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Effects of ectoparasites on survivorship and  
reproduction of *Peromyscus leucopus*.

Stephanie Dea

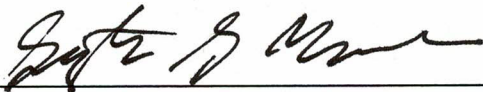
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Bachelor of Sciences

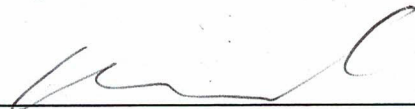
Submitted in partial fulfillment of the requirements for

College Honors

Departmental Distinction in Biology



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Title: Effects of ectoparasites on survivorship and reproduction of *Peromyscus leucopus*

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## **Effects of ectoparasites on survivorship and reproduction of *Peromyscus leucopus*.**

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### *Introduction*

White-footed mice (*Peromyscus leucopus*) are abundant habitat generalists in eastern deciduous and mixed forests. These mice play an important role in seed and fungus dispersal and as potential prey items (Lackey et al. 1985; Cary & Johnson 1995). White-footed mouse populations are often regulated by factors such as forest patch area (Nupp & Swihart 1996), food availability (Batzli 1997), and parasite population (Pederson & Greives 2008). These factors may have stronger effects on different aspects of the mouse populations. For example, Pederson and Greives (2008) suggest that food availability may only strongly influence host population growth while parasite presence strongly influences population crashes. Some of the parasites commonly found on white-footed mice are bot flies (*Cuterebra* spp.), fleas (order Siphonaptera), and ticks (*Ixodes scapularis*) (Vandergraft et al. 2008).

Bot flies are common in North America (Wecker 1962) and frequently infect many small mammal species, particularly white-footed mice (Burns et al. 2005). The larvae penetrate the skin of their hosts and remain there until they mature, which takes an average of 24-30 days (Wecker 1962). Although the flies are classified as parasitic, infected mice remain longer on trapping grids than uninfected mice (Burns et al. 2005; Cramer & Cameron 2006) resulting in increased survivorship estimates. A potential cause for increased survivorship is a decrease in activity, as the swellings caused by multiple larvae can impede movement (Dalmat, 1943; Wolf & Batzli 2001). Decreasing activity can increase survivorship by reducing the risk of predation, as the mice are less likely to be exposed to predators if they remain in their burrows. Another

potential explanation for increased survivorship of mice infected with bot fly larvae is that the larvae may actively extend the longevity of their hosts (Burns et al. 2005). A mechanism to increase the survivorship of a host benefits parasites that require long periods for development, such as the bot fly.

Bot fly larvae typically infect the mice in the inguinal region, and infected mice experience a period of sterility while the larva develops (Hensley 1976). Timm and Cook (1979) also found that reproduction of subadult males specifically was affected by bot fly infection. Male mice are more affected by bot fly infection than female mice, as the larvae can displace testicles and cause castration (Arnaud et al. 2016).

Bot fly infection may also influence mass and the overall health of the host. Mice with greater masses are more often infected with bot fly larvae (Phillips & Mech, unpublished data). The correlation of infestation with mass suggests a minimal effect on quality of the individual. However, mice infected with bot fly larvae may be more susceptible to subsequent infections by other parasites, such as flesh flies (*Wohlfahrtia vigil*), that can negatively impact the host (Craine & Boonstra 1986).

Other parasites that commonly infect white-footed mice include fleas and ticks. The effects of fleas on mice are not well studied, and we found no published evidence that the fleas' feeding on their host's blood affects the mice. Ticks are hosts for various diseases, including Lyme disease. White-footed mice are the most competent reservoirs for the spirochete (*Borrelia burgdorferi*) which causes Lyme disease (Schmidt et al. 1999). The ticks contract *B. burgdorferi* while feeding on mice during the larval bloodmeal. However, high tick burdens do not affect mouse survivorship (Ostfeld et al. 1996; Hersh et al. 2014).

Nolde Forest is a state park near Reading, PA. In the fall and spring of 2012/13, the Pennsylvania Department of Conservation of Natural Resources harvested timber from various areas in Nolde to improve forest health, as well as generate income for the park. The harvesting levels varied, ranging from clear cutting to selective harvesting, with most areas completely unaffected. Some of this logging has created areas of edge habitat, which can be ideal habitat for some ectoparasites, such as bot flies (Wolf & Batzli 2001). Edge habitat may result in an increased population density (Nupp & Swihart 1996) and loss of other vertebrate species that may be hosts for parasites. For example, Allan et al. (2003) found increased parasitism by ticks on white-footed mice in small forest patches, likely as a result of the loss of other species that might act as hosts for the ticks or predators of the mice.

We explored the effects of forest management practices on the ectoparasite load of mice and the subsequent impact of common ectoparasites on white-footed mice populations. We tested three hypotheses: 1) the frequency of infestation will be greater in a disturbed site than an undisturbed site; 2) mice with greater numbers of parasites will have reduced cues of reproductive ability (e.g., pregnancy rates, lactation, and scrotal size); and 3) mice with bot flies will have a greater survivorship over the course of the trapping period.

### *Methods*

We trapped two sites in Nolde Forest State Park: a select cut site that was selectively logged to remove only dead and dying trees, and a control site, which was unaffected by any logging. At the select cut site, we set 64 Sherman® live traps set in eight lines of eight traps each spaced 15 m apart, and at the control site we set 25 traps set in five lines of five traps each. We trapped for three consecutive nights each week for five weeks through the summer and two

consecutive nights each week during the fall. We recorded sex, age, mass, and reproductive status on all mice captured. We implanted PIT tags (Oregon RFID 8mm x 1.4mm FDX-B) in each mouse for future identification, and we examined each mouse for presence of parasites in the field. Presence of parasites was determined by counts of individual ticks or bot flies, and estimated flea infection using an ordinal scale from 0 to 2. An individual was considered infected with a parasite if they had been recorded with that parasite at any point throughout the trapping period.

Using standard mark-recapture analysis in Rcapture (Rivest & Baillargeon 2014), we estimated population size and survivorship rates for each site. We also examined sex ratios and parasite infection rates between the sites. We used nested log-linear models in the MASS package for R (Venables & Ripley 2002) to determine relationships between infection status, site, sex, age, and reproductive status. Using  $\chi^2$  statistical analysis we tested for differences in infestation rates between sites. Methods were approved by Albright College ACUC (Protocol #14-02) and follow the approved field methods of the American Society of Mammalogists (Sikes et al. 2016).

## *Results*

We had a total of 496 captures of 106 individuals at the select cut site and 269 captures of 61 individuals at the control site. The majority (70.89% select cut, 76.60% control) of individuals at both sites were infected with some parasite. Most individuals at both sites were infected with ticks (61.32% select cut, 54.10% control), while fewer individuals were infected with fleas (32.08% select cut, 42.62% control) and bot flies (22.64% select cut, 32.79% control). The

proportions of individuals infected by two or three of the parasites were 39.34% (control) and 32.08% (select cut) and 9.84% (control) and 7.55% (select cut), respectively.

There was a significant relationship between bot fly infection status, sex, and site ( $D = 7.7703$ ,  $df = 1$ ,  $p = 0.0053$ ). The proportions of males infected at both sites were not significantly different ( $\chi^2 = 0.5271$ ,  $df = 1$ ,  $p = 0.4678$ ). Females were more likely to be infected by bot flies at the control site than at the select cut site ( $\chi^2 = 7.967$ ,  $df = 1$ ,  $p = 0.0048$ ; Figure 1).

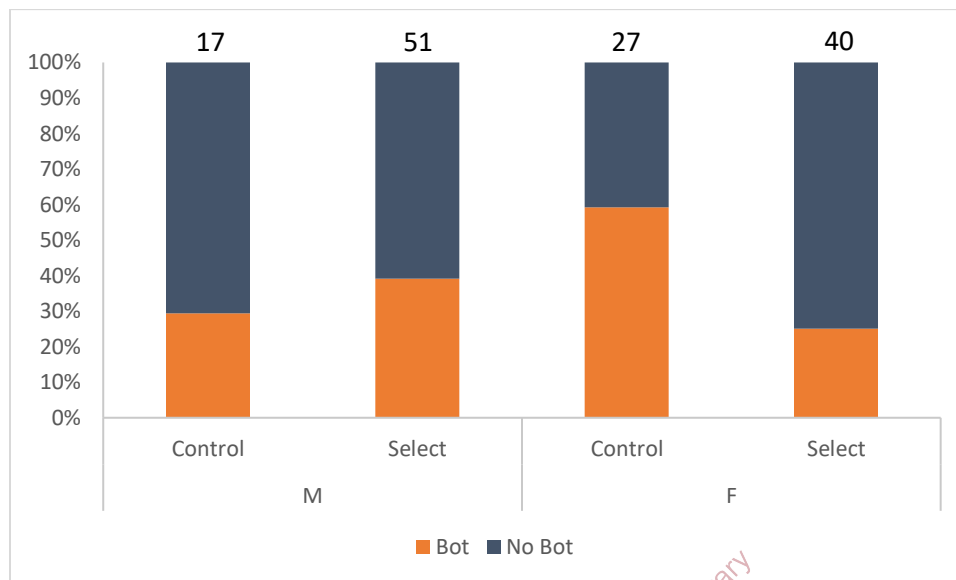


Figure 1. Proportion of males and females infected with bot flies at each site. Values at the tops of the bars are sample size.

Flea infection status was significantly related to sex and site ( $D = 5.381$ ,  $df = 1$ ,  $p = 0.0204$ ), age and site ( $D = 7.311$ ,  $df = 2$ ,  $p = 0.02585$ ), and sex and reproductive status ( $D = 9.510$ ,  $df = 1$ ,  $p = 0.0020$ ). Equal proportions of males were infected with fleas at each site ( $\chi^2 = 0.1778$ ,  $df = 1$ ,  $p = 0.6733$ ), while a greater proportion of females was infected at the select cut site than females at the control site ( $\chi^2 = 6.094$ ,  $df = 1$ ,  $p = 0.0136$ ; Figure 2). The proportions of



individuals infected with fleas is about equal at both sites for adults ( $\chi^2 = 0.0477$ ,  $df = 1$ ,  $p = 0.8271$ ) and subadults ( $\chi^2 = 0.1007$ ,  $df = 1$ ,  $p = 0.7509$ ). However, there is a greater proportion of juveniles infected with fleas at the control site than the select cut site ( $\chi^2 = 8.430$ ,  $df = 1$ ,  $p = 0.0037$ ; Figure 3). The proportions of reproductively competent and non-reproductively competent females were not significantly different ( $\chi^2 = 2.808$ ,  $df = 1$ ,  $p = 0.0938$ ). A greater proportion of males who were reproductively competent were infected than non-reproductive males and any females ( $\chi^2 = 4.401$ ,  $df = 1$ ,  $p = 0.0359$ ; Figure 4).

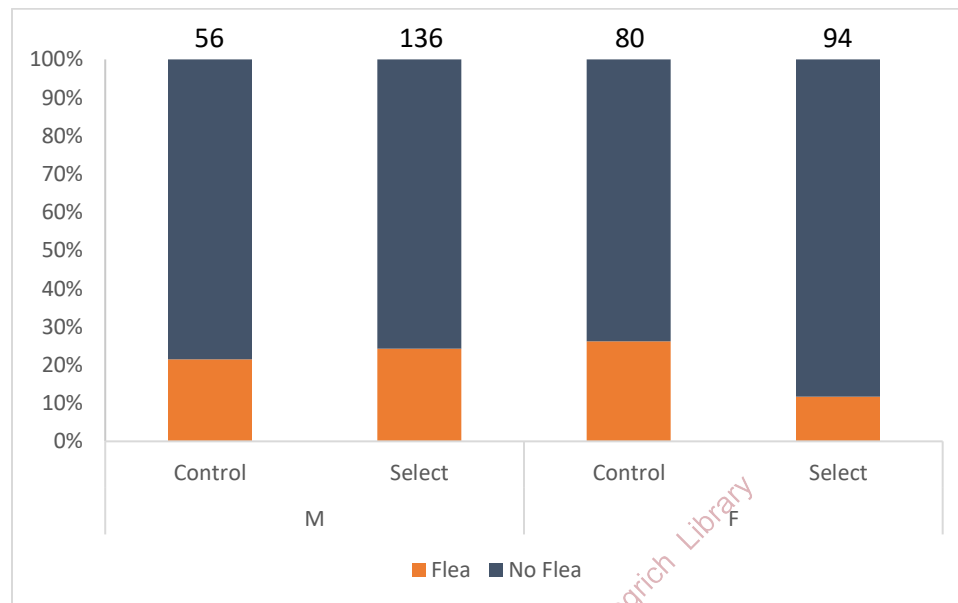


Figure 2. Proportion of males and females infected with fleas at each site. Values at the tops of the bars are sample size.

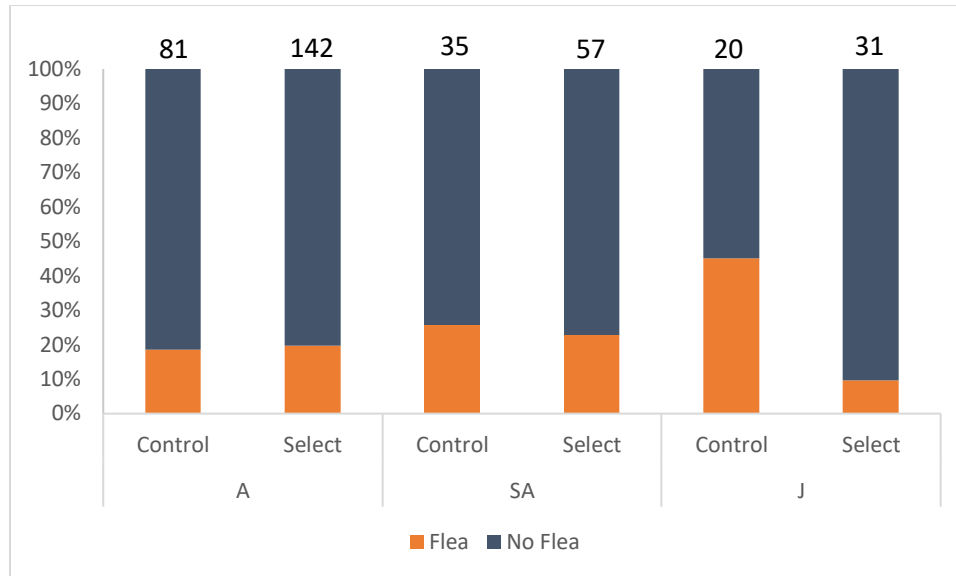


Figure 3. Proportion of adults (A), subadults (SA), and juveniles (J) infected with fleas at each site. Values at the tops of the bars are sample size.

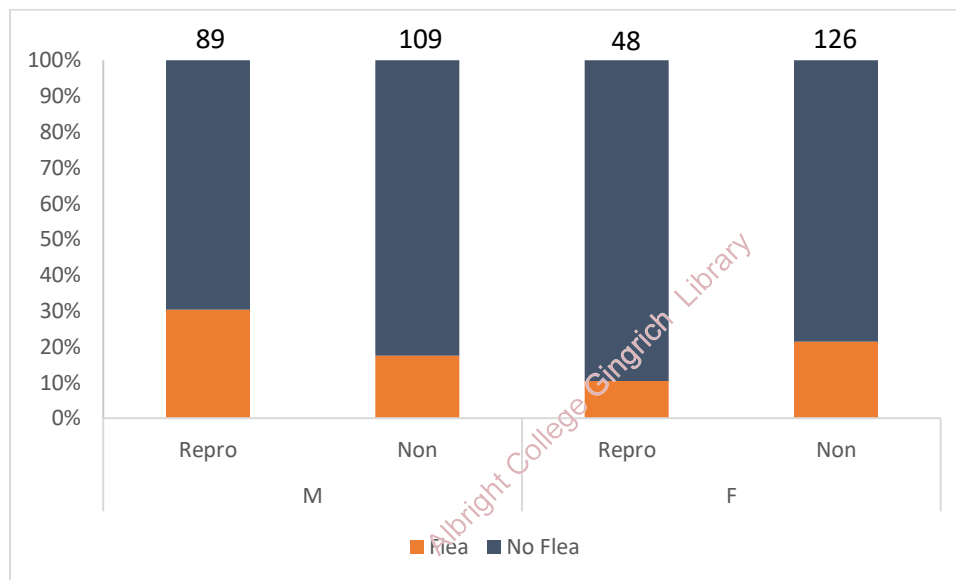


Figure 4. Proportion of males and females infected with fleas that are reproductively competent (Repro) or not (Non). Values at the tops of the bars are sample size.

There were significant relationships between tick infection status and site ( $D = 4.450$ ,  $df = 1$ ,  $p = 0.0349$ ) and age ( $D = 16.17$ ,  $df = 2$ ,  $p = 0.1364$ ). The select cut site had a greater proportion of individuals infected with ticks than the control site ( $\chi^2 = 5.858$ ,  $df = 1$ ,  $p = 0.0155$ ; Figure 5). A greater proportion of adults was infected than any other age group ( $\chi^2 = 40.97$ ,  $df = 2$ ,  $p \lll 0.0001$ ; Figure 6).

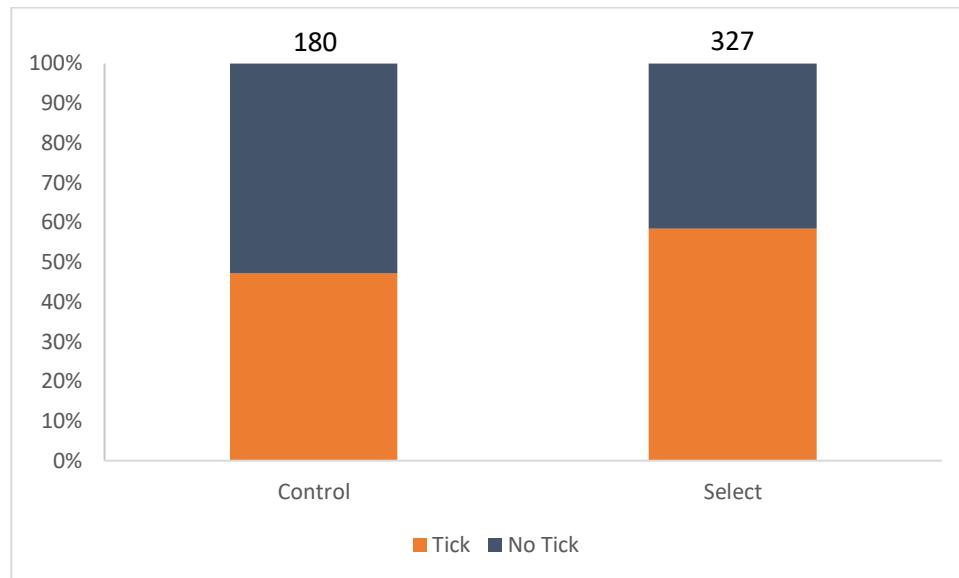


Figure 5. Proportion of individuals infected or uninfected with ticks at the select cut and control sites. Values at the tops of bars are sample size.

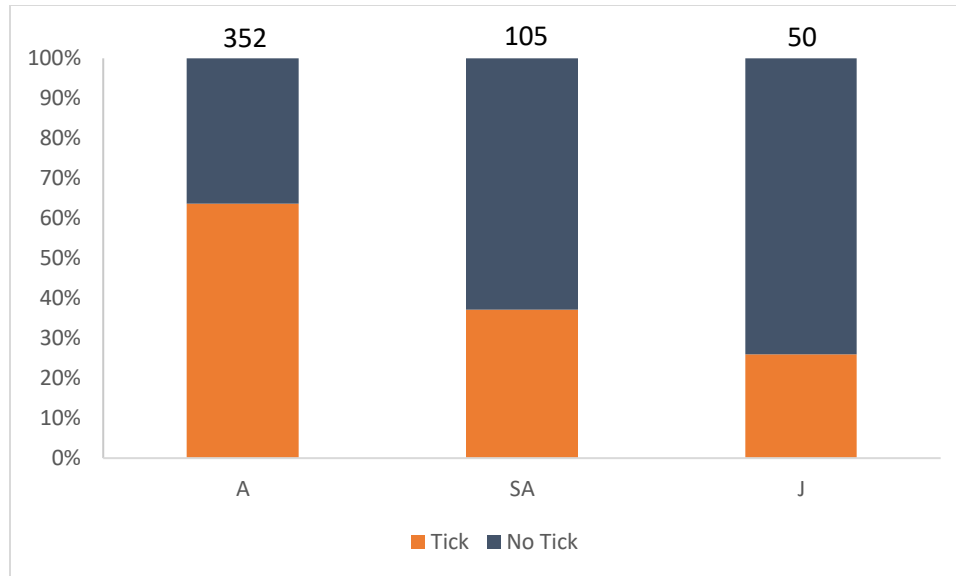


Figure 6. Proportion of adults (A), subadults (SA), and juveniles (J) infected with ticks at each site. Values at the tops of the bars are sample size.

The mass of individuals infected with fleas and those infected with ticks was significantly greater than the mass of uninfected individuals (Tables 1 & 2). The average mass ( $\pm$  se) of flea-infected individuals was  $17.60 \pm 1.04$  g at the control site and  $16.72 \pm 1.03$  g at the select cut site, while the average mass for individuals unaffected by fleas was  $14.31 \pm 1.04$  g at the control and  $14.32 \pm 1.03$  g at the select cut site. Tick-infected individuals, on average, weighed  $17.84 \pm 0.62$  g at the control and  $17.04 \pm 0.44$  g at the select cut site. There was a significant interaction between site and bot fly infection status for mass (Table 3). Individuals at the control site that were infected with a bot fly weighed more than individuals not infected with bot fly. Bot fly-infected individuals at the control site weighed an average of  $18.27 \pm 0.82$  g, while uninfected individuals at the control site weighed  $15.55 \pm 0.58$  g. At the select cut site, bot fly-infected

individuals weighed, on average,  $15.92 \pm 0.75$  g, and uninfected individuals weighed an average of  $16.24 \pm 0.40$  g.

Table 1. ANOVA table for average mass for mice with and without fleas. Significant relationships denoted with three asterisks.

|             | Sum Sq | Df  | F value | Pr(>F)      |
|-------------|--------|-----|---------|-------------|
| Status      | 1.22   | 1   | 25.5392 | <<0.0001*** |
| Site        | 0.02   | 1   | 0.5124  | 0.4751      |
| Status:Site | 0.03   | 1   | 0.5326  | 0.4666      |
| Residuals   | 7.72   | 161 |         |             |

Table 2. ANOVA table for average mass for mice with and without ticks. Significant relationships denoted with three asterisks.

|             | Sum Sq | Df  | F value | Pr(>F)     |
|-------------|--------|-----|---------|------------|
| Status      | 262    | 1   | 21.54   | <<0.001*** |
| Site        | 9      | 1   | 0.7451  | 0.3893     |
| Status:Site | 4      | 1   | 0.291   | 0.5903     |
| Residuals   | 1961   | 161 |         |            |

Table 3. ANOVA table for average mass for mice with and without bot flies. Significant relationships denoted with an asterisk.

|             | Sum Sq | Df  | F value | Pr(>F)    |
|-------------|--------|-----|---------|-----------|
| Status      | 45     | 1   | 3.3124  | 0.07056   |
| Site        | 22     | 1   | 1.6079  | 0.20657   |
| Status:Site | 72     | 1   | 5.3076  | 0.02247 * |
| Residuals   | 2246   | 166 |         |           |

Population density was much greater at the control site than the select cut site. All individuals, regardless of infection status, had relatively high survivorship throughout the trapping period until around week 35. At this point, survivorship sharply declines at both sites (Figure 7).

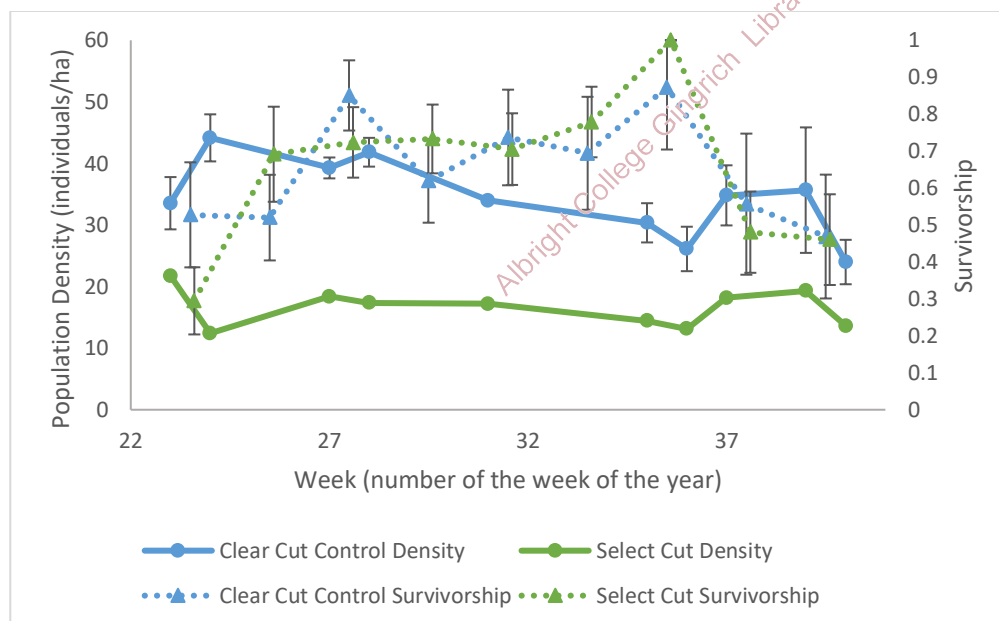


Figure 7. Survivorship and population density (individuals/ha) of the select cut and control sites over time. Error bars represent standard error.

Individuals infected with bot flies at each site had a greater survivorship than their uninfected peers. Survivorship of individuals without bot flies increased, before dropping towards the end of the trapping period at both sites. The survivorship of bot fly-infected individuals, however, remained relatively constant before also decreasing in the last few weeks (Figure 8). We were not able to calculate survivorship information for individuals infected and uninfected with fleas and ticks, likely due to small sample size for these specific groups. For the select cut site, there was a greater number of individuals that were uninfected with bot flies than those infected with bot flies. The number of individuals that were infected with bot flies increased throughout the trapping period, while the number of uninfected individuals generally decreased.

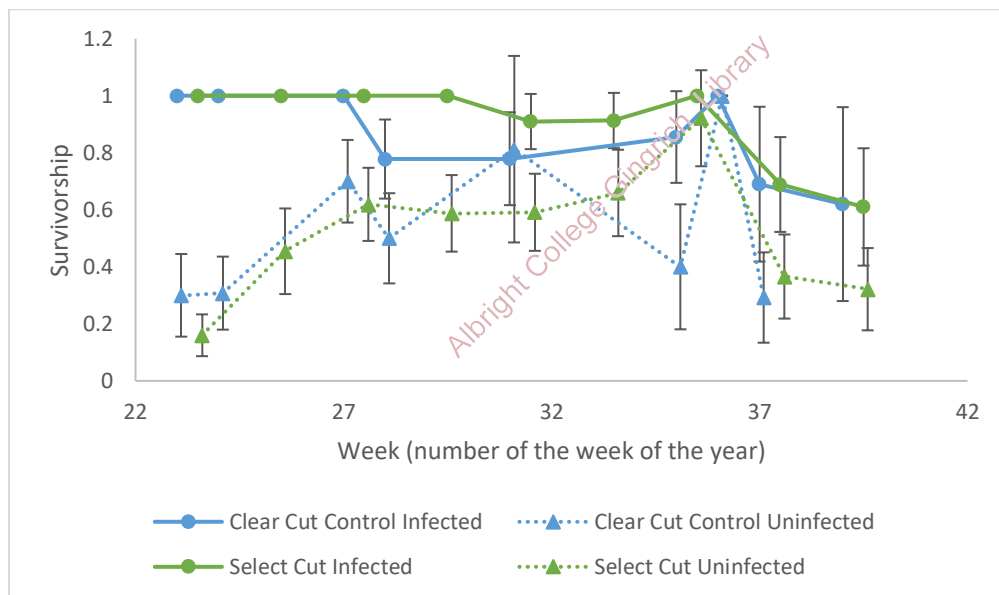


Figure 8. Survivorship of individuals infected and uninfected with bot fly larvae at both the select cut and control sites. Error bars represent standard error.

### *Discussion*

Our first hypothesis that the frequency of ectoparasite infection would be greater at the disturbed site than the undisturbed site was only partially supported. The second hypothesis, that mice infected with ectoparasites would exhibit reduced cues of reproductive ability was not supported. Our third hypothesis that mice infected with bot flies would have greater survivorship was supported. The effects of the individual ectoparasites will be examined in the following paragraphs.

The greater proportion of bot fly-infected females at the control site was not expected, as bot flies are more common in edge habitat (Wolf & Batzli 2001), which was more prevalent at the select cut site. However, the control site has a trail that divides the trapping grid in half. This trail may have created a large enough area of edge habitat to influence the bot fly population, therefore affecting infection rates at the control site. Additionally, the control site has had some large trees fall, followed by an increased proportion of wineberry (*Rubus phoenicolasius*) and blackberry plants (*Rubus* genus), which are edge species, further supporting that the control site may be an area of edge habitat (D. Osgood, pers. comm.).

The greater proportion of female mice infected with fleas at the control site is also not explained by the literature. Generally, ectoparasites such as fleas are more likely to infect male hosts than female hosts because of the males' weakened immune system as well as increased activity (Khokhlova et al. 2011). This trend may also explain the greater proportion of reproductive males being infected with fleas than non-reproductive males. Perhaps female mice



at the control site have a weakened immune system or are more active than the male mice in the area, leading to a trend different from that suggested by the literature. This relationship should be investigated further, with a specific focus on the movement patterns and overall health of the female mice at each site to determine if there is an effect of habitat on either of these factors, which may influence flea infection rates.

The greater proportion of bot fly- and flea-infected individuals at the control site may be a result of the control site consisting of an edge habitat that may be more favorable for these parasites than the select cut site or individuals at the control site having weakened immune systems or different movement patterns. However, population density may also play a role in the infection rates for these parasites (Arneberg et al. 1998). As Nupp and Swihart (1996) suggest, population density can be regulated by the habitat quality. We were unable to collect enough data to investigate whether population density, habitat quality, or both influenced parasite infection rates in the present study. Therefore, the relationship between population density, habitat quality, and bot fly and flea infection rates should be investigated further.

The larger proportion of juveniles at the control site were infected with fleas. One explanation for this general pattern of infection is the “poorly fed host” hypothesis, which suggests that fleas sometimes infect juveniles more than older age groups because organisms can be more vulnerable in the younger stages of their lives (Hawlena et al. 2005). Fleas are more likely to follow the “poorly fed host” hypothesis when their population densities are low and may become more likely to prey upon older individuals if the flea population density increases (Hawlena et al. 2005).

We captured a greater proportion of mice infected with ticks at the select cut site than the control site. Ticks are most common in wooded areas and areas of edge habitat (Schulze et al.

1991). The large area of edge habitat created by the select cut site is likely quality habitat for ticks, making the mice more likely to become infected if the tick population is thriving. Other abiotic features such as soil, geology, and climate can also affect tick abundance (Guerra et al. 2002). These other factors may be worth investigating to further understand the larger system influencing the interactions between ticks and their hosts.

Tick infection rates differed by age, with adults more likely to be infected than subadults or juveniles. Krasnov et al. (2006) also saw this trend with fleas and small mammals and suggest that the pattern is an effect of the natural history of the host. Older individuals are more mobile than younger ones, and so have greater chance of being exposed to ectoparasites. Individuals infected with fleas and individuals infected with ticks weighed, on average, more than their respective uninfected peers. Hawlena et al. (2006) found no significant difference in the masses of gerbils (*Gerbillus andersoni*) parasitized and not parasitized by fleas, but acknowledged individual variation. For ticks, Perkins et al. (2003) found that adult males that weighed more were more heavily parasitized than their lighter peers. We found individuals infected with bot flies at the control site had a greater average mass than uninfected individuals at the control site and both bot fly-infected and uninfected individuals at the select cut site. Similarly, Dunaway et al. (1967) found that *Peromyscus* infested with bot fly larvae tend to weigh as much, if not more, than un-infested mice. The correlation of infestation with mass for bot flies suggests a minimal effect of infection on quality of the individual, but this interaction between sex, site, and bot fly infection for mass should be investigated further.

The high survivorship of individuals infected with bot flies in this study supports previous findings that mice infected with bot flies have greater survivorship than individuals that are uninfected (Burns et al. 2005; Wolf & Batzli 2001). This increase in survivorship may be

caused by a decrease in the host's activity due to the size of the bot fly larvae (Dalmat, 1943; Wolf & Batzli 2001). This decrease in activity can increase host survivorship by reducing the risk of predation. The other potential explanation for increased survivorship of mice infected with bot fly larvae is that the larvae actively extend the longevity of their hosts (Burns et al. 2005). We have yet to analyze the data examining the differences in movement between infected and uninfected individuals. Further studies should be conducted to determine the exact mechanism which may be acting to increase bot fly host survival.

Although there appear to be relatively few major negative effects of infection by ectoparasites, and even some benefits, an individual infected with parasites may experience an accumulation of minor effects that lead to an overall degradation of host health. Booth et al. (1993) found that rock doves with high loads of feather-feeding lice had significantly higher metabolisms than rock doves with low loads of the lice. This difference in metabolism was due to an indirect effect of the lice consuming skin debris and feathers. Regardless, the indirect effects of other parasites may not affect an individual's survivorship, but this relationship is not well-studied (Booth et al. 1993). Parasites can also negatively impact the host's health if the host expends energy on parasite removal or in developing a resistance to the parasite (Stjernman et al. 2008). Such indirect effects were not addressed in this study, but may be worth investigating in the future. As overwinter survivorship is a critical point in small mammal population dynamics (Pulliam 1988), exploring the impact of summer ectoparasite load on subsequent overwinter survival may reveal long-term costs of parasite infection.

Our data show that different management strategies, including creation of edge habitat, may influence ectoparasite infection rates of white-footed mice differently. It may be important to explore the effects of edge habitat and ways in which different types or amounts of edge

habitat can influence ectoparasite infection. Understanding how different types of edge habitat influence parasite infection rates can provide a better understanding of what factors influence white-footed mouse population dynamics and subsequent forest health. Additionally, this will lead to a better understanding of the dynamics of the parasite populations and the risk for any zoonotic diseases they may carry, particularly with ticks (Despommier et al. 2007). Therefore, while our data suggest that host-parasite interactions may be affected by forest management, further research should be done to fully understand this difference.

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