

## TISSUE AND GASTROINTESTINAL PARASITES OF COLONIZING NINE-BANDED ARMADILLOS AT THE EDGE OF THEIR NORTHERN RANGE

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### KEY WORDS ABSTRACT

Nine-banded armadillo  
*Dasypus novemcinctus*  
Nonnative species  
*Trypanosoma cruzi*  
Chagas' disease  
*Mycobacterium leprae*  
Leprosy  
Hansen's disease  
*Oncicola canis*  
*Brachylaemus virginianus*  
*Physaloptera* sp.  
*Raillietina* sp.

Originally endemic to South America, the nine-banded armadillo (*Dasypus novemcinctus*) has recently expanded its range northward to Illinois. With this range expansion comes concern regarding potential incoming pathogens; our research, conducted during 2012–2020, consisted of screening armadillos for the presence of helminths, *Trypanosoma cruzi*, and *Mycobacterium leprae*. We screened for the presence of *T. cruzi* and *M. leprae*, 2 pathogens known to infect humans, using polymerase chain reaction and enzyme-linked immunosorbent assay, respectively. All 80 samples screened for *T. cruzi* and all 25 samples screened for *M. leprae* were negative. No parasite specific to the nine-banded armadillo, such as *Aspidodera sogandaresi*, was detected. This lack of infection is consistent with the idea that animals may be isolated from their common parasites during periods of range expansion. Lack of infection by *T. cruzi* in an endemic area suggests that these mammals may not be exposed to the infective stages at this early phase of their colonization. Presently, the armadillo has become established in Illinois, yet they have not introduced their parasites into the area. Our study represents the first effort to document the parasitological record of the expanding armadillo within 30 yr of their initial record in Illinois and the American Midwest. This helminthological record of armadillos in Illinois sets the timeline to observe the establishment of *A. sogandaresi* in the Midwest.

Globalization and anthropogenic disturbance, such as land-use change and habitat fragmentation, have contributed to species range shifts and accelerated the spread of nonnative species around the world (Kolar and Lodge, 2001; Crowl et al., 2008; Hulme, 2009). Important direct effects include the spread of disease and parasites, which can also have serious effects on native communities (Begon and Bowers, 1995; Prenter et al., 2004; Young et al., 2016); for example, parasites can cause reduced fitness of host species through decreased fecundity, body mass, or survivorship of wildlife populations (Newey and Thirgood, 2004; Torchin and Mitchell, 2004; Roy et al., 2011).

Invasive species can be potential hosts that can alter host–parasite relationships of native species by introducing nonnative parasites that can reduce the fitness of natives (i.e., spillover; Begon and Bowers, 1995) or by serving as a reservoir for endemic parasites, known as spillback (Kelly et al., 2009). However, the effect of invasive species will depend on environmental conditions, their interaction with the native fauna, and their relative success. In certain cases organisms may be successful upon invasion because of their reduced parasite loads, a phenomenon

explained by the enemy release hypothesis (Torchin et al., 2003). Alternatively, nonnative species may benefit native species by regulating vector populations or by serving as incompatible hosts for parasites, thus acting as a sink for infective parasite stages (Kelly et al., 2009; Miller et al., 2018). In this manner, native species benefit from the presence of invasive organisms by lowering the probability of encountering infective stages of native parasites and consequently reducing parasite intensities (Keesing et al., 2006).

Host–parasite dynamics can also change over time (Scott, 1988; Torchin et al., 2003). For example, repeated introductions of a species can increase the chance of the co-introduction of nonnative parasites, and invasive species can begin to accumulate endemic parasite species from the introduced region. Additionally, anthropogenic disturbance can exacerbate changes to parasite–host dynamics through the reduction of suitable habitat (Scott, 1988; Brearley et al., 2013). To study these changes through time, records of parasite species infected with nonnative species in the early stages of colonization must be established.

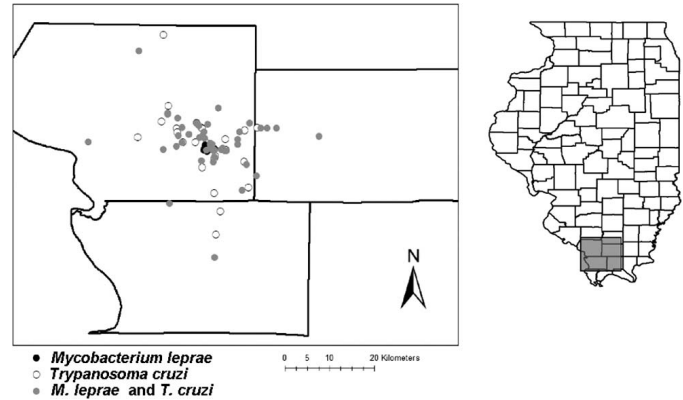
Originally endemic to South America, the nine-banded armadillo (*Dasypus novemcinctus* L., hereafter armadillo) has colonized much of the southern United States in less than 200 yr (Loughry and McDonough, 2013). The current distribution of armadillos now includes 15 states, and populations are expected to expand farther north (Taulman and Robbins, 2014; Feng and Papeş, 2015). In Illinois, the armadillo was first recorded in the late 1970s, and sightings have increased dramatically since the early 2000s, with breeding populations now established in the state (Van Deelen et al., 2002; Hofmann, 2009; Taulman and Robbins, 2014; Haywood et al., 2021a). Although the armadillo is naturalized in portions of the United States (FWC, 2021; TPW, 2021), expansion of its range into Illinois brings concern about its potential role in transmitting zoonotic pathogens such as *Mycobacterium leprae* (Hansen, 1880) and *Trypanosoma cruzi* Chagas, 1909. Although these species are not specific to armadillos, they are 2 of the most prominent pathogens these mammals carry (Loughry and McDonough, 2013). Further, the armadillo-specific nematode *Aspidodera sogandaresi* Jiménez-Ruiz, Gardner and Varela-Stokes, 2006 has been documented in Florida and Texas (Chandler, 1946; Jiménez-Ruiz et al., 2006; Varela-Stokes et al., 2008), which indicates that these regions provide appropriate habitat for armadillos and the proper conditions for the transmission of some of their parasites. It is also common to find armadillos infected with native parasites contracted by the ingestion of insects throughout their established range in the United States (Chandler, 1946, Radomski et al., 1991; Varela-Stokes et al., 2008).

We screened for the presence of *T. cruzi*, *M. leprae*, and various intestinal parasites in a recently established population of armadillos in Illinois. We expected this parasite to spill back into armadillos for 2 reasons. First, 2 species of competent vectors for *T. cruzi*, namely *Triatoma sanguisuga* Le Conte, 1855 and *Triatoma lecticularia* Stal, 1859, are present in Illinois, and second, *Trypanosoma cruzi* was recently detected in raccoons, *Procyon lotor*, in this region (Vandermark et al., 2018). Thus, following the premise that host species experience lower parasite loads on the expansion front, we expected armadillos to be free of infection of the parasites that are common in them, in this case *M. leprae* and *A. sogandaresi* (Dogiel, 1964). Our findings have important implications for expanding armadillo populations, their effect on native wildlife, and the alteration of parasite–host dynamics by colonizing species.

## MATERIALS AND METHODS

### Study area

We sampled armadillos in central and southern Illinois with emphasis on Jackson, Williamson, and Union counties (91,466 km<sup>2</sup>, U.S. Census Bureau, 2019). This region is the northernmost current range of the species (Haywood et al., 2021a) and consisted of fluvial plains of elevation ranging from 104 to 324 m (Illinois State Geological Survey 2020). Climate is temperate, with cold winters, wet springs, and hot, humid summers (Changnon et al., 2004), and mean annual temperature and precipitation of 13.1 C and 123.6 cm, respectively (Illinois State Water Survey, 2018). Land cover is a mixture of forest (42%), row-crop agriculture and pasture (39%), development (9%), wetland (6%), and open water (4%) (Yang et al., 2018). The current mean human density is 40 persons/km<sup>2</sup> (U.S. Census Bureau, 2019).



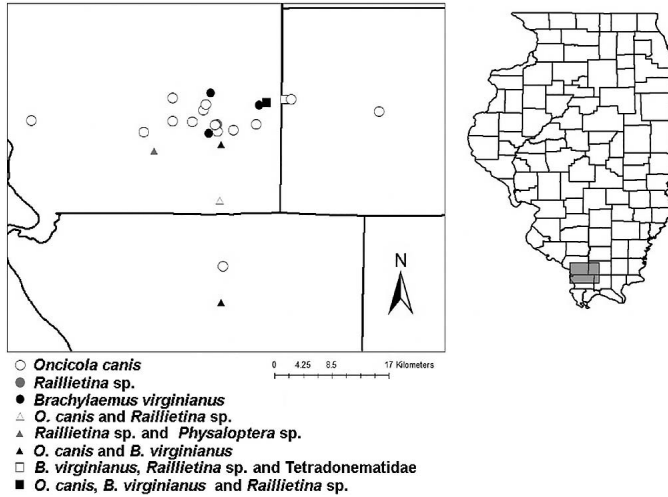
**Figure 1.** Locations of nine-banded armadillos tested for *Mycobacterium leprae* and *Trypanosoma cruzi* in southern Illinois during 2012–2020.

### Sample collection

Specimens were collected under state-issued permits and protocols approved by the Institutional Animal Care and Use Committee (17-024). Road-killed and live armadillos were sampled for this study (Figs. 1, 2). Armadillo road-kills ( $n = 80$ ) were collected during May 2012–February 2020. Live animals ( $n = 7$ ) were trapped during May–August 2019 using double-lined dip nets (71-cm diameter) and 2-door Tomahawk® traps (91 cm × 30 cm × 30 cm; Tomahawk Live Trap, Hazelhurst, Wisconsin) (Haywood et al., 2021b). The heart ( $n = 42$  samples), lungs ( $n = 47$ ), and intestines ( $n = 55$ ) of road-killed armadillos ( $n = 57$ ) were extracted and stored at  $-80$  C and deposited in our laboratory. Blood and serum taken from road-killed and live animals were soaked in 2 Nobuto strips (Advantec, Dublin, California) and dehydrated at room temperature (Loughry et al., 2009). Blood was collected from live armadillos during the surgical implantation of intraabdominal radio transmitters (Hernandez et al., 2010) for a separate movement study, either by drawing blood from the tail or by absorbing blood with a sterile Nobuto strip (Advantec) at the surgery site. Digestive tracts were screened for parasites following conventional techniques (Jiménez-Ruiz et al., 2006), whereas heart and lungs were sectioned and examined with the aid of a dissecting microscope.

### Screening for *T. cruzi* infection

Deoxyribonucleic acid (DNA) was extracted from the heart ( $n = 69$  samples), diaphragm ( $n = 56$ ), and spleen ( $n = 56$ ) of road-killed armadillos ( $n = 80$ ) using a DNeasy blood and tissue kit (QIAGEN, Valencia, California) following the manufacturer's instructions. After extraction, the presence of *T. cruzi* was determined using polymerase chain reaction (PCR). PCRs used approximately 100 ng of genomic DNA in volumes of 20  $\mu$ l, using 5 pM of primers and reagents included in the Taq PCR Core Kit (QIAGEN) or reagents included in the high-yield PCR kit (SYD labs Inc., Hopkinton, Massachusetts) following manufacturer's recommendations. The primers targeted the hypervariable region of kinetoplast DNA minicircle (S35/S36, Sturm, et al. 1989) and the highly repetitive genomic satellite DNA (Tcz1/Tcz2; Moser, et al. 1989). Every set of reactions included a negative control of distilled water and positive control of *T. cruzi* DNA (strain TcIV)



**Figure 2.** Locations of intestinal parasites in nine-banded armadillos in southern Illinois during 2012–2020.

following the thermal profiles optimized by Vandermark et al. (2018).

### Screening for *M. leprae* infection

Nobuto strips from road-killed specimens ( $n = 59$ ) were sent to the National Hansen's Disease Clinical Center in Baton Rouge, Louisiana (Health Resources and Services Administration, 2020). Samples were tested for the presence of anti-PGL1 and anti-LID 1 serum antibodies using enzyme-linked immunosorbent assay as previously described (Engvall and Perlmann 1972; Duthie et al., 2011).

Statistical analyses were performed using Quantitative Parasitology (QPWeb) software version 1.0.13 (Reiczigel et al., 2019). Metrics used for quantifying infection were prevalence and intensity (Margolis et al., 1982; Shaw et al., 2018). Ninety-five percent confidence intervals for prevalence were calculated using Clopper–Pearson confidence limits, and bias-corrected and accelerated bootstrap was used to calculate 95% confidence intervals for mean intensity to account for the skewed nature of parasite distributions (Reiczigel et al., 2019).

## RESULTS

Of 80 road-killed armadillos tested for *T. cruzi*, none was positive; 59 samples tested for *M. leprae* were also negative. Fifty-seven roadkill specimens screened for intestinal parasites (Table 1) harbored 5 helminth taxa, including cystacanths of *Oncicola canis* (Kaupp, 1909), the adult *Brachylaemus virginianus* (Dickerson, 1930), tapeworms of an unidentified species of *Raillietina*, larvae from the genus *Physaloptera*, and adults of an unidentified species of Tetradonematidae (Nematoda: Enoptia). Among those, *O. canis* had a prevalence of 33.9% and a mean intensity of 4.3, whereas *B. virginianus* occurred in 16.1% with a mean intensity of 8, *Raillietina* sp. had a prevalence of 8.9% and a mean intensity of 7.4, and both *Physaloptera* sp. and the unidentified Tetradonematidae occurred with a prevalence of 1.8% (Table 1).

## DISCUSSION

No infection with any armadillo-specific parasite was detected in armadillos in Illinois. Further, we found 2 larval taxa (*O. canis* and *Physaloptera* sp), immature cestodes (*Raillietina* sp.), and an unnamed Tetradonematidae. Typically, helminths of these taxa use arthropods as intermediate or definitive hosts and arthropods are a major component of the armadillo diet (McBee and Baker, 1982). Our results are consistent with the helminthological records of armadillos at the northern limit of their range (Radomski et al., 1991) and consistent with the general observations that vertebrates experience lower parasite loads at the edge of their range (Dogiel, 1964). The species richness ( $S$ ) of helminths present in armadillos in Florida ( $S = 2$ , Varela-Stokes et al., 2008), Georgia ( $S = 3$ , Radomski et al., 1991), Texas ( $S = 6$ , Chandler, 1946), and Illinois ( $S = 5$ ) is poor in comparison with helminthological records from Argentina ( $S = 11$ , Ríos, 2020), Brazil ( $S = 13$ , Hoppe and do Nascimento, 2007;  $S = 11$ , Gomes et al., 2011), and Paraguay ( $S = 12$ , Fujita et al., 1995). From the helminths infecting armadillos in the United States, only *A. sogandaresi* and *B. virginianus* are adults, whereas the rest are immature or larval forms. Armadillos in the United States typically host fewer parasites than sympatric species of similar body size such as opossums, raccoons, and skunks (Chandler, 1946; Storrs, 1971).

The only helminth specific to armadillos recorded for the United States (*A. sogandaresi*) was not found; neither were several other parasites found in the armadillo's native range (Chandler, 1946; Jiménez et al., 2013a, 2013b), suggesting that armadillos

**Table 1.** Prevalence and mean intensity of intestinal parasite infection of 57 nine-banded armadillos in southern Illinois during 2012–2020. Confidence intervals for prevalence were calculated using Clopper–Pearson confidence limits; confidence intervals for mean intensity were calculated through bias-corrected and accelerated bootstrap. Representative specimens were deposited in the Harold W. Manter Laboratory of Parasitology (HWML), University of Nebraska, Lincoln, Nebraska.

Parasite species	HWML No.	% Prevalence	Lower and upper confidence limits for prevalence	Mean intensity	Lower and upper confidence limits for mean intensity
<i>Oncicola canis</i>	HWML216702, 216703	33.9	21.8–47.8	4.32	2.44–8.81
<i>Brachylaemus virginianus</i>	HWML216704, 216705	16.1	7.6–28.3	8	1.78–25.3
<i>Raillietina</i> sp.	Not deposited	8.9	3.0–19.6	7.4	1.4–18.6
<i>Physaloptera</i> sp.	HWML216701	1.8	0.0–9.6	—*	—
Tetradonematidae gen. sp.	HWML112257	1.8	0.0–9.2	—	—

\* It is not possible to provide a value here.

have not brought parasites from their native range into Illinois. Rather, armadillos are likely acquiring parasites including *B. virginianus*, *O. canis*, *Physaloptera* sp., and *Raillietina* sp. from sympatric species in Illinois. Armadillos likely became infected with *B. virginianus* after consuming the intermediate hosts for these parasites, which regularly use opossums as definitive hosts; *B. virginianus* was first recorded in armadillos in Texas, which was the first time the species was found in a host other than opossums (Chandler, 1946). As an adult, *O. canis* is commonly found in canids (*Canis latrans* and *Canis lupus familiaris*) and pigs (*Sus scrofa domestica*); armadillos may serve as a sink for this species, rather than a source of infection to other hosts. This is supported by the observation that most encysted cystacanths were dead or calcified (Chandler, 1946; Radomski et al., 1991). Our study was no exception, as almost all specimens were found encysted in the intestinal wall, and in the individual with the highest intensity (n = 28 acanthocephalans), most cystacanths were calcified. Armadillos appear to act as a paratenic host to *Physaloptera* sp., which infect armadillos incidentally after armadillos ingest the arthropod hosts (Radomski et al., 1991). Infection with the adults of the unknown Tetradonematidae was most likely incidental, as only 1 armadillo was infected with these nematodes. Our report of infection of an unidentified *Raillietina* is the first for armadillos throughout their range. *Taenia* sp. and *Mathevotaenia surinamensis* (Buchanan, 1956) are the only cestodes previously recorded in armadillos. Species of *Raillietina* are common parasites of homeotherm tetrapods such as lagomorphs and birds (Reid et al., 1938; Bartel, 1965). The armadillos infected with this cestode probably ingested an intermediate host such as a beetle (Reid et al., 1938) or an ant (Bartel, 1965).

The absence of *T. cruzi* in armadillos was unexpected because of the presence of both the pathogen and the vector in the study area. In particular, *Triatoma sanguisuga* is abundant in the forested areas of southern Illinois, yet time delay between blood consumption and defecation may reduce the probability of pathogens being inoculated into wild animals (Wood, 1951). The prevalence of *Trypanosoma cruzi* in armadillos in the United States has only been studied in Louisiana (Yaeger, 1988; Barr et al., 1991; Paige et al., 2002), Illinois (Vandermark et al., 2018), and Texas (Packchianian, 1942), and prevalence values are highly variable. In armadillos sampled in 3 independent studies in Louisiana, the prevalence of infection with *T. cruzi* was 1.1% (Barr et al., 1991) and 3.5% (Paige et al., 2002), whereas a population only 80 km away had a prevalence of 28% (Yaeger, 1988). Whether the difference in results was due to a disparity in testing methods or environment was unclear (Paige et al., 2002). The aggregate prevalence of *T. cruzi* from these studies (16.6%) was low in comparison with prevalence values in raccoons (36.4%), wood rats (*Neotoma* spp., 32.5%), opossums (22.9%), and striped skunks (*Mephitis mephitis*, 25.6%) in the United States (Hodo and Hamer, 2017). In Illinois, *T. cruzi* was detected in 18.9% of screened raccoons (Vandermark et al., 2018). Because prevalence may be as low as 1.1% in armadillos, there is a chance that these pathogens are present in wild populations but at levels not detected by our sample of 80 armadillos.

The difference in the infection between raccoons and armadillos in Illinois cannot be explained by diet, as the diet of raccoons consists of up to 40% insects (Llewellyn and Uhler, 1952), whereas up to 64% of armadillo diet is insects (McBee and Baker, 1982; Dikes et al., 1990; Whitaker et al., 2012). On the basis of

this reasoning alone, armadillos should consume more triatomine insects than raccoons, and therefore have higher rates of infection. Rather, this disparity may be explained by the population densities of each species. Oral transmission of *T. cruzi* is dependent on host density (Kribs-Zaleta, 2010); populations at the margins of the armadillo's range, such as those in Illinois, likely have lower densities than populations in the core of their range and are less likely to encounter the vector (Hengeveld and Haek, 1982; Phillips et al., 2010). Conversely, raccoon numbers in Illinois are unnaturally high because of mesopredator release and habitat fragmentation (Schmidt, 2003). Raccoons and other mesopredators may be controlling vector populations, further decreasing the chance of consumption of triatomines by armadillos. Alternatively, the difference in infection between raccoons and armadillos can be explained by the habitat and host preference of the vector. However, we believe this is unlikely, as *Triatoma sanguisuga* habitat preferences include both raccoon and armadillo nests (Klotz et al., 2014), and a recent study found that host feeding frequency of *T. sanguisuga* collected from homes in Louisiana was comparable between raccoons and armadillos (Dumontail et al., 2020).

The negative results for *M. leprae* were consistent with our prediction. The probability of parasites of invaders arriving in the new species' range is decreased because invading individuals are a small subset of the original rangewide population, and thus only a fraction of the parasites will be present in the new region (Dogiel, 1964; Torchin et al., 2003). In addition, leprosy is considered to have density-dependent transmission (Smith, 2016). In the initial stages of colonization, density-dependent pathogens will be unable to persist in the population because of low host densities (Kermack and McKendrick, 1927; Torchin and Mitchell, 2004). *Mycobacterium leprae* is also a specialist pathogen and therefore cannot easily shift hosts, making establishment more difficult (Cornell and Hawkins, 1993). Furthermore, there is no evidence of vertical transmission of leprosy from parent to offspring (Morgan and Loughry, 2009), meaning that if by chance adult founders carry the pathogen, the next generation will be free of infection, further decreasing the chance that individuals at the expanding front will carry leprosy (Phillips et al., 2010).

Within the first 100 yr of its dispersion across the United States, *A. sogandaresi*, a parasite specific to armadillos, became established in the Houston Bay (Chandler, 1946) and it was detected in Central Texas and Florida by 1991 (Jiménez-Ruiz et al., 2006; Varela-Stokes et al., 2008). Given the accelerated dispersion of armadillos across the southeastern United States, it may be relevant to anticipate the concomitant dispersion of this parasite. The life cycle of *A. sogandaresi* is believed to be direct; it does not require an intermediate host to be transmitted and their survival may depend on the conditions that allow egg viability. It may be possible for eggs of *A. sogandaresi* to remain viable in southern Illinois, since another species of the same genus, *Aspidodera raillieti* Travassos, 1913, is already present in the region (Alden, 1995; Jiménez et al., 2013a, 2014). The codispersion of an armadillo host and a parasite has occurred elsewhere, as the invasive big hairy armadillo, *Chaetophractus villosus* (Desmarest), was introduced into Tierra del Fuego. On this island, the big hairy armadillo has become established, yet only 1 species of their parasites has been documented in this new habitat; this parasite has a direct transmission (Ezquiaga et al., 2016). This

helminthological record of armadillos in Illinois sets the timeline to observe the establishment of *A. sogandaresi* in the Midwest.

It is imperative that testing be conducted in the future as armadillo numbers increase in areas of northerly expanding populations. Although the chance of northward expansion of the etiological agent of leprosy is low, testing should be conducted in states such as Missouri and Tennessee, given leprosy has spread to populations that were previously believed to be leprosy-free in Alabama, Georgia, and Florida within the last decade (Loughry et al., 2009). Currently, armadillo populations at the edge of their range have very low prevalence and intensity of various pathogens, aiding in the colonization of the area. However, as more individuals colonize this area, there is an increased chance that their parasites and pathogens may begin to arrive (Phillips et al., 2010), and density-dependent pathogens such as *M. leprae* may become established in the population (Kermack and McKendrick, 1927; Torchin and Mitchell, 2004; Smith, 2016). Parasites may also adapt over time to increase their transmissibility as a way of increasing dispersal capability (Phillips et al., 2010). Although armadillos positive for *M. leprae* may increase the risk of infection to humans (Balamayooran et al., 2015), a higher density of armadillos could benefit wildlife and humans by acting as definitive hosts of *Trypanosoma cruzi*, as high diversity of compatible hosts can lead to a decrease in disease risk in individuals of different species (i.e., via the dilution effect; Keesing et al., 2006; Civitello et al., 2015). Armadillos could also decrease the risk of Chagas' disease by predation of triatomine insects. Reducing vector density will in turn reduce the chance of native wildlife or humans encountering the vector and contracting the disease (Keesing et al., 2006).

#### ACKNOWLEDGMENTS

The authors assert that all applicable international, national, and institutional guidelines for the care and use of animals were followed. Funding was provided by the Illinois Department of Natural Resources via Federal Aid Project W-135-R. C.J.H. was supported by NSF-DUE 1564969. L. Adams at the National Hansen's Disease Clinic in Baton Rouge, Louisiana aided us in screening blood samples for *M. leprae* (AAI21005-000-0000). We thank R. Zollars, M. Kinkade, S. Arreguin, and R. Flores for their assistance with screening for intestinal parasites; J. Martin and the citizen naturalists of Illinois T. Gettelman, A. Wilson, and M. Deutsch assisted with armadillo capture.

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