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Effects of climate and density on the survival of whiteooted mice (Peromyscus leucopus)

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EFFECTS OF CLIMATE AND DENSITY ON THE SURVIVAL OF WHITE-FOOTED

MICE (*PEROMYSCUS LEUCOPUS)*

By

Eric Richard Wengert

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EFFECTS OF CLIMATE AND DENSITY ON THE SURVIVAL OF WHITE-FOOTED

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Short-lived rodents are sensitive to changes in environmental conditions and exhibit annual fluctuations under seasonal environments in northern temperate regions. I analyzed 34 years of monthly live-trapping data on white-footed mice (*Peromyscus leucopus*) collected in Carter Woods, Ohio. I used a theoretic-information approach to select the best approximating models and analysis of deviance to infer effects of climate and density on survival of mice. I tested for a cost of reproduction to females and found no difference in survival between reproductive states. Directions and magnitudes of effects of climate and density varied over time. Increased variability in temperature reduced effects of density on survival. I detected an Allee effect and density dependent effects on survival. Long-term trapping data are needed to study temporal effects of climate and density on the demography of rodents. Recruitment had a greater impact on population growth rate than survival.

ACKNOWLEDGEMENTS

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CHAPTER I

INTRODUCTION

The effect of climate change on ecosystems is one of the most critical issues of
this century (Krebs and Berteaux 2006; Stenseth et al. 2002). The debate regarding the
roles of density dependence and density independence in population dynamics has
particular relevance to this issue. The interaction of population density and climate
change affects survival and reproduction of animals and is manifested as changes in
population growth rate and density. Therefore, understanding effects of density and
climate on demographic processes will allow us to make better predictions of changes in
animal populations.

The density paradigm, a traditional approach to studying effects of density, is to
relate population growth rates to population density and is often extended to include
climatic variables as covariates. Krebs (2002) has argued that the density paradigm has
been remarkably insufficient for understanding why populations change in size and
advocates using the mechanistic paradigm, which assumes that no predictions of
population dynamics can be described by relationships between vital rates and population
density without identifying the ecological mechanisms that drive those rates (Krebs
2002). With this assumption, the mechanistic paradigm asks how survival and
reproduction of individuals in the population are influenced by intrinsic and extrinsic

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factors and recognizes that individual responses vary (Krebs 2002). However, few studies have used the mechanistic approach or detailed demographic models to investigate effects of climate on population dynamics of mammals (Hone and Clutton-Brock 2007; Krebs and Berteaux 2006; Williams and Liebhold 2002). This study uses the mechanistic approach and maximum likelihood estimation to investigate effects of climate and density on survival of white-footed mice.

Effects of identical weather conditions can differ because age and gender structures of a population can fluctuate independently of population size (Coulson et al. 2001). Coulson et al. (2001) found that simulated populations with the same weather and initial population size, but with different initial gender and age structures, experienced different population trajectories. Likewise, in addition to the negative effects of high densities, low densities also can have negative effects on population growth rates. The Allee effect, originally proposed by Warder Clyde Allee (1931, 1938, 1949), refers to inverse density dependence at low population size (Courchamp et al. 1999). This effect posits that below a certain size a population will trend toward extinction, whereas above this size the population growth rate increases until density dependent effects begin influencing the population. Proposed mechanisms of this relationship include inbreeding depression, difficulties in finding mates, social dysfunction, and demographic stochasticity (Courchamp et al. 1999; McCarthy 1997). Yunger (2002) attributed the absence of a population increase of white-footed mice in response to supplemental food to difficulties in finding mates at low density. Thus, it is plausible to expect time-varying effects of densities and/or climate on the demography of mice.

The white-footed mouse (*Peromyscus leucopus*) is distributed widely in the deciduous forests of the United States (King 1968). Understanding population changes in white-footed mice is important because the species is a primary reservoir of Lyme disease, a threat to human health (Schauber et al. 2005). Increased understanding of the mechanisms influencing populations of white-footed mice is critical to predicting the spread and relative risk of contracting Lyme disease. Moreover, white-footed mice are a predator of gypsy moths (*Lymantria dispar;* Elkinton et al. 1996). Periodic outbreaks of gypsy moths defoliate eastern deciduous forests and cause enormous economic loss in the eastern United States (Campbell and Schlarbaum 1994). White-footed mice are important seed predators (Schnurr et al. 2004; Whitaker 1966; Wolff 1996) and prey species for avian, mammalian and reptilian predators (Derting 1989; Marti 1976; Reinert et al. 1984).

Many studies have used population modeling to suggest that climate and density dependence influence survival of white-footed mice, but few studies directly estimated survival probabilities of white-footed mice using a probabilistic model (Kesner and Linzey 1997; Lewellen and Vessey 1998a, 1998b; Schug et al. 1991, but see Reed and Slade 2007). Previous examinations have used ad-hoc modeling, which relates survival estimates to densities or seasons using regressions or t tests, to determine that survival of *Peromyscus leucopus* is seasonal and density-dependent (Blair 1948; Goundie and Vessey 1986; Reed and Slade 2007; Wolff 1986). Schug et al. (1991) estimated survivorships of *Peromyscus leucopus* in Carter Woods, Bowling Green, Ohio, USA by regressing log survivors against ages with a subset of trapping data collected from 1982 to 1988 and found that 30 to 90 days after weaning, autumn-born mice experience greater

mortality than spring-born mice (Schug et al. 1991), which suggests seasonal differences of weather or density effects on survival. In years of peak population density, survival from birth to adulthood was found to be as low as 10% (Schug et al. 1991). Therefore, seasons and densities may affect survival of *Peromyscus leucopus*. However, the results of seasonal and density effects on *Peromyscus leucopus* survival in Carter Woods, OH have not been confirmed using more complete data from 1973 to 2006 and probabilistic models, which estimate probabilities of survival and capture as a function of densities, climate variables, and seasons.

Life history theory predicts that reproductive effort should lead to a decrease in either survival or future reproduction (Williams 1966). White-footed mice are regarded as "income breeders", increasing consumption to compensate for the energetic requirement of reproduction (Jacquot and Vessey 1998; Millar 1978). Direct measures of reproductive effort are difficult to quantify in the field (Gadgil and Solbrig 1972); however, the multistate model can be used to estimate breeding proportions and tests about the cost of reproduction from mark-recapture data (Nichols et al. 1994). The multistate model allows movement of animals to different states or sites and calculates state specific parameters.

Previous studies of the *Peromyscus leucopus* population in Carter Wood, OH mainly have used multivariate time series models to determine the effects of density and weather on population growth rate (Lewellen and Vessey 1998a; 1998b), but did not estimate survival of white-footed mice using the Cormack-Jolly-Seber (CJS) model (Cormack 1964; Jolly 1965; Seber 1965). The CJS models are probabilistic models that examine only the recapture histories of marked animals and provide estimates of apparent

survival and recapture probability (Amstrup et al. 2005). Probabilistic models use

maximum likelihood to produce less biased estimates with good properties over a broad

array of conditions (Amstrup et al. 2005). I analyzed 34 years of monthly live-trapping

data using probabilistic models in Program MARK to assess effects of intrinsic (density

and reproduction) and extrinsic (temperature and precipitation) factors on seasonal

survival of *Peromyscus leucopus* in Carter Woods, Ohio, using program MARK (White

and Burnham 1999). In addition, previous studies of this population have used minimum

number alive as an index of population size rather than estimates from probabilistic

models as recommended by Nichols and Pollock (1983). By investigating effects of

intrinsic and extrinsic factors on survival instead of population growth rate, I sought to

test the mechanistic causes of changes in survival.

This study addressed the following objectives:

1) Compare Jolly-Seber estimates to an index (minimum number alive, MNA) of
   population size.

2) Assess importance of survival and recruitment in population growth rates of white-
   footed mice.

3) Determine seasonal pattern of survival.

4) Test the hypothesis that reproduction incurs costs to survival of female white-footed
   mice.

5) Test for time-varying effects of density and climate on survival.

6) Test for effects of food on over-wintering survival.

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CHAPTER II

SURVIVAL, FECUNDITY, AND POPULATION SIZE OF WHITE-FOOTED MICE

OBJECTIVES

1.   Compare the minimum number alive (MNA) and Jolly – Seber (JS)

estimates of white-footed mouse population size.

2.   Determine relative importance of recruitment and survival in the

population dynamics of white-footed mice.

METHODS

Study site

The study site (Carter Woods) is an isolated 2-ha woodlot located in northwest

Ohio, USA (41º23'N, 83º35'W). The dominant tree species are shagbark hickory (*Carya*

ovata) and red oak (*Quercus rubrum*). Carter Woods is surrounded by agricultural fields

planted with corn (*Zea mays*), soybeans (*Glycine max*) or wheat (*Triticum aestivum*) that

are usually tilled in autumn. The eastern edge of the study site has a drainage ditch ~1 m

deep that runs parallel to a paved road and the nearest woodlot is 1.5 km away (Lewellen

and Vessey 1998). Monthly temperature ranged from -11.9°C to 31.4°C with a mean of

9.5°C over the study period. Monthly precipitation ranged from 0.3 cm to 27.6 cm with a mean of 7 cm. Owls werethe only nocturnal predators observed and were only observed during periods with very high mouse densities (Lewellen and Vessey 1998).

Data collection

Stephen H. Vessey and his students have conducted monthly trapping in Carter Woods, for 34 years (March 1973-November 2006) with winter months missing in some years. Beginning in 1973, a 13 × 26 trap grid was established across the entire woodlot with one trap per station and 7.6 m between stations. In January 1988, the grid was expanded to 15 × 26 to cover the eastern edge of the woodlot. Sherman and Leathers live traps (Sherman Traps, Inc., Tallahassee, FL. Model # LNATDG, size ca. 7.5 by 7.5 by 23 cm; Leathers live traps of similar size) were baited with oatmeal and peanut butter and cotton or polyester insulation was supplied during cold weather. The woodlot was divided into four sections and two sections were trapped in a calendar week, resulting in a two-week trap period, from April 1973 to March 1977, April 1978 to June 1978, and December 1982 to April 1983. The entire woodlot was trapped simultaneously for all intervening and subsequent trapping periods yielding a 2-day trap period. Individuals were ear-tagged or toe-clipped upon capture, and age, gender, reproductive status, and location were recorded for each individual (Lewellen and Vessey 1998a). *Peromyscus leucopus* accounted for 97% (> 40,000) of the captures; other species captured during the study were the short-tailed shrew (*Blarina brevicauda*) and meadow vole (*Microtus pennsylvanicus*) (Lewellen and Vessey 1998a; Vessey and Vessey 2007). In most years, trapping was not conducted during winter and thus was not continuous. However, 4

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periods (March 1973 - October 1975, April 1979 – September 1980, April 1982 –

October 1983, and April 1986 – October 1988) were continuous for > 12 months. The

trapping and handling of white-footed mice in this research followed American Society

of Mammalogists guidelines (Gannon et al. 2007).

Peromyscus leucopus density

MNA estimates were calculated by accumulating individuals from those mice

caught during one trap session and those mice caught at any time both before and after,

but not during the trap session (Krebs 1966). I calculated population size using the

POPAN model in program MARK (White and Burnham 1999). POPAN differs from the

original JS formulation by creating a super-population of all animals that would ever be

born in the population, and parameters b_i, which represent the probability that an animal

from the super-population will enter the population (probability of entrance, PENT).

Previous studies of this population have used MNA as an index of abundance (Lewellen

and Vessey 1998, 1999). Accurate Jolly-Seber estimates of population size require > 10

animals per sampling period (Seber 1982). Of the 293 months used, 17 had $\leq$ 10 animals

caught. Nine of these months occurred during spring (March, April, May), 5 were in

winter (December, January, February) and 3 were in autumn (September, October,

November). Due to the confounding of parameters, the first and last population estimates

for each time period are suspect and were not included in this analysis. This resulted in

estimates for only 5 of the 17 months with $\leq$ 10 captures.

Recruitment

I used the Pradel survival and recruitment model to estimate recruitment in program MARK (White and Burnham 1999). The Pradel model uses a "trick" to estimate recruitment. By reversing the encounter histories the model finds the probability that if alive at time *i,* the animal also was alive and in the population at time *i*-1. Eight models were constructed from the parameters, survival (phi), recapture (p) and recruitment (f) either time specific (t) or constant (.) with a general model of Phi(t)p(t)f(t) to obtain monthly recruitment estimates. I used model averaging to estimate recruitment and account for all model uncertainty. This gave me an estimated number of recruits per individual per month.

Survival

I used the CJS model in program MARK (White and Burnham 1999) to estimate monthly survival. Sixteen models of all possible combinations of time and gender effects were created from the general model phi(g*t)p(g*t), where phi is survival and p is recapture probability, using gender as a group (g) and time as either time-specific (t) or constant (.). These 16 models were run for each year (1973-2006). Four time periods of continuous data, two periods of 2 years and two periods of 3 years also were analyzed. I adjusted for over-dispersion using the ĉ approach described by White and Burnham (1999). I found no gender effects on survival and excluded all models with gender effects in the survival function. I left gender effects in the recapture probabilities because gender influences behavior that may lead to different recapture probabilities. The

exclusion resulted in 8 candidate models, phi(t) and phi(.), with 4 possible recapture probabilities: p(g*t), p(g), p(t), and p(.).

I selected the most parsimonious models among the candidate models by using Akaike's information criterion (AICc) adjusted for small sample size and quasi-Akaike's information criterion (QAICc) with data over-dispersion being corrected for with the factor ĉ (Burnham and Anderson 2002). The most parsimonious models had the least AICc and were used to estimate parameter values. The difference between AICc values (ΔAICc) is used to compare and rank models, and when ΔAICc or ΔQAICc is >10 the model has essentially no support (Burnham and Anderson 2002). When ΔAICc or ΔQAICc < 2, models are considered to be competing and I used model averaging to obtain survival estimates.

Population growth rate

I calculated population growth rate with the equation:

$$r = \ln(N_t) - \ln(N_{t-1}) \tag{2.1}$$

where N_t is population estimate in month t. I assessed the importance of survival and recruitment to population growth rate using quadratic regression of monthly population growth rate on survival or recruitment.

RESULTS

I found that MNA and Jolly-Seber estimates followed the same trend and Jolly-Seber estimates were generally greater than MNA (Figures 2.1-2.3). As expected the greatest differences between Jolly-Seber estimates and MNA occurred when I had low

recapture probability (November 1987, 2001, February 2002, and December 2003, with

capture probabilities of 0.0999, 0.1230, 0.0989, and 0.0791 respectively). A correlation

between the POPAN estimates and MNAs gives an R^2 of 0.568 (Figure 2.4) and

removing the 4 months with low capture probabilities resulted in an R^2 of 0.680 (Figure

2.5). Jolly-Seber estimates were greater than and showed greater variation than MNA

($\bar{x} = $ 102 and 63.67 with standard deviations of 85.8 and 45.36 respectively).

I examined how Jolly-Seber estimates performed when the number of captures

was $\leq$ 10 (Figure 2.6) and $\leq$ 50 (Figure 2.7). A declining trend in JS estimates as

captures increased to 10 (Figure 2.6) and an increasing trend from 11 to 50 captures

(Figure 2.7) indicates that below 10 captures JS estimates are unreliable. This result is

consistent with Seber (1982).

Recruitment and survival both affected population growth rate with R^2 of 0.70

and 0.30 respectively (Figure 2.8 and 2.9). However, rcruitment had a greater effect on

growth rate than survival. In most years recruitment peaked when population peaked

(Figure 2.10).   Survival did show a relationship with population size; however the

relationship is not as distinct as the one with apparent recruitment. Apparent recruitment

predicted population size better than survival (Figure 2.12 and 2.13).

DISCUSSION

Previous studies have concluded that MNA population indices are proportional to

population size and are robust (Boonstra 1985; Hillborn et al. 1976; Slade and Blair

2000). My comparison of MNA and JS is consistent with the findings of Slade and Blair

(2000). MNA provided an index of population size exhibiting a population trend parallel

to the Jolly-Seber estimates although the JS estimates usually are greater than MNA (Figure 2.1-2.4). Although the JS estimator is assumed to be less biased and closer to true (Nichols and Pollock 1983), I did find instances where JS estimates were clearly wrong (e.g., periods with low recapture probability such as November 2001 with an estimate of almost 700 individuals and $p = 0.123$) which is consistent with Carothers (1973). However, Nichols and Pollock (1983) and Boonstra (1985) recommend using the JS estimator for population size estimation as it is usually less biased. The relationship between JS estimates and number of captures suggests that > 10 captures per trapping period is needed to estimate population size with the JS estimator (Figure 2.6), which is consistent with Seber (1982). Therefore, I used the JS estimator in my subsequent analysis as I had few months when the number of captures was less than 10.

White-footed mice are a non-outbreak species with an intra-annual cycle caused by seasonally varying intrinsic growth rates and density dependence in Carter Woods, Ohio (Lewellen and Vessey 1998). In most years, population size starts out low (< 50 and as low as 9 over the study site), peaks to 150-200 individuals in mid-summer or early autumn (July – October) then falls back to low levels at the end of the year (Figures 2.1-2.3). This annual cycle is the result of recruitment during the breeding season and either dispersal or a decline in survival during autumn. Another possible explanation for the autumnal decline could be increased dispersal. Carter Woods is an isolated woodlot surrounded by agricultural fields with limited dispersal. No mice have been found in the nearest woodlot (1.5 km away); however the mice have dispersed to nearby farmsteads (Vessey and Vessey 2007).

Populations of long-lived species that mature slowly and have few offspring are more responsive to adult survival than recruitment (Harvey et al. 1989; Heppell et al. 2000). Species that mature quickly and have many offspring are more responsive to fecundity than survival (Heppell et al. 2000; Read and Harvey 1989). My results support these conclusions as recruitment followed the trend of population size better than survival (Figure 2.8-2.11). Recruitment is greatest in April and May ($\bar{x} = 0.79$ and 0.77 recruits per individual per month, respectively) with a decline in summer and a slight increase in September and October (Figure 2.11). These time periods correspond to the bimodal breeding of white-footed mice at this latitude (Goundie and Vessey 1986). White-footed mice of Carter Woods usually begin breeding in late March or early April (Schug et al. 1991). Young mice should reach trappable size ($\geq 8g$) and disperse from their natal sites approximately two months after birth as gestation and weaning each require ~ 1 month (Lewellen and Vessey 1998). The Pradel model can not differentiate between reproduction and immigration. Therefore, there is the possibility the mice that moved into agricultural fields and their offspring may account for some of the recruitment when immigrating back to the woodlot after crops are harvested in autumn.

My estimated population sizes were inconsistent with my survival results that showed relatively stable apparent survival for much of the year with a decline in autumn (September – November). Stable apparent survival throughout the year allows an increase in population with increased recruitment and the decline in apparent survival corresponds to the decline in autumn. One possible reason for this decline in survival is immigration from harvested crops results in high densities in October and this increased density incurs lowered survival through density dependence. Another possible

explanation for this trend may be that mast crops in autumn allowed for greater densities and the variability of nut crops may explain some of the variation seen in autumnal survival.

My results are consistent with previous studies that found MNA indices are proportional to JS estimates. Assuming that JS estimates are less biased than enumeration methods and that trap response is common in small mammal recapture studies (Nichols and Pollock 1983) JS estimates should be preferred over indices. Life history posits that small, short-lived animal populations are more sensitive to changes in recruitment than survival. My results support previous studies that have reached this conclusion using elasticity analysis (Harvey et al. 1989; Read and Harvey 1989).

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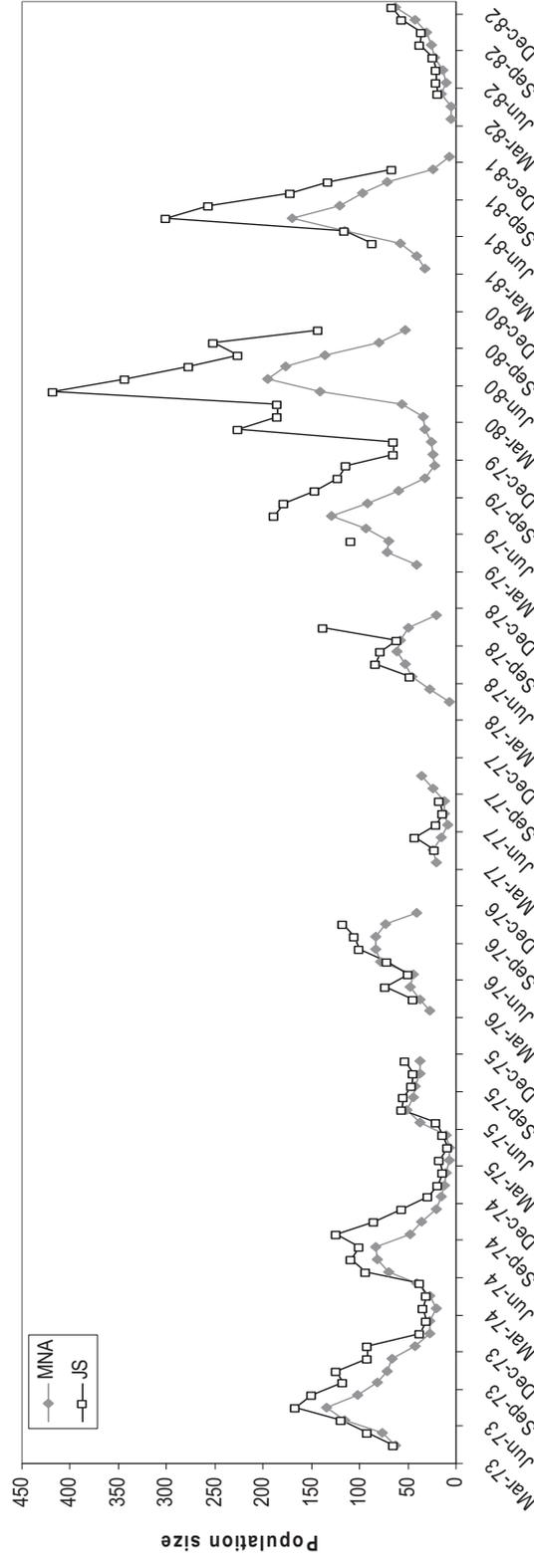
Figure 2.1: Comparison of minimum number alive (MNA) and Jolly-Seber population estimates of white-footed mice in Carter Woods, Ohio for 1973-1982.
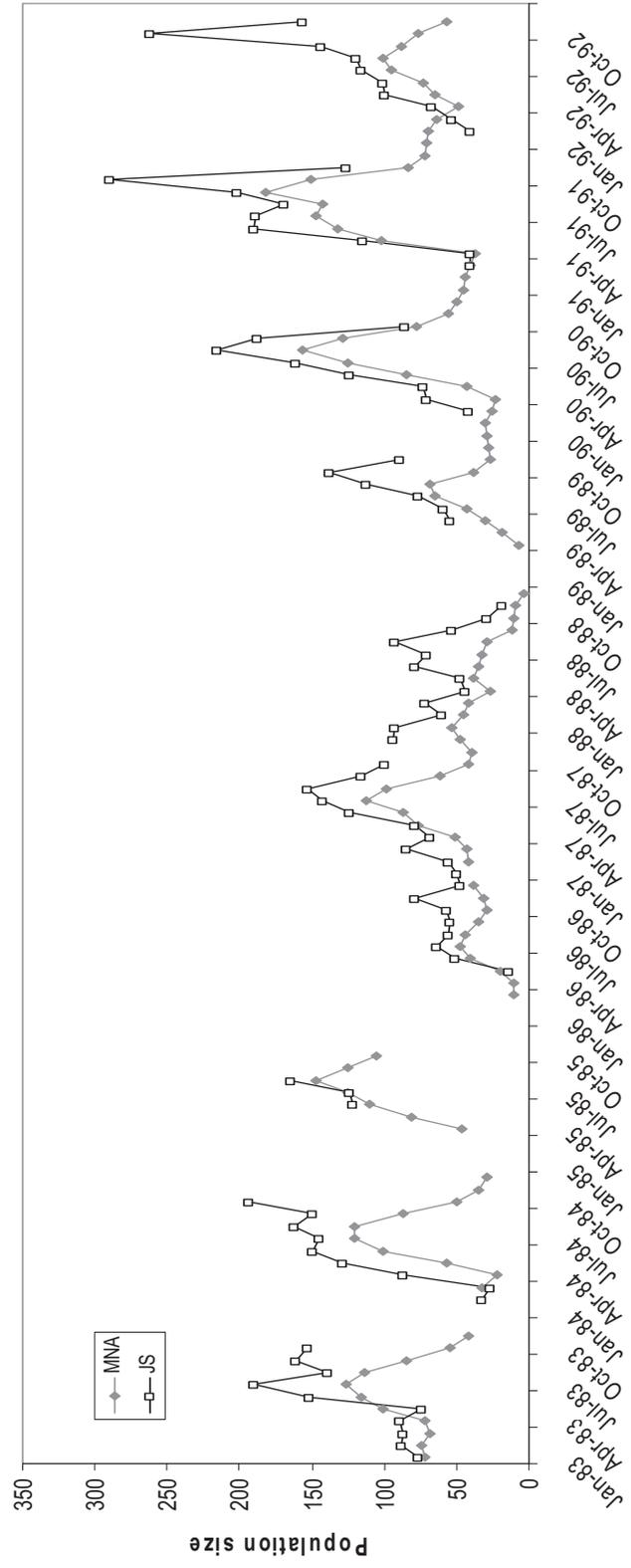
Figure 2.2: Comparison of minimum number alive (MNA) and Jolly-Seber population estimates of white-footed mice in Carter Woods, Ohio for 1983-1992.

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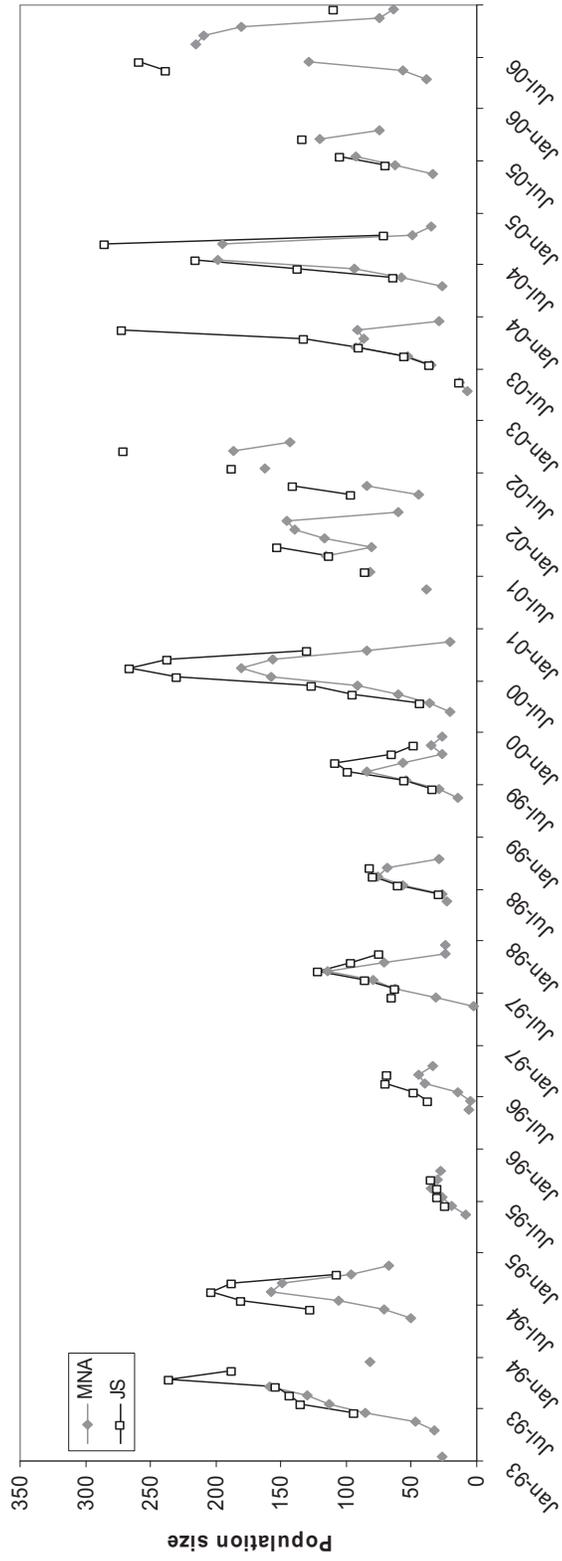
Figure 2.3: Comparison of minimum number alive (MNA) and Jolly-Seber population estimates of white-footed mice in Carter Woods, Ohio for 1993–2006.
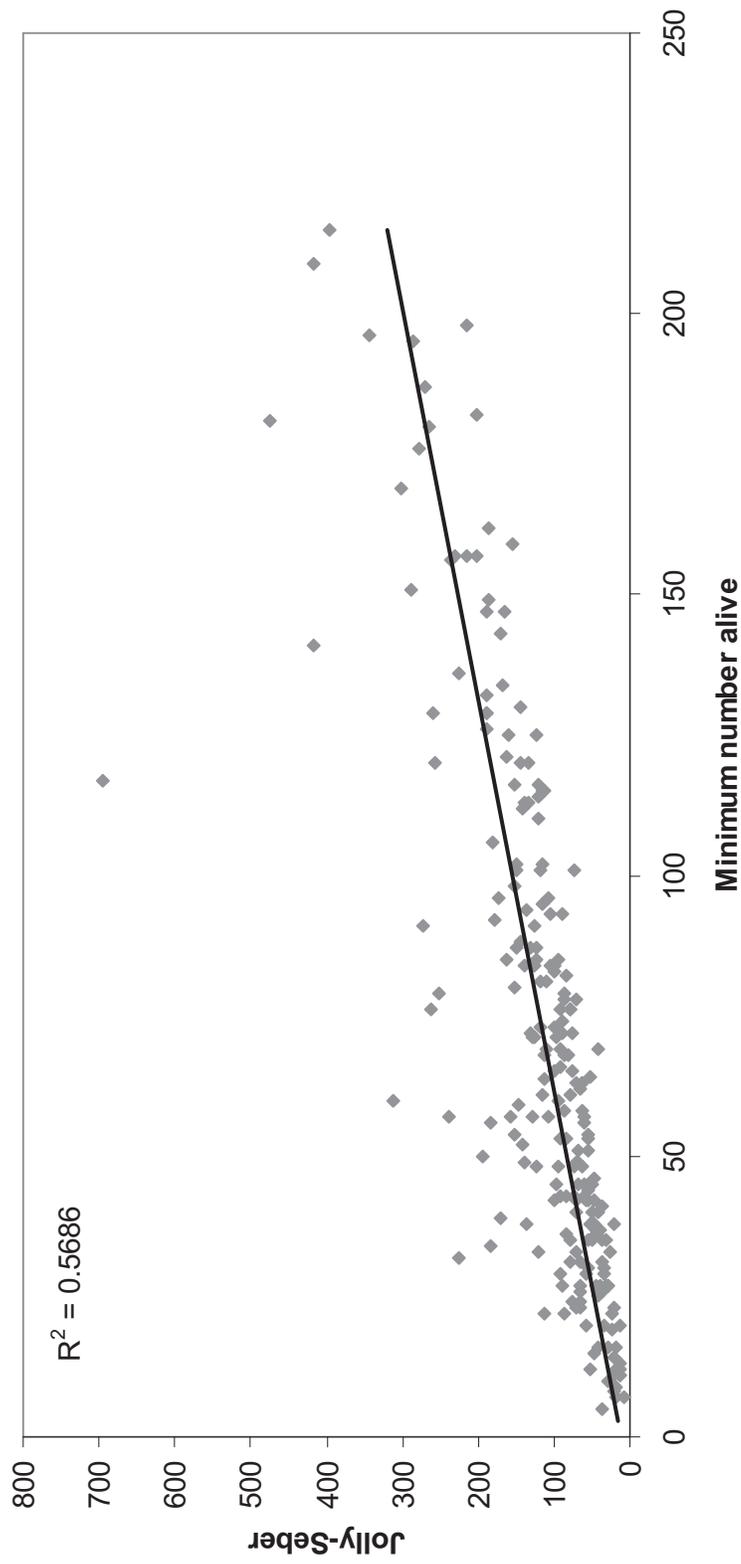
Figure 2.4: Regression of minimum number alive (MNA) and Jolly-Seber population estimates of white-footed mice in Carter Woods, Ohio for 1973-2006.
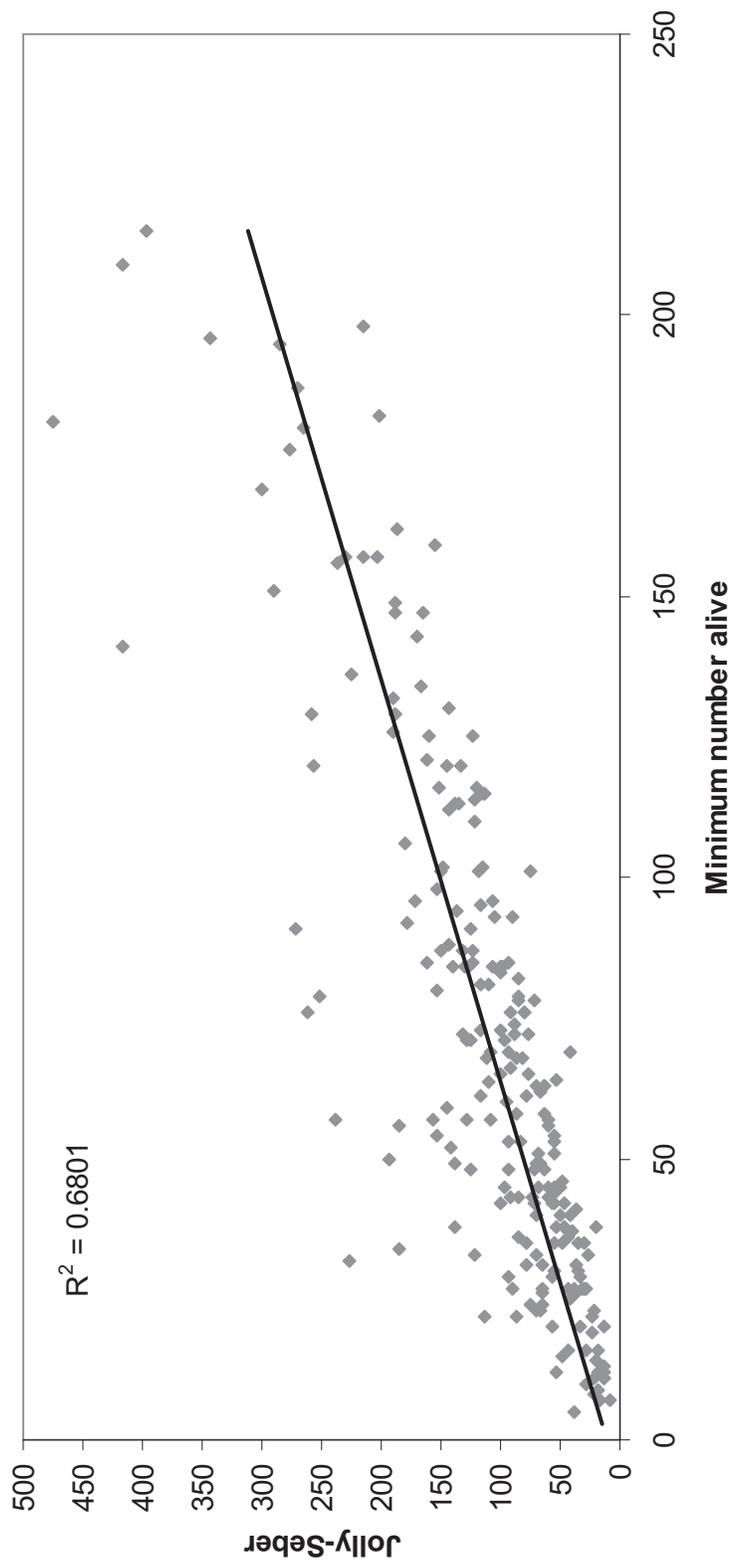
Figure 2.5: Regression of minimum number alive (MNA) and Jolly-Seber population estimates with low recapture probability months removed in Carter Woods, Ohio from 1973-2006.
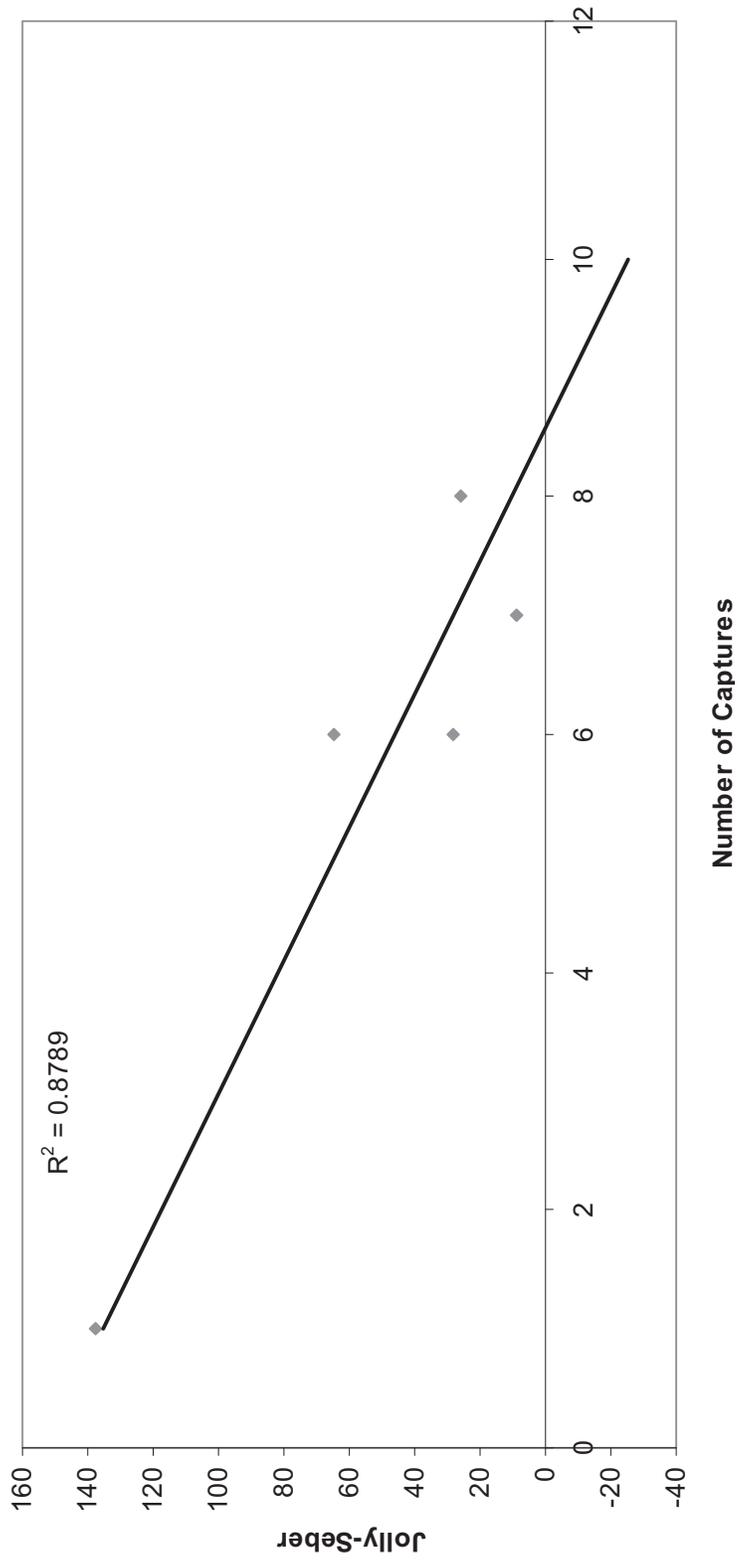
Figure 2.6: Relationship between Jolly-Seber estimates and number of captures when number of captures is ≤ 10 in Carter Woods, Ohio for 1973–2006.
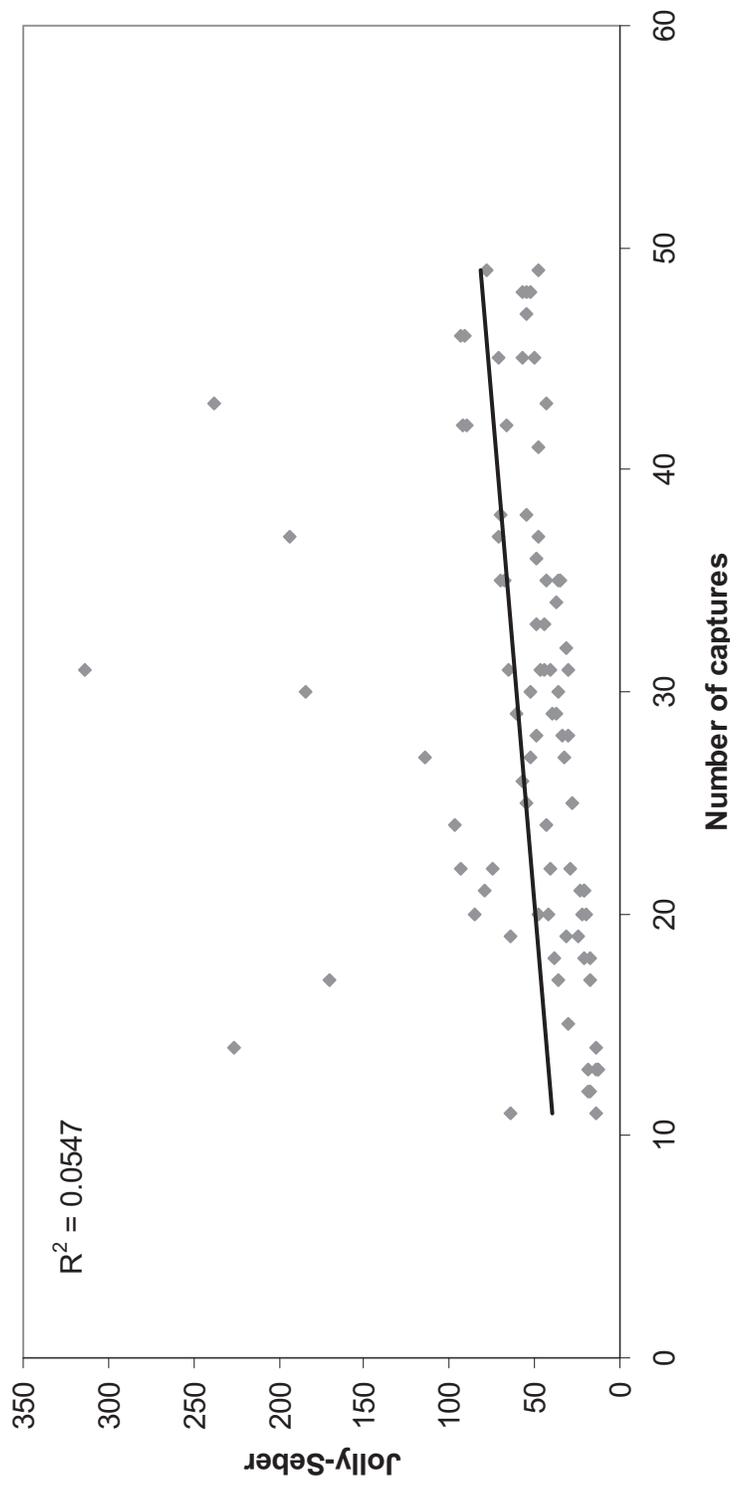
Figure 2.7: Relationship between Jolly-Seber estimates and number of captures when number of captures is ≤ 50 in Carter Woods, Ohio for 1973-2006.
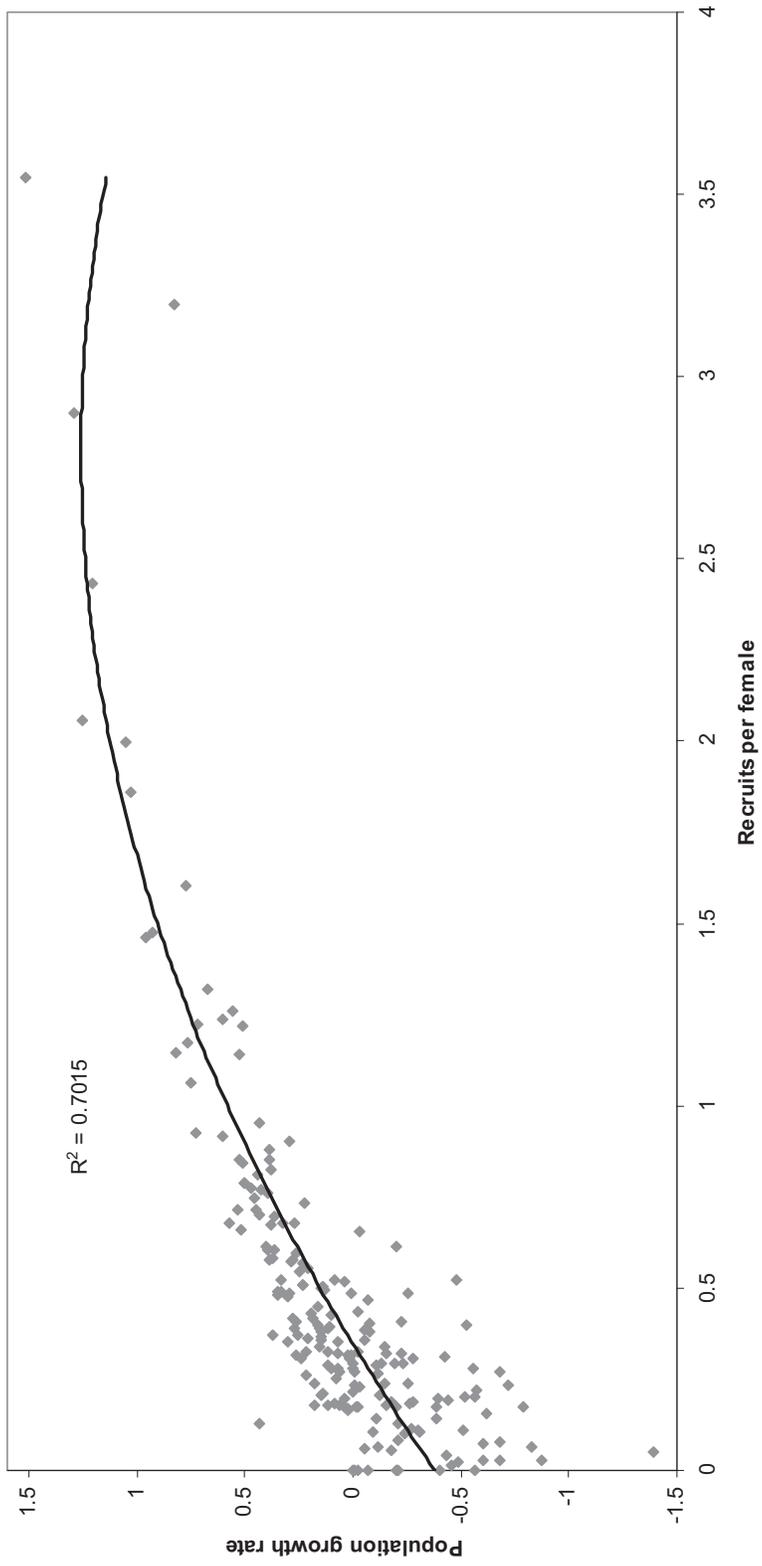
Figure 2.8: Relationship between population growth rate and recruitment of white-footed mice in Carter Woods, Ohio for 1973-2006

$R^2 = 0.7015$

Recruits per female

Population growth rate
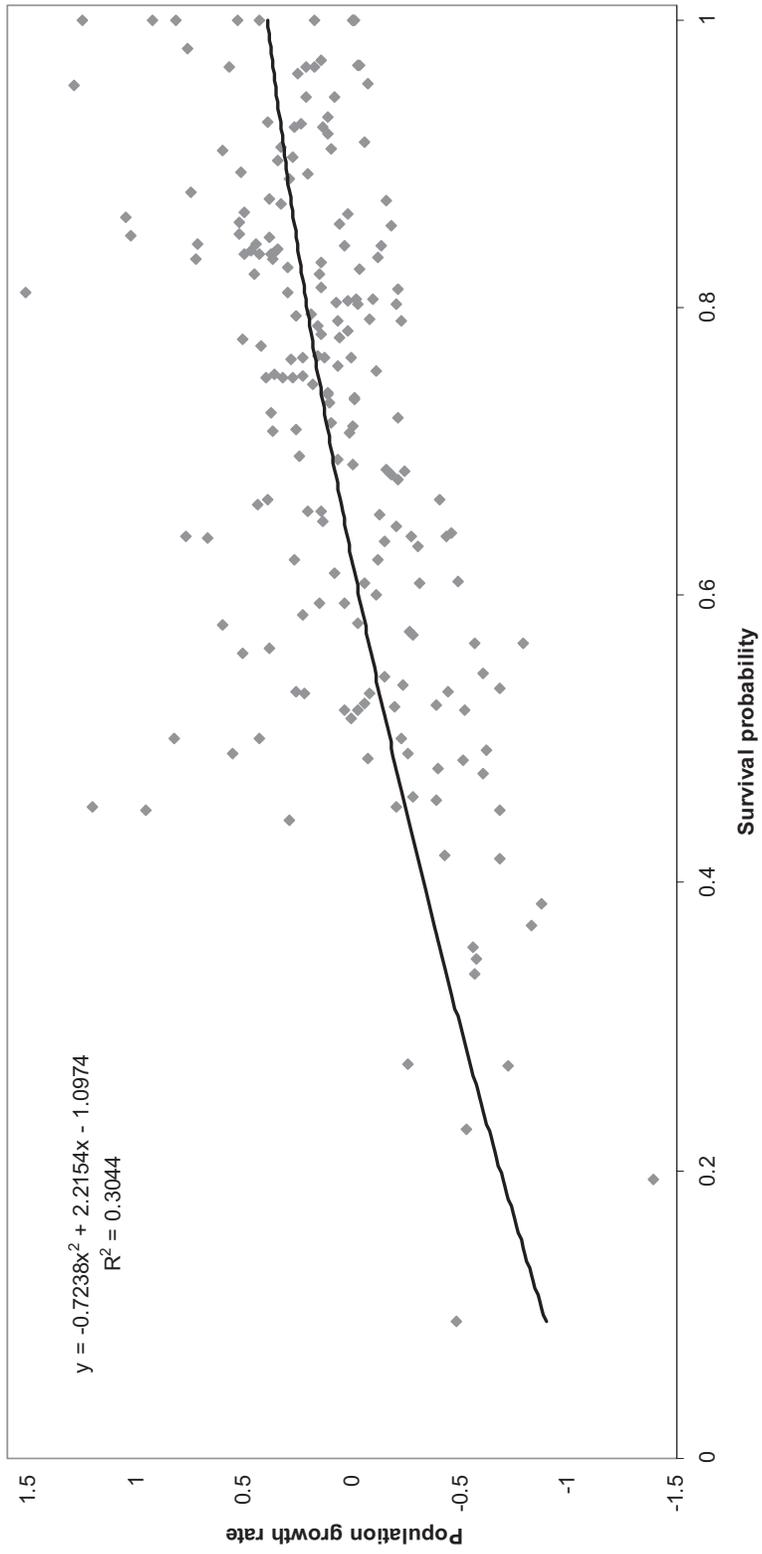
Figure 2.9: Relationship between population growth rate and survival of white-footed mice in Carter Woods, Ohio for 1973–2006.

The figure shows a scatter plot with the trend line equation:

$$y = -0.7238x^2 + 2.2154x - 1.0974$$
$$R^2 = 0.3044$$

where the x-axis is labeled "Survival probability" (ranging from 0 to 1) and the y-axis is labeled "Population growth rate" (ranging from -1.5 to 1.5).
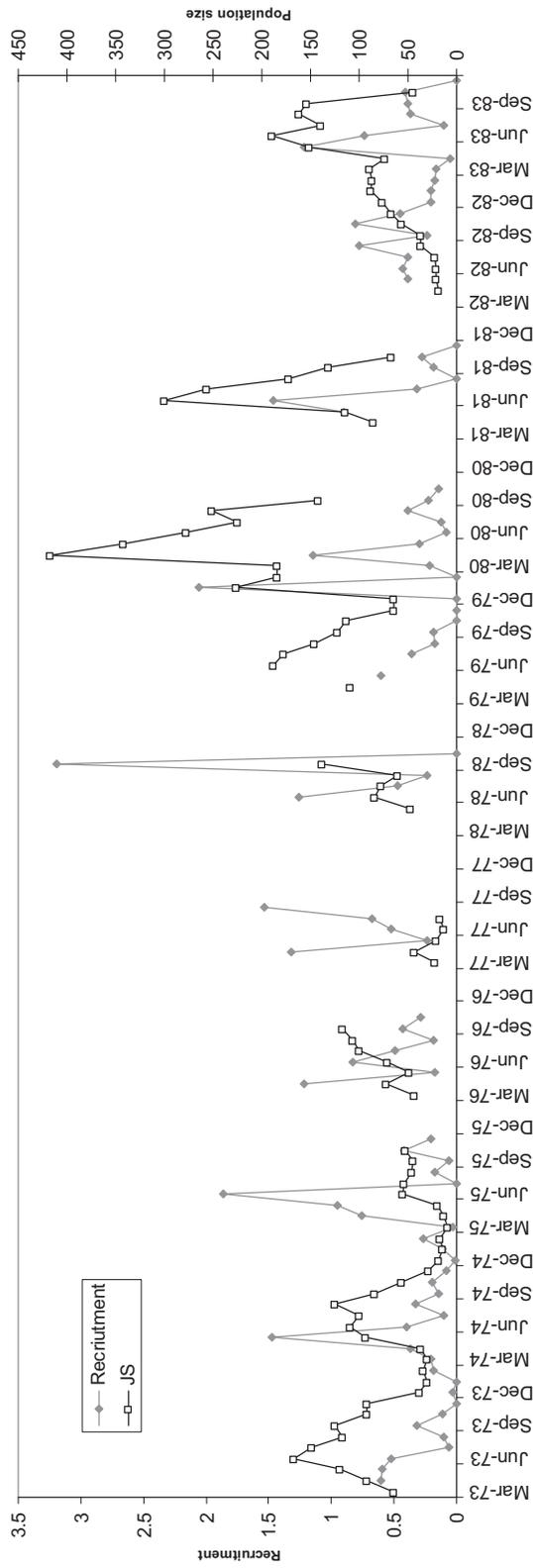
Figure 2.10: Recruitment and population size of white-footed mice in Carter Woods, Ohio for 1973 to 1983.
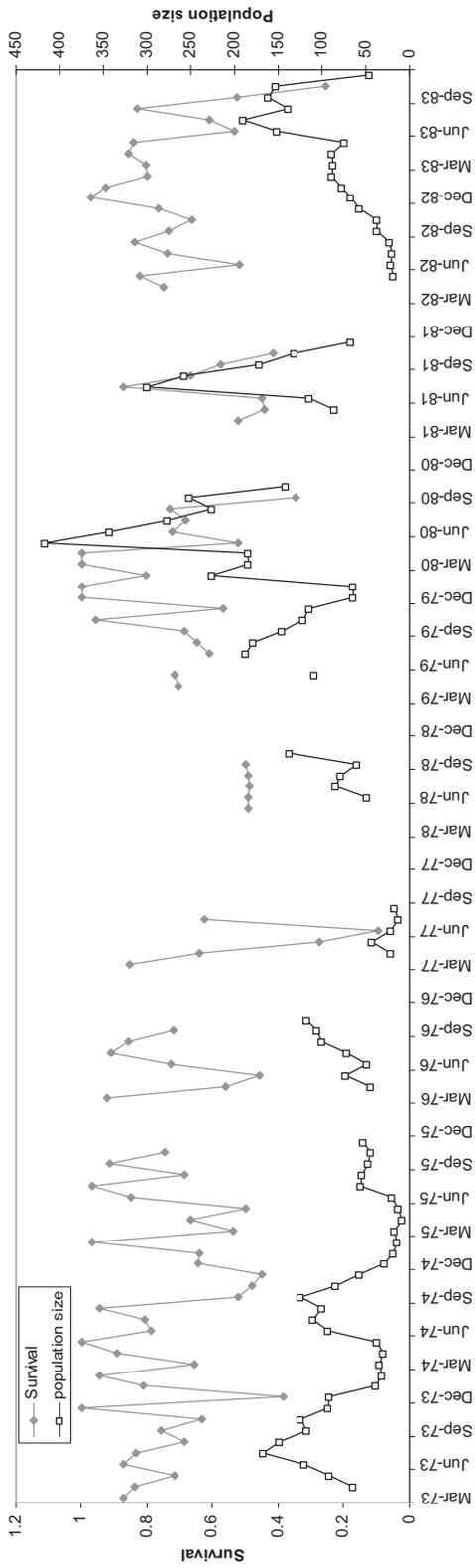
Figure 2.11: Survival and population size of white-footed mice in Carter Woods, Ohio for 1973 to 1983

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$R^2 = 0.0553$

Population Size
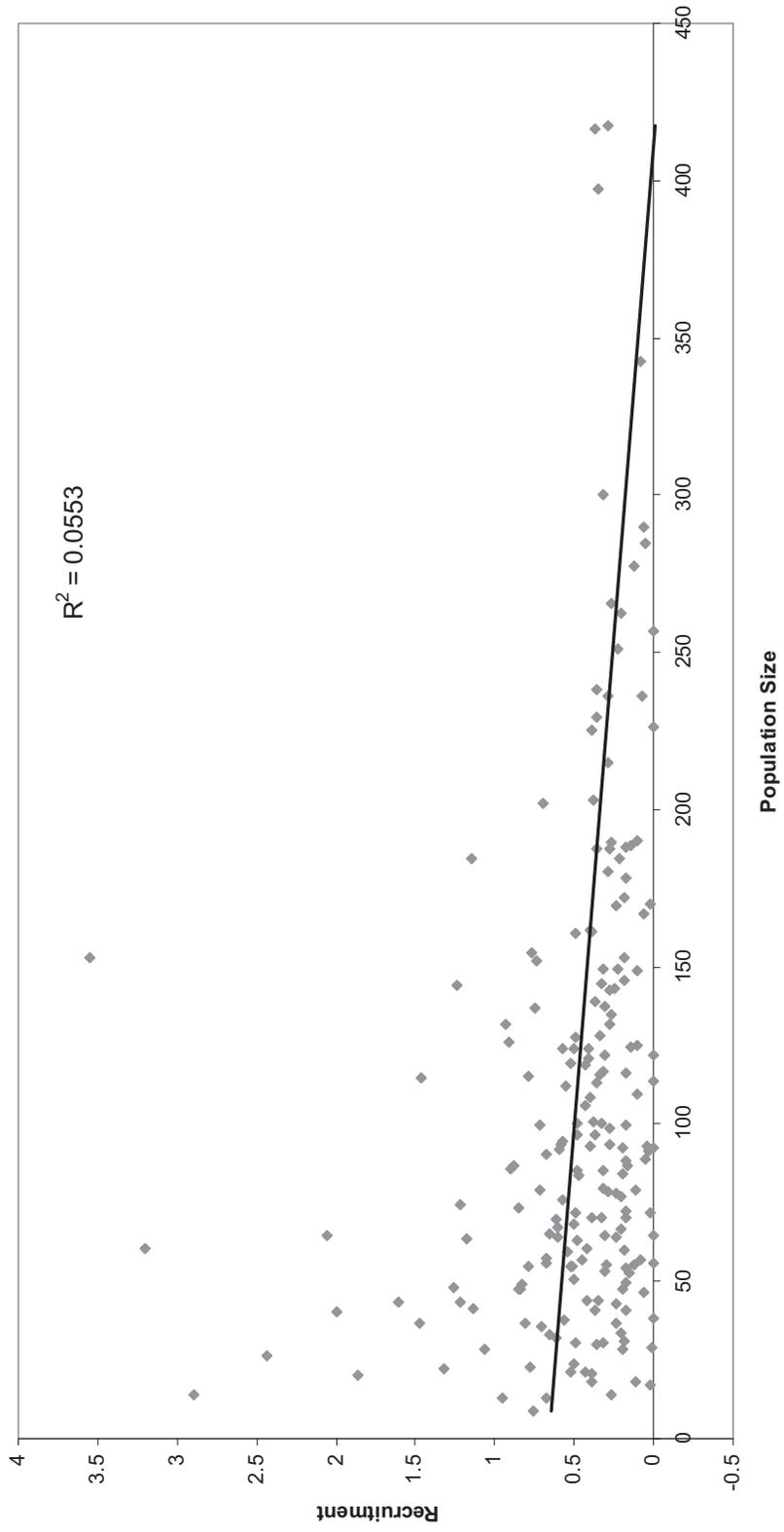
Recruitment

Figure 2.12: Relationship of recruitment and population size of white-footed mice in Carter Woods, Ohio for 1973 to 2006

$R^2 = 0.0162$

Apparent Survival
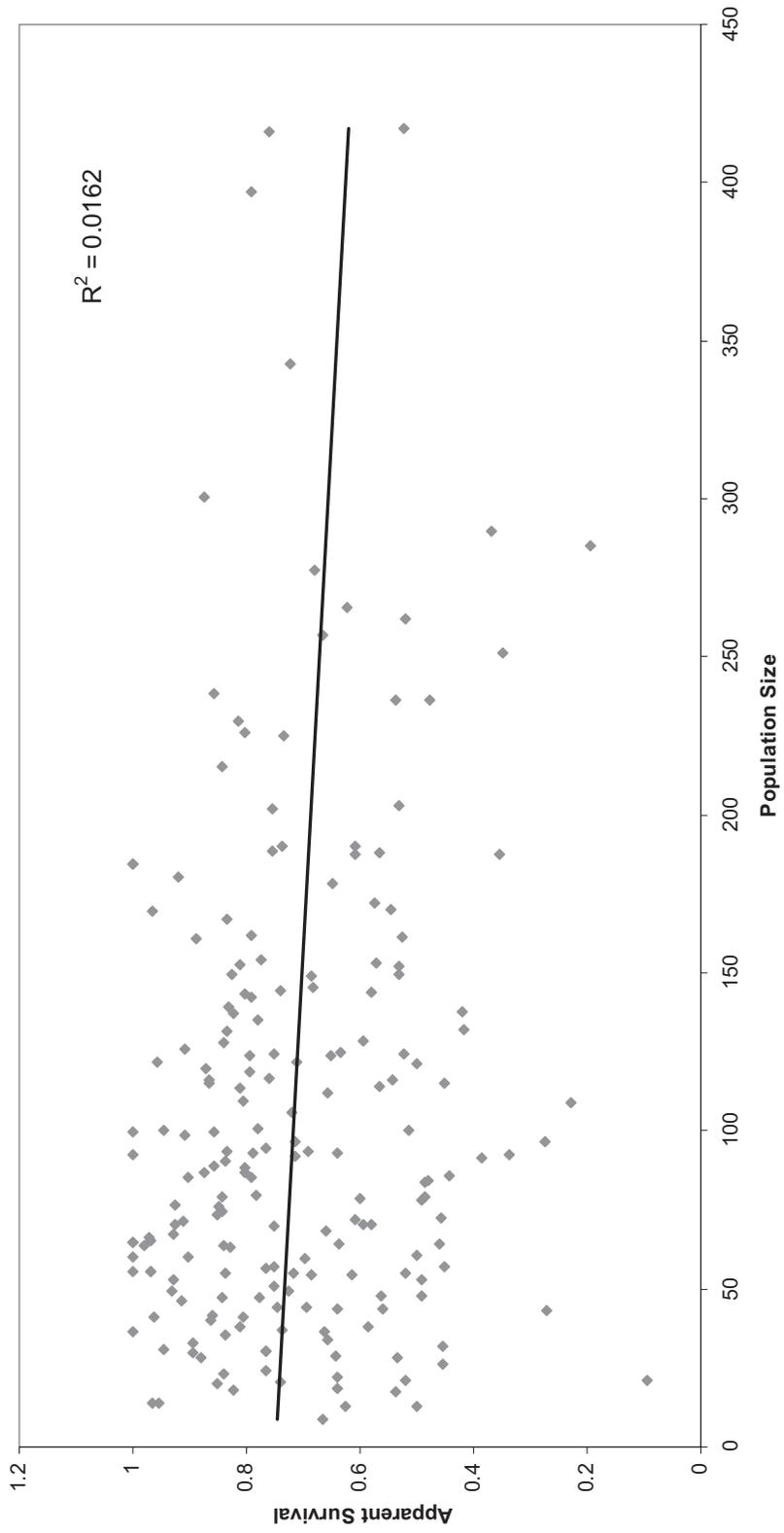
Population Size

Figure 2.13: Relationship of survival and population size of white-footed mice in Carter Woods, Ohio for 1973 to 2006

CHAPTER III

EFFECTS OF CLIMATE, FOOD AND DENSITY ON SURVIVAL OF WHITE-

FOOTED MICE

OBJECTIVES

1. Determine seasonal pattern of survival.

2. Test for effects of climate and density on survival.

3. Test for costs of reproduction to females.

4. Test for effects of mast on overwinter survival.

METHODS

Study site

The study site (Carter Woods) is an isolated 2-ha woodlot located in northwest

Ohio, USA (41º23'N, 83º35'W). See the study site section of Chapter II for details

Data collection

See data collection section of Chapter II.

Weather data

The closest National Weather Service station was located at the Bowling Green
sewage treatment plant, approximately 3 km southwest of Carter Woods (Lewellen and
Vessey 1998a). I obtained the monthly average temperature and total monthly
precipitation data collected at this station from the National Climatic Data Center
(http://www.ncdc.noaa.gov/oa/mpp/). Temperature and precipitation were converted to
degrees Celsius and centimeters respectively.

Peromyscus leucopus **density**

Based on my comparison of MNA and JS estimates, JS estimator was chosen for
my estimates of population size. I used the POPAN model in program MARK (White
and Burnham 1999) to estimate mouse density. Accurate JS model estimates require >
10 animals per sampling period (Seber 1982). Of the 293 months I used, 17 had ≤ 10
animals caught. Nine of these months were in spring (March, April, May), 5 were in
winter (December, January, February), and 3 were in autumn (September, October,
November). Due to the confounding of parameters, the first and last population estimates
for each time period are suspect. This resulted in estimates for only 5 of the 17 months
with ≤ 10 captures. For these 5 months and the one instance when JS estimated almost
700 individuals (November 2001), I used linear regression to estimate population size.
This regression gave me the equation:

$$y = 1.4008x + 10.996, \tag{3.1}$$

where y is JS and x is the MNA index of population size.

Seasonal survival

  I used the CJS model in program MARK (White and Burnham 1999) to estimate

monthly survival and determine the pattern of seasonal survival. Sixteen models of all

possible combinations of time and gender effects were created from the general model

phi(g*t)p(g*t), where phi is survival and p is recapture probability, using gender as a

group (g) and time as either time-specific (t) or constant (.). These 16 models were run

separately for each year due to missing live trapping data during the winters (1973-2006).

Four time periods of continuous data, two periods of 2 years and two periods of 3 years,

also were analyzed. I adjusted for over-dispersion using the ĉ approach described by

White and Burnham (1999). The ĉ is a measure known as a variance inflation factor that

adjusts for the lack of fit of a model to the data. When the general model fit poorly, I

used program U-CARE (Pollock 1982) to calculate the ratio of the chi-square goodness

of fit tests over the degrees of freedom to calculate the ĉ. I found no gender effects on

survival and excluded all models with gender effects in the survival function. I left

gender effects in the recapture probability models because gender influences behavior

that may lead to different recapture probabilities. The exclusion resulted in 8 candidate

models, phi(t) and phi(.), with 4 possible recapture probabilities: p(g*t), p(g), p(t), and

p(.). I did not include age in my analysis because age data are biased toward older

juveniles that are heavy enough to be caught, ≥ 8 grams (Lewellen and Vessey 1998a).

Reed and Slade (2007) did not detect age effects on survival of *P. leucopus* in Kansas,

USA.

  I selected the most parsimonious models among the candidate models by using

Akaike's information criterion (AICc) adjusted for small sample size and quasi-Akaike's

information criterion (QAICc) with data over-dispersion being corrected for with the factor ĉ (Burnham and Anderson 2002). The most parsimonious models had the least AICc and were used to estimate parameter values. The difference between AICc values (ΔAICc) is used to compare and rank models, and when ΔAICc or ΔQAICc is > 10 the model has essentially no support (Burnham and Anderson 2002). When ΔAICc or ΔQAICc < 2, models are considered to be competing and I used model averaging to obtain survival estimates.

Cost of reproduction

I used the multi-state model in program MARK (Brownie et al. 1993; White et al. 2006) to test for current and future costs of reproduction to females. The multi-state model offers estimation of survival rates and transition probabilities between states (e.g., reproductive condition) and allows for estimating the cost of reproduction (Liu et al. 2009; Nichols et al. 1994; White et al. 2006). I used biweekly trapping data from March 1973 to December 1983 for this analysis. This span was used because the biweekly trapping allowed better estimation of breeding status than monthly trapping data.

My state variable was breeding condition with three states defined as (1) sexually immature (SI), (2) reproductively active (RA), and (3) reproductively inactive (RI). New captures less than 17g or with no signs of breeding were assumed never to have bred. Breeding was assigned to mice that had changes of weight > 5 g between successive trapping periods, were obviously pregnant, captured with offspring, or lactating. Probabilities for the transitions of RA or RI to SI were fixed to zero because these transitions are not logical. While an animal could go from SI to RI if not captured during

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RA, I would have no evidence of the animal reaching RA and it would remain SI therefore the movement probability of SI to RI was fixed to zero. I developed 8 models to explain variation in survival between states. To determine if there was a difference between states I used state (g) or constant (.) for survival (phi), recapture (p) and transition probability (psi) with a general model of phi(g)p(g)psi(g). I did not include time in any of the functions because of small sample sizes in some months and the temporal nature of these states.

Effects of climate and density

I reduced my eight candidate models to two: the most parsimonious model and a model using only the recapture function from the most parsimonious model, then added the effects of climate and density as covariates. The design matrix was used to incorporate monthly density (D), total precipitation (R) of the current month, and monthly average temperature (C) of the current month into the survival function as covariates.

Significant covariates of survival often are identified by using AICc (Lebreton et al. 1992). However, Link (1999) found that time-dependent models were invariably preferred over covariate models when using the AIC approach in large data sets with strong temporal variation in survival. The preliminary results for my multiple-year continuous data sets showed this same pattern. Therefore, I used analysis of deviance (ANODEV) F-tests (Skalski et al. 1993) and proportion of variation explained by covariates (analogous to R^2 in regression) (Schemper 1990) to identify effects of

covariates. I used ANODEV for all time periods to be consistent in my analysis.

ANODEV is calculated as:

$$F = \frac{[DEV(.) - DEV(\text{cov})]/[(n_{\text{cov}})]}{[DEV(\text{cov}) - DEV(t)]/[n - n_{\text{cov}} - 1]},$$ (3.2)

where DEV is the deviance of models with constant (.), covariate (cov) and time-specific

(t); n is number of parameters of the time-specific model and n_{cov} is number of covariates

included in cov. Deviance is a measure of how poorly a model fits the data. The

proportion of variation explained by covariates is calculated as:

$$R^2 = \frac{DEV(\text{cov}) - DEV(.)}{DEV(t) - DEV(.)}.$$ (3.3)

I also used mixed models to assess effects of monthly temperature and

precipitation with 1- or 2-month lags on *P. leucopus* survival. I used years as a random

factor and the order-1 autocorrelated error to account for temporal autocorrelation in

survival.

Overwinter survival and mast

I used the robust design model (Pollock 1982) to determine effects of mast on

overwintering survival. The robust design model combines the CJS and closed capture

models. Instead of using only one capture occasion the robust model uses multiple

capture occasions; primary sampling sessions in which gains and losses to the population

occur and secondary sampling sessions of shorter intervals in which the population is

closed (Kendall et al. 1995). My primary periods were May and October and a secondary

period of 2 consecutive days was used. Immigration parameters were set to Markov,

random or no emigration. Markov emigration describes the future capture probability of

an animal depending on current location of the animal. Under random emigration a marked animal may leave and reenter the population, but capture probability is the same for all individuals. I selected the most parsimonious models among the candidate models by using Akaike's information criterion (AICc) adjusted for small sample size. I did not use ANODEV because the deviance of all models was zero.

RESULTS

Seasonal survival

I found little difference in survival between genders: of 34 years, 4 years showed gender effects in the most parsimonious model and 6 years had models with gender effects as competing models (ΔAICc <2). Despite these effects, the survival estimates between genders did not differ significantly as 95% confidence intervals overlapped and shared the same trend. Male recaptures were zero during January and March of 2002 and May of 2005; thus, survival estimates for males were not estimatable, which may explain the detection of an effect of gender on survival for those years. Combining live trapping data over genders also increased sample size and allowed for greater precision in estimates of survival. The monthly pattern of survival shows a relatively constant survival rate, with a slight decrease and large amount of variation during autumn (Figure 3.1). Mean survival ranged from 0.74 to 0.80 over 30 days for most of the year; however, in autumn mean survival ranged from approximately 0.59 to 0.63.

Cost of reproduction

I found no differences in female survival among the three breeding states, indicating no cost of reproduction on survival. The most parsimonious model in 4 of the 7 trapping periods showed no group effect. The survival estimates of the remaining 3 trapping periods did not differ significantly as 95% confidence intervals overlapped (Figure 3.2). Differences seen in 1978 are most likely due to low sample size.

Effects of climate and density

Effects of density, precipitation, and temperature on survival varied across years. Fourteen trapping periods representing 20 years were significantly affected by at least one covariate. Temperature had positive effects in 9 years and negative effects in 5 years whereas precipitation had positive effects in 5 years and negative effects in 4 years. Density had positive effects in 3 years and negative effects in 5 years. I also found an inverse relationship between the coefficient of variation of temperature and amount of variation explained (R^2) by density (Figure 3.3). My mixed models did not detect effects of temperature and precipitation of either 1- or 2- month lags ($\Delta AIC > 10$).

Overwinter survival

The Markov movement model was the most parsimonious and no models had ΔAIC values < 2. My results showed that survival was greater in summer and less during winter (Figure 3.5). However, my capture data was insufficient to detect an effect of mast on overwinter survival.

DISCUSSION

The greater variation in apparent survival during autumn (Figure 3.1) is probably the result of several factors. Autumn recruitment has been shown to be as low as 12% in this population (Goundie and Vessey 1986). Reed and Slade (2007) found a similar pattern in survival among juvenile *P. leucopus* and attributed the decline to increased dispersal. Dispersal may increase in autumn; however, I find this unlikely in this study as Carter Woods is an isolated woodlot. Furthermore, few mice were caught in the surrounding fields and those mice usually returned to the woodlot after crops were harvested (Cummings and Vessey 1994; Goundie and Vessey 1986; Schug et al. 1991). *Peromyscus leucopus* reaches peak densities in late summer and early autumn, particularly in the year following high acorn or nut production (Falls et al. 2007; Ostfeld 1996; Vessey and Vessey 2007). Hickory nuts at this site may have a similar effect on this mouse population and may account for the variation in survival observed in autumn. However, I did not have sufficient data to test for the effects of hickory nuts on survival. High autumn densities may result in increased competition and reduce survival. Survival has been known to decline sharply during August and September while no decline occurred following nonpeak years (Falls et al. 2007).

I found that breeding does not have a detectable cost to current or future survival (Figure 3.2). This result is consistent with previous studies of this population that detected no cost of reproduction (Jacquot and Vessey 1998). *Peromyscus leucopus* is regarded as an "income breeder," increasing consumption during breeding rather than using energy reserves to compensate for the increased energy requirements of reproduction (Millar 1978). Income breeders are not expected to suffer tradeoffs between

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current reproduction and future survival. Previous studies have estimated recruitment rates (percent that reached weaning age) for this population to be as high as 40% in spring and as low as 12% in autumn (Goundie and Vessey 1986; Jacquot and Vessey 1998). With low recruitment rates and an average lifespan of 10 weeks (Rintamaa et al. 1976), *P. leucopus* should be evolutionarily selected to produce as many litters as possible (Jacquot and Vessey 1998; Morris 1986). Given this life history, a cost of reproduction should not be expected as females are not likely to survive long enough for a survival cost to be detected. An alternative explanation is the covariation hypothesis that breeding individuals are already in good condition whereas nonbreeding individuals do not have the resources necessary to reproduce (Descamps et al. 2009; Weladji et al. 2008). However, reproductive activities are unlikely to shape the seasonal survival pattern of *P. leucopus* because the species increases consumption to compensate for the energetic requirement of reproduction during the breeding season.

Effects of temperature, precipitation and density on survival vary over time. Increased variability in temperature reduces the importance of density dependence in the population dynamics of white-footed mice (Figure 3.3). High densities can result in decreased survival through increased intraspecific competition (Nicholson 1933). However, an increasing population at low density can have a positive effect on survival by increasing the chances of locating mates (Allee 1949). Likewise, an increase in precipitation can result in an increase in survival mediated through food (Lewellen and Vessey 1998a), but also may flood ground nests and decrease survival. High temperatures in winter may result in increased survival by reducing the energy costs of

thermoregulation and increased access to food. However, warmer summer temperature may reduce in utero and pup survival (Lewellen and Vessey 1998a).

Previous studies (Linzey and Kesner 1991; Wolff et al. 1983) have found increased aggression and declining female reproductive effort with increasing population size. In contrast, Yunger (2002) examined effects of supplemental food at low density and ascribed the lack of an increase in density with supplemental food to the Allee effect for *P. leucopus* caused by difficulty in finding mates. In the present study the overall effect of density in 1982-83 was negative; however, densities varied substantially between 1982 and 1983 (average population sizes were 32 and 114 respectively) (Figure 3.4). When 1982-83 was split into 2 years the beta estimate of density was positive in 1982 and negative in 1983, indicating positive effects of density in 1982 and negative effects in 1983. Positive density effects occurred at population sizes < 35 and were also seen in 1995. At population sizes < 35, males are vagrants in search of females; as population size increases males establish territories (Vessey 1987). This increased movement resulting from a difficulty in finding mates may be responsible for the detected Allee effect. For population sizes between 35 and 150 there was little competition for resources, but when population size was > 150 the effects of density dependence were evident (Figure 4). My results from 1995 and the time period 1982-83 suggest an Allee effect for this population.

Positive density effects on survival also were found in 1981 and 2001; however, these results are confounded by effects of precipitation. June of 1981 produced double the average precipitation (21 cm vs. 9 cm on average), whereas estimated population size and apparent survival approximately doubled in July. Greater than average precipitation

was recorded in May and autumn (September – November) of 2001, corresponding to an increase in population size. Lewellen and Vessey (1998b) found a positive correlation between rate of increase and contemporaneous precipitation in autumn, most likely the result of increased pup survival or reduced dispersal.

I found that effects of density and climate varied over time. My results are consistent with the findings of Link (1999) and Coulson et al. (2001). For instance, the time periods 1973-75 and 1986-88 had very similar densities and climatic conditions but have different effects of covariates. Both periods were affected by temperature and precipitation; density remained below average for 2 out of 3 years with peak densities in 1973 and 1987. However, effects of temperature and precipitation are reversed, with 1973-75 having positive effects and 1986-1988 having negative effects. Precipitation and temperatures over the periods were very similar. A possible explanation for these differing effects could be differing age structures. Coulson et al. (2001) found that simulated populations with the same initial population size and climate conditions but different gender or age structures had different population trajectories. I did not look at age structure as trapping data are biased toward older juveniles > 8 grams (Lewellen and Vessey 1998a). The exact causes of different effects are unknown.

Under the expected global warming, winter temperatures will likely increase more than summer temperatures at northern latitudes (IPCC 2001). I predict that warmer winters may ameliorate the autumnal decline of *P. leucopus,* resulting in greater abundance the following year. Abundance of mice is known to be correlated positively with the incidence of Lyme disease (Schauber et al. 2005). Greater than average winter temperatures resulted in increased survival and breeding in one warm winter (1982-83).

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This effect is most likely the result of increased access to resources that would usually be covered by snow during winter. Greater winter temperature also may reduce energy cost of thermoregulation during winter and subsequently reduce food demands.

My results indicate the need for long-term data sets because the use of short-term data sets may lead to spurious conclusions. Typical 2 to 3 year studies would not have captured the variation in the effects of precipitation, temperature and density that I documented here. The varying effects I discovered are supported by the conclusions of Coulson et al. (2001), who determined that age and gender structure can influence the response of a population to climate. However, the results of Coulson et al. (2001) were found for a long-lived species (Soay sheep) and the application of their results to short-lived species needs to be examined further.

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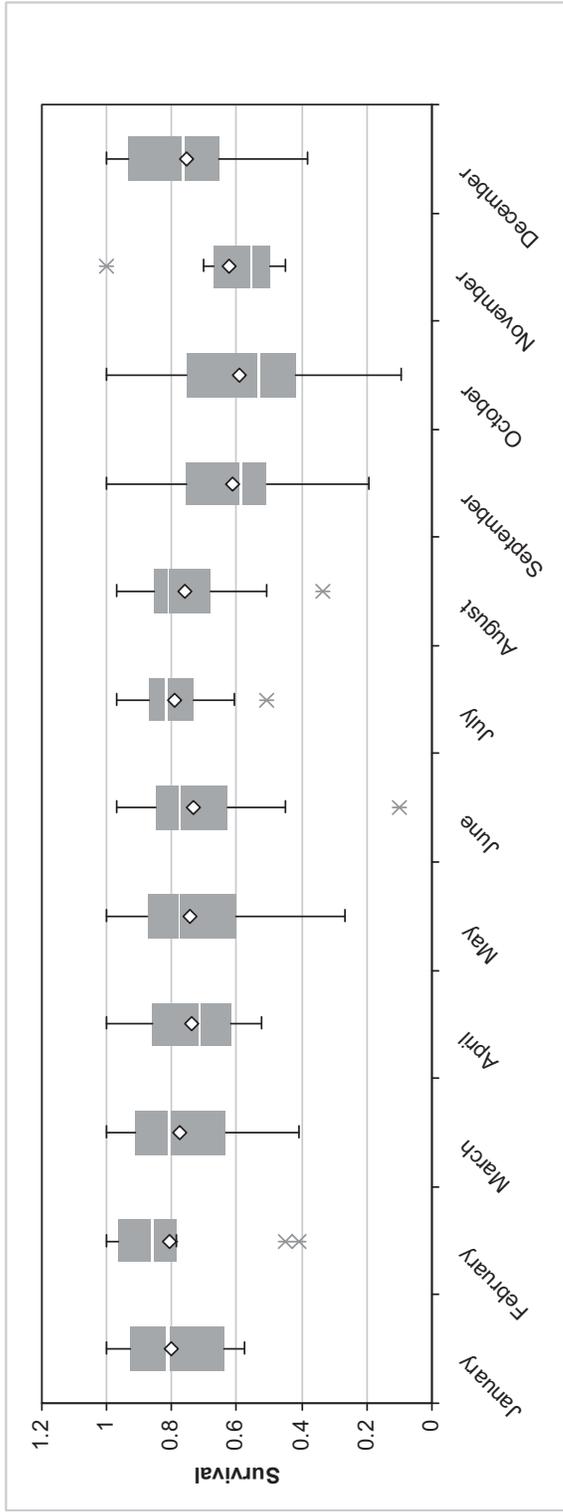
Figure 3.1:   Box plot of monthly survival (30 days) of white-footed mice in Carter Woods, Ohio, from 1973-2006 with outliers (✳).
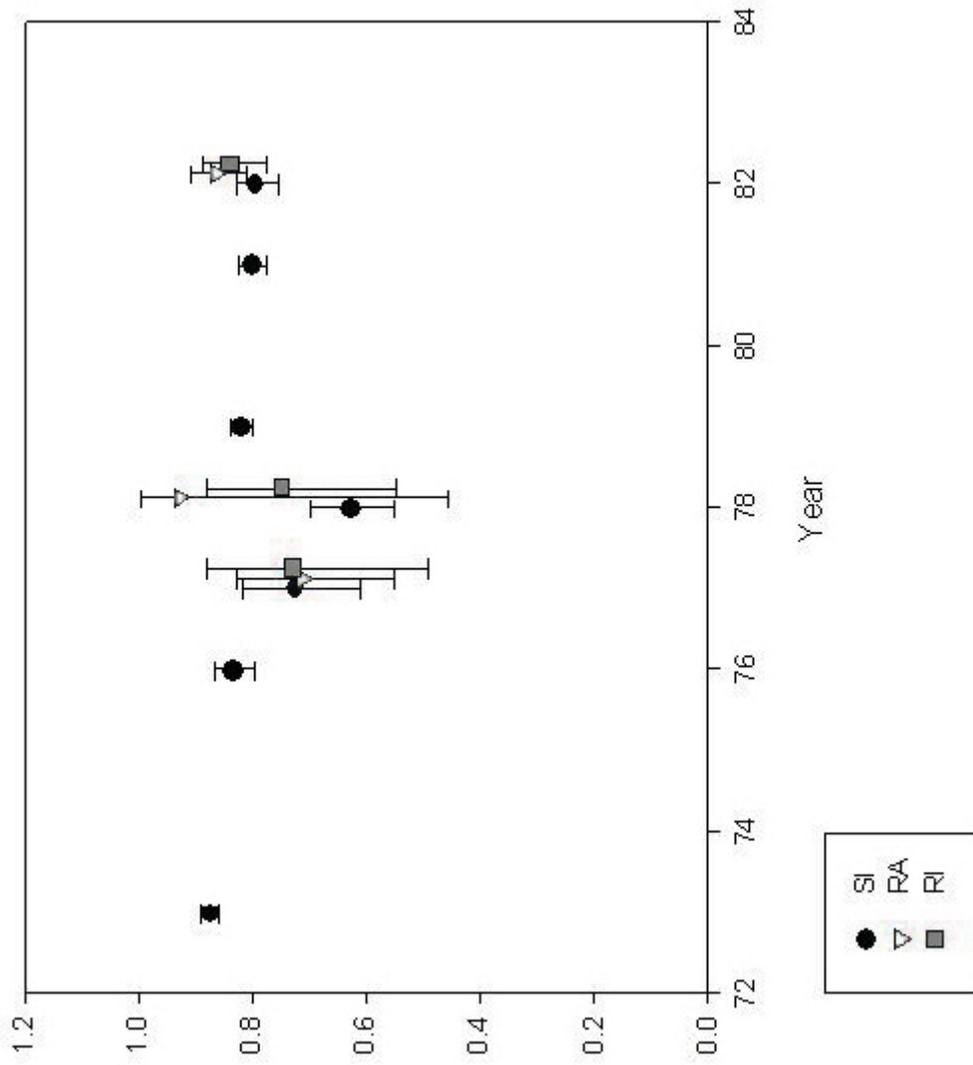
Figure 3.2: State-specific survival of female white-footed mice in different reproductive strata. SI is sexually immature, RA is reproductively active and RI is reproductively inactive in Carter Woods, Ohio for 1973 to 1983.
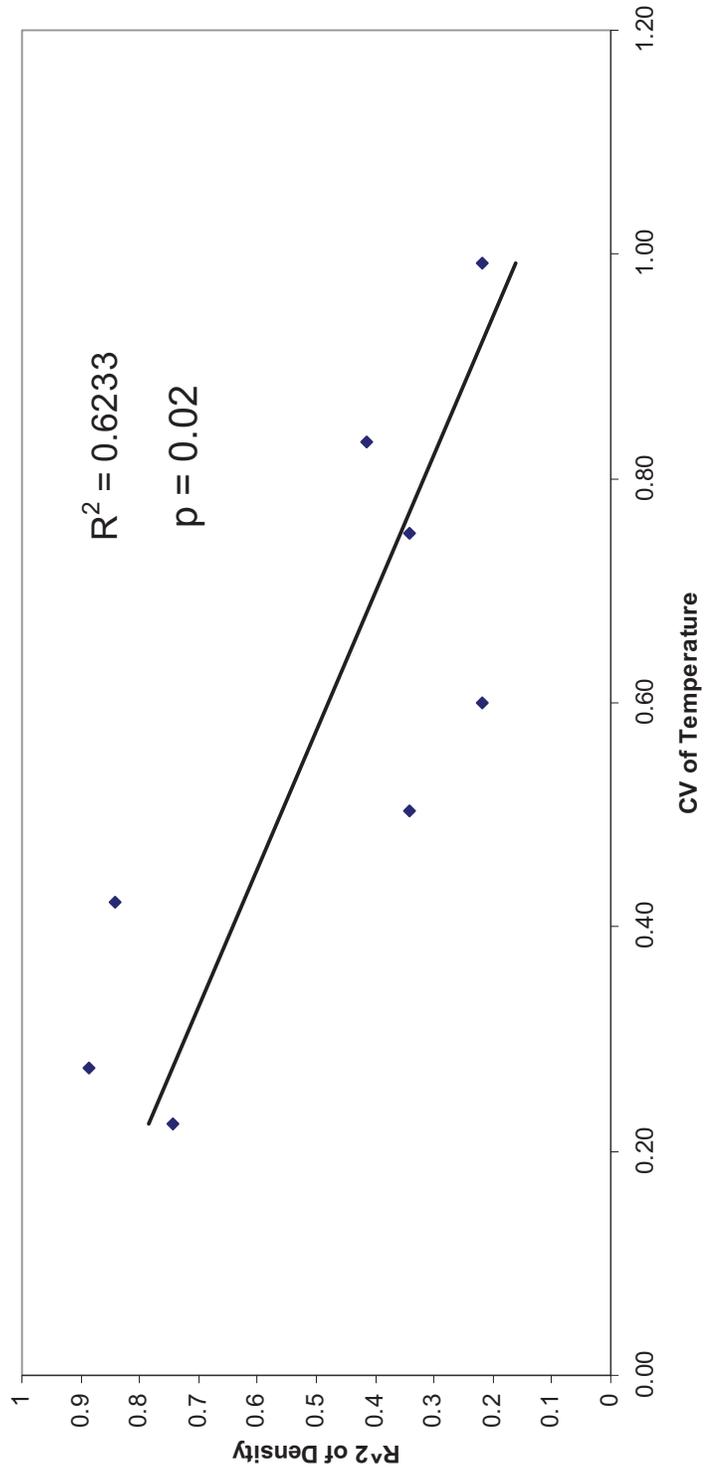
Figure 3.3: The inverse relationship between the coefficient of variation of temperature and percentage of variability in survival explained by population density (R^2) in Carter Woods, Ohio for 197-2006.
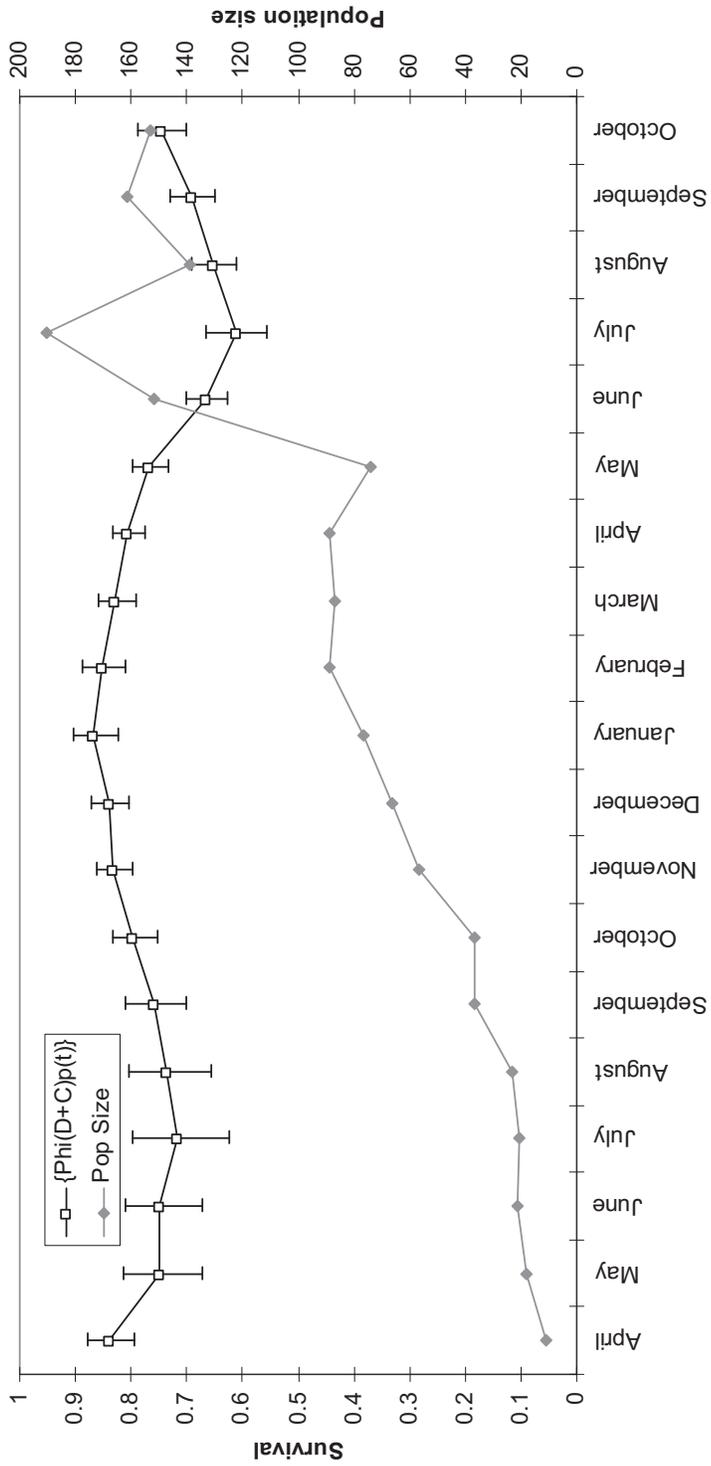
Figure 3.4: Survival estimates (phi) from the density (D) and temperature (C) model (phi(D+C)p(t)) in comparison to white-footed mouse population size (D) in Carter Woods, Ohio for 1982 to 1984.
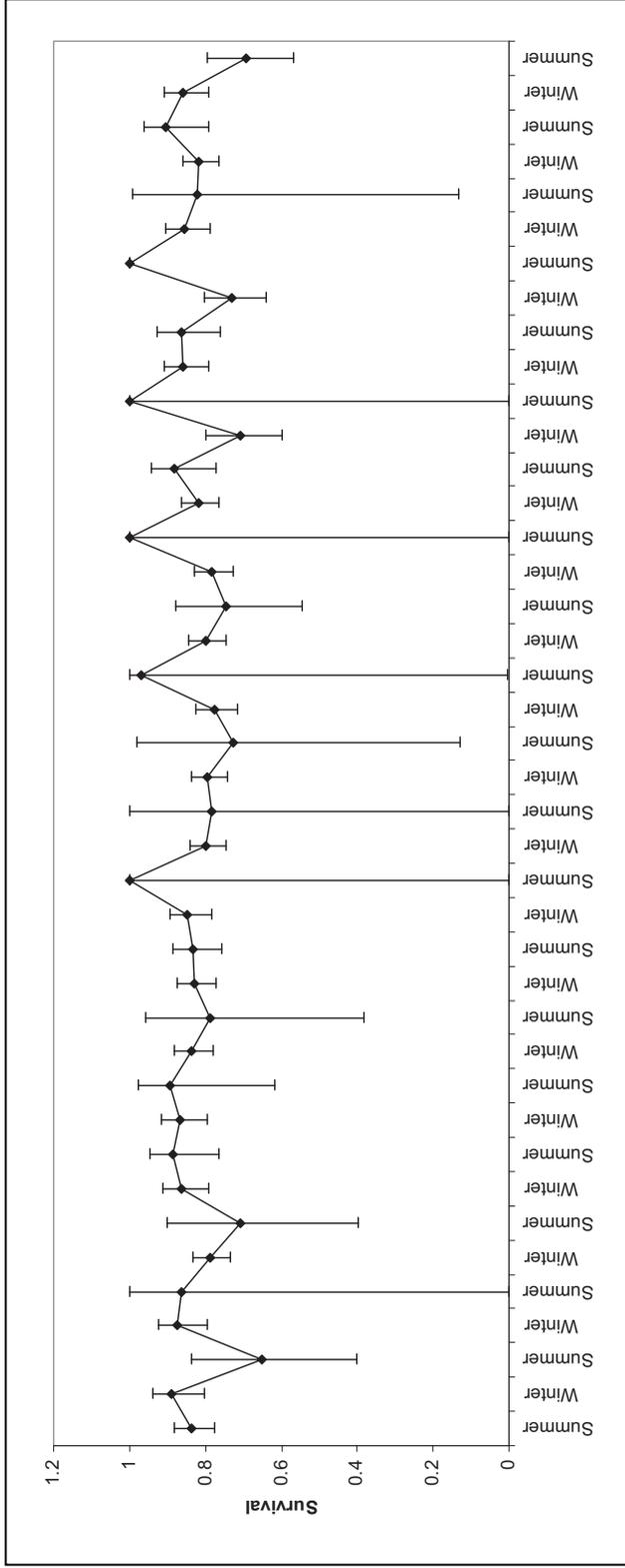
Figure 3.5: Summer and winter survival of white-footed mice using hickory nut crop as a covariate in Carter Woods, Ohio for 1986-2006.

CHAPTER IV

IMPLICATIONS FOR NATURAL RESOURCE MANAGEMENT

TRAPPING FREQUENCY AND SAMPLE SIZE FOR MONITORING SMALL MAMMAL POPULATIONS

My results on the effects of mast on overwintering survival indicate the need for more intensive trapping. Trapping should be conducted at least quarterly or every other month to determine how mast affects survival as the average lifespan of wild white-footed mice is approximately 10 weeks (Rintamaa et al. 1976). This supports Lewellen and Vessey's (1998) argument for evaluating the species and community to identify the time scale that factors affect the population. Summer data was found to be insufficient and this is most likely due to low population sizes and therefore low captures during spring. This indicates that 2 consecutive days may be insufficient to collect an adequate sample size. Therefore, I recommend trapping four consecutive days to provide a large enough sample size.

The results of this study indicate the need for adequate trapping effort. When the number of captures is ≤ 10, or when recapture probability is low, I found Jolly-Seber estimates were unreliable, which is consistent with the findings of Seber (1982) and Carothers (1973). Therefore, an adequate number of traps and trap nights are required to capture more than 10 individuals per trapping occasion. More traps and days of trapping

also may increase recapture probability and thus increase the reliability of Jolly-Seber estimates. While this study likely had enough traps, the 2 day trapping scheme may have been insufficient, as all 4 months with low recapture probability, and 15 of the 17 months with ≤ 10 captures, occurred while using this design.

EFFECTS OF CLIMATE CHANGE ON *PEROMYSCUS LEUCOPUS* POPULATIONS UNDER FUTURE WARMING

Climate change models indicate that temperature and precipitation will become more variable over the next 100 years (IPCC 2001). My result in Chapter 3, of increasing variation in temperature resulting in the release of the population from density dependence, indicates that as climate becomes more variable, mouse populations should be affected more by local weather events than density. Temperature can affect survival through vegetative growth and influencing the energetic costs of homeostasis. Precipitation can affect survival through flooding, drought and influences on vegetative growth. Under the expected global warming, winter temperatures will likely increase more than summer temperatures at northern latitudes (IPCC 2001). I found greater than average winter temperatures produced an increase in survival and breeding occurred in one warm winter (1982-83; Figure 4.1). This effect is most likely the result of increased access to resources that would usually be covered by snow during winter. Greater winter temperature also may reduce energetic costs of thermoregulation during winter and combined with torpor, reduce food demands. Greater mouse densities in spring may result in an increase in the incidence of Lyme diseases as abundance of mice is known to be correlated positively with the incidence of Lyme disease (Schauber et al. 2005).

Warmer temperatures, during early May when gypsy moth eggs hatch, are associated with greater acreage defoliation (Miller et al. 1989a). This increase in gypsy moths may increase survival of white-footed mice through increased food resources (moth pupae). However, warmer summer temperatures have been shown to affect negatively the survival of young mice and have been implicated in causing the summer lull in breeding (Lewellen and Vessey 1998).

Mid and high latitudes in the Northern Hemisphere have experienced an increase in extreme precipitation events during the last several decades (IPCC 2001). I did detect one month where more than double the average precipitation fell and resulted in a contemporaneous decline in survival of white-footed mice (Figure 4.2). This extreme precipitation event may have resulted in flooding and caused direct mortality of mice as ground nests flooded or collapsed. The collapse or flooding of ground nests would also make these nests unavailable this may result in indirect mortality through increased predation risk and increased competition for available nests if nest sites were limiting (Goundie and Vessey 1986). If extreme precipitation events are also associated with wind events arboreal nests may be affected negatively. However, extreme precipitation events may also result in increased survival as plant growth responds and insects respond to that growth. This increase in food resources may account for the increase in survival (Figure 4.2) and the population size reaching a peak of approximately 300 individuals in the months following the event. However, one month is not sufficient to indicate the effect of extreme precipitation events is consistent. Despite increases in precipitation, rising temperatures are predicted to increase evaporation and lead to drought conditions (National Assessment Synthesis Team 2001). Drought negatively affects mouse

populations through decreased food resources (Jones and Kitron 2000; Lewellen and Vessey 1998).

Overall, increasing, fluctuating winter temperatures and declining snow cover (National Assessment Synthesis Team 2001) may result in increased overwinter survival and greater mouse densities in spring. However, increases of extreme precipitation events may result in immediate declines in mouse survival while increasing food resources and mouse survival in later months. Greater temperatures resulting in increased evaporation and drought conditions would also influence food resources negatively and decrease survival of mice. Therefore, mouse survival may increase immediately after extreme precipitation events then decline as drought conditions ensue. Hickory mast crops may increase as a result of this increased precipitation and extreme precipitation events, however if drought conditions are more prevalent hickory crops would presumably be smaller on average. Therefore, overwintering survival of mice may decline.

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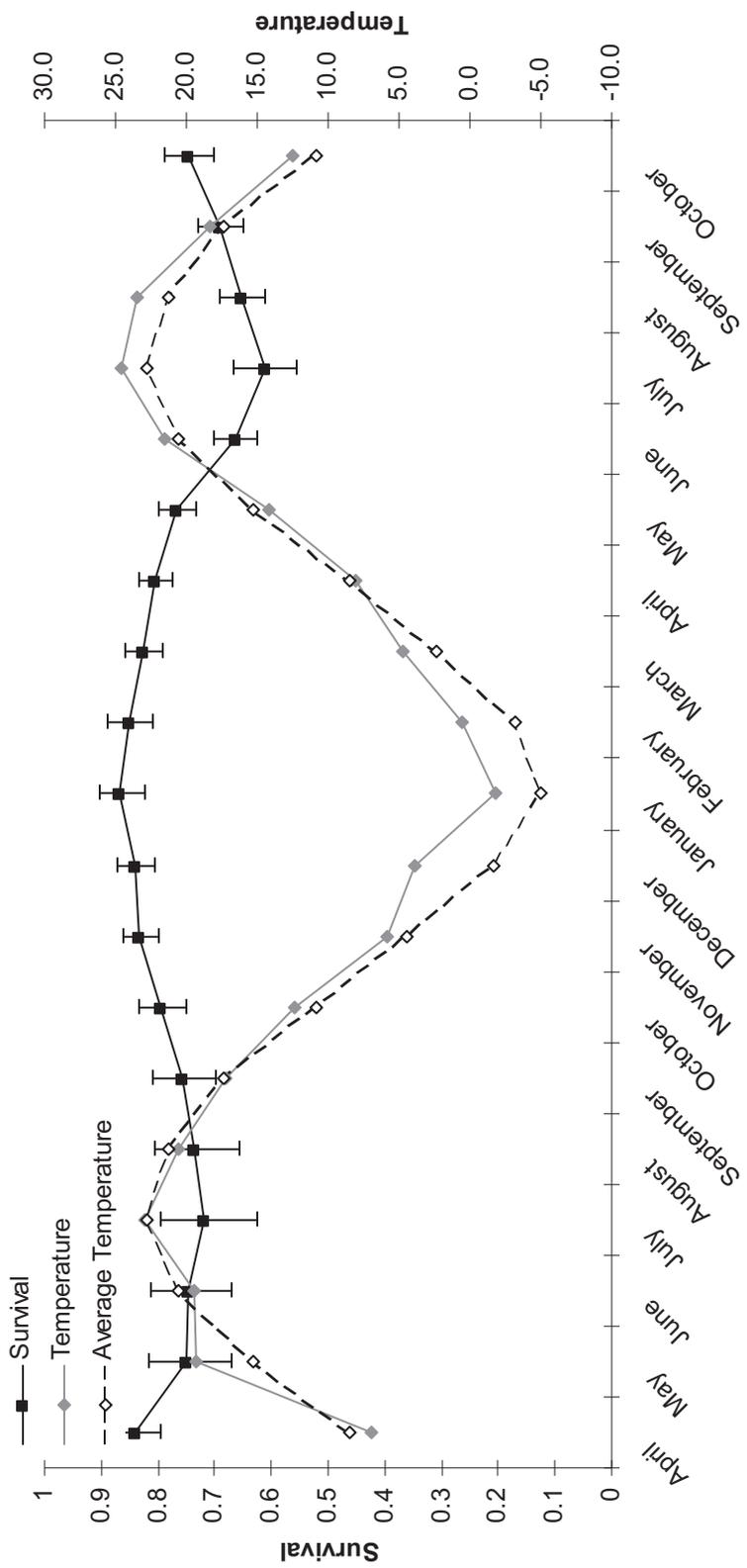
Figure 4.1: Effect of warm winter on survival of white-footed mice in Carter Woods, Ohio in the winter of 1982-83
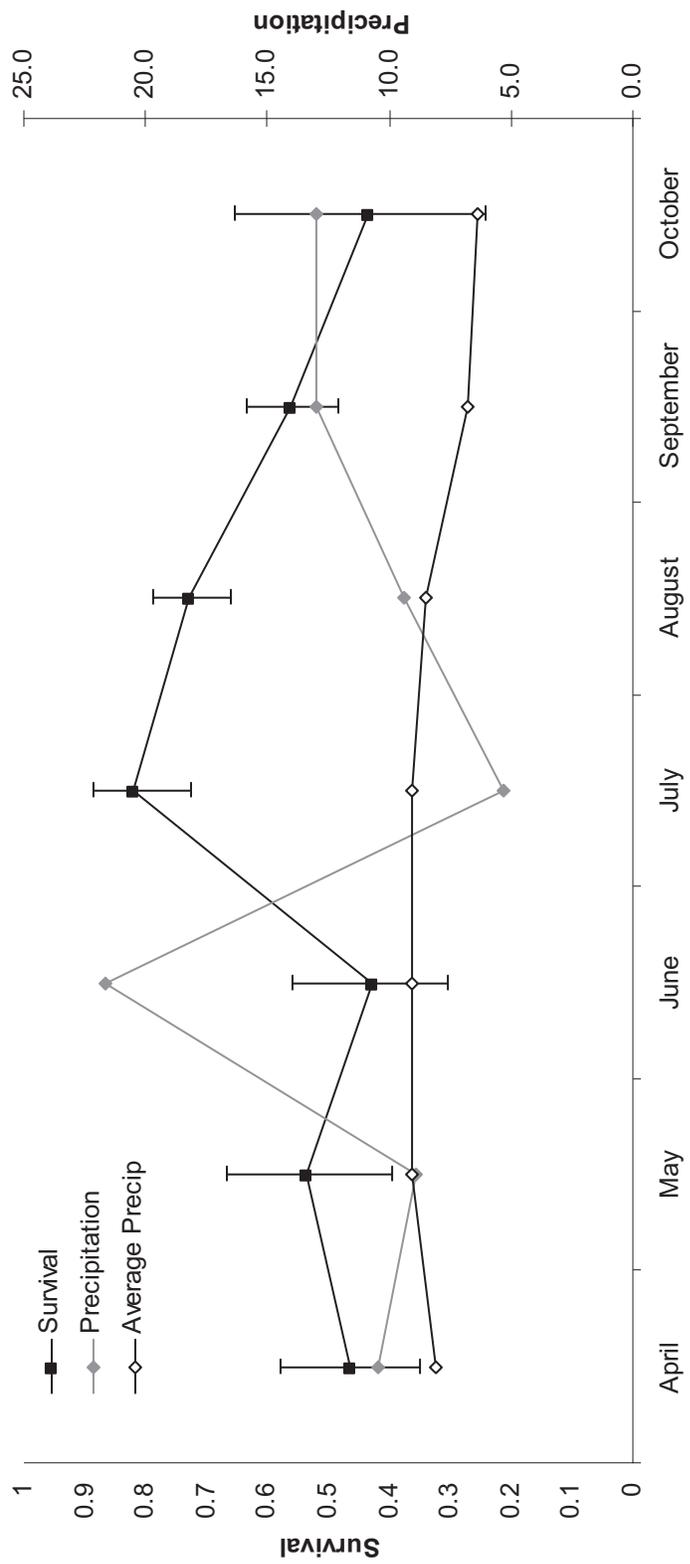
Figure 4.2: Effect of a flood event on white-footed mouse survival in Carter Woods, Ohio during 1981.
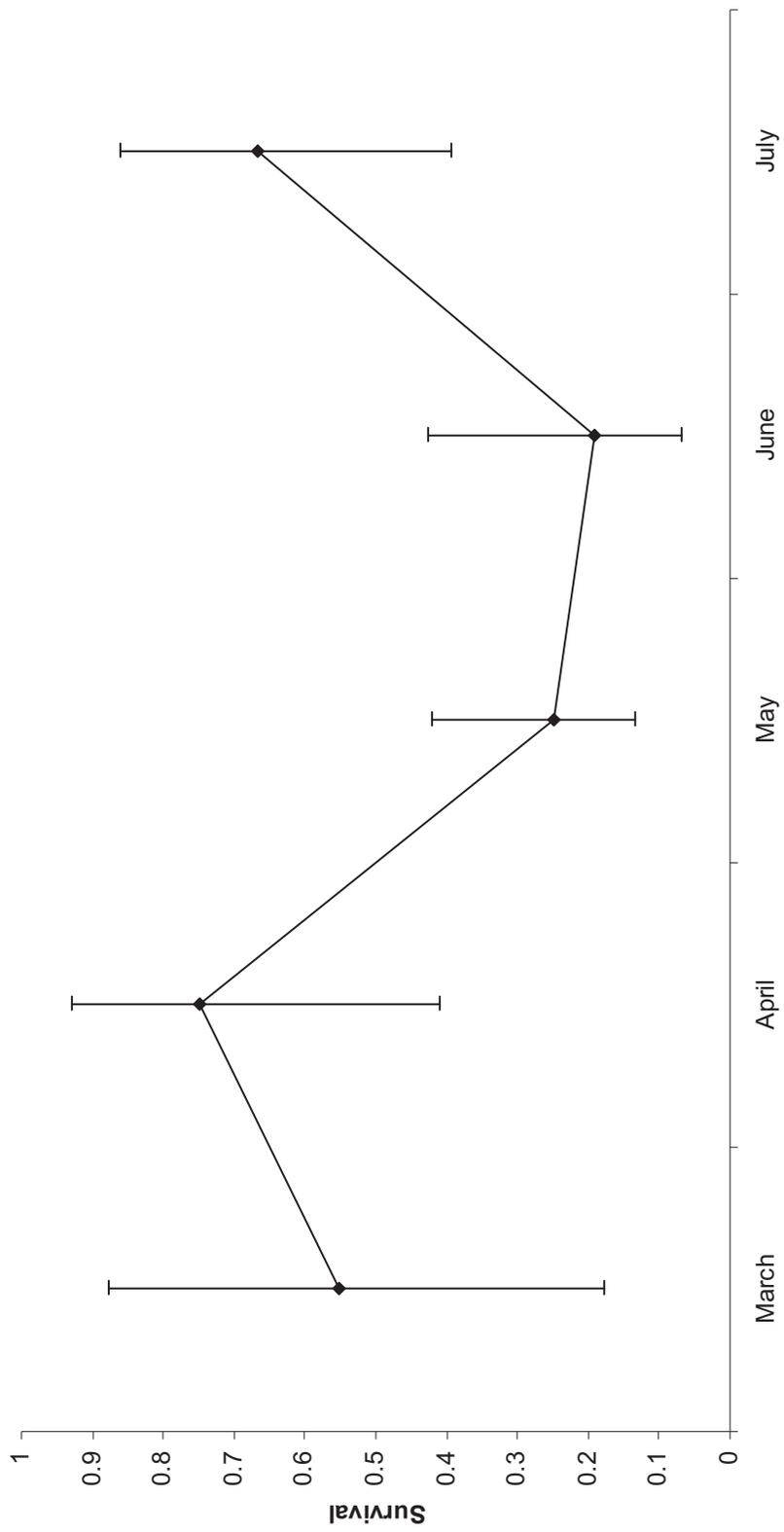
Figure 4.3: Survival of white-footed mice in Carter Woods, Ohio in 1977.