Changes in transmission of *Baylisascaris procyonis* to intermediate hosts as a function of spatial scale

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Physical changes in landscapes alter the abundance and distribution of species. Higher-order effects can occur when changes in ecological processes result in altered interspecific interactions and subsequent changes in a species' abundance or persistence. *Baylisascaris procyonis*, a roundworm parasite of raccoons (*Procyon lotor*), is pathogenic to numerous small vertebrates that serve as intermediate hosts, including white-footed mice (*Peromyscus leucopus*). Raccoons have responded positively to agriculturally induced changes in landscapes, with potential consequences for intermediate hosts of *B. procyonis*. We examined white-footed mice from a homogeneous, predominantly forested landscape in south-central Indiana and a heterogeneous, predominantly agricultural landscape in northwestern Indiana for presence of larval *B. procyonis*. We compared prevalence of infection, intensity of infection, and average number of larvae per mouse between the landscapes, and among forest patches within the highly fragmented agricultural landscape. Prevalence, intensity of infection, and average number of larvae were significantly higher in the highly fragmented landscape. Within the agricultural landscape, regression models predicted probability of infection, intensity of infection, and average number of larvae per mouse per patch as functions of forest patch area and isolation. We conclude that positive responses of raccoons to agriculturally induced fragmentation of forests have resulted in increased encounter rates between white-footed mice and infective stages of *B. procyonis* between and within landscapes, resulting in increased transmission of the parasite to intermediate hosts.

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Agriculture and urbanization have been primary agents of landscape change, resulting in extensive fragmentation of native habitat (Iverson 1988, Anderson et al. 1996). As a process, habitat fragmentation has two components, habitat loss and insularization (Wilcox and Murphy 1985, Noss and Csuti 1994). If physical changes in landscapes alter species' abundance, distribution, and the resulting spatial structure of populations (Saunders et al. 1991, Noss and Csuti 1994), ecological processes within the landscape may also be altered (Gilpin 1987, Hanski and Gilpin 1991). In addition, higher-order effects can occur when changes in

ecological processes result in altered interspecific interactions and subsequent changes in a species' abundance or persistence (e.g., Taylor and Merriam 1996). These effects may be direct, with one species affecting another through predation, herbivory, or parasitism, or indirect as a result of the presence of a third species (Strauss 1991, Wootton 1994).

Raccoons (*Procyon lotor*) have responded positively to changing land-use practices. They are abundant in landscapes characterized by a diversity of habitat types (Oehler and Litvaitis 1996), especially in areas that have been moderately to highly fragmented by agriculture

(Pedlar 1994). Over the past 100 years, raccoon populations have increased throughout the midwest (Lehman 1977), presumably as a result of conversion of native forest, prairie, and wetland to agricultural use. All aspects of the landscape mosaic resulting from conversion of native habitat to agricultural use are positively exploited by raccoons, including greater-than-expected use of agricultural fields (Fritzell 1978, Sherfy and Chapman 1980). As a consequence, fragmentation-induced changes in regional and landscape-level processes may alter higher-order effects involving raccoons.

Fragmentation of forest is a common form of landscape change that can result in altered interactions between species. We propose that spatial elements of a predominantly agricultural landscape have altered the historic distribution of raccoons, and therefore may impact the abundance and distribution of other smaller vertebrates with which raccoons interact. For example, predation by raccoons has been implicated as an important source of mortality in ground-nesting birds (Paton 1994), especially in fragmented habitats with a high edge to interior ratio (Wilcove 1985).

Within fragmented landscapes, predation is not the only higher-order effect that might result in changes in the abundance and distribution of resident species. Parasite-host relations might also be altered, especially when complex life cycles are involved. Van Buskirk and Ostfeld (1998) demonstrated how spatial variation in the risk of Lyme disease is related to the ecological responses and altered interactions of hosts inhabiting heterogeneous habitats. Here, we investigate a parasite-host system and ask whether ecological responses of hosts at the landscape and regional level can alter the risk of infection. Raccoons are the definitive host of a parasitic nematode, *Baylisascaris procyonis*, which lives and reproduces in the small intestine (Kazacos 1983, Kazacos and Boyce 1989). In the midwestern United States, prevalence of infection among raccoons is high and has been documented in 68–82% of raccoons (Kazacos and Boyce 1989). Small vertebrates are common intermediate hosts, and in these animals larvae undergo aggressive somatic migration, often entering the central nervous system (CNS) resulting in clinical disease (Kazacos and Boyce 1989). *Baylisascaris procyonis* is the most commonly recognized cause of clinical larva migrans in vertebrates, with neurologic disease documented in more than 50 species of mammals and birds (Kazacos 1997, Sheppard and Kazacos 1997). Rodent species, including white-footed mice (*Peromyscus leucopus*), are considered the most common intermediate hosts for *B. procyonis* and become infected by ingesting infective eggs (Tiner 1953a, b, Wirtz 1982, Sheppard and Kazacos 1997). Tiner (1954) estimated that 5% of mortality in populations of white-footed mice occupying woodlots in a predominantly agricultural area of Illinois was due to CNS migration of *B. procyonis*. Transmission of *B. procyonis* to intermediate

hosts likely occurs at raccoon latrines, where accumulated raccoon feces serve as foci of infective eggs (Jacobson et al. 1982, Cooney 1989, Sheppard and Kazacos 1997, Page et al. 1998). Transmission of *B. procyonis* to raccoons occurs via egg ingestion (in young raccoons) and predation or scavenging on infected intermediate hosts or their carcasses (Kazacos 1983, Kazacos and Boyce 1989).

We hypothesize that interactions between *B. procyonis* and hosts are affected by responses of hosts to changes in spatial elements of fragmented landscapes. Dynamics of parasite life cycles may be affected by landscape alterations, especially if interactions between parasites and hosts are altered. Encounter rates, and thus the prevalence of resulting parasitic infections, may change as potential hosts have altered behavior and movements in fragmented landscapes (Taylor and Merriam 1996). In complex parasite life cycles, responses to fragmentation by several host species must be considered. Because species potentially perceive landscape configuration and continuity at different scales, what appear to be small changes in resource or parasite distribution to one host species may result in dramatic responses by another. For example, isolation and reduction of forest patches by conversion to agricultural fields might not dramatically affect the movements and distribution of raccoons. However, agriculturally induced fragmentation might significantly alter the movements and distribution of white-footed mice in such a landscape. Therefore, it is important to investigate aspects of parasite-host and host-host interactions at multiple spatial scales. For instance, different rates of infection at a regional scale suggest that host species may have differential responses to changes in landscape structure (Taylor and Merriam 1996).

Our objective was to compare prevalence and intensity of larval *B. procyonis* infections in an intermediate host, white-footed mice, from two regions that differ greatly in the extent to which they have been fragmented. One region is characterized by a highly fragmented landscape dominated by agriculture, whereas the other is typified by a relatively homogeneous forest landscape. At a finer spatial scale, we also test whether prevalence and intensity of infection in white-footed mice varies among patches within a landscape. We hypothesize that changes in land use have altered interactions between raccoons (definitive host) and white-footed mice (intermediate host). Specifically, we predict that raccoon abundance should be greater in regions dominated by agriculture than in otherwise similar regions dominated by forest (Pedlar 1994). This, in turn, should result in increased prevalence and intensity of infection of mice by *B. procyonis* in agricultural areas. Because of their smaller size, white-footed mice presumably perceive fragmentation at a finer scale than raccoons (Lima and Zollner 1996). Thus, we suspect that variation in the prevalence and intensity of *B.*

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procyonis of infection in mice might also vary among forest patches within a landscape, and specifically, we predict higher rates of infection among mice in more isolated forest patches.

Methods

Study area

We examined prevalence of larval *B. procyonis* infections in populations of white-footed mice in a highly fragmented, predominantly agricultural landscape and in a slightly fragmented, predominantly forested landscape of Indiana, USA. Two study areas, separated by 160 km, were chosen because they were similar in climate but exhibited different land-use patterns. The agricultural landscape contained the Indian Pine Natural Resources Area in northwestern Indiana. Indian Pine is a 259-km^2 area including two major watersheds in Tippecanoe and Warren counties (40°25′N, 86°54′W). Portions of adjacent Benton county also were included in our study. Eighty-two percent of the landscape is cultivated, and small farmland woodlots and wooded riparian strips comprise 16% of the area (Sheperd and Swihart 1995). The predominantly forested landscape was located on the Naval Surface Warfare Center-Crane Division (NSWCC) in south-central Indiana. Crane is a 253-km^2 area in Martin, Green, and Lawrence counties (38°51′N, 86°50′W). Eighty-nine percent of the area is forested (D. Pointer pers. comm.), and none of the site is cultivated (Weakland 1995).

Data on abundance

An index of raccoon abundance compiled by the Indiana Department of Natural Resources, Division of Fish and Wildlife (1994, 1995, 1996, 1997) was used to compare the relative abundance of raccoons at each study site, and subsequently to predict prevalence of *B. procyonis* at a regional scale. The number of raccoons sighted by bowhunters per 1000 h of observation was recorded in each of the six fur districts throughout Indiana. Fur district boundaries correspond closely to the six natural physiographic regions of the state (Petty and Jackson 1966). Indices for 1992 through 1996 were used in this study. To compare raccoon abundance as it related to regional differences in land use and degree of forest fragmentation, landscape attributes were ranked among each of the six fur districts and correlated with the bowhunter index. These landscape attributes included forest area, forest proximity, current extent of agriculture, and the historical heterogeneity of habitat. Ranks of forest area and proximity were based on maps created by Spetich et al. (1997) using geographical information system (GIS) data layers.

Trapping data was used to determine mouse densities in forested portions of both Indian Pine and NWSCC (Nupp and Swihart 1996, 1998, Page 1998). Density was calculated as the number of captures/100 trap nights. Comparisons of densities in Indian Pine and NWSCC were made using a two-sample *t*-test.

White-footed mice were collected at 17 small farmland woodlots (0.6 ha–32 ha) and three larger forested areas (approximately 1500 ha) within and adjacent to Indian Pine using Sherman™ live traps (7.5 × 9.0 × 30 cm) spaced 15–20 m, and arrays of 1–16 pit-fall traps placed randomly throughout forest patches (Kolozsvary 1998). The number of pit-fall arrays within the forested plots was roughly proportional to the rank ordering of patch size. Because NWSCC is predominantly homogeneous forest, identification of distinct forest patches was problematic. Instead, mice were collected within five 1748-ha sampling units spaced an average of 9200 m apart. Mice were collected from bluebird nest boxes during fall and winter months, and by trapping using Sherman™ live traps (7.5 × 9.0 × 30 cm).

To estimate densities of raccoon latrines, forest patches within Indian Pine, and at four locations within NWSCC, were surveyed for latrines using line transects at 15-m spacing. Latrines were identified based on the presence of raccoon fecal piles (Yeager and Rennels 1943). At Indian Pine, 0.5-ha grids were searched within each forested sampling unit. At NSWCC, searches were limited to four 0.64-ha grids.

Assessing *Baylisascaris procyonis*

Following capture, mice were euthanized using Methoxyflurane (Metofane™) inhalant anesthetic and refrigerated until they were examined for larval *B. procyonis*. Because CNS infection/disease is a possible manifestation of larval *B. procyonis* infections, brains were removed and analyzed separately by pressing them between glass plates (12.7 cm diameter) and examining them for larvae under a dissecting microscope. Larvae in remaining tissues were recovered by digestion using acid-pepsin solution (1% pepsin and 1% hydrochloric acid in 0.85% saline) (Sheppard and Kazacos 1997). Larvae were counted, fixed in hot acetic acid-formalin-alcohol (AFA), and identified (Kazacos 1997), taking care to separate them from other larvae and gastrointestinal nematodes which might be present.

We computed the proportion of white-footed mice from each woodlot that were infected with *B. procyonis*. Prevalence of *B. procyonis* infection among white-footed mice was calculated for each sampled woodlot or forest patch. Average intensity of larval infection, measured as the number of larvae per infected white-footed mouse, and the average per capita number of larvae among all sampled mice were also calculated for each woodlot and forest patch.

Statistical analysis

At the regional scale we sampled from multiple landscapes at each of the two areas. However, we chose to present data pooled across landscapes within each area. We understand the problems associated with lack of replication at the regional scale (Hurlbert 1984); however, pooling of landscapes simplified interpretation and yielded similar results in terms of statistical significance to tests conducted on multiple landscapes within each region.

A Wilcoxon rank-sum test (Conover 1980) was used to compare latrine densities between Indian Pine and NSWCC. In addition, prevalence of larval infection in mice was compared between Indian Pine and NSWCC using a chi-square test of homogeneity of proportions (Zar 1984), and a Wilcoxon rank-sum test (Conover 1980) was used to compare average infection intensity and per capita number of larvae between the two regional study areas.

Arcview (ESRI) was used to obtain landscape variables from digitized maps of Indian Pine and NWSCC. We calculated variables, such as patch size and measures of isolation, which describe patch attributes and spatial distributions of patches throughout landscapes. Landscape statistics used in this study include patch area and the proportion of forested habitat within three buffer zones (150 m, 1 km, 3 km) around each patch, because variables related to area and isolation tend to be the most important predictors of patch occupancy in a metapopulation (Moilanen and Hanski 1998). The three buffer sizes were chosen to represent the differing scales of perception between mice and raccoons (Zollner and Lima 1999, Zollner 2000).

A $\log_{10}$ transformation of patch area ($\log_{10}$ A) and arcsine square-root transformation of forested area within each buffer (ARCSIN 150, ARCSIN1K, ARCSIN3K) were performed prior to analysis to improve the distributional properties of regression residuals. $\log_{10}$ A and its square were centered by subtracting the mean before analysis to reduce collinearity (Neter et al. 1990). After centering $\log_{10}$ A to yield $\log_{10}$ AC, and the squared term ($\log_{10}$ AC2), we computed best possible subsets multiple regression models from $\log_{10}$ AC, $\log_{10}$ AC2, ARCSIN150, ARCSIN1K, ARCSIN3K, and a term for latrine density to predict the arcsine square-root transformed proportion (ASP) of infected mice, intensity of larval infection in individual mice, and average number of larvae/infected mouse within woodlots where ≥ 10 mice were captured. A stepwise logistic regression model also was constructed to predict prevalence of infection as a function of these same explanatory variables. Because NWSCC was so homogeneous that all mice were collected from the same forest patch as defined by ARCVIEW, regression models were developed only for the Indian Pine Study area.

Results

Raccoons and latrines were more abundant in the agricultural landscape

Relative abundance of raccoons throughout Indiana was related to landscape features and human land use. The rate of raccoon sightings by bowhunters increased as both forest area ($r = -0.94$, $p = 0.02$) and forest proximity ($r = -1.00$, $p = 0.01$) declined across the fur districts. Although only marginally significant, relative abundance of raccoons also increased as the proportion of cultivated land increased ($r = 0.83$, $p = 0.10$). However, historical habitat heterogeneity was not related to current indexes of raccoon abundance ($r = 0.26$, $p > 0.50$). Greater sighting rates of raccoons were recorded for the fur district containing Indian Pine than for the district containing NSWCC for the period 1992–1996 (Fig. 1).

Raccoon latrines were located at all 20 sites within the Indian Pine study area, and densities ranged from 10 to 44 latrines/ha. Latrines were located at three of four grids at NSWCC, and densities ranged from 3 to 13 latrines/ha. Latrine density was significantly greater at Indian Pine than at NSWCC ($Z = -2.75$, $p = 0.005$).

Mouse densities and rates of parasitism were greater in the agricultural landscape

Three hundred and seventy-nine white-footed mice were collected from 20 locations in the Indian Pine study area, and an additional 108 mice were collected from five sites at NSWCC. Mouse density was signifi-
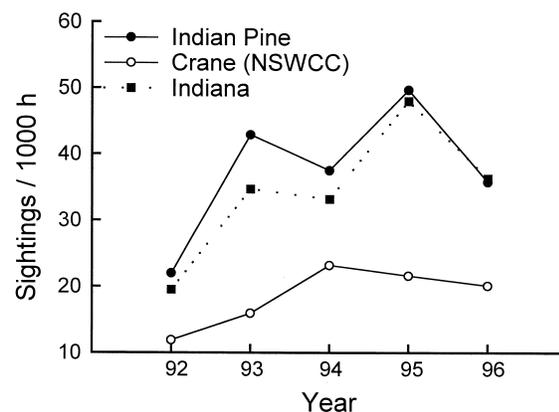

Fig. 1. Indiana Department of Natural Resources, Division of Fish and Wildlife Bowhunter Indices for 1992 through 1996. The Indian Pine curve represents the northwest physiographic region, whereas the Crane (NSWCC) curve represents the south-central physiographic region of Indiana. The dotted line represents the overall average for the state.

Table 1. Estimated coefficients (β), standard errors, and significance levels for explanatory variables predicting attributes of parasitism of white-footed mice by *Baylisascaris procyonis* in an agricultural landscape of Indiana. Models 1–3 were fitted using best subsets multiple regression, whereas model 4 was fitted using stepwise logistic regression.

Dependent variable	Independent variable	β	SE	t	p
Infection	Intercept	0.881	0.104	8.46	0.000
	$\log_{10}(AC)$	0.158	0.045	3.50	0.004
	$\log_{10}(AC2)$	−0.075	0.029	−2.55	0.025
	ARCSIN3K	−0.600	0.201	−2.98	0.012
Intensity of infection	Intercept	15.644	4.34	3.61	0.004
	$\log_{10}(AC)$	5.361	1.88	2.86	0.015
	$\log_{10}(AC2)$	−2.157	1.23	−1.76	0.105
	ARCSIN3K	−14.188	8.39	−1.69	0.117
Average no. of larvae	Intercept	9.75	2.71	3.60	0.004
	$\log_{10}(AC)$	3.40	1.17	2.90	0.013
	$\log_{10}(AC2)$	−1.59	0.768	−2.07	0.061
	ARCSIN3K	−12.22	5.24	−2.33	0.038
Prevalence	Intercept	0.512	0.374	1.87	0.171
	$\log_{10}(AC)$	0.839	0.201	17.40	<0.001
	$\log_{10}(AC2)$	−0.404	0.120	11.39	0.001
	ARCSIN3K	−2.270	0.791	11.04	0.001

cantly ($t = -2.57$, d.f. = 18, $p = 0.019$) higher (mean ± SE: 7.87/100 trap nights ± 0.83) for the Indian Pine study site than at NSWCC (4.39/100 trap nights ± 0.66).

Larval *B. procyonis* infections were documented at all 20 sites within the Indian Pine study area. Of the 379 mice sampled from Indian Pine, 105 individuals (28%) were infected. At NSWCC, only two of five sampling localities yielded infected mice, and only 6 of 108 individuals (6%) were infected overall. Prevalence of *B. procyonis* larval infection was significantly higher at Indian Pine than at NSWCC ($\chi^2 = 23.5$, $p < 0.001$, d.f. = 1).

Ten or more mice were captured at 16 sites within Indian Pine. Intensity of larval infection among mice from these sites ranged from 2.5 to 23.6 larvae/infected mouse. Intensity among mice from the five sites at NWSCC ranged from 0 to 2 larvae/infected mouse. The median intensity of infection was significantly greater at Indian Pine than at NSWCC ($Z = 3.19$, $p = 0.0014$).

Average numbers of larvae in mice from forest patches at Indian Pine ranged from 0.3 to 15.7. At NWSCC, average numbers of larvae in mice sampled within each of 5 sites ranged from 0 to 0.2. The median number of larvae in mice at Indian Pine was significantly greater than at NSWCC ($Z = 3.27$, $p = 0.001$).

Patch area and isolation were related to parasitism

Attributes of parasitism increased with forest patch area, but at an ever-decreasing rate for all four regression models. Likewise, levels of parasitism increased as the proportion of forested habitat within a 3-km buffer declined in all four models (Table 1). A significant ($\chi^2 = 22.4$, $p = 0.0001$) logistic regression model was developed which predicted the probability of larval infection (p) for individual mice from Indian Pine and correctly classified 74.7% of mice:

$$\log_e\left(\frac{p}{1-p}\right) = 0.52 - 2.63(\text{ARCSIN3K}) + 0.84(\log_{10} AC) - 0.40(\log_{10} AC2)$$

All explanatory variables in the model were highly significant ($p < 0.001$, Table 1).

The proportion of infected mice within forested patches of Indian Pine (ASP) was significantly ($R^2 = 0.56$, $p = 0.017$) related to forest area and the fraction of forested habitat within a 3-km buffer as

$$ASP = 0.88 + 0.16(\log_{10} AC) - 0.08(\log_{10} AC2) - 0.60(\text{ARCSIN3K})$$

The intensity of infection was marginally ($R^2 = 0.41$, $p = 0.086$) related to forest area and the fraction of forested habitat within a 3-km buffer as

$$\text{Intensity} = 15.64 + 5.36(\log_{10} AC) - 2.15(\log_{10} AC2) - 14.18(\text{ARCSIN3K})$$

The average number of larvae per mouse was marginally ($R^2 = 0.45$, $p = 0.057$) related to forest area and the fraction of forested habitat within a 3-km buffer as

$$\text{Average larvae} = 9.75 + 3.40(\log_{10} AC) - 1.60(\log_{10} AC2) - 12.22(\text{ARCSIN3K})$$

Discussion

Raccoon populations in Indiana have responded positively to changes in land-use practices that involve conversion of native vegetation to agriculture. Raccoons are more abundant in northern portions of the state where native vegetation is isolated as small woodlots among a matrix of cultivated fields, whereas fewer raccoons are found in the large homogeneous forests of southern Indiana. Raccoons are habitat generalists (Lotze and Anderson 1979). Thus, one explanation for such a result is that the current patterns of relative abundance could be due to differences in the historical heterogeneity of habitat across the state. However, our analysis indicates that the current distribution and abundance of Indiana raccoon populations is not related to the historical heterogeneity of plant communities throughout the state. Rather, increasing numbers appear to be directly related to changes in land use. Our results demonstrate increased raccoon abundance as a result of the interrelated changes of decreased forest area, increased isolation of forest patches, and increased agriculture. Altered raccoon abundance and distribution as a function of physical changes in the environment may have important implications in the transmission dynamics of *B. procyonis*.

Our results support the hypothesis that *B. procyonis* infection in intermediate hosts is increased in areas where raccoons respond positively to agriculturally induced fragmentation of forest. Ultimately raccoons as the definitive host determine the distribution of *B. procyonis* in a landscape. However, responses of intermediate hosts to changing land-use practices presumably interact with responses of the definitive host to determine parasite prevalence in a region. White-footed mice also have responded positively to agriculture (Nupp and Swihart 2000), and the increased densities of mice and raccoons in forest patches of Indian Pine have resulted in increased levels of parasitism.

Differences in physical attributes of the landscapes at each study site, by virtue of their effects on raccoons and mice, likely explain a portion of the variation in parasite prevalence at a regional scale. Larval *B. procyonis* infections were found in mice from both the Indian Pine and the NSWCC study sites. However, prevalence, intensity, and average numbers of larvae per capita were significantly greater from the predominantly agricultural Indian Pine landscape. Within the Indian Pine study area, larval *B. procyonis* infections were documented in 28% of white-footed mice sampled, and infections were documented in all 20 patches. Larval infections in mice from the heavily forested NSWCC landscape occurred in only two of the five sampling locations and involved only 6% of all mice sampled.

When host species alter behavior or movements as a result of changes in landscapes, interactions between species of definitive hosts and intermediate hosts change, and rates of parasite transmission may be altered (Taylor and Merriam 1996). In complex life cycles, changes in numbers and movements of the definitive host may increase the encounter rate between the parasite and the intermediate host. In our study, this was demonstrated by the elevated number of raccoons in the fur district containing Indian Pine, which coincided with a significantly higher prevalence of *B. procyonis* infection in mice residing in forest patches there.

Although differential responses of raccoons to land-use patterns appear sufficient to explain the regional differences in parasitism that we observed, the cause of variation in infection risk at smaller spatial scales is more difficult to ascertain. We suspected that latrine density would be an important determinant of variation in infection risk among forest patches in the Indian Pine landscape, because latrines are foci of *B. procyonis* infection to white-footed mice (Page et al. 1998). Surprisingly, though, latrine density was not an important predictor of parasite prevalence at this smaller scale, even though latrine density on a regional scale varied significantly, with greater densities occurring in the agricultural landscape of Indian Pine. White-footed mice presumably perceive aspects of the landscape at a smaller spatial scale than raccoons; therefore, the density of latrines within a forest patch may be less important in transmission of *B. procyonis* to mice than is the distribution of the latrines.

Within the Indian Pine landscape, forest patch area and connectivity, indexed by measuring the fraction of forested habitat surrounding each forest patch, were related to probability of infection, intensity of infection, and average larval load of *B. procyonis* in mice (Table 1). We suspect that a combination of factors interact to create this association in such a highly fragmented landscape, and we propose four underlying mechanisms that could produce such a pattern.

One factor that likely affects infection risk within an agricultural landscape is the use of trees as denning sites by raccoons. Raccoons respond positively to increased fragmentation and isolation of forest patches, especially when agriculture is the intervening matrix (Rivest and Bergeron 1981, Pedlar 1994, Pedlar et al. 1997). The relation between levels of parasitism in a patch and the fraction of 3-km buffer comprised of forest are consistent with these findings; use of isolated patches by raccoons can be heavy, potentially leading to increased levels of parasitism in mice. Isolated forest patches are valuable to raccoons because they provide the only access to denning sites, which quite possibly are limiting in such a landscape. Consequently, forest isolates may serve as focal areas from which raccoons emanate (Pedlar et al. 1997). Because of their size, larger isolates typically will provide a greater array of den sites and thus may harbor more raccoons. Thus, larger isolates are more likely to contain latrines with feces deposited by infected raccoons.

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A second factor influencing infection risk is the heavy use of corn as a food resource by raccoons. Raccoons are opportunistic omnivores (Stains 1956, Sonenshine and Winslow 1972, Lotze and Anderson 1979, Rivest and Bergeron 1981, Mumford and Whitaker 1982), and corn is an especially important dietary component in agricultural landscapes (Giles 1940, Sonenshine and Winslow 1972, Rivest and Bergeron 1981, Mumford and Whitaker 1982). When raccoon diets consist primarily of corn, berries, or other mast, the composition of their feces is dominated by undigested seed. Such an accumulation of seed provides a prime source of food for granivorous rodents and birds, and foraging at raccoon latrines is common (Page 1998, Page et al. in press). Corn is more likely to be present in raccoon feces deposited in isolated forest patches, because these patches frequently are surrounded by cultivated fields. Thus, raccoons presumably enhance the risk of infection of white-footed mice in forest isolates by importing corn as a supplemental food resource.

A third factor that predisposes mice in forest isolates to infection by *B. procyonis* is their preference for corn. Granivores vary in their preferences for types of seed, and raccoon feces containing unpreferred items likely would receive little attention unless competition for food was severe. However, corn is preferred over other common seeds, and white-footed mice increase their visitation rates to latrines when corn is present in raccoon feces (Page 1998, Page et al. in press). Mice may be reluctant to forage in fields away from woody cover (Cummings and Vessey 1994). Thus, the apparent preference of mice for corn, coupled with the importation of corn to forest isolates by raccoons, likely enhances transmission of *B. procyonis* to mice.

Finally, population-level responses of mice to fragmentation may alter rates of transmission across a fragmented landscape. In the Indian Pine landscape, local densities of white-footed mice are greater in forest patches than in continuous forest, presumably because larger species of granivorous rodents are absent from woodlots (Nupp and Swihart 1996, 1998). However, release from interspecific competition ultimately could increase levels of intraspecific competition in forest isolates, particularly as population levels of white-footed mice increase. When this occurs, the value of raccoon latrines as a food resource would be increased.

In conclusion, differences in the prevalence of *B. procyonis* infection in white-footed mice at a regional scale appear to be due to population-level responses of raccoons to differences in forest area, forest proximity, and extent of agriculture. Transmission of *B. procyonis* is greater in landscapes where native vegetation exists as small patches within a matrix of cultivated fields. Within an agricultural landscape, increased parasite prevalence is related in a complex fashion to changes in patch area and isolation which affect the densities and movements of raccoons and their interactions with white-footed mice. Our study demonstrates the important role of agriculture in altering the extent and distribution of a parasite-host interaction, in this case mediated by defecation behavior of the definitive host and foraging behavior of the intermediate host.

References

Anderson, B., Crow, T. R., Lietz, S. M. and Stearns, F. 1996. Transformation of a landscape in the upper mid-west, USA: the history of the lower St. Croix river valley, 1830 to present. – Landscape Urban Planning 35: 247–267.

Conover, W. J. 1980. Practical nonparametric statistics, 2nd ed. – Wiley.

Cooney, T. A. 1989. Environmental contamination with *Baylisascaris procyonis* in an urban park. – M.S. thesis, Purdue Univ., West Lafayette, IN.

Cummings, J. R. and Vessey, S. H. 1994. Agricultural influences on movement patterns of white-footed mice (*Peromyscus leucopus*). – Am. Midl. Nat. 132: 209–218.

Fritzell, E. K. 1978. Habitat use by prairie raccoons during the waterfowl breeding season. – J. Wildl. Manage. 42: 118–127.

Giles, L. W. 1940. Food habits of the raccoon in eastern Iowa. – J. Wildl. Manage. 4: 375–382.

Gilpin, M. E. 1987. Spatial structure and population vulnerability. – In: Soulé, M. E. (ed.), Viable populations for conservation. Cambridge Univ. Press, pp. 125–139.

Hanski, I. and Gilpin, M. E. 1991. Metapopulation dynamics: brief history and conceptual domain. – Biol. J. Linn. Soc. 42: 3–16.

Hurlbert, S. H. 1984. Pseudoreplication and the design of ecological field experiments. – Ecol. Monogr. 54: 187–211.

Indiana Department of Natural Resources, Division of Fish and Wildlife. 1994. Indiana statewide wildlife research 1993-1994 progress and final reports. Pittman-Robertson project no. W-26-R-25.

Indiana Department of Natural Resources, Division of Fish and Wildlife. 1995. Indiana statewide wildlife research 1994-1995 progress and final reports. Pittman-Robertson project no. W-26-R-26.

Indiana Department of Natural Resources, Division of Fish and Wildlife. 1996. Indiana statewide wildlife research 1995-1996 progress and final reports. Pittman-Robertson project no. W-26-R-27.

Indiana Department of Natural Resources, Division of Fish and Wildlife. 1997. Indiana statewide wildlife research 1996-1997 progress and final reports. Pittman-Robertson project no. W-26-R-28.

Iverson, L. R. 1988. Land-use changes in Illinois, USA: the influence of landscape attributes on current and historic land use. – Landscape Ecol. 2: 45–61.

Jacobson, J. E., Kazacos, K. R. and Montague, F. H., Jr. 1982. Prevalence of eggs of *Baylisascaris procyonis* (Ne-

matoda: Ascaridoidea) in raccoon scats from a rural and urban community. – J. Wildl. Dis. 18: 461–464.

Kazacos, K. R. 1983. Raccoon roundworms (*Baylisascaris procyonis*). A cause of animal and human disease. – Bulletin No. 422, Purdue Univ. Agricultural Experiment Station, West Lafayette, IN.

Kazacos, K. R. 1997. Visceral, ocular, and neural larva migrans. – In: Connor, D. H., Chandler, F. W., Schwartz, D. A. et al. (eds), Pathology of infectious diseases. Vol. II. Appleton and Lange, pp. 1459–1473.

Kazacos, K. R. and Boyce, W. M. 1989. *Baylisascaris* larva migrans. Journal of the American Veterinary Medical Association 195: 894-903. Addendum. 1995. – In: Zoonosis updates from the Journal of the American Veterinary Medical Association. 2nd ed. American Veterinary Medical Association. Schaumburg, IL, pp. 29–30.

Kolozsvary, M. B. 1998. Effects of agriculturally induced fragmentation on amphibian assemblages in west-central Indiana. – M.S. thesis, Purdue Univ., West Lafayette, IN.

Lehman, L. E. 1977. Population ecology of the raccoon on the Jasper-Pulaski wildlife study area. – Indiana Dept of Natural Resources Publication, Pittman-Robertson Bull. No. 9.

Lima, S. L. and Zollner, P. A. 1996. Towards a behavioral ecology of ecological landscapes. – Trends Evol. Ecol. 11: 131–135.

Lotze, J.-H. and Anderson, S. 1979. *Procyon lotor*. Mammalian Species Number 119. American Society of Mammalogists.

Moilanen, A. and Hanski, I. 1998. Metapopulation dynamics: effects of habitat quality and landscape structure. – Ecology 79: 2503–2515.

Mumford, R. E. and Whitaker, J. O., Jr. 1982. Mammals of Indiana. – Indiana Univ. Press.

Neter, J., Wasserman, W. and Kutner, M. H. 1990. Applied linear statistical models, 3rd ed. – Richard D. Irwin.

Noss, R. F. and Csuti, B. 1994. Habitat fragmentation. – In: Meffe., G. K. and Carroll., C. R. (eds), Principles of conservation biology. Sinauer, pp. 237–264.

Nupp, T. E. and Swihart, R. K. 1996. Effect of forest patch area on population attributes of white-footed mice (*Peromyscus leucopus*) in fragmented landscapes. – Can. J. Zool. 74: 467–472.

Nupp, T. E. and Swihart, R. K. 1998. Influence of forest fragmentation on population attributes of white-footed mice and eastern chipmunks. – J. Mammal. 79: 1234–1243.

Nupp, T. E. and Swihart, R. K. 2000. Landscape-level correlates of small-mammal assemblages in forest fragments of farmland. – J. Mammal. 81: 512–526.

Oehler, J. D. and Litvaitis, J. A. 1996. The role of spatial scale in understanding responses of medium-sized carnivores to forest fragmentation. – Can. J. Zool. 74: 2070–2079.

Page, L. K. 1998. Ecology and transmission dynamics of *Baylisascaris procyonis*. – Ph.D. thesis, Purdue Univ., West Lafayette, IN.

Page, L. K., Swihart, R. K. and Kazacos, K. R. 1998. Raccoon latrine structure and its potential role in transmission of *Baylisascaris procyonis* to small vertebrates. – Am. Midl. Nat. 140: 180–185.

Page, L. K., Swihart, R. K. and Kazacos, K. R. in press. Seed preference and foraging by granivores at raccoon latrines in transmission dynamics of raccoon roundworm (*Baylisascaris procyonis*). – Can. J. Zool.

Paton, P. W. C. 1994. The effect of edge on avian nest success: how strong is the evidence? – Conserv. Biol. 8: 17–26.

Pedlar, J. H. 1994. Variation in raccoon and skunk abundance along an agricultural intensity gradient across two spatial scales. – M.S. thesis, Carleton Univ., Ottawa, ON, Canada.

Pedlar, J. H., Fahrig, L. and Merriam, H. G. 1997. Raccoon habitat use at 2 spatial scales. – J. Wildl. Manage. 61: 102–112.

Petty, R. O. and Jackson, M. T. 1966. Plant communities. – In: Lindzey., A. A. (ed.), Natural features of Indiana. Indiana Academy of Science, Indianapolis, IN, pp. 264–296.

Rivest, P. and Bergeron, J. M. 1981. Density, food habits, and economic importance of raccoons (*Procyon lotor*) in Quebec agrosystems. – Can. J. Zool. 59: 1755–1762.

Saunders, D. A., Hobbs, R. J. and Margules, C. R. 1991. Biological consequences of ecosystem fragmentation: a review. – Conserv. Biol. 5: 18–32.

Sheperd, B. F. and Swihart, R. K. 1995. Spatial dynamics of fox squirrels (*Sciurus niger*) in fragmented landscapes. – Can. J. Zool. 73: 2098–2105.

Sheppard, C. H. and Kazacos, K. R. 1997. Susceptibility of *Peromyscus leucopus* and *Mus musculus* to infection with *Baylisascaris procyonis*. – J. Parasitol. 83: 1104–1111.

Sherfy, F. C. and Chapman, J. A. 1980. Seasonal home range and habitat utilization of raccoons in Maryland. – Carnivore 3: 8–18.

Sonenshine, D. E. and Winslow, E. L. 1972. Contrasts in distribution of raccoons in two Virginia localities. – J. Wildl. Manage. 36: 838–847.

Spetich, M. A., Parker, G. A. and Gustafson, E. J. 1997. Spatial and temporal relationships of old-growth and secondary forests in Indiana, USA. – Nat. Areas J. 17: 118–130.

Stains, H. J. 1956. The raccoon in Kansas. – Misc. Publ. Mus. Nat. Hist. Univ. Kans. 10: 1–76.

Strauss, S. Y. 1991. Indirect effects in community ecology: their definition, study and importance. – Trends Ecol. Evol. 6: 206–210.

Taylor, P. D. and Merriam, G. 1996. Habitat fragmentation and parasitism of a forest damselfly. – Landscape Ecol. 11: 181–189.

Tiner, J. D. 1953a. Fatalities in rodents caused by larval *Ascaris* in the central nervous system. – J. Mammal. 34: 153–167.

Tiner, J. D. 1953b. The migration, distribution, in the brain, and growth of ascarid larvae in rodents. – J. Infect. Dis. 92: 105–113.

Tiner, J. D. 1954. The fraction of *Peromyscus leucopus* fatalities caused by raccoon ascarid larvae. – J. Mammal. 35: 589–592.

Van Buskirk, J. and Ostfeld, R. S. 1998. Habitat heterogeneity, dispersal, and local risk of exposure to Lyme disease. – Ecol. Appl. 8: 365–378.

Weakland, C. A. 1995. Density, nesting success, and habitat selection of neotropical migratory songbirds at forest-road edges in southern Indiana. – M.S. thesis, Purdue Univ., West Lafayette, IN.

Wilcove, D. S. 1985. Nest predation in forest tracts and the decline of migratory songbirds. – Ecology 66: 1211–1214.

Wilcox, B. A. and Murphy, D. D. 1985. Conservation strategy: the effects of fragmentation on extinction. – Am. Nat. 125: 879–887.

Wirtz, W. L. 1982. Cerebrospinal nematodiasis due to the raccoon ascarid, *Baylisascaris procyonis*. – M.S. thesis, Purdue Univ., West Lafayette, IN.

Wootton, J. T. 1994. The nature and consequences of indirect effects in ecological communities. – Annu. Rev. Ecol. Syst. 25: 443–466.

Yeager, L. E. and Rennels, R. G. 1943. Fur yield and autumn foods of the raccoon in Illinois river bottomlands. – J. Wildl. Manage. 7: 45–60.

Zar, J. H. 1984. Biostatistical analysis, 2nd ed. – Prentice-Hall.

Zollner, P. A. 2000. Comparing landscape level perceptual abilities of forest sciurids in fragmented landscapes. – Landscape Ecol. 15: 523–533.

Zollner, P. A. and Lima, S. L. 1999. Illumination and the perception of remote habitat patches by white-footed mice. – Anim. Behav. 58: 489–500.