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New records of the nine-banded armadillo, *Dasypus novemcinctus*, in southeast Tennessee, and their implications

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Abstract For over 150 years the nine-banded armadillo, *Dasypus novemcinctus*, has been expanding its range into the southern United States. Previous studies have suggested an average expansion rate of 7.8 km/year, with the fastest expansion rates in the Gulf Coast of Florida at 17.2 km/year and the southern Great Plains at a rate of 11 km/year. Beginning in July 2007, we collected 11 road-killed specimens of *D. novemcinctus* from southeast Tennessee; one from Hamilton County, one from Rutherford County, three from Marion County, and six from Franklin County. These records represent an extension of approximately 325 km to the east and 375 km to the north of previously published range limits. The new records imply an expansion rate in far excess of previous maximum estimates. The six Franklin County specimens were collected atop the Cumberland Plateau at elevations of 446, 462, 570, 583 (two specimens), and 606 m asl. These elevation records suggest further northward and eastward expansion of the species is likely. The ecological implications of this increased rate of geographic expansion are discussed.

Keywords: Dasypodidae, *Dasypus novemcinctus*, nine-banded armadillo, range, southeast United States, zoogeography

Nuevos registros del armadillo de nueve bandas, *Dasypus novemcinctus*, en el sureste de Tennessee y sus implicaciones

Resumen Por más de 150 años, el armadillo de nueve bandas (*Dasypus novemcinctus*) ha extendido su distribución en el sur de los Estados Unidos. Investigaciones anteriores indican que la velocidad media de expansión es de 7,8 km/año; la velocidad más rápida de expansión se registró en Florida, en la región de la costa del Golfo de México (17,8 km/año) y en el sur de las planicies centrales ("Great Plains"; 11 km/año). Desde julio de 2007 se colectaron 11 especímenes atropellados de *D. novemcinctus* en el sureste del estado de Tennessee; uno en el condado de Hamilton, uno en el condado de Rutherford, tres en el condado de Marion y seis en el condado de Franklin. Estos especímenes representan una gran extensión de la distribución publicada, de aproximadamente 325 km hacia el este y 375 km hacia el norte. Los datos implican una velocidad de expansión superior a las máximas estimaciones anteriores. Los seis especímenes del condado de Franklin fueron coleccionados en la Meseta de Cumberland ("Cumberland Plateau"), a elevaciones de 446, 462, 570, 583 (dos especímenes) y 606 msnm. Estos datos sugieren que podrían ocurrir expansiones adicionales hacia el norte y el este. En este trabajo se discuten las implicaciones ecológicas del aumento en la velocidad de expansión geográfica de *D. novemcinctus*.

Palabras clave: armadillo de nueve bandas, Dasypodidae, *Dasypus novemcinctus*, distribución, sureste de Estados Unidos, zoogeografía

Introduction

The geographic distribution of modern xenarthrans is almost exclusively confined to the Neotropics, with only one species found in the Nearctic, the nine-banded armadillo *Dasypus novemcinctus*. This species holds the largest geographic range of any xenarthran (Abba & Superina, 2010) and is the only xenarthran currently undergoing significant range expansion (Aguiar & Fonseca, 2008). It has been expanding the northern limits of its North American range for over 150 years, and has become common, even ubiquitous in much of the southeastern United States (Audubon & Bachman, 1854; McBee & Baker, 1982; Taulman & Robbins, 1996; Aguiar & Fonseca, 2008). It was first documented in extreme southwestern Tennessee in the early 1980s, but has been known from the southern portions of the neighboring states of Georgia and Alabama for at least a decade prior to this (Humphrey, 1974; Kennedy & Harvey, 1980; Taulman & Robbins, 1996). Occurrences of *D. novemcinctus* have now been reported from as far north as Illinois and Indiana (Van Deelen *et al*., 2002; Whitaker, 2010). The biogeography of *D. novemcinctus* is particularly intriguing in that expansion has occurred in historic times when many other mammalian species have exhibited population declines. Reproductive features such as polyembryony and delayed implantation (Humphrey, 1974; McBee & Baker, 1982; Storrs *et al*., 1988; Peppler, 2008) undoubtedly heighten the ability of the species to reach population carrying capacity in areas where they dwell, expedite dispersal into adjacent unoccupied land, and allow populations to be founded outside of previously established territory by solitary mature females pregnant with male offspring. **Fig. 1** details the historic trends in *D. novemcinctus* colonization of the United States.

Taulman & Robbins (1996) estimated rates of range expansion between 1972 and 1994 for *D. novemcinctus* based on literature records and their own communications with several hundred wildlife officers. They estimated the average rate of expansion across the range was 7.8 km per year, with maximum expansion rates of 11 km per year in the

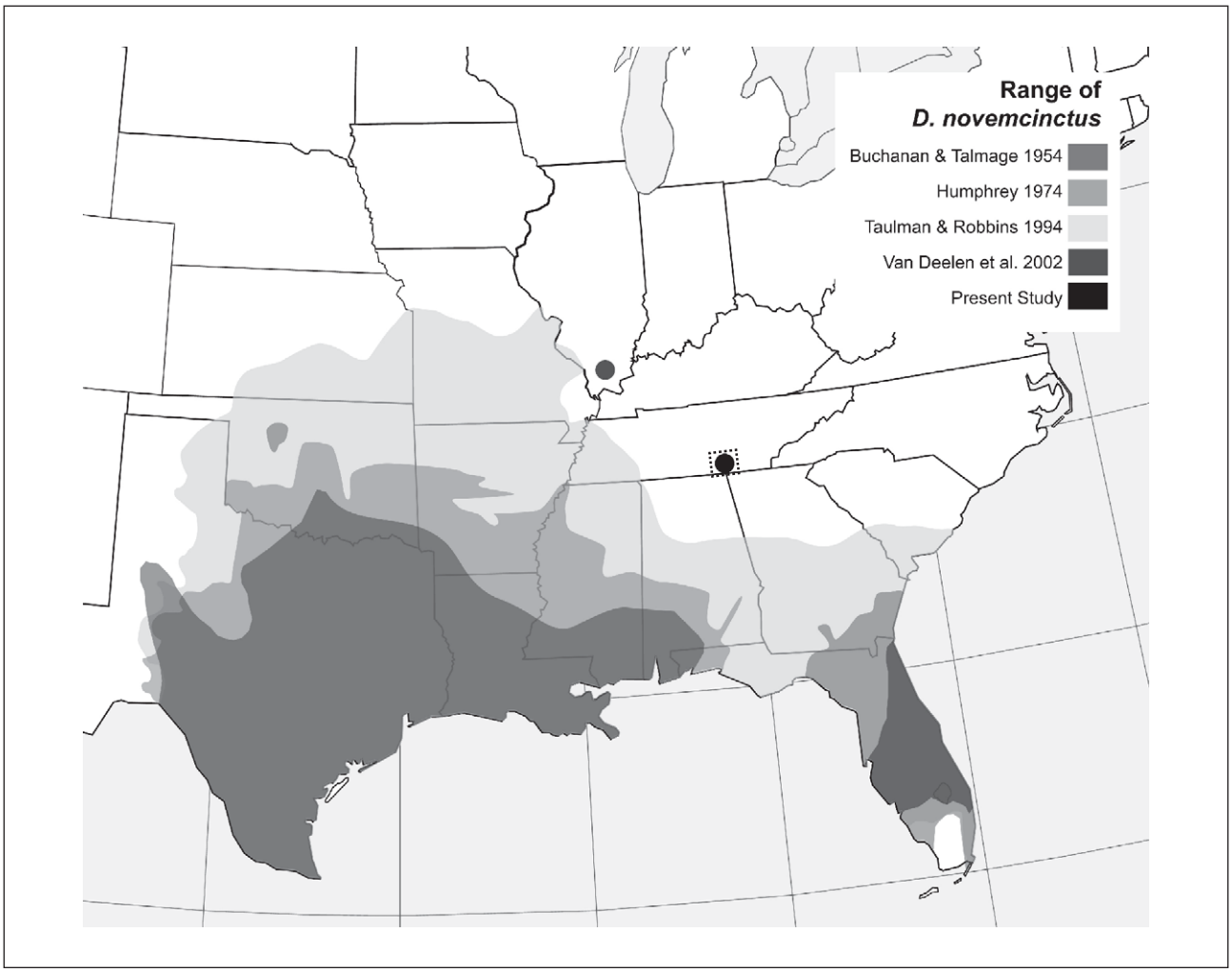

Figure 1. Illustration of historical expansion of *D. novemcinctus* in the southeastern United States based upon previously published range estimates, especially those of Taulman & Robbins (1996). The contemporary range for the species likely includes all or most of Georgia, Alabama and South Carolina, western Kentucky, all of Tennessee west of the area of present study, and southern North Carolina and Illinois. The dotted line indicates the area that is amplified in **Fig. 2**.

Midwest and 17.2 km per year in the Gulf Coast of Florida. They suggested that the timing of the U.S. invasion and rapid spread of this species likely related to anthropogenic activities of the past two centuries and predicted that two primary factors would ultimately limit its dispersal. The first was a precipitation limit, restricting the territory of *D. novemcinctus* to regions receiving at least 38 cm of precipitation per year. The second limiting factor was winter temperature. Areas with a mean January temperature above 0 °C with less than 24 annual freeze days were expected to be suitably warm for persistent populations. Based on their analysis, Taulman & Robbins (1996) predicted the potential maximum for northern range expansion to be 41° N latitude along the East Coast and 39° N latitude in the Appalachians and Midwest.

The first published record of *D. novemcinctus* in east Tennessee came from Rhea County, where a road-killed specimen was discovered and subsequently preserved for Bryan College in 1980 (Henning, 1980). This individual, a pregnant female, was likely an accidental record or the result of human introduction. There are no documented cases of an armadillo occurring in this region from 1980 to 2007. The aim of the present study is to report new records of *D. novemcinctus* from southeast Tennessee, including the Cumberland Plateau, spanning the years of 2007 to 2011. As noted before, the only previous records of a persistent *Dasypus* population in this state are from extreme southwest Tennessee (Kennedy & Harvey, 1980; Taulman & Robbins, 1996) so these new records represent a significant range extension. The specimens collected from the Cumberland Plateau are also likely elevation records for this species east of the Mississippi River. The ecological implications of these new records are discussed.

Materials and Methods / Results

In the course of present study (2007–2011), 11 vouchered specimens of *D. novemcinctus* have been collected from roadsides in Franklin County, Marion County, Rutherford County, and Hamilton County, TN. All were apparently killed by automobile traffic and all were males. Franklin and Marion County collection sites all lie within a 26 km radius. Specimens are listed by their University of Tennessee at Chattanooga Natural History Museum catalogue number, as indicated by the UTCM prefix. Collection date, locality, total body length, tail length, hind foot length, ear length measurements (in mm), and mass (in kg) are reported when available. Because all are road-killed individuals, reported masses are almost certainly underestimates, the degree of underestimation being determined by the circumstances of the individual's death and time elapsed between death and collection. **Fig. 2** provides a map denoting specimen localities within the collection region.

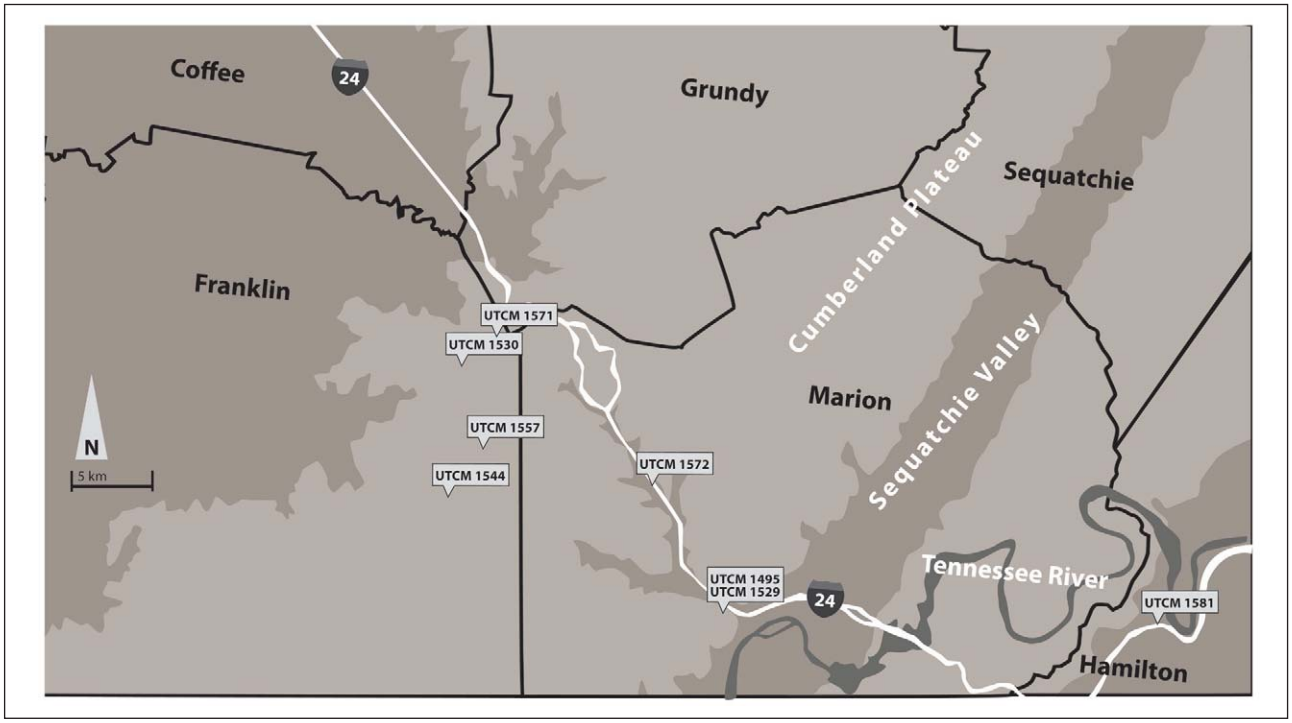

Figure 2. County map of southeastern Tennessee depicting localities where *Dasypus novemcinctus* specimens were collected from 2007–2011. This is an amplification of the present study area noted by the dotted line in Fig. 1. Individual specimens are identified by their museum accession numbers. Lighter areas of the map represent the Cumberland Plateau (elevation >400 m asl). The lower margin of the map represents the border between Tennessee and Alabama/Georgia. UTCM 1580 was collected in Rutherford County along I-24, approximately 30 km north of the uppermost bound of the map.

Franklin County specimens have been collected from the Cumberland Plateau at elevations up to 606 m asl. These specimens were found along two-lane roads including Highway 41, Highway 156, and Gudger Road. These thoroughfares roughly outline the north, east, and west overlooks of Lost Cove near Sewanee. Specimen information is as follows (measurements in parentheses: total body length–tail length–hind foot length–ear length, all in mm): UTCM 1557 (July 2007, 35°09′43″N, 85°52′55″W, 570 m asl, measurements 597–224–87–42, 3.7 kg, vouchered skin, skull, and skeleton), UTCM 1530 (August 2009, 35°12′22″N, 85°42′00″W, 583 m asl, measurements not obtained due to the extreme degree of degradation, vouchered skull, and skeleton), UTCM 1544 (September 2009, 35°07′48″N, 85°55′12″W, 462 m asl, measurements 735–347–96–44, 3.9 kg, vouchered skin, skull and skeleton), UTCM 1571 (May 2010, 35°13′01″N, 85°53′10″W, 606 m asl, unmeasured due to degradation, vouchered skull), and UTCM 1725 (March 2011, 35°06′11″N, 85°33′50″W, 446 m asl, measurements 702–248–91–37, 3.5 kg, vouchered skull, skeleton, and partial skin). An additional specimen obtained in November 2011 near the location of UTCM 1530 has yet to be catalogued. It is vouchered as a frozen, unmeasured carcass awaiting preparation.

Marion County specimens were collected in Kimball along Interstate 24 near the mouth of Battle Creek, a Tennessee River tributary in close proximity to Sequatchie Valley. Specimen information is as follows: UTCM 1495 (August 2008, 35°03′40″N, 85°43′26″W, 190 m asl, unmeasured due to degradation, vouchered skull; **Fig. 3**), UTCM 1529 (August 2009, 35°03′40″N, 85°43′26″W, 190 m asl, unmeasured due to degradation, vouchered skull), and UTCM 1572 (May 2010, 35°07′48″N, 85°46′01″W, 262 m asl, measurements 821–359–82–46, 4.3 kg, vouchered skull).

Specimens from Rutherford County and Hamilton County were collected along Interstate 24. The Rutherford specimen was found near Wartrace: UTCM 1580 (May 2010, 35°24′04″N, 86°09′32″W, 288 m asl, unmeasured due to degradation, vouchered skull). The Hamilton County specimen was found between Lookout Mountain and a bow of the Tennessee River called Moccasin Bend: UTCM 1581 (June 2010, 35°00′50″N, 85°12′40″W, 218 m asl, vouchered as a frozen, unmeasured carcass awaiting preparation).

Figure 3. Specimen of *Dasypus novemcinctus* collected in southeastern Tennessee in 2008. Skull and mandible of UTCM 1495. Skull shown in ventral view, complete right and nearly complete left mandible in lateral view.

Discussion

Specimens of *D. novemcinctus* have now been documented from the southern Cumberland Plateau of Tennessee and neighboring areas over the course of several successive years. A contemporary zoological survey of Russell Cave National Monument in Jackson County, Alabama, adjacent to Marion County (Grow & Kennedy, 2010) has also detected the presence of *D. novemcinctus*. This evidence suggests that at least a stable seasonal population of *D. novemcinctus* has become established through north Alabama and into the Cumberland Plateau and Sequatchie Valley of Tennessee. This is further confirmed by news reports and other anecdotal sightings.

We still hope to confirm the presence of *D. novemcinctus* in the winter months in our study area. Although the collection of multiple specimens over the course of four years strongly suggests the presence of a resident population, the fact that specimens were collected only from March to November leaves open the possibility that the Tennessee population is presently seasonal, dying back in the winter and reestablishing in spring. The measurements of a specimen acquired on the seventh day of spring (27 March 2011; UTCM 1725) imply the specimen may be a yearling (McBee & Baker, 1982). Loughry & McDonough (2001) suggest it is unlikely that a yearling armadillo has traveled farther than a half-kilometer from the burrow in which it was born, though the distances traveled by dispersing yearlings and the implications of this specimen remain uncertain. Although *D. novemcinctus* is known to decrease activity levels during cold periods (McNab, 1980; Layne & Glover, 1985), locating an active burrow during the summer and monitoring its status through the winter could resolve this question of seasonal persistence.

The new southeast Tennessee records constitute a range extension for this species of approximately 325 km to the east and 375 km to the north of Taulman & Robbins' range estimates published in 1996 (based on data collected through 1994), as shown in **Fig. 1**. Furthermore, the altitudes at which the Franklin County specimens have been collected represent likely elevation records for this species in the southeastern United States east of the Mississippi River. If temperature is a regulator of expansion, the presence of *D. novemcinctus*

at elevations over 500 m asl confirms a capacity for colonization throughout most of Tennessee, given a decrease of -3.25 °C in annual mean temperature per 500 m elevation increase (COESA, 1976).

Given the elapse of 13 years (1994–2007) from the end of Taulman & Robbins' (1996) data collection to our first record, the rate of expansion necessary to colonize southeastern Tennessee would be approximately 26 km per year from the west and/or 29 km per year from the south. As noted previously, the maximum rate of range expansion calculated for this species by Taulman & Robbins (1996) was 11 km per year in the Midwest and 17 km per year in Florida's Gulf Coast, with an average expansion rate of 7.8 km per year in North America at large. The rate of range expansion in this region therefore exceeds previously recorded maximums by 65%.

The factors responsible for the amplified rate of expansion of *D. novemcinctus* in the southeast are unknown. Because the species has been expanding for many years across its range (Taulman & Robbins, 1996; Van Deelen *et al*., 2002) it may be assumed that the reasons for the accelerated expansion rates do not relate to conditions local to southeast Tennessee. There are several possibilities that seem plausible. These include the spread of fire ants (*Solenopsis invicta*) or other invasive insect species, lack of large predators, succession of farmland into fields and forests, and increased development of residential areas with accompanying ecological disturbance and global climate change. Of these, the first two seem less likely, as ants in general represent a fairly minor component of armadillo diets in North America (McDonough & Loughry, 2008), and McDonough & Loughry (1997) and Loughry *et al*. (2002) report significant levels of predation on *D. novemcinctus*, particularly among juveniles.

Between 1987 and 2007, farmland in Tennessee, Georgia and Alabama decreased by 1,467,983 acres (USDA Census of Agriculture 1877–2007, 2007). Blackberry (*Rubus fruticosus*) and other thorny plants are often dominant species in areas undergoing early succession in the southeast. Blackberry is known to be a foodstuff of interest to *D. novemcinctus* (Kalmbach, 1943) and, with its tough carapace, *D. novemcinctus* is likely less hindered by prickly thickets than potential competitors such as opossum (*Didelphis virginiana*) and raccoon (*Procyon lotor*). Areas in succession also seem likely to support a greater food supply of arthropod biomass than fields under cultivation. The southeastern U.S. has also seen rapid population development over the past two decades. The population of Georgia increased 18.3% from 2000 to 2008 compared to a national average of 8.0% (U.S. Census Bureau, 2008). Compromised ecosystems are more readily colonized by invasive species than those that are intact (Williams & Meffe, 1998).

If temperature plays a part not only in the limits of dispersal, but also in the rate at which it proceeds, then the overall temperature rise of the past two decades may be spurring the advance of *D. novemcinctus*. The mean January temperature of Chattanooga, TN during the 1980s was 2.54 °C. This has risen through the 1990s and early 21st century to 6.05 °C, as of 2009 (NASA GISS Surface Temperature Analysis, 2009). If cold temperatures retard the spread and stabilization of *D. novemcinctus* populations, then current trends in climate may be facilitating an increased rate of expansion and suggest that range expansion of this species may continue beyond the latitudinal limits previously suggested by Taulman & Robbins (1996). It is also possible that the rate of expansion will continue to increase as climate warms.

The reasons for accelerated expansion may also be attributable to an inherent niche plasticity within the species that is as yet unrealized. Smith & Redford (1990) compared the morphology and feeding habits of *D. novemcinctus* with those of the six-banded armadillo *Euphractus sexcinctus*. They noted that where these two armadillo species were sympatric, their diets differed in a manner that could be predicted by the morphology of their feeding apparatus, with *D. novemcinctus* subsisting primarily on ants and termites and *E. sexcinctus* exhibiting generalized omnivory. However, in North America, *D. novemcinctus* exhibits a level of dietary opportunism that rivals that of *E. sexcinctus* (Smith & Redford, 1990). It may be that the realized niche of *D. novemcinctus* as a myrmecophage over much of its range is a result of competition with armadillos more broadly adapted to omnivory (Smith & Redford, 1990). Lacking this close niche competition in the United States, the species may be broadening its ecological horizons to fill a fundamental niche more varied and generalized than previously anticipated by morphology alone.

The present study documents an accelerated rate of expansion for *D. novemcinctus* in the southeast United States. The new records suggest that *D. novemcinctus* will fill its potential range to the predicted limits of dispersal more rapidly than previously expected, perhaps even dispersing beyond predicted latitudinal limits. Although we believe climate change and anthropogenic activity to be the most likely factors responsible for the amplified rate of expansion, determining the underlying causes with greater certainty will require further study. Most ecological studies of *D. novemcinctus* focus on two aspects alone, diet and home range size (McDonough & Loughry, 2008). Additional ecological studies, especially of seasonal/temperature related variations in habitat use, may prove particularly important in increasing our understanding of the ecological factors acting to hasten range expansion.

We close this paper with an appeal for better documentation of *D. novemcinctus* populations at the margins of their range. *Dasypus novemcinctus* populations are relatively easy to document, as their distinctive appearance allows them to be readily identified and they are common road-killed animals in areas where they occur. Anecdotal evidence suggests that *D. novemcinctus* are more widely distributed than any published report suggests, including this one. For example, newspapers in Somerset, KY, Evansville, IN, and Knoxville, TN have all made reports of local armadillo sightings (Mardis, 2006; Potter, 2008; Venable, 2009). As of January 2010 the North Carolina Wildlife Resource Commission has permitted year-round hunting of armadillos as well as seasonal trapping due to local sightings along the South Carolina border (North Carolina Wildlife Resources Commission Public Hearings 2010–2011, 2011). We have also received unofficial reports of armadillo sightings from Cleveland, TN (J. Hisey, Lee University) and Nashville, TN (D. Withers, Tennessee Natural Heritage Program). However, the lack of vouchered museum specimens and published records from refereed journals hinders scientific efforts to document the ongoing biogeographic changes in this species. Indeed, records from areas like middle Tennessee, northern Alabama, and northern Georgia could have provided critical data on the migration trends that led to the establishment of the South Cumberland population and yielded further insight into when and how the rates of expansion have changed in this species. Going forward, such data will be vital in improving our understanding of the location, rate, and underlying causes of the biogeographic expansion of *D. novemcinctus*.

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