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DEPARTMENT OF VETERINARY AND BIOMEDICAL SCIENCES

THE EFFECT OF PARASITISM ON THE POPULATION DYNAMICS OF THE
WHITE-FOOTED MOUSE (*PEROMYSCUS LEUCOPUS*)

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ABSTRACT

Population cycles have been recorded for a number of animal species and can have major impacts on society, accounting for numerous disease outbreaks and considerable losses in agricultural crops. However, there still exists a lack of clear evidence in the scientific community regarding the mechanisms driving these population cycles. Previous studies have demonstrated that endoparasites may have the ability to regulate the growth of host populations, although few empirical studies have tested this claim. We examined the impact of parasitism by helminthes on the population dynamics of the white-footed mouse (*Peromyscus leucopus*), a species with unstable population dynamics, and found that administration of anthelmintic significantly increased the average proportion of individuals in breeding condition and the average proportion of females pregnant. Additionally, administration of the anthelmintic significantly increased the average mass, average body length and average growth rate of male *P. leucopus*. However, the anthelmintic did not influence the survival or the population estimates of *P. leucopus*. The white-footed mouse served as a model organism, but the results may be applicable to other species that exhibit population cycles as well.

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Chapter 1

Introduction

Fluctuations in animal numbers, known as population cycles, have been recorded for a number of species (Elton and Nicholson, 1942; Elton, 1924; Hudson et al., 1992; Krebs et al., 1973; Peterson et al., 1984). These cycles can have major impacts on society, accounting for numerous infestations which lead to famine and disease (Beck et al., 1959; Singleton et al., 2001; Vanbuskirk and Ostfeld, 1995; Williamson and Oyston, 2012). Outbreaks of bubonic plague, caused by the bacterium *Yersinia pestis*, were increased by abundance in the black rat population (*Rattus rattus*) (Williamson and Oyston, 2012). This bacterium claimed the lives of over sixty-five million people throughout the course of three pandemics, most notably the Black Plague which extirpated one-third of Europe's population in the 14th century (Williamson and Oyston, 2012). Another devastating example involves the periodic density peaks of the house mouse (*Mus domesticus*) throughout southeastern, grain-growing regions of Australia (Singleton et al., 2001). *M. domesticus* densities have reached exceedingly high levels, and these animals have diminished crops (Singleton et al., 2001). Despite their impact, the mechanisms driving population fluctuations are poorly understood.

Charles Elton, an English zoologist and ecologist, was one of the first to recognize the importance of understanding population cycles (Elton and Nicholson, 1942; Elton, 1924) . As a biological consultant to the Hudson's Bay Company, Elton collected trapper records dating back to the 18th century which allowed him to describe population fluctuations in fur bearing animals (Elton and Nicholson, 1942). Through these records, he demonstrated that snowshoe hare and Canadian lynx population cycles strongly correlated with one another, implying that predation

was driving changes in snowshoe hare abundance (Elton and Nicholson, 1942). Elton also recognized the importance of studying population cycles in less conspicuous animals, because their impact can be great. For this reason, Elton devoted a portion of his career studying rodent population cycles. He stated in his paper, *Periodic Fluctuations in the Number of Animals: Their Causes and Effects (1924),* "We have seen that the numbers of many different orders of mammals fluctuate in a periodic way, and the phenomenon is obviously of wide occurrence in mammals. The rodents show it most clearly, but it occurs as well in insectivores, carnivores, and marsupials. Further work will, no doubt, disclose its existence in other groups of mammals,"(Elton, 1924). Although Elton made a major contribution to the knowledge of population cycles, there is a need to understand the mechanisms driving these fluctuations and to identify how general these cycles may be.

Another attempt to understand population cycles was made in the early 20th century by Alfred J. Lotka through the proposal of the Lotka-Volterra model, a pair of equations that define predator-prey relations (Lotka, 1925). This model is recognized as one of the most fundamental theories in the field of ecology, as it is commonly referred to in scientific literature. Nevertheless, the model makes a number of assumptions that oversimplify population dynamics, making the classic model impractical in many ecological studies. For example, the model predicts that the enrichment of a system will lead to an increase in the equilibrium density of the predator, but will create no change in the equilibrium density of the prey (Hairston et al., 1960), destabilizing the community equilibrium (Rosenzwe.Ml, 1971). This prediction, however, is challenged by several biological studies (Arditi and Ginzburg, 1989; McCauley and Murdoch, 1987). Another example is referred to as the "biological control paradox" (Arditi and Berryman, 1991; Luck, 1990). The Lotka-Volterra model predicts that maintaining a very low and stable prey equilibrium density is not plausible; however, there are several examples of predator introductions that result in the prey population being maintained at a low, but stable density (Debach, 1974; Hagen and Franz, 1973;

Turnbull and Chant, 1961). Although, the research of Lotka contains many gaps, his work provides an excellent foundation for further research that aims to define the mechanisms driving population cycles.

Roy M. Anderson and Robert M. May, leading experts in epidemiology, further developed population models, but applied them to host-parasite interactions (Anderson and May, 1978; May and Anderson, 1978). Under certain conditions, parasites play an analogous role to predators in which they suppress the growth of the prey population. They do this in two ways: by decreasing fecundity and increasing mortality of the host population (Anderson and May, 1978; May and Anderson, 1978). Anderson and May (1978) defined three specific conditions which strengthen the regulatory influence of the parasite population and create a stabilizing host-parasite interaction: First, aggregation of the parasites within the host population, in which relatively few members of the host population harbor the majority of the parasites. Second, the parasite population is constrained by density-dependent factors; and third, host mortality positively correlates with parasite burden at a rate greater than the linear (Anderson and May, 1978; May and Anderson, 1978). May and Anderson (1978) also defined three specific conditions which weaken the regulatory influence of the parasite population and create a destabilizing host-parasite interaction: First, the parasites' effect on fecundity is large compared to their effect on morbidity. Second, the parasites are distributed randomly throughout the host population; and third, there exist time delays in parasite reproduction and transmission (Anderson and May, 1978; May and Anderson, 1978). True parasite-host relationships exhibit all six of these conditions presented by Anderson and May (1978), such that the final dynamics are a tension between these factors (Anderson and May, 1978; May and Anderson, 1978). The population models developed by Anderson and May are significant, because they provide a framework to test whether parasite-host relationships are in balance between a stabilizing and destabilizing interaction, and whether parasites have the ability to regulate the growth of host populations.

Although, Anderson and May made a major contribution in the understanding of parasite-host population dynamics, relatively few studies have been performed to test these models. The parasite-host interaction is often overlooked in ecological studies, because the effect on mortality is small in comparison to predation. However, its effects on morbidity can be great. Parasites have the ability to affect predation, reduce aggression in the host, increase susceptibility to disease and reduce access to resources (Vandegrift and Hudson, 2009). In addition, parasites can reduce fecundity in the host population (Vandegrift et al., 2008), which affects population growth and can lead to the instability in host population dynamics and even the generation of population cycles (Dobson and Hudson, 1992; Hudson et al., 1992). Red grouse (*Lagopus lagopus scoticus*) are well known to exhibit population cycles. In a classic study, Hudson et. al. (1992) gathered the necessary data on the vital rates of the avian species and the dominant intestinal parasite, *Trichostrongylus tenius* and used these data to parameterize the Anderson and May models. They were subsequently able to demonstrate that the removal of the parasitic nematode *T. tenuis* with anthelmintic stopped the cyclic population crash of the red grouse in northern England. The removal of this parasite led to an increase in fecundity and an elimination of the population cycle (Dobson and Hudson, 1992; Hudson et al., 1992). This study is the first recorded empirical evidence to demonstrate that parasites can control population cycles, and supports the hypothesis that parasites may control population cycles in other species.

The North American white-footed mouse (*Peromyscus leucopus*) is also known to exhibit population cycles. The *P. leucopus* populations in northeastern North America exhibit a peculiar breeding pattern, in which females cease breeding during the midsummer. This phenomenon is referred to as the "midsummer breeding hiatus" (Brown, 1964; Burt, 1940; Cornish and Bradshaw, 1978; Rintamaa et al., 1976; Terman, 1998; Wolff, 1985) and has not been explained through food shortage (Wolff, 1986) or lack of sexually mature individuals (Terman, 1998). In an attempt to understand the population cycles of the North American white-footed mouse,

Vandegrift et. al. (2008) gathered data on the necessary vital rates of the rodent species and the dominant nematode in their parasite community (*Pterygodermatites peromysci*) and parameterized the data into the Anderson and May models. They determined that *P. peromysci* and *P. leucopus* appear to satisfy the criteria for an unstable parasite-host relationship: The parasite burden has a minimal effect on mortality, large effect on fecundity and the parasites are not aggregated (Anderson and May, 1978; May and Anderson, 1978; Vandegrift and Hudson, 2009). Through the administration of anthelmintic, Vandegrift et. al. (2008) were able to reverse the midsummer breeding hiatus, suggesting that *P. peromysci* may cause instability in the *P. leucopus* populations (Vandegrift et al., 2008).

Population cycles of rodents can have major impacts on human society, leading to famine and disease. Rodents are major carriers of zoonotic diseases. Hantavirus pulmonary syndrome (HPS), monkeypox, leptospirosis, Lassa fever and bubonic plague are only a few examples of potentially fatal diseases that rodents transmit to humans (Ostfeld and Holt, 2004). When rodent population levels rise, these diseases become a serious threat to human health. The ultimate objective of this study is to understand the effect of parasitism on population dynamics in the white-footed mouse. We designed an experiment to monitor the survival, reproductivity and demographics of 12 *P. leucopus* populations. We predict that anthelmintic treated mice will have higher reproductive rates, higher survival rates and better physiological conditions compared with control mice. Learning to control rodent populations through parasitic manipulation may lead to the development of techniques that will reduce disease transmission and infestation levels from these animals. These techniques may be applicable to other species as well.

Chapter 2

Materials and Methods

2.1 General Methodology

The fieldwork occurred in open hardwood forest within the Pennsylvania State University's Experimental Forest which is located 20 kilometers south of State College, Pennsylvania. The experimental design consisted of a total of 12 grids, each separated by at least 500 m. Each grid consisted of 64 live traps in 15 meter trap intervals (105 m^2/grid). The trapping of small mammals was performed using Ugglan live-traps. Trapping occurred bi-weekly from May 24, 2011 until November 23, 2011, with a 3 week interval between trapping sessions. A total of 9 trapping sessions occurred. Captured animals were processed (as described below) and released at the point of capture.

The grids were randomly assigned as control or treatment, with 6 grids in each category. Beginning the second trapping session (June 14, 2011), captured mice in the treatment group were given anthelmintic (1 μL g^{-1} Levamisole hydrochloride™; dose: 36 mg kg^{-1}) once within each trapping session, and captured mice in the control group were given an equal dose of sterile water once within each trapping session. All handing procedures and data retrieval were approved through the Institutional Animal Care and Use Committee (IACUC) at the Pennsylvania State University.

2.2 Field Techniques

Physical measurements were taken from each individual animal and included mass, body

length, sex and molting stage. Animals were classified as reproductive or non-reproductive.

Males were considered reproductive if they had descended testes and females were considered

reproductive if they had a perforated vagina, were lactating or were pregnant. Animals were

classified as juveniles if they had a mass at or below 15.0 grams; they were classified as sub-

adults if they had a mass between 15.1 and 19.9 grams, and they were classified as adults if they

had a mass of 20.0 grams and above. The burden and location of ectoparasites were recorded,

including ticks, botflies, mites and fleas. Presence and location of wounds were also noted, and

included torn ears, bot fly scars and other wounds or scars. External factors were recorded and

included time and weather conditions. Each individual over 8 grams received a Trovan™ Passive

Induced Transponder (PIT) tag or an ear tag. The feces from each capture was collected and

tested for the presence of helminth eggs via the McMasters technique (using 10 mL of $MgSO_4$ per

gram of feces, giving a minimal resolution of 37 eggs per gram). Individuals captured and treated

more than one trapping session (either with the anthelmintic or the placebo) were considered

residents, and those captured and treated only one trapping session were considered non-

residents.

2.3 Statistical Analysis

Two-tailed, unpaired t-tests were used to determine the statistical significance of the

data, and the results were considered statistically significant when the probability (P) values were

<0.05. The t-statistics (t) and degrees of freedoms (df) were included in the calculations, with t-

statistics of >2.0 or <-2.0 considered statistically significant. When plotting results based on the

effects of the anthelmintic, only data from resident animals were used, because newly caught

animals had yet to receive their first treatment. These first captures or new animals were analyzed independently and were indicators of population level effects. The population estimates were calculated using the Jolly-Seber model (Pollock et al., 1990). Growth rates were measured as the slope of the regression line drawn through the plot of mass versus days known alive. Body conditions were estimated by the cube root of individual mass divided by body length. The days known alive were natural log transformed, and only included data from resident animals that did not perish (either within the trap or during processing) during any portion of the study.

Chapter 3

Results

A total of 3752 *Peromyscus leucopus* captures occurred over 13,824 trap nights between May 24, 2011 and November 23, 2011. Of the 1005 individually tagged animals, 423 were residents, meaning that they were captured and treated more than one time. Residents were caught and treated an average of 3.7 times.

Effect of treatment on the population estimate and survival

Based on the Jolly-Seber population model (Pollock et al., 1990), there was no influence of deworming on *Peromyscus leucopus* population levels (Fig. 1). Data from trapping sessions 2 through 9 indicated that the average population estimates were not significantly different from control and anthelmintic treated grids before or after treatment (average P>0.05).

The use of anthelmintic did not significantly influence survival in resident *P. leucopus* measured as the natural log transformed days known alive (P=0.82, t=0.23, df=10) (Fig. 2A, Table 1). In addition, anthelmintic treatment did not significantly influence survival in resident female *P. leucopus* (P=0.64, t=0.48, df=9) (Fig. 2B, Table 1) or resident male *P. leucopus* (one-tailed P= 0.13, t=-1.2, df=10) (Fig. 2B, Table 1). To determine whether the anthelmintic altered survival in *P. leucopus* caught initially as adults and subadults, the average log transformed days alive was compared between these individuals on control and anthelmintic treated grids, but no significant difference was observed (P=0.87, t=0.18, df=9) (Fig. 2C, Table 1). Additionally, the average log transformed days alive was calculated for *P. leucopus* caught initially as juveniles to determine whether the anthelmintic affected survival in this group, however the difference in the

average log transformed days alive between these individuals on control and anthelmintic treated grids was not statistically significant (P=0.67, t=0.43, df=10) (Fig. 2D, Table 1).

Table 1. Average days known alive (natural log transformed) of resident *Peromyscus leucopus* given for control and anthelmintic treated grids, males and females on control and anthelmintic treated grids, individuals caught initially as subadults or adults on control and anthelmintic treated grids and individuals caught initially as juveniles on control and anthelmintic treated grids. The standard errors were calculated by the grid means (n=6).

Group	Average ln(days alive+1)	Standard Error
Residents on control grids	3.94	0.042
Residents on anthelmintic treated grids	3.95	0.051
Female residents on control grids	4.01	0.054
Female residents on anthelmintic treated grids	3.97	0.079
Male residents on control grids	3.89	0.051
Male residents on anthelmintic treated grids	3.97	0.041
Subadult/adult residents on control grids	4.02	0.045
Subadult/adult residents on anthelmintic treated grids	4.01	0.067
Juvenile residents on control grids	3.69	0.093
Juvenile residents on anthelmintic treated grids	3.63	0.11

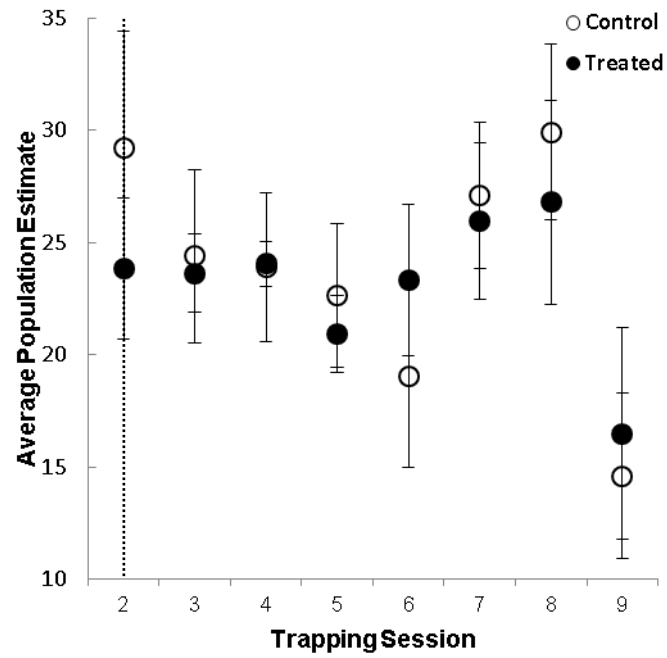**Fig. 1.** Average population estimates of *Peromyscus leucopus* on control grids (unfilled circles, n=6) and anthelmintic treated grids (filled circles, n=6) from trapping sessions 2 (June 14, 2011) through 9 (November 29, 2011), using the Jolly-Seber population model (Pollock et al., 1990). The dotted line represents the start of treatment. Error bars represent the ± standard error of the grid means (n=6).
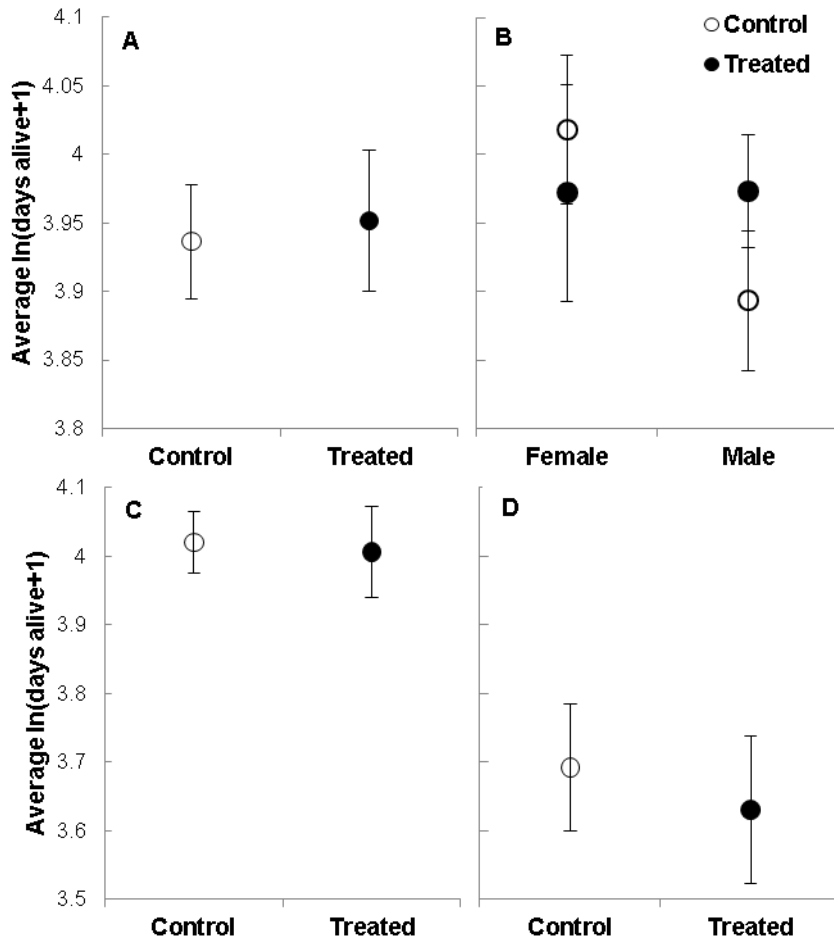
Fig. 2. Survival of resident (those captured and treated more than once) *Peromyscus leucopus*, measured as the average ln(days alive+1), where days alive equaled the time between the first treatment and last capture of each individual (with treatments administered between June 14, 2011 and November 23, 2011). Survival was compared between (A) control grids (unfilled circle, n=6) and anthelmintic treated grids (filled circle, n=6); (B) females on control grids (unfilled circle, n=6), females on anthelmintic treated grids (filled circle, n=6), males on control grids (unfilled circle, n=6), males on anthelmintic treated grids (filled circle, n=6); (C) individuals caught initially as subadults (between 15.0 and 19.9 grams) or adults (at least 20.0 grams) on control grids (unfilled circle, n=6) and anthelmintic treated grids (filled circle, n=6); (D) individuals caught initially as juveniles on control grids (unfilled circle, n=6) and anthelmintic treated grids (filled circle, n=6) . Error bars represent the ± standard error of the grid means (n=6).

Effect of treatment on mass and growth rate

The difference in the average masses of residents on control and anthelmintic treated grids tended toward significant (P>0.10), although it was not statistically significant at a 5% level (one-tailed P=0.085, t=-1.5, df=10) (Fig. 3A, Table 2). Therefore, anthelmintic treatment may have increased the mass of *P. leucopus*, but there was a lack of strong statistical support. Additionally, the average masses of residents on control and anthelmintic treated grids did not differ significantly before treatment (trapping sessions 1 and 2) or after treatment (trapping sessions 3 through 9), indicating that deworming did not affect the average mass of residents overall (average P>0.05) (Fig. 3C). The average masses also did not vary significantly between anthelmintic treated resident females and control resident females (one-tailed P=0.18, t=-0.95, df=10) (Fig. 3B, Table 2). However the average mass of anthelmintic treated resident males was 5.00% higher than control resident males, which was statistically significant (one-tailed P=0.031, t=-2.2, df=8) (Fig. 3B, Table 2). This indicated that the anthelmintic increased the average mass in resident males.

The average growth rates on control grids and anthelmintic treated grids were not significantly different (one-tailed P=0.22, t=-0.085, df=5) (Fig. 4A, Table 3). Because pregnancy can considerably affect the mass of *P. leucopus*, we calculated the average growth rates of residents on control and anthelmintic treated grids that were not determined pregnant at any time of the study. The average growth rates of non-pregnant control residents and non-pregnant anthelmintic treated residents did not vary significantly (one-tailed P=0.19, t=-0.95, df=7) (Fig. 4B, Table 3). Although, the average growth rates of females on control grids and females on anthelmintic treated grids were not significantly different (P=0.14, t=1.73, df=5) (Fig. 4C, Table 3), the average growth rate of males on anthelmintic treated grids was 63.5% higher than the average growth rate of males on control grids, which was statistically significant (one-tailed

P=0.044, t=-2.03, df=6) (Fig. 4C, Table 3). This suggests that the administration of the

anthelmintic increased the growth rate in male residents.

Table 2. Average masses of resident *Peromyscus leucopus* given for control and anthelmintic treated grids, and males and females on control and anthelmintic treated grid. The standard errors were calculated by the grid means (n=6).

Group	Average mass (grams)	Standard Error
Residents on control grids	19.8	0.34
Residents on anthelmintic treated grids	20.6	0.43
Female residents on control grids	19.5	0.52
Female residents on anthelmintic treated grids	20.2	0.53
Male residents on control grids	20.0	0.24
Male residents on anthelmintic treated grids	21.0	0.39

Table 3. Average growth rates of resident *Peromyscus leucopus* given for control and anthelmintic treated grids, individuals not determined pregnant at any portion of the study on control and treated grids, and males and females on control and anthelmintic treated grid. The standard errors were calculated by the grid means (n=6).

| Group	Average growth rate	Standard Error
Residents on control grids	0.0453	0.00094
Residents on anthelmintic treated grids	0.0517	0.0075
Non-pregnant residents on control grids	0.0454	0.0049
Non-pregnant residents on anthelmintic treated grids	0.0560	0.010
Female residents on control grids	0.0611	0.0011
Female residents on anthelmintic treated grids	0.0507	0.0059
Male residents on control grids	0.0312	0.0026
Male residents on anthelmintic treated grids	0.0510	0.0094
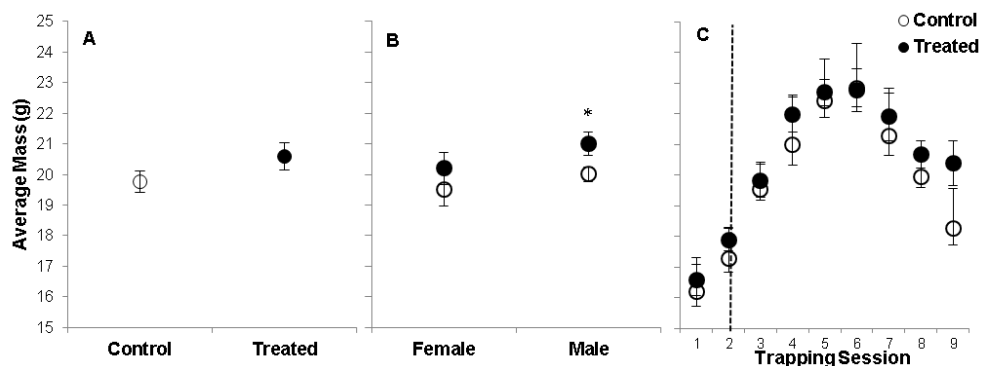
Fig. 3. Average masses of *Peromyscus leucopus* measured in grams, compared between (A) resident mice (those captured and treated more than once) on control grids (unfilled circle, n=6) and anthelmintic treated grids (filled circle, n=6); (B) resident females on control grids (unfilled circle, n=6), resident females on anthelmintic treated grids (filled circle, n=6), resident males on control grids (unfilled circle, n=6), resident males on anthelmintic treated grids (filled circle, n=6); (C) resident mice on control grids (unfilled circles, n=6) and anthelmintic treated grids (filled circles, n=6) from trapping sessions 1 (May 24, 2011) through 9 (November 23, 2011). Trapping sessions 1 and 2 represent all captures, since treatment was not administered until the second trapping session. Trapping sessions 3 through 9 only represent resident mice. The dotted line represents the start of treatment. A star indicates statistical significance, based on a P-value of >0.05. Error bars represent the ± standard error of the grid means (n=6).
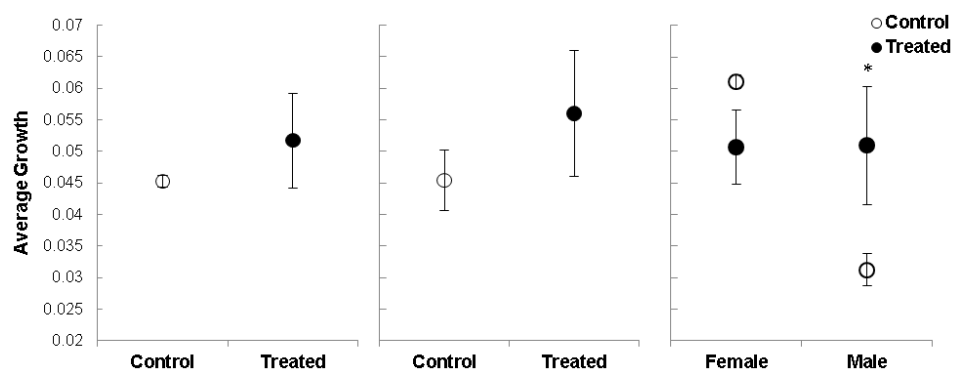
Fig. 4. Average growth rates of resident (those captured and treated more than once) *Peromyscus leucopus,* measured as the slope of the regression line drawn through the plot of mass (g) versus days known alive, compared between (A) control grids (unfilled circle, n=6) and anthelmintic treated grids (filled circle, n=6); (B) individuals that were not determined pregnant at any point during the experiment on control grids (unfilled circle, n=6) and anthelmintic treated grids (filled circle, n=6); (C) females on control grids (unfilled circle, n=6), females on anthelmintic treated grids (filled circle, n=6), males on control grids (unfilled circle, n=6), males on anthelmintic treated grids (filled circle, n=6). A star indicates statistical significance, based on a P-value of >0.05. Error bars represent the ± standard error of the grid means (n=6).

Effect of treatment on reproduction

The administration of the anthelmintic significantly increased the average proportion of

residents in breeding condition (i.e. presence of at least one of the following conditions:

perforated vagina, pregnant, lactating, descended testes) overall. The average proportion of

residents in breeding condition was 26.7% higher on anthelmintic treated grids compared to

control grids (Fig. 5A, Table 4). Although, this result was statistically significant (one-tailed

P=0.043, t=-1.9, df=9), the average proportion of anthelmintic treated residents in breeding

condition was not statistically significant during each trapping session (average P>0.05). The

proportion of females in breeding condition was higher on anthelmintic treated grids compared to

control grids, and this difference tended toward significant (P>0.10), although it was not

statistically significant at a 5% level (one-tailed P=0.072, t=-1.6, df=9) (Fig. 5B, Table 4), which

was also true for resident males (one-tailed P=0.078, t=-1.53, df=10) (Fig. 5B, Table 4).

The anthelmintic significantly increased the average proportion of female residents

pregnant. The average proportion of anthelmintic treated females pregnant was 28.4%

(SE=0.035), which was substantially higher than control females whose average proportion of

females pregnant was 14.8% (SE=0.061) (Fig. 6A). Although, this result was statistically

significant (one-tailed P=0.043, t=-2.0, df=8), the average proportion of anthelmintic treated

females pregnant was not statistically significant during each trapping session (average P>0.05)

(Fig. 7B).

The average proportion of resident males with descended testes on anthelmintic treated

grids was 47.8% (SE=0.040) which was substantially higher compared to the value for resident

males on control grids, which was 39.1% (SE=0.040). This difference tended toward significant

(P>0.10), although the value was not statistically significant at a 5% level (one-tailed P=0.078,

t=-1.15, df=10) (Fig. 5B). The proportions of control and anthelmintic treated males with

descended testes during each trapping session were not statistically different (average P>0.05)

(Fig. 7C).

Table 4. Average proportions of individuals in breeding condition of resident *Peromyscus leucopus* given for control and anthelmintic treated grids and males and females on control and anthelmintic treated grids. The standard errors were calculated by the grid means (n=6).

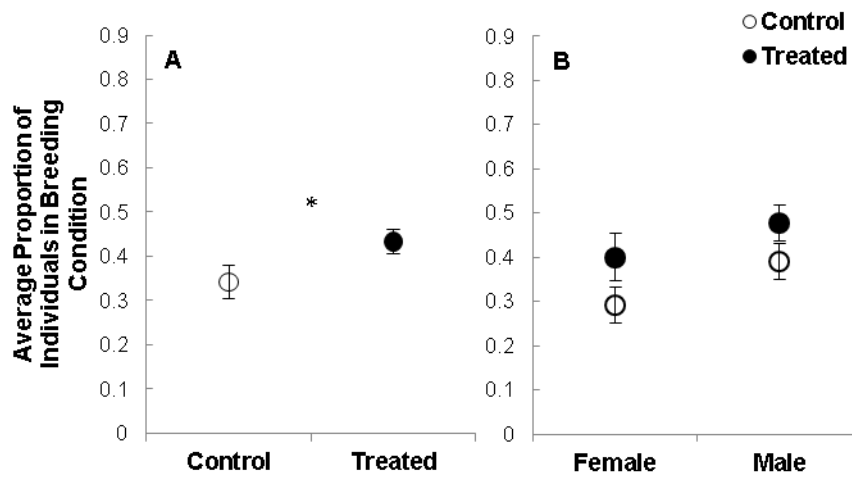| Group	Average Proportion of Individuals in Breeding Condition	Standard Error
Residents on control grids	0.342	0.038
Residents on anthelmintic treated grids	0.433	0.029
Female residents on control grids	0.293	0.040
Female residents on anthelmintic treated grids	0.400	0.054
Male residents on control grids	0.391	0.040
Male residents on anthelmintic treated grids	0.478	0.040

Fig. 5. Average proportions of individual *Peromyscus leucopus* in breeding condition (i.e. presence of at least one of the following conditions: perforated vagina, pregnant, lactating, descended testes) compared between (A) resident mice (those captured and treated more than once) on control grids (unfilled circle, n=6) and treated grids (filled circle, n=6); (B) resident females on control grids (unfilled circle, n=6), resident females on treated grids (filled circle, n=6), resident males on control grids (unfilled circle, n=6), resident males on treated grids (filled circle, n=6). A star indicates statistical significance, based on a P-value of >0.05. Error bars represent the ± standard error of the grid means (n=6).

Fig. 6. (A) Average proportions of female *Peromyscus leucopus* pregnant, compared between (A) resident (those treated more than once) females on control grids (unfilled circle, n=6) and treated grids (filled circle, n=6); (B) Average proportions of male *P. leucopus* with descended testes, compared between resident males on control grids (unfilled circle, n=6) and treated grids (filled circle, n=6). A star indicates statistical significance, based on a P-value of >0.05. Error bars represent the ± standard error of the grid means (n=6).
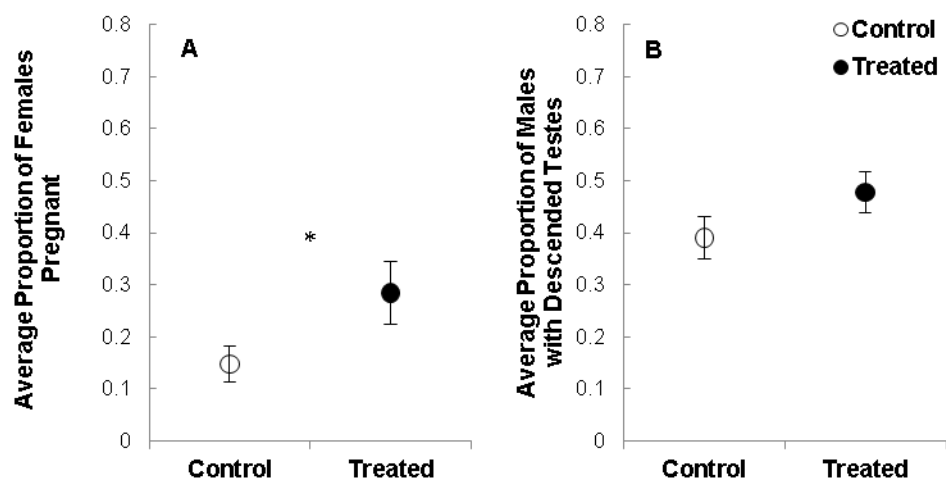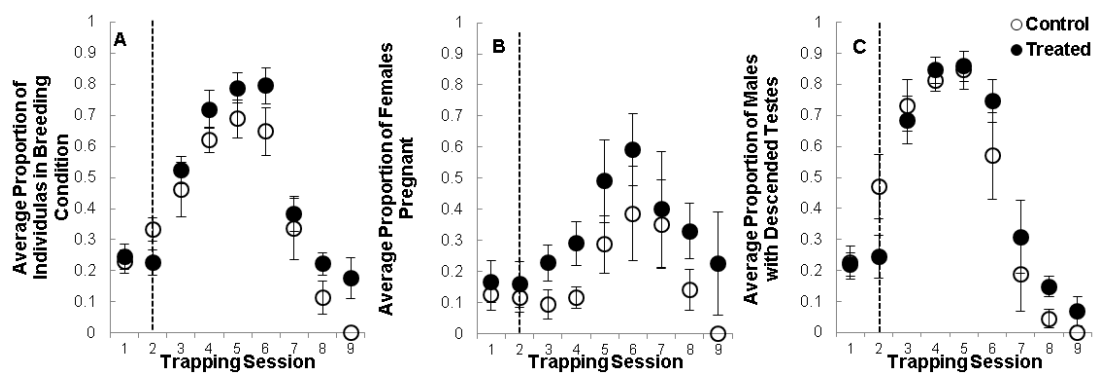
Fig. 7. (A) Average proportions of individual *Peromyscus leucopus* in breeding condition (i.e. presence of at least one of the following conditions: perforated vagina, pregnant, lactating, descended testes) compared between control grids (unfilled circles, n=6) and treated grids (filled circles, n=6) from trapping sessions 1 (May 24, 2011) through 9 (November 23, 2011). (B) Average proportions of females *P. leucopus* pregnant compared between control grids (unfilled circles, n=6) and treated grids (filled circles, n=6) from trapping sessions 1 through 9. (C) Average proportions of male P. leucopus with descended testes compared between control grids (unfilled circles, n=6) and treated grids (filled circles, n=6) from trapping sessions 1 through 9. For each graph, trapping sessions 1 and 2 represent all captures, since treatment was not administered until the second trapping session. Trapping sessions 3 through 9 only represent resident mice (those captured and treated more than once). The dotted line represents the start of treatment. Error bars represent the ± standard error of the grid means (n=6).

Effect of treatment on body length and body condition

Administration of the anthelmintic did not significantly increase the average body length (measured from the tip of the rostrum to the base of the tail) in resident *Peromyscus leucopus* overall (one-tailed P=0.20, t=-0.89, df=10) (Fig. 8A, Table 5). The average body lengths in resident females also did not differ significantly between anthelmintic treated females and control females (P=0.70, t=-0.40, df=10) (Fig. 8B, Table 5). However, the anthelmintic did significantly increase the average body length of male resident *P. leucopus*. Anthelmintic treated resident males were 1.26% longer, compared to control resident males, which was statistically significant (one-tailed P=0.047, t=-1.8, df=10) (Fig. 8B, Table 5).

The average body condition in *P. leucopus*, measured as the cube root of the mass divided by body length was not influenced by the administration of the anthelmintic. The average body conditions between anthelmintic treated residents and control residents were not significantly different (one-tailed P=0.23, t=-0.78, df=9) (Fig. 8C, Table 6). Similarly, the average body conditions between anthelmintic treated female residents and control female residents were not significantly different (one-tailed P= 0.20, t=-0.88, df=9) (Fig.8D, Table 6), as was also true for resident males (P=0.52, t=-0.68, df=8) (Fig. 8D, Table 6).

Table 5. Average body lengths of resident *Peromyscus leucopus* given for control and anthelmintic treated grids and males and females on control and anthelmintic treated grids. The standard errors were calculated by the grid means (n=6).

Group	Average body length (mm)	Standard Error
Residents on control grids	87.0	0.67
Residents on anthelmintic treated grids	87.8	0.61
Female residents on control grids	86.5	0.97
Female residents on anthelmintic treated grids	87.0	0.82
Male residents on control grids	87.5	0.39
Male residents on anthelmintic treated grids	88.6	0.41

Table 6. Average body conditions of resident *Peromyscus leucopus* given for control and anthelmintic treated grids and males and females on control and anthelmintic treated grids. The standard errors were calculated by the grid means (n=6).

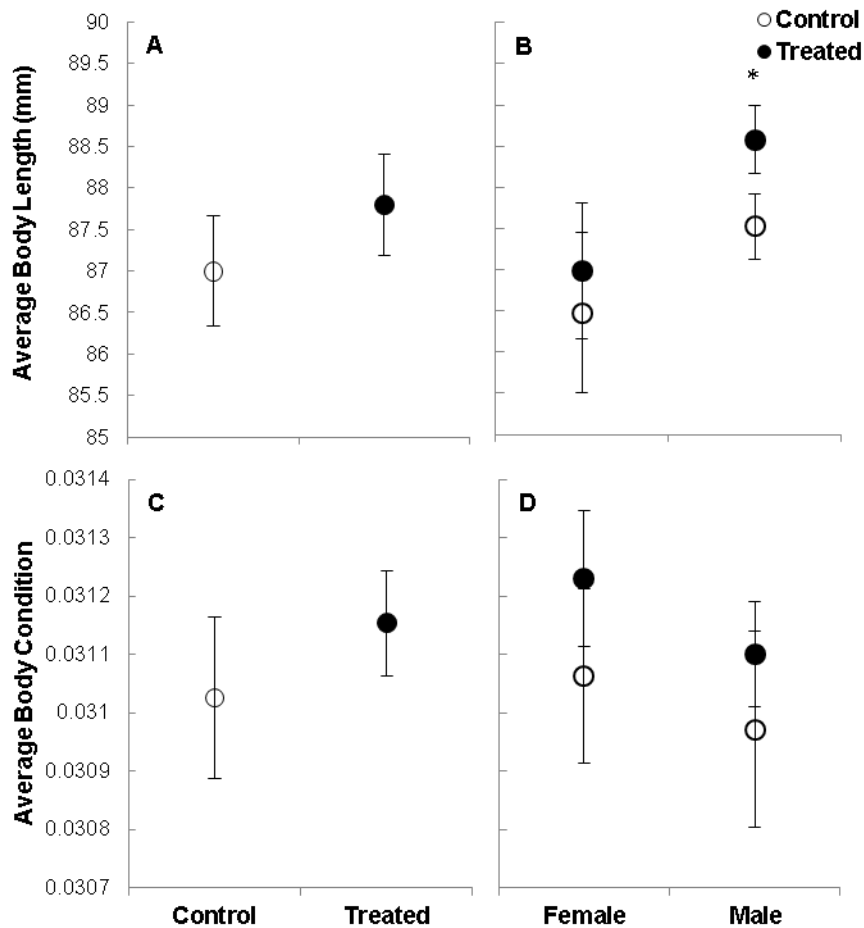| Group	Average body condition	Standard Error
Residents on control grids	0.0310	0.00014
Residents on anthelmintic treated grids	0.0312	0.000090
Female residents on control grids	0.0311	0.00015
Female residents on anthelmintic treated grids	0.0312	0.00012
Male residents on control grids	0.0310	0.00017
Male residents on anthelmintic treated grids	0.0311	0.000090

Fig. 8. Average body lengths (from the tip of the rostrum to the base of the tail) of resident (those treated more than once) *Peromyscus leucopus* measured in millimeters, compared between (A) control grids (unfilled circle, n=6) and anthelmintic treated grids (filled circle, n=6); (B) females on control grids (unfilled circle, n=6), females on anthelmintic treated grids (filled circle, n=6), males on control grids (unfilled circle, n=6), males on anthelmintic treated grids (filled circle, n=6). Average body conditions of resident *P.leucopus* measured as the cube root of the mass (g) divided by body length (mm) with outliers taken out of the equation, compared between (C) control grids (unfilled circle, n=6) and anthelmintic treated grids (filled circle, n=6); (D) females on control grids (unfilled circle, n=6), females on anthelmintic treated grids (filled circle, n=6), males on control grids (unfilled circle, n=6), males on anthelmintic treated grids (filled circle, n=6). A star indicates statistical significance, based on a P-value of >0.05. Error bars represent the ± standard error of the grid means (n=6).

Effect of treatment on ectoparasitism

The average proportions of *Peromyscus leucopus* residents parasitized by ectoparasites (i.e. botflies, fleas, mites, ticks) were not significantly different between control and anthelmintic treated grids, indicating that deworming did not significantly influence ectoparasitism. The average proportion of residents on control grids parasitized by at least one ectoparasite was 46.9% (SE=0.052), and the average proportion of residents on anthelmintic treated grids parasitized by at least one ectoparasite was 43.6% (SE=0.045), which were not significantly different (one-tailed P=0.32, t=0.48, df=8) (Fig. 9A). Additionally, the average proportions of residents parasitized by ectoparasites on control and anthelmintic treated grids did not differ significantly before treatment (trapping sessions 1 and 2) or after treatment (trapping sessions 3 through 9) (average P>0.05), indicating that deworming did not affect ectoparasitism on residents overall (Fig. 9C).

The average proportions of *P. leucopus* residents parasitized by botflies were not significantly different between control and anthelmintic treated grids, indicating that deworming did not significantly influence the presence of botflies in *P. leucopus*. The average proportion of residents on control grids parasitized by at least one botfly was 7.6% (SE=0.039), and the average proportion of residents on treated grids parasitized by at least one botfly was 6.3% (SE=0.016), which were not significantly different (P=0.74, t=0.34, df=7) (Fig. 9B). In addition, data from trapping sessions 1 through 9 indicated that the average proportions of residents parasitized by at least one botfly were not significantly different on control and treated grids (average P>0.05), both before and after the start of treatment (Fig. 9D).
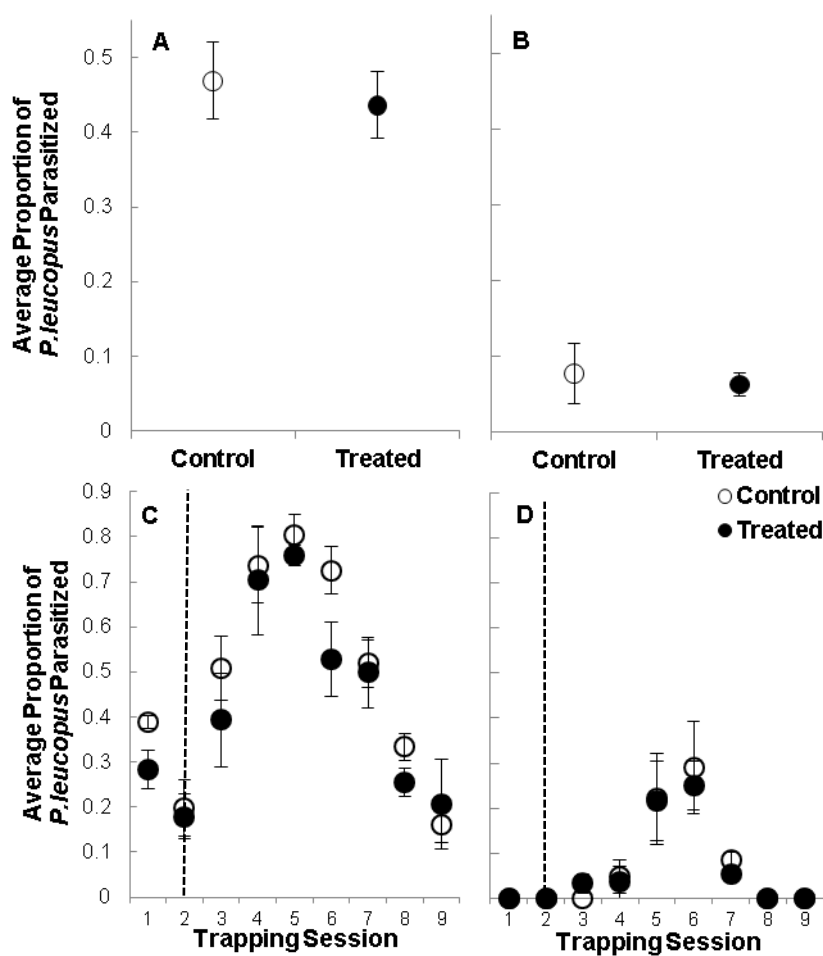
Fig. 9. Average proportions of *Peromyscus leucopus* parasitized by ectoparasites (botflies, fleas, mites, ticks), compared between (A) resident mice (those treated more than once) on control grids (unfilled circle, n=6) and anthelmintic treated grids (filled circle, n=6); (B) control grids (unfilled circles, n=6) and anthelmintic treated grids (filled circles, n=6) from trapping sessions 1 (May 24, 2011) through 9 (November 23, 2011). Trapping sessions 1 and 2 represent all captures, since treatment was not administered until the second trapping session. Trapping sessions 3 through 9 only represent resident mice. The dotted line represents the start of treatment. The average proportions of *P. leucopus* parasitized by botflies, compared between (C) resident mice on control grids (unfilled circle, n=6) and anthelmintic treated grids (filled circle, n=6); (D) control grids (unfilled circles, n=6) and anthelmintic treated grids (filled circles, n=6) from trapping sessions 1 through 9. Trapping sessions 1 and 2 represent all captures, since treatment was not administered until the second trapping session. Trapping sessions 3 through 9 only represent resident mice. The change is represented by a dotted line. Error bars represent the ± standard error of the grid means (n=6).

Chapter 4

Discussion

Administration of the anthelmintic led to a significant increase in the average proportion of *Peromyscus leucopus* in breeding condition and a significant increase in the average proportion of female *P. leucopus* pregnant. This supports our hypothesis that helminthes can reduce reproductivity in the *P. leucopus* populations, which is a destabilizing host-parasite interaction (Anderson and May, 1978; May and Anderson, 1978). This finding is substantial because it suggests that helminthes have a destabilizing effect on *P. leucopus* populations and may be able to regulate the growth of white-footed mouse populations (Anderson and May, 1978; May and Anderson, 1978). Therefore, this study supports the findings of Hudson et. al. (1992) who discovered that the removal of helminthes increased fecundity in the red grouse (*Lagopus lagopus scoticus*) in northern England (Dobson and Hudson, 1992; Hudson et al., 1992). Additionally, our study supports the findings of Vandegrift et. al. (2008) who discovered that the removal of helminthes increased fecundity in *P. leucopus* and led to the reversal of the mid-summer breeding hiatus within this species (Vandegrift et al., 2008).

The anthelmintic also led to an increase in the average body length and average growth rate of male *P. leucopus*. This is consistent with our hypothesis and the findings of Vandegrift et. al. (2008) (Vandegrift et al., 2008), that helminthes have a negative effect on the physiological health and vital rates of males in *P. leucopus* populations. The anthelmintic also led to a statistically significant increase in the average mass of male *P. leucopus*, although the difference was so low that it was likely biologically insignificant. The average mass, body length and growth rate were also higher for residents overall on anthelmintic treated grids compared to control grids, however the differences were not statistically significant. Additionally, the average mass and body length were higher for female residents on anthelmintic treated grids compared to

control grids, although these results were not statistically significant. The average growth rate was actually higher for female residents on control grids compared to anthelmintic treated grids, although the difference was not significantly different. In order to determine whether helminthes truly do affect the average mass, average body length and average growth rate of *P. leucopus* overall and female *P. leucopus*, another study should be conducted with a larger sample size and the study should be performed over a longer period of time.

Based on the Jolly-Seber population model, administration of the anthelmintic did not influence the average population estimates of *P. leucopus*. This finding does not support our hypothesis, since helminthes can reduce fecundity and increase morbidity of host populations (Dobson and Hudson, 1992; Hudson et al., 1992; Vandegrift and Hudson, 2009; Vandegrift et al., 2008), which we expect would have an indirect effect on population estimates of the host as well. However, these findings were consistent with those observed in the study performed by Vandegrift et. al. (2008) (Vandegrift et al., 2008), who also found that anthelmintic treated *P. leucopus* did not exhibit significantly different population estimates compared to control *P. leucopus*.

Furthermore, the anthelmintic did not significantly affect survival of *P. leucopus*, measured as the natural log transformed days known alive. Although, the average natural log transformed days known alive was higher for anthelmintic treated residents compared to control grids, these results were not significantly different. These results do not support our hypothesis, since helminthes can reduce fecundity and increase morbidity in host populations (Dobson and Hudson, 1992; Hudson et al., 1992; Vandegrift and Hudson, 2009; Vandegrift et al., 2008), which we expect would have an indirect effect on survival. These results were also inconsistent with those found by Vandegrift et. al. (2008) (Vandegrift et al., 2008), who discovered that anthelmintic treated *P. leucopus* residents and anthelmintic treated *P. leucopus* resident males exhibited higher survival rates. Further studies with a larger sample size conducted over a longer

period of time should be performed to determine if helminthes do indeed affect survival in *P. leucopus*.

Although, the anthelmintic significantly increased the average proportion of *P. leucopus* in breeding condition, it did not significantly increase the average proportion of females and males in breeding condition. Vandegrift et. al. (2008) also found that anthelmintic treatment did not significantly increase the average proportion of male *P. leucopus* in breeding condition, but they did find that anthelmintic treatment did significantly increase the average proportion of female *P. leucopus* in breeding condition (Vandegrift et al., 2008). The lack in statistical significance of the results may be due to the deficiency in an adequate sample size.

The average body condition was not significantly higher in anthelmintic treated *P. leucopus* residents overall and anthelmintic treated resident female and male *P. leucopus*. This is inconsistent with our hypothesis, since helminthes have been shown to decrease physiological condition and increase morbidity in the host species (Dobson and Hudson, 1992; Hudson et al., 1992; Hudson, 2002). Vandegrift et. al. (2008) demonstrated that the removal of helminthes increased the average body condition of male *P. leucopus*, but their results did not demonstrate that anthelmintic treatment influenced average body condition in *P. leucopus* overall or female *P. leucopus* (Vandegrift et al., 2008).

Lastly, the anthelmintic did not significantly influence the presence of ectoparasites in *P. leucopus*. This supports our hypothesis, because the anthelmintic (Levamisole hydrochloride™) is designed for the treatment of helminthes, not ectoparasites. Although, we expected anthelmintic treated mice to exhibit better overall physiological conditions, environmental factors are likely to play a larger role in the ectoparasitism of individual mice compared to internal factors (e.g. mass, length, fecundity, etc.) that may have varied between anthelmintic treated and control *P. leucopus* (Durden and Wilson, 1991; Wharton and Cross, 1956).

Possibly the greatest weakness in this study was an insufficient sample size. Most of the results corresponded with our hypotheses, but they were not statistically significant to actually support our hypotheses. In order to determine the adequate sample size, a power analysis should be conducted. Performing another study with an adequate sample size, as determined by the power analysis would provide a stronger indication of the effect of parasitism on *P. leucopus* population dynamics.

Although, there have been few empirical studies to determine the effect of endoparasitism on population dynamics in animal species, there is supporting evidence that helminthes may cause instability in some host populations (Anderson and May, 1978; Dobson and Hudson, 1992; Hudson et al., 1992; May and Anderson, 1978; Vandegrift et al., 2008). In the future, we suggest that similar studies be performed on other species of animals in order to have a greater understanding of the effect of helminthes on population dynamics. Additionally, we suggest that further studies be performed on *P. leucopus* to further understand the effect of parasitism on population dynamics in this species, and also to understand why anthelmintic treatment significantly increased the average mass, length and growth rate in *P. leucopus* males, but not in females.

Overall, our study suggests that helminthes have a negative effect on breeding condition and pregnancy in *P. leucopus*, and they also decrease the average mass, length and growth rate of *P. leucopus* males. These results are consistent with those of other studies (Anderson and May, 1978; Dobson and Hudson, 1992; Hudson et al., 1992; May and Anderson, 1978; Vandegrift and Hudson, 2009; Vandegrift et al., 2008) and suggest that helminthes may have the ability to drive population cycles in the white-footed mouse.

Population cycles have been recorded in several animal species and can have major impacts on society, leading to famine and disease. In particular, rodents are major carriers of zoonotic diseases and are often responsible for disease outbreaks and agricultural losses in human

populations (Ostfeld and Holt, 2004; Singleton et al., 2001; Williamson and Oyston, 2012). By understanding the effect of parasitism on population dynamics in the white-footed mouse, we may learn how to control rodent populations through parasitic manipulation, which could significantly improve human health and well-being. These techniques may be applicable to other species as well.

REFERENCES

Anderson, R.M., May, R.M., 1978. Regulation and stability of host-parasite population interactions. 1. Regulatory processes. Journal of Animal Ecology 47, 219-247.

Arditi, R., Berryman, A.A., 1991. The biological-control paradox. Trends in Ecology & Evolution 6, 32-32.

Arditi, R., Ginzburg, L.R., 1989. Coupling in predator prey dynamics- ratio-dependence. Journal of Theoretical Biology 139.

Beck, J., Osgood, S., Smith, M., 1959. The Oregon meadow mouse interruption of 1957-1959. Federal Cooperation Extension Service, Oregon State College, Corvallis.

Brown, L.N., 1964. Reproduction of the brush mouse and white-footed mouse in the central United States. Amer Medland Natur 72.

Burt, W., 1940. Territorial behavior and populations of some small mammals in southern Michigan. Miscellaneous Publication of the Museum of Zoology 45, 1-51.

Cornish, L., Bradshaw, W., 1978. Patterns in twelve reproductive parameters for the white-footed mouse (*Peromyscus leucopus*). Journal of Mammology 59, 731-739.

Debach, P., 1974. Biological control by natural enemies. Biological Control by Natural Enemies.

Dobson, A.P., Hudson, P.J., 1992. Regulation and stability of a free-living host-parasite system-*Trichostrongylus-tenuis* in red grouse .2. Population-models. Journal of Animal Ecology 61.

Durden, L.A., Wilson, N., 1991. Parasitic and phoretic arthropods of sylvatic and commensal white-footed mice (*Peromyscus leucopus*) in central Tennessee, with notes on Lyme disease. The Journal of Parasitology 77, 219-223.

Elton, C., Nicholson, M., 1942. The ten-year cycle in numbers of the lynx in Canada. Journal of Animal Ecology 11.

Elton, C.S., 1924. Periodic fluctuations in the numbers of animals - Their causes and effects. British Journal of Experimental Biology 2.

Hagen, K., Franz, J., 1973. A history of biological control. History of Entomology, 433-476.

Hairston, N.G., Smith, F.E., Slobodkin, L.B., 1960. Community structure, population control, and competition. American Naturalist 94.

Hudson, P.J., Newborn, D., Dobson, A.P., 1992. Regulation and stability of a free-living host-parasite system- *Trichostrongylus-tenius* in red grouse .1. Monitoring and parasite reduction experiments. Journal of Animal Ecology 61.

Hudson, P.J.e.a., 2002. The Ecology of Wildlife Diseases. Oxford University Press.

Krebs, C.J., Gaines, M.S., Keller, B.L., Myers, J.H., Tamarin, R.H., 1973. Population cycles in small rodents. Science 179.

Lotka, A., 1925. Elements of physical biology, Baltimore.

Luck, R.F., 1990. Evaluation of natural enemies for biological-control - A behavioral-approach. Trends in Ecology & Evolution 5.

May, R.M., Anderson, R.M., 1978. Regulation and stability of host-parasite population interactions .2. Destabilizing processes. Journal of Animal Ecology 47, 249-267.

McCauley, E., Murdoch, W.W., 1987. Cyclic and stable-populations - Plankton as paradigm. American Naturalist 129.

Ostfeld, R.S., Holt, R.D., 2004. Are predators good for your health? Evaluating evidence for top-down regulation of zoonotic disease reservoirs. Frontiers in Ecology and the Environment 2.

Peterson, R.O., Page, R.E., Dodge, K.M., 1984. Wolves, moose, and the allometry of population-cycles. Science 224.

Pollock, K.H., Nichols, J.D., Brownie, C., Hines, J.E., 1990. Statistical-inference for capture-recapture experiments. Wildlife Monographs, 1-97.

Rintamaa, D.L., Mazur, P.A., Vessey, S.H., 1976. Reproduction during 2 annual cycles in a population of *Peromyscus-leucopus-noveboracensis*. Journal of Mammalogy 57.

Rosenzwe.Ml, 1971. Paradox of enrichment- destabilizing of exploitation ecosystems in ecological time. Science 171.

Singleton, G., Krebs, C.J., Davis, S., Chambers, L., Brown, P., 2001. Reproductive changes in fluctuating house mouse populations in southeastern Australia. Proceedings of the Royal Society of London Series B-Biological Sciences 268.

Terman, C.R., 1998. Early-summer reproductive curtailment in wild white-footed mice and reproductive recovery in the laboratory. Journal of Mammalogy 79.

Turnbull, A.L., Chant, D.A., 1961. Practice and theory of biological control of insects in Canada. Canadian Journal of Zoology 39.

Vanbuskirk, J., Ostfeld, R.S., 1995. Controlling Lyme-disease by modifying the density and species composition of tick hosts. Ecological Applications 5.

Vandegrift, K.J., Hudson, P.J., 2009. Could parasites destabilize mouse populations? The potential role of *Pterygodermatites peromysci* in the population dynamics of free-living mice, *Peromyscus leucopus*. International Journal for Parasitology 39, 1253-1262.

Vandegrift, K.J., Raffel, T.R., Hudson, P.J., 2008. Parasites prevent summer breeding in white-footed mice, *Peromyscus leucopus*. Ecology 89, 2251-2258.

Wharton, G.W., Cross, H.F., 1956. Studies on the feeding habits of 3 species of Laelaptid mites. Journal of Parasitology 42, 45-50.

Williamson, E., Oyston, P., 2012. The natural history of incidence of *Yersinia pestis* and prospects for vaccination. Journal of Medical Microbiology 61, 911-918.

Wolff, J., 1986. The effects of food on mid-summer breeding activity in *Peromyscus leucopus* in southwestern Virginia. Canadian Journal of Zoology 64, 855-858.

Wolff, J.O., 1985. Comparative population ecology of *Peromyscus-leucopus* and *Peromyscus-maniculatus*. Canadian Journal of Zoology-Revue Canadienne De Zoologie 63.

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