A COMPARISON OF TRAPPING METHODOLOGIES AND GRID SIZE FOR SMALL MAMMAL RESEARCH

by

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ABSTRACT

This study was designed to compare two distinct trapping systems in their ability to assess small mammal abundance, and to determine the optimal number of days to adequately sample populations. The hypothesis tested was that trapping for short periods of time throughout the field season would yield a more frequent regime of results, compared to trapping for longer periods two or three times a year. The study area was in Summerland, British Columbia, where deer mice (*Peromyscus maniculatus*), montane voles (*Microtus montanus*) and Great Basin pocket mice (*Perognathus parvus*) were live-trapped in grasslands on six 1-ha replicate grids from June to October 1997. Three of the grids were sampled for two consecutive nights, every three weeks, from June to October. The other three grids were trapped for ten consecutive nights in June, August and October. I suggest that trapping for short periods of time throughout the year or field season will give a better estimate of small mammal population dynamics. A minimum of two and maximum of four night trapping sessions throughout the field season is recommended.

An additional objective of this study was to evaluate the differences between estimates of small mammal population densities from grids of different sizes, and to determine the optimal grid size in estimating abundance. The hypothesis tested was that 1-ha grids would be as precise as larger grids in assessing small mammal abundance. Study areas were located in Vernon, Penticton, Kamloops and Prince George, British Columbia. For Experiment A, deer mice and northwestern chipmunks (*Tamias amoenus*) were trapped on 5-ha grids from May to October 1991 and 1992, and population estimates from 1- and 2-ha grids within the 5-ha grids were compared. For Experiment B, Northwestern chipmunks were sampled on 1- and 9-ha grids from May to August, 1990 and 1991. One ha grids were found to be as precise as 2-and 5-ha grids for density estimation of deer mice and northwestern chipmunks. However, estimates from the 1-ha grids were higher than estimates from the 9-ha grids. Additional research should focus on using identical methodologies and trap type for both 1- and 9-ha grids.

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GENERAL INTRODUCTION

Problems in estimating small mammal abundance are common in wildlife management studies and environmental impact assessments. Part of the difficulty is a lack of general consensus on trapping methodologies, grid size and estimators of population density. Accurate estimation of population density is an important prerequisite to better understanding behavioral ecology and management of a given species. Small mammals contribute to biodiversity of many habitats, both to the diversity of species and life forms and to the functional diversity of ecosystems (Carey and Johnson 1995). In addition, the importance of reliable density estimates can hardly be minimized since they are used for calculations in studies of bioenergetics, mineral cycling, population ecology and in studies of mammals as disease vectors (Smith *et al.* 1971).

Two distinct trapping systems are generally being used for small mammal research. The first prescribes intensive trapping for five to ten consecutive nights a few times a year, usually in June and October or once in August (Smith *et al.* 1971; Hansson, 1975; Radvanyi 1980; Cross *et al.* 1985; Medin and Clary 1990; Thompson 1986; Rosenberg and Anthony 1993; Carey and Johnson 1995; Hayes *et al.* 1995; Brooks *et al.* 1998; Menzel *et al.* 1999). In the second system, trapping is done for two or three consecutive nights and is conducted throughout the year, or the field season, usually May to October, at two-to-four week intervals (Krebs 1966; Krebs *et al.* 1969; Redfield *et al.* 1977; Sullivan and Sullivan 1982b; Boonstra 1985; Bondrup-Nielsen 1987; Desy *et al.* 1989; Ritchie and Sullivan 1989; Runciman and Sullivan 1996; Fryxell *et al.* 1998; Sullivan *et al.* 1998b; Van Horne, 1982).

Criticism for both methods arises mainly on the reliability to survey an adequate sample of the small mammal populations. Some argue that five-to-ten night trapping periods twice during the year is not enough to get a realistic estimate of population abundance and diversity. Trapping is not conducted during the summer months, and hence no data can be recorded on reproduction, weight and survival, all of which are important population parameters. In addition, chances of trapping transient animals may be increased and there is a greater likelihood of stressing animals from confinement in

traps if individuals are captured repeatedly over a ten-day period. However, it has also been argued that two night trapping periods every three weeks, for example, is not intensive enough to provide an adequate sample size from the population for that period. Accurate estimation of small mammal population parameters often requires a large number of observations (Swihart and Slade, 1985). Trapping for as long as ten nights two or three times every year might give precise estimates and would likely reduce the risks of autocorrelation between estimates since sampling periods are separated by longer intervals. However, trapping for a few nights ten to 20 times every year would yield a more accurate estimate of the real population size. The long time frame of such a study would ensure that sample size and trapping intensity is sufficiently large to yield accurate estimates despite the autocorrelated nature of the observations. My study assessed both methods in the field to evaluate the differences between them, if any, in estimating abundance.

Data from the "ten night" trapping periods were analyzed using the program CAPTURE (Otis *et al.* 1978) while data from the "two night" intervals were analyzed using the Jolly-Seber model of population estimation (Seber 1982). Both were also analyzed using minimum number of animals known to be alive (MNA) (Krebs 1966).

Grid size has also been very controversial in recent years. While some argue that 1-ha grids are large enough to adequately sample a small mammal population, others advocate the use of grids as large as 5-ha. Grids ranging from 0.7- to 1.4-ha have been used in many small mammal studies (Krebs *et al.* 1976; Redfield *et al.* 1977; Sullivan 1979a; Renzulli *et al.* 1980; Sullivan and Sullivan 1982b; Boonstra 1985; Sullivan *et al.* 1993; Zimmerling and Sullivan 1994; Runciman and Sullivan 1996; Hayward *et al.* 1997; Brooks *et al.* 1998; Von Trebra *et al.* 1998; Menzel *et al.* 1999), but grid size is still one of the major criticisms of many reviewers (Bondrup-Nielsen, 1983; Ritchie and Sullivan 1989, Smith, 1999; Sullivan *et al.* 1999). This design has been described as inappropriate to adequately report absolute densities of small mammals since the 1-ha grid is too small in relation to the home range of small mammals. This discrepancy results in a large "edge effect" (Smith *et al.* 1975; Swift and Steinhorst 1976; Van Horne 1982; White *et al.* 1982; Bondrup-Nielsen 1983; Wilson and Anderson 1985a; Wilson and Anderson 1985b). On average, 1-ha grids are trapped from May to October, at two- to three-week

intervals for two nights. When larger grids are used, the trapping intensity tends to decrease to one to three trapping periods which last from five to ten nights (Van Vleck 1968; Smith *et al.* 1971; Hansson, 1975; Jones and Sherman, 1983; Radvanyi 1980; Medin and Clary 1990; Hallett *et al.* 1991, Kohler 1993; Rosenberg and Anthony 1993; Hayes *et al.* 1995).

When the size of live-trapping grid used is less than approximately four times the average home range size, marked overestimates of population size will occur. At ratios of less than 16 (grid size to home range size), the variation in overestimate caused by home range shape and dispersion is considerable (Bondrup-Nielsen 1983). My study looked at the differences between population estimates (number of animals/ha) from 1- and 2- ha grids taken from 5 ha grids to evaluate if there really is a need for larger sample areas. Another comparison was made using 9- and 1-ha grids located in the same study areas, and were sampled at consecutive periods.

CHAPTER 1

A COMPARISON OF NUMBER OF TRAP NIGHTS FOR MEASURING POPULATION DYNAMICS

INTRODUCTION

Rodents are widely distributed in many terrestrial ecosystems including forests, agricultural lands and urban areas. The need to study and census small mammal populations arises for many reasons. Assessing the effects of forest management on population dynamics, controlling the damage to plantations and orchards, and evaluating trophic relationships of endangered species are examples of small mammal studies. The small mammals themselves may be the primary food source of an endangered predator species. The estimation of abundance is central to basic and applied ecology and capture-recapture methods are widely used to gather information for this and other various parameters of animal populations. Of the many techniques available for estimating population size, mark-recapture is one of the more common methods used (Menkens and Anderson 1988). The difficulty arises when a general consensus on trapping methodology is not met. Several studies have investigated the differences between widely used methods of analysis (Manly 1970, Boonstra 1985, Hallett *et al.* 1991, Boulanger and Krebs 1994, Manning *et al.* 1995), but no one has looked at the root cause of the problem: how should the data be collected to estimate, as accurately as possible, population size. Two different trapping procedures are generally used for small mammal population studies, each of which has different assumptions and characteristics and are usually associated with specific data analysis methods.

Small mammal sampling conducted from May to October at two- to four- week intervals is one of the commonly used trapping systems (Krebs 1966; Krebs *et al.* 1969; Redfield *et al.* 1977; Sullivan and Sullivan 1982b; Boonstra 1985; Desy *et al.* 1989; Ritchie and Sullivan 1989; Runciman and Sullivan 1996; Fryxell *et al.* 1998; Sullivan *et*

al. 1998b; Van Horne 1982). Data collected using this method is usually analyzed using the Jolly-Seber (Seber 1982) and minimum number known to be alive (MNA) (Krebs 1966) models. Supporters of this method argue that population size is better estimated when trapping is done throughout the year (or May to October), since the population is closely monitored. In addition to evaluating population size, this method also enables the measurement of parameters such as survival, body mass, recruitment, reproduction and trappability, all of which can be very useful to determine the condition of a population. Sampling of small mammals in such a way, and the use of Jolly-Seber and MNA models, assume that the population sampled is open (i.e. immigration, emigration, births and deaths are incorporated). In addition, the Jolly-Seber model makes the following assumptions: 1) every animal in the population has the same probability of being captured in the *i*th sample ($i = 1,...K$), given that it is alive and in the population when the sample is taken; 2) every animal has the same probability of surviving from the *i*th to the $(i + 1)$th sample, given that it is alive and in the population immediately after the *i*th release; 3) marked animals do not lose their marks and all marks are reported on recovery; and 4) the actual time spent sampling occupies a short period (Nichols and Pollock 1983). Furthermore, sampling must be random, survival rates and probabilities of survival must be unaffected by the marking of animals, and survival rates must be independent of the age of the animals (Manly 1970).

Another commonly used trapping system advocates an extended trapping effort over six to ten consecutive nights twice a year, generally in May and October (Smith *et al.* 1971; Hansson, 1975; Radvanyi 1980; Thompson 1986; Rosenberg and Anthony 1993; Carey and Johnson 1995; Hayes *et al.* 1995; Brooks *et al.* 1998; Menzel *et al.* 1999). Data collected using this method is generally analyzed using program CAPTURE (Otis *et al.* 1978). The assumption of demographic closure, that is, no births, deaths, immigration or emigration during the study, is one of the defining features of program CAPTURE and is largely what differentiates the two population estimators. In addition to the closure assumption, CAPTURE makes specific assumptions about an animal's capture probability. Three sources of variation can be incorporated into capture probabilities: 1) time; 2) behavioural (or trap) response; and 3) individual heterogeneity (Otis *et al.* 1978). CAPTURE models assume that time is a factor influencing capture

probabilities and allow these probabilities to change between trap periods. Behavioural response models infer that all animals initially have the same probability of being captured. After being captured, however, an animal may become "trap-happy" (increased probability of capture) or "trap-shy" (decreased probability of capture). Individual heterogeneity-based models permit each animal to have a unique capture probability that could be influenced by age, sex, social status or other innate characteristics. It can also be caused by unequal access to traps by different animals (Otis *et al.* 1978). Program CAPTURE consists of 8 models, five with estimators, for estimating population size when these variations in capture probabilities act independently or in combination. CAPTURE models are: the constant capture probability model, *M*o; the time variation model, *M*t; the behavioral response model, *M*b; the individual heterogeneity model, *M*h; and a combination of the last three models, *M*bh, *M*th, *M*tb, and *M*tbh (Menkens and Anderson 1988). It is difficult to decide on the most appropriate model, and therefore a model selection procedure has been implemented into program CAPTURE. However, the low power of the selection routine is well documented (Menkins and Anderson 1988; Otis *et al.* 1978; Boulanger and Krebs 1994). As suggested by Boulanger and Krebs (1994), only one model of consistent bias was used for this study. The Jackknife estimator was used for all data analysis as it is considered to be the most robust of all CAPTURE estimators (Otis *et al.* 1978; Manning *et al.* 1995), and is recommended for cases in which there is a high number of recaptures, as in this study. Jackknife was also found to be the less biased of all estimators (Hallett *et al.* 1991; Manning *et al.* 1995; Rosenberg *et al.* 1995).

This study was designed to evaluate the most efficient way to sample small mammals to yield population density estimates which are as accurate as possible. Each sampling method resulted in data collection which was later analyzed using the model most often associated with the methodology used.

The two major objectives were to: 1) determine the difference between two distinct trapping systems in assessing small mammal abundance; and 2) determine the optimal number of sample days for adequate estimation of small mammal populations.

Based on these objectives, specific hypotheses, phrased as predictions, were: 1) trapping for short periods (two nights) throughout the season (from May to October) will

give a more precise estimate of small mammal population dynamics than will trapping for longer periods of time (ten nights) in each of June and October; and 2) there will be no difference between trapping small mammals for five or ten nights, as the number of new animals captured significantly declines after the fifth night.

MATERIALS AND METHODS

Study Area and Experimental Design

Small mammals were studied in grassland-sagebrush habitats near Summerland, British Columbia, from June to October 1997. The climate is classified as semi-arid, characterized by warm, dry summers and cool, dry winters. Average annual precipitation is 281 mm with 2021 hours of annual sunlight. Mean low (January) and high (July) temperatures are –6.3 °C and 27.8 °C, respectively. A slight degree of cooling (1.6 to 2 °C) and an increase in precipitation (53 mm) occurs from north to south, however, there is generally little variation from these data (Sullivan *et al.* 1987). The dominant coniferous species is Ponderosa pine (*Pinus ponderosa*) and vegetation consists mainly of big sagebrush (*Artemisia tridentata*), common rabbit-brush (*Chrysothamnus nauseosus*), diffuse knapweed (*Centaurea diffusa*) and grasses and herbs. These vegetative conditions provided excellent habitat for small mammals.

Six experimental units were selected in areas which were identified as being similar in terms of parameters such as vegetation, elevation, temperature, and precipitation. All grids were separated by at least 150 m to minimize animal movement between them and enough to make them true replicates of each other (Figure 1).

One live-trapping grid was located in each experimental unit. These units were established in a randomized design, with three being used for ten night trapping periods in June, August and October, and three used for two night trapping periods every three weeks from June to October.

Small Mammal Populations

All six grids had 49 (7 x 7) trap stations located at 14.29-m intervals with one Longworth live-trap (Penlon Limited, United Kingdom) placed within a 2-m radius of each station. Longworth traps have been specifically designed to capture small mammals and will sample the majority of rodents and insectivores in a given area. Several studies have used Longworth traps to capture all known forest floor small mammals in forests and grasslands (Sullivan and Sullivan 1982b; Boonstra 1985; Bondrup-Nielsen 1987; Sullivan 1990; Zimmerling and Sullivan 1994; Runciman and Sullivan 1996; Von Trebra

Figure 1. Aerial photograph of the research site and grid locations near Summerland, BC - 1:15 000 scale.

et al. 1998). Voles are particularly sensitive to confinement and must be provided with warm and dry accommodation, such as is offered in the nest box of the Longworth trap (Ritchie and Sullivan 1989). Sampling of small mammals was done from June 20 to October 20, 1997 (Table 1). For each grid, a two-week pre-baiting period preceded sampling. Baited traps were left at each station with doors locked open to enable animals to familiarize themselves with the traps. Voles may avoid entering traps newly placed in their environment (Chitty and Kempson 1949) and therefore, prebaiting is a common technique in small mammal trapping. Small mammals were live-trapped for 10 consecutive nights in June, August and October on grids 1, 2 and 3 and for 2 consecutive nights every three weeks from June to October for grids 4,5 and 6 (7 trap sessions). In most experiments using ten-night trapping periods, the data were collected only twice a year (usually May and October). However, for this study, data were also collected in August to look at differences, if any, between population density for that month and May and October. Traps were set on the afternoon of day 1, checked on the morning of day 2, set again on the late afternoon of day 2, and checked on the morning of day 3 for grids 4, 5 and 6. The same procedure was continued until day 11 for grids 1, 2 and 3. Intense heat during the day (25-35 ° C) prevented trapping during the afternoon. Traps were all baited with oats and a slice of carrot; coarse brown cotton was supplied as bedding. They were also covered with a piece of wood to offer protection from rain and direct sunlight. All traps were locked open between trapping sessions. For each capture, animals were marked with serially numbered metal ear-tags (National Band and Tag, Newport, Kentucky, USA), and the location, body mass (± 0.5 g on a Pesola spring balance), gender, and breeding condition recorded. The breeding condition of males was evaluated through palpation of the testes. Females were considered in breeding condition if they were obviously pregnant (high body mass and distended lower abdomen), lactating (verified through palpation), or had developed nipples and mammae that showed signs of nursing (Krebs *et al.* 1969). Animals were released at point of capture immediately following data collection.

Table 1. Fieldwork schedule for each small mammal sampling grid near Summerland BC.

GRIDS 1-2-3	Week 1	June 21-July 1, 1997
	Week 8	August 7-17, 1997
	Week 17	October 10-20, 1997
GRIDS 4-5-6	Week 1	June 19-21, 1997
	Week 4	July 8-10, 1997
	Week 7	July 30-August 1, 1997
	Week 10	August 23-25, 1997
	Week 13	September 10-12, 1997
	Week 16	October 1-3, 1997
	Week 19	October 20-22, 1997

Population Dynamics

Population density (animals/ha), minimum survival, reproduction and male body mass were estimated on all grids for the three most frequently captured small mammal species: *Peromyscus maniculatus* (deer mouse), *Microtus montanus* (montane vole), and *Perognathus parvus* (pocket mouse). Comparisons of minimum survival at every 21 days, proportion of breeding animals and male body weight between the six experimental units were used to establish that the six replicates were similar. Minimum survival was calculated for each trap period i and is defined as the total number of marked animals in the population just before the $(i + 1)$th sample, divided by the total number of marked animals in the population immediately after sample i (Nichols and Pollock 1983). The proportion of breeding males and females from June to October was used to evaluate reproduction. An animal was recorded as breeding if it was in this condition at least once during the study. Comparisons of body mass were based on the mean mass of each resident male and averaged for all males on each grid. Only male body weights were used to avoid overestimates of female body weight from pregnant or lactating individuals.

For grids 1, 2 and 3, size of the population was estimated using the program CAPTURE (Otis *et al.* 1978). CAPTURE tests for closure, for assumptions concerning how capture probabilities vary with respect to time, behavior and heterogeneity, and the

Model Selection Procedure selects the best fitting model and associated estimator for the data from each trapping period (Hallett *et al.* 1991). The Jackknife estimator, which has been recommended by Burnham and Overton (1979) as a general estimator, was used in all cases. It was reported to yield reliable estimates when capture probabilities were heterogeneous and the population was assumed closed during the sampling period (Otis *et al.* 1978). Complete enumeration using minimum number of animals known to be alive (MNA) (Krebs 1966) also provided density values for the three trapping periods at each of the three sites. This model provides sufficiently accurate estimates for a trapping design in which 80% or more of the animals are caught at each sampling time (Hilborn *et al.* 1976). MNA is the number of animals that can be identified as alive at a certain time *i*, and can be defined as the total number of animals caught at time *i*, plus the number of animals that were caught and marked before *i*, and caught alive again after *i*. This argument rests on the assumption that, while "death" may include permanent emigration, temporary emigration is not occurring (Jolly and Dickson 1983).

Population density for grids 4, 5 and 6 was calculated using the Jolly-Seber model (Seber 1982), which is designed for mark-recapture samples taken from open populations on three or more occasions (Krebs 1989). However, the reliability of the Jolly-Seber model declines when population sizes are very low, and no marked animals are captured (Krebs *et al.* 1986). Therefore, minimum number alive (MNA) was also calculated and replaced Jolly-Seber estimates for some sampling weeks or for some species when it was biologically unreasonable and could not be calculated. MNA also served as the only common method of analysis between the six grids and was used to compare population densities between them. Population density for grids 1, 2 and 3 was calculated using MNA and CAPTURE (Otis *et al.* 1978), which is available as computer software. Minimum survival and population density (Jolly-Seber and MNA) for grids 4, 5 and 6 were calculated using *Small Mammal Programs for Mark-Recapture Data Analysis* (Krebs 1991).

Statistical Analysis

Reproduction, male body mass and minimum survival rates were compared between the six replicates to evaluate the differences, if any, between them. Reproduction for males and females was compared between the six grids using an analysis of variance (ANOVA). Arcsine transformations were performed on the percentages of breeding males and females and on survival percentages to alter the binomially distributed proportions to resultant data which have an underlying distribution that is normal (Zar 1996). Male body mass was also compared using an ANOVA for each species. Minimum survival rates for males and females were also compared between the six replicates using an ANOVA.

For grids 1, 2 and 3, CAPTURE and MNA estimates for weeks 1, 8 and 17 were compared using ANOVA, which was also used to compare population densities from Jolly-Seber and MNA for grids 4, 5 and 6. CAPTURE estimates from grids 1, 2 and 3 were compared to Jolly-Seber estimates from grids 4, 5 and 6, and finally MNA estimates from grids 1, 2 and 3 were compared to MNA estimates from grids 4, 5 and 6. All comparisons were done using a split plot analysis of variance, with time as a split plot. Standard errors were calculated on the averages of the three grids for each estimator (Jolly-Seber, MNA and CAPTURE) and are presented in the graphs. CAPTURE and MNA estimates from grids 1, 2 and 3 calculated for 2, 4, 6, 8 and 10 nights were compared using a split plot analysis of variance on the population estimate for each grid at each week, with each week representing a treatment, each grid a block, and each night a split plot. Furthermore, significant differences between nights were determined using the Bonferroni Multiple Comparisons test. Statistical analysis for all population density estimates was conducted using the SPSS statistical analysis package. All previously described analyses were performed for each species.

For grids 1, 2 and 3, CAPTURE and MNA estimates were averaged over three replicates for weeks 1, 8 and 17. For grids 4, 5 and 6, Jolly-Seber and MNA estimates were averaged over three replicates for weeks 1, 4, 7, 10, 13, 16 and 19. For CAPTURE, the Jackknife estimator was used in all cases.

ANOVA tables for all population density analyses can be found in Appendix A and B. For all statistical comparisons, the level of significance was set at $P= 0.05$.

RESULTS

P. maniculatus and *M. montanus* were the most abundant small mammals on each of the six grids, and therefore major conclusions from the analyses of population parameters are dominated by these two species. However, data from the less common species, *P. parvus*, are presented as supporting evidence. Very low numbers of this species were captured on some grids, and consequently, reliable data analysis was not always possible. Northwestern chipmunks (*Tamias amoenus*) were also captured on some occasions on the six grids but dependable data analysis was not possible for this species. Only three long-tailed voles (*M. longicaudus*) were caught on different grids during the study, and therefore will not be part of the data analysis.

Reproduction

The start of the breeding season was the time of capture of the first scrotal male or lactating female; the end of the breeding period was the week in which the last breeding animal was recorded. *P. maniculatus* had the longest breeding season of all species from mid- to late-June to the end of September. *M. montanus* and *P. parvus* had more restricted breeding seasons. There was little difference in the proportion of breeding males and females between the six grids from June to October. The overall percentage of male *P. maniculatus* in breeding condition ranged from 27.5% to 53.3% and the percentage of breeding females ranged from 20.0% to 60.7%. (Table 2). There were no significant differences among grids in the proportion of male ($F_{1,4} = 0.04$, $P > 0.5$) and female ($F_{1,4} = 1.35$, $P > 0.5$) deer mice in breeding condition.

The breeding season for *M. montanus* started in mid- to late July and ended in mid-October. Although *M. montanus* had the second longest breeding season, the number of breeding males and females were highest for this species. Only one male was captured on grid 1 therefore yielding a breeding percentage of 100%. The proportion of breeding males ranged from 34.5% to 100% and from 28.0% to 58.6% for females (Table 2). There were no significant differences among grids in the proportion of breeding males ($F_{1,4} = 0.01$, $P > 0.5$) and females ($F_{1,4} = 3.61$, $P = 0.15$).

Table 2. *P. maniculatus* - *M. montanus* - *P. parvus*: Sample size and percentages of breeding males and females.

MALES	*P. maniculatus*		*M. montanus*		*P. parvus*	
	n	%	n	%	n	%
GRID 1	58	32.8	1	100	17	52.9
GRID 2	30	43.3	29	34.5		
GRID 3	54	37.0	22	54.6	14	64.3
GRID 4	40	27.5	15	66.8	11	18.2
GRID 5	40	37.5	32	71.9	5	20.0
GRID 6	15	53.3	25	84.0	6	16.7
FEMALES	*P. maniculatus*		*M. montanus*		*P. parvus*	
	n	%	n	%		
GRID 1	52	23.1	8	50.0	19	31.6
GRID 2	44	22.7	25	28.0		
GRID 3	61	31.2	31	48.4	6	16.8
GRID 4	43	39.5	15	53.3	12	8.3
GRID 5	28	60.7	44	56.8	4	0
GRID 6	25	20.0	29	58.6	5	20.0

On average, male *P. parvus* were breeding from weeks two (late June) to eight (early August), while females were recorded reproductively active from weeks two to four (early July). No *P. parvus* were captured on grid 2 during the study. The percentage of males in breeding condition ranged from 16.7% to 64.3% and from 0.0% to 31.6% for females (Table 2). A significant difference was found among grids in the proportion of breeding males ($F_{1,3} = 87.7$, $P = 0.003$), but no difference was found for female *P. parvus* ($F_{1,3} = 1.91$, $P > 0.5$).

Body Weight

Body weights of male *P. maniculatus* were similar ($F_{1,4} = 0.22$, $P > 0.5$) across the six grids and ranged from 21.2 g to 25.2 g (Table 3). Average body weight of male *M. montanus* ranged from 31.3 g to 44.0 g. There was no significant difference among grids for mean adult body weight of *M. montanus* ($F_{1,4} = 0.29$, $P > 0.5$) (Table 3). *P. parvus* was the smallest species sampled, with average male body weight ranging from

Table 3. *P. maniculatus* - *M. montanus* - *P. parvus*: Sample size and mean male body mass with 95% confidence intervals.

MALES	*P. maniculatus*		*M. montanus*		*P. parvus*	
	n	MASS (g)	n	MASS (g)	n	MASS (g)
GRID 1	58	25.2 ± 1.9	1	38.0 ± 0.0	17	20.4 ± 2.3
GRID 2	30	21.2 ± 2.7	29	31.3 ± 3.6		
GRID 3	54	23.0 ± 1.5	22	44.0 ± 4.6	14	22.6 ± 2.1
GRID 4	40	23.5 ± 2.2	15	40.2 ± 3.8	11	23.9 ± 2.3
GRID 5	40	23.8 ± 1.7	32	39.7 ± 4.2	5	22.2 ± 5.5
GRID 6	15	23.7 ± 2.2	25	39.2 ± 3.4	6	22.8 ± 2.7

20.4 g to 23.9 g. There was no significant difference among grids in body weight ($F_{1,3}$ = 0.43, $P > 0.5$) (Table 3).

Survival

Minimum survival rates per 21 days of male ($F_{1,4}$ = 2.91, $P > 0.5$) and female ($F_{1,4}$ = 1.43, $P > 0.5$) *P. maniculatus* were similar across the six grids and averaged 45.6% (grids 1, 2 and 3) and 61.2% (grids 4, 5 and 6) for males and 47.1% (grids 1, 2 and 3) and 56.2% (grids 4, 5 and 6) for females (Table 4).

Similarly, no significant difference was found between minimum survival rates per 21 days of males ($F_{1,4}$ = 1.40, $P > 0.5$) and females ($F_{1,4}$ = 1.37, $P > 0.5$) of *M. montanus*. Average survival rates for males were 21.4% (grids 1, 2 and 3) and 38.4% (grids 4, 5 and 6) while for females, the estimates averaged 34.2% (grids 1, 2 and 3) and 58.3% (grids 4, 5 and 6) (Table 4).

The analysis of minimum survival rates per 21 days for *P. parvus* showed no significant difference between the six grids for either males ($F_{1,3}$ = 0.86, $P > 0.5$) or females ($F_{1,3}$ = 5.01, P = 0.25). Average survival rates for males and females were 34.4% (grids 1, 2 and 3), 20.2% (grids 4, 5 and 6), 9.4% (grids 1, 2 and 3), and 39.4% (grids 4, 5 and 6), respectively (Table 4).

Table 4. *P. maniculatus* - *M. montanus* - *P. parvus*: Sample size and minimum survival rates per 21 days estimates.

MALES	*P. maniculatus*		*M. montanus*		*P. parvus*	
	n	%	n	%	n	%
GRID 1	58	36.1	1	0.0	17	31.3
GRID 2	30	51.7	29	30.8		
GRID 3	54	49.1	22	33.3	14	37.5
GRID 4	40	47.9	15	21.4	11	23.1
GRID 5	40	74.5	32	42.6	5	0.0
GRID 6	15	61.1	25	51.2	6	37.5
FEMALES	*P. maniculatus*		*M. montanus*		*P. parvus*	
	n	%	n	%		
GRID 1	52	37.9	8	0.0	19	18.8
GRID 2	44	51.6	25	69.2		
GRID 3	61	51.9	31	33.3	6	0.0
GRID 4	43	53.3	15	52.9	12	53.8
GRID 5	28	68.0	44	62.1	4	20.0
GRID 6	25	47.3	29	60.0	5	44.4

Population Density

P. maniculatus

Average population densities per ha from CAPTURE and MNA for grids 1, 2 and 3 ranged from 50.7 to 67.0 for CAPTURE and 41.7 to 56.0 for MNA (Fig. 2). Both estimators show a low in August and a peak in October. There was no significant difference between estimates from CAPTURE and MNA for the three trapping periods ($F_{1,4} = 0.42$, $P = 0.55$).

Average population densities from Jolly-Seber and MNA estimates for grids 4, 5 and 6 and ranged from 21.7 to 35.4 for Jolly-Seber and 20.3 to 24.8 for MNA (Fig. 3). While MNA showed a relatively stable population, Jolly-Seber estimates displayed a low in early July and a peak in late July- early August, only to stabilize for the remainder of the study. The ANOVA showed there were no significant differences between Jolly-Seber and MNA estimates from weeks 4 to 16 ($F_{1,4} = 3.34$, $P = 0.14$).

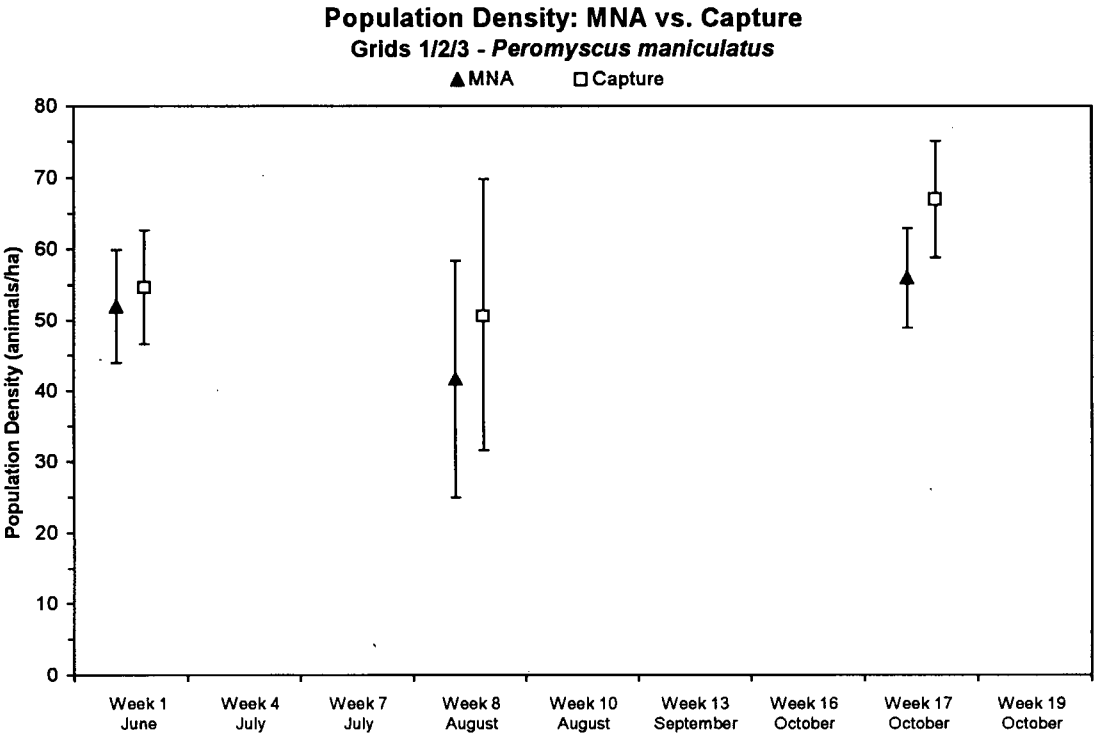


Figure 2. Average population densities ± S.E. of *P. maniculatus* (CAPTURE and MNA) for grids 1, 2 and 3.

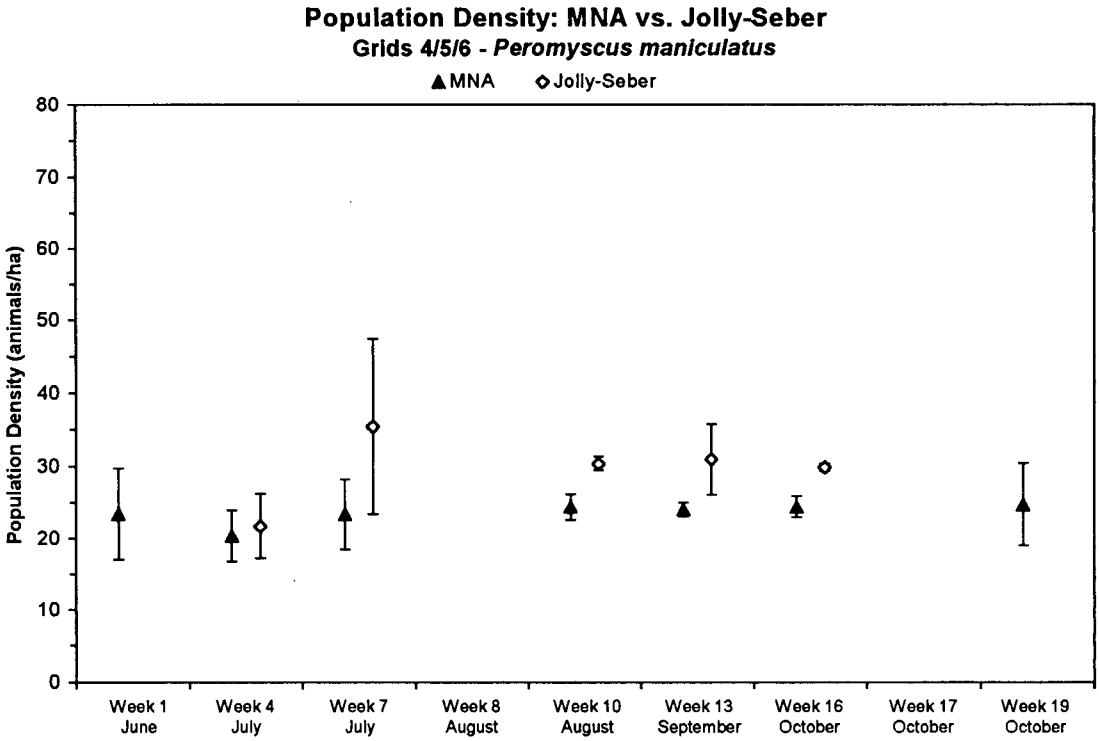


Figure 3. Average population density ± S.E. of *P. maniculatus* (Jolly-Seber and MNA) for grids 4, 5 and 6.

CAPTURE population estimates from grids 1, 2 and 3 were compared to Jolly-Seber population estimates from grids 4, 5 and 6 (Fig. 4). Weeks were paired for the analysis of variance in the following manner: weeks 1 (CAPTURE) and 4 (Jolly-Seber), weeks 8 (CAPTURE) and 7 (Jolly-Seber) and finally weeks 17 (CAPTURE) and 16 (Jolly-Seber). Population estimates from CAPTURE were found to be significantly higher than estimates from Jolly-Seber ($F_{1,4} = 14.03$ $P = 0.02$).

MNA estimates from grids 1, 2, 3 and 4, 5, 6 were also compared (Fig. 5). Weeks were paired as follows: week 1, weeks 7 and 8 and weeks 16 and 17. A significant difference was found between MNA estimates from grids 1, 2, 3 and 4, 5, 6 ($F_{1,4} = 8.07, P = 0.045$).

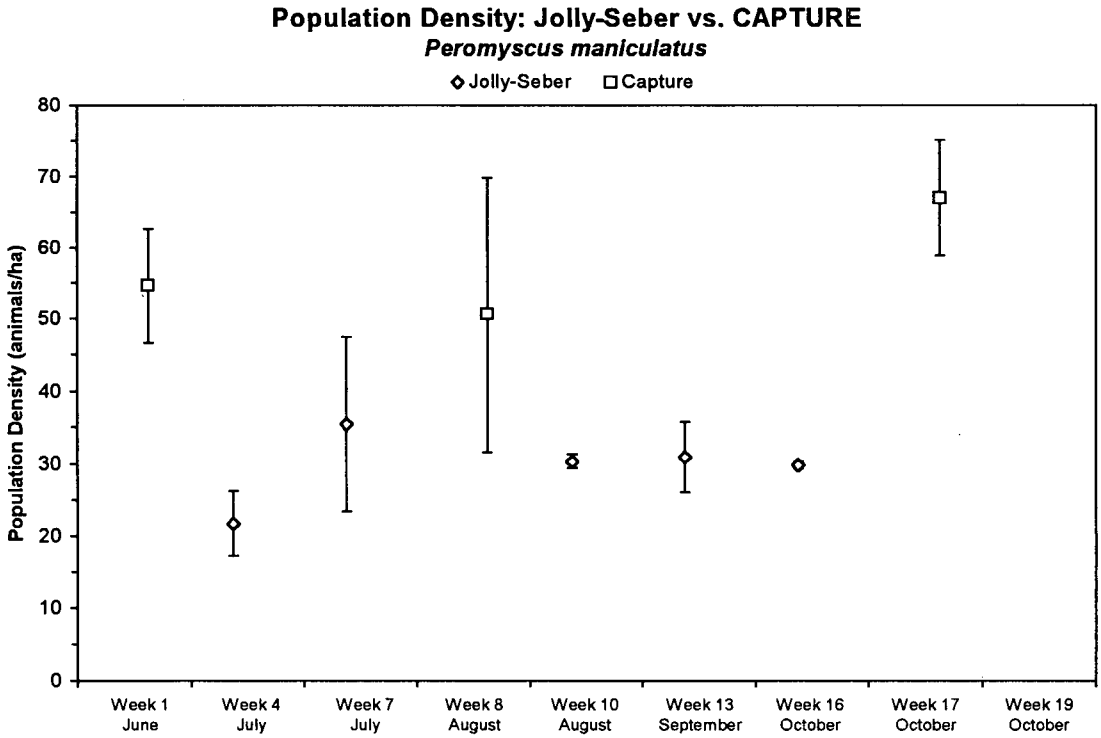


Figure 4. Average population density ± S.E. of *P. maniculatus* for grids 1, 2 and 3 (CAPTURE) and grids 4, 5 and 6 (Jolly-Seber).

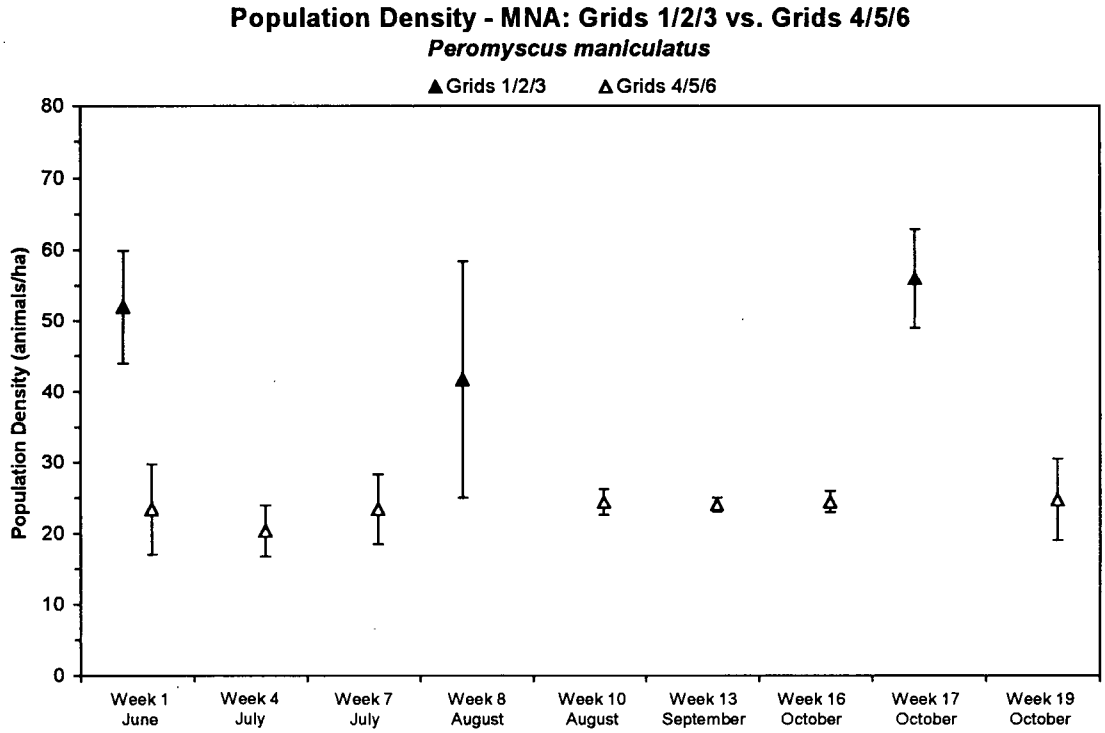


Figure 5. Average population densities (MNA) ± S.E. of *P. maniculatus* for grids 1,2,3 and 4,5,6.

Data from grids 1, 2 and 3, collected over 10 nights, were also fragmented into five different trapping sessions: two, four, six, eight and 10 nights, for each of which population estimates using CAPTURE and MNA were calculated.

In each case, population estimates increased slowly over the five periods but in general, the increase slowed considerably after the sixth night (Figs. 6 and 7). The data were blocked to account for the variation between the three grids. Each of the three trapping weeks were classified as a treatments, with the three grids as block, and nights were treated as subplots. This approach was taken because nights were not randomly allocated. For the data analyzed using CAPTURE, a randomized block analysis of variance on the population estimates for each grid resulted in significant differences between the five estimates ($F_{4,23} = 19.22$, $P < 0.001$). However, the Bonferroni multiple comparisons test revealed that although estimates from the two night trapping period was significantly different from all other estimates, there was no significant difference between estimates from four, six and eight nights. Furthermore, no significant difference

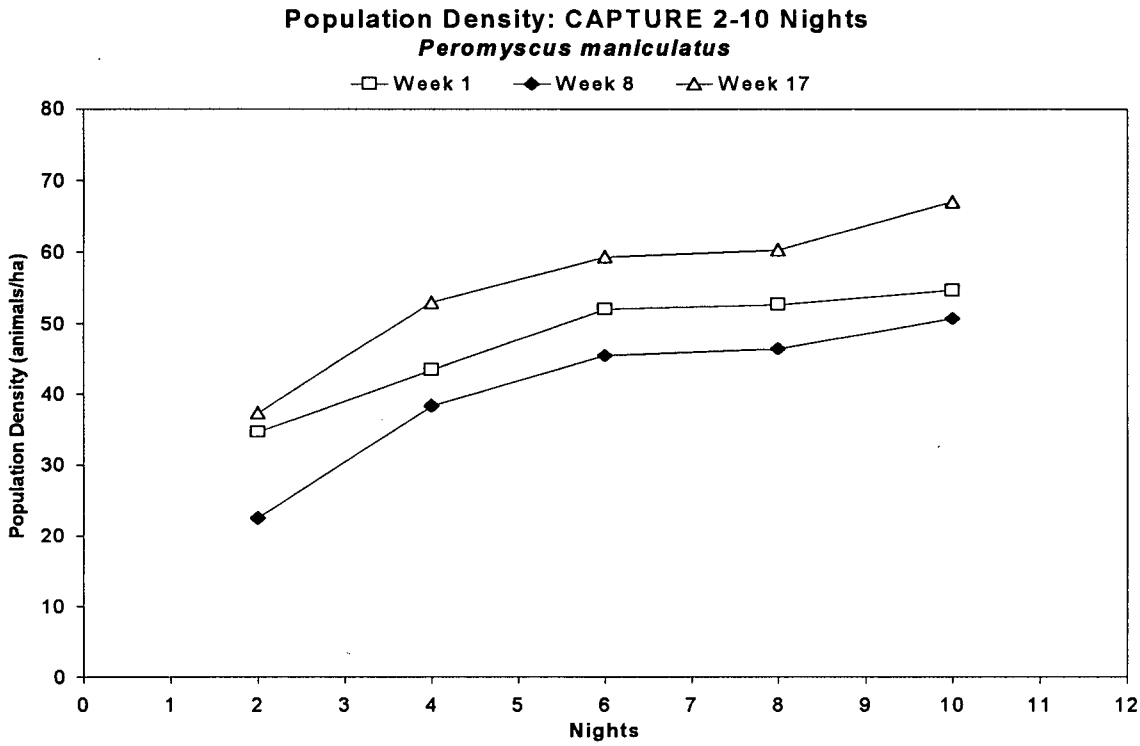


Figure 6. Average population density of *P. maniculatus* (CAPTURE) for weeks 1, 8 and 17; 2 to 10 night trapping sessions.

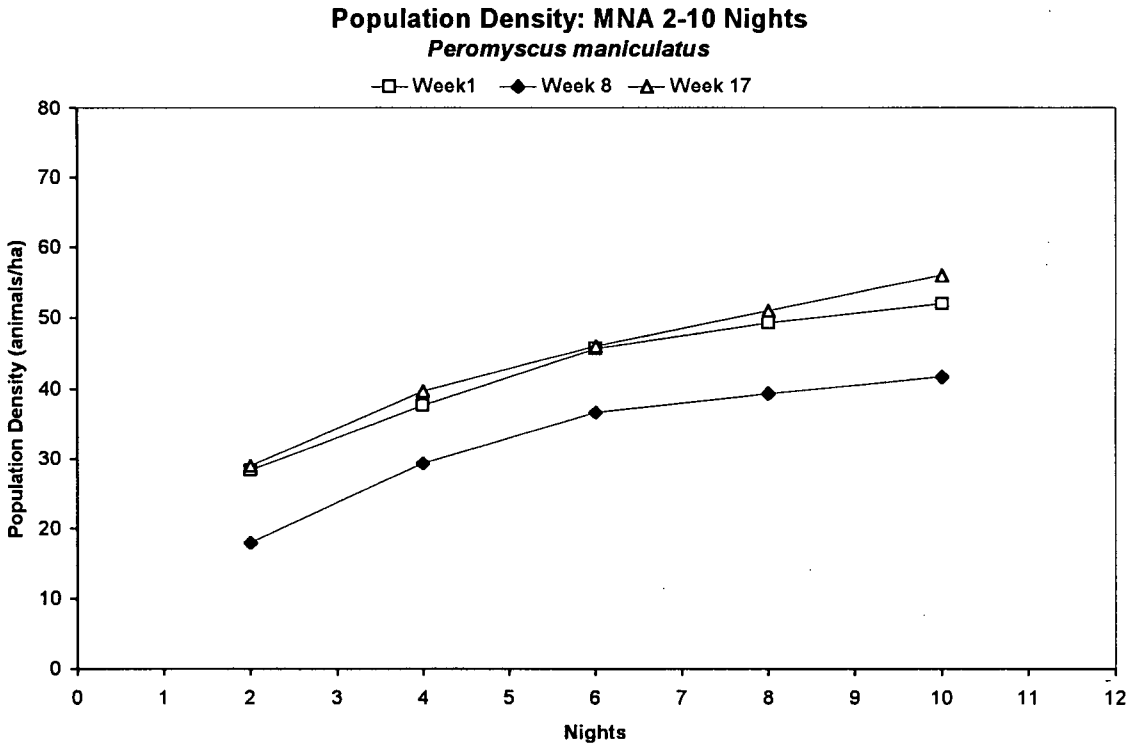


Figure 7. Average population density of *P. maniculatus* (MNA) for weeks 1, 8 and 17; 2 to 10 night trapping session.

was found between estimates from six, eight and ten nights. A significant difference was found between estimates from four and ten nights (App. B). A significant difference was also found for population estimates from MNA between the means of each grid ($F_{4,24}$ = 42.53, $P < 0.001$). However, once again the Bonferroni test showed that while estimates from two and four nights were significantly different from each other as well as from all other estimates, no significant difference was found between estimates from six and eight nights as well as estimates from eight and ten nights. A significant difference was found between estimates from six and ten nights (App. B).

In addition, the number of newly caught animals decreased considerably after four nights of trapping during each week (Figs. 8, 9 and 10). On average, recaptured animals consisted of 95% or more of the total number of animals caught on a particular night on night 8 for week 1, night 10 for week 8, and did not apply for week 17. Recaptured animals consisted of 90% or more of the total number of animals caught on one night on night 7 for week 1, 8 for week 8, and 6 for week 17. During the first week of trapping, a total of 156 animals were caught on the three grids, 113 (72%) of these animals were caught on the first four nights of trapping while only 43 (28%) new animals were caught on the last six nights. For the eighth week, a total of 108 animals were caught among the three grids, 76 (71%) animals were caught during the first four checks and only 32 (29%) newly captured *P. maniculatus* were caught on the last six nights. For the last week of trapping, a total of 174 animals were captured on the three grids, 123 (71%) during the first four nights and 51 (29%) during the last six (Table 5). During week 1, 23 (53%) of the 43 animals caught during the last six nights were never caught again, 11 (26 %) were caught in only one of the following trapping sessions (either week 8 or 17), and nine animals (21 %) were caught on both subsequent trapping sessions. For week 8, 18 (56%) of the 32 animals captured after the fourth night were never caught again, and 14 (44 %) were caught during the last trapping session.

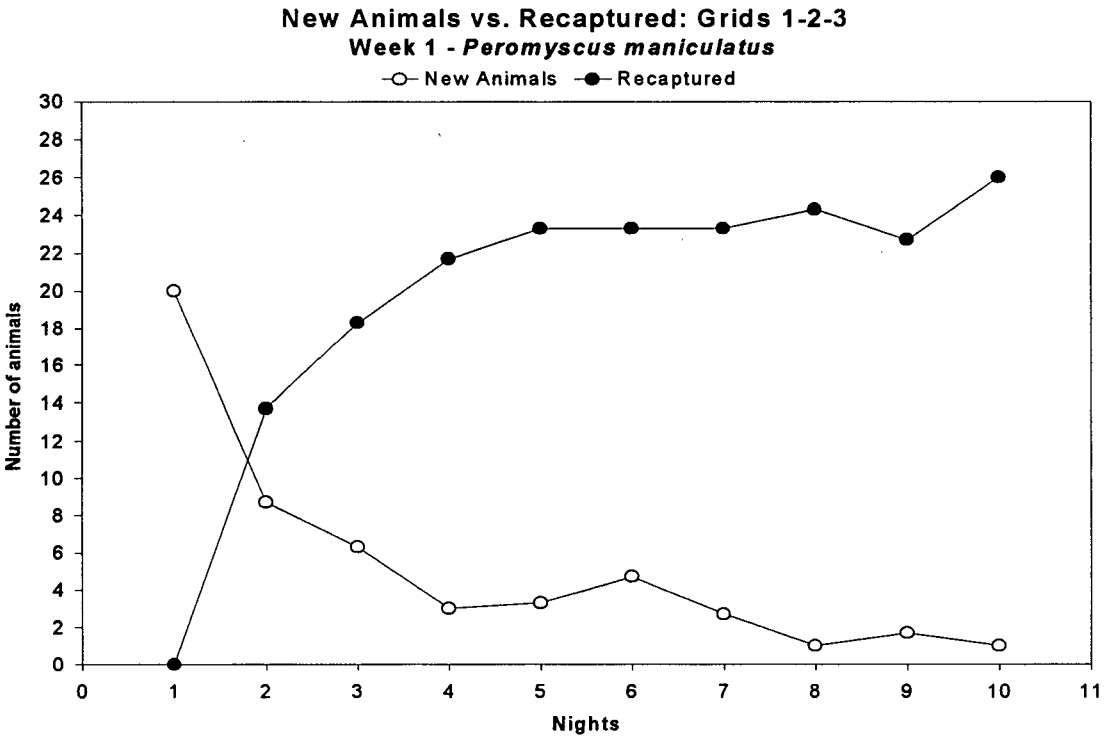


Figure 8. Number of new and recaptured *P. maniculatus* over a 10-night period. Grids 1, 2 and 3 - Week 1.

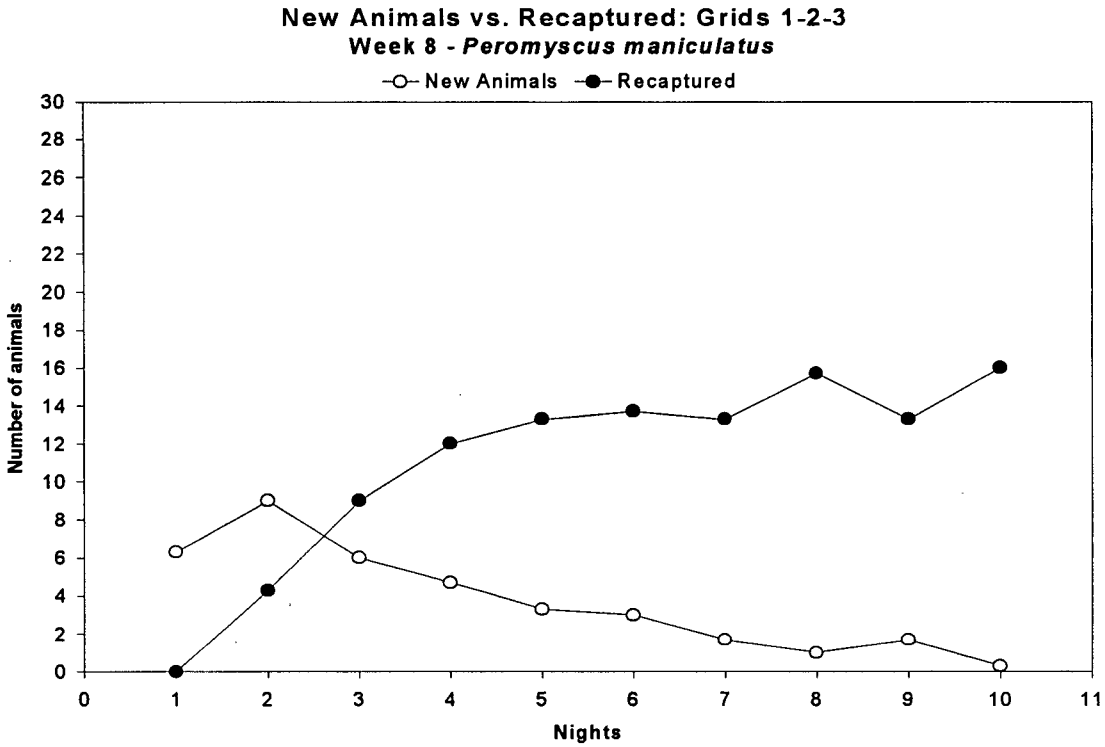


Figure 9. Number of new and recaptured *P. maniculatus* over a 10-night period. Grids 1, 2 and 3 – Week 8.

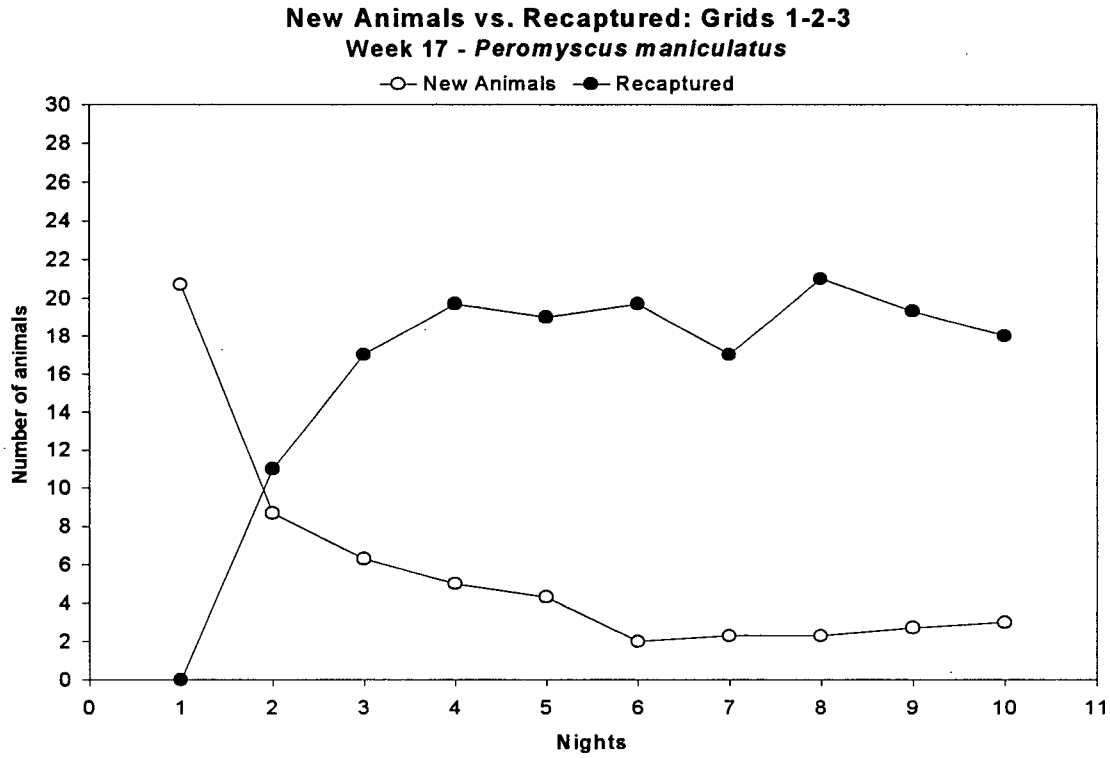


Figure 10. Number of new and recaptured *P. maniculatus* over a 10-night period. Grids 1, 2 and 3 – Week 17.

Table 5. Number of *P. maniculatus* captured over 10 nights – Grids 1, 2 and 3.

	WEEK 1		WEEK 8		WEEK 17	
	Nights 1-4	Nights 5-10	Nights 1-4	Nights 5-10	Nights 1-4	Nights 5-10
Grid 1	35	14	11	4	48	21
Grid 2	27	13	15	5	36	11
Grid 3	51	16	50	23	39	19
Total	113	43	76	32	123	51
Total	156 animals		108 animals		174 animals	

M. montanus

Average population densities per ha obtained from CAPTURE for grids 1, 2 and 3 ranged from 8.3 for week 1 to 48.7 for week 17, while MNA density estimates ranged from 3.3 for week 1 to 31.7 for week 17 (Fig. 11). In a similar manner as *P. maniculatus,* populations of *M. montanus* increased significantly in numbers in October. However, numbers for this species were lower in late June. There was no significant difference between estimates of CAPTURE and MNA for weeks 1, 8 and 17 ($F_{1,4} = 0.53$, $P = 0.51$).

Average population densities from Jolly-Seber and MNA estimates for grids 4, 5 and 6 ranged, for Jolly-Seber, from 6.7 and 32.4 for weeks 4 and 16 (Fig. 12). MNA population estimates ranged from 1.7 for week 1 to 26.7 for week 16. Both estimators show a definite increase in population density through time and follow one another closely to a peak in early October. A first decline in numbers of *M. montanus* started at the end of the same month. No significant difference was found between Jolly-Seber and MNA estimates from weeks 4 to 16 ($F_{1,4} = 0.20$, $P = 0.68$).

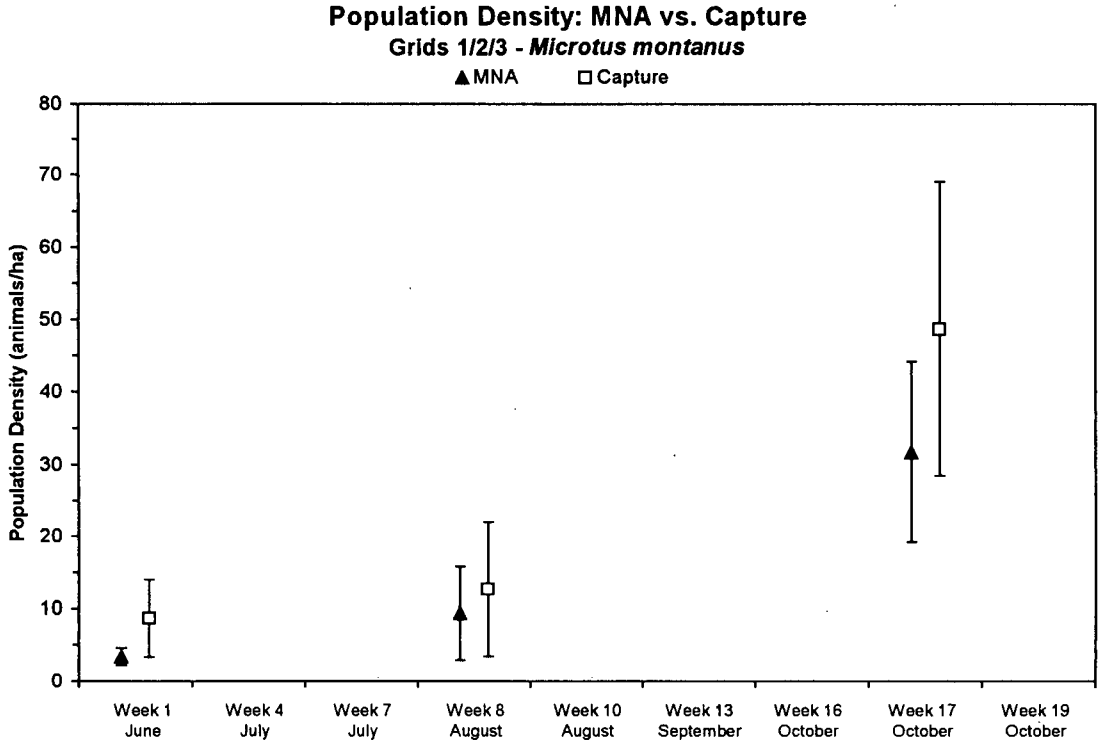


Figure 11. Average population densities ± S.E. of *M. montanus* (CAPTURE and MNA) for grids 1, 2 and 3.

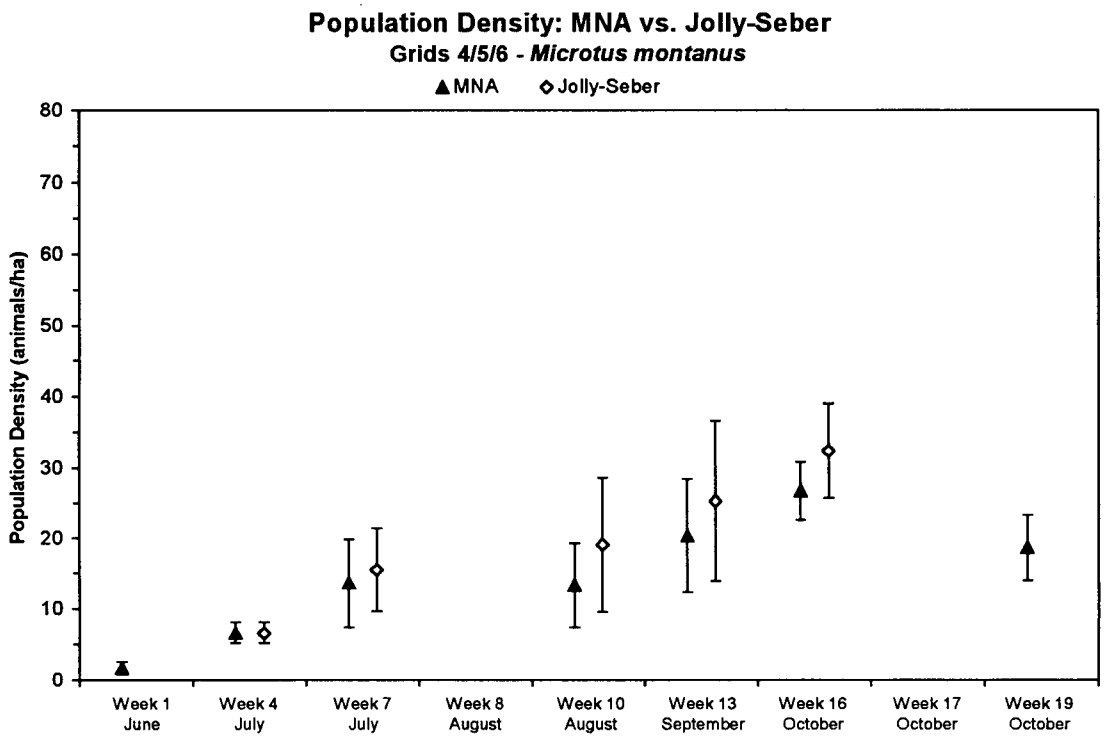


Figure 12. Average population density ± S.E. of *M. montanus* (Jolly-Seber and MNA) for grids 4, 5 and 6.

Population estimates from CAPTURE (grids 1, 2 and 3) were compared to estimates from Jolly-Seber (grids 4, 5 and 6) (Fig. 13). *M. montanus* population estimates from CAPTURE and Jolly-Seber were very closely correlated, with the Jolly-Seber estimate for week 7 being higher than the CAPTURE estimate for week 8. Weeks 1 (CAPTURE) and 4 (Jolly-Seber) were paired for the analysis of variance as well as weeks 8 and 7, and 17 and 16 for CAPTURE and Jolly-Seber, respectively. There was no significant difference between estimates from CAPTURE and Jolly-Seber ($F_{1,4} = 0.22$, $P = 0.66$). There was no significant difference ($F_{1,4} = 0.01$, $P = 0.92$) between MNA estimates from grids 1, 2, 3 and 4, 5, 6 (Fig. 14).

The data from grids 1, 2 and 3 were divided into five different trapping sessions for which population densities were calculated using CAPTURE and MNA. For both estimators, population estimates over the ten-night periods experienced little or no variation through time for weeks 1 and 8. Estimates increased slowly and steadily for week 17 for both CAPTURE and MNA (Figs. 15 and 16).

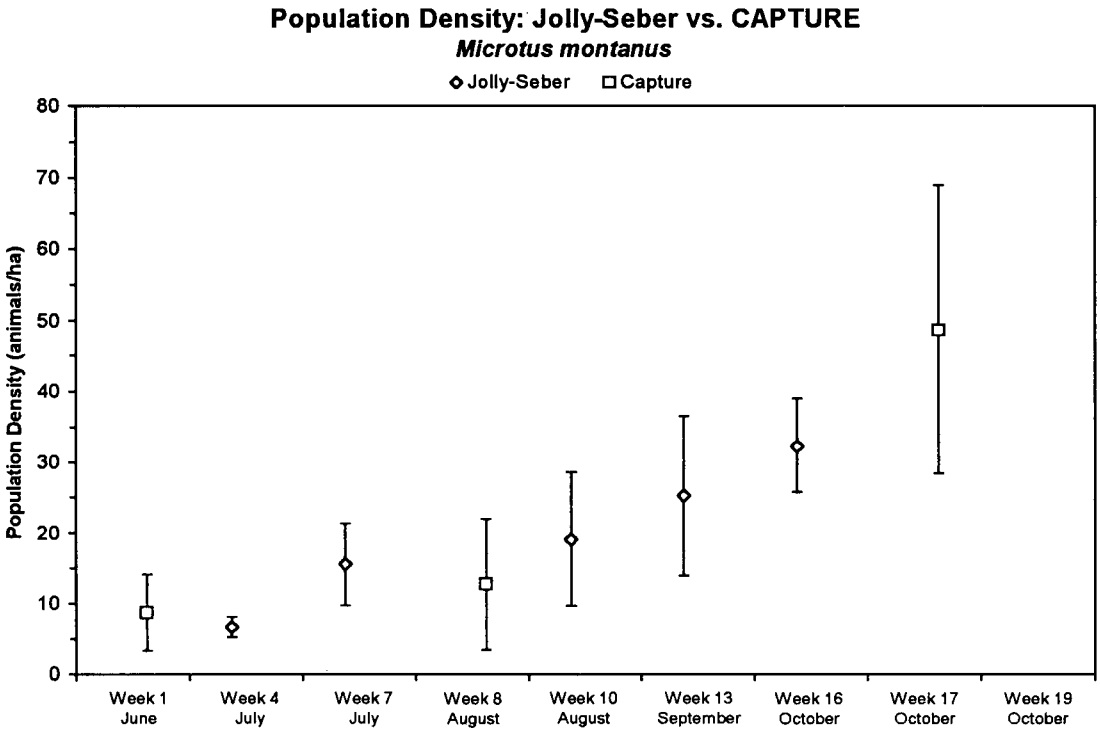


Figure 13. Average population density ± S.E. of *M. montanus* for grids 1, 2 and 3 (CAPTURE) and 4, 5 and 6 (Jolly-Seber).

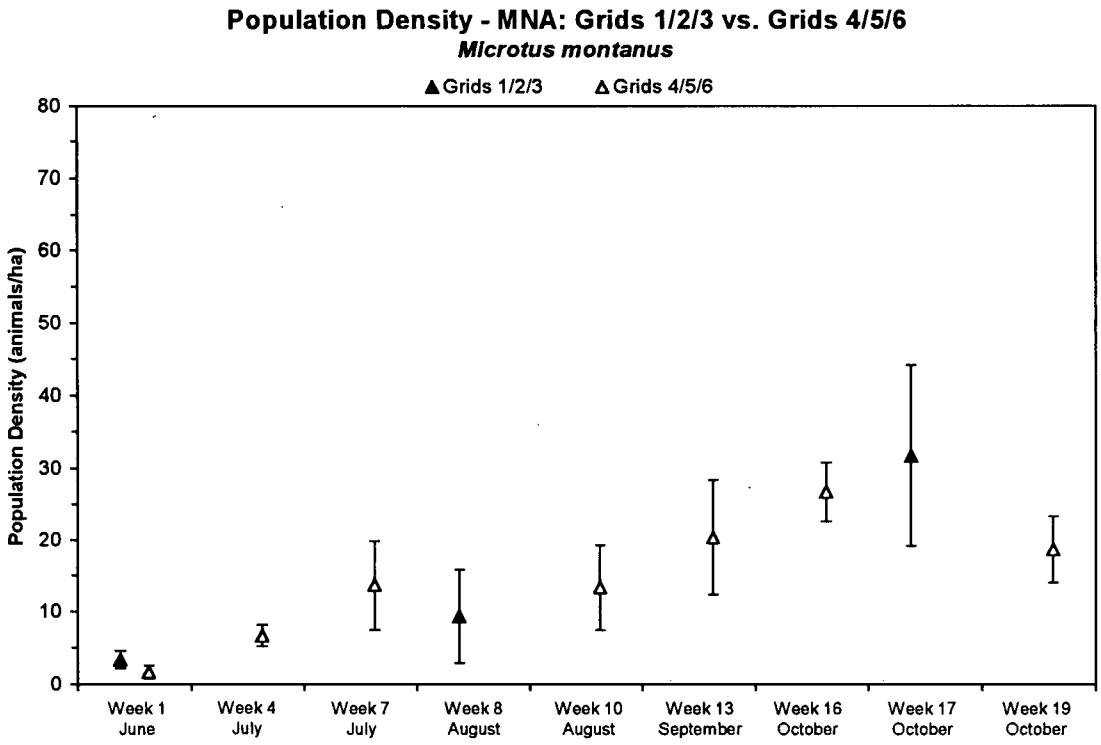


Figure 14. Average population densities (MNA) ± S.E. of *M. montanus* for grids 1,2,3 and 4,5,6.

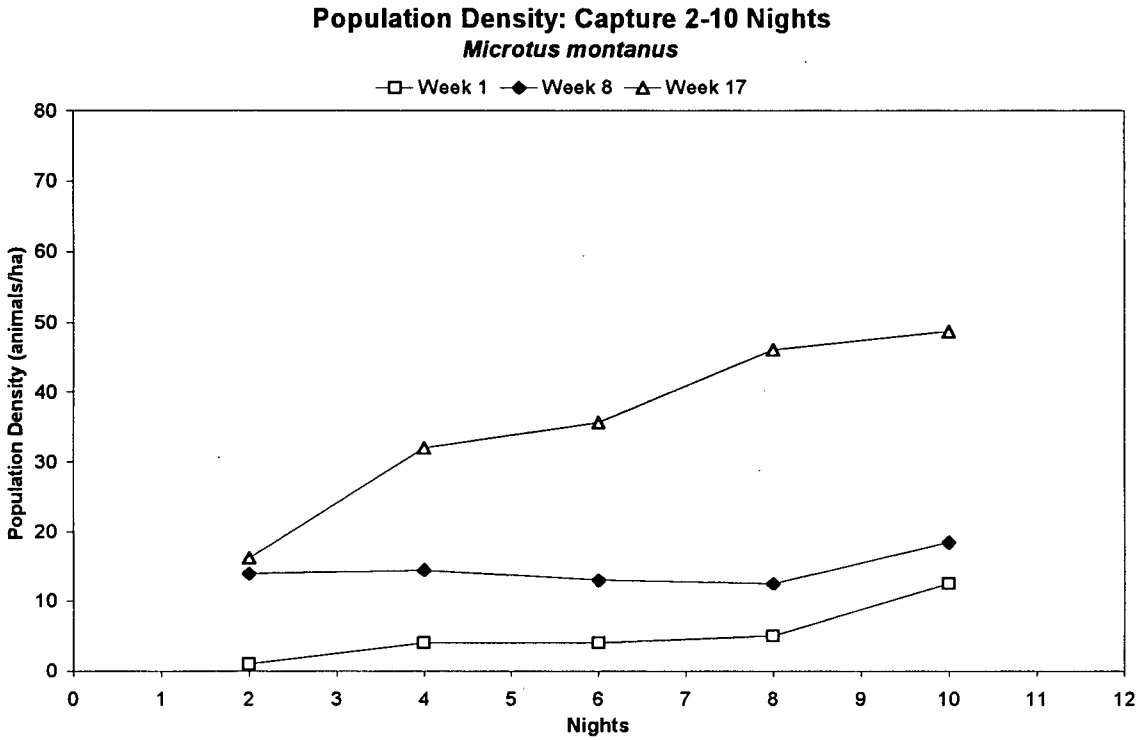


Figure 15. Average population density of *M. montanus* (CAPTURE) for weeks 1, 8 and 17; 2 to 10 night trapping sessions.

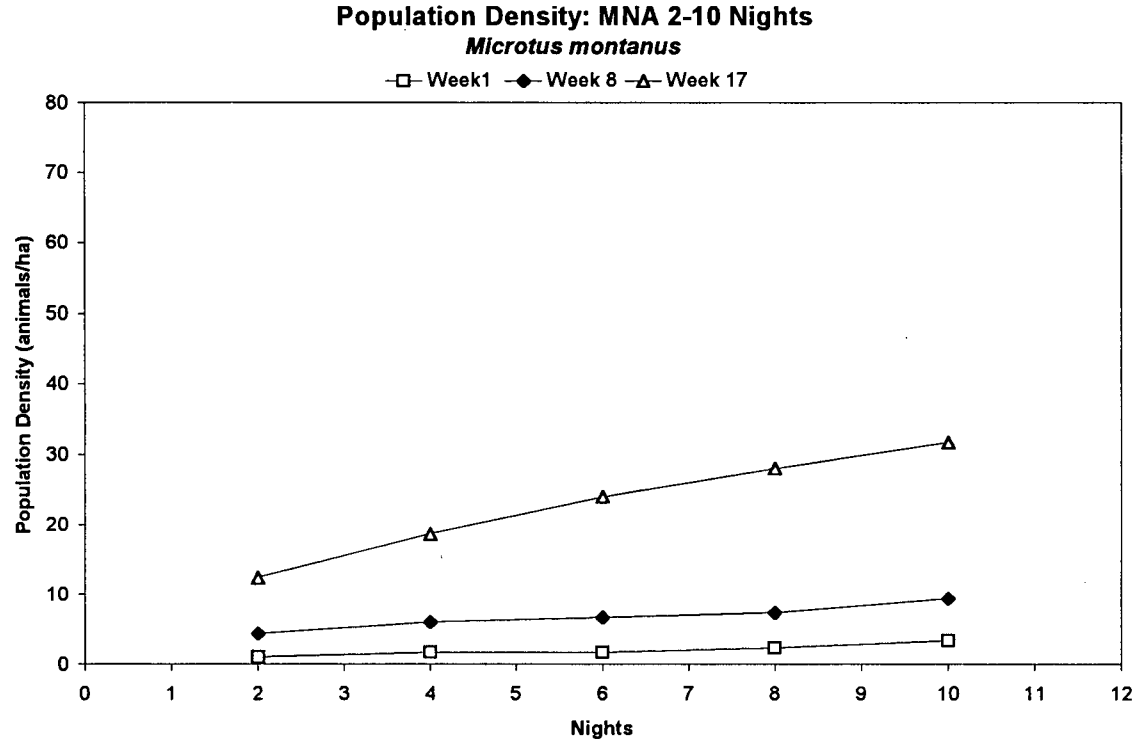


Figure 16. Average population density of *M. montanus* (MNA) for weeks 1, 8 and 17; 2 to 10 night trapping sessions.

Data analysis for *M. montanus* was performed as described for *P. maniculatus*. A significant difference was found between the five CAPTURE estimates ($F_{4,19} = 3.91$, $P = .02$). However, the Bonferroni test showed there was no significant difference between the estimates of two, four, six and eight nights. Furthermore, no significant difference was found between the estimates of four, six, eight and ten nights. A significant difference was found between estimates from two and ten nights (App. B). A significant difference was also found between MNA estimates of the five nights ($F_{4,24} = 7.34$, $P = 0.00$), however, no significant difference was found between estimates of two, four and six nights. Also, no significant difference was found between estimates of four, six and eight nights as well as six, eight and ten nights. There was a significant difference between estimates from two and ten as well as from four and ten nights (App. B).

Numbers of newly caught animals versus the number of recaptured ones was difficult to analyze for *M. montanus* as the number of animals captured for weeks 1 and 8 was, on average, too low to give meaningful information. However, by week 17, the number of animals on each grid was large enough to show a decline in the number of new animals after the fifth night, associated with an increase in the number of recaptured ones (Fig. 17). On average, recaptured animals consisted of 95% or more of the total number of animals caught on a particular night during the sixth night for week 1, the third night for week 8 and was never reached for week 17. The number of recaptured animals consisted of 90% or more of the total number of animals caught during the sixth night for week 1, the third for week 8 and once more did not apply for week 17.

During the first week of trapping, a total of ten *M. montanus* were caught on the three grids, five (50 %) on the first four nights and five (50%) on the last six. During the second trapping period, a total of 27 animals were captured on the three grids, 18 (67%) during the first four nights and nine (33%) new animals during the last six. And finally, during the last week of trapping, a total of 96 animals were captured, 57 (59%) during the first four nights and 39 (41%) newly captured animals during the last six (Table 6). During the first week, three (60%) of the five animals captured on the last six nights were never caught again, one (20%) was caught in only one of the following trapping sessions and one (20%) was caught in the two following trapping sessions. For the eight weeks,

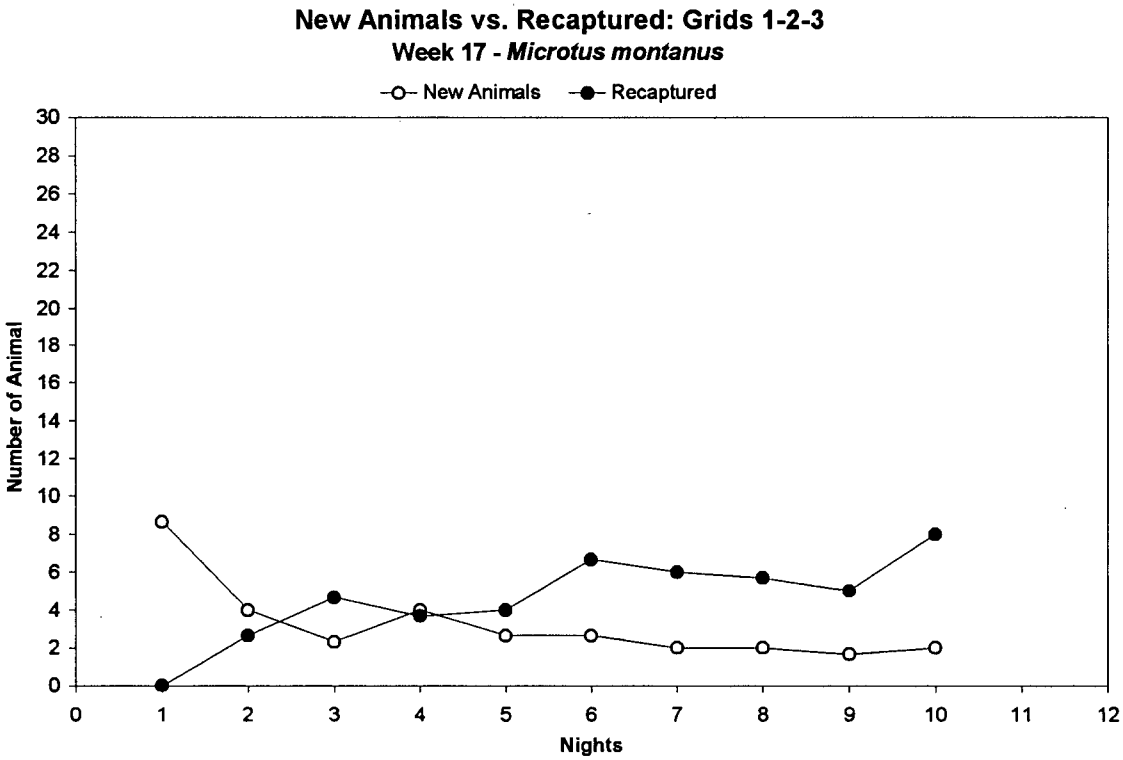


Figure 17. Number of new and recaptured *M. montanus* over a 10-night period. Grids 1, 2 and 3 – Week 17.

Table 6. Number of *M. montanus* captured over 10 nights – Grids 1, 2 and 3.

	WEEK 1		WEEK 8		WEEK 17	
	Nights 1-4	Nights 5-10	Nights 1-4	Nights 5-10	Nights 1-4	Nights 5-10
Grid 1	1	0	1	0	6	1
Grid 2	2	2	15	7	25	17
Grid 3	2	3	2	2	26	21
Total	5	5	18	9	57	39
Total	10 animals		27 animals		96 animals	

six (67%) of the nine animals captured during the last six nights of trapping were never caught again and three (33%) were caught in the last week of trapping.

P. parvus

Average population densities per ha for grids 1, 2 and 3 ranged from 7.3 to 17.3 for CAPTURE and 4.7 to 12.7 for MNA (Fig. 18). Both estimators indicate a peak in *P. parvus* population numbers for week 8, and a sharp decline in numbers for week 17. MNA numbers are at their lowest for that period, while CAPTURE numbers are lower for the first trapping period. There was no significant difference between estimates from CAPTURE and MNA for grids 1, 2 and 3 ($F_{1,4} = 0.25$, $P = 0.65$).

Average population densities per ha for grids 4, 5 and 6 estimated from Jolly-Seber and MNA ranged from 1.7 to 8.9 for Jolly-Seber and 0.7 to 8.0 for MNA (Fig. 19). Both show a steady increase in density from early June to early September, only to decline dramatically in October. There was no significant difference ($F_{1,4} = 0.14$, $P = 0.73$) between estimates from Jolly-Seber and MNA for grids 4, 5 and 6.

The ANOVA showed there was no significant difference ($F_{1,4} = 0.89$, $P = 0.40$) between the paired weeks from CAPTURE (grids 1, 2 and 3) and Jolly-Seber (grids 4, 5 and 6) (Fig. 20). MNA estimates from grids 1, 2, 3 and 4, 5, 6 were also compared (Fig. 21). No significant difference ($F_{1,4} = 1.25$, $P = 0.33$) was found between MNA estimates from paired weeks of grids 1, 2, 3 and 4, 5, 6.

Data from grids 1, 2 and 3, collected over ten nights were divided into five periods: two, four, six, eight and 10 nights. CAPTURE population estimates for weeks 1, 8 and 17 were variable, and fluctuated from two to 10 nights (Fig. 22). This variation may be explained by the small sample size available for *P. parvus*, in particular for the first few nights of trapping. MNA population estimates for the three trapping sessions show a slow increase from two to 10 nights, with little variation (Fig. 23).

No significant difference was found between CAPTURE estimates for the five nights ($F_{4,8} = 3.08$, $P = 0.08$). However, a significant difference was found between the five MNA estimates ($F_{4,12} = 14.29$, $P = 0.00$). The Bonferroni test showed that there was no significant difference between estimates from two and four nights as well as estimates from four and six nights. In addition, no significant difference was found between estimates from six, eight and ten nights. A significant difference was found between estimates from two and ten nights as well as estimates from four and ten nights (App. B).

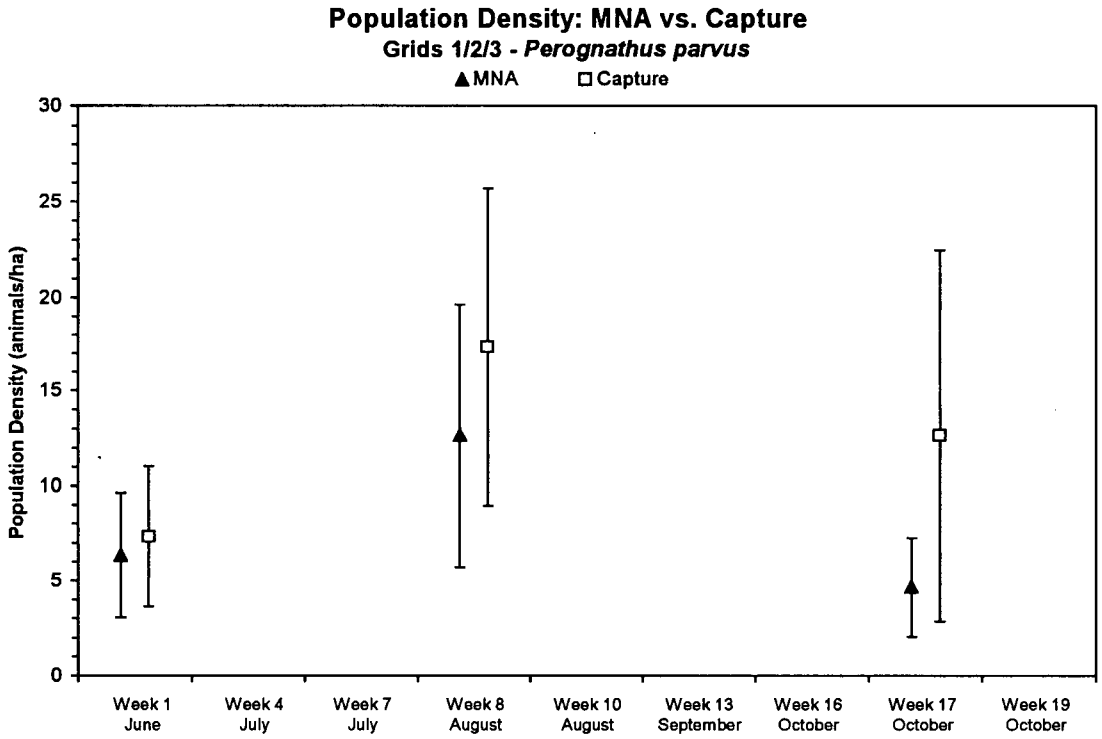


Figure 18. Average population density ± S.E. of *P. parvus* (CAPTURE and MNA) for grids 1, 2 and 3.

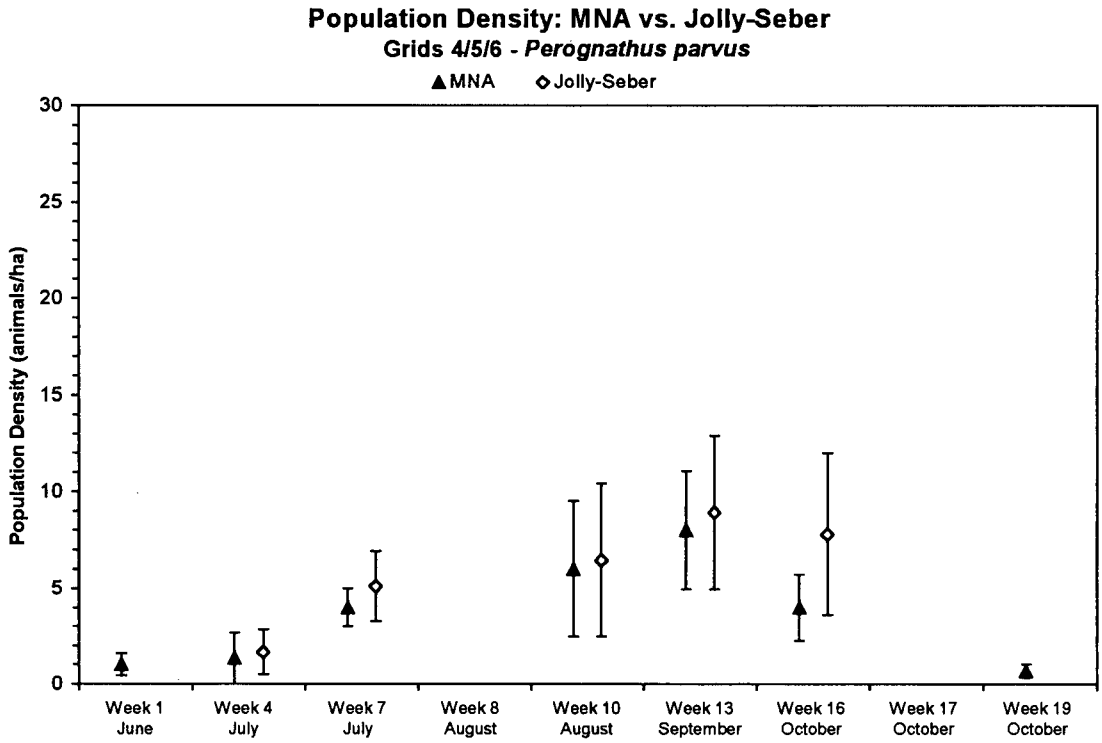


Figure 19. Average population density ± S.E. of *P. parvus* (Jolly-Seber and MNA) for grids 4, 5 and 6.

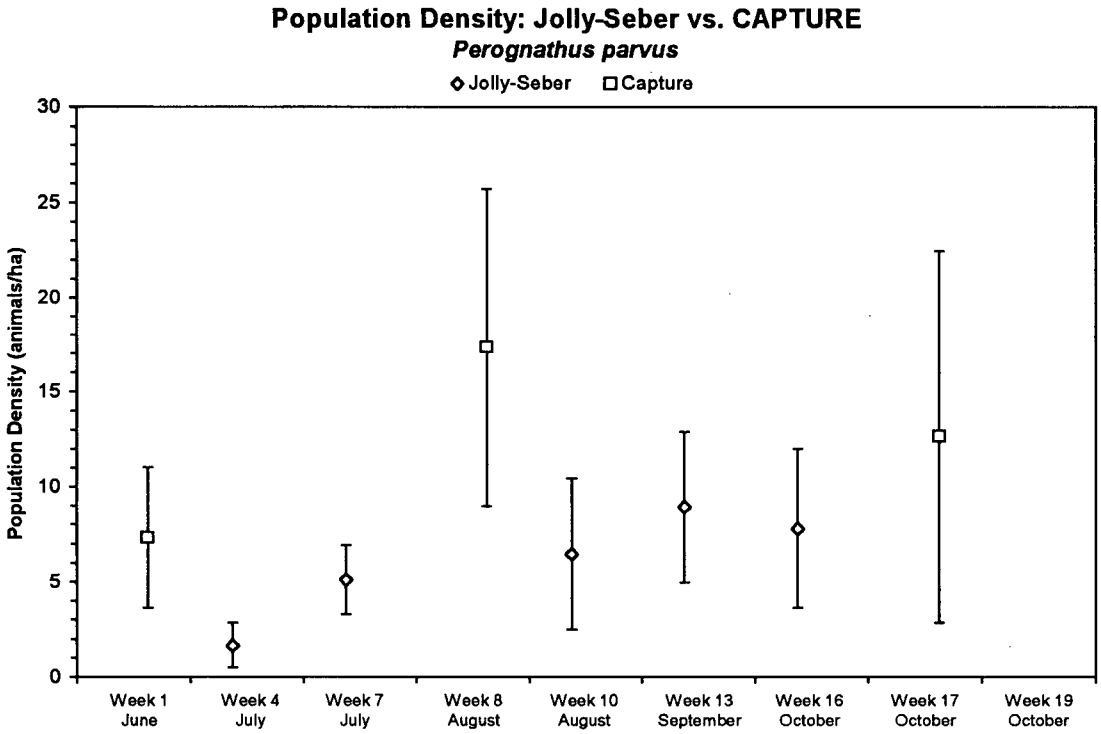


Figure 20. Average population density ± S.E. of *P. parvus* for grids 1, 2 and 3 (CAPTURE) vs. 4, 5 and 6 (Jolly-Seber).

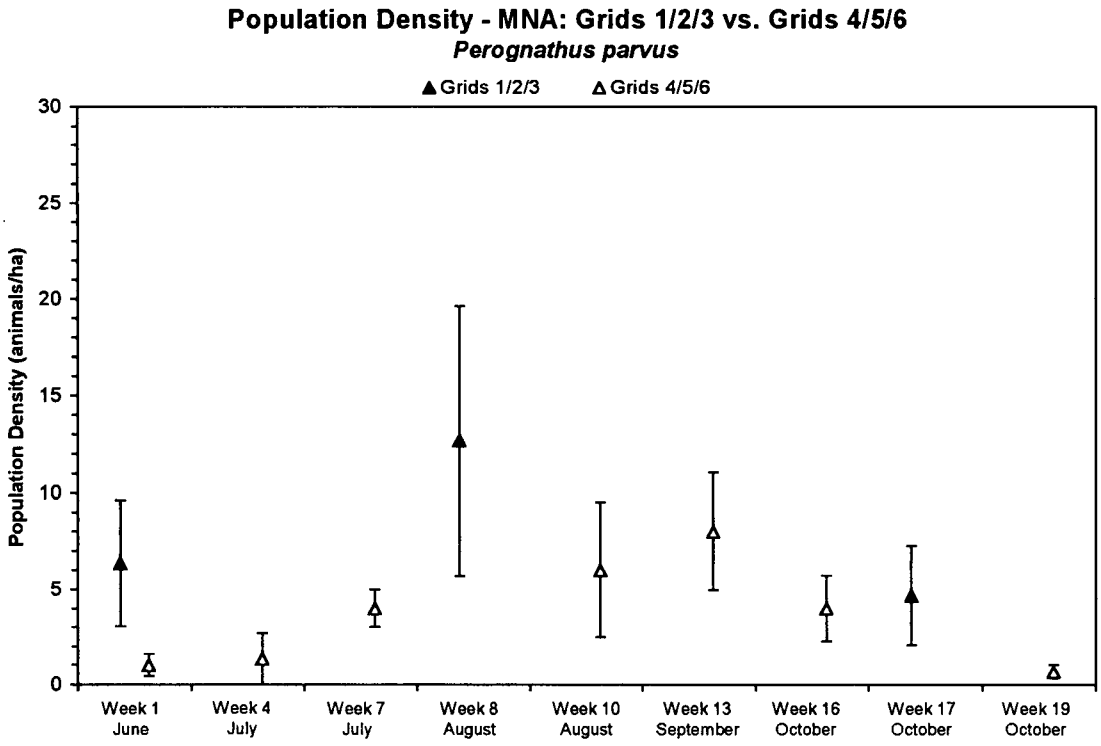


Figure 21. Average population densities (MNA) ± S.E. of *P. parvus* for grids 1, 2, 3 and 4, 5, 6.

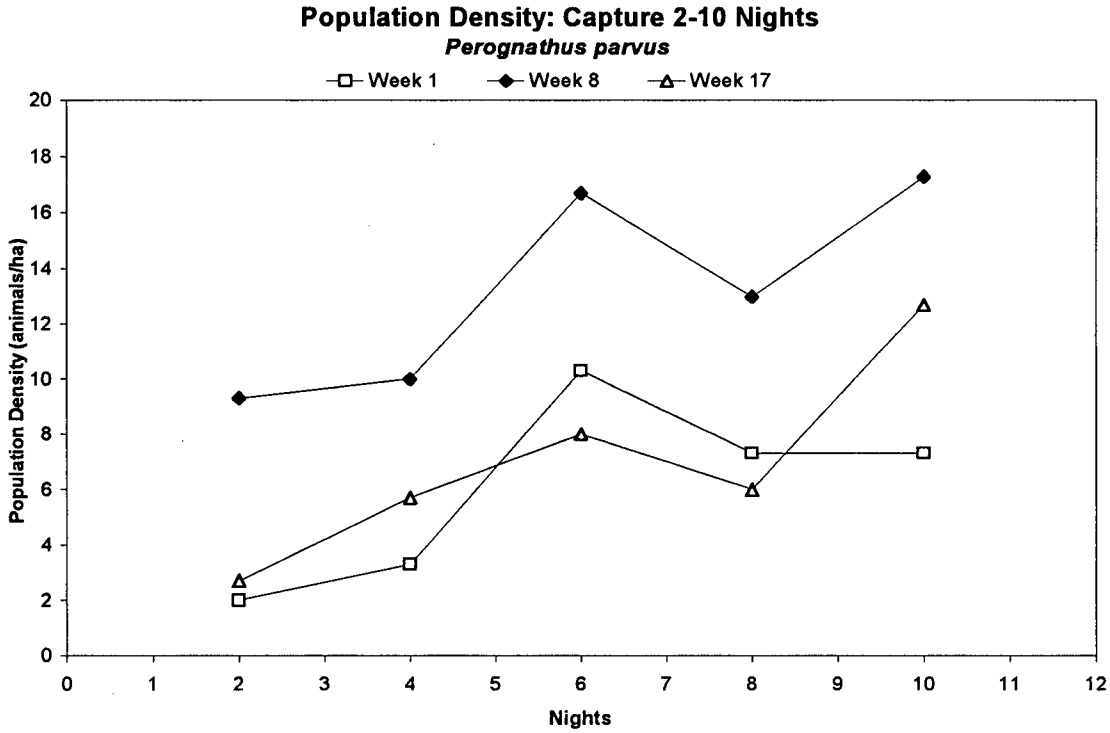


Figure 22. Average population density of *P. parvus* (CAPTURE) for weeks 1, 8 and 17; 2 to 10 night trapping sessions.

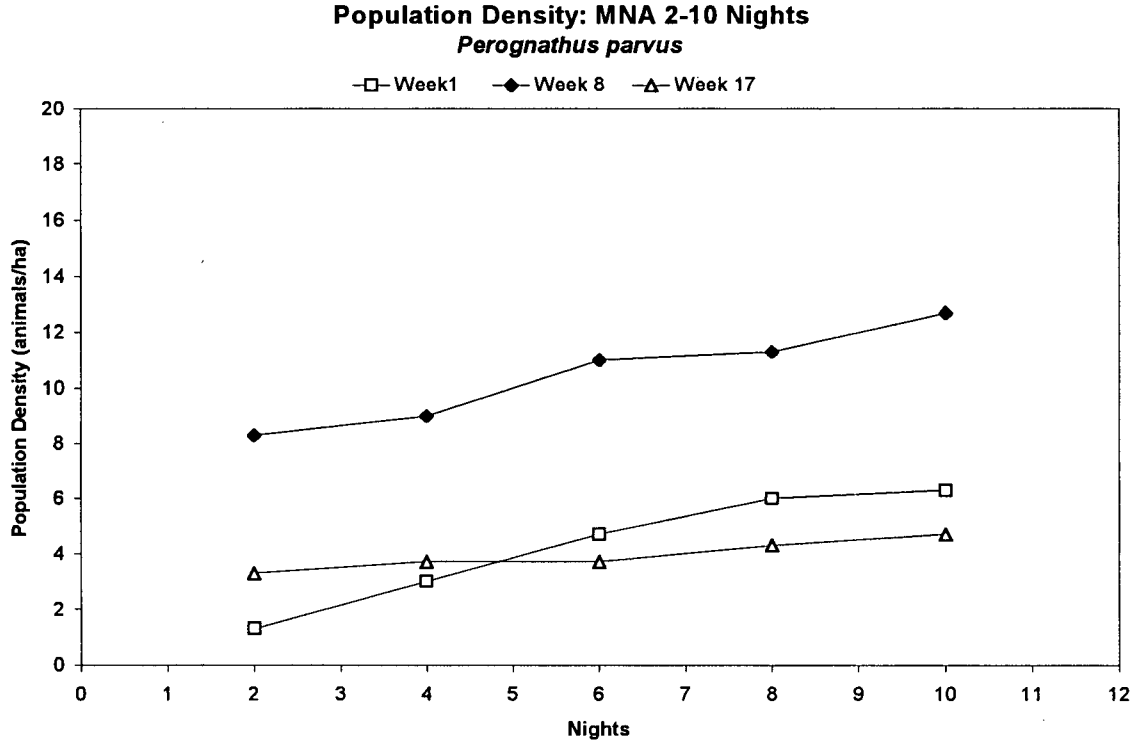


Figure 23. Average population density of *P. parvus* (MNA) for weeks 1, 8 and 17; 2 to 10 night trapping sessions.

Although numbers fluctuate heavily for week 1, the number of newly caught animals started to decrease after days 5 and 7 (Figs. 24, 25 and 26). During the second and last trapping periods, the number of newly captured animals decreased considerably after the third day.

On average, recaptured animals consisted of 95% or more of the total number of animals caught on a single day on night 9 for week 1, night 3 for week 8 and night 4 for week 17. Recaptured animals consisted of 90% or more of the total number of animals caught on a particular night on these same respective nights for each week.

During the first week of trapping, a total of 18 animals were captured on the three grids, nine (50%) during the first four days and nine (50%) new animals during the last six. For the eight week period, a total of 40 *P. parvus* were caught, 28 (70%) of which were caught on the first four days, while 12 (30%) were captured during the last six nights. Finally, a total of 16 animals were caught during the last week of trapping, 13 (81%) during the first four days and only three (19%) new animals were captured during the last six (Table 7). For the first trapping week, four (44%) of the nine animals caught during the last six nights were never caught again, five (56%) were caught in only one of the following trapping periods (week 8 or 17) and no animals were caught on both week 8 and 17. For week 8, nine (75%) of the 12 animals were never caught again and three (25%) animals were captured once again during the last week of trapping.

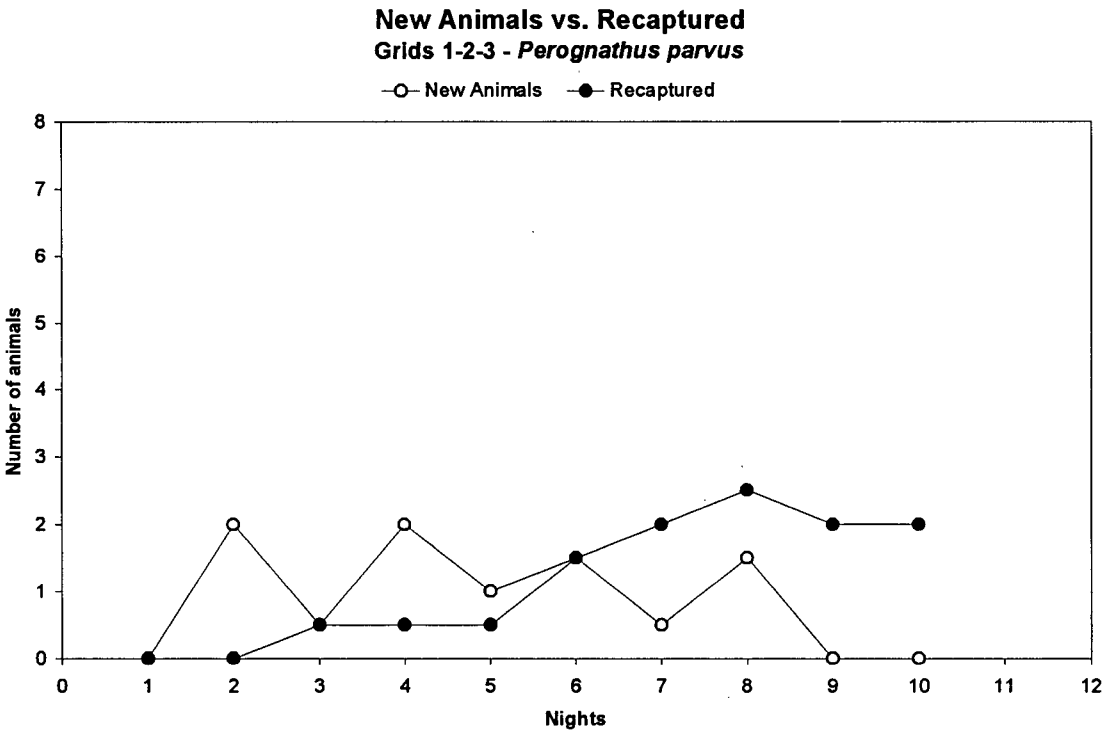


Figure 24. Number of new and recaptured *P. parvus* over a 10-night period. Grids 1, 2 and 3 – Week 1.

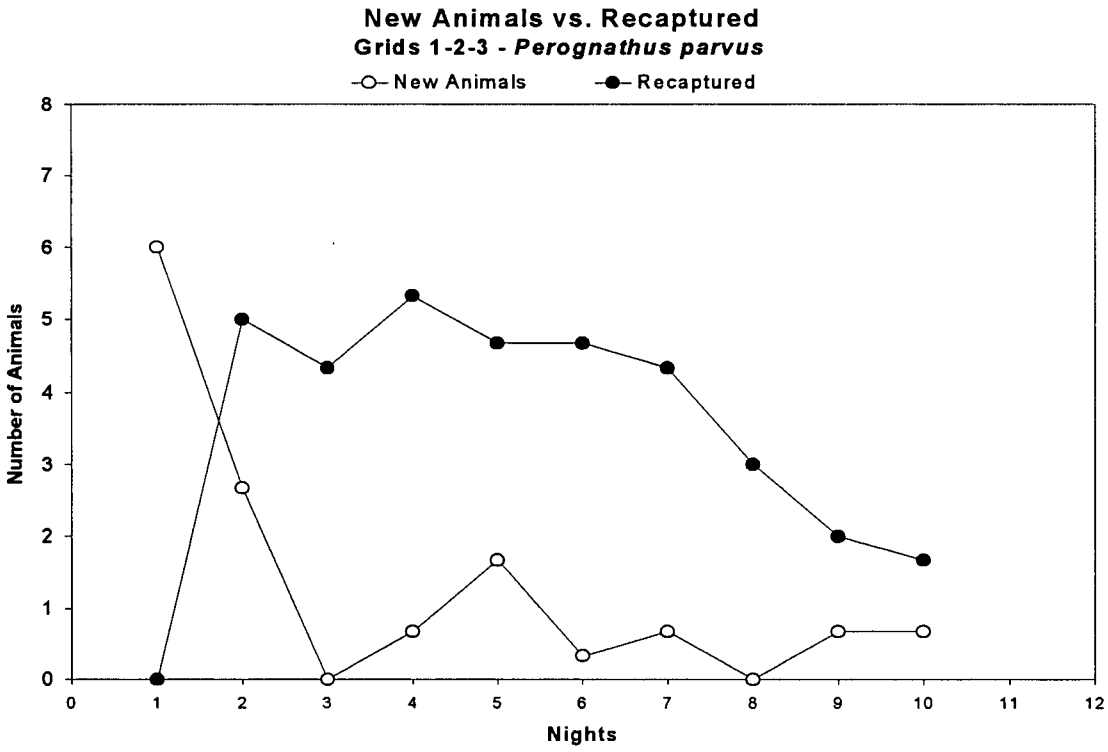


Figure 25. Number of new and recaptured *P. parvus* over a 10-night period. Grids 1, 2 and 3 – Week 8.

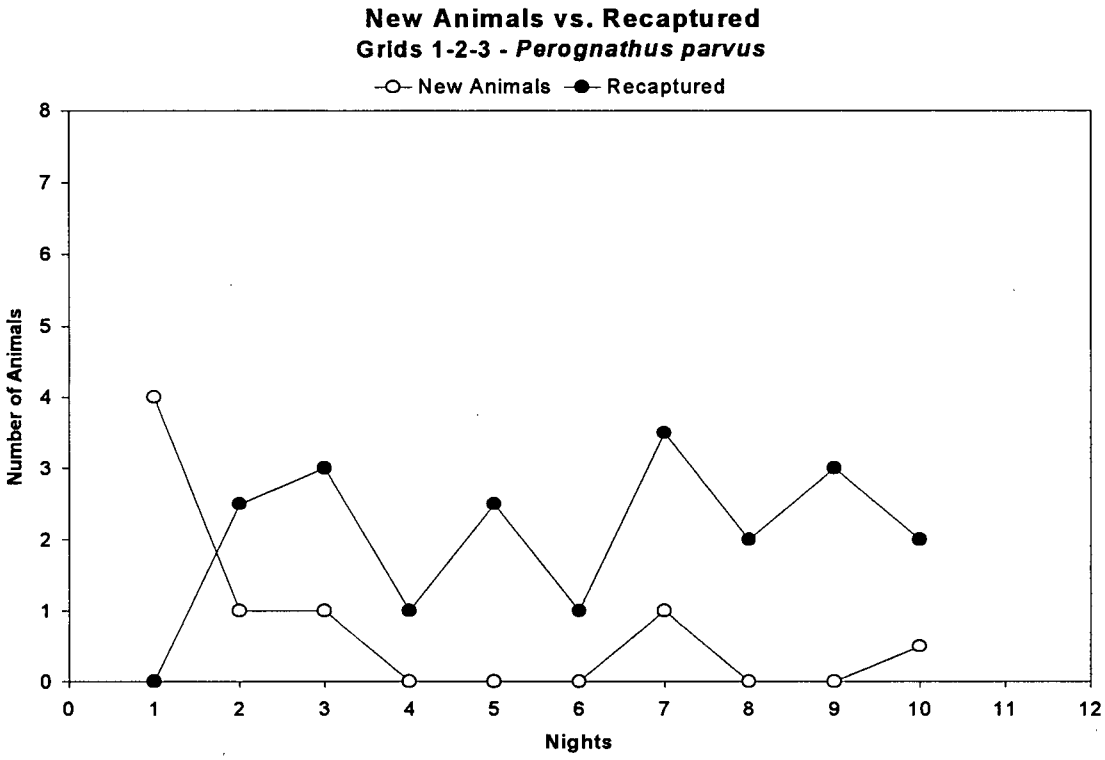


Figure 26. Number of new and recaptured *P. parvus* over a 10-night period. Grids 1, 2 and 3 – Week 17.

Table 7. Number of *P. parvus* captured over 10 nights – Grids 1, 2 and 3.

	WEEK 1		WEEK 8		WEEK 17	
	Nights 1-4	Nights 5-10	Nights 1-4	Nights 5-10	Nights 1-4	Nights 5-10
Grid 1	5	5	15	9	9	1
Grid 2	0	0	1	1	0	0
Grid 3	4	4	12	2	4	2
Total	9	9	28	12	13	3
Total	18 animals		40 animals		16 animals	

DISCUSSION

Experimental Design

The systematic design used to intersperse the six replicates, the spatial independence of each experimental unit from each other, as well as the high degree of homogeneity between each unit during the premanipulation period all diminished the likelihood of incidence of pseudoreplication (Hurlbert 1984). Three replicates per treatments (six experimental units) were determined to be sufficient to yield reliable estimates of population density of small mammals. Although additional replicates might have increased the precision of results, they were not economically justifiable. No movement of animals between each unit was recorded throughout the study, all of which were on government land and were not visited by anyone but the researcher.

Reproduction / Body Mass / Survival

These population parameters were evaluated to indicate any variation between the six experimental units and as supporting evidence that all replicates were relatively similar throughout the duration of the study.

The percentages of breeding males and females, body weight of males and minimum survival rates of *P. maniculatus* from the six grids all showed no significant variation among grids from May to October. The average male weight, the proportion of breeding male and female and minimal survival rates of *P. maniculatus* on the six grids were consistent with findings from other studies (Sullivan 1977; Sullivan 1979b; Sullivan and Krebs 1981; Runciman and Sullivan 1996; Von Trebra *et al.* 1998). The same holds true for *M. montanus*, while for *P. parvus*, only the proportion of breeding males indicated a difference between grids. These results indicate that the similarities between population parameters of all species on the six grids provided a reasonable opportunity for comparing abundance estimates derived from different sampling and analysis methods. It was assumed that all experimental units experienced the same environmental conditions throughout the study.

Population Densities

P. maniculatus

In the habitat sampled for this study, *P. maniculatus* was the most common species. The population analysis from grids 1, 2 and 3, using the full ten-day sessions and analyzed using CAPTURE and MNA yielded significantly higher density estimates than did Jolly-Seber and MNA for grids 4, 5 and 6. CAPTURE and MNA estimates from grids 1, 2 and 3 were compared to Jolly-Seber and MNA estimates from grids 4, 5 and 6, respectively, and both analyses indicated significant differences. The unusually high numbers of *P. maniculatus* captured on grids 1, 2 and 3 may explain this difference. CAPTURE estimates averaged 57.4 animals per ha throughout the study for grids 1, 2 and 3, while Jolly-Seber estimates for grids 4, 5 and 6 were much lower and averaged 29.8 animals per ha. Similarly, MNA estimates for the first three grids were averaged to 49.9 animals per ha, while estimates for the last three grids averaged 23.5 animals per ha. Estimates from grids 1, 2 and 3 may have been reliable but are higher than normal, while estimates from grids 4, 5 and 6 are more closely related to population density estimates found in literature. Previous studies reporting *P. maniculatus* density estimates from forested areas include: Sullivan and Sullivan (1982a), which reported average MNA estimates ranging from 12.0 to 20.8 per ha over a three-year period; Sullivan *et al.* (1993) reported MNA estimates ranging from 8.0 to 26.3 animals per ha, and Jolly-Seber estimates ranging from 12.0 to 29.0 animals per ha; while Zimmerling (1993) calculated MNA estimates from 9.5 to 24.7 animals per ha over a two-year period. Other studies reporting *P. maniculatus* population density in forested areas include Sullivan (1979b); Sullivan (1980); Sullivan and Sullivan (1982b); Carey and Thompson 1995; Runciman and Sullivan (1996); Hayward *et al.* 1997; Sullivan *et al.* (1998b); Von Trebra *et al.* (1998). In all cases, average density estimates per ha ranged from zero to numbers in the high twenties and low thirties. In one case, MNA estimates reached 55 animals per ha (Sullivan and Sullivan 1982b), but these numbers do not reflect the general trend in population density for *P. maniculatus* found in literature. In orchards and grassland settings, population density estimates per ha ranged from zero to high thirties and low forties, but were on average in the twenties (Redfield *et al.* 1977; Sullivan and Krebs 1981; Sullivan *et al.* 1998a).

These numbers indicate that density estimates from CAPTURE and MNA for grids 1, 2 and 3, are overestimated. In addition, since *P. maniculatus* is a territorial species, high population densities given by CAPTURE and MNA from grids 1, 2 and 3 would put considerable stress and pressure on a population and are therefore not likely to be biologically achievable. Furthermore, *P. maniculatus* occurring in grasslands are known to be subordinate to voles. Experimental studies have shown that *Microtus* species competitively exclude *P. maniculatus* from grassland areas (Grant 1971; Redfield *et al.* 1977), and while the two species are also known to co-habit (Sullivan and Krebs 1981), high numbers of *P. maniculatus*, such as computed for this study, in an area inhabited by *M. montanus* are probably unlikely. Consequently, it would appear that trapping for short periods throughout the field season gave a more precise and less biased estimate of abundance of *P. maniculatus* than did trapping for a longer period only twice or three times a year.

When CAPTURE data from the ten night trapping periods were sub-divided into five, there was no difference between trapping for six, eight or ten nights. Results from MNA suggested no difference between eight and ten trapping nights. These results indicate that while some researchers advocate that trapping for longer periods of time is necessary to thoroughly sample the study area and get reliable population density estimates, such intense trapping may not be needed. Although CAPTURE and MNA population estimates increased over the ten nights, the rate of increase slowed considerably after the sixth night. Furthermore, the number of new animals captured on the three grids decreased considerably after the fourth night of trapping, corroborating the hypothesis that trapping for more than four to six nights is unnecessary in measuring population densities of *P. maniculatus*.

For each of the three trapping sessions on grids 1, 2 and 3, over 70% of new animals captured were caught during the first four nights, and over 50% of the animals which were captured during the last six nights were never captured again. On average, over 90% of animals captured on night seven had been caught once before on that particular trapping session. Again, these results not only show how trapping *P. maniculatus* for more than four nights is unnecessary, but how animals captured in subsequent nights are more likely to be transients therefore resulting in overestimates of

abundance. Transients, or single-capture animals might be attracted during the last trapping days by food provided as bait, thereby increasing the "edge effect". Trapping for ten days is then more likely to yield positively biased estimates because of these single captures. Various filters could be applied to the data from grids 1, 2, and 3 to see if removing animals which were only captured once would greatly influence estimates and reduce them to numbers more closely related to the density estimates calculated for grids 4, 5 and 6. This could also be done for *M. montanus* and *P. parvus*, although estimates for these species did not seem to be as influenced by transients as *P. maniculatus*. Moreover, intense trapping sessions resulting in a high number of recaptured animals, such as is the case for this study, increases the likelihood of animals being handled too often, which could have negative effects on some individuals, especially during hot weather or pregnancy. Thus, for a very common species such as *P. maniculatus*, there is no difference between trapping for four nights and trapping for ten nights. Trapping for a shorter period of time reduces handling of animals and disturbance of the sampling area.

M. montanus

The population analysis results from grids 1, 2 and 3 (CAPTURE and MNA) and grids 4, 5 and 6 (Jolly-Seber and MNA) were similar throughout the study, with estimates from grids 1, 2 and 3 being generally higher than estimates from grids 4, 5 and 6. For all six grids, numbers of *M. montanus* were lower in June but increased to peak densities in October. Such an increase is explained by the high rate of birth in the late summer, as microtines are known to delay reproduction during the hot summer months (Krebs 1966). No difference was found between CAPTURE and Jolly-Seber estimates of paired weeks from grids 1, 2, 3 and 4, 5, 6, nor for estimates from the six grids from MNA. In this case, there was no difference between trapping for four and ten nights between all three experimental units. Because of the lower densities of *M. montanus*, reducing but not eliminating the chance of trapping transients in the area sampled, as well as the "edge effect", estimates of population density on grids 1, 2 and 3 did not seem to be unusually high. On average, density estimates ranged from under five to approximately 35 and these results were consistent with findings from Sullivan *et al.* 1998a. For *M. montanus*,

trapping for short periods of time throughout the field season gave similar results as did intensive trapping for ten consecutive nights, two or three times a year. Therefore, both methods gave accurate estimates of population density for a given area.

For the first two trapping sessions on grids 1, 2 and 3, the number of animals from nights two to ten were similar. During week 17, there was a slow and steady increase from the second night to the tenth, explained again by the higher rate of birth associated with this period. However, for each session, over 50% of new animals were captured during the first four nights of trapping and an average of 64% of the animals captured during the last six nights were never caught again during the following weeks. On average, for week 1 and 8, over 90% of animals captured on the fifth night were recaptures. Again, these results provide evidence that trapping for more than four or five nights is unnecessary for estimating *M. montanus* population density. The high percentage of animals never captured again, after being caught on the last six nights of trapping, is probably due to transients to the area. In this case, while trapping for more than a few nights did not seem to result in overestimating population density, it does not seem like an efficient method, with respect to time, energy and cost. Resources used during these extra trapping days could be applied to other grids, thereby increasing the number of replicates, or to the number of trapping periods, both of which can improve the quality and quantity of data. As for *P. maniculatus,* unnecessary prolonged trapping can result in handling the animals excessively and could be detrimental to some individuals like lactating females. For *M. montanus*, trapping for shorter periods throughout the field season is recommended as opposed to prolonged trapping. The number of animals captured after the fourth and fifth nights does not change population density estimates calculated from these initial nights of trapping.

P. parvus

On all grids, the number of *P. parvus* slowly increased during the spring and summer, but a sharp decline was noticed in October. This decline was probably related to the high number of *P. parvus* going into hibernation at that time of year (Verts and Kirkland 1988). Population analysis results from grids 1, 2 and 3 using CAPTURE and MNA yielded somewhat higher estimates than did Jolly-Seber and MNA for grids 4, 5

and 6. As was shown for *M. montanus*, this again indicated that both methods of trapping gave similar and likely accurate estimates of the true population density of *P. parvus*. These results strongly suggest that trapping for short periods yields similar and accurate results as does trapping for extended periods.

Estimators used on grids 1, 2 and 3, CAPTURE and MNA, showed a slow increase in numbers from the second night to the tenth, nevertheless, CAPTURE estimates from two, four, six, eight and ten nights were not significantly different from one another for *P. parvus*. MNA population estimates were different, but no difference was found between estimates from six and ten nights. These results not only show that trapping for ten consecutive nights is unnecessary, but that for uncommon species such as *P. parvus*, trapping for two to four nights is enough to collect sufficient information to yield accurate estimates of population density. On average, recaptured animals consisted of 95% or more of the total number of animals captured on the fifth night of trapping. In addition, over 67% of all animals captured on grids 1, 2 and 3 during the three trapping sessions were caught during the first four nights of trapping, and 60% of the animals captured during the last six nights were never caught again.

Trapping Methodologies

Both trapping methods used for this study offer definite advantages and disadvantages, and ultimately, it becomes the experimenter's decision to use one or the other. Trapping for extensive periods (up to ten consecutive nights) a few times a year will generally involve assumptions of population closure: no death, birth, immigration or emigration from the population, and studies using this trapping methodology regularly use CAPTURE (Otis *et al.* 1978) as a tool for data analysis. Advocates of this method will argue that to thoroughly sample a study area, trapping for only a few nights is not enough for adequate sampling of small mammal populations. But while extensive trapping might be desirable, it has many limitations. It requires a great commitment of time, effort and money. Intensive live trapping may result in disruption of social structure and frustrate predation since the animals can spend a lot of time in traps (Renzulli *et al.* 1980). Chitty and Kempson (1949) and Tanaka (1956) have suggested that once individuals have been captured once, they are more likely to be captured again.

Such behavior could increase occurrences of trap-related deaths and injuries, especially during hot weather and pregnancy, as animals may wait near traps and enter them as soon as they are set, increasing time spent in confinement. Secondly, this method generally involves trapping during the spring and fall, thereby ignoring potentially important processes happening in the population during other periods of the year. Trapping once or twice a year yields only a minimum and maximum with no reference point in time for comparison, which could easily result in a misleading interpretation about the true population dynamics. Hallett *et al.* (1991) concluded that it is not possible to meet all guidelines of program CAPTURE for long-term population studies of medium-sized mammals. Thirdly, this technique does not allow reliable data collection about population parameters such as body weight, survival, reproduction, recruitment, sex ratios, animal movement and trappability, all of which can be important in determining the quality and viability of a population.

In addition, while trapping for ten nights might ensure complete sampling of a population, it also significantly increases the chances of capturing transient animals to the area, and thereby overestimating population densities. The movement patterns by individual animals for this study are unknown, but some small mammals are known to travel great distances (Gentile and Cerqueira 1995; Juskaitis 1997; Basquill and Bondrup-Nielsen 1999; Bias and Morrison 1999; Owadowska 1999; Macdonald *et al.* 2000). Reasons for small mammals to travel or disperse to other habitats can include movement patterns by juvenile members of a population which can be influenced by competition for mates or for resources (Jensen 1996; Wolff and Schauber 1996; Juskaitis 1997; Byrom and Krebs 1999). Seasons (Twigg *et al.* 1998; Bias and Morrison 1999; Macdonald *et al.* 2000) or the sex of an individual (Twigg *et al.* 1998; Priotto and Steinmann 1999) can also influence its mobility. Habitat quality, food type and abundance, and landscape structure can also affect movement between areas (Macdonald *et al.* 1997; Stapp 1997; Basquill and Bondrup-Nielsen 1999; Ouin *et al.* 2000). Although it is not possible to positively identify resident and transient animals for my study, it is very likely, considering the large number of single and double captures, that transient animals were caught during the ten night trapping periods. This again would support assumptions that estimates from grids 1, 2, and 3 are over-inflated. As previously mentioned, deleting

these single-captures from data for grids 1, 2, and 3, could yield closer estimates to estimates from grids 4, 5, and 6. Moreover, it would be interesting to evaluate if these transients or single-capture animals can be classified, for instance, as mostly juveniles or adults, males or females, breeding or non-breeding.

Intensive trapping requires laborious efforts from the experimenter and it can be argued that such efforts could be used to sample other grids or replicates. For all of these reasons, intensive trapping is not necessarily the best approach.

Trapping for a few nights at regular intervals throughout the year, or field season, involves assumptions of demographically open populations in which births, deaths, immigration and emigration are taken into consideration. Data collected in this fashion are usually analyzed using the Jolly-Seber (Seber 1982) or minimum number of animals known to be alive (MNA) (Krebs 1966) models. The Jolly-Seber estimator is described as one of the best by Nichols and Pollock (1983), even in cases of heterogeneity and trap-happy responses which are the two sources of unequal capture probability most likely to arise in small mammal studies. Supporters of this method argue that trapping throughout the field season is the only method that provides sufficient and reliable information on the population and its changes through time. The collection of time-series data for small mammals allows analysis of the effects of a perturbation, such as habitat alteration, on the demographic characteristics of a distinct population. Such characteristics might change from season to season and year to year, and it is therefore necessary to have continuity in the sampled populations to evaluate the potential effects of an experimental treatment accurately and stringently (Ritchie and Sullivan 1989). Since only a few nights every two to four weeks are necessary, the trapping effort is reduced and the chances of trapping transients are close to zero. But trapping every few weeks also means the experimenter has to be close to the area trapped, and some might argue that sampling for only a few days may not be enough to collect an adequate sample of the population. Nevertheless, this method, as well as the Jolly-Seber format, permits the acquisition of data enabling the analysis of parameters such as body weight, survival, trappability, recruitment, sex ratios, reproduction and movement of marked individuals. In addition, handling of animals is kept to a minimum.

Which of the two techniques results in the best density estimates? The answer to this question is still not an absolute one since the real density is not known. However, data collected while trapping for a few nights every two- to four- weeks and assessed using the Jolly-Seber and MNA models seemed to yield less biased estimates and rest on fewer assumptions than the other method.

From data collected in this study and in light of the strengths and weaknesses of both methods, it is suggested that trapping for short periods throughout the year, or field season, will give a better estimate of small mammal population abundance. The methodology selected should, however, reflect the experimental goals of the study to be undertaken as well as the experimental design. The judicious ecologist will choose a method that optimizes the quantity and quality of data gathered. Trapping duration within a sampling period should be a compromise between being long enough for maximum trap exposure for resident animals, but short enough to neither attract transients, nor stress animals from extended confinement (Ritchie and Sullivan 1989). As was previously reported, different methods could be applied to different species, but as a general rule, a diversity of small mammals could be sampled from three to five nights at every two- to four-week intervals and data collected would yield reliable population density estimates. Any trapping beyond this recommended period would only result in an increase in recaptured animals and transients resulting in overestimation of population density. Excessive animal handling may also be detrimental to some individuals or some species, leading to an increase in trapping related deaths.

CONCLUSIONS AND RECOMMENDATIONS

This study was conducted to determine the difference, if any, between two distinct small mammal trapping methodologies used in assessing population abundance, as well as to determine the optimal number of trapping days required to adequately sample a population. The results suggest that trapping for three to five nights yields reliable estimates of small mammal population density in an area. Additional replicates may have increased the precision of these results but such a design was not economically feasible. Future work in this area could include conducting this study over a two- or three-year period to determine the differences in populations through time. Such a study would likely reinforce the results and conclusions reached from this experiment. Data collected every few weeks throughout the year would certainly provide useful information about population dynamics of the species sampled, the kind of interpretation that could not be reached from trapping for only a few, specific periods in the year. This study could also be replicated in a different habitat, such as in a forested area, to evaluate the difference, if any, between grassland and forest populations of small mammals under different experimental methodologies.

One of the major inconveniences of this study was not knowing the actual population size of *P. maniculatus, M. montanus* and *P. parvus*. It would have been interesting to follow each population using radiotelemetry, but such a study would have required additional time, energy and money which was not available. Replicating this study on an island would also provide an excellent means of comparison, as some small mammal populations could be extensively sampled to provide a more accurate estimation of densities than would be established by trapping in an open environment such as grassland or forested areas.

CHAPTER 2

A COMPARISON OF GRID SIZE FOR ESTIMATION OF ABUNDANCE

INTRODUCTION

A grid system of traps is one of the most effective method for monitoring all demographic parameters of various small mammal populations in an area (Smith *et al.* 1975). It provides a greater probability of an animal encountering a trap and being captured. Therefore, a grid may provide a more representative sample of all species, both common and rare, living in a given area than would a line of traps. From grids, density estimates are readily obtained and may be compared between different areas, seasons, and years (Ritchie and Sullivan 1989). Although grids are used more often than trapping lines for small mammal research, there has been much controversy regarding grid size to adequately sample a population and yield reliable density estimates. The reliability of results derived from a study depends on the effectiveness of the trapping methods to capture a representative sample of a small mammal population. It as been argued that 1-ha grids are too small to do so (Smith *et al.* 1975; Swift and Steinhorst 1976; Van Horne 1982; White *et al.* 1982; Bondrup-Nielsen 1983; Wilson and Anderson 1985a; Wilson and Anderson 1985b; Smith, 1999).

A common grid configuration for mice and voles is a 1-ha matrix with 49 (7 x 7) trap stations set at 14.3-m intervals (Ritchie and Sullivan 1989). One trap per station is usually sufficient for monitoring purposes, but two traps per station may be used at high densities. This system provides estimates for 1-ha and is an ideal size for replication, as well as for acquiring reliable density estimates of all small mammal species in an area (Sullivan and Sullivan 1982a). Trapping grids ranging from 0.7- to 1.4-ha have been widely used for many small mammal research projects (Myers and Krebs 1971; Krebs *et al.* 1976; Redfield *et al.* 1977; Sullivan 1979a; Renzulli *et al.* 1980; Sullivan and Sullivan 1982b; Boonstra 1985; Sullivan *et al.* 1993; Zimmerling and Sullivan 1994; Runciman

and Sullivan 1996; Sullivan and Boateng 1996; Hayward *et al.* 1997; Brooks *et al.* 1998; Von Trebra *et al.* 1998; Menzel *et al.* 1999).

In other studies, larger grids have been used for small mammal research (Van Vleck 1968; Smith *et al.* 1971; Hansson 1975; Radvanyi 1980; Jones and Sherman 1983; Bondrup-Nielsen 1987; Medin and Clary 1990; Hallett *et al.* 1991; Kohler 1993; Rosenberg and Anthony 1993; Hayes *et al.* 1995). While studies using 1-ha grids are usually sampled for 2 nights at every two- to three-week interval, larger grids are generally, but not exclusively, sampled for a longer period of time (five to ten nights) usually only a few times a year. This difference can probably be related to the high trapping effort required to trap such large grids. The debate over grid size is one that arises based primarily on the belief that a 1-ha grid design is too small in relation to the home range sizes of small mammals. Such a design results in a large "edge effect", where for a large proportion of animals, the home range only overlaps the study area (Dice 1938; Tanaka 1972; White *et al.* 1982; Wilson and Anderson 1985a; Wilson and Anderson 1985b).

In addition, Smith *et al.* (1975), Swift and Steinhorst (1976), Van Horne (1982) and Bondrup-Nielsen (1983) argued that census grids usually cover only a small proportion of the area utilized by small mammal populations, except when sampling is done on small islands or when animals are restricted to isolated habitat patches where the whole population can be enumerated. Since animals trapped on the grids occupy a larger area, proportionately more animals will be captured in the other perimeter of the grid, resulting in "edge effect". Furthermore, results from Bondrup-Nielsen's model showed that when the size of the trapping grid used for small mammal sampling is less than about four times the average home range size, overestimation of population density occurs.

The two major objectives of this chapter were to: 1) determine the differences between small mammal population estimates (number of animals/ha) taken from grids of different sizes; and 2) determine the optimal grid size for adequate estimates of small mammal population abundance. Based on these objectives, a specific hypothesis, phrased as a prediction is: one-ha grids will be as accurate in estimating small mammal abundance as two- or five-ha grids.

MATERIALS AND METHODS

Study Area Description and Experimental Design

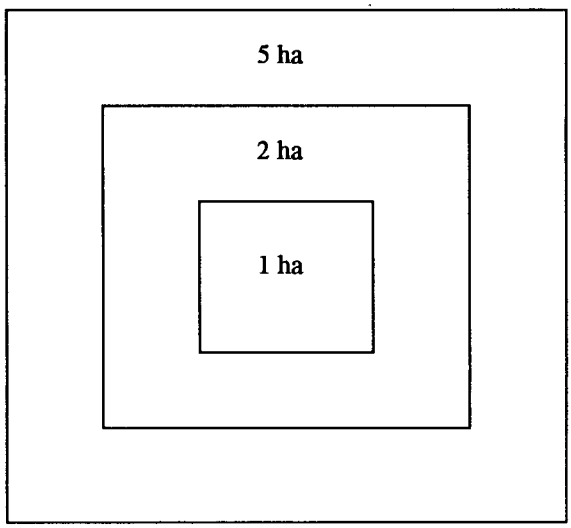
Experiment A

Data was collected 25 km north-west of Vernon, in the south central interior of British Columbia, between the latitudes of 50° 21.5′ to 50° 22.8′ N, and longitudes of 119° 35.3′ to 119° 36.5′ W, near the northwest end of Okanagan Lake from June to October in 1991 and 1992. Site elevation ranged from 1356 m to 1478 m, in the MSdm biogeoclimatic zone (Meidinger and Pojar 1991). The climate is characterized by warm, dry summers and cold, dry winters with mean July and January temperatures of 16° and -10° C respectively, and a mean annual precipitation of 40 cm. Chris M. Kohler and his field assistants collected the data used for this experiment in 1991 and 1992. In mature stands, the predominant coniferous species are western red cedar (*Thuja plicata*), Douglas-fir (*Pseudotsuga menziesii*), subalpine fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelmannii*), white spruce (*P. glauca* x *P. engelmannii*) hybrid, western larch (*Larix occidentalis*), and lodgepole pine (*Pinus contorta*) (Kohler 1993).

Two replicate experimental units of thinned and fertilized lodgepole pine stands (age 21 and 28 years), approximately 36 ha each, were selected for large-scale food supplementation. Two other thinned and fertilized stands of 17.8 and 38.8 ha, aged 28 and 20 years, respectively, were used as control (no food supplementation) replicates. The average dbh of trees on control and treatment blocks ranged from 13.8 ± 0.2 cm to 18.8 ± 0.3 cm (Kohler 1993).

A randomized block design was used with two control and two treatment replicate units. Small mammal sampling was conducted on 5-ha grids within the center of each unit. All treatment units were separated by at least 100 m to minimize animal movement between grid areas. From within these four 5-ha grids, two additional sampling grids, 1 ha and 2 ha, were used to compare population estimates of small mammals among three grid sizes (Fig. 27).

Figure 27. 1-, 2- and 5-ha grids layout: Experiment A



Experiment B

This experiment was located at three replicate study areas: Penticton, Kamloops and Prince George and data were collected from May to August in 1991 and 1992.

The Penticton creek study area was located in south central British Columbia, 15 km northeast of Penticton (49°34′ N; 119°27′ W). This region is within the Interior Douglas-fir (IDF_{dk}) biogeoclimatic zone (Meidinger and Pojar 1991). Topography in the area is hilly with sandy loam soil at 1340 to 1500 m elevation and southeast aspect, with an average slope of 10%. The climate is characterized by warm, dry summers and cool winters. The average temperature is below 0°C for 2-5 months, and above 10°C for 3-5 months, with mean annual precipitation ranging from 30 to 75 cm. Open to close forests of Douglas-fir (*Pseudotsuga menziesii*) cover much of this zone, with even-aged lodgepole pine (*Pinus contorta*) stands at higher elevations. Several thousand hectares was burned by wildfire in 1970, salvage logged in 1971, and planted with lodgepole pine in 1972. Natural regeneration increased the density to a range of 18,500-30,300 stems/ha. Other species in the stands included Douglas-fir, Engelmann spruce (*Picea engelmannii*), western larch (*Larix occidentalis*), willow (*Salix* spp.), Sitka alder (*Alnus sinuata*) and trembling aspen (*Populus tremuloides*) (Sullivan *et al.* 1996).

The Kamloops study area was located 30 km south of Kamloops, British Columbia (50°28′ N; 120°32′ W) within the Montane Spruce (MS_{dm}) biogeoclimatic zone (Meidinger and Pojar 1991). Engelmann and hybrid spruce (*P. engelmannii* X *P. glauca*) and varying amounts of subalpine fir (*Abies lasiocarpa*) are the characteristic tree species. Due to past wildfires, successional forests of lodgepole pine, Douglas-fir and trembling aspen are common. This zone has a cool, continental climate characterized by cold winters and moderately short, warm summers. The mean temperature is below 0°C for 5 months of the year and above 10°C for 2-4 months. The mean annual precipitation range from 38 to 90 cm. The topography is hilly at 1400 to 1500 m elevation, with northerly aspects. This area was burned by wildfire in 1960 and regenerated naturally to lodgepole pine with a mean density of 20,000 stems/ha. Other species present are Engelmann spruce, subalpine fir, willow, Sitka alder and trembling aspen (Sullivan *et al.* 1996).

The Prince George study area was located 60 km west of Prince George, British Columbia (53°52′ N;123°32′ W) in the Sub-boreal Spruce (SBS_{dw}) biogeoclimatic zone (Meidinger and Pojar 1991). The general topography is gently rolling, at 800 m elevation and variable aspects. In mature stands, hybrid Engelmann X white spruce and subalpine fir is mixed with extensive stands of lodgepole pine, which regenerated after wildfires. Stands of young lodgepole pine covered ≈ 1000 ha; this area was harvested during 1966-1972 and left to natural regeneration of pine. Stand densities ranged from 2,700 to 4,700 stems/ha. Minor components of the stands included white spruce, black spruce (*P. mariana*), Douglas-fir, willow, alder and aspen (Sullivan *et al.* 1996).

For each study area, five stands of lodgepole pine were chosen in a randomized block design. Stand A was low density (500 stems/ha); Stand B was medium density (1,000 stems/ha); Stand C was high density (2,000 stems/ha); Stand D was unthinned (> 2,000 stems/ha) and Stand E was old growth (Sullivan *et al.* 1996).

Small Mammal Populations

Experiment A

For each replicate stand, 225 Longworth live-traps (Penlon Limited, United Kingdom) were used and located at 14.3-m intervals in a checkerboard pattern on 16

lines (16 by 15). One trap was placed at each station for the duration of the project so that animals would become accustomed to their presence, therefore keeping trappability high. Trapping was conducted from May to October in 1991 and 1992, at 2-week intervals. For each station, traps were set on the afternoon of day 1, checked on the morning and afternoon of day 2, and again on the morning of day 3. They were left locked open between trapping periods. All traps were baited with oats, peanut butter mixed with sunflower seed oil and a slice of carrot. Cotton was provided as bedding. For each capture, new animals were ear-tagged with serially numbered fish fingerling tags. Information on gender, reproductive condition (by palpation of male testes and mammaries of the females) (Krebs *et al.* 1969), species, body weight (using Pesola spring scales) and tag number was recorded.

Experiment B

At each study area, small mammal populations were sampled in all five stands (A, B, C, D and E) on 1-ha and 9-ha live-trapping grids. Each 1-ha grid had 49 (7 x 7) trap stations located at 14.3-m intervals with one Longworth live-trap placed within a 2-m radius of each station. Traps were baited with oats and a slice of carrot; coarse brown cotton was supplied as bedding. They were also covered with a piece of wood to offer protection from rain and sunlight. Traps were set on the afternoon of day 1, checked on the morning and afternoon of day 2, and checked on the morning of day 3. Traps were left open between trapping periods.

Each 9-ha grid had either 96 (6 X 16) or 100 (10 X 10) stations at 30-m intervals, with one Tomahawk live-trap (Tomahawk Live-trap co., Tomahawk, Wisconsin, USA) at every other station, resulting in $\approx$ 5 traps/ha. Traps were baited with sunflower seeds, set shortly after dawn and checked 4-6 hours later on two consecutive days in a given trapping period. Traps on all grids were closed and left permanently in the field between trapping periods. Live-trapping was conducted every 2 weeks from May to August 1990 and 1991 (Sullivan *et al.* 1996). For each capture, animals were handled as described for Experiment A.

Population Dynamics

Experiment A

Population densities for both *P. maniculatus* and *T. amoenus* were estimated using the Jolly-Seber (Seber 1982) and minimum number alive (MNA) (Krebs 1966) models. Densities were calculated for the 5-ha grids as well as for the 1- and 2-ha grids. All estimates were reduced to the number of animals per ha. To evaluate the differences, if any, between estimates from the three grid sizes, only data from the summer (June to early August) and fall (late August to October) periods, where animals are known to be most abundant, were analyzed. Population density for both species was calculated using *Small Mammal Programs for Mark-Recapture Data Analysis* (Krebs 1991).

Experiment B

Population density estimates for *T. amoenus* used Jolly-Seber (Seber 1982) and MNA (Krebs 1966) models. Estimates were calculated for all 1-ha and 9-ha grids. Mean length of movement between trapping periods was also calculated for each grid and year. This was done to evaluate the average home range of *T. amoenus* to further assess the effective trapping area (ETA) for each grid. Jolly-Seber and MNA estimates were then reduced to number of animals per effective trapping area. For this study, data from 1990 and 1991 summer periods (June to August) were averaged and analyzed. Population density and mean length of movement for *T. amoenus* were calculated using *Small Mammal Programs for Mark-Recapture Data Analysis* (Krebs 1991).

Statistical Analysis

Experiment A

Because the 1-, 2- and 5-ha grids were nested and therefore not independent from one another, population estimates of *P. maniculatus* and *T. amoenus* from Jolly-Seber and MNA were analyzed using the means for each period (summer and fall) and associated standard errors. Standard errors and averages (animals/ha) from the summer and fall of each year were compared for the 1-, 2- and 5-ha grids on grids A, B, C and D.

Experiment B

Population estimates of *T. amoenus* from Jolly-Seber and MNA were analyzed using a randomized block ANOVA (Zar 1996). Analyses were performed for each grid separately (A, B, C, D and E) since each of the stands were of different tree densities and therefore of different environmental conditions (Sullivan *et al.* 1996). The two years, 1990 and 1991, were kept separate as was each location for analysis. The data were blocked, resulting in six blocks for each grid (three locations x two years). Averages (animals/ha) from the summer of each year were compared for the 1- and 9-ha grids. ANOVA analyses are presented in Appendix C. For all statistical analyses, the level of significance was set at $P= 0.05$.

RESULTS

Population Density

Experiment A

P. maniculatus

Averaged summer and fall population estimates and associated standard errors for *P. maniculatus* over the two year period for the 1-, 2- and 5-ha grids, are illustrated in Figs. 28 to 31, for grids A, B, C and D, respectively. It has been shown that when standard error intervals overlap, the means are never significantly different (Browne 1979). These intervals are used to establish if densities calculated for the 1-, 2- and 5-ha grids are similar.

Jolly-Seber and MNA estimates for grid A were all very low (Fig. 28). In most cases, estimates from the 1-, 2- and 5-ha grids were very similar. During summer 1991 and fall 1992, estimates from the 5-ha grids were significantly different from the other two grids. Density estimates from Jolly-Seber for grid B were the highest of all grids, with numbers in the low fifties (Fig. 29). Although all estimates for 1991 and the fall of 1992 were very similar, marked differences were found between 1-, 2- and 5-ha grids during the summer of 1992.

Estimates from grid C were the most variable (Fig. 30). Only Jolly-Seber population density estimates from the summer of 1991 and MNA estimates from the summer and fall of 1992 were found to be comparable. Although the other estimates were very much alike, a significant difference was found between Jolly-Seber estimates for fall of 1991, summer and fall of 1992, and MNA estimates for 1991. Density estimates for grid E were fairly high and very similar (Fig. 31), only Jolly-Seber estimates for the summer of 1991 were found to be different. No significant differences were found between all other estimates.

Higher numbers on treatment grids B and D are likely related to the food supplementation experiment conducted using these grids, while grids A and C were used as control. Because of the different experimental conditions occurring in all grids, differences between estimates among grids should not be analyzed.

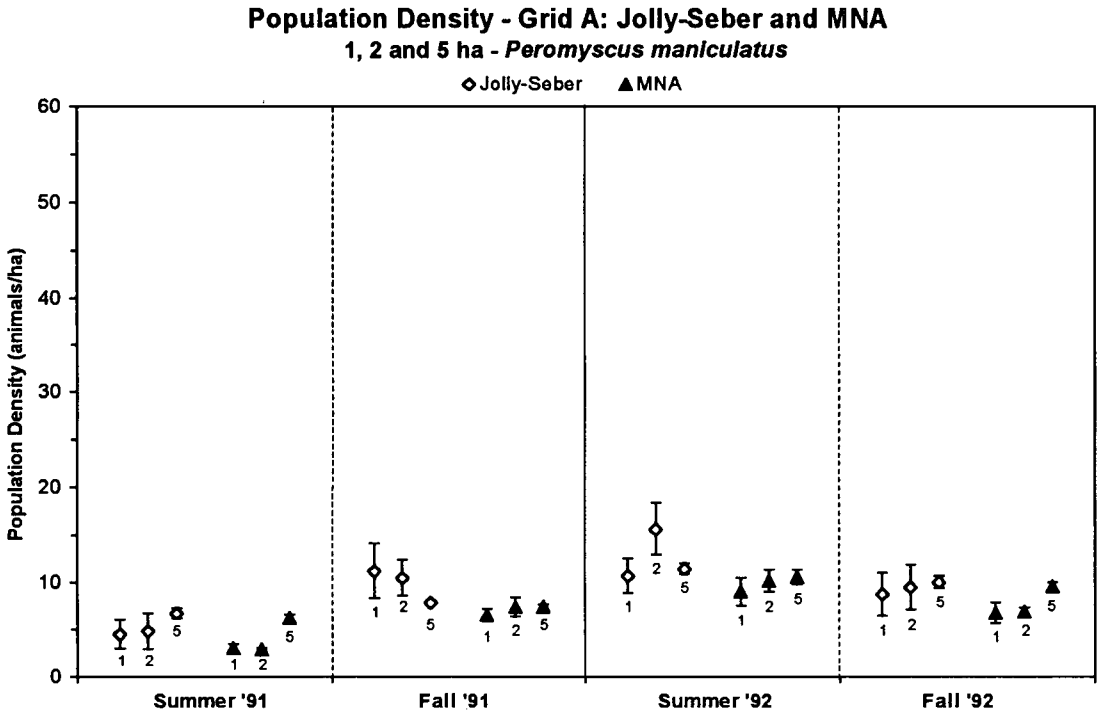


Figure 28. *P. maniculatus*: Population density for 1-, 2-, and 5-ha grids from Jolly-Seber and MNA ± S.E.: Grid A - 1991 and 1992.

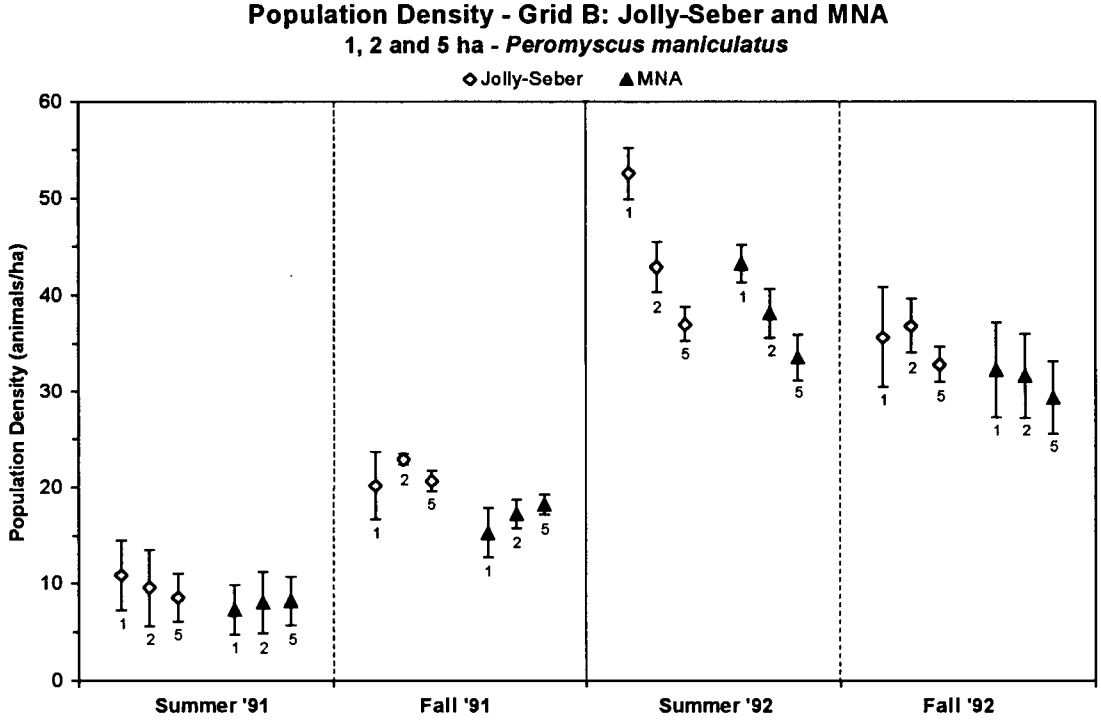


Figure 29. *P. maniculatus*: Population density for 1-, 2-, and 5-ha grids from Jolly-Seber and MNA ± S.E.: Grid B - 1991 and 1992.

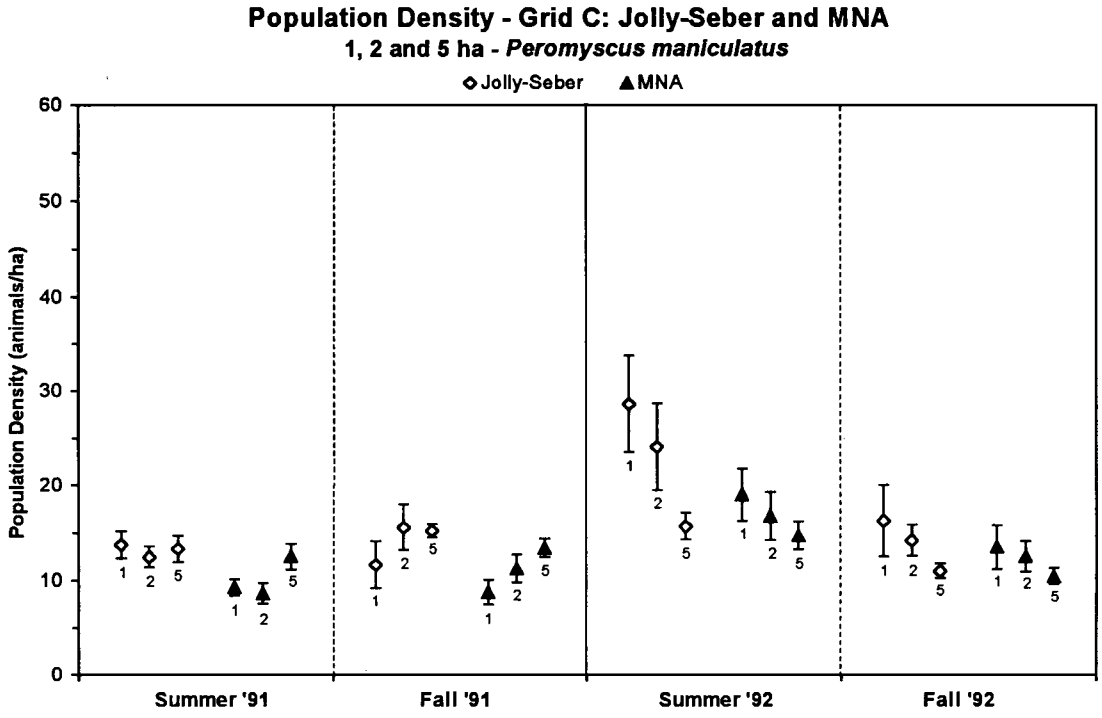


Figure 30. *P. maniculatus*: Population density for 1-, 2-, and 5-ha grids from Jolly-Seber and MNA ± S.E.: Grid C - 1991 and 1992.

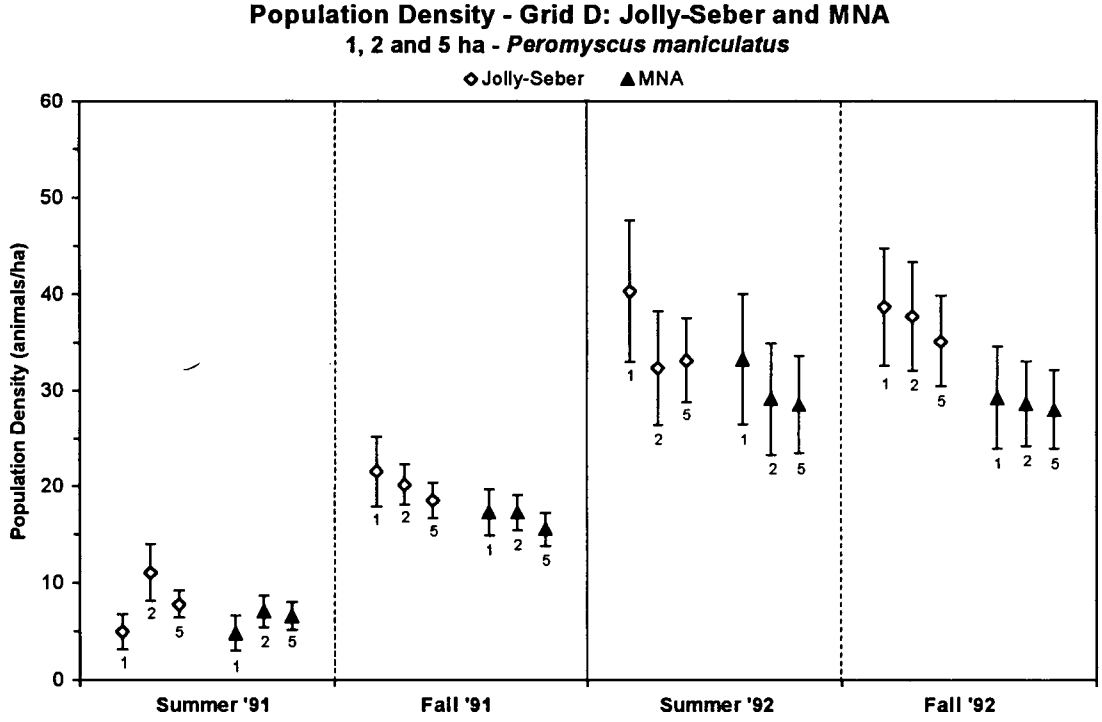


Figure 31. *P. maniculatus*: Population density for 1-, 2-, and 5-ha grids from Jolly-Seber and MNA ± S.E.: Grid D - 1991 and 1992.

T. amoenus

Summer and fall averaged population estimates of *T. amoenus* with associated standard errors for grids A, B, C and D over the two year period for the 1-, 2- and 5-ha grids from Jolly-Seber and MNA are presented in Figs. 32 to 35. Although the general trend of the population (high and low population estimates) is followed by the three grid sizes for *T. amoenus*, there is more variation between the 1-, 2- and 5-ha grids for this species.

Population estimates for grid A varied slightly but stayed under ten animals per ha (Fig. 32). Only Jolly-Seber numbers for the fall of 1991 and 1992 as well as MNA numbers from the fall of 1992 were found to be similar. Grid B estimates were more comparable (Fig. 33) and no significant differences were found between Jolly-Seber estimates from the fall of 1991 and 1992. MNA estimates were all similar except for the summer of 1992.

Population estimates for grid C were fairly high (Fig. 34). No significant differences were found for both estimators for the fall of 1991, and for 1992. Estimates were different for Jolly-Seber and MNA for the summer of 1991. Grid D experienced the most variation (Fig. 35), where only MNA estimates for 1991 and both estimators for the fall of 1992 showed no significant difference. Estimates from the 1-ha grids were generally significantly lower than estimates from the 2- and 5-ha grids.

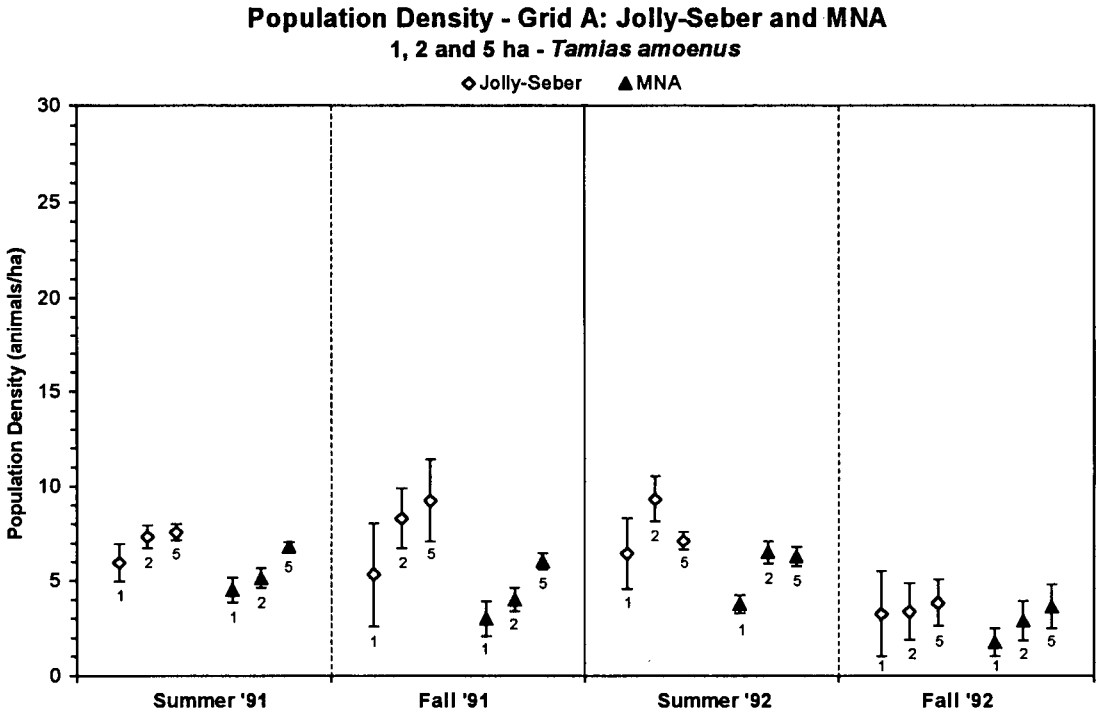


Figure 32. *T. amoenus*: Population density for 1-, 2-, and 5-ha grids from Jolly-Seber and MNA ± S.E.: Grid A - 1991 and 1992.

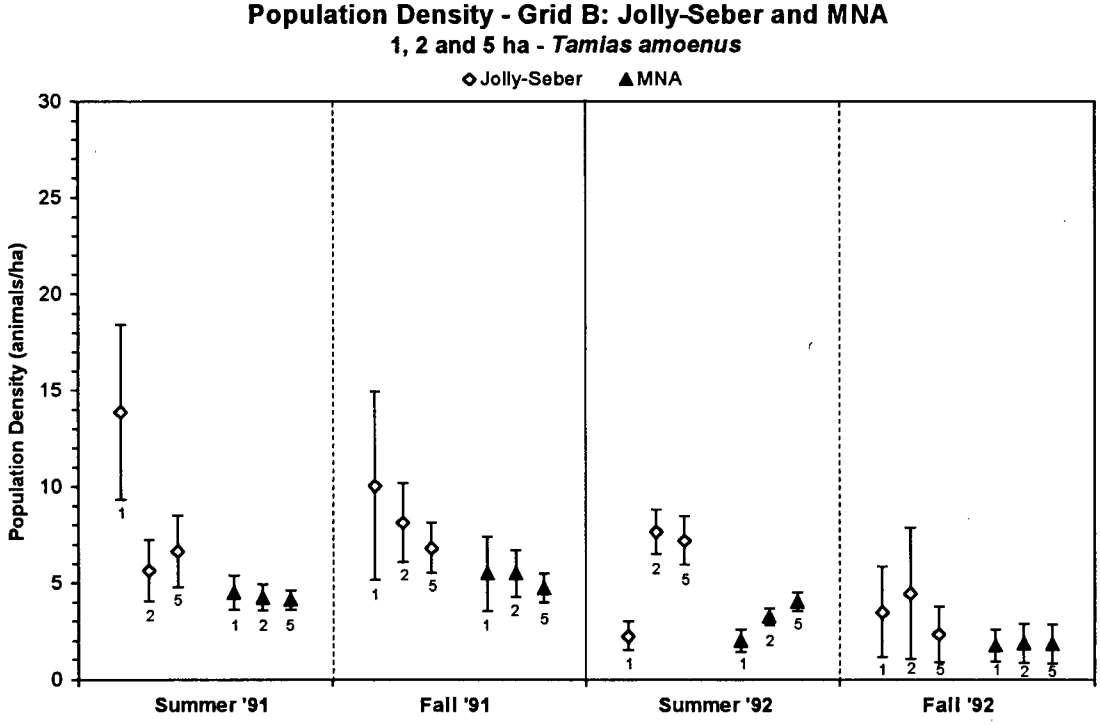


Figure 33. *T. amoenus*: Population density for 1-, 2-, and 5-ha grids from Jolly-Seber and MNA ± S.E.: Grid B - 1991 and 1992.

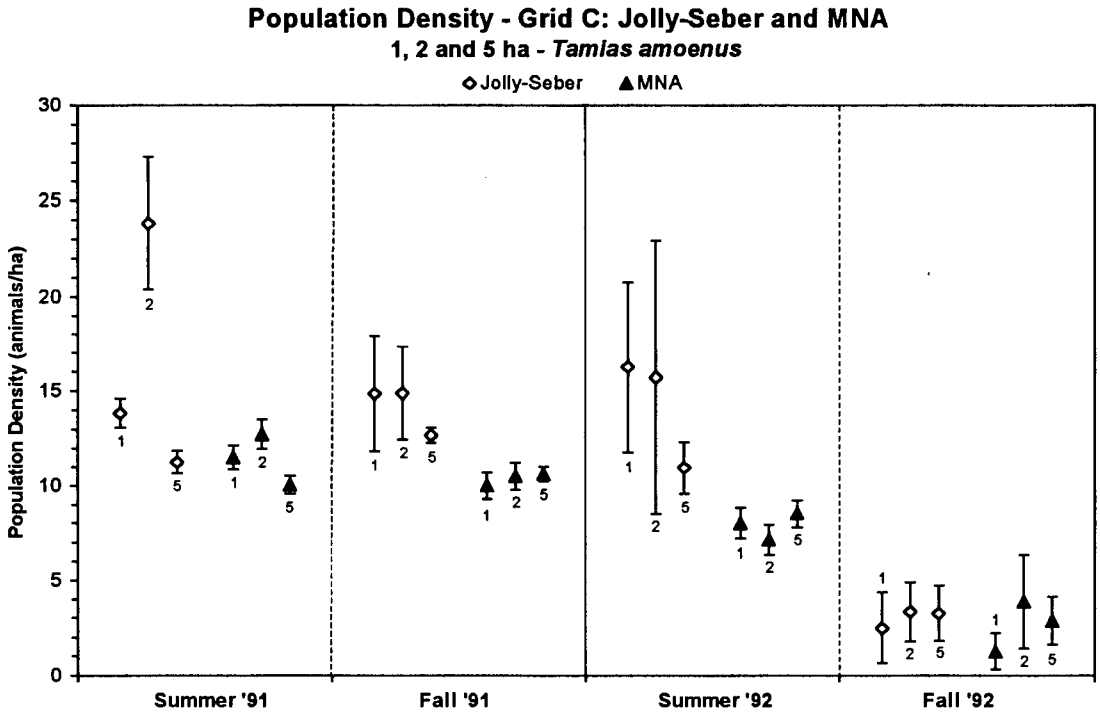


Figure 34. *T. amoenus*: Population density for 1-, 2-, and 5-ha grids from Jolly-Seber and MNA ± S.E.: Grid C - 1991 and 1992.

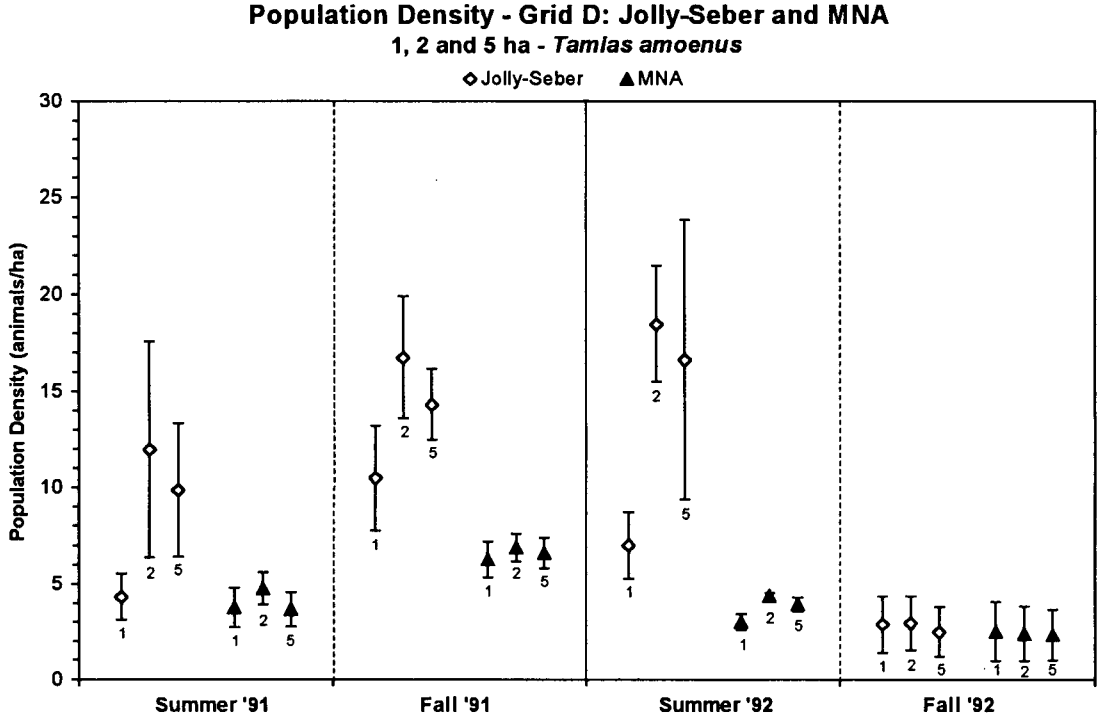


Figure 35. *T. amoenus*: Population density for 1-, 2-, and 5-ha grids from Jolly-Seber and MNA ± S.E.: Grid D - 1991 and 1992.

Population Density

Experiment B

T. amoenus

Mean length of movement from all grids at the three locations ranged from 0.0 m to 55.2 m on the 1-ha grids and 0.0 m to 152.0 m on the 9-ha grids. These movements resulted in 1- and 9-ha grids corrected for edge effect ranging from 1- to 2.4-ha and 9- to 20.4-ha, respectively.

Population densities of *T. amoenus* were lower on the 9-ha grids than on the 1-ha grids for Penticton, Kamloops and Prince George: grids A (Fig. 36); B (Fig. 37); C (Fig. 38); D (Fig. 39); and E (Fig. 40). Density estimates per ha for Jolly-Seber from grid A for the three locations ranged from 0.5 to 11.7 on the 1-ha grids, and 0.7 to 3.5 on the 9-ha grids. MNA estimates per ha ranged from 0.2 to 8.1 on the 1-ha grids, and 0.2 to 2.9 on the 9-ha grids. Estimates from Jolly-Seber on grids B ranged from 0.6 to 12.7 animals per ha for the 1-ha grids, and 0.7 to 1.6 animals per ha for the 9-ha grids. MNA estimates ranged from 0.6 to 9.4 and 0.1 to 1.5 animals per ha for the 1- and 9-ha grids, respectively. For grid C, Jolly-Seber estimates per ha ranged from 0.5 to 14.2 on the 1-ha grids, and 0.2 to 3.7 on the 9-ha grids. MNA estimates per ha ranged from 0.0 to 7.9 on the 1-ha grids, and 0.2 to 2.9 on the 9-ha grids. Jolly-Seber estimates per ha from grids D ranged from 0.5 to 11.3 for the 1-ha grids, and 0.2 to 2.5 for the 9-ha grids. MNA estimates per ha ranged from 0.0 to 10.6 for the 1-ha grids, and 0.1 to 2.0 for the 9-ha grids. Finally, estimates from Jolly-Seber from grids E ranged from 0.5 to 7.0 and 0.0 to 0.8 animals per ha on 1- and 9-ha grids, respectively, while MNA estimates ranged from 0.0 to 7.0 and 0.0 to 0.5 animals per ha on 1- and 9-ha grids, respectively.

Jolly-Seber estimates from all locations calculated from the 1 and 9-ha grids were significantly different for grid A ($F_{1,5} = 13.75$, $P = 0.03$), grid B ($F_{1,5} = 27.80$, $P = 0.00$), grid C ($F_{1,5} = 21.12$, $P = 0.01$), grid D ($F_{1,5} = 7.22$, $P = 0.04$) and grid E ($F_{1,5} = 13.23$, $P = 0.02$). In all cases, estimates from the 1-ha grids were significantly higher than estimates from the 9-ha grids. Similar conclusions were reached from data analyzed using MNA, for which a significant difference was found between population estimates from grid A ($F_{1,5} = 12.37$, $P = 0.02$), grid B ($F_{1,5} = 20.05$, $P = 0.01$), grid C ($F_{1,5} = 20.69$, $P = 0.01$), and grid E ($F_{1,5} = 11.84$, $P = 0.02$). No significant difference was found between MNA

estimates from 1- and 9-ha on grid D ($F_{1,5} = 6.55$, $P = 0.05$). Once again, estimates from the 1-ha grids were significantly higher than estimates from the 9-ha grids.

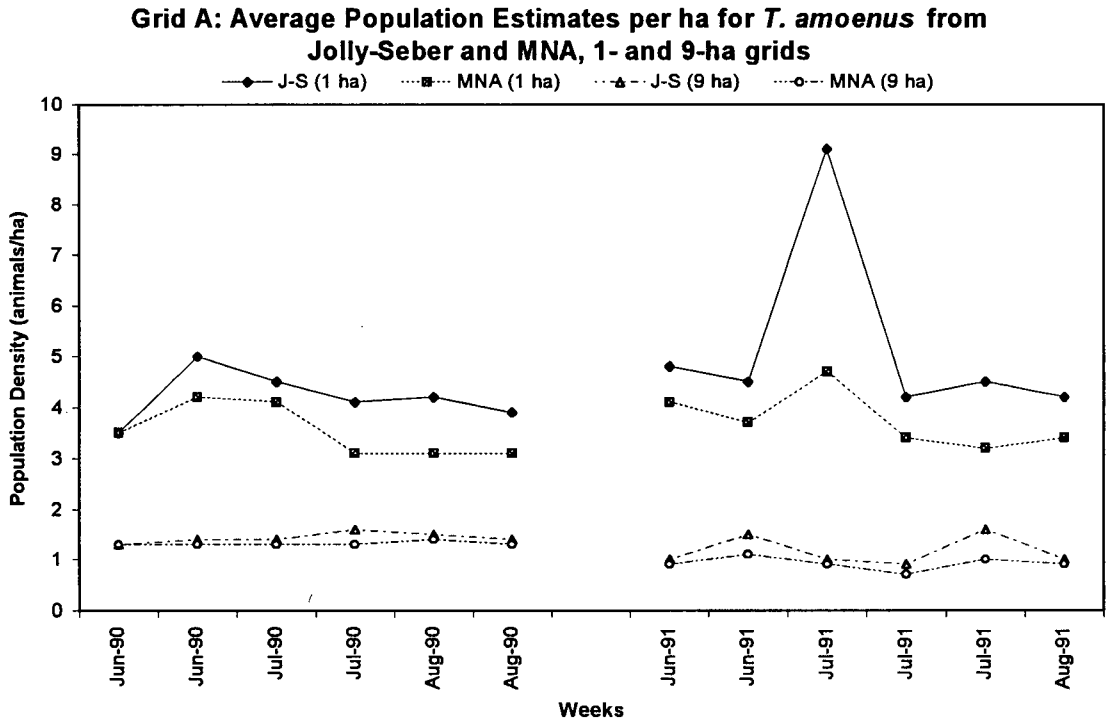


Figure 36. Grid A: Average population estimates per ha of *T. amoenus* from Jolly-Seber and MNA, 1-and 9-ha grids: 1990, 1991: Penticton-Kamloops-Prince George.

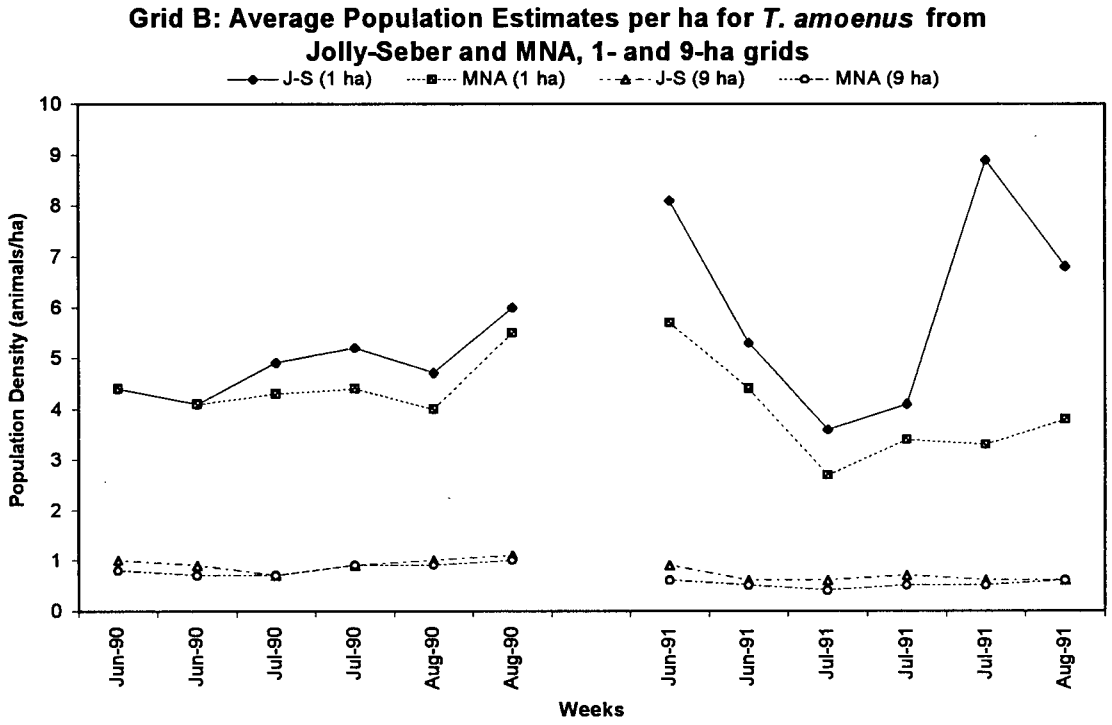


Figure 37. Grid B: Average population estimates per ha of *T. amoenus* from Jolly-Seber and MNA, 1-and 9-ha grids: 1990, 1991: Penticton-Kamloops-Prince George.

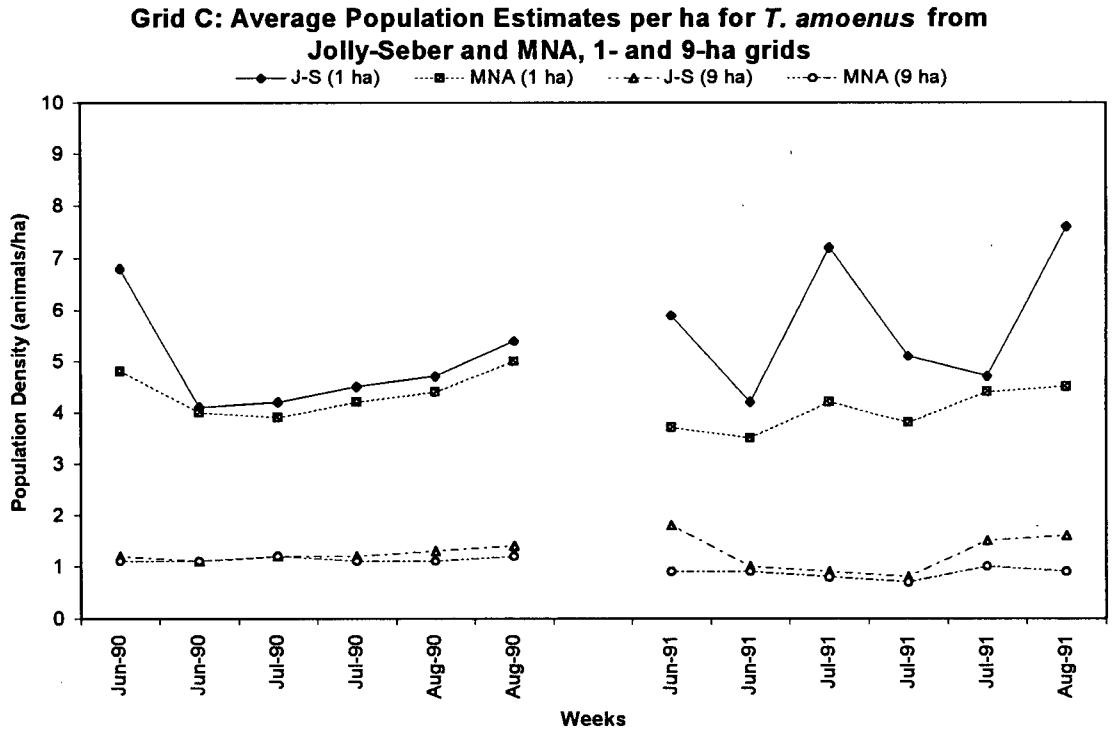


Figure 38. Grid C: Average population estimates per ha of *T. amoenus* from Jolly-Seber and MNA, 1-and 9-ha grids: 1990, 1991: Penticton-Kamloops-Prince George.

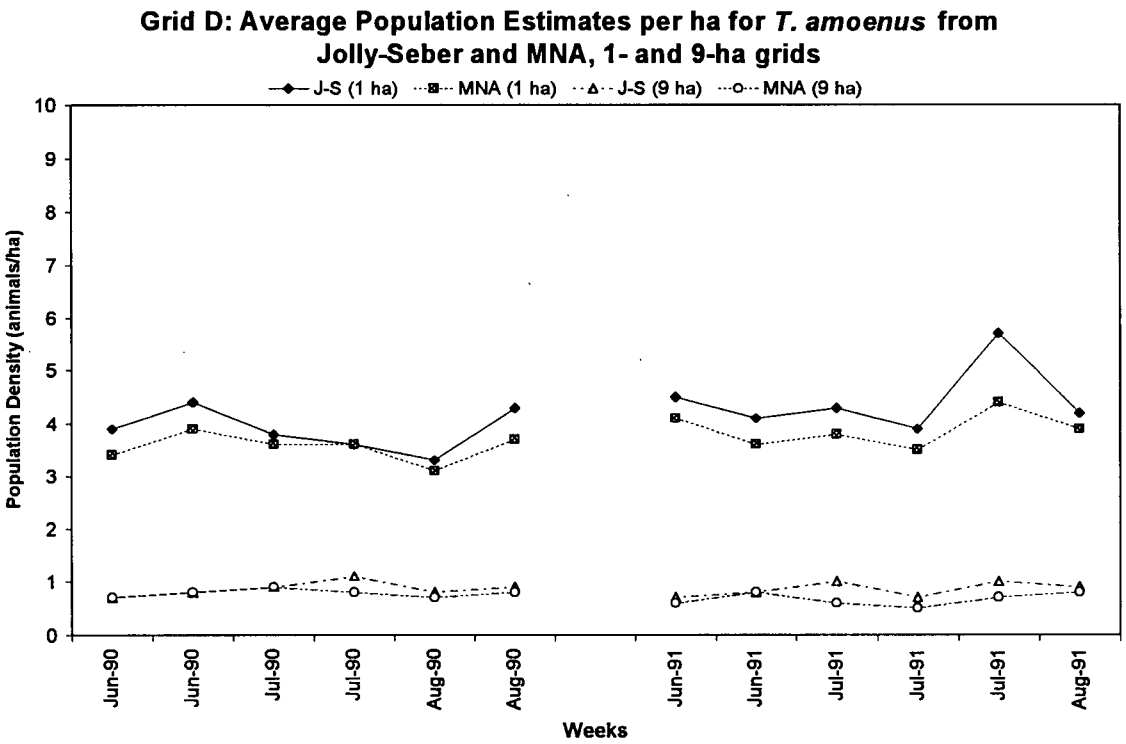


Figure 39. Grid D: Average population estimates per ha of *T. amoenus* from Jolly-Seber and MNA, 1-and 9-ha grids: 1990, 1991: Penticton-Kamloops-Prince George.

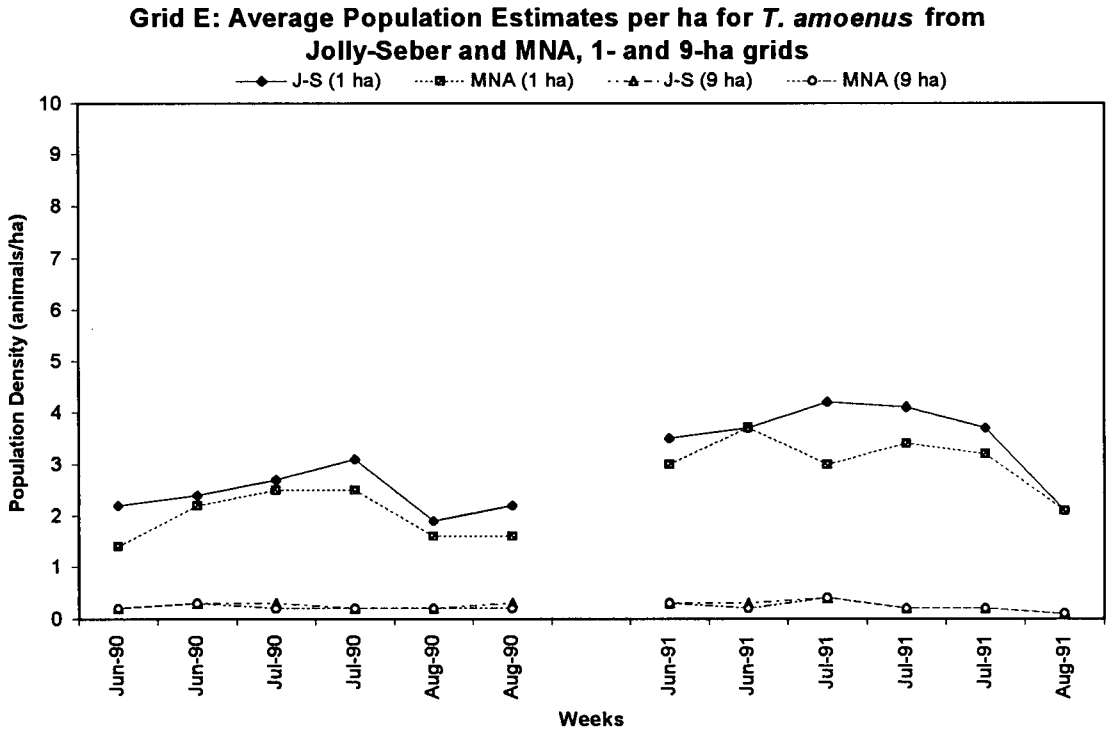


Figure 40. Grid E: Average population estimates per ha of *T. amoenus* from Jolly-Seber and MNA, 1-and 9-ha grids: 1990, 1991: Penticton-Kamloops-Prince George.

DISCUSSION

Experiment A

Population Densities

Since there was little or no consistent difference in Jolly-Seber and MNA summer and fall population estimates between the three grid sizes, it can be concluded that when studying *P. maniculatus* populations, 1-ha grids are suitable in evaluating densities. As reported in Chapter 1, previous studies citing density estimates for *P. maniculatus* in forested areas include Sullivan (1980); Sullivan and Sullivan (1982a); Sullivan *et al.* (1993); Zimmerling and Sullivan (1994); Carey and Johnson (1995); Runciman and Sullivan (1996); Hayward *et al.* 1997; Sullivan *et al.* (1998b) and Von Trebra (1998). On average, density estimates reported in these studies are similar to estimates per ha determined for this research from the 1-, 2- and 5- ha grids.

Although the difference between estimates of *T. amoenus* from the three grid sizes appeared more apparent, most of the estimates from Jolly-Seber and MNA for 1991 and 1992 were very similar. Although some estimates were shown to be significantly different, they were often very closely related and showed biological significance. Previous studies reporting *T. amoenus* population densities in orchards and forest settings include: Sullivan (1990); Sullivan *et al.* (1998a); Sullivan and Klenner (2000). In orchards, the density of *T. amoenus* ranged from 0.8 to 7.8 and averaged 3.1 animals per ha, while in forested areas, population densities per ha ranged from 0.1 to 8.0, but were on average lower than 5 per ha. Although estimates calculated from the three grid sizes are, on average, somewhat higher than what was reported in previous studies, they do reflect findings from Sullivan and Klenner (2000), who reported higher abundance of *T. amoenus* in low density stands. Banfield (1974) and Sutton (1992) discussed preference of *T. amoenus* for early successional stages of young forests, and relatively open habitats. Three stands sampled in this study had previously been thinned, which therefore created more "open" conditions with respect to tree cover than would be found in unthinned or old-growth stands.

Grid Size

A major limitation of this study is not knowing the actual population size of *P. maniculatus* and *T. amoenus* at the time of sampling. However, as was previously established, the density of both species reflect densities reported from prior studies. Results from this study suggest that 1-ha grids are large enough to adequately sample small mammal populations. Traps which are set in an open area capture animals whose home range and exploratory movements only partially overlap the trapping grid. This "edge effect" is often reflected by higher captures at the perimeter of the grid and could result in overestimates of population densities (Van Horne 1982; Bondrup-Nielsen 1983). Although edge effect may have been a factor in overestimating animal density for the 5-ha grids, it was not an issue for the 1- and 2-ha grids since estimates were calculated from grids taken from inside the 5-ha grids and therefore did not experience a higher volume of animals to the edges of the grids. This could mean that the edge factor, in this case, did not influence density estimates since no difference was found between estimations from the three grid sizes.

Length of transects, dimensions of grids, and the distance between trap stations are considerably variable in the literature and are cause for debate. These dimensions should reflect the home range of the species to be studied. White *et al.* (1982) suggested a trapping configuration of four traps per average home range on the area to be studied. Nevertheless, differences in home range size in relation to sex, age, breeding and non-breeding periods within a species is a problem, as is studying species with different home ranges (Priotto and Steinmann 1999). It then becomes important to compromise between the highest probability of capturing the desired species and the most effective use of trapping equipment and time (Ritchie and Sullivan 1989). Results from Bondrup-Nielsen's (1983) mathematical model and computer simulations suggest that when the size of the trapping grid is less than four times the average home range size of the animals to be studied, marked over-estimations of population size occur. To minimize the effects of home range size on results, grid sizes at least 16 times larger than the average home range should be used. Average home ranges of male *P. maniculatus* is reportedly 1.2 ha, while female average home ranges are significantly smaller at 0.6 ha (Ribble and Millar 1996). The average home range of *T. amoenus* usually remains very stable from

year to year, indicating a strong attachment to an area which varies from 0.8- to 1.0-ha, depending on food availability (Martinsen 1968; Sullivan and Klenner 2000).

According to Bondrup-Nielsen (1983), the optimal grid size for adequate sampling should be 19.2- and 9.6-ha for male and female *P. maniculatus*, respectively, and 12.8- to 16.0-ha for *T. amoenus*. Another problems associated with Bondrup-Nielsen's model is if census grids are sized according to the home range of a particular species, it could mean that these grids would be appropriate to sample only one species or even only one sex of a single species. Results from live-trapping species are often used to evaluate differences or similarities in demography between different species or the same species between different habitats (Krebs *et al.* 1969; Redfield *et al.*1977; Sullivan 1979b; Carey and Johnson 1995; Gentile and Cerqueira 1995; Menzel *et al.* 1999), or to discuss demographic strategies based on sex ratios (Hansson 1978; Jannett 1981). It would be highly impractical and unrealistic to have different grid sizes for each species or even each sex. My study clearly showed that there was no difference between large grids (5- and 2-ha) and 1-ha grids. Although only four traps per average home range might not be enough to thoroughly sample *P. maniculatus* and *T. amoenus* populations, 1-ha grids are considered adequate in accomplishing this task. This may also be true for other frequently studied small mammals such as various *Microtus* spp., shrews and other mouse species.

Differences between results and conclusions from Bondrup-Nielsen's mathematical model and computer simulations (1983) and results and conclusions from this study might be due to a difference in several underlying assumptions between the mathematical model and the Jolly-Seber and MNA models (as described in Chapter 1).

Even though 1-, 2- and 5-ha grids gave similar density estimates for *T. amoenus*, larger grids may be more accurate in estimating population densities, as discussed for Experiment B.

Overall, my study clearly showed that 1-ha grids are as precise as 2- and 5-ha grids in estimating small mammal abundance.

Experiment B

Population Density

Density estimates from the 1- and 9-ha grids at the three locations were significantly different on all grids. In practically all cases, estimates from the 1-ha grids were much higher than estimates from the 9-ha grids. For this study, not only different grid sizes were used to sample *T. amoenus*, but also different traps, different trap locations and different trapping methodologies. Thus, this study conveys information on how different grid sizes may influence the estimation of abundance, and on how animals might respond to Tomahawk versus Longworth traps, and day versus night trapping.

Previous studies (Broadbooks 1958; Broadbooks 1970; Sullivan 1990; Sullivan *et al.* 1998a; Sullivan and Klenner 2000) have reported densities which are, in most cases, more closely related to estimates from the 9-ha grids. This is certainly the case for the low density stands (grids A, B, and C), while the 1-ha estimates from the unthinned and old growth stands (grids D and E) are more closely related to estimates from the 9-ha grids and are also closer to estimates of *T. amoenus* found in literature.

The mean lengths of movement were much higher on the 9-ha than on the 1-ha grids, suggesting that chipmunks move more than indicated from the analysis of the 1-ha grids. This would imply that 1-ha grids, corrected for effective trapping area, might increase by more than is indicated in this study. In addition, the high activity on the 1-ha grids may have resulted in overestimates of the population. According to Bondrup-Nielsen's (1983) mathematical model, grids as large as 16.0-ha should be used for *T. amoenus* to reduce the probability of overestimating population size. Although I believe there is no need for such large grids, it seems from the results obtained from Experiment B that there may be a need for grids larger than 1-ha when sampling *T. amoenus.*

Differences between estimates from the 1- and 9-ha grids are likely a direct result of the different trap types and different trapping methods used for this study. Numbers from the 9-ha grids appear to more closely reflect density estimates found in literature. The reality is that Longworth versus Tomahawk traps, as well as day versus night trapping may have played a major influence in determining density estimates. Animals may have been attracted to the 1-ha grids due to the higher density of traps per ha

providing food and shelter. They may also have a preference for Longworth traps, which more closely simulate their natural living quarters.

Overall, this part of my study showed that 1- and 9-ha grids give different results in estimating *T. amoenus* abundance when different trap types and methodologies are used, and therefore identifies the need for careful selection of trap type and methodology to fit the hypotheses being tested.

CONCLUSIONS AND RECOMMENDATIONS

The objectives of this study were to evaluate the difference between small mammal population estimates taken from grids of different sizes, and to determine the optimal grid size to adequately sample populations and yield reliable estimates of population abundance.

Results from Experiment A clearly suggest that 1-ha grids are just as adequate as 2- or 5-ha grids in assessing small mammal abundance in forested areas. One of the major limitations of this study was that the 1- and 2-ha grids were taken from the same original 5-ha grids, and while the four grids were true replicates of one another, the 1- 2- and 5-ha grids were not independent. In fact, all animals had equal chance of being captured on the whole grid and, in many cases, were probably caught in more than one grid size during the duration of the project. Accordingly, additional replicates of 1-, 2- and 5-ha, segregated from each other, would greatly improve the study design and would provide independent, more precise results from a well replicated study. In addition, it would be interesting to conduct this study over a 3- to 5-year period. This would help determine if the fluctuations known to happen in many small mammal populations through time are truly reflected from smaller grid sizes, or if in time of greater numbers, larger grids provide better estimates. An alternative to using larger grids at higher densities could be to use two traps per station. This system has been used in studies to provide 1-ha density estimates while obtaining a reliable sample size of all resident small mammal species (Runciman and Sullivan 1996; Sullivan *et al.* 1998a). Another option is to reduce the distance between traps to 7.6 m so that while the grid remains the same size, the number of traps is doubled (Boonstra 1985; Renzulli *et al.* 1980). This study could also be replicated in a different habitat, such as in grasslands, to look at the difference, if any, between grassland and forest populations of small mammals under different experimental conditions.

Results from Experiment B clearly suggest that 1- and 9-ha grids give different results when assessing *T. amoenus* abundance in forested areas. One of the major limitations of this experiment was that different trap types and trapping methodologies were used. It would be interesting to conduct similar research over several years with 1-

and 9-ha replicates using the same traps and methodologies, and compare not only the difference between estimates from the different grid sizes, but also the difference between estimates from Longworth versus Tomahawk, and day versus night trapping. Another major problem is that *T. amoenus* is very often studied as a secondary species to various other squirrel species. Therefore, grids are set and trapped in an effort to maximize the likelihood of capturing these animals. It would be prudent to conduct a study to determine the optimal grid size for a study focusing on *T. amoenus*. I believe such a grid would very likely range between 2- and 4-ha.

Once again, a major challenge of this study was not knowing the actual population size of *P. maniculatus* (Experiment A) and *T. amoenus* (Experiments A and B). Future studies could replicate these experiments using radiotelemetry to investigate the difference between trapping and radiotelemetry results and to determine how density estimates compare to the real population size.

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APPENDIX A

ANOVA tables for *P. maniculatus*: Population density analyses computed using alpha = .05

Source		Type III Sum of Squares	df	Mean Square	*F*	Sig.	Noncent. Parameter	Observed Power
Intercept	Hypothesis	51842.000	1	51842.000	84.786	.001	84.786	1.000
	Error	2445.778	4	611.444				
TREAT	Hypothesis	256.889	1	256.889	.420	.552	.420	.080
	Error	2445.778	4	611.444				
TREAT (REP)	Hypothesis	2445.778	4	611.444	1.703	.242	6.812	.318
	Error	2872.222	8	359.028				
TIME	Hypothesis	706.333	2	353.167	.984	.415	1.967	.166
	Error	2872.222	8	359.028				
TIME*TREAT	Hypothesis	56.778	2	28.389	.079	.925	.158	.058
	Error	2872.222	8	359.028				
TREAT (TIME*REP)	Hypothesis	2872.222	8	359.028	.	.	.	.
	Error	.000	0	.				

CAPTURE estimates grids 1, 2 and 3 versus MNA estimates grids 1, 2 and 3.

Source		Type III Sum of Squares	df	Mean Square	*F*	Sig.	Noncent. Parameter	Observed Power
Intercept	Hypothesis	20988.075	1	20998.075	230.421	.000	230.421	1.000
	Error	364.343	4	91.086				
TREAT	Hypothesis	304.008	1	304.008	3.338	.142	3.338	.291
	Error	364.343	4	91.086				
TREAT (REP)	Hypothesis	364.343	4	91.086	1.417	.273	5.668	.341
	Error	1028.477	16	64.280				
TIME	Hypothesis	241.717	4	60.429	.940	.466	3.760	.233
	Error	1028.477	16	64.280				
TIME*TREAT	Hypothesis	88.650	4	22.162	.345	.844	1.379	.108
	Error	1028.477	16	64.280				
TREAT (TIME*REP)	Hypothesis	1028.477	16	64.280	.	.	.	.
	Error	.000	0	.				

Jolly-Seber estimates grids 4, 5 and 6 versus MNA estimates grids 4, 5 and 6.

Source		Type III Sum of Squares	df	Mean Square	*F*	Sig.	Noncent. Parameter	Observed Power
Intercept	Hypothesis	28385.502	1	28385.502	191.981	.000	191.981	1.000
	Error	591.424	4	147.856				
TREAT	Hypothesis	2073.680	1	2073.680	14.025	.020	14.025	.797
	Error	591.424	4	147.856				
TREAT (REP)	Hypothesis	591.424	4	147.856	.289	.877	1.157	.087
	Error	4089.676	8	511.209				
TIME	Hypothesis	1387.874	2	693.937	1.357	.311	2.715	.214
	Error	4089.676	8	511.209				
TIME*TREAT	Hypothesis	564.963	2	282.482	.553	.596	1.105	.113
	Error	4089.676	8	511.209				
TREAT (TIME*REP)	Hypothesis	4089.676	8	511.209	.	.	.	.
	Error	.000	0	.				

CAPTURE estimates grids 1, 2 and 3 versus Jolly-Seber estimates grids 4, 5 and 6.

Source		Type III Sum of Squares	df	Mean Square	*F*	Sig.	Noncent. Parameter	Observed Power
Intercept	Hypothesis	24494.222	1	24494.222	64.952	.001	64.952	1.000
	Error	1508.444	4	377.111				
TREAT	Hypothesis	3042.000	1	3042.000	8.067	.047	8.067	.575
	Error	1508.444	4	377.111				
TREAT (REP)	Hypothesis	1508.444	4	377.111	2.466	.129	9.863	.448
	Error	1223.556	8	152.944				
TIME	Hypothesis	197.444	2	98.722	.645	.550	1.291	.124
	Error	1223.556	8	152.944				
TIME*TREAT	Hypothesis	136.333	2	68.167	.446	.665	.891	.100
	Error	1223.556	8	152.944				
TREAT (TIME*REP)	Hypothesis	1223.556	8	152.944	.	.	.	.
	Error	.000	0	.				

MNA estimates grids 1, 2 and 3 versus MNA estimates grids 4, 5 and 6.

ANOVA tables for *M. montanus*: Population density analyses computed using alpha = .05

Source		Type III Sum of Squares	df	Mean Square	*F*	Sig.	Noncent. Parameter	Observed Power
Intercept	Hypothesis	6536.056	1	6536.056	10.446	.032	10.446	.680
	Error	2502.889	4	625.722				
TREAT	Hypothesis	329.389	1	329.389	.526	.508	.526	.088
	Error	2502.889	4	625.722				
TREAT (REP)	Hypothesis	2502.889	4	625.722	2.710	.107	10.840	.487
	Error	1847.111	8	230.889				
TIME	Hypothesis	4086.111	2	2043.056	8.849	.009	17.697	.878
	Error	1847.111	8	230.889				
TIME*TREAT	Hypothesis	163.444	2	81.722	.354	.712	.708	.089
	Error	1847.111	8	230.889				
TREAT (TIME*REP)	Hypothesis	1847.111	8	230.889	.	.	.	.
	Error	.000	0	.				

CAPTURE estimates grids 1, 2 and 3 versus MNA estimates grids 1, 2 and 3.

Source		Type III Sum of Squares	df	Mean Square	*F*	Sig.	Noncent. Parameter	Observed Power
Intercept	Hypothesis	9673.256	1	9673.256	19.11	.012	19.111	.897
	Error	2024.601	4	506.150				
TREAT	Hypothesis	99.736	1	99.736	.197	.680	.197	.064
	Error	2024.601	4	506.150				
TREAT (REP)	Hypothesis	2024.601	4	506.150	11.422	.000	45.688	.999
	Error	709.019	16	44.314				
TIME	Hypothesis	1792.135	4	448.034	10.111	.000	40.442	.997
	Error	709.019	16	44.314				
TIME*TREAT	Hypothesis	40.122	4	10.030	.226	.920	.905	.087
	Error	709.019	16	44.314				
TREAT (TIME*REP)	Hypothesis	709.019	16	44.314	.	.	.	.
	Error	.000	0	.				

Jolly-Seber estimates grids 4, 5 and 6 versus MNA estimates grids 4, 5 and 6.

Source		Type III Sum of Squares	df	Mean Square	*F*	Sig.	Noncent. Parameter	Observed Power
Intercept	Hypothesis	7758.427	1	7758.427	14.270	.019	14.270	.803
	Error	2174.696	4	543.674				
TREAT	Hypothesis	119.094	1	119.094	.219	.664	.219	.066
	Error	2174.696	4	543.674				
TREAT (REP)	Hypothesis	2174.696	4	543.674	2.952	.090	11.808	.524
	Error	1473.324	8	184.166				
TIME	Hypothesis	3636.701	2	1818.351	9.873	.007	19.747	.911
	Error	1473.324	8	184.166				
TIME*TREAT	Hypothesis	297.768	2	148.884	.808	.479	1.617	.144
	Error	1473.324	8	184.166				
TREAT (TIME*REP)	Hypothesis	1473.324	8	184.166	.	.	.	.
	Error	.000	0	.				

CAPTURE estimates grids 1, 2 and 3 versus Jolly-Seber estimates grids 4, 5 and 6.

Source		Type III Sum of Squares	df	Mean Square	*F*	Sig.	Noncent. Parameter	Observed Power
Intercept	Hypothesis	3726.722	1	3726.722	16.910	.015	16.910	.861
	Error	881.556	4	220.389				
TREAT	Hypothesis	2.722	1	2.722	.012	.917	.012	.051
	Error	881.556	4	220.389				
TREAT (REP)	Hypothesis	881.556	4	220.389	2.753	.104	11.012	.494
	Error	640.444	8	80.056				
TIME	Hypothesis	2208.444	2	1104.222	13.793	.003	27.586	.975
	Error	640.444	8	80.056				
TIME*TREAT	Hypothesis	67.111	2	33.556	.419	.671	.838	.097
	Error	640.444	8	80.056				
TREAT (TIME*REP)	Hypothesis	640.444	8	80.056	.	.	.	.
	Error	.000	0	.				

MNA estimates grids 1, 2 and 3 versus MNA estimates grids 4, 5 and 6.

ANOVA tables for *P. parvus*: Population density analyses
computed using alpha = .05

Source		Type III Sum of Squares	df	Mean Square	*F*	Sig.	Noncent. Parameter	Observed Power
Intercept	Hypothesis	1800.000	1	1800.000	5.554	.078	5.554	.436
	Error	1296.444	4	324.111				
TREAT	Hypothesis	80.222	1	80.222	.248	.645	.248	.068
	Error	1296.444	4	324.111				
TREAT (REP)	Hypothesis	1296.444	4	324.111	9.478	.004	37.914	.968
	Error	273.556	8	34.194				
TIME	Hypothesis	192.333	2	96.167	2.812	.119	5.625	.402
	Error	273.556	8	34.194				
TIME*TREAT	Hypothesis	37.444	2	18.722	.548	.599	1.095	.112
	Error	273.556	8	34.194				
TREAT (TIME*REP)	Hypothesis	273.556	8	34.194	.	.	.	.
	Error	.000	0	.				

CAPTURE estimates grids 1, 2 and 3 versus MNA estimates grids 1, 2 and 3.

Source		Type III Sum of Squares	df	Mean Square	*F*	Sig.	Noncent. Parameter	Observed Power
Intercept	Hypothesis	852.267	1	852.267	8.748	.042	8.748	.608
	Error	389.675	4	97.419				
TREAT	Hypothesis	13.200	1	13.200	.136	.731	.136	.060
	Error	389.675	4	97.419				
TREAT (REP)	Hypothesis	389.675	4	97.419	16.004	.000	64.018	1.000
	Error	97.392	16	6.087				
TIME	Hypothesis	157.541	4	39.385	6.470	.003	25.882	.956
	Error	97.392	16	6.087				
TIME*TREAT	Hypothesis	12.075	4	3.019	.496	.739	1.984	.138
	Error	97.392	16	6.087				
TREAT (TIME*REP)	Hypothesis	97.392	16	6.087	.	.	.	.
	Error	.000	0	.				

Jolly-Seber estimates grids 4, 5 and 6 versus MNA estimates grids 4, 5 and 6.

Source		Type III Sum of Squares	df	Mean Square	*F*	Sig.	Noncent. Parameter	Observed Power
Intercept	Hypothesis	1295.405	1	1295.405	4.852	.092	4.852	.392
	Error	1067.964	4	266.991				
TREAT	Hypothesis	236.894	1	236.894	.887	.400	.887	.114
	Error	1067.964	4	266.991				
TREAT (REP)	Hypothesis	1067.964	4	266.991	8.948	.005	35.792	.959
	Error	238.702	8	29.838				
TIME	Hypothesis	143.503	2	71.752	2.405	.152	4.809	.351
	Error	238.702	8	29.838				
TIME*TREAT	Hypothesis	36.081	2	18.041	.605	.569	1.209	.119
	Error	238.702	8	29.838				
TREAT (TIME*REP)	Hypothesis	238.702	8	29.838	.	.	.	.
	Error	.000	0	.				

CAPTURE estimates grids 1, 2 and 3 versus Jolly-Seber estimates grids 4, 5 and 6.

Source		Type III Sum of Squares	df	Mean Square	*F*	Sig.	Noncent. Parameter	Observed Power
Intercept	Hypothesis	533.556	1	533.556	6.188	.068	6.188	.474
	Error	344.889	4	86.222				
TREAT	Hypothesis	107.556	1	107.556	1.247	.327	1.247	.140
	Error	344.889	4	86.222				
TREAT (REP)	Hypothesis	344.889	4	86.222	8.945	.005	35.781	.959
	Error	77.111	8	9.639				
TIME	Hypothesis	76.444	2	38.222	3.965	.064	7.931	.537
	Error	77.111	8	9.639				
TIME*TREAT	Hypothesis	48.444	2	24.222	2.513	.142	5.026	.364
	Error	77.111	8	9.639				
TREAT (TIME*REP)	Hypothesis	77.111	8	9.639	.	.	.	.
	Error	.000	0	.				

MNA estimates grids 1, 2 and 3 versus MNA estimates grids 4, 5 and 6.

APPENDIX B

Bonferroni Multiple Comparisons tables for *P. maniculatus*: Two to ten night trapping period comparisons computed using alpha = .05

Nights I	Nights J	Mean Difference (I – J)	Std Error	Sig.	95% Confidence Intervals	
					Lower	Upper
2	4	-12.2639	3.311	.012	-22.5397	-1.9880
	6	-19.5972	3.311	.000	-29.8731	-9.3214
	8	-19.8194	3.311	.000	-30.0953	-9.5436
	10	-24.9306	3.311	.000	-35.2064	-14.6547
4	2	12.2639	3.311	.012	1.9880	22.5397
	6	-7.3333	3.212	.320	-17.3024	2.6357
	8	-7.5556	3.212	.276	-17.5246	2.4135
	10	-12.6667	3.212	.006	-22.6357	-2.6976
6	2	19.5972	3.311	.000	9.3214	29.8731
	4	7.3333	3.212	.320	-2.6357	17.3024
	8	-.2222	3.212	1.000	-10.1913	9.7468
	10	-5.3333	3.212	1.000	-15.3024	4.6357
8	2	19.8194	3.311	.000	9.5436	30.0953
	4	7.5556	3.212	.276	-2.4135	17.5246
	6	.2222	3.212	1.000	-9.7468	10.1913
	10	-5.1111	3.212	1.000	-15.0802	4.8579
10	2	24.9306	3.311	.000	14.6547	35.2064
	4	12.6667	3.212	.006	2.6976	22.6357
	6	5.3333	3.212	1.000	-4.6357	15.3024
	8	5.1111	3.212	1.000	-4.8579	15.0802

CAPTURE population estimates, 2 to 10 nights – *P. maniculatus*

Nights I	Nights J	Mean Difference (I – J)	Std Error	Sig.	95% Confidence Intervals	
					Lower	Upper
2	4	-10.4444	2.141	.001	-17.0613	-3.8276
	6	-17.6667	2.141	.000	-24.2835	-11.0498
	8	-21.4444	2.141	.000	-28.0613	-14.8276
	10	-24.7778	2.141	.000	-31.3946	-18.1609
4	2	10.4444	2.141	.001	3.8276	17.0613
	6	-7.2222	2.141	.025	-13.8391	-.6054
	8	-11.0000	2.141	.000	-17.6168	-4.3832
	10	-14.3333	2.141	.000	-20.9502	-7.7165
6	2	17.6667	2.141	.000	11.0498	24.2835
	4	7.2222	2.141	.025	.6054	13.8391
	8	-3.7778	2.141	.904	-10.3946	2.8391
	10	-7.1111	2.141	.029	-13.7280	-.4943
8	2	21.4444	2.141	.000	14.8276	28.0613
	4	11.0000	2.141	.000	4.3832	17.6168
	6	3.7778	2.141	.904	-2.8391	10.3946
	10	-3.3333	2.141	1.000	-9.9502	3.2835
10	2	24.7778	2.141	.000	18.1609	31.3946
	4	14.3333	2.141	.000	7.7165	20.9502
	6	7.1111	2.141	.029	.4943	13.7280
	8	3.3333	2.141	1.000	-3.2835	9.9502

MNA population estimates, 2 to 10 nights – *P. maniculatus*

Bonferroni Multiple Comparisons tables for *M. montanus*: Two to ten night trapping period comparisons computed using alpha = .05

Nights I	Nights J	Mean Difference (I – J)	Std Error	Sig.	95% Confidence Intervals	
					Lower	Upper
2	4	-6.9821	3.810	.826	-19.0738	5.1095
	6	-7.9821	3.810	.498	-20.0738	4.1095
	8	-11.8571	3.810	.057	-23.9488	.2345
	10	-13.9683	3.710	.013	-25.7422	-2.1943
4	2	6.9821	3.810	.826	-5.1095	19.0738
	6	-1.0000	3.681	1.000	-12.6816	10.6816
	8	-4.8750	3.681	1.000	-16.5566	6.8066
	10	-6.9861	3.577	.657	-18.3386	4.3664
6	2	7.9821	3.810	.498	-4.1095	20.0738
	4	1.000	3.681	1.000	-10.6816	12.6816
	8	-3.8750	3.681	1.000	-15.5566	7.8066
	10	-5.9861	3.577	1.000	-17.3386	5.3664
8	2	11.8571	3.810	.057	-.2345	23.9488
	4	4.8750	3.681	1.000	-6.8066	16.5566
	6	3.8750	3.681	1.000	-7.8066	15.5566
	10	-2.1111	3.577	1.000	-13.4636	9.2414
10	2	13.9683	3.710	.013	2.1943	25.7422
	4	6.9861	3.577	.657	-4.3664	18.3386
	6	5.9861	3.577	1.000	-5.3664	17.3386
	8	2.111	3.577	1.000	-9.2414	13.4636

CAPTURE population estimates, 2 to 10 nights – *M. montanus*

Nights I	Nights J	Mean Difference (I – J)	Std Error	Sig.	95% Confidence Intervals	
					Lower	Upper
2	4	-2.8889	1.785	1.000	-8.4067	2.6289
	6	-4.8889	1.785	.115	-10.4067	.6289
	8	-6.6667	1.785	.010	-12.1845	-1.1489
	10	-8.8889	1.785	.000	-14.4067	-3.3711
4	2	2.8889	1.785	1.000	-2.6289	8.4067
	6	-2.000	1.785	1.000	-7.5178	3.5178
	8	-3.7778	1.785	.449	-9.2956	1.7400
	10	-6.0000	1.785	.026	-11.5178	-.4822
6	2	4.8889	1.785	.115	-.6289	10.4067
	4	2.0000	1.785	1.000	-3.5178	7.5178
	8	-1.7778	1.785	1.000	-7.2956	3.7400
	10	-4.0000	1.785	.346	-9.5178	1.5178
8	2	6.6667	1.785	.010	1.1489	12.1845
	4	3.7778	1.785	.449	-1.7400	9.2956
	6	1.7778	1.785	1.000	-3.7400	7.2956
	10	-2.2222	1.785	1.000	-7.7400	3.2956
10	2	8.8889	1.785	.000	3.3711	14.4067
	4	6.0000	1.785	.026	.4822	11.5178
	6	4.0000	1.785	.346	-1.5178	9.5178
	8	2.2222	1.785	1.000	-3.2956	7.7400

MNA population estimates, 2 to 10 nights – *M. montanus*

Bonferroni Multiple Comparisons tables for *P. parvus*: Two to ten night trapping period comparisons computed using alpha = .05

Nights I	Nights J	Mean Difference (I – J)	Std Error	Sig.	95% Confidence Intervals	
					Lower	Upper
2	4	-1.3333	.813	1.000	-4.1210	1.4543
	6	-3.1667	.813	.021	-5.9543	-.3790
	8	-4.3333	.813	.002	-7.1210	-1.5457
	10	-5.3333	.813	.000	-8.1210	-2.5457
4	2	1.3333	.813	1.000	-1.4543	4.1210
	6	-1.8333	.813	.436	-4.6210	.9543
	8	-3.0000	.813	.031	-5.7876	-.2124
	10	-4.0000	.813	.004	-6.7876	-1.2124
6	2	3.1667	.813	.021	.3790	5.9543
	4	1.8333	.813	.436	-.9543	4.6210
	8	-1.1667	.813	1.000	-3.9543	1.6210
	10	-2.1667	.813	.206	-4.9543	.6210
8	2	4.3333	.813	.002	1.5457	7.1210
	4	3.0000	.813	.031	.2124	5.7876
	6	1.1667	.813	1.000	-1.6210	3.9543
	10	-1.0000	.813	1.000	-3.7876	1.7876
10	2	5.3333	.813	.000	2.5457	8.1210
	4	4.0000	.813	.004	1.2124	6.7876
	6	2.1667	.813	.206	-.6210	4.9543
	8	1.0000	.813	1.000	-1.7876	3.7876

MNA population estimates, 2 to 10 nights – *P. parvus.*

APPENDIX C

ANOVA tables for *T. amoenus*: Grid size comparison study
Penticton / Kamloops / Prince George data

	SS	DF	MS
TOTAL	82.94	11	
TREATMENTS	34.95	1	34.95
BLOCKS	35.27	5	
REMAINDER	12.71	5	2.54

Grid A - Jolly-Seber: 1990-1991

	SS	DF	MS
TOTAL	49.70	11	
TREATMENTS	19.05	1	19.05
BLOCKS	22.95	5	
REMAINDER	7.70	5	1.54

Grid A - MNA: 1990-1991

	SS	DF	MS
TOTAL	97.73	11	
TREATMENTS	65.75	1	65.75
BLOCKS	20.15	5	
REMAINDER	11.83	5	2.37

Grid B - Jolly-Seber: 1990-1991

	SS	DF	MS
TOTAL	61.30	11	
TREATMENTS	36.44	1	36.44
BLOCKS	15.78	5	
REMAINDER	9.09	5	1.82

Grid B - MNA: 1990-1991

	SS	DF	MS
TOTAL	97.54	11	
TREATMENTS	50.84	1	50.84
BLOCKS	34.66	5	
REMAINDER	12.04	5	2.41

Grid C - Jolly-Seber: 1990-1991

	SS	DF	MS
TOTAL	58.02	11	
TREATMENTS	30.56	1	30.56
BLOCKS	20.07	5	
REMAINDER	7.39	5	1.48

Grid C - MNA: 1990-1991

	SS	DF	MS
TOTAL	104.71	11	
TREATMENTS	32.70	1	32.70
BLOCKS	49.35	5	
REMAINDER	22.66	5	4.53

Grid D - Jolly-Seber: 1990-1991

	SS	DF	MS
TOTAL	91.18	11	
TREATMENTS	27.00	1	27.00
BLOCKS	43.59	5	
REMAINDER	20.60	5	4.12

Grid D - MNA: 1990-1991

	SS	DF	MS
TOTAL	42.72	11	
TREATMENTS	22.39	1	22.39
BLOCKS	11.88	5	
REMAINDER	8.46	5	1.69

Grid E - Jolly-Seber: 1990-1991

	SS	DF	MS
TOTAL	31.69	11	
TREATMENTS	15.66	1	15.66
BLOCKS	9.41	5	
REMAINDER	6.61	5	1.32

Grid E - MNA: 1990-1991