



Season and prey identity mediate the effect of predators on parasites in rodents: a test of the healthy herds hypothesis

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Abstract

The healthy herds hypothesis (HHH) suggests that predators decrease parasitism in their prey. Repeated tests of this hypothesis across a range of taxa and ecosystems have revealed significant variation in the effect of predators on parasites in prey. Differences in the response to predators (1) between prey taxa, (2) between seasons, and (3) before and after catastrophic disturbance are common in natural systems, but typically ignored in empirical tests of the HHH. We used a predator exclusion experiment to measure the effect of these heterogeneities on the tri-trophic interaction among predators, parasites and prey. We experimentally excluded mammalian predators from the habitats of hispid cotton rats (*Sigmodon hispidus*) and cotton mice (*Peromyscus gossypinus*) and measured the effect of exclusion on gastrointestinal parasites in these rodents. Our experiment spanned multiple seasons and before and after a prescribed burn. We found that the exclusion of the same predators had opposite effects on the parasites of small mammal prey species. Additionally, we found that the effect of mammal exclusion on parasitism differed before versus after fire disturbance. Finally, we saw that the effect of predator exclusion was highly dependent on prey capture season. Significant effects of exclusion emerged primarily in the fall and winter months. The presence of so many different effects in one relatively simple system suggests that predator effects on parasites in prey are highly context dependent.

Keywords Fire · Parasitism · Predation · Predator–parasite interaction · Seasonality

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Introduction

Ecological theory suggests that predators keep herds “healthy” by decreasing parasitism in their prey (Packer et al. 2003). Predators cull infected individuals from populations, often selectively (Hudson et al. 1992; Stephenson et al. 2016; Gehman and Byers 2017), and decrease densities of both infected and susceptible hosts, limiting transmission (Dobson 1990; Arneberg et al. 1998). The *healthy herds hypothesis* (HHH) summarizes these predictions (Packer et al. 2003). However, empirical tests of the HHH have yielded conflicting results (Lafferty 2004; Groner and Relyea 2015; Koprivnikar and Urichuk 2017; Buss and Hua 2018; Richards et al. 2022). Heterogeneities in a variety of factors have been found to explain the presence, strength, and direction of responses in trophic cascades, a better studied type of tri-trophic interaction (Norrdahl et al. 2002; Schmitz et al. 2004), suggesting that similar factors may be important to understanding predator–prey–parasite (PPP) interactions. As a result, it is unsurprising that empirical tests of the HHH consistently fail to support the underlying theory,

because the theory assumes that systems are composed of a single generalist predator and a single homogeneous prey population, and that non-predation components of systems remain constant through time. Although additional theory has been developed to explore the outcome of violating a number of these assumptions of homogeneity (e.g. Choisy and Rohani 2006; Holt and Roy 2007), empirical work has largely focused on testing the central hypothesis. Explicit empirical tests of the violation of homogeneity assumptions are required to make reliable predictions about the potential effects of predator loss or reintroduction on parasites.

Variability among host/prey species is one major source of heterogeneity that can influence PPP interactions. Most theoretical and empirical tests of the HHH measure the effects of predator pressure on a single host/prey species (but see Hofmeester et al. 2017), obscuring important variation in how predators can influence parasites in different prey species. Some predators may show strong preferences based on prey species identity or body mass (Pearre 1982; Dickman et al. 1991; Koivunen et al. 1996a, b; Post et al. 2000). This type of variation can result in differences among prey species in the effect of predation on the density and age, body mass, or sex structure of the population, each of which can in turn influence parasitism (Schalk and Forbes 1997; Begon et al. 2002; Wilson et al. 2002). For example, the exclusion of mammalian predators increases the mean body mass of cotton rats in a population, suggesting that mammalian predators preferentially prey on larger, older, rats (Morris and Conner 2019). Since parasites are often highly aggregated in older and larger individuals (Pacala and Dobson 1988; Wilson et al. 2002), the loss of mammalian predation should have a larger consumptive effect (defined in this paper as effects of predators on parasites mediated by consumption of a shared prey/host) on cotton rat parasites than on parasites of other host species whose body mass distributions are unaffected by predation. Thus, by changing the size distribution of prey or reducing prey density, consumptive effects of predators may tend to decrease parasitism in prey. Additionally, differences in prey behavioral response to predation risk can also lead to variation in the non-consumptive effects of predators on prey (defined here as effects of predators on parasites mediated by changes in prey behavior or physiology; Preisser and Orrock 2012). These non-consumptive effects of predators can have both positive and negative effects on parasitism, but increases in parasitism are more likely because prey responses to predation typically increase contact rates between hosts and/or host physiological susceptibility to parasites (Koprivnikar et al. 2014; Stephenson et al. 2015; Buss and Hua 2018). The parasites of prey species which experience clear effects of predation on population size, size structure, or sex ratio are expected to be most strongly influenced by consumptive effects of predation. In these species, we would expect

predators to decrease parasitism in their prey, when prey density decreases or predation preferences and infection biases align. The absence of measurable consumptive effects on hosts might suggest that non-consumptive effects of predators will increase parasitism in the prey species.

Seasonal variation can also introduce heterogeneities that shape PPP interactions. For example, in systems where predators are seasonal migrants (e.g. migrating birds of prey; Smith et al. 2006; Farmer et al. 2007), the impact of predation on parasitism in prey is expected to occur primarily in the seasons when predators are present. Even resident predators show decreased activity in some seasons (e.g. some mammals and snakes; Gibbons and Dorcas 2005; Conner et al. 2011), suggesting that seasonal variation in predator activity should have strong effects on PPP interactions. Moreover, prey population size and behavior often vary seasonally, due to changes in food availability, reproduction, and torpor or hibernation (Merritt et al. 2001; Morris et al. 2011b, c), all of which can alter the relative availability of prey to different predator species affecting parasite distributions in prey populations. Consequently, we expect the effect of most predators on parasitism in prey to also vary seasonally.

Abundance and behavior of predators and prey also vary in response to disturbance events. In particular, fire frequently alters the distribution of animals on a landscape because some species vacate recently burned areas, while others colonize these areas; other species do not survive the fire itself, and still others remain essentially unaffected (Hatchell 1964; Fox 1982; Kelly et al. 2018). These effects of fire on prey arise, in part, because fire affects food availability and vegetation structure influencing the carrying capacity of burned patches, the foraging behavior of resident organisms, and interactions between predators and prey (Johnston and Odum 1956; DellaSala and Hanson 2015). Fire can also affect parasitism directly, for example, by destroying parasites which typically persist in the environment or in an intermediate host (Albery et al. 2021). As a result, the effect of predation on parasitism in prey populations is likely to vary according to the recent history of disturbances like fire. If predation tends to decrease abundance or shift body mass and sex structure towards more heavily parasitized individuals in some seasons or burn regimes but not others, then we would expect the largest reductions in parasitism in response to predation during these periods. If, instead, disturbance-based changes in the effects of predation on parasitism are decoupled from effects of predation on prey abundance or population structure, then non-consumptive effects are likely primarily responsible for predator–parasite effects and they are more likely to increase parasitism (Richards et al. 2022).

Experimental exclusion of predators is a common method of quantifying the effect of predators on prey populations (Krebs et al. 1995; Morris et al. 2011c). In

this study, we used this type of manipulative approach to quantify the effects of predator exclusion on parasitism in prey populations, and to evaluate whether these effects depended on (1) prey/host identity, (2) seasonal variation, and (3) fire disturbance. We focused on a small mammal prey community subject to avian, mammalian, and snake predation and dominated by two rodent species: hispid cotton rats (*Sigmodon hispidus*) and cotton mice (*Peromyscus gossypinus*) (Smith et al. 2006; Morris et al. 2011b, c). Cotton rats are (50–250 g) solitary, omnivorous, ground nesting rodents that breed primarily in the spring and summer and rapidly decline in population after prescribed burns due to emigration, fire-dependent mortality, and increased predation pressure (Conner et al. 2011; Morris et al. 2011a, b). Cotton rat size structures but not abundances respond to terrestrial mammal predation pressure as rats are larger when terrestrial predators are excluded. This shift in rodent body mass is likely due to a large-size refuge to the avian and snake predation which compensates for the loss of mammal predation (Conner et al. 2011; Morris and Conner 2019). Cotton mice are (10–45 g) semi-arboreal, omnivorous, rodents that breed primarily in the fall–winter (Morris et al. 2011c). Cotton mice experience increased survival and decreased predation in response to prescribed fire but their size structure is not influenced by terrestrial mammal predator exclusion, likely because even the largest cotton mice are still easy prey for snakes and birds of prey (Morris et al. 2011c; Karmacharya et al. 2012). We performed a large-scale manipulative experiment to study the effect of predator removal on this small mammal community. The experiment consisted of a large-scale mammalian meso-predator exclusion, in which we monitored gastrointestinal parasites of both study species for two years, encompassing two full seasonal cycles and one prescribed burn event. We asked three questions about the context-dependency of PPP interactions: (1) Does the exclusion of mammalian predators differentially affect parasites of different prey species? (2) Does the effect of predator exclusion vary seasonally, and/or (3) in response to prescribed burning? We predicted that excluding mammalian predators would elevate parasitism in cotton rats, due to elevated cotton rat body mass in predator exclosures (Morris and Conner 2019). We predicted that this exclusion would elevate parasitism in cotton mice only in the time following prescribed burns due to increases in their survival in predator exclosures after burns (Morris et al. 2011c). We also expected that seasonality in the effects of predation would result from differences between effects in winter, when mammal predation is rarest and spring/summer when mammal predation is most common (Conner et al. 2011).

Materials and methods

Terrestrial mammal predator exclusion experiment

Our terrestrial mammalian predator exclusion experiment was conducted at The Jones Center at Ichauway in Baker County, Georgia, United States (31.22°, –84.48°). Longleaf pine (*Pinus palustris*) and wiregrass (*Aristida beyrichiana*) cover much of the 12,000-ha property, and the community of small mammals in this habitat is dominated by cotton rats and cotton mice. Longleaf pine ecosystems are fire-dependent and all sites were burned in February–March during odd years according to a 2-year prescribed burn regime beginning in 2001, though the area has been regularly burned since the 1930s (Atkinson et al. 1996). Prescribed fires were conducted by licensed practitioners using drip torches. A mixture of backing fires and strip fires were used for ignition while roads through the site served as firebreaks. These prescribed fires are typically fast-moving, low intensity fires which primarily affect the understory of the longleaf pine-wiregrass savanna ecosystem. Previous research in our study sites has found that cotton rats and cotton mice were affected by fire in different ways. Cotton rat populations declined precipitously due to predation and emigration immediately following a burn (Conner et al. 2011; Morris et al. 2011b). Cotton mouse populations persisted through fire and exhibited increased survival after fire in the absence of mammalian predators (Morris et al. 2011c). Understory vegetation recovers quickly in response to fire (Atkinson et al. 1996) and so we consider only seasons in the 12 months following the fire as “burn” treatments for the purposes of this experiment. Both rodent species were reliably trapped seasonally in the predator manipulation plots (Morris et al. 2011b, c), and both were subject to predation from multiple predator guilds, including raptors, meso-mammalian carnivores, and snakes (Smith et al. 2006; Derrick et al. 2010; Conner et al. 2011). Cotton rats and mice also host a suite of gastrointestinal parasites (Kinsella 1974, 1991; Bergstrom et al. 2019; Thompson et al. 2019), making this system highly tractable for addressing questions about PPP interactions.

In 2002, the Jones Center constructed four ~40 ha terrestrial meso-predator exclosures and four control plots within similar habitat (Fig. 1). The predator exclosures are surrounded by 1.2-m-tall woven wire fences with electrified lines running along them to discourage mammals from climbing over or digging under the fence. The size of the fence weave excludes meso-mammals but allows small mammals to pass through. Excluded predator species included coyotes (*Canis latrans*), gray foxes (*Urocyon cinereoargenteus*), red foxes (*Vulpes vulpes*), raccoons

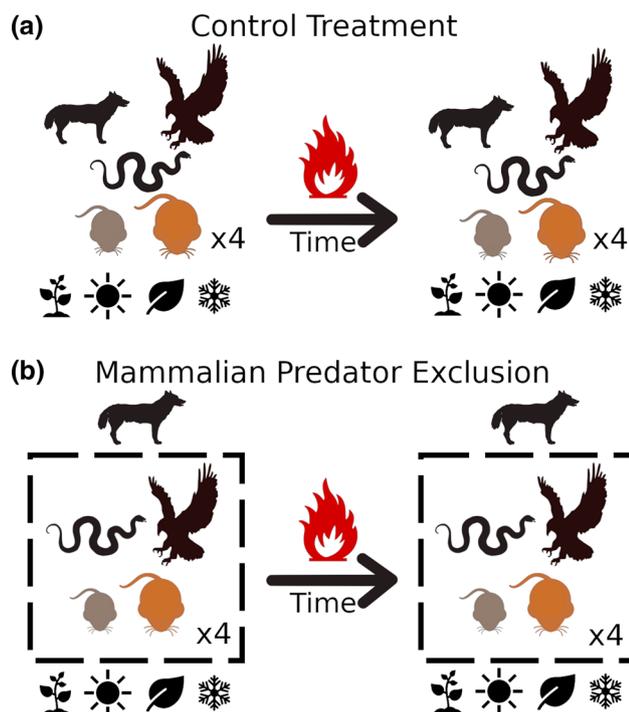


Fig. 1 The predator exclusion experiment was conducted over a span of 2 years in 8 patches of longleaf pine savanna habitat. **a** 4 patches were left open to predation by terrestrial mammal predators, avian predators, and snake predators. **b** Electric fences were erected around 40 ha areas ~15 years prior to the experiment in 4 patches. These fences excluded terrestrial mammal predators but allowed all other predators access to cotton mouse and cotton rat prey/hosts. All patches were burned once during the experiment and were trapped once each calendar season (spring, summer, fall, winter) before and after prescribed burning. Biometric measurements and fecal samples were taken from cotton mice (small gray) and cotton rats (large brown) during each trapping event

(*Procyon lotor*), Virginia opossums (*Didelphis virginiana*), striped skunks (*Mephitis mephitis*), spotted skunks (*Spilogale putorius*), and nine-banded armadillos (*Dasypus novemcinctus*). All of these species, except for armadillos, are common predators of small mammals in this system and predation pressure peaks in the spring (Conner et al. 2011). Raptors and snakes were not excluded and have been shown both to commonly prey on these species and to vary seasonally in density and activity, with snake predation and activity lowest in the winter months and avian predation pressure strongest in the winter (Smith et al. 2006; Conner et al. 2011, Howze et al. Unpublished data). Snakes were also less abundant in the year following a prescribed burn (Howze et al. Unpublished data). Relative predator species abundances and preferences for our two focal prey species are not well understood in this system. Total mammal predator presence in control and predator exclusion plots was monitored regularly with track counts (Conner et al. 2010; Morris et al. 2011b).

Although mammal predators occasionally penetrated the fence, the predator exclusions reduced meso-predator presence by approximately 90% in prior studies (Conner et al. 2011). We collected data on mammalian predator presence in both control and predator exclusion plots for 3 nights (when small mammals were not trapped) each season, using counts of predator tracks in five 1.5 m by 0.5 m raked sandy areas in each plot. Tracks were checked in the morning by experts in mammalian track identification and then raked clean of debris and old tracks. The effect of mammalian predator exclusions on other rodent predators is well characterized in this system. There was no difference in the proportion of cotton rat mortality due to snakes in the predator exclusions historically (Conner et al. 2011) and the abundance of snakes did not significantly differ between predator exclusion and control plots during the years of the study (Howze et al. Unpublished data). The proportion of cotton rat mortality due to avian predators was significantly greater in predator exclusion plots than control plots, but this increase was largely compensatory for lost mammal predation resulting in no overall change in predation rates (Conner et al. 2011). Neither avian predator prevalence nor predation rates were directly measured during the period of this study.

Each control and predator exclusion plot contained a 12 trap × 12 trap small mammal trapping grid with 15-m spacing between traps. Within predator exclusion plots these grids were placed in the center of exclusions so that the home ranges of all trapped rodents should fall entirely within the exclusion (Morris et al. 2011a, c), though gaps in fences were sufficiently large for rodents to pass through. The longleaf pine habitat was generally consistent throughout the plot. For this study, grids were trapped four times per year (once each season; Fall: September–November, Winter: December–February, Spring: March–May, Summer: June–August) from October 2016 through August 2018 (Table S2). Trapping in a grid occurred on 4 consecutive nights each season and one predator exclusion and one control plot were trapped at the same time. We used Sherman live traps baited with a mixture of birdseed and oats (H.B. Sherman Traps, Tallahassee, FL, USA) and checked traps each morning. The prescribed burn occurred between the Winter 2017 and Spring 2017 trapping seasons. Granular insecticide (Bifen L/P Insecticide Granules, Control Solutions, Inc, Pasadena, TX, USA) was sprinkled around each trap to deter fire ants. New captures were marked individually with metal ear tags. Data recorded for all captures included site, trap location, species, sex, mass, reproductive condition (for males, testes descended or not, and for females, pregnant and/or lactating or not), and hind foot length. Fecal samples were collected from traps after animal release and stored on ice packs while in the field and then at ~4 °C in the lab until processing.

Parasite analysis

A modified double centrifugation method was used to quantify the number of helminth parasite eggs present in fecal samples (Foreyt 2013). Briefly, fecal samples were weighed, homogenized in water and then concentrated by centrifugation. Pellets were resuspended in sugar solution (specific gravity = 1.27) and concentrated on a single microscope cover slip. Helminth eggs found on the cover slip were identified to taxonomic group and morphotype according to size and morphological characteristics and quantified under a compound microscope at 40× magnification. Fecal egg counts were used as a proxy for parasite abundance within the host (Cabaret et al. 1998; Pedersen and Antonovics 2013). Common parasites of cotton rats included two strongyle nematode morphotypes (strongyle 1 and strongyle 2, Figure S1a and b), one cestode morphotype (Figure S1d) and one spirurid nematode morphotype (Figure S1d; Table S3, Table S4). Common parasites of cotton mice included the same two strongyle nematode morphotypes and the cestode morphotype described in cotton rats (Figure S1a, b, and d; Table S3, Table S5). The spirurid morphotype was extremely rare in cotton mice (Tables S3, S5) and was excluded from all analyses.

We were not able to positively identify the parasites to species level, but strongyle nematodes of rodents are generally transmitted between host individuals via a fecal oral route (Streicker et al. 2013), while spirurid nematodes of cotton rats typically have an insect intermediate host (Schell 1952; Kinsella 1974). All of these parasite taxa are well described in our focal mammal species, but their prevalence and abundance can vary between habitats (Kinsella 1974, 1991). While there is limited evidence on the fitness costs of parasitism in our study system, evidence from the literature suggests that intestinal helminths of rodents can impose morbidity, fecundity, and mortality costs that are proportional to the intensity of infection (Pedersen and Greives 2008; Schwanz 2008; Shanebeck et al. 2022).

Statistical analysis

We used a (Gaussian) generalized linear mixed model (GLMM) to test for the effect of the predator exclusion treatment on the number of mammalian predator track counts per observation night as an index of mammalian predator abundance. Models included terrestrial mesopredator exclusion treatment (hereafter exclusion treatment), season, burn status and all two-way interactions with exclusion treatment as fixed effects and plot as a random effect. We also used (Gaussian) GLMMs to test for the effect of the exclusion treatment, season, burn status, and interactions on the natural log of the estimated abundance of cotton rats and cotton mice in each plot.

Abundances were estimated using Huggins closed population models for each plot in each season (Huggins 1989). For grid seasons with fewer than 4 individual capture histories, we instead used the minimum number known alive (Krebs 1966) to estimate abundance due to constraints of the Huggins closed population models. Additionally, we tested for the effect of exclusion treatment on both host species individual body mass (Gaussian) and sex ratio (binomial) using GLMMs with fixed effects of treatment, season, burn status, and all two-way interactions (sex model), and sex, treatment, season, burn status, and all two-way interactions (body mass model) with a random effect of plot in both models. All models were checked for fit using diagnostic plots.

We also used GLMMs to test for a relationship between exclusion treatment and parasite abundance. In this case, models were fit with both negative binomial and zero-inflated negative binomial distributions to account for aggregation in parasite count data. The best-fitting model was selected using the corrected Akaike Information Criterion (Anderson and Burnham 2002). All parasite models included the random effects of individual, nested within trapping plot, to control for consistent variation in parasite abundances among individuals and plots. Predator exclusion treatment, individual body mass, sex, season, burn status, and the interactions of all the latter terms with exclusion treatment were included as fixed effects. All models were assessed for violation of assumptions of distribution and uniformity of residuals using residuals plots. A type III analysis of variance was performed on all models to assess the significance of main effects and interaction terms (Fox 2015; Fox and Weisberg 2019). When interactions with exclusion treatment were significant, we conducted a post hoc analysis of differences between the marginal means of exclusion treatments across levels of the interacting factor while controlling for multiple comparisons using the Tukey method (Searle et al. 1980; Lenth 2020).

All analyses were performed using the R programming software (R Core Team 2020). Small mammal abundances were estimated using the *F.huggins.estim* function of the *mra* package (McDonald 2018). GLMMs were fit using the *glmmTMB* function from the *glmmTMB* package (Brooks et al. 2017), and model comparison was performed using the *model.sel* function from the *MuMIn* package (Barton 2019). Residual plots were produced using the *simulateResiduals* function of the *DHARMA* package (Hartig 2020), and ANOVAs were conducted using the *Anova* function of the *car* package (Fox & Weisberg 2019). Posthoc analyses were performed using the *emmeans* and *pairs* functions of the *emmeans* package (Lenth 2020) and the *glht* function of the *multcomp* package (Hothorn et al. 2008).

Results

Mammalian predator abundance

There was a significant effect of enclosure treatment on predator track counts per observation night ($\chi^2 = 15.37$, $df = 1$, $p < 0.001$, Figure S6, Table S7). On average, 88.8% fewer tracks were found in predator enclosures than controls. No other factors (e.g. season, burn treatment) were significant predictors of mammal predator track counts.

Small mammal abundance, body mass, and sex ratio

We failed to detect an effect of the predator enclosure treatment or any interactions on estimated cotton rat abundance, though the effect of burn treatment was significant ($\chi^2 = 15.217$, $df = 1$, $p < 0.001$; Table S8), with more cotton rats in non-burn years (Figure S9). Cotton mouse abundances also showed no response to enclosure treatment but did significantly vary by season ($\chi^2 = 15.617$, $df = 3$, $p = 0.001$; Table S10), with the lowest abundances in the fall (Figure S11).

There was no significant effect of enclosure treatment or any of its interactions on cotton rat or cotton mouse sex ratio (Table S12, Table S15), though season and burn treatment did affect cotton rat sex ratio (Table S12) with more males in the winter and in non-burn years (Figure S13, Figure S14). There was also no significant effect of enclosure treatment or interactions on cotton mouse body mass, though again both season and burn treatment were important (Table S16), with the highest masses in the fall and in non-burn years and the lowest masses in the spring (Figure S17, Figure S18). We did find a significant effect of enclosure treatment ($\chi^2 = 22.10$, $df = 1$, $p < 0.001$) and its interaction with season ($\chi^2 = 19.33$, $df = 3$, $p < 0.001$) on cotton rat mass (Table S19, Figure S20). This pattern was driven by significantly higher body masses in predator enclosure plots than in control plots in the fall ($t = -3.31$, $df = 1028$, $p < 0.001$), while there was no difference in winter ($t = -0.096$, $df = 1028$, $p = 0.924$), spring ($t = 1.60$, $df = 1028$, $p = 0.11$), or summer ($t = 0.998$, $df = 1028$, $p = 0.319$).

Cotton rat parasites

We found strong seasonality of parasitism in cotton rats and of the predator–parasite interaction. Four parasite taxa (Strongyle 1, Strongyle 2, Spirurid, and Cestode) were observed infecting cotton rats in the predator exclusion experiment (Figure S1, Table S2, Table S3). Strongyle 1 and Strongyle 2 were very weakly but significantly negatively correlated in cotton rat hosts (Spearman's $\rho = -0.07$,

$p = 0.03$), all other parasite pairs were not significantly related (Table S21). For two parasite taxa (Strongyle 1 and 2), we failed to detect a significant effect of the enclosure treatment or its interactions on parasite abundance (Table 1). However, the abundance of both parasites varied significantly with capture season (Table 1). Strongyle 1 abundance was generally highest in summer and winter, while Strongyle 2 abundance was generally highest in fall and spring (Figure S22, Figure S23). The interaction between enclosure treatment and season had a clear effect on the third parasite, the Spirurid. In this case, capture season, predator treatment, and the interaction between enclosure treatment and capture season were significant predictors of abundance (Table 1). Specifically, Spirurid abundance differed between treatment types in winter ($t = -2.681$, $df = 1028$, $p = 0.030$), but not in spring ($t = 1.884$, $df = 1028$, $p = 0.219$), summer ($t = 1.494$, $df = 1028$, $p = 0.441$), or fall ($t = -0.151$, $df = 1028$, $p = 0.999$; Fig. 2a). There was also a significant interaction between cotton rat abundance and predator treatment (Table 1). Parasites increased with host abundance in controls (slope = 0.0132, SE = 0.0048) but not enclosures (slope = -0.0080, SE = 0.0080; Fig. 2b). Overall, the effects of the predator treatment occurred in the Spirurid during the winter, when predator enclosures increased parasite abundances, and predator exclusion eliminated any relationship between host abundance and parasite abundance. None of our predictor variables explained Cestode presence in cotton rats (Table 1).

Cotton mouse parasites

For cotton mice, the effects of predator enclosure treatment on parasite abundance depended on capture season or burn treatment. Three parasite taxa (Strongyle 1, Strongyle 2 and a Cestode) were observed to commonly infect cotton mice in the predator exclusion experiment (Figure S1, Table S2, Table S5). None of these parasites were significantly correlated (Table S21). For Strongyle 1, both capture season and the interaction between enclosure treatment and capture season were significant predictors of abundance, while enclosure treatment alone was not (Table 1). The effect of the interaction was such that Strongyle 1 abundance differed between treatment types in winter ($t = 3.887$, $df = 604$, $p < 0.001$) and summer ($t = 3.757$, $df = 604$, $p < 0.001$), when predator enclosures decreased parasite abundance, but not in fall ($t = -1.919$, $df = 604$, $p = 0.204$) or spring ($t = 1.070$, $df = 604$, $p = 0.739$; Fig. 3a). For Strongyle 2, the effect of predator enclosures on parasite abundance varied both seasonally and between burn treatments. The main effect of burn year, the interaction between enclosure treatment and burn, and the interaction between enclosure treatment and capture season were all significant predictors of Strongyle 2 abundance, while enclosure treatment alone was not

Table 1 Full results of generalized linear models for parasite abundance in cotton rats and cotton mice, during our mammalian predator exclusion experiment

Variable	Cotton rats				Cotton mice		
	Strongyle 1	Strongyle 2	Spirurid	Cestode	Strongyle 1	Strongyle 2	Cestode
Intercept	270.8₁ (<0.0001)	609.5₁ (<0.0001)	10.45₁ (0.001)	0.000 ₁ (0.999)	0.7097 ₁ (0.400)	20.197₁ (<0.0001)	9.392₁ (0.002)
Sex	14.49₁ (0.0001)	8.135₁ (0.004)	0.0158 ₁ (0.900)	0.000 ₁ (0.999)	0.0336 ₁ (0.855)	6.289₁ (0.012)	0.008 ₁ (0.928)
Predator treatment	1.677 ₁ (0.195)	0.0498 ₁ (0.823)	4.434₁ (0.035)	0.000 ₁ (0.999)	0.0133 ₁ (0.908)	2.439 ₁ (0.118)	1.063 ₁ (0.303)
Body mass	12.83₁ (0.0003)	45.945₁ (<0.0001)	38.588₁ (<0.0001)	1.127 ₁ (0.289)	0.1281 ₁ (0.720)	2.153 ₁ (0.142)	0.178 ₁ (0.673)
Season	18.98₃ (0.0003)	23.895₃ (<0.0001)	52.242₃ (<0.0001)	1.565 ₃ (0.667)	24.911₃ (<0.0001)	3.436 ₃ (0.329)	13.261₃ (0.004)
Burn treatment	1.605 ₁ (0.205)	4.753₁ (0.029)	0.7278 ₁ (0.394)	0.000 ₁ (0.999)	6.603₁ (0.010)	19.619₁ (<0.0001)	2.531 ₁ (0.112)
Host abundance	16.78₁ (<0.0001)	1.192 ₁ (0.275)	0.315 ₁ (0.575)	–	9.447₁ (0.002)	0.4823 ₁ (0.487)	2.092 ₁ (0.148)
Predator treatment*sex	2.600 ₁ (0.107)	0.1789 ₁ (0.672)	1.004 ₁ (0.316)	3.104 ₁ (0.078)	1.788 ₁ (0.181)	0.2112 ₁ (0.645)	0.001 ₁ (0.969)
Predator treatment*body mass	0.2654 ₁ (0.606)	1.074 ₁ (0.300)	0.0366 ₁ (0.848)	0.612 ₁ (0.434)	0.3956 ₁ (0.530)	1.592 ₁ (0.207)	1.257 ₁ (0.262)
Predator treatment*season	1.266 ₃ (0.737)	4.720 ₃ (0.194)	16.64₃ (0.0008)	7.410 ₃ (0.060)	15.01₃ (0.002)	19.151₃ (0.0002)	6.417 ₃ (0.093)
Predator treatment*burn treatment	0.3049 ₁ (0.581)	0.0386 ₁ (0.844)	0.3250 ₁ (0.567)	0.000 ₁ (0.999)	0.440 ₁ (0.507)	10.56₁ (0.001)	5.858₁ (0.016)
Predator treatment*host abundance	1.018 ₁ (0.313)	0.0673 ₁ (0.795)	5.052₁ (0.025)	–	1.928 ₁ (0.165)	3.561 ₁ (0.059)	0.011 ₁ (0.918)
Random effect of individual (variance)	0.6886, 0.0633	0.7730, <0.0001	1.973	274.3	2.368, 0.0092	0.8536, 0.2703	771.5
Random effect of plot pair (variance)	0.2083, 0.6297	<0.0001, 0.3432	<0.0001	<0.0001	0.0664, 0.3233	<0.0001, 0.0916	0.0002

Statistics show the chi-squared value, degrees of freedom, and (*p* value). Significant effects are displayed in bold. The final 2 entries for each model represent the variance explained by random intercept effects if two values for random intercepts are presented, the first is in the count model, and the second in the zero-inflation model

(Table 1). With respect to the season by enclosure treatment interaction, Strongyle 2 abundance differed between enclosure and control treatment types in fall ($t = -3.253$, $df = 604$, $p = 0.005$) and winter ($t = 1.632$, $df = 604$, $p = 0.038$), but not in spring ($t = -0.973$, $df = 604$, $p = 0.800$) or summer ($t = 0.003$, $df = 604$, $p = 1.00$ Fig. 3b). Interestingly, predator enclosures increased Strongyle 2 abundance in fall, while in winter predator enclosures decreased Strongyle 2 abundance. For the burn by enclosure treatment interaction, Strongyle 2 abundance differed between treatment types in the year without a burn ($t = -2.533$, $df = 604$, $p = 0.023$), increasing when predators are excluded. There was no effect in the burn year ($t = 2.009$, $df = 604$, $p = 0.088$; Fig. 3c). For the cestode, the effect of predator exclusion on presence also significantly varied between burn treatments (Table 1). The effect of predator exclusion trended in opposite directions during the

burn year and the non-burn year but neither difference was significantly different from zero (burn: $t = 1.448$, $df = 623$, $p = 0.275$; non-burn: $t = -1.934$, $df = 623$, $p = 0.104$).

Discussion

We tested for effects of seasonality, disturbance, and variation in prey species identity on the predictions of the healthy herds hypothesis. The HHH posits that, because predators remove infected prey from a population and control prey population density, the loss of predators should increase parasitism in prey (Packer et al. 2003). However, we found, as we predicted, that mammalian predator enclosures had variable effects on parasitism in prey. First, we found that both the strength and direction of the effect of predator

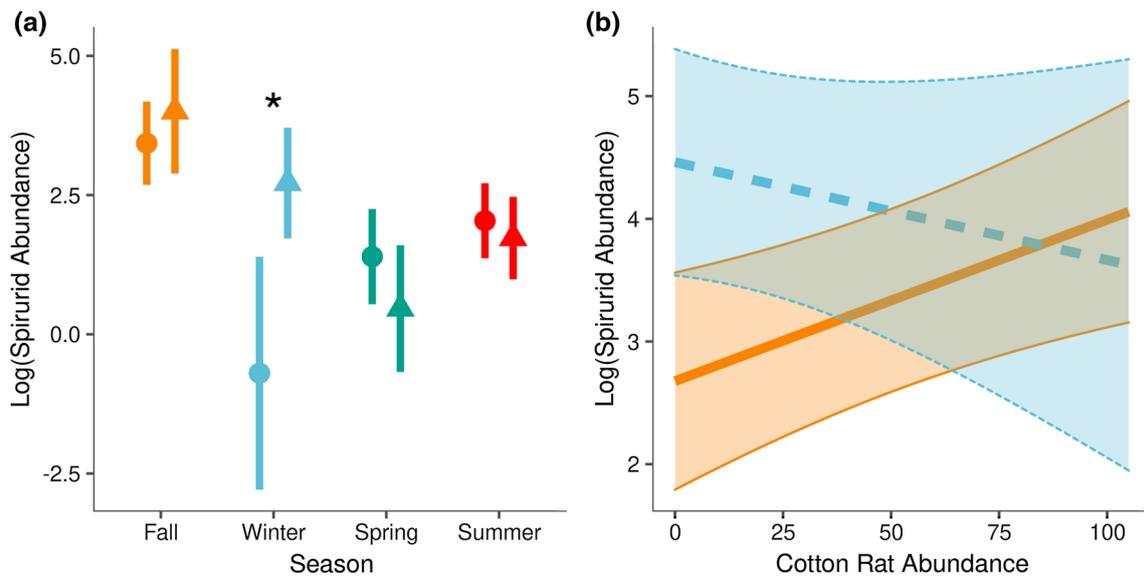


Fig. 2 Mean parasite eggs per gram of feces of a Spirurid in cotton rats **a** in predator exclusion (triangle) and control (circle) plots of our terrestrial mesopredator exclusion experiment separated by season

and **b** over the range of cotton rat abundance separated into predator exclusion (solid line) and control (dashed line). Points are presented on a natural log scale. Error bars represent 95% confidence intervals

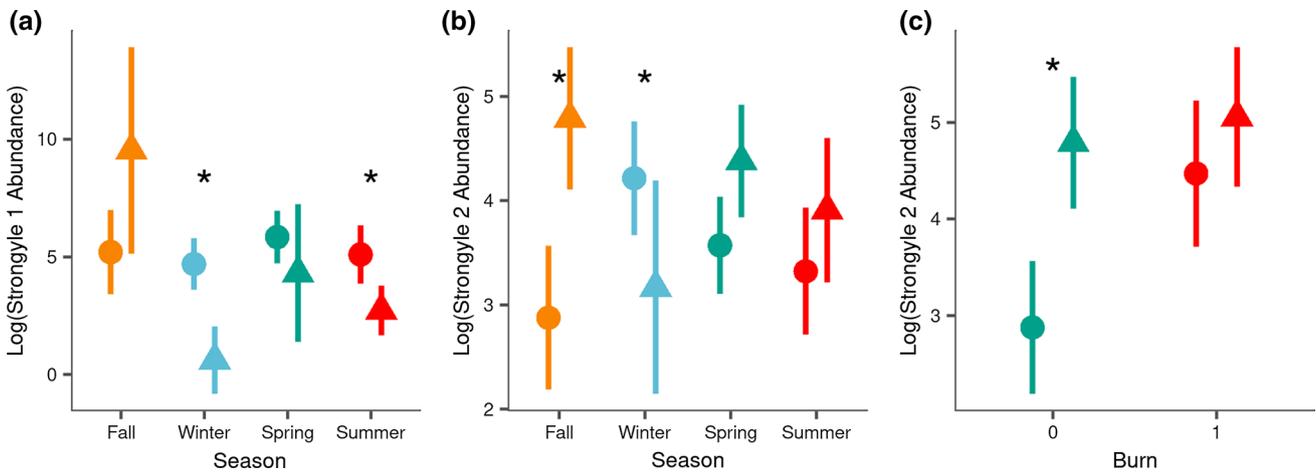


Fig. 3 Mean parasite eggs per gram of feces in predator exclusion (triangle) and control (circle) plots of our terrestrial mesopredator exclusion experiment in cotton mice for **a** Strongyle 1 and **b, c** Strongyle 2, separated by **a, b** season or **c** burn treatment history (1—burn, 0—non-burn). Points are presented on a natural log scale. Error bars represent 95% confidence intervals

gyle 2, separated by **a, b** season or **c** burn treatment history (1—burn, 0—non-burn). Points are presented on a natural log scale. Error bars represent 95% confidence intervals

enclosures on small mammal parasites varied seasonally, with effects concentrated in the fall and winter months. Second, we found that fire disrupted the effect of predators on parasites in cotton mice. Finally, we found that the direction of the effect of predator exclusions varied with host species identity. These findings suggest that taxonomic and seasonal variation in predator–prey interactions shape how predation affects parasitism in prey.

Seasonality influenced the effect of predators on parasite abundance in our experiment. Terrestrial mammal predator exclusions affected parasite abundances in cotton

rats and cotton mice in the fall, winter, and summer. The importance of seasonality in our study system may be explained by seasonality in the predator, the prey, or the predator–prey interaction itself. First, the focal predators that were excluded may vary seasonally in their abundance or behavior, making their exclusion most apparent during seasons when they would otherwise be present or active. However, based on track surveys, we saw no sign of seasonal variation in mammal predator presence, and prior studies found that winter months had the lowest proportional mammalian predation pressure (Conner et al. 2011). Second, the

vegetation phenology and structure of our system varies seasonally. This variation almost certainly alters the interactions between predator and prey species. Notably, changes in vegetative cover and food availability alter rodent risk-taking behavior during foraging as well as predator foraging preferences. For example increased vegetation cover decreases the amount of high-risk open foraging by prey (Schooley et al. 1996; Cherry et al. 2016), but the data collected in this study do not allow us to effectively test this mechanism. Third, it is possible that seasonal changes in the abundance of unmanipulated predators magnified the effects of our predator manipulations during certain periods. For example, in addition to meso-mammals and raptors, snakes are well-known predators of rodents (Gibbons and Dorcas 2005; Conner et al. 2011) whose abundance was not influenced by our enclosure treatments (Howze et al. Unpublished Data, Conner et al. 2011). However, in much of the southeastern United States snakes enter a seasonal torpor during colder months, eliminating the predation pressure on focal prey species during this period (Gibbons and Dorcas 2005; Conner et al. 2011). Thus, the loss of snake predation during the fall and winter may have magnified the importance of meso-mammal and avian predation for controlling both prey and parasite populations. We find limited evidence of this mechanism in the effect of predator enclosures on cotton rat body mass in the fall, which is when snake predation began to decline in prior studies (Conner et al. 2011). When mammalian predators are excluded and snakes are becoming dormant, avian predator preference for smaller prey items (Dickman et al. 1991; Koivunen et al. 1996a) produces a shift in average host body mass without changes in density in predator enclosures. This pattern occurs just before the winter months when we see a strong, negative effect of predation on parasitism by Spirurids, a parasite aggregated in larger individuals in our system.

No measures of cotton mouse population abundance or demography varied with exclusion treatment. As a result, the seasonal effects of predators on parasites in cotton mice are unlikely to be directly consumptive in nature. Predators can have non-consumptive effects on the behavior and physiology of their prey (Schmitz et al. 2004; Preisser et al. 2007), which can in turn influence parasitism (Raffel et al. 2010; Bertram et al. 2013). These non-consumptive effects of predators on parasites may themselves be seasonal for many of the reasons discussed above, but seasonality in prey behavior may be relevant as well. In southern Georgia, cotton mice primarily breed during the fall and winter, the same period in which predator effects are concentrated (Morris et al. 2011c). As a result, we hypothesize that changes in cotton mouse behavior between the peak and non-peak breeding season generate differences in prey behavioral or physiological responses to predators which increase parasite susceptibility or transmission rates. Therefore, our study

points to the seasonality of PPP interactions arising due to seasonality in consumptive effects of predators in cotton rats, versus seasonality in non-consumptive effects of predators in cotton mice. Overall, our work suggests that seasonal variation is central to shaping PPP interactions. Consequently, short-term experiments that fail to consider seasonality are inadequate for drawing inferences about the HHH in natural systems.

Periodic disturbances, such as prescribed fire, can alter predator–prey interactions (Torre and Díaz 2004; Lyons et al. 2015; Leahy et al. 2016). We found that predator enclosures only affected the abundance of a single cotton mouse parasite in the year without a burn. In this “non-burn” year, we observed a classic healthy herds effect, with significantly higher parasite abundance in predator enclosure plots. Burning drastically alters the ground cover and plant community (Glitzenstein et al. 1995; Brockway and Lewis 1997) in ways that influence both predator and prey behavior (Fordyce et al. 2015; Lyons et al. 2015). In our system, fire has strong short-term effects on small mammal survivorship and predation-associated mortality (Conner et al. 2011; Morris et al. 2011b, c). Of particular relevance to our findings, the effect of predator enclosures on cotton mouse survival varies with recent fire history, with increased survival in predator enclosures after burns (Morris et al. 2011c). It therefore follows that recent fire history should also influence PPP interactions in cotton mice, and indeed we found that predator exclusion leads to increased parasitism only in the non-burn years (Fig. 2c). However, over the time period of our study, we did not detect an effect of fire on differences between enclosure treatments in any factors relevant to cotton mouse predation. This lack of alignment between consumptive effects on cotton mice and predator effects on their parasites again supports the potential importance of non-consumptive effects of predators on parasites of cotton mice, via changes to prey behavior or physiology. For example, parasitism may be uniformly high during burn-years due to burrow and refuge use by mice following a fire (Derrick et al. 2010) increasing contact rates, while in non-burn years mouse contact rates may depend on the perceived threat of predation. Our results highlight the important role fire also plays in the ecology of the parasites associated with predator–prey systems subject to this type of disturbance.

The effects of mammalian predator enclosures varied by prey species and parasite taxon but the drivers of these differences require further consideration. While exclusion of meso-predators increased parasite abundance in cotton rats during winter, in cotton mice the abundance of parasites decreased under the same conditions. The cotton mouse result is the opposite of what the HHH predicts (Packer et al. 2003). Moreover, the opposing pattern in cotton rats vs. mice suggests an important difference in the nature of predation pressure experienced by these two species during the winter.

Given evidence of seasonal variation in consumptive effects of predators on cotton rats (see above) that aligns with the effects on parasites, and an absence of similar effects in cotton mice, this finding provides additional support for a difference in the mechanisms of predator effects on parasites in the two rodent species (i.e. predator effects on parasites are primarily consumptive in cotton rats and primarily non-consumptive in cotton mice). Future work should measure behavioral and physiological effects of predators, such as space-use behavior and stress or immune function, to better characterize the actual mechanisms mediating the non-consumptive effects in cotton mice.

In our study, we also found that different parasite taxa showed variable responses to predation. Most notably only the indirectly transmitted Spirurid showed a response to the enclosure treatment in cotton rats, while the directly transmitted Strongyle nematodes did not. The most plausible explanation for this difference is the way the size-distribution of the parasites in cotton rats interacts with size-selective predation. Spirurid abundance was strongly positively correlated with cotton rat body mass while Strongyle 1 was negatively associated and Strongyle 2 weakly positively associated with host body mass (Table 1). As a result, the shift to larger sized rats in the enclosure treatment could have affected the positively size-structured parasite (the Spirurid) most. Another interesting observation is that the burn treatment interacts significantly with the exclusion treatment for Strongyle 2 but not for Strongyle 1. This pattern is more difficult to explain but we hypothesize that Strongyle 2, given its higher prevalence and abundance in cotton mice, could be more transmissible. Therefore, while both parasites showed an increase in transmission due to the increased burrow and refuge use by mice in the period following a burn (Table 1), only the more transmissible parasite (Strongyle 2) showed a significant response to the more subtle difference in contact rates due to perceived predator pressure. While these parasite-specific explanations for the patterns we observed are speculative at this point, they provide additional context for our results.

Overall, our exclusion experiment highlights the importance of species identity, seasonality, and disturbance in shaping the effect of predators on parasites in their prey. Given these findings, we propose that future investigations of the HHH explicitly consider the role of these factors in PPP interactions to improve the accuracy of study predictions. While it may be daunting to consider the large number of possible drivers of tri-trophic PPP interactions, a path forward has already been paved by research on other three-species interactions, such as competition (Gurevitch et al. 1992, 2000) and trophic cascades (Shurin et al. 2002; Schmitz et al. 2004). A key weakness of our own study is the lack of manipulation of all possible predator species. This limitation obscures potentially important ways that different

predator taxa may differentially, additively, or multiplicatively influence parasitism in their shared prey. Thus, to draw meaningful and generalizable conclusions about the role of different heterogeneities in shaping PPP interactions, future studies should move beyond the paradigm of measuring parasitism in a single host with or without a single predator over a short period of time.

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Author contribution statement RLR, VOE, JMD, and LMC conceived the ideas and designed the study; LMC and GM designed and maintain the long-term predator exclusion experiment, RLR and GM collected the data, RLR analyzed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Availability of data and material The data were deposited in the figshare repository at <https://doi.org/10.6084/m9.figshare.17194619>. Available at <https://doi.org/10.6084/m9.figshare.17194619> prior to publication.

Code availability The code to reproduce these results is deposited in the figshare repository at <https://doi.org/10.6084/m9.figshare.17194619>. Available at <https://doi.org/10.6084/m9.figshare.17194619> prior to publication.

Declarations

Conflict of interest We declare no competing interests.

Ethics approval Animal experiments and use of samples were approved by the University of Georgia Animal Care and Use Committee (#A2016 04-024-Y3-A6) and complies with current laws of the USA and the state of Georgia.

Consent to participate Not applicable.

Consent for publication Not applicable.

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