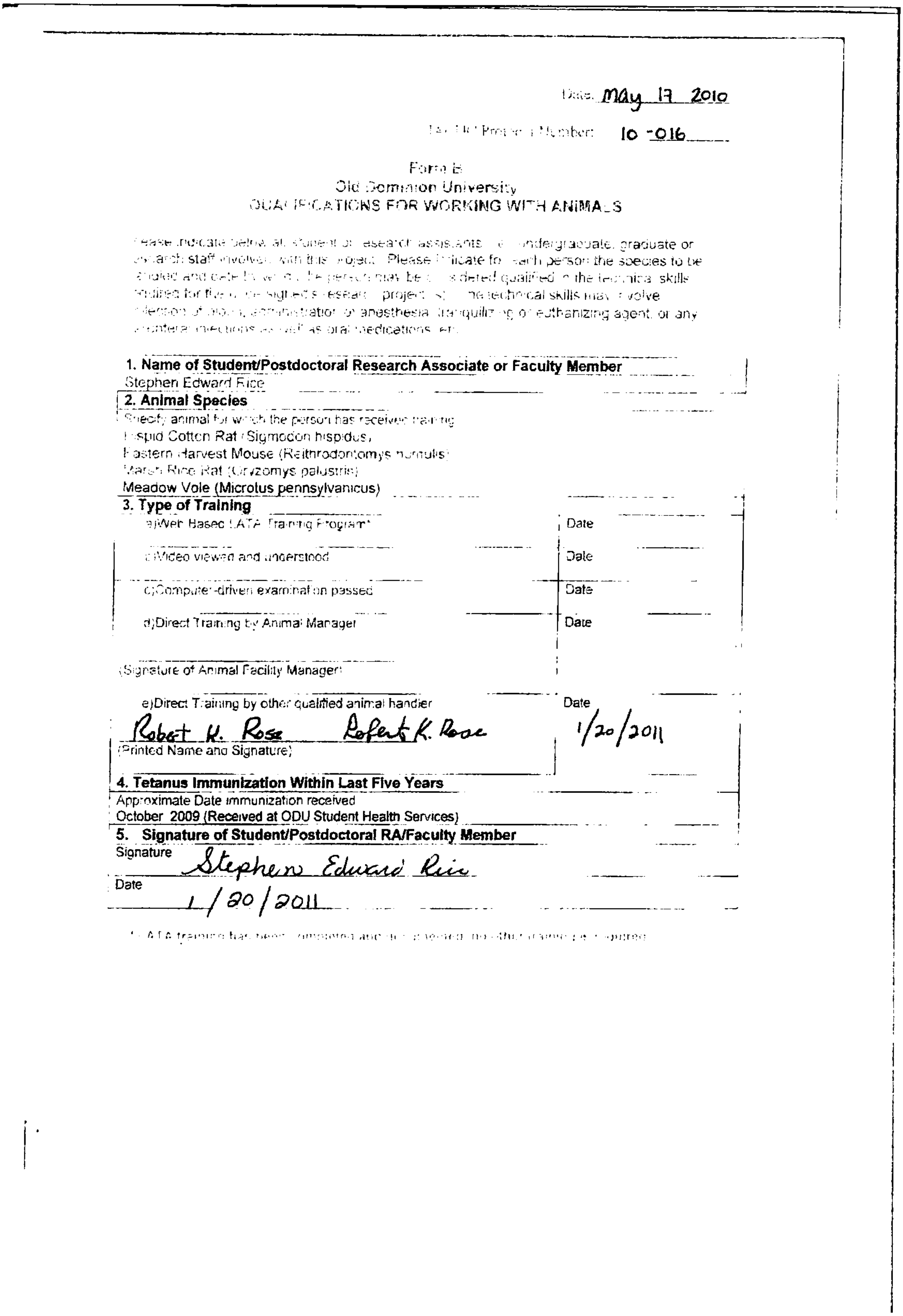
Dear Dr. Rose,

This letter is to inform you that your protocol, "Demography of *Sigmodon hispidus*, the hispid cotton rat, in oldfield habitat" (IACUC protocol #10-016), has been approved by the Old Dominion University IACUC. You are authorized to begin your work immediately.

Your start date for initiating work on this project is May 17, 2010.

Regards,

Adam J. Rubenstein
Research Compliance Coordinator



Date: May 17 2010

IACUC Protocol Number: 10 -016

Form B
Old Dominion University
QUALIFICATIONS FOR WORKING WITH ANIMALS

Please indicate below all student or research assistants (i.e. undergraduate, graduate or research staff) involved with this project. Please indicate for each person the species to be handled and date by which the person may be considered qualified in the technical skills required for the undersigned's research project. The technical skills may involve collection of blood, administration of anesthesia, tranquilizing or euthanizing agent, or any parenteral injections as well as oral medications, etc.

1. Name of Student/Postdoctoral Research Associate or Faculty Member

Stephen Edward Rice

2. Animal Species

Specify animal for which the person has received training

Hispid Cotton Rat (Sigmodon hispidus)
Eastern Harvest Mouse (Reithrodontomys humulis)
Marsh Rice Rat (Oryzomys palustris)
Meadow Vole (Microtus pennsylvanicus)

3. Type of Training

a) Web Based LATA Training Program* Date
b) Video viewed and understood Date
c) Computer-driven examination passed Date
d) Direct Training by Animal Manager Date

(Signature of Animal Facility Manager)

e) Direct Training by other qualified animal handler Date

Robert K. Rose Robert K. Rose 1/20/2011
(Printed Name and Signature)

4. Tetanus Immunization Within Last Five Years

Approximate Date immunization received
October 2009 (Received at ODU Student Health Services)

5. Signature of Student/Postdoctoral RA/Faculty Member

Signature Stephen Edward Rice
Date 1/20/2011

* If LATA training has been completed and is accepted, no other training is required.

VITA

Stephen E. Rice *curriculum vitae*

Contact Information

Dept. of Biological Sciences
Old Dominion University
Norfolk, VA 23529

Education

M.S. -	Old Dominion University *Biology, Advisor: Robert K. Rose*	(4.0/4.0)	2011
B.A. -	University of North Carolina - Asheville *Biology, Concentrations: Ecology/Evolution; Molecular/Cellular*	(2.98/4.0)	2003

Professional Employment

Teaching Assistant – Anatomy and Physiology *Old Dominion University*	Norfolk, VA	2010-2011
Research Technician *ODU, Animal Care Facility*	Norfolk, VA	2009-2011
Online Life Sciences Instructor *Crescent Preparatory High School*	Dania Beach, FL	2009-2011
Middle School Science Instructor/Dean of Students *Downtown Academy of Technology and Arts*	Ft Lauderdale, FL	2006-2008
Laboratory Supervisor *Natural Immunogenics, Inc*	Ft Lauderdale, FL	2005-2006

Memberships

American Society of Mammalogists, Animal Care and Use Committee (ASM), Virginia Academy of Science, ODU Biology Graduate Student Organization

Presentations

Rice, S. R., and R. K. Rose. 2011. Patterns of transience, sex bias, and body mass in open-habitat rodent populations. 91st annual meeting of the American Society of Mammalogists poster exhibition, University of Oregon, Portland OR.

Rice, S. R., and R. K. Rose. 2011. Patterns of residence, sex bias, and body mass in open-habitat rodent populations. 89th annual meeting of the Virginia Academy of Science, University of Richmond, Richmond, VA.

Rice, S. R., and R. K. Rose. 2011. Patterns of transience, sex bias, and body mass in open-habitat rodent populations. Biology Graduate Student Organization Spring Symposium, Old Dominion University, Norfolk, VA.

Honors and Awards

BGSO Spring Symposium 3rd Place Award	ODU	2011