

A PRESCRIPTION FOR LONGER LIFE? BOT FLY PARASITISM OF THE WHITE-FOOTED MOUSE

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Abstract. Investigation of host–parasite interactions typically reveals a negative impact of parasitism on the host species. In contrast, mounting evidence indicates that bot fly (*Cuterebra* sp.) infestation enhances the survival of white-footed mice (*Peromyscus leucopus*). We propose that life history trade-offs, namely, between reproduction and survival, can explain this counterintuitive observation. By using an extensive data set spanning a decade, 12 sites in two states, and over 30 000 mouse captures, we offer a new perspective on the effects of bot fly parasitism on white-footed mice. Analysis of persistence time corroborated earlier studies that showed significantly higher survival rates of infested mice. Although a higher proportion of infested than uninfested females were in breeding condition, secondary reproductive success appeared to be negatively impacted by parasitism via declines in the number of litters and the total number of offspring produced by infested females. Population growth rates were negatively correlated with infestation prevalence, further indicating a negative effect of parasitism. Based on the negative impact of parasitism on reproduction, we propose that enhanced survival of infested mice can be explained by the diversion of resources from reproduction to body maintenance. Parasite-induced life history shifts in which mice decrease current reproduction to promote future reproduction, such as increasing the age at maturity, may also contribute to the decline in population growth rate observed in years of high infestation prevalence.

Key words: bot fly; bot fly impact on *Peromyscus* hosts; *Cuterebra*; host–parasite interactions; life history trade-offs; parasite; parasitism; *Peromyscus leucopus*; population dynamics; reproduction; survival; white-footed mouse.

INTRODUCTION

Parasites, by definition, have a negative impact on their host (Gotelli 1998). Some parasites minimally affect hosts through limited reductions in the efficiency of physiological processes, such as digestion, or by causing minor shifts in movement patterns (Munger and Karasov [1991, 1994] and Cranford and Tomblin [1993] document these effects in *Peromyscus*). Other parasites, however, can markedly decrease survival and reproduction, in some cases leading to death or sterility of the host (including near-complete castration in crabs [Shields and Wood 1993, Alvarez et al. 1995]). Parasites can also trigger changes in life history strategies of the host by operating on trade-offs between life history traits. Physiological trade-offs in life history traits occur when energy must be allocated between two or more functions competing for limited resources within the same individual (Stearns 1992). Life history trade-offs have been widely observed in natural populations, including the negative correlation often observed between current and future reproduction, and between

reproduction and survival (see reviews by Bell and Koufopanou 1986, Stearns 1992, and Roff 2002). Possible impacts of parasitism on life history traits include shifting the timing of reproduction (Minchella 1985, Forbes 1993, Perrin and Christie 1996, Agnew et al. 2000, Krist 2001), changing the optimal litter/brood size (Moller 1991, Richner and Heeb 1995, Richner 1998, Fitze et al. 2004, Kristan 2004), altering reproductive effort (including provisioning of resources to offspring; Richner 1998, Richner and Tripet 1999, Fitze et al. 2004), and increasing the probability of predation via infestation-induced changes in host movement patterns (Thornhill 1980, Gwynne and Dodson 1983, Thiemann and Wassersug 2000).

Alteration of a specific life history trait by parasitism, however, implies that correlated life history traits might change in a compensatory manner. Consequently, although the net effects of parasitism on host fitness, by definition, must be negative, an apparent positive effect might be postulated if only a subset of the key life history traits is measured. For example, if parasitism reduced reproductive rates, the energy usually expended for reproduction could then be spent on foraging and metabolic costs, leading to a subsequent increase in body condition or survival. Such life history trade-offs may offer a general explanation for cases in

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which parasitism appears to prolong the life of the host, as has been shown for estuarine snails parasitized by trematodes (Curtis et al. 2000), for white-footed mice with heavy burdens of the blacklegged tick (*Ixodes scapularis*) (Ostfeld et al. 1996b), and with bot fly infestations (details follow).

Bot flies (*Cuterebra* sp.) are long known to associate with white-footed mice (*Peromyscus leucopus*). Bot fly larvae, which embed within the dermis of mouse hosts, can reach over 2 cm in length and weigh >1 g (5% or more of adult mouse body mass) when fully developed (Wecker 1962, Munger and Karasov 1994). Mounting evidence indicates that bot fly infestation enhances survival of white-footed mice (Wecker 1962, Goertz 1966, Hunter et al. 1972, but see Miller and Getz 1969). Early explanations for this apparent positive effect of infestation were attributed not to any real positive effect on the host, but to alleged decreased movement of infested individuals (Wecker 1962), and to the potential for long-term residents having increased exposure to bot fly infestation (Hunter et al. 1972). More recently, however, controlled laboratory experiments (Munger and Karasov 1991) and studies of natural populations (Clark and Kaufman 1990) have provided additional evidence that infested mice do exhibit lower rates of attrition than naturally uninfested individuals. On the other hand, bot fly parasitism has been shown to negatively impact gonadal development in male *Peromyscus* (Wecker 1962, Timm and Cook 1979), and to decrease both survival and reproduction in voles (Boonstra et al. 1980).

We sought to determine whether trade-offs between survival and reproduction could explain the observed pattern of increased persistence in parasitized white-footed mice. We examined the consequences of bot fly parasitism for rates of survival, reproduction, and population growth in white-footed mice, using an extensive data set spanning over 10 years of live-trapping, at 12 locations in two states, and including more than 30 000 captures. Our goals were to: (1) reassess the alleged pattern of increased persistence of parasitized mice, (2) determine whether parasitism compromises mouse reproduction (evidence for a life history trade-off), and (3) assess the population-level consequences of bot fly parasitism (population density, growth rate, and density-dependent infestation prevalence).

METHODS

Study sites

Data were obtained from ongoing experiments investigating population dynamics and demography of white-footed mice in southeast New York (NY) during 1991–2001, and in northeast Connecticut (CT) during 2000–2002, at a total of 12 sites. Nine sites were studied in NY at the Institute of Ecosystem Studies. Six of these sites covered 2.25 ha each, dominated by oak trees (*Quercus* sp.), two of these sites were trapped

from 1991 through 2001 and the remaining four from 1995 through 2001. Three additional sites in NY were trapped from 1999–2001. These latter three sites covered 3–4 ha each, with half of each site in oak-dominated forest and the other half in non-oak-dominated forest. The three sites in CT were located at the Yale-Myers Research Forest. Each site in CT covered 3–4 ha, and encompassed a mosaic of habitat types including oak-dominated forest, white-pine forest (*Pinus strobus*), old-fields, and wetlands.

Small-mammal sampling

Trapping was conducted with Sherman live traps at stations (one trap per station in CT and two traps per station in NY) separated by 15 meters. Live-traps were set for 2–3 consecutive nights every 3–4 weeks from April/May through November at all NY sites, and for three consecutive nights monthly from May through September/October at all CT sites. Trapping was suspended in inclement weather (extreme cold or rain) at CT sites, and resumed the next suitable evening. Traps were baited with crimped oats, and supplemented with black oil sunflower seeds and cotton batting during cold nights. Traps were set in the evening before dusk and were checked and closed by mid-morning the following day. Once captured, *Peromyscus* were marked with numbered metal ear tags (National Band & Tag Company, Newport, Kentucky, USA), and data were recorded on capture location, body mass, sex, pelage, reproductive condition, and parasite load. Animals were subsequently released at the point of capture. To supplement movement and survival data and to gain more precise estimates of the reproductive portion of the population, nest boxes were placed at 30-m intervals across each site. Boxes were freely accessible to *Peromyscus* residents through a 2.5-cm hole in the bottom or side of the pine box, and were attached to trees at a height of approximately one meter. Cotton batting was used as bedding and was replaced as needed. Nest boxes were checked for occupants every 1–3 weeks from March through December, and data collected as described for live-trapping. Although nest-box data were collected at all sites in both states, data were only used from the CT sites for the analyses described in this paper, as bot fly infestation status of nest-box inhabitants at NY sites was not surveyed routinely.

Statistical procedures: individual-level analyses

Persistence times of infested and uninfested mice were compared using survival analysis (Cox proportional-hazards model; Cox 1972, Hosmer and Lemeshow 1999). All age classes were pooled. Mice were assigned to groups by infestation status, including those with zero, one, and two or more bot flies. Mice from both sexes were pooled for analysis when no significant differences were found between male and female persistence (in accord with Clark and Kaufman [1990]). Here we were interested in whether bot fly infestation

increased or decreased survival of individual mice (as assessed by persistence on the trapping grid). To minimize the possibility that any positive correlation between bot fly infestation and persistence was due to greater probability of exposure for longer-lived mice (Hunter et al. 1972), we followed discrete cohorts of individuals through time (as in Clark and Kaufman [1990]). Only individuals captured after the first observation of bot fly infestation, and before mid-way through the bot fly season were included in the analysis of persistence time to ensure equal exposure of all mice to the possibility of bot fly infestation. The cohort used for survival analysis was therefore limited to infested and uninfested mice present during an average period of one month (4–5 weeks). For all analyses, we defined the “bot fly season” as the period spanning the first date of observed bot fly infestation through the last day of *Peromyscus* monitoring in a given year. An individual’s presence on a site prior to the onset of the bot fly season was not included in that individual’s persistence time, nor were mice that became infested, or that dispersed onto a site, after the season’s mid-point included in the analysis. In addition to infestation status, site and year were incorporated into the survival analysis to account for any inter-annual or site-specific variation in survival rates.

The relationship between infestation status and breeding condition for individual mice was computed for all adult females captured during the bot fly season using χ^2 analysis and logistic regression. Females were scored as reproductive if lactating or pregnant. Mice recorded with brown pelage were considered adults. For the analysis of persistence times and reproduction, each individual was only counted once. For example, if a female was pregnant or lactating at any point during the bot fly season, she was counted as “reproductive.” Similarly, if an individual was observed to have a bot fly infestation at any point during the season, it was counted as an infested mouse. If an animal experienced reinfestation later in the season, it was placed in the bot fly category corresponding with the maximum number of bot flies observed at any one time. Reinfestation rates were extremely low given the characteristic peak in infestation prevalence and the long duration of larval development within the host (Catts 1982). In addition, we used *t* tests to compare litter size, the number of litters produced, and the total number of offspring produced per female for infested and uninfested females found in nest boxes at CT sites during the duration of the bot fly season.

Statistical procedures: population-level analyses

Multiple linear regression was used to assess the relationships between annual population density, population growth rate, the proportion of the population breeding, and infestation prevalence. Monthly population density at each site was calculated as the minimum number known alive (MNA), based on live-trap-

ping data for each month. The value used to represent the annual population density for each site was computed as the maximum density obtained during monthly trapping sessions. Population growth rate during the bot fly season was calculated as the density (MNA) observed during the last week of the season minus the density observed the first week of bot fly infestation, divided by the number of weeks in between (the length of the bot fly season). The percentage of breeding females, a proxy for reproductive activity, was calculated as the percentage of all adult females recorded during the bot fly season that were observed to be lactating or pregnant.

We could not similarly assess male breeding activity with respect to bot fly infestation. Breeding condition in male white-footed mice is typically assessed by the position of testes (descended or scrotal testes indicate reproductive activity, and ascended or abdominal testes indicate inactivity). However, because larval bot flies typically embed in or near the inguinal area and cause scrotal swelling in males, we could not reliably assess the position of testes. Parasitized males have been shown in dissection studies to have considerably compromised gonadal development, including smaller testes, epididymides, and seminal vesicles (Wecker 1962, Timm and Cook 1979).

Infestation prevalence was calculated as the percentage of *Peromyscus* observed to have at least one bot fly infestation, out of all mice captured between the onset and termination of the bot fly season. SAS, S-Plus, and SPSS statistical packages were employed for these analyses. Data from NY and CT sites were first analyzed separately, and then combined when no differences between these locations were found to be significant. For all regressions, the trapping location (“site”) was initially included as an independent variable, but was subsequently dropped from the model for cases where site did not significantly influence the response variable.

In addition, to adjust for possible effects of nonhomogeneity of variances, potentially problematic for Models 3 and 8 (Table 1), these two regressions were also computed using a weighting factor (the reciprocal of the deviation of each point from its expected value on the regression line). This places higher emphasis on points close to the regression line and less emphasis on points far from the regression line. The slope and intercept of the weighted regressions were in all cases indistinguishable from the nonweighted regressions, supporting the validity of the simpler model. Therefore, results of the nonweighted regressions are presented.

We also asked whether (1) infestation prevalence varied significantly between different habitat types on heterogeneous sites (habitats classified by dominant overstory vegetation), using a two-way ANOVA for habitat type and year, (2) mean bot fly infestation differed among sampling sites in any given year, again using a two-way ANOVA; and (3) movement patterns

TABLE 1. Multiple linear-regression models used to assess the relationships between bot fly infestation prevalence and *Peromyscus* population-level effects; for each model, statistics are provided for the overall regression model and for each independent variable.

Response variable (current year)	Model no.	Independent variables				
		Percentage infested			Mouse density	
		Year	<i>t</i>	<i>P</i>	Year	<i>t</i>
Mouse density	1	Current	-1.04	0.30	Prev.	-2.22
	2	Previous	0.72	0.48	Prev.	-2.67
Population growth (no. mice/wk)	3	Current	-1.96	0.05	Curr.	-5.05
	4	Previous	0.99	0.33	Curr.	-2.74
Percentage of females reproductive	5	Current	0.02	0.99	Curr.	-4.12
	6	Previous	0.41	0.68	Curr.	-3.34
Percentage infested‡	7	Curr.	-1.46
	8	Prev.	3.13

† Site (trapping location) was initially included for all regression as an independent variable but was subsequently dropped from the model whenever site did not significantly influence the response variable.

‡ Models 7 and 8 assessed the effect of *Peromyscus* density on bot fly infestation prevalence.

differed significantly between infested vs. uninfested and pregnant vs. non-pregnant individuals. We computed each mouse's movement as the maximum displacement (the distance between the two most distant capture locations) that each mouse exhibited during the study. The mean maximum displacement of infested vs. uninfested or pregnant vs. nonpregnant females were compared using a *t* test. We also compared the distributions of maximum displacements for the various groups using Kolmogorov-Smirnov tests (Zar 1996).

RESULTS

There were no significant differences in bot fly infestation prevalence between the different habitat types at heterogeneous sites (even after controlling for year with a two-way ANOVA). Therefore, all results presented below represent data for entire sites, regardless of habitat type. In addition, bot fly infestation prevalence, determined over a trapping site, varied significantly between years (two-way ANOVA, $F = 5.84$, $P = 0.02$) and between sites (two-way ANOVA, $F = 2.79$, $P = 0.01$); but the interaction was not significant (two-way ANOVA, $F = 1.00$, $P = 0.46$) (Fig. 1). Mean bot fly loads at many of the sites seemed to be synchronized.

Effects of bot fly infestation on Peromyscus persistence, movement, and reproduction

Peromyscus persistence time was positively associated with bot fly infestation (Table 2). Results presented separately for CT (Connecticut, USA) and NY (New York, USA) sites identify interactions apparent at NY sites, but absent in CT sites. At the three CT sites, bot fly infestation was positively correlated with persistence time, with site and year insignificant factors in determining persistence time (Fig. 2). All interaction terms were not significant. Survival analysis for individuals at the nine NY sites also indicated a significant, positive effect of increasing bot fly infestation preva-

lence on *Peromyscus* persistence. At NY sites, site, year, and the interaction between site and bot fly infestation status were also significant determinants of persistence time.

Bot fly infestation may enhance individual persistence because infested mice move less than uninfested mice, thereby causing mice to remain on a trapping grid longer or experience decreased predation risk. Over all trapping years and sites, there were 6381 mice with multiple captures at the same site. Both infested and uninfested mice had average maximum displacements of ~35 m (mean \pm 1 SE of 36.8 ± 1.6 m and 35.2 ± 0.4 m for infested and uninfested mice, respectively), and these were not significantly different ($t = 0.90$, $df = 6379$, $P = 0.37$). The distributions of maximum displacements were also indistinguishable between infested and uninfested mice (Kolmogorov-Smirnov test; $D = 0.05$, $P = 0.39$).

Altogether, 354 (13.8%) of the 2570 adult females captured during the bot fly season were infested. A significantly higher proportion of reproductive females was infested (19.0%; 159/839) compared with nonreproductive females (11.3%; 195/1731; Pearson $\chi^2 = 28.11$, $P < 0.001$; logistic regression *t* ratio = 5.25, $P < 0.001$). Furthermore, reproductive females showed the same patterns of movement as the overall mouse population—with no differences in average maximum displacements (36.9 ± 4.1 m and 33.3 ± 0.7 m [mean \pm 1 SE] for infested and uninfested mice, respectively; *t* test, $t = 1.04$, $df = 1401$, $P = 0.30$) nor in distributions of maximum displacements (Kolmogorov-Smirnov test; $D = 0.11$, $P = 0.55$).

Although the proportion of females in breeding condition (pregnant or lactating) is a standard metric of reproductive status, it might not accurately measure reproductive output by mice. Our assessment of litter sizes and frequencies for females captured in nest boxes revealed a different pattern. Although no significant difference in litter size was detected between infested and uninfested females (4.22 ± 0.27 and 4.41 ± 0.17

TABLE 1. Extended.

Independent variables			Overall model				
Mouse density	Site†		F	df	P	R ²	
P	t	P					
0.03	4.60	2, 52	0.02	0.15	
0.01	4.27	2, 52	0.02	0.14	
<0.001	13.20	2, 62	<0.001	0.30	
0.01	3.94	2, 50	0.03	0.14	
<0.001	11.74	3, 63	<0.001	0.36	
0.002	5.58	2, 52	0.01	0.15	
0.15	2.18	0.01	5.00	2, 64	0.01	0.14	
0.003	2.08	0.04	7.22	2, 52	0.002	0.22	

[mean ± SE], respectively; $t = 0.60$, $df = 47$, $P = 0.55$), the number of litters produced per female (log-transformed) was significantly reduced for infested vs. uninfested females (0.07 ± 0.07 and 0.34 ± 0.07 [mean ± SE], respectively; $t = 2.28$, $df = 47$, $P = 0.03$; untransformed mean ± SE of 1.13 ± 0.13 and 1.53 ± 0.12). The overall effect of bot fly parasitism on female reproductive success was a (nonsignificant) trend toward a decrease in the total number of offspring produced by infested females during the bot fly season (4.67 ± 0.47 and 6.04 ± 0.50 [mean ± SE] for infested and uninfested females, respectively; $t = 1.82$, $df = 39$, $P = 0.08$).

Bot fly impact on population dynamics of Peromyscus

Effects of bot fly infestation on individual-level persistence and reproduction could translate into population-level parameters such as population growth rate, maximum annual density, and proportion of females breeding. We tested these expectations using multiple linear regression, with annual bot fly infestation prevalence in either the current or previous year as an independent variable. We included mouse density, in ei-

ther the current or the previous year, as a second independent variable to account for any density-dependent effects on the response variables. In addition, to determine whether *Peromyscus* population dynamics in turn impacted bot fly infestation rates, we asked whether bot fly infestation prevalence was affected by mouse density in the current or previous year. No significant differences were found between NY and CT sites, therefore the results presented represent data pooled from both states.

The maximum density of mice observed in a given year was not significantly affected by bot fly infestation prevalence in either the current year (Table 1: Model 1) or the previous year (Table 1: Model 2), when variation due to *Peromyscus* density the previous year was taken into account. More specifically, a high prevalence of bot fly infestation did not result in a significantly lower peak population density during that year or the following year. However, the maximum density recorded in a given year was significantly impacted by the maximum density of mice recorded the previous year. In other words, years of high *Peromyscus* density were generally followed by years of low density, and vice versa, irrespective of bot fly infestation prevalence.

However, population growth rates were significantly negatively impacted by the bot fly infestation prevalence in the current year (Table 1: Model 3; Fig. 3). Growth rates were not significantly affected by bot fly infestation prevalence in the previous year (Table 1: Model 4). Mouse population growth rate was also negatively affected by maximum mouse density in the current year, indicating density-dependent population regulation. Although the maximum density of mice at a site clearly has strong effects on population growth rate, with high-density years showing slower population growth, our analyses suggest that bot fly infestation rates independently play a role in determining population growth rate in this species.

The reduction in population growth rate we observed in years of high bot fly infestation was not caused by a reduction in the proportion of females in breeding

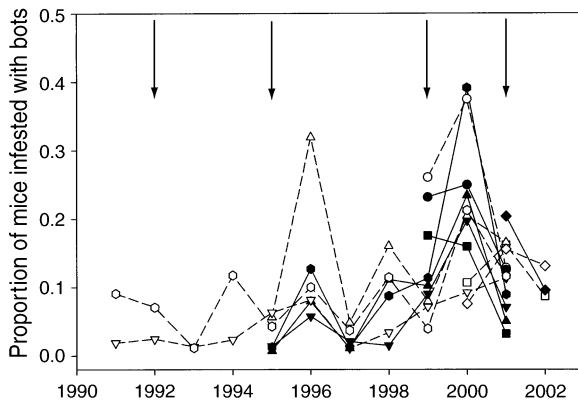


FIG. 1. Bot fly infestation prevalence for all Connecticut (CT) and New York (NY) sites, 1991–2002. Arrows indicate years of peak *Peromyscus* density (1992, 1995, 1999, 2001). Each of 12 sites is denoted with a unique symbol.

TABLE 2. Survival analysis of bot fly-infested and uninfested *Peromyscus*.

Factor	New York			Connecticut		
	Exp. coef.†	<i>z</i>	<i>P</i>	Exp. coef.†	<i>z</i>	<i>P</i>
Infestation status of <i>Peromyscus</i>	0.612	-7.31	<0.001	0.768	-2.79	0.005
Site	0.962	-5.02	<0.001	1.120	1.46	0.140
Year	0.975	-4.68	<0.001	0.907	-1.19	0.230
Site × infestation status	1.034	2.72	<0.007			

Note: Survival analysis statistics (Cox proportional hazards model [Cox 1972]) are presented, with values obtained for NY and CT sites listed separately.

† The exponent coefficient represents the factor by which survival changes for each incremental change in the target variable. For example, an increase in *Peromyscus* infestation status from zero to one bot fly results in survival enhanced by a factor of 0.768 at the CT sites, and by a factor of 0.612 at the NY sites.

condition. The percentage of females reproductive in a given year was significantly negatively affected by the current population density, but was not affected by the percentage of the population infested in either the current or previous year (Table 1: Models 5 and 6).

Peromyscus population density in a given year did not have significant impact on the percentage of mice infested by bot flies in that year, when site-specific variation was taken into account (Table 1: Model 7). We did observe a time lag, however, in which the infestation prevalence in the current year was significantly positively correlated with mouse population density the previous year, again, once site-specific variation was accounted for (Table 1: Model 8; Figs. 4 and 5).

DISCUSSION

Live slow and die old? Bot fly effects on survival and reproduction

Consistent with previous findings in the field (Wecker 1962, Goertz 1966, Hunter et al. 1972, Clark and Kaufman 1990) and in the laboratory (Munger and Karasov 1991), mice infested with bot fly larvae persisted

significantly longer than uninfested mice, and those with two or more bot fly larvae persisted longer than those with only one larva (Fig. 2). Wecker (1962) suggested that decreased activity of infested animals would enhance the likelihood of their repeated capture, thereby causing an artificially inflated persistence time for these individuals compared with uninfested animals that would be more likely to move outside the boundaries of the study site. Analysis of movement for the individuals in this study, aimed to explore this hypothesis, revealed no significant differences in distance moved (maximum displacement) between infested and uninfested mice. Given this result, enhanced survivorship of infested individuals appears to be an authentic, albeit counterintuitive, response to bot fly infestation. From the perspective of a parasite, particularly one requiring a considerable amount of time for development within its host, an increase in the life span of the

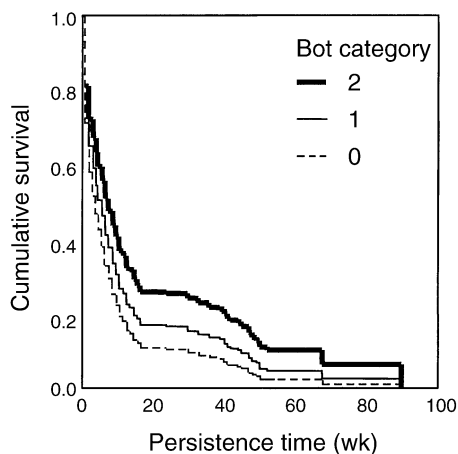


FIG. 2. Persistence time for *Peromyscus* infested with zero, one and two or more bot flies (CT sites, all years); Cox proportional-hazards model, $z = -2.79$, $P = 0.005$.

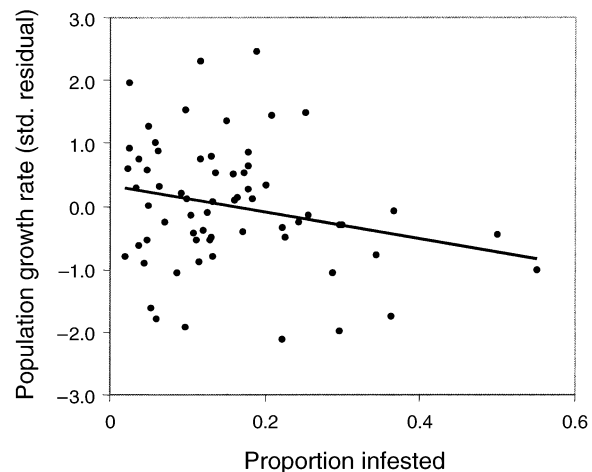


FIG. 3. Residuals from the regression of population growth rate on density in the current year plotted against the proportion of *Peromyscus* infested. *Peromyscus* population growth rate decreases in years of high bot fly infestation prevalence ($t = -1.96$, $P = 0.05$), when variation due to the impact of *Peromyscus* population density (in the current year) on population growth is taken into account (multiple linear regression, $F_{2,62} = 13.20$, $R^2 = 0.30$, $P < 0.001$).

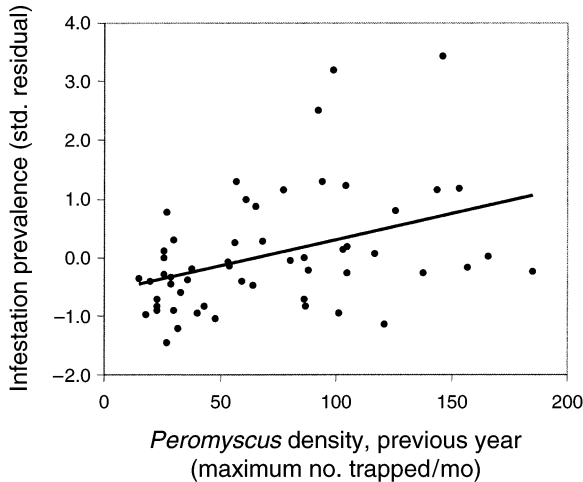


FIG. 4. Percentage of *Peromyscus* with bot fly infestations as a function of *Peromyscus* density in the previous year ($t = 3.13$, $P = 0.003$), once site-specific variation is taken into account (multiple linear regression, $F_{2,52} = 7.22$, $R^2 = 0.22$, $P = 0.002$). Residuals from the regression of infestation prevalence with site are plotted against the density of *Peromyscus* in the previous year. The density is the highest number observed in one month in any given year.

host would be extremely beneficial. Bot flies, which require 3–4 weeks for development (King 1968, Catts 1982), fall into this category, suggesting that bot fly infestation should not strongly reduce, and may facilitate an increase in, the longevity of their hosts.

The mechanism by which bot flies increase persistence of individual hosts, however, remains previously unexplored. As has been reported for many kinds of organisms (Stearns 1992, Roff 2002), energy constraints can result in trade-offs between life history traits such as survival and reproduction. For example, a factor causing a decrease in the probability of survival could indirectly cause the reproductive schedule to be moved forward, or litter size to be increased. Conversely, in the case of white-footed mice, if reproduction is compromised by bot fly infestation, survival might increase owing to increased allocation to maintenance or to the avoidance of risk associated with reproductive activities. In our assessment of breeding activity (pregnant or lactating females), we did not detect a decrease in the percentage of females reproductive in years of high bot fly infestation prevalence. This is corroborated by an earlier study showing that parasitism did not result in decreased numbers of embryos, corpora lutea, or placental scars in infested females (Timm and Cook 1979). In fact, our observations of breeding condition indicated that infested females actually exhibited disproportionately high rates of breeding activity compared with uninfested females. This suggests that (1) bot fly infestation enhances reproductive success, (2) reproductive females are more susceptible to infestation, (3) upon infestation, females allocate more resources to current reproduction (Forbes

1993, Perrin and Christe 1996, Agnew et al. 2000), or (4) external examination of breeding condition is a misleading indicator of reproductive success.

Our analysis of the number and size of litters produced by infested and uninfested females demonstrated that, despite being more often in breeding condition (pregnant or lactating), infested females produced fewer litters and (possibly) fewer offspring than did their uninfested counterparts. These data undermine hypotheses (1) through (3) above, support hypothesis (4), and suggest that the negative effects of infestation on females may be most strongly manifest through secondary impacts on reproductive success. The effect of parasitism on male reproduction appears to be more direct, given previous dissection studies documenting impaired gonadal development of parasitized males (Wecker 1962, Timm and Cook 1979).

The total number of offspring produced by infested vs. uninfested females is a somewhat crude metric of

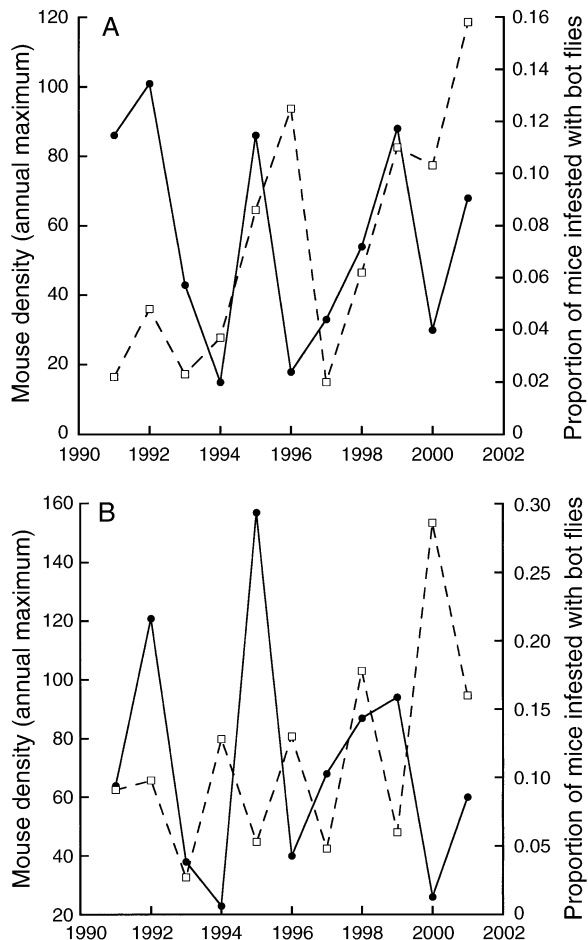


FIG. 5. Maximum annual population density (solid line) and infestation prevalence (dashed line) recorded at two oak-dominated NY sites, (A) HCG (Henry control grid) and (B) TCG (Teahouse control grid), from 1991 to 2001. Maximum annual population density is the highest monthly density recorded in a given year.

parasite effects on reproductive success of individual females. Infested mice may also employ life history strategies that decrease current reproduction to promote future reproduction (Forbes 1993, Perrin and Christe 1996, Richner 1998). Infested juveniles may delay the date of first reproduction (Agnew et al. 2000), and infested adults may shift the order of litter sizes within their life cycle (Cole 1954). These life history shifts can also have negative impacts on population dynamics by lengthening generation time (Cole 1954). Whether parasitism primarily causes an immediate decrease in offspring production (for which we provide evidence), or a delay in the timing of reproduction (not measured in this study), the consequent benefit to individual survival and detriment to population growth rate remains the same. In either case, the observation of increased persistence of infested mice with coincident declines in population growth rate in years of high parasitism indicates a life history trade-off between current reproduction and survival.

Bot fly parasitism has also been shown to increase the persistence times of other small-mammal species, including the eastern woodrat (*Neotoma floridana*; Clark and Kaufman 1990), the western harvest mouse (*Reithrodontomys megalotis*; Clark and Kaufman 1990), and the deer mouse (*Peromyscus maniculatus*; Hunter et al. 1972). In contrast, Boonstra et al. (1980) reported that survival and reproduction of voles (*Microtus townsendii*) were both strongly negatively impacted by bot fly parasitism. Boonstra et al. (1980) suggested that the increased severity of parasitism on *Microtus* compared to *Peromyscus* might be attributed to the poor adaptation of bot flies to voles. The apparent reduced severity of parasitism on *Peromyscus* hosts in particular suggests that *Microtus* is a "less natural host" than *Peromyscus* (Boonstra et al. 1980:1691). This idea is supported by the lack of site specificity (i.e., infestations were found all over the body) observed by Boonstra et al. (1980) and by Getz (1970) with *Microtus pennsylvanicus*.

A two-way street: feedback between bot fly and Peromyscus population dynamics

We have shown that bot flies have negative consequences for their host's population growth rate, with decreased population growth rate of *Peromyscus* during years of intense bot fly infestation. This effect holds when variability in population growth rate due to density dependence within the mouse population is accounted for. In addition, population fluctuations of white-footed mice appear to have significant effects on the infestation prevalence patterns of bot flies, and therefore presumably on bot fly population dynamics (although not directly measured in this study). Bot fly infestation prevalence was found to be significantly higher immediately following years of peak mouse density, and lower following low years in the *Peromyscus* population (Figs. 1 and 4). Given the ~1-year time lags

in positive feedback from *Peromyscus* population density to bot flies, and the negative repercussions of bot fly infestation on white-footed mice, it seems likely that bot flies comprise a destabilizing (anti-regulating) force on mouse population dynamics (cf. Lidicker 1978, Hanski et al. 2001). Although fluctuations in mouse population size have typically been attributed to the bottom-up effects of food supply (positive response to oak mast events occurring every 3–4 years; Ostfeld et al. 1996a, Wolff 1996, Schnurr et al. 2002), we suggest that parasitism by bot flies might exacerbate the variability introduced by fluctuating food supply. For example, high-density populations would likely experience both greater competition for food and greater impacts of bot fly parasites.

In conclusion, observation of enhanced survival of infested mice, combined with decreased population growth rates in years of high-infestation prevalence, is outwardly contradictory. In one case, bot fly infestation appears to positively affect individual hosts, and in the other, a negative population-level response is found. We suggest that life history trade-offs between survival and reproduction can explain this contradiction. We provide evidence that bot fly infestation reduces the reproductive success of individual mice, at least in the short term, despite external signs of breeding activity. While life history shifts to favor future reproduction may partially ameliorate the long-term effects of parasitism on individuals, the effects of bot flies on *Peromyscus* population growth are distinctly negative.

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