Seed preferences and foraging by granivores at raccoon latrines in the transmission dynamics of the raccoon roundworm (*Baylisascaris procyonis*)

L. Kristen Page, Robert K. Swihart, and Kevin R. Kazacos

**Abstract:** Raccoons (*Procyon lotor*) habitually defecate at preferred sites (latrines). Feces at latrines often harbor eggs of the roundworm *Baylisascaris procyonis*, a parasite of raccoons that is pathogenic to numerous species of small vertebrates. Undigested seeds are also commonly found in raccoon feces, the composition varying with availability of seed types. Thus, feces at latrines may serve as a source of food and pose a mortality risk for small granivores. To examine this interaction, we manipulated the seed composition in feces at simulated raccoon latrines and tested for differences in vertebrate visitation rates as a function of seed type. Treatments involved placing seeds, including corn, cherry (*Prunus virginiana*), dogwood (*Cornus racemosa*), and a combination of the three types, at simulated raccoon latrines. Using Trailmaster™ camera systems we documented 2406 vertebrate visits by 16 mammal and 11 bird species during 455 camera-nights. Small granivorous mammals, including white-footed mice (*Peromyscus leucopus*) and eastern chipmunks (*Tamias striatus*), were the most common visitors. Visitation by white-footed mice was significantly greater when corn, the most preferred seed type, was present in raccoon feces. Visitation by eastern chipmunks and other vertebrate species did not vary with seed type. Active foraging was documented for five vertebrate species and accounted for 10% of all recorded events. We conclude that raccoon latrines are routinely visited by a variety of vertebrate species, especially small granivores. Active foraging for seeds in raccoon feces is an important risk factor for transmission of *B. procyonis* to small vertebrates, and white-footed mice may suffer elevated rates of infection when corn is present in raccoon feces.

**Résumé :** Les ratsons-laveurs (*Procyon lotor*) ont habituellement des sites de préférence pour déposer leurs déjections (latrines). Les fèces recueillies dans ces latrines contiennent souvent des œufs de *Baylisascaris procyonis*, un ver rongeur parasite des ratsons-laveurs, qui a des effets pathogènes chez de nombreuses espèces de petits vertébrés. On trouve aussi dans les fèces des graines non digérées dont la composition varie selon leur disponibilité saisonnière. Les fèces trouvées dans les latrines peuvent aussi servir de source de nourriture et comportent un risque de mortalité pour les petits granivores. Pour étudier cette interaction, nous avons manipulé la composition du stock de graines dans les fèces à des latrines simulées de ratson-laveur et examiné les variations des visites des vertébrés en fonction des types de graines. Nous avons procédé à différents traitements, graines de maïs, de cerisier (*Prunus virginiana*), de cornouiller (*Cornus racemosa*) et une combinaison de graines, dans des latrines simulées. Au moyen de systèmes de caméras Trailmaster™, nous avons enregistré 2406 visites de vertébrés appartenant à 16 espèces de mammifères et 11 espèces d'oiseaux en 455 nuit-caméras. Les petits mammifères granivores, dont la Souris à pattes blanches (*Peromyscus leucopus*) et le Tamia rayé (*Tamias striatus*), étaient les visiteurs les plus assidus. Les visites des Souris à pattes blanches étaient significativement plus fréquentes quand les fèces contenaient des graines de maïs, leurs graines préférées. Les visites des tamias et des autres espèces de vertébrés ne variaient pas en fonction du type de graines présentes. La recherche active de nourriture a été suivie chez cinq espèces de vertébrés et représente 10% de tous les événements enregistrés. Nos résultats indiquent que les latrines des ratsons-laveurs sont visitées régulièrement par plusieurs vertébrés, en particulier par les petits granivores. La recherche de nourriture dans les fèces des ratsons-laveurs comporte un important facteur de risque de transmission de *B. procyonis* aux petits mammifères et, chez les Souris à pattes blanches, la fréquence des infections est plus élevée lorsque les fèces contiennent du maïs.

[Traduit par la Rédaction]

**Introduction**

Raccoons (*Procyon lotor*) habitually defecate in preferred locations (latrines), where feces accumulate (Giles 1939; Yeager and Rennels 1943; Stains 1956). In forested locations, raccoon latrines are found most often at the base of trees, in raised crotches of trees, and on large logs, stumps, rocks, tree limbs, and other horizontally oriented structures.
(Yeager and Rennels 1943; Stains 1956; Cooney 1989; Kazacos and Boyce 1989, 1995; Page et al. 1998). Active raccoon latrines may be utilized by many individual raccoons over extended periods of time, therefore large amounts of feces can accumulate at these sites (personal observation).

Raccoons are opportunistic omnivores (Stains 1956; Lotze and Anderson 1979; Rivest and Bergeron 1981; Mumford and Whitaker 1982). Plant foods such as berries, nuts, and seeds are an important part of raccoon diets (Giles 1940; Yeager and Rennels 1943; Tester 1953; Mumford and Whitaker 1982). In agricultural areas, corn is an especially important food for raccoons (Giles 1940; Rivest and Bergeron 1981; Mumford and Whitaker 1982). When raccoon diets consist primarily of berries, corn, or other seeds, the composition of their feces is dominated by undigested seeds. Such an accumulation of seeds provides a prime potential source of food for granivorous rodents and birds.

Raccoons are the definitive host of Baylisascaris procyonis, a parasitic nematode that lives and reproduces in the small intestine (Kazacos 1983; Kazacos and Boyce 1989, 1995). Eggs of B. procyonis are shed with raccoon feces, therefore locations where feces accumulate, i.e., raccoon latrines, serve as foci of these eggs. The prevalence of B. procyonis infection is high, especially in the midwestern and northeastern United States, where B. procyonis has been documented in 68–82% of raccoons (Kazacos and Boyce 1989, 1995). Small vertebrates are common intermediate hosts in the life cycle of B. procyonis, and in these animals the larvae undertake an aggressive somatic migration, often entering the central nervous system, which leads to clinical cerebrospinal nematodiasis (Kazacos and Boyce 1989, 1995). Baylisascaris procyonis is the most commonly recognized cause of clinical larva migrans in animals, producing fatal or severe neuropathic disease in over 50 species of mammals and birds (Kazacos 1997; Sheppard and Kazacos 1997).

Small vertebrates are susceptible to infection with B. procyonis through accidentally ingesting infective eggs (Kazacos 1983; Kazacos and Boyce 1989, 1995; Sheppard and Kazacos 1997). Contact with infective eggs likely occurs at raccoon latrines, where egg-laden feces accumulate (Tiner 1952; Wirtz 1982). Female B. procyonis are prolific egg producers and, on average, infected raccoons shed 20,000 eggs per gram of feces (Kazacos 1983). Because B. procyonis eggs are extremely resistant to environmental conditions, they may remain viable and infective at raccoon latrines for years (Kazacos 1983; Kazacos and Boyce 1989, 1995). Therefore, raccoon latrines represent important foci of infective eggs and serve as long-term sources of B. procyonis infection for susceptible animals, especially those that forage for undigested seeds in raccoon feces (Tiner 1952; Wirtz 1982).

Understanding the dynamics of transmission of B. procyonis to small vertebrates is important in understanding the potential impact of this parasite on their populations. Because raccoon latrines are foci of infective eggs, they appear to play an important role in transmission of B. procyonis to intermediate hosts (Tiner 1952; Wirtz 1982; Sheppard and Kazacos 1997). We suspect that the species most at risk are those which forage for undigested seeds, corn, or other potential food material in raccoon feces. In previous visitation studies, foraging for seeds in feces was documented for the white-footed mouse (Peromyscus leucopus), eastern chipmunk (Tamias striatus), Virginia opossum (Didelphis virginiana), and white-breasted nuthatch (Sitta carolinensis) (Page et al. 1998, 1999).

Although most granivorous vertebrates are polyphagous, distinct preferences for certain types of seeds are often evident (e.g., Hart 1929; Dolan and Carter 1977; Briggs and Smith 1989; Harlow and Doyle 1990; Pyare et al. 1993; Kropowski 1994a, 1994b). Because numerous seeds can be found in raccoon feces, the attractiveness of latrines as foraging sites could vary among granivore species and over time in accordance with the seed composition in feces. Our objective in this study was to examine whether the frequency of vertebrate visitation at raccoon latrines varied as a function of seed type present in raccoon feces at simulated latrine sites. We used corn, cherry (Prunus virginiana), dogwood (Cornus racemosa), or a combination of the three seed types. These seeds were chosen because they are common in raccoon diets (Mumford and Whitaker 1982). We hypothesized that the frequency of visitation by different species would vary as a function of seed type present in feces.

**Methods**

We examined visitation by vertebrates at simulated raccoon latrines in six large forested tracts (>1000 ha) and four small farmland woodlots (8.2, 0.6, 4.6, 0.8 ha) in Tippecanoe and Warren counties in west-central Indiana. Among the 10 study sites, 23 simulated raccoon latrines were established as the centers of 100-m² grids. Grids established in large forested tracts were spaced 200 m apart. In 2 of the small woodlot sites, the grids were spaced 150 m apart. Twelve grids were established and monitored from September to December 1996 and 11 grids from September to December 1997.

Livetrapping and marking of granivorous rodents were conducted for 5 nights prior to the establishment of simulated latrines in order to estimate the abundance of small mammals and mark individuals for identification. Individual identification was necessary to estimate per-capita rates of visitation at latrines (see below). At each of the 23 grids, Sherman live traps (7.5 x 9.0 x 30 cm) were spaced at 20-m intervals and Tomahawk live traps (15 x 15 x 60 cm) at 40-m intervals. Sherman traps were baited with a mixture of rolled oats, peanut butter, and sunflower seeds and Tomahawk traps were baited with English walnuts and corn. Trapped mice (P. leucopus), chipmunks (T. striatus), and tree squirrels (Sciurus niger, Sciurus carolinensis, Tamiasciurus Hudsonicus) were examined to determine sex, reproductive condition, and body mass. Each individual was uniquely marked with a numbered ear tag and released at point of capture. Abundance of each species was estimated using the minimum number known alive (MINKA; Krebs 1966).

Individual white-footed mice, chipmunks, and tree squirrels were also marked with unique color combinations to facilitate estimation of per-capita rates of visitation at latrines. Paint pens (Uni®) were used to mark the pelage in unique combinations. Individuals were divided into three zones (head, midsection, and rump) (Hurst 1988) and a color was assigned to each section. In 1997, mice were marked by painting the ears and tail in unique combinations.

Trials were conducted at simulated latrines using the three types of seed. Simulated latrines were constructed on horizontal structures characteristic of raccoon latrines (Page et al. 1998), but with no visible raccoon feces present within 5 m. Raccoon feces were collected from captive raccoons that were not infected with B. procyonis. Fecal piles were created by mixing 40 g of feces with approximately equal volumes of corn (60 g), cherry seed (40 g), or
dogwood seed (34 g). Four treatments were tested, using each seed type separately and all types combined. Treatments were randomly assigned to a 5- to 7-day period during each trial. Three fecal piles were placed at each simulated latrine during each treatment. For the combination treatment, one fecal pile of each seed type was placed at the simulated latrine. All fecal material was removed from simulated latrines between trials.

Selection of seed types by white-footed mice was also tested in laboratory trials. Measured amounts of the three seed types used in the field experiments were given to 11 captive mice for a 24-h period. Corn (20 g) and cherry (9 g) and dogwood (7 g) seeds were presented to mice at the same time. After 24 h, all seed was removed from cages and weighed to determine the amount consumed. To account for unequal availability of seed types, we computed forage ratios for each seed type, i.e., $p_i/p_s$, where $p_i$ is the fraction of all consumed seeds that were of type $i$ and $p_s$ is the fraction of all available seeds that were of type $i$ (reviewed by Manly et al. 1993). A forage ratio of 1 signifies that seed type $i$ was eaten in proportion to its availability, a ratio less than 1 indicates avoidance, and a ratio greater than 1 indicates selection. Analysis of variance and a Newman–Keuls multiple-comparison test were used to determine whether seed consumption varied with type.

Trailmaster™ 1500 camera systems were used to monitor animal visitation at the 23 simulated latrines during each treatment. The infrared trip beam of each unit was aligned over the three fecal piles and was approximately 0.5 cm above the surface of each simulated latrine. The infrared pulse for the receivers was such that a 0.10-s break (pulse = 2) in the infrared beam would register an event. This setting was sensitive enough to detect mouse-sized vertebrates. Counters recorded the time and date of each break in the infrared beam. Cameras were also triggered by breaks in the beam. To prevent repeated photographing of an individual during a single foraging episode, and increase the likelihood that film would last for 24-h periods, cameras were set to allow a 15-min delay after each photograph. Kodak Royal Gold™ 1000 speed film was used in the cameras.

Twenty-eight percent of all events were recorded during periods when cameras were inoperative, therefore we used photographic data to infer which vertebrate species was responsible for each unconfirmed event. Multiple logistic regression was used in conjunction with photographic data to develop models for predicting the probability of visitation by each species at a latrine as a function of Julian date, hour, and study site. These models were then used to infer which species were represented by counter data that did not include photographs. An event for which a photograph was not obtained was assigned to the species for which the greatest probabil-

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**Table 1.** Species of mammals and birds visiting simulated raccoon latrine sites in west-central Indiana, documented photographically.

<table>
<thead>
<tr>
<th>Activity</th>
<th>Located in proximity</th>
<th>Foraging</th>
</tr>
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<tbody>
<tr>
<td>White-footed mouse (<em>Peromyscus leucopus</em>)</td>
<td>x</td>
<td>x</td>
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<tr>
<td>Meadow jumping mouse (<em>Zapus hudsonius</em>)</td>
<td>x</td>
<td>x</td>
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<tr>
<td>Eastern chipmunk (<em>Tamias striatus</em>)</td>
<td>x</td>
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<tr>
<td>Fox squirrel (<em>Sciurus niger</em>)</td>
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<td>x</td>
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<tr>
<td>Gray squirrel (<em>Sciurus carolinensis</em>)</td>
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<td>x</td>
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<tr>
<td>Red squirrel (<em>Tamiasciurus hudsonicus</em>)</td>
<td>x</td>
<td>x</td>
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<tr>
<td>Southern flying squirrel (<em>Glaucomys volans</em>)</td>
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<td>x</td>
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<tr>
<td>Woodchuck (<em>Marmota monax</em>)</td>
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<td>x</td>
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<tr>
<td>Eastern cottontail (<em>Sylvilagus floridanus</em>)</td>
<td>x</td>
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<tr>
<td>Virginia opossum (<em>Didelphis virginiana</em>)</td>
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<tr>
<td>Raccoon (<em>Procyon lotor</em>)</td>
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<tr>
<td>Long-tail weasel (<em>Mustela frenata</em>)</td>
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<tr>
<td>Domestic cat (<em>Felis catus</em>)</td>
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<tr>
<td>Red fox (<em>Vulpes vulpes</em>)</td>
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<tr>
<td>Domestic dog (<em>Canis familiaris</em>)</td>
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<tr>
<td>White-tailed deer (<em>Odocoileus virginianus</em>)</td>
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<tr>
<td>White-breasted nuthatch (<em>Sitta carolinensis</em>)</td>
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<tr>
<td>Hermit thrush (<em>Catharus guttatus</em>)</td>
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<td>Swainson’s thrush (<em>Catharus ustulatus</em>)</td>
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<tr>
<td>Wood thrush (<em>Hylocichla mustelina</em>)</td>
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<tr>
<td>Downy woodpecker (<em>Picoides pubescens</em>)</td>
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<tr>
<td>Northern flicker (<em>Colaptes auratus</em>)</td>
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<tr>
<td>Yellow-rumped warbler (<em>Dendroica coronata</em>)</td>
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<tr>
<td>Cardinal (<em>Cardinalis cardinalis</em>)</td>
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<tr>
<td>American robin (<em>Turdus migratorius</em>)</td>
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<tr>
<td>Tufted titmouse (<em>Parus bicolor</em>)</td>
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<td>x</td>
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<tr>
<td>Carolina wren (<em>Thryothorus ludovicianus</em>)</td>
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</tr>
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**Note:** Species in which cases of clinical cerebrospinal nematodiase have been confirmed (Jacobson et al. 1976; Kazacos et al. 1981; Roth et al. 1982; Kazacos 1983; Evans and Tangredi 1985; Thomas 1988; Kazacos and Boyce 1989, 1995; Rudmann et al. 1996; Sheppard 1995; Tseng 1997, K.R. Kazacos, personal observation) are shown in boldface type. An asterisk indicates a species that was found to be susceptible to experimental infection (Tiner 1953; Wirtz 1982; Snyder 1983; Sheppard 1996; Sheppard and Kazacos 1997, K.R. Kazacos, personal observation).
Fig. 1. Rates of visitation by vertebrates at simulated raccoon latrines in west-central Indiana, U.S.A., as a function of seed type present in raccoon feces.

![Graph showing visitation rates for different seed types]

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footed mice and fox squirrels in Illinois woodlots where raccoons were abundant. He estimated that 5% of natural mortality of white-footed mice in these woodlots could be attributed to *B. procyonis*. Tseng (1997) and K.R. Kazacos (personal observation) have documented natural infections with *B. procyonis* in gray squirrels (*Sciurus carolinensis*). Clinical disease resulting from natural infections with *B. procyonis* larvae has been documented for 50 species of mammals and birds (Sheppard 1995; Kazacos 1997). Seven of the 16 species of mammals that visited the simulated latrines have been documented with naturally acquired infections, and 2 additional species have been documented as being susceptible experimentally (Sheppard 1996) (Table 1).

Forest granivores may perceive raccoon latrines as an abundant source of food when they contain concentrations of feces with a high seed content. Granivorous rodents locate seeds primarily by olfaction (Howard et al. 1968; Jacobs and Liman 1991; Vander Wall 1993, 1995, 1998). Increased substrate moisture appears to play an important role in the ability of rodents to locate seed by olfaction (Vander Wall 1993, 1995, 1998). Moisture in feces at raccoon latrines may therefore facilitate the location of seeds in feces by granivores. The pungent odor of the feces also may contribute to the location of seeds at latrine sites. Memory probably plays an important role in the ability of an individual to return to and forage at a latrine once it is located (Jacobs and Liman 1991; Vander Wall 1995).

When all vertebrate species were considered collectively, rates of visitation at simulated raccoon latrines did not vary as a function of seed type. This result is not entirely unex-
pected because granivores can vary considerably in their preferences for certain food types (Ivan and Swihart 2000). Our best data on visitation were for white-footed mice. Rates of visitation by this species were significantly higher when corn was present in feces (Fig. 1). Corn was also the most preferred seed in laboratory foraging trials. The fact that visitation by white-footed mice increased when corn was present in feces suggests that mice locate seeds at latrines and return more frequently when a preferred food is available there. Some evidence suggests that white-footed mice, unlike fox squirrels (Shepherd and Swihart 1995) and perhaps other larger bodied granivores, are reluctant to enter fields adjacent to woodlots after harvest (Whitaker 1967; Cummings and Vessey 1994). The smaller home ranges of white-footed mice might also limit access to corn for individuals occupying forest interiors. Thus, raccoons appear to serve as importers of a preferred but otherwise rarely available food item to white-footed mice in forest patches surrounded by agricultural fields. This implies that forest-dwelling mice in agricultural landscapes may experience elevated rates of B. procyonis transmission relative to mice in non-agricultural areas.

In agricultural areas, corn is the primary component of raccoon diets during the fall months prior to and following harvest (Rivest and Bergeron 1981; Mumford and Whitaker 1982). Interestingly, an increase in patency of raccoons infected with B. procyonis coincides with this seasonal shift in raccoon diets (Kidder et al. 1989). It follows that an increase in the number of B. procyonis eggs coinciding with the presence of a preferred food such as corn in raccoon feces would result in increased transmission to intermediate hosts. Moreover, we predict that this increased transmission will occur following harvest in agricultural areas. Photographs of white-footed mice carrying large pieces of raccoon feces laden with corn suggest that individuals are caching seed-laden feces for future consumption. Eggs of B. procyonis become infective to potential intermediate hosts approximately 3–4 weeks after being shed and, with adequate moisture, can remain viable for years (Kazacos and Boyce 1989, 1995). Because the shedding of B. procyonis eggs by raccoons increases at the time when raccoon diets shift to corn, white-footed mice are at an increased risk of infection at that time, especially if they cache feces for future seed consumption.

Although foraging among raccoon feces is the most likely mode of B. procyonis transmission, other activities carried out in close proximity to feces may also increase the risk of infection for small vertebrates. Numerous vertebrate species utilize habitat structures associated with latrines in a variety of ways that may increase the risk of transmission. For example, white-footed mice and eastern chipmunks use horizontal habitat features such as travel paths and escape cover (Barnum et al. 1992; McMillan and Kaufman 1995). If grooming occurs following travel across a latrine site, ingestion of eggs adhering to fur could occur. Vertebrates might also ingest eggs when they ingest soil or other materials. Many wildlife species ingest soil as a source of vital elements (Beyer et al. 1994). If soil in the vicinity of raccoon latrines is ingested, B. procyonis eggs could also be ingested. Page et al. (1998) and Cooney (1989) found B. procyonis eggs in 13–14% of soil and fecal samples taken <1 m from raccoon latrines. In our study, vertebrate activity in close proximity to raccoon feces at latrines was frequent. Therefore, species that frequently visit raccoon latrines are likely to come in contact with raccoon feces containing B. procyonis eggs, and are thus at increased risk of infection with B. procyonis.

Our results show that vertebrate activity at raccoon latrines is common, and frequently includes foraging in feces. The increase in rates of visitation by white-footed mice when corn was present in feces suggests that infection rates are likely to be high during harvest months and in winter, especially if caching occurs. By virtue of their abundance in woodlots (Nupp and Swihart 1996, 2000) and their frequent visitation at latrines, white-footed mice are likely the most common intermediate host of B. procyonis in landscapes dominated by agriculture.

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