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BAYLISASCARIS PROCYONIS INFECTION IN WHITE-FOOTED MICE: PREDICTING PATTERNS OF INFECTION FROM LANDSCAPE HABITAT ATTRIBUTES

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ABSTRACT: There is a growing body of evidence that habitat fragmentation resulting from anthropogenic land use can alter the transmission dynamics of infectious disease. *Baylisascaris procyonis*, a parasitic roundworm with the ability to cause fatal central nervous system disease in many mammals, including humans, is a zoonotic threat, and research suggests that parasite recruitment rates by intermediate hosts are highly variable among forest patches in fragmented landscapes. During 2008, we sampled 353 white-footed mice (*Peromyscus leucopus*) from 22 forest patches distributed throughout a fragmented agricultural ecosystem to determine the influence of landscape-level habitat attributes on infection rates of *B. procyonis* in mice. We characterized each mouse in terms of infection status and intensity of infection, and calculated (on a patch-wide basis) prevalence, mean abundance of *B. procyonis*, and mean intensity of infection. We used an information-theoretic approach to develop a suite of candidate models characterizing the influence of landscape attributes on each of our measured characteristics of *B. procyonis* infection in white-footed mice, based on previous knowledge of raccoon (*Procyon lotor*) ecology and *B. procyonis* distribution in agricultural ecosystems. We observed evidence of *B. procyonis* infection in mice across all 22 habitat patches sampled. However, parasite recruitment rates and intensity were highly variable among patches, and the results of our analyses suggest that spatial variability in *B. procyonis* infections was primarily driven by emergent properties of fragmented ecosystems. In particular, prevalence, abundance, and intensity of *B. procyonis* infections in mice were negatively associated with the size and connectivity of forest patches. These results support previous studies indicating that habitat fragmentation can alter the transmission dynamics of infectious disease, and suggest that factors below the scale of landscape, i.e., fine-scale habitat structure or demographic and behavioral attributes of intermediate and/or definitive hosts, also may be important for predicting patterns of *B. procyonis* infection in intermediate hosts.

Baylisascaris procyonis is a parasitic roundworm recognized as a zoonotic threat that uses the raccoon (*Procyon lotor*) as its definitive host (Sorvillo et al., 2002; Wise et al., 2005; Pai et al., 2007). White-footed mice (*Peromyscus leucopus*) and other small rodents are the most common intermediate hosts, often becoming infected while foraging upon undigested seeds within raccoon scat, particularly if corn is present in the feces (Page et al., 2001a, 2001c). However, some exposure to *B. procyonis* eggs by small mammals may occur simply as a consequence of their normal movement behavior, as raccoon latrines, i.e., defecation sites, usually are located within important travel corridors for these species (Page et al., 1998). Exposure risk also may be elevated in fragmented ecosystems, where white-footed mice and raccoons often are ubiquitous and abundant, and movements of both species are concentrated in remnant forest fragments (Nupp and Swihart, 2000; Moore and Swihart, 2005; Beasley and Rhodes, 2010).

There are 2 key factors underlying the increased potential for *B. procyonis* infections in white-footed mice in fragmented landscapes. First, both *B. procyonis* in raccoons and the density of latrines are higher in fragmented landscapes than in continuously forested settings (Kazacos, 2001; Page et al., 2001b; Smyser et al., 2010). Reflecting these patterns, larval infections in white-footed mice also are elevated in fragmented landscapes relative to individuals in heavily forested ecosystems (Page et al., 2001b). Second, raccoon populations thrive in landscapes fragmented by agriculture, where densities greatly exceed those of populations in less disturbed ecosystems (Beasley et al., 2011; Houle et al., 2011). Within fragmented agricultural ecosystems, raccoons are highly dependent upon agricultural food resources, and thus their

movements are primarily concentrated within forest remnants and along forest-agricultural interfaces (Rivest and Bergeron, 1981; Beasley, DeVault, and Rhodes, 2007; Beasley, DeVault, Retamosa et al., 2007; DeVault et al., 2007; Beasley and Rhodes, 2010). The combination of high densities, intensive use of forested habitats, extensive use of corn, and high prevalence of *B. procyonis* exhibited by raccoons in agricultural ecosystems all increase the probability that white-footed mice are being exposed to raccoon latrines with infected *B. procyonis* larvae (Page et al., 2001b).

Despite a growing awareness that habitat fragmentation can alter the transmission dynamics of infectious disease (Allan et al., 2003; LoGiudice et al., 2003; Brownstein et al., 2005), few data exist pertaining to factors affecting the spatial distribution of *B. procyonis* infection in agricultural ecosystems. Page et al. (2001b) did demonstrate that prevalence of *B. procyonis* increases in response to habitat fragmentation, although their study did not include samples from highly fragmented populations, where raccoon densities and roundworm prevalence are likely to be highest. Given the widespread and increasing distribution of agriculturally dominated landscapes, it is clear that the relationship between landscape attributes and the transmission dynamics of *B. procyonis* to intermediate hosts should be further evaluated in these systems. Thus, our goal in the present study was to determine the influence of landscape-level habitat attributes on the spatial distribution of *B. procyonis* infection in white-footed mice in fragmented agricultural ecosystems. To achieve this goal, we used an information-theoretic approach to develop models for predicting the prevalence, mean abundance, and mean intensity of *B. procyonis* infection in white-footed mice among 22 forest patches in a fragmented agricultural ecosystem in northern Indiana.

MATERIALS AND METHODS

Study area

This study took place in portions of the Upper Wabash River Basin (UWB) in north-central Indiana. The UWB is a highly deforested region with ~66% of the land used for agricultural production (only ~13% is

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forested), with corn and soybeans comprising the main crops. The remaining forest land (mainly oak-hickory-maple [*Quercus-Carya-Acer*] forest) is highly fragmented, with the only contiguous tracts reserved to areas unfit for agriculture, i.e., floodplains and steeply sloped terrain (for study area map, see Beasley et al., 2013).

White-footed mouse trapping

We live-trapped mice from 22 habitat patches distributed throughout the UWB during late spring through summer 2008 in accordance with ASM guidelines and protocols approved by the Purdue University Animal Care and Use Committee (PACUC protocol 07-025). Study patches were selected to represent the range of woodlot sizes and degrees of isolation from other forested areas present in this landscape. Trapping grids generally consisted of 30 Sherman live-traps (H. B. Sherman Traps, Tallahassee, Florida) placed in 5 rows of 6 traps each that were 20 m apart.

We also placed 2 raccoon-size Tomahawk live traps (Tomahawk Live Trap Co., Tomahawk, Wisconsin) at opposite corners of each grid to curtail predator damage to small mammal traps. Small mammal bait consisted of rolled-oats mixed with peanut butter, and we used commercial cat food for predator bait. A trapping round consisted of 3 days, and all mice trapped during the 3-day period (up to a maximum of 20 for each site) were killed by cervical dislocation (PACUC protocol 07-025). After the initial 3-day period, we retrapped any site not producing ≥ 15 mice for an additional 3 days to increase sample size. All mice were characterized by sex, age, and weight.

Assessment of *B. procyonis* infection

The protocol for assaying mice for larval *B. procyonis* infection prevalence followed that of Page et al. (2001b), with some modifications. We prepared mice for the *B. procyonis* assay in the field by removing and discarding the skin, fur, tail, and feet, opening and washing the digestive tract, and storing samples in bags at 4 C until processing. We removed the head in order to examine the brain separately, which was accomplished by removing the brain from the skull, pressing it between clear plastic plates, and examining it for the presence of *B. procyonis* larvae using a dissecting microscope.

To assess for evidence of *B. procyonis* larvae, we cut each mouse carcass into smaller pieces and blended them with 100 ml of acid pepsin solution (1% pepsin, 1% hydrochloric acid, 0.85% saline) to obtain a smooth, homogeneous mixture. We then transferred this solution to a flask and gently mixed it in an incubator shaker for 3 hr at 30 C. After incubation, we poured the solution through cheesecloth into a conical glass, added water to fill the glass, and allowed the solution to settle for 30 min. After settling had occurred, we drew the water off the top until approximately 10 ml of solution remained. We again added water to the glass until full, and the solution was allowed to settle for another 30 min, at which point water was drawn off the top until approximately 10 ml of solution remained. We transferred the remaining 10 ml of solution to a Petri dish and examined it for larvae using a dissecting scope. We counted and identified each larva, and then fixed them in a 70% ethanol solution. We then characterized each mouse with the following metrics for each patch: prevalence, defined as the proportion of mice infected with *B. procyonis*; mean abundance, defined as the average number of larvae per mouse (including non-infected mice); and mean intensity, defined as the average number of larvae per infected mouse (Bush et al., 1997).

Landscape attributes

We quantified landscape-level attributes associated with each sampled forest patch using a GIS coverage developed from 1998 U.S. Geological Survey digital orthophotos (DOQs) of 1-m resolution (Retamosa et al., 2008). In this GIS, habitats were defined into 8 land-use classes: forest (closed-canopy forests); shrubland (scattered trees in an open matrix to open-canopy forests); corridors (habitat with trees greater than 3 m and less than 30 m in width spanning a distance between 2 larger habitats); grassland (open areas not allocated to agriculture, including pasture and hay fields); agriculture (all type of crops, excluding tree plantations); water (open non-linear water bodies, rivers, and streams >3 m wide); anthropogenic (cities, farm houses delineated by the mowing line, and animal holding facilities), and roads (Retamosa et al., 2008). We used ArcMap 9.1 to obtain estimates of patch- and landscape-level attributes,

e.g., patch area and proportion of habitat types in surrounding buffer area, associated with each white-footed mouse population sampled.

Statistical analyses

We tested for correlations among each of our dependent variables (prevalence, mean abundance, mean intensity of infection) using Pearson correlation coefficients. Based on previous studies of *B. procyonis* infection in mice and raccoon spatial ecology (Beasley, DeVault, Retamosa et al., 2007; Page et al., 2001b; Beasley and Rhodes, 2010), we identified 7 variables to include in our models of *B. procyonis* infection in white-footed mice. These variables included forest patch size (Psize), the amount (ha) of forest (For150, For3,000) and anthropogenic (Anth150, Anth3,000, i.e., farmsteads, animal holding facilities, and cities) habitat within a 150-m and 3,000-m buffer of trapped patches, and the length of streams (km) (Streams150, Streams3,000) within a 150-m and 3,000-m buffer. Buffers were selected to characterize processes of infection occurring at both fine and broad spatial scales. We tested for collinearity among each of our habitat variables by examining Pearson correlation coefficients and only included combinations of uncorrelated variables ($P > 0.05$) in subsequent models.

We used generalized linear models to evaluate the influence of landscape-level habitat characteristics on *B. procyonis* infection status and intensity of infection. Although endoparasite infections often are aggregated in wildlife populations and thus overdispersed (Wilson et al., 1996; Shaw et al., 1998), dispersion parameters from preliminary models utilizing a negative binomial model with a logit-link function did not differ from zero. Therefore, prevalence was transformed with the use of a logit-link function and modeled using a Gaussian distribution, whereas mean abundance and mean intensity of infection (as defined previously) were modeled using a Poisson distribution with a log-link function. For each dependent variable, we developed 14 models representing a priori predictions of landscape-level influences on *B. procyonis* infections based on previous knowledge of raccoon ecology and *B. procyonis* distribution in agricultural ecosystems (Page et al., 2001b; Beasley and Rhodes, 2010; Beasley et al., 2011). We ranked models using bias-corrected Akaike's Information Criterion (AIC_c) scores and calculated Akaike weights to aid in model selection (Burnham and Anderson, 2002). All statistical tests were implemented in SAS 9.3 (SAS Institute Inc., Cary, North Carolina).

RESULTS

In total, 353 white-footed mice were trapped, with the number of mice removed ranging from 9 to 20 among patches ($\bar{x} = 16.05$, SE = 0.73). All sites revealed evidence of larval *B. procyonis* infection within their respective white-footed mice populations, and prevalence ranged from 5 to 70% ($\bar{x} = 29.25\%$, SE = 3.93%) among habitat patches. Mean abundance of *B. procyonis* ranged from 0.05 to 6.67 larvae per mouse ($\bar{x} = 1.44$, SE = 0.41), and mean intensity of infection ranged from 1 to 20 larvae per infected mouse ($\bar{x} = 3.77$, SE = 0.95).

Pearson correlation tests indicated a high degree of correlation among our infection parameters ($P < 0.05$). Results of our regression analyses produced 3 models with moderate support for each dependent variable (Table I). Variables included in supported models were consistent among analyses, although the ranking of these models differed slightly. All measures of *B. procyonis* infection status in white-footed mice (prevalence, mean abundance, mean intensity of infection) were primarily influenced by emergent properties of habitat fragmentation. In particular, forest patch size, and the availability of forest, i.e., index of habitat connectivity, immediately surrounding sampled habitat patches were the most influential variables for predicting *B. procyonis* infections among white-footed mouse populations based on model weights and rankings, although the availability of forest within the broader landscape surrounding sampled patches also was included in a single supported model for each

TABLE I. Model selection results and regression equations for regression models examining the influence of habitat variables (forest patch size [Psize]; amount [ha] of forest [For150, For3,000]) on the prevalence, mean abundance, and mean intensity of infection of *Baylisascaris procyonis* in white-footed mice (*Peromyscus leucopus*) sampled across 22 forest patches in north-central Indiana, USA.

Model*	K^\dagger	AIC _c	Δ AIC _c	w_i^\ddagger
Prevalence				
0.17–(0.06)Psize–(0.08)For150	2	–22.0	0	0.56
–0.06–(0.11)Psize	1	–20.9	1.1	0.32
0.06–(0.10)Psize–(0.003)For3000	2	–18.3	3.7	0.09
Mean abundance				
0.99–(0.08)Psize	1	72.84	0	0.49
1.19–(0.05)Psize–(0.05)For150	2	74.24	1.4	0.24
1.22–(0.07)Psize–(0.0006)For3000	2	75.03	2.2	0.16
Mean intensity of infection				
1.93–(0.02)Psize–(0.05)For150	2	124.48	0	0.42
2.02–(0.03)Psize–(0.0009)For3000	2	125.55	1.1	0.25
1.66–(0.03)Psize	1	125.65	1.2	0.23

* Only models deviating ≤ 4 Akaike's Information Criterion (AIC_c) from the top model are displayed.

$^\dagger K$, the number of parameters.

‡ Model weights calculated from all models including those deviating > 4 AIC_c from the top model.

analysis (Table I). The regression coefficients for each of these variables were negative for all dependent variables, indicating that the prevalence, average number of larvae per mouse, and mean intensity of infection all decreased as patch size and habitat connectivity increased (Fig. 1). No stream or anthropogenic variables were present in any supported model, i.e., ≤ 4 AIC_c.

DISCUSSION

Despite a growing awareness that habitat fragmentation can have a profound influence on transmission dynamics of infectious disease (Allan et al., 2003; LoGiudice et al., 2003; Brownstein et al., 2005; Dharmarajan et al., 2012), investigation of the ways in which epidemiological processes are influenced by attributes of fragmented ecosystems remains an understudied area of research (Ostfeld et al., 2005). Here, we demonstrate that landscape attributes contribute to spatial variability in *B. procyonis* infections in an intermediate host, white-footed mice. Prevalence, mean abundance, and mean intensity of *B. procyonis* infection in mice all were highly correlated and positively associated with emergent properties of habitat fragmentation, with mice in smaller and less contiguous forest patches exhibiting increased parasite burdens. Although only 3 large forest patches were sampled in this study, i.e., > 60 ha, due to their limited availability in our study area, this inverse relationship held among patches < 20 ha. These data suggest that factors below the scale of landscape, such as fine-scale habitat structure or demographic and behavioral attributes of mice and/or raccoons within forest patches, likely are important drivers of intermediate host infection with *B. procyonis* as well (Alder and Wilson, 1987; Gortazar et al., 1998; Calvete et al., 2004; Brouat et al., 2007).

Other studies investigating spatial patterns of infectious disease have demonstrated that both host demography and attributes of landscape composition and configuration can directly affect

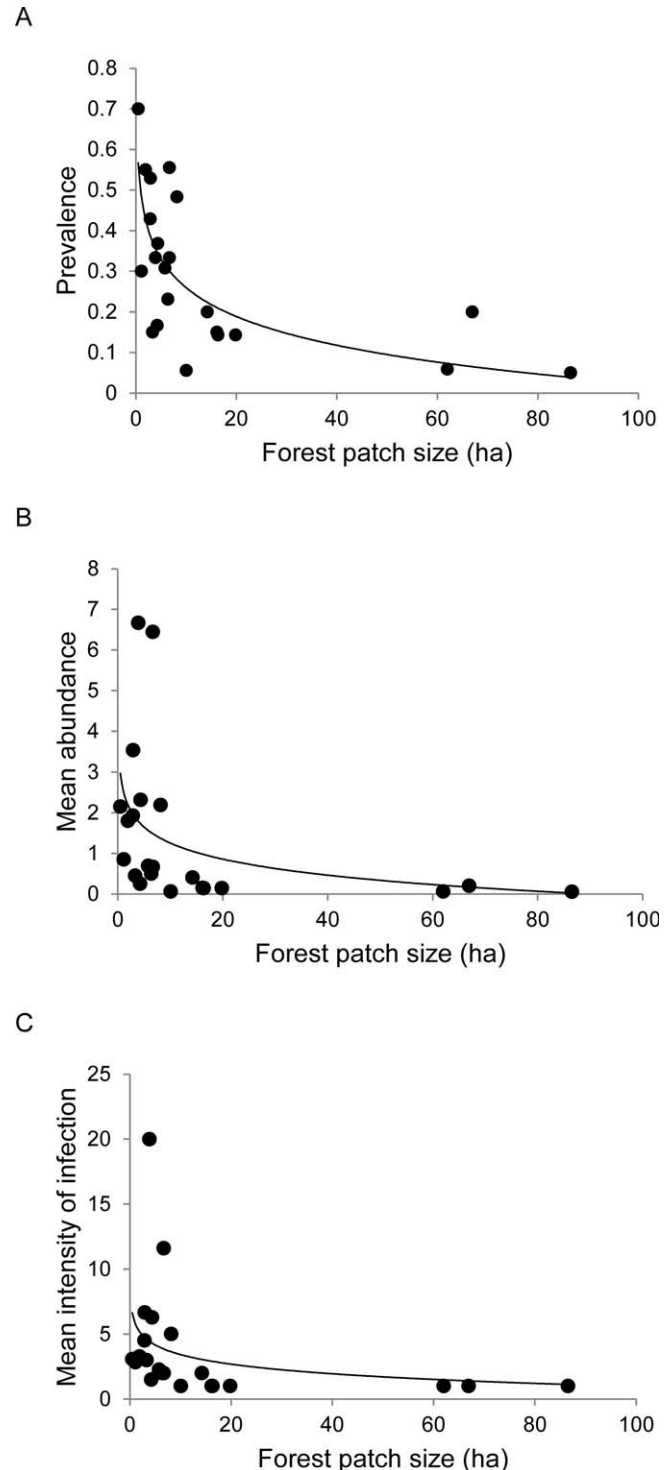


FIGURE 1. Linear regression plots showing the relationship between forest patch size (ha) and the (A) prevalence, (B) mean abundance, and (C) mean intensity of *Baylisascaris procyonis* infection in white-footed mice (*Peromyscus leucopus*) in a fragmented agricultural landscape in Indiana.

infection parameters (e.g., Jones et al., 1998; Langlois et al., 2001; Page et al., 2001b; Allan et al., 2003; Su et al., 2009; Dharmarajan et al., 2012). For example, a similar pattern of decreasing infection prevalence with increasing patch area has been observed for larval ticks infected with *Borrelia burgdorferi*

(Allan et al., 2003; Brownstein et al., 2005), likely due to increased densities of white-footed mice in smaller habitat patches (Nupp and Swihart, 1998, 2000). In the case of *B. procyonis*, elevated infections in white-footed mice inhabiting small, isolated forest fragments may reflect differences in raccoon movement behavior, and subsequently latrine distribution among forest patches varying in size. Corn comprises a significant food resource for raccoons when available, and thus raccoon movements (Pedlar et al., 1997; Dijak and Thompson, 2000; Beasley and Rhodes, 2010) and latrines (Page et al., 1998) often are concentrated along forest-agricultural interfaces in landscapes containing abundant agricultural resources. Given that the proportion of edge to interior habitat is inversely related to patch size, intermediate hosts in small forest patches may encounter raccoon latrines more frequently due to greater overlap with areas of higher raccoon activity. Moreover, densities of white-footed mice also increase as patch size decreases (Nupp and Swihart, 1998, 2000), presumably resulting in increased competition among habitat patches of varying size. Increased latrine encounter rates, coupled with elevated densities of white-footed mice in small forest patches, suggest that the importance and availability of raccoon latrines as a food resource likely increase as forest patch size decreases.

Variability in the extent of raccoon movements among forest patches also may have contributed to the patterns observed in this study. The probability of acquiring an infectious disease increases as the extent of an individual's movements increases (Rogers et al., 1998; Vicente et al., 2007). Given that raccoon home range size is negatively correlated with forest patch area in agricultural ecosystems (Beasley and Rhodes, 2010), spatial variability in *B. procyonis* acquisition by raccoons likely exists due to differences in raccoon movement behavior among forest patches of varying size. However, the relationship between *B. procyonis* recruitment and raccoon home range size currently is unknown.

Interestingly, the nature of the relationship between *B. procyonis* infection and patch area differed between the present study and that of Page et al. (2001b). Across 20 forest patches sampled in a moderately fragmented landscape, Page et al. (2001b) observed a positive relationship between *B. procyonis* prevalence in white-footed mice and forest patch area as well as the amount of forest within a 3-km buffer of sampled patches. However, their models predicting mean abundance and mean intensity of infection were only marginally significant ($P = 0.06$ and $P = 0.09$, respectively; Page et al., 2001b). Moreover, although their work was performed in a fragmented agricultural landscape, it is important to note that their study area contained ~100% more forest habitat than the present study. These contrasting results suggest there are fundamental differences in the relationship between transmission dynamics of *B. procyonis* and habitat attributes among landscapes with varying levels of habitat fragmentation. Such inconsistencies likely reflect differences in landscape composition and fine-scale habitat attributes among study sites. Alternatively, differences in host (intermediate or definitive) density or movement behavior among study sites could have contributed to the disparate patterns of infection observed among studies (LoGiudice et al., 2003; Wright and Gompper, 2005). For example, average densities of mice within habitat patches in the moderately fragmented landscape sampled by Page et al. (2001b) were 41% higher ($\bar{x} = 34.6/\text{ha}$; Nupp and Swihart, 1998) than those in our study area ($\bar{x} = 20.4/\text{ha}$; Eagan, 2009).

Ultimately, both the present research and that of Page and her colleagues (2001b) support the hypothesis that the size and context of remnant habitat patches in fragmented ecosystems play important roles in the transmission dynamics of *B. procyonis*. However, forest remnants in fragmented ecosystems can exhibit considerable variation in both the demographic and behavioral attributes of the species that inhabit them, as well as the fine-scale structure and composition of patch-specific plant communities (Fleishman et al., 2002; Holland and Bennett, 2007; Schooley and Branch, 2009). Thus, differences in the nature of the relationship between landscape attributes and *B. procyonis* infection parameters among studies point to the need to examine factors affecting transmission dynamics of this parasite at finer scales of spatial and biological resolution in highly fragmented agricultural ecosystems.

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