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Ecology of Botfly Parasitism in White-Footed Mice (Peromyscus leucopus)

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Ecology of botfly parasitism in white-footed mice (*Peromyscus leucopus*)

A Senior Honors Thesis

Presented in Partial Fulfillment of the Requirements
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ABSTRACT.—White-footed mice (*Peromyscus leucopus*) are an abundant species in eastern deciduous forests. The objective of this study was to examine the ecology of botfly parasitism in a white footed mouse population in the Brockport Woods, Brockport, NY. I analyzed data collected by live trapping in May and September from 1993 to 2009. Males and females exhibited similar levels of botfly infestation. When a greater percentage of mice was infected with botflies, there was a significant increase in average body mass. I also found that as fall trap success increased, the proportion of mice with botflies decreased, but the number of infected mice remained relatively constant over time. This may be due to the fluctuation of *P. leucopus* populations, which is characterized by rapid increases and sudden collapses, so there may not be enough botflies to take advantage of all the available hosts at high densities. Botfly infection did not have an impact on overwinter survival. Lastly, spring abundance was most affected by trap success in the previous fall and two weather variables; spring abundance increased when fall trap success and mean January temperature increased and when total January snowfall decreased. These three variables, however, did not explain all of the observed variability in abundance. Population fluctuations in *P. leucopus* are complex, so future studies should look at other factors that could be responsible for driving abundance of this species.

INTRODUCTION

White-footed mice (*Peromyscus leucopus*) are common in eastern deciduous forests (Cramer and Cameron 2007). Previous studies have shown that *P. leucopus* populations exhibit unstable dynamics (Terman 1968, Vandegrift and Hudson 2009). They increase when food is abundant, leading to greater survival during the winter and greater subsequent breeding (Jones et al. 1998, Falls et al. 2007). The eventual population decline is thought to be due to resource

overexploitation. However, parasitism may also contribute to destabilization of populations (Vandegrift and Hudson 2009), because parasites can decrease body condition and breeding success (Vandegrift et al. 2008). *P. leucopus* are common hosts to the botfly (*Cuterebra fontinella*), an obligate parasite that completes its life cycle in mouse hosts (Jaffe et al. 2005, Cramer and Cameron 2007). Botflies lay their eggs in late spring and early summer (Cramer and Cameron 2007) and mice become infected when they come in contact with the eggs. The larvae develop in the host for about one month (Cogley 1991).

It is still unclear how parasites influence population dynamics and whether they have a significant effect on host abundance and reproduction (Jaffe et al. 2005, Cramer and Cameron 2007). According to Ewald (1994), a successful parasite needs to exhibit a level of virulence in its host that does not compromise its own survival and transmission. Therefore, the parasite would be expected to have little effect on its host. However, previous research has produced contradictory results in regards to the effect of botflies on *P. leucopus* (Munger and Karasov 1994, Jaffe et al. 2005, Cramer and Cameron 2007, Vandegrift and Hudson 2009).

The objective of this study was to examine botfly parasitism in a *P. leucopus* population to determine whether, and to what extent, botflies affect population abundance. I analyzed data collected by live trapping in the Brockport Woods in May and September from 1993 to 2009. I investigated the relationship between rate of botfly infection and overwinter survival, and also examined the relationship between population density and botfly infection, hypothesizing that as *P. leucopus* abundance increases, the proportion of individuals infected will also increase, due to increased crowding and thus a higher probability of contact with the parasite. I then examined the impact of botfly infection on body mass. Last, I looked at the effect of fall abundance, botfly infection, and weather conditions on white-footed mouse abundance in the spring, to develop a

model with spring abundance as the response variable. This project is especially important, because of limited availability of long-term studies on *P. leucopus* populations. The analysis of a 16-year data set hopefully will allow me to answer important ecological questions regarding botfly parasitism in this species. Even though other studies have found that botfly infection alone does not affect survivorship (Jaffe et al. 2005, Cramer and Cameron 2007), there have been no previous studies, to my knowledge, examining whether and how the interaction between botflies and weather or other conditions affect *P. leucopus* abundance.

MATERIALS AND METHODS

The trapping grid was located in the Brockport Woods, a sugar maple (*Acer saccharum*) dominated deciduous forest with down logs and a sparse understory, on the SUNY Brockport campus, Brockport, Monroe Country, NY. Mammal residents of these woods include white-footed mice, white-tailed deer (*Odocoileus virginianus*), and eastern chipmunks (*Tamias striatus*). The size of our 10 x 6 grid was approximately 1 ha. The study employed Sherman live traps placed 15 m apart. Live trapping was done during 4-night trapping sessions every May and September from 1993 to 2009. Rolled oats were placed in traps in the evening and the traps were checked in the early morning. A wad of polyester batting was also placed in traps to provide insulation and prevent mortality at low temperatures. White-footed mice captured were ear tagged and released, after their mass, sex, age, reproductive condition, and botfly infection were recorded. Age classification was based on mass; mice that weighed ≤ 15 g were considered juveniles, mice that weighed between 15 and 20 g were considered subadults, and mice that weighed ≥ 20 g were considered adults. When other small mammals were captured, they were released after recording the species.

I performed a χ^2 goodness-of-fit test to determine whether there was a difference in the proportion of males and females in the population. I arcsin transformed infection rates of males and females and used a paired t-test to compare them. I then performed regression analysis to see how average mass of mice changed with percentage of mice infected with botflies. I also used linear regression to investigate the relationship between population density and botfly infection rate. Last, I performed best subsets regression to identify the model that best explained variability in spring abundance. The response variable was spring abundance and the covariates were fall trap success, botfly infection rate, and several weather variables: January snowfall, April snowfall, total snowfall from December to March, mean January temperature, mean February temperature, mean April temperature, mean December to March temperature, January snowfall/January temperature, heating degree days from December to March, snow depth on March 1, snow depth on April 1, and date of last snow in April. In all of these analyses, trap success was used as a measure of *P. leucopus* abundance. Trap success was calculated by dividing the total number of white-footed mice captured by the number of traps available for use by white-footed mice. Minitab 15 was used for all statistical analyses; *p*-values < 0.05 were considered statistically significant.

RESULTS

A χ^2 goodness-of-fit test showed no statistically significant difference in the number of males and females captured (χ^2 = 2.44, *df* = 1, *P* = 0.119), which was 269 and 234, respectively. There was also no statistically significant difference in botfly infection between males and females throughout the study period (*t*=-0.55, *df*=13, *P*=0.588). Regression analysis showed that as the

percentage of mice infected increased, the average mass of the mice increased (F=11.80, $R^2(adj)$=43.6%, P=0.004; Figure 1).

I found that as fall trap success, and thus fall abundance, increased, the percentage of mice infected with botflies decreased (F=7.00, $R^2(adj)$=28.6%, P=0.019; Figure 2). However, the number of mice infected did not change much as fall trap success increased (F=0.07, $R^2(adj)$=0.00%, P=0.789; Figures 3 and 4). The range in number of infected mice throughout the study period was 1 to 17, whereas the average number of infected mice captured each fall was 5.8. A change in the percentage of mice infected in the fall did not have an effect on spring trap success the following year (F=0.00, $R^2(adj)$=0.00%, P=0.978; Figure 5).

To evaluate the importance of botfly infection rate in driving *P. leucopus* abundance the following spring, I first used univariate regression. The results showed that botfly infection alone does not significantly affect spring abundance (F=0.09, $R^2(adj)$=0.00%, P=0.773; Figure 6). Multivariate regression was then performed, using botfly infection rate as one of the predictor variables. None of the simple models that were generated explained the variation in spring abundance to a satisfactory degree. One of the models included eight variables and had an R^2 value of 86.6%, but it was considered too complex due to the large number of variables included in the model. Multivariate regression was performed again, with fewer variables as predictors. Based on the results of this analysis, the model determined to be the best included three variables: fall trap success in the previous year, total January snowfall, and mean January temperature ($R^2(adj)$=31.4%, Mallows Cp=1.4). Stepwise regression showed that spring trap success increased with decreasing fall trap success (t=-1.65, P=0.129), increasing January temperature (t=2.19, P=0.053), and increasing January snow (t=1.34, P=0.211).

Males and females exhibited similar levels of botfly infestation. When mice are infected with botflies, they may experience a significant increase in body mass; even though this analysis showed that the increase was statistically significant, it is unclear whether it is also biologically significant. It should also be noted that some of the increase may be due to the mass of the botfly itself. Previous studies have reported that larva can grow to 5% of the host's body mass (Munger and Karasov 1994, Jaffe et al. 2005). Cramer and Cameron (2007) also found that botfly infection increases male body size and thus improves their mating success, since females show a preference for larger males.

As fall trap success increased, the proportion of mice with botflies decreased, but the number of infected mice remained relatively constant through time. This may be due to the fluctuation of *P. leucopus* populations, which is characterized by rapid increases and sudden collapses (Vandegrift and Hudson 2009). Therefore, there may not be enough botflies to take advantage of all available hosts at higher densities. Another possibility is that good conditions for mice are bad conditions for botflies, leading to an increase in the former and a decrease in the latter. Since changes in the percentage of mice infected in the fall did not affect spring trap success the following year, botfly infection did not have an impact on overwinter survival. This finding is consistent with previous studies, which found that botfly infection alone does not affect survivorship (Jaffe et al. 2005, Cramer and Cameron 2006).

As far as the results of statistical modeling are concerned, botfly infection does not appear to affect spring abundance. Based on the results of the multivariate regression analysis, spring abundance is mostly driven by fall trap success, total January snowfall, and mean January temperature. Spring abundance tends to be higher when fall abundance in the previous year is

lower, probably because of decreased intraspecific competition for resources in the winter and thus lower mortality. Spring abundance is also higher in years with higher total snowfall in January. This may due to the fact that *P. leucopus* use the subnivean zone as shelter during the winter, so a thicker layer of snow would provide increased insulation and protection from predators. Last, a higher mean January temperature leads to higher spring abundance, since *P. leucopus* need to expend less energy for thermoregulation at milder ambient temperatures. Also, when weather conditions are better, food resources may become available relatively earlier in the year. Kesner and Linzey (1997) found that the most important predictor of density in a given month was density in the previous month. A small amount of variance was also explained by two weather variables: deviation from mean precipitation with a 5-month lag and high temperature with a 2-month lag (Kenser and Linzey 1997).

A potential problem of this study was that trap success was used as a population index, but factors other than abundance can lead to variation in trap success. For example, on a night with a clear sky and full moon, *P. leucopus* may be more wary due to increased predation risk and thus wander less, decreasing trap exposure. However, it is unlikely that this caused significant errors, so the results of this study are robust.

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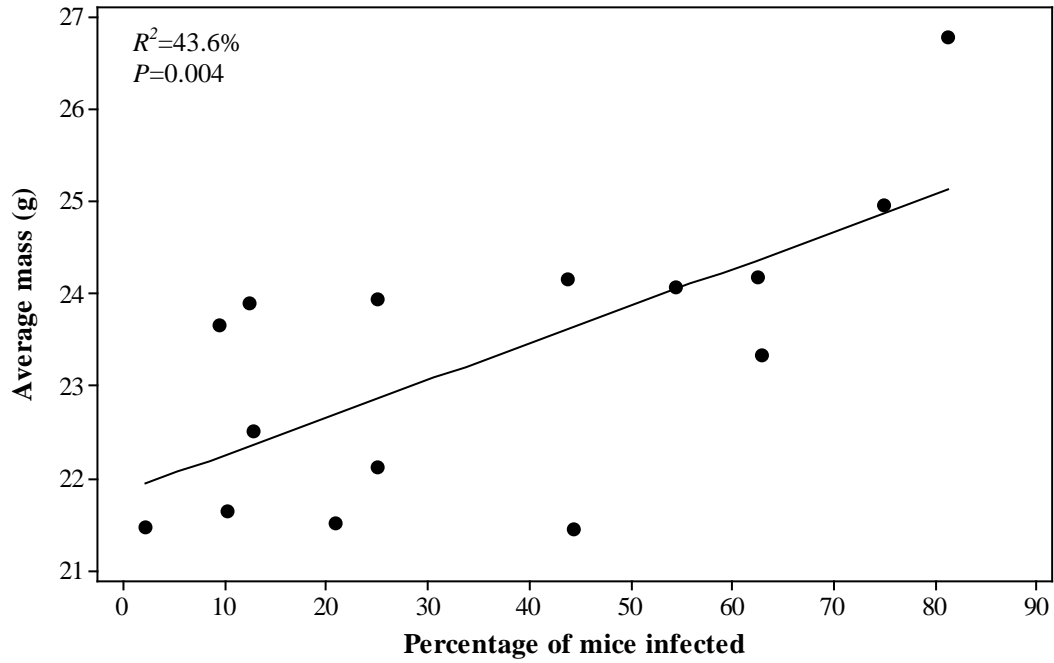
Figure 1. Regression line showing that as the percentage of infected mice increases, the average mass of the mice also increases.
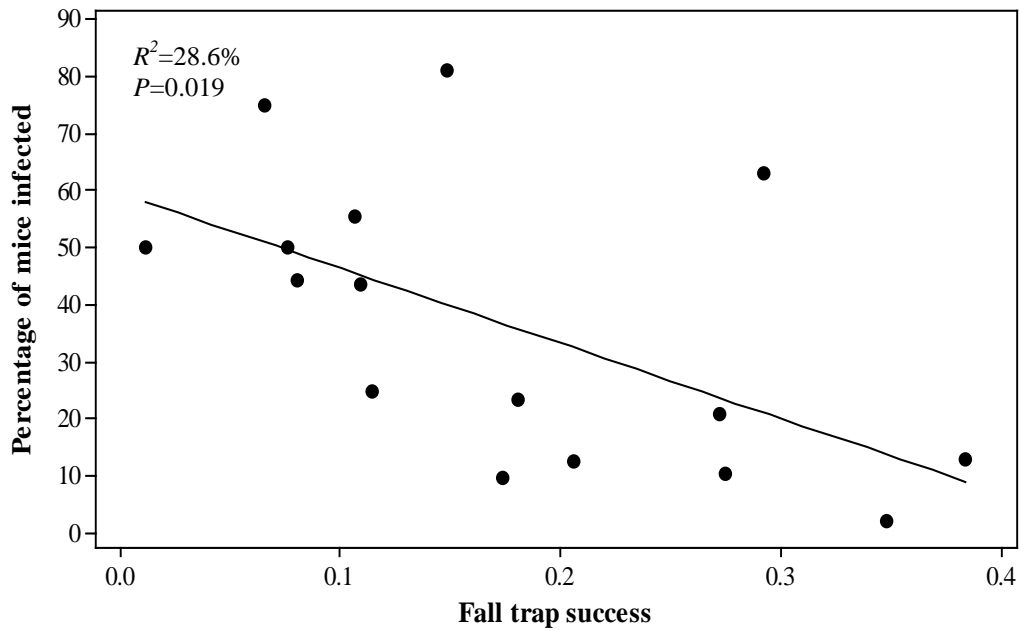

Figure 2. Regression line showing that as fall trap success, and thus fall abundance, increases, the percentage of infected mice in the population decreases.
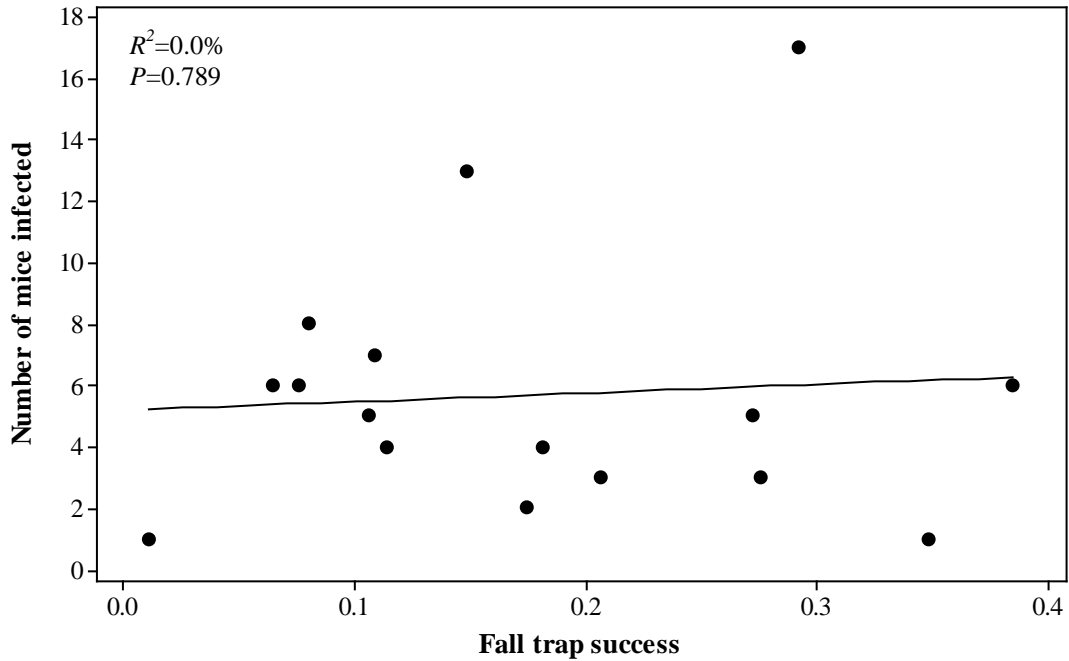
Figure 3. Regression line showing that number of infected mice does not change with changes in fall trap success.
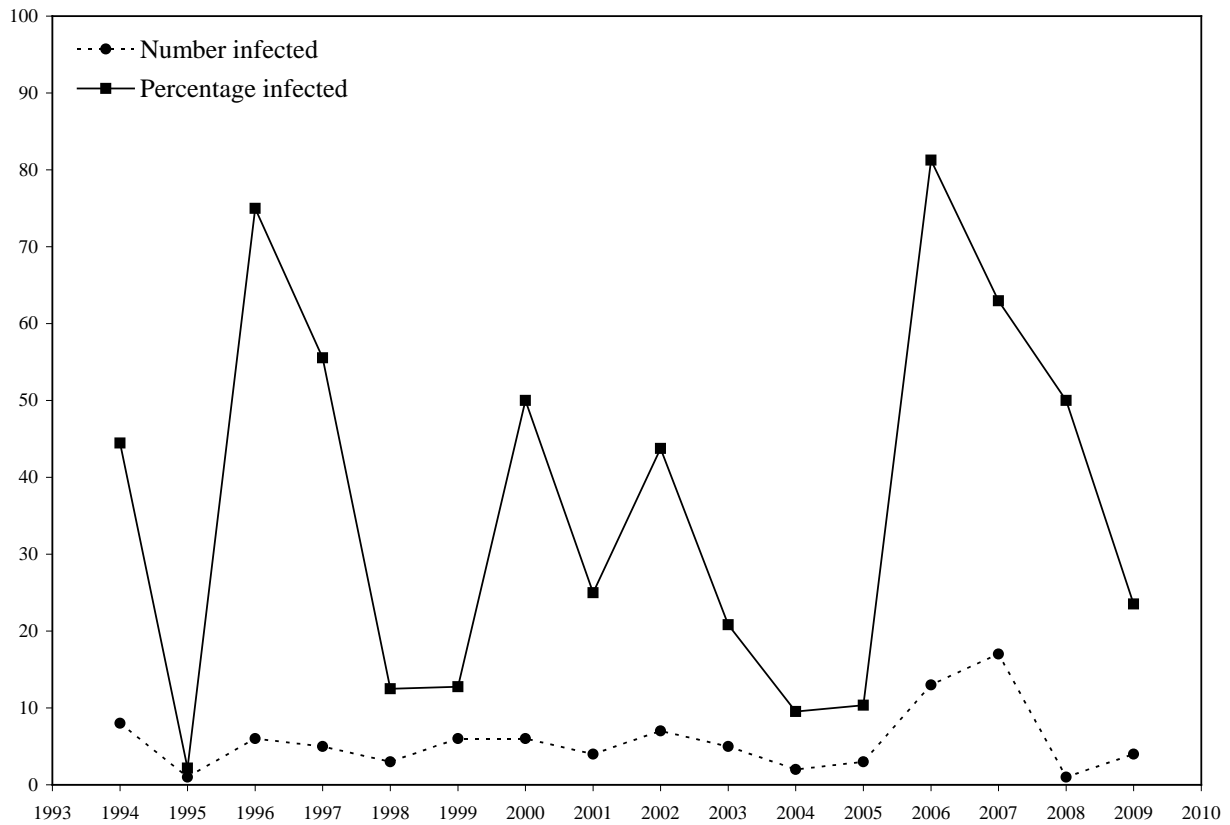

Figure 4. Number and percentage of infected mice over time. The number of infected mice remained relatively constant throughout the study period.
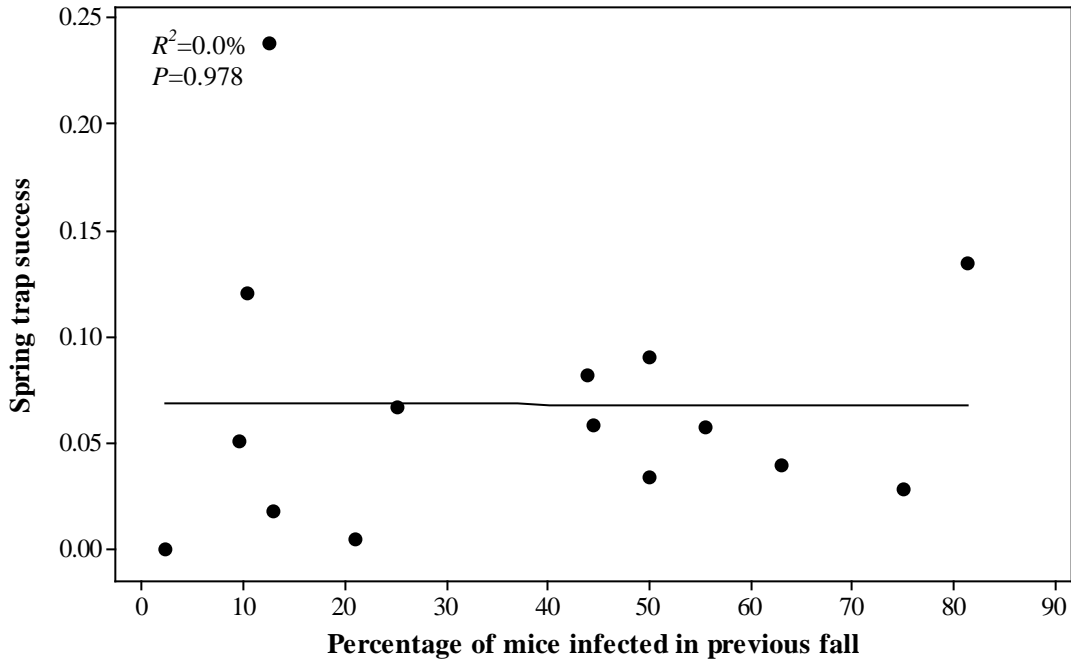
Figure 5. Regression line showing that spring abundance is not affected by the percentage of infected mice in the previous fall.
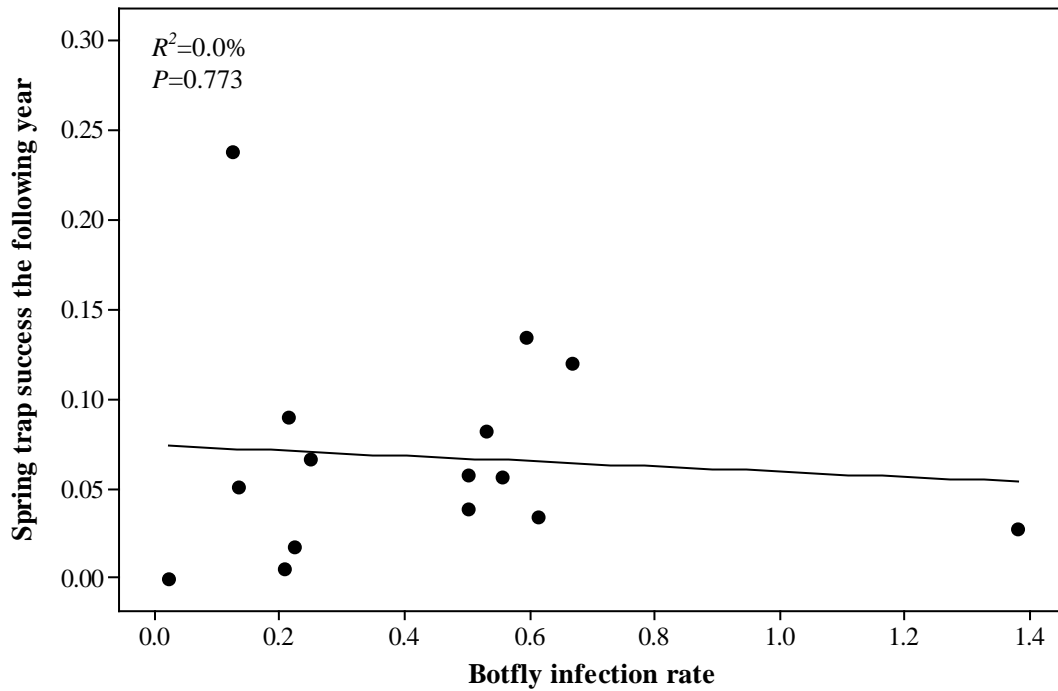

Figure 6. Regression line showing that botfly infection rate does not drive changes in the spring abundance.