



Original Article

Identification of an Attractant for the Nine-Banded Armadillo, *Dasypos novemcinctus*

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ABSTRACT The nine-banded armadillo (*Dasypos novemcinctus*) is considered by many to be one of the greatest nuisance wildlife species in the Southeastern United States. Management is difficult because no repellents, toxicants, or fumigants are currently registered for this species; exclusion is laborious because armadillos are adept burrowers; and no effective trapping attractants have been identified. If a suitable lure were discovered, trap capture success could increase and the frequency of nuisance complaints could decrease. We compared the behavioral attractiveness to captive armadillos of 15 commercially available food materials, as well as scents collected from conspecifics, in Florida, USA, 2008–2009. According to 3 distinct behavioral measures, 4 materials consistently elicited the most attraction responses from armadillos: pond worms (*Lumbricus terrestris*), crickets (*Acheta domesticus*), red worms (*Eisenia fetida*), and wigglers (*Pheretima harwayanus*). Recognizing that all of these materials were live prey, we devised a second series of experiments to evaluate the relative importance of olfactory cues versus auditory–vibrational cues in evoking a response from armadillos. Results suggested auditory–vibrational cues were meaningful. Finally, we measured sound pressure and vibration levels produced by the most preferred and less preferred prey items. Sound and vibrational cues decreased rapidly below background noise levels within 10–30 cm from baits. Because of this, and because the perceptual range of armadillos to the olfactory cues from these baits appears limited, traps baited with any worm or cricket are unlikely to lure armadillos from great distances. Development of an effective baiting system will require further investigation into the possibility of enhancing the ability of stimuli to travel over long distances. © 2011 The Wildlife Society.

KEY WORDS armadillos, attractants, baits, capture, *Dasypos novemcinctus*, lures, nuisance, odors, trap.

The nine-banded armadillo (*Dasypos novemcinctus*) is abundant throughout the southeastern United States, as a result of both natural range expansion and repeated translocations by humans (Fitch et al. 1952, Neill 1952, Humphrey 1974, Taulman and Robbins 1996). Human population growth throughout the Southeast during the past century has coincided with range expansion of the species, leading to an increase in the frequency of contact between armadillos and humans. This contact is of medical concern because nine-banded armadillos from Texas, Louisiana, Arkansas, Mississippi, and Alabama are the only known nonhuman endemic natural host of the bacteria that causes Hansen's Disease or leprosy (Burchfield 1999, Truman 2005, Loughry

et al. 2009). Recent research indicates armadillos may transmit leprosy to humans (Truman et al. 2011).

The nine-banded armadillo is capable of expanding its distribution rapidly in part because of both high fecundity and survival: females regularly give birth to genetically identical quadruplets (Prodöhl et al. 1996), and the species has few predators, an abundant prey base, and an affinity for a wide variety of habitats. Two factors believed to be most limiting to further northward expansion are rainfall (≥ 38 cm rainfall/yr) and the annual number of days below freezing (< 24 days/yr; Taulman and Robbins 1996). Climate changes resulting from global warming may enable the species to spread farther north in the future, leading to even greater need for efficient control techniques.

Armadillos are considered one of the most significant nuisance pests in the Southeast, comprising a large proportion of complaints against wildlife (Armstrong 1991, Bruggers et al. 2002, Mengak 2003). Armadillo foraging activity causes damage in a wide range of urban and suburban

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locations such as golf courses, sports fields, nurseries, orange groves, cemeteries, lawns, and flower and vegetable gardens, while burrowing activity can cause structural instabilities when it occurs around and under buildings (Neill 1952, Chamberlain 1980). Armadillo foraging activity can also pose a considerable threat to species of conservation concern such as northern bobwhite quail (*Colinus virginianus*; Staller et al. 2005), gopher tortoises (*Gopherus polyphemus*; Douglass and Winegarner 1977), and sea turtles (loggerhead, *Caretta caretta*; leatherback *Dermochelys coriacea*; and green *Chelonia mydas*; Drennen et al. 1989, Engeman et al. 2005). Because armadillos have small home ranges (4–11 ha; Layne and Glover 1977, Loughry and McDonough 1998, McDonough 2000, Gammons et al. 2009), it is common for individual animals to become chronic pests to homeowners and land managers. Wildlife professionals rank both 1) the development of effective lures to live trap armadillos and 2) improvement upon methods used to census armadillos to strengthen control programs focused on protecting species of conservation concern, as high-priority research needs in the wildlife damage-management field (Bruggers et al. 2002).

Presently, there are no cost-effective, reliable methods to deter or capture wild armadillos. Most of the methods typically used to reduce damage caused by wildlife are not suitable for use with armadillos. Exclusion attempts are often ineffective because armadillos are adept at both burrowing and climbing; currently no repellents, toxicants, or fumigants are registered for use with armadillos; and no efficient methods exist for luring armadillos into traps. Although these animals occasionally enter live traps set in combination with fencing materials, capture rates in traps are extremely low (i.e., 1 capture/133 trap-nights in GA; Gammons et al. 2005).

Identification of a substance that effectively functions as a lure for armadillos could increase capture success and, thereby, reduce the frequency of nuisance complaints. Despite great interest among homeowners and commercial businesses in managing nuisance armadillos, we are aware of only one published attempt to systematically evaluate the relative attractiveness of various materials that could function as lures to armadillos (Gammons et al. 2005). This study compared capture success in live traps baited with various materials, and experienced such low capture rates that it is questionable whether armadillo preferences were truly measured (1 capture/133 trap-nights). Assessing preferences in a more controlled setting would be a more efficient means of evaluating the efficacy of potential materials as lures. We posit that the 2 types of materials most likely to generate interest from wild armadillos and, thus, worthy of evaluation as potential lures are food materials and odors from conspecifics.

Armadillos are considered opportunistic foragers, consuming a wide variety of food materials. Approximately 50–95% of their diet is insects, depending on site and season studied (reviewed by McDonough and Loughry 2008), with Coleoptera comprising the largest component of this (Kalmbach 1943, Fitch et al. 1952, Nesbitt et al. 1977, Sikes et al. 1990, Anacleto 2007). The remainder of the

diet consists of other invertebrates, small vertebrates, fruit, and other vegetative matter.

Chemical signals produced by armadillos also have potential for exploitation as lures. Most mammal species produce several types of individual-specific odors that communicate information to conspecifics on their sex, reproductive state, and identity (Halpin 1986, Johnston 2003, Conover 2007). These odors are used for a variety of functions, ranging from mate attraction to alarm announcements. Chemical communication in armadillos is probable, given that juveniles are capable of recognizing their own odor, discriminating the odors of kin from nonkin, and are more interested in the odors of siblings than their own odors (Loughry and McDonough 1994). Furthermore, behaviors exhibited during courtship strongly suggest the use of chemical cues (Yaksh 1967, McDonough 1997).

We conducted choice experiments in a large test arena to document armadillo responses to a variety of materials with the goal of identifying materials that could be exploited to lure animals into traps. These initial experiments suggested that mobile materials (live prey) seemed to be more attractive than other materials. To explore this finding further, we conducted a second set of behavioral experiments to assess the relative role of different combinations of olfactory or auditory–vibrational cues in attracting armadillos. Finally, we measured amplitudes and spectra of sounds and vibrations produced by highly preferred and less preferred live prey items in a laboratory setting in an attempt to explain differences in detectability of these items by armadillos.

STUDY AREA

We captured armadillos from 3 study areas in Gadsden and Leon Counties in North Florida, USA: Joe Budd Wildlife Management Area (30°30'33"N, 84°32'19"W), North Florida Research and Education Center (30°32'42"N, 84°35'39"W), and Tall Timbers Research Station (30°39'24"N, 84°12'32"W). Each of these study areas is located within 40 km of one another and has a diverse combination of vegetative community types including upland pines, bottomland hardwoods, and agricultural areas.

MATERIALS AND METHODS

Between August 2008 and November 2009, we captured 40 individual armadillos using long-handled dip nets (McDonough 1994) at Joe Budd Wildlife Management Area ($n = 30$), North Florida Research and Education Center ($n = 5$), and Tall Timbers Research Station ($n = 5$). Each individual was housed singly in captivity for a maximum of 14 days, and then released at the site of capture (as approved by the University of Florida Institutional Animal Care and Use Committee protocol 200801663 and a permit from the Florida Fish and Wildlife Conservation Commission).

Animal Maintenance in Captivity

We developed a captive environment with conditions as similar as possible to those experienced by armadillos in the wild. We constructed an outdoor enclosure area that

measured 12.1 m × 12.1 m, surrounded by 1.8-m-high chain-link fence to keep predators out. A tall frame made of polyvinyl chloride pipe was erected over this entire area to support a large sheet of shade cloth that limited exposure of the animals to direct sunlight. Within this protected area, we constructed 3 3-m × 3-m holding pens and 3 3-m × 3-m bioassay pens. Each pen was surrounded by sheet metal buried 0.9 m in the ground to prevent armadillos from digging underneath and 0.9 m above ground to prevent armadillos from jumping or climbing over. Pens were situated such that each holding pen was adjacent to a same-sized bioassay pen, with movable doors between the 2 areas to facilitate voluntary movement of animals.

Pens had naturally occurring dirt floors to allow animals to dig burrows in the soil. We placed the top half of a plastic pet carrier in each holding pen to provide a means of escaping rain and sun if a test animal did not dig a burrow. We provided hay in each holding pen for use as bedding material in burrows or pet carriers.

We provided water at all times through an automatic pet watering device. Either cat or dog food soaked in water was provided daily. On the days of experimental trials, we provided food after testing to limit the likelihood of nonparticipation due to satiation.

Bioassay and Acoustic Measurement Procedures

We constructed a virtual grid in each bioassay pen by placing reference points on the side walls, spaced 0.3 m apart. The intersections of these grid lines formed the 49 location points where test materials could be placed. For each experimental trial, we determined the locations of materials to be tested within this grid system using randomly generated numbers. Materials were presented in sterilized plastic bowls (10.2-cm diam and 7.6-cm depth; sterilized in a 3-step procedure by first scrubbing with a detergent, followed by a thorough rinsing, followed by a 10-min immersion in a solution of

1 Tbs bleach to 1 quart water) sunk into the soil at these randomly selected locations.

To reduce the chances of contamination of the bioassay pen between animals (through scent marking, food remains, etc.), we laid a plastic sheet on the ground in each bioassay pen and covered it with approximately 8 cm of top soil taken from a pit dug in another location on the property. After each animal was released to the wild, this layer of soil and the plastic sheeting were removed and replaced prior to the introduction of a new animal into the pen. We sterilized all walls, kennels, and waterers within the holding pen between animals as well (using a detergent and a scrub brush, followed by a thorough rinsing with water, followed by spraying with a solution of 1 Tbs [14.79 mL] bleach to 1 quart [0.95 L] water).

Following a 2-day period of acclimation to captive conditions, each animal was given the opportunity to participate in 1–3 experimental trials per day, depending upon the speed with which they completed each trial (mean no. of trials/animal/day = 1.6). At the start of each experimental trial, we placed the materials to be tested at randomly selected locations in the bioassay pen adjacent to the assigned animal, and we opened the door between the pens, allowing the test animal to begin participating whenever it chose. We conducted all trials between 1900 hours and 0100 hours.

We used video cameras (Sony Handycam DCR-SR85 [Tokyo, Japan]) to record armadillo behaviors during experimental trials. Infrared lights (CCTV 48 LED Camera Infrared Illuminator Night Vision) provided light for video recording after sunset. Videotaping of each trial began when the adjoining door between the 2 pens was opened and ended when the animal exited the bioassay pen.

Experiment 1: evaluation of potential bait materials.—Fifteen commercially available food materials previously reported to be consumed by the species were used as test materials (Table 1). All live invertebrates were presented in bowls

Table 1. Materials presented during experimental trials that evaluated the utility of potential lures for captive nine-banded armadillos in Florida, USA, 2008–2009.

Reason for testing	Materials	Quantity
Odors associated with food materials, expected to stimulate hunger	Mealworms (<i>Tenebrio molitor</i>)	10
	Millipedes (<i>Diplopoda</i> spp.)	10
	Wigglers (<i>Pheretima harwayanus</i>)	5
	Red worms (<i>Eisenia fetida</i>)	5
	Big red worms (<i>E. hortensis</i>)	3
	Glow worms (<i>E. hortensis</i> , injected with brightly colored dyes to entice fish)	3
	Pond worms (<i>Lumbricus terrestris</i>)	3
	Crickets (<i>Acheta domesticus</i>)	3
	Chicken eggs	1
	Quail eggs	1
	Avocado	Approx. 2 Tbsp (29.57 mL)
	Banana	Approx. 2 Tbsp (29.57 mL)
	Strawberry	Approx. 2 Tbsp (29.57 mL)
	Peanut butter	Approx. 2 Tbsp (29.57 mL)
	Vanilla wafer cookies	3
Odors associated with conspecifics, expected to stimulate curiosity or animosity	Feminine hygiene pad containing anal secretions or feces from animals of same gender	1/3
	Feminine hygiene pad containing anal secretions or feces from animals of opposite gender	1/3
Control	Unscented feminine hygiene pad	1/3

containing a thin layer of the rearing medium in which they were purchased, with the exception of crickets (*Acheta domesticus*) and mealworms, which were placed into empty bowls. In addition, we tested intraspecific odors collected from anal glands and fecal material of other animals upon capture (Table 1). Odors from armadillos were collected by wiping a feminine hygiene pad (Kotex ultra thin; Kimberly-Clark, Neenah, WI) repeatedly across the anal glands of animals, and were stored in double ziplock bags in the freezer at -20° C until required for experimental trials (Loughry and McDonough 1994). We also included unscented feminine hygiene pads in some trials to control for the possibility that the pads themselves could attract animals. Three materials were randomly selected from the list of 18 options to present during each experimental trial.

We used 3 behavioral metrics to infer the relative interest of armadillos in test materials. These metrics were quantified from all videotapes by the same observer (L.W.D.), starting when an animal entered the bioassay pen and ending when 5 min elapsed after the animal had wandered from the vicinity (1 body length) of any of the test materials. We used the metric “time to first contact” (mean no. of sec between animal entry into bioassay pen and first visit of animal to each material) as a measure of the relative ability of each test material to evoke a response from armadillos. If a particular test material was never contacted during the trial, the end time of the experiment was assigned to that material. Second, the metric “number of attraction events” (mean no. of times animal’s head was oriented toward each material when animal was within 1 body length of that material) was chosen as a measure of the relative strength of each test material to evoke a response indicating interest. Finally, we used the metric “duration of interest” (mean no. of sec an animal spent oriented toward each material when animal was within 1 body length of that material) as a measure of the relative ability of each test material to sustain the interest of armadillos. Relative “palatability” of test materials is simply reported as the mean proportion of each test material consumed per trial per animal.

Experiment 2: comparison of the relative importance of auditory and olfactory cues.—We devised 2 bioassays to assess the relative importance of auditory–vibrational versus olfactory cues in attracting the attention of armadillos, hereafter referred to as the “prey presence” and “prey mobility” tests. For both tests, we set up 6 randomly located stations within each bioassay pen. The “prey presence” test contained 2 stations with soil and live prey (pond worms [*Lumbricus terrestris*], red worms [*Eisenia fetida*], or wigglers [*Pheretima hawayanus*]), 2 stations with soil that had recently contained the same prey type but no actual prey items (i.e., worms had been removed from the soil shortly before the trial began), and 2 stations with empty bowls. The “prey mobility” test contained 2 stations with live prey items (crickets, pond worms, red worms, or wigglers), 2 stations with the same type of prey frozen 1–2 hr prior to the experiment (so that they were immobile), and 2 stations with empty bowls. In both of these tests, it was assumed that stations with live prey items provided both olfactory and auditory–vibrational cues,

stations with either soil or frozen prey items provided olfactory but not auditory–vibrational cues, and stations with empty bowls provided neither olfactory nor auditory–vibrational cues but allowed us to quantify the relative interest of animals in the bowls themselves. Because we were interested solely in the ability of materials to attract armadillo attention in these experiments, we limited analyses to 1 metric: time to first contact.

For both experiments 1 and 2, we used linear mixed-effects models (Pinheiro and Bates 2000) to evaluate the attractiveness of potential baits while taking into account repeated measurements within a trial or for each animal. For experiment 1, the full model contained fixed effects to describe all factors of interest: the identity of the test materials, sex of the animal, trial number (to account for a potential change in behavior over the course of repeated trials), and seasonality (prebreeding [Apr–May], breeding [Jun–Aug], or postbreeding [Sep–Oct]; Jacobs 1979, McDonough 2000). For analyses pertaining to time to first contact, we also included distance between the entrance of the bioassay pen and the test materials as a fixed effect to account for the possibility that the physical layout of the materials in each pen influenced results. For each analysis in experiment 1, we used an iterative process whereby whichever test material explained the least variability was lumped into the category “other” and a likelihood ratio test was used to compare the resulting reduced model to the full model. This process was repeated until the likelihood ratio was significantly different, indicating the best model had been identified (Diggle et al. 2002). Interactions between season and test materials and between sex and test materials were considered for top-ranking materials only. For experiment 2, we limited analyses to assessments of the importance of test materials and distance between the entrance to the bioassay pen and the test materials. All analyses were conducted in R version 2.10.0, using the *nlme* package (Pinheiro et al. 2009), and all tests were considered significant at $P \leq 0.05$.

Experiment 3: comparisons of sounds and vibrations produced by live prey.—We examined the amplitudes and spectral characteristics of sounds and vibrations produced by several species of live prey in a vibration-insulated anechoic chamber (Wenninger et al. 2009). We conducted separate trials with 6 species: crickets, pond worms, wigglers, red worms, big red worms (*Eisenia hortensis*), and mealworms (*Tenebrio molitor*). We recorded each species in the same condition as they had been presented to armadillos (i.e., with or without medium in plastic bowls, as described above). A microphone (model 4145; Brüel and Kjær [B&K], Nærum, Denmark) was suspended approximately 2 cm above the top of the center of each bowl, and the accelerometer (model 4370; B&K, Nærum, Denmark) was clamped to the side. We digitized accelerometer and microphone signals simultaneously at 25 kHz using 2 channels of a CSL speech analysis system (model 4300B; Kay Elemetrics, Lincoln Park, NJ), and we analyzed general characteristics of the signals using Raven 1.3 (Charif et al. 2008). Sound and vibration impulse amplitudes and times were measured for approximately 1-hr periods using a customized signal analysis program, DAVIS

(Mankin et al. 2000). The DAVIS program counts individual impulses or bursts of impulses, and calculates the mean sound–pressure levels of sound bursts and the mean vibration levels of vibration bursts (Mankin and Benshemesh 2006). Differences among pairs of 180-s samples recorded from bowls with different species were assessed using analysis of variance.

RESULTS

Experiment 1

We used information from 28 individual animals collected over the course of 202 trials to assess the relative potential of test materials to function as lures.

Time to first contact varied from 5 s to 3,709 s, with a median of 352.5 s. Of the 18 materials tested, the mean time to first contact of 4 materials was significantly less than that of all others, with no significant differences among them: pond worms ($\bar{x} = 61.4$ s), wigglers ($\bar{x} = 74.0$ s), crickets ($\bar{x} = 87.1$ s), and red worms ($\bar{x} = 96.7$ s; Fig. 1). The only other variables that remained in the best model were distance of test materials from the entrance door and number of trials. Time to first contact increased slightly as the distance of test materials from the entrance door within the bioassay pens increased (0.32 s/m) and decreased exponentially with the number of trials an animal participated in.

Number of attraction events varied from 0 to 11, with a median of 3 events. Animals repeatedly oriented toward 4 materials significantly more often than they did the remaining 14 materials, with no significant differences among them: pond worms ($\bar{x} = 2.6$ orientations), crickets ($\bar{x} = 2.2$ orientations), red worms ($\bar{x} = 2.1$ orientations), and wigglers ($\bar{x} = 2.0$ orientations; Fig. 2). The only other variable that occurred in the best model was number of trials. The mean number of attraction events increased slightly with the number of trials an animal participated in (0.004 orientations/trial).

Duration of interest varied from 0–718 s, with a median of 24.0 s, and results provided further evidence of preferences

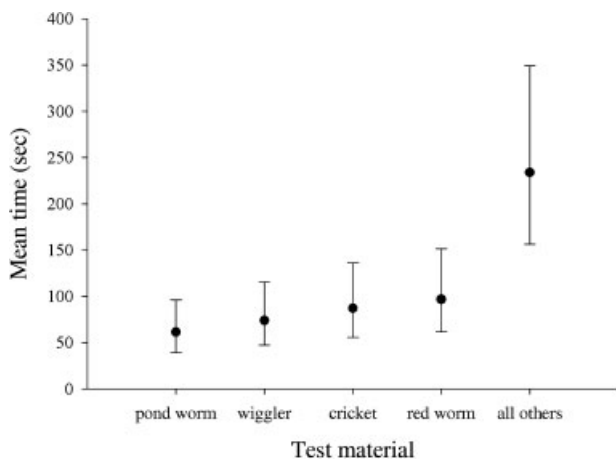


Figure 1. Mean time (s) to first contact (amt of time elapsed between a captive nine-banded armadillo's entrance to the bioassay pen and the first contact of that animal with each material), in experimental trials conducted in Florida, USA, 2008–2009. Error bars represent 95% confidence intervals.

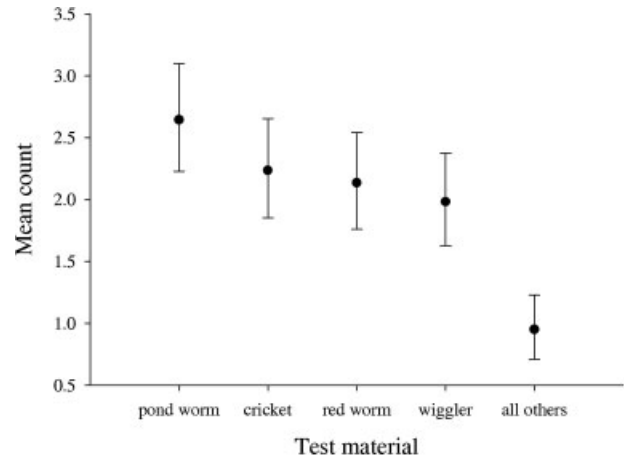


Figure 2. Mean number of attraction events (no. of times a captive nine-banded armadillo's head was oriented toward a material when the animal was within 1 body length of that material), in experimental trials conducted in Florida, USA, 2008–2009. Error bars represent 95% confidence intervals.

for many of the same materials. Animals spent significantly more time oriented toward 4 materials than they did all other 14 materials: pond worms ($\bar{x} = 18.2$ s), red worms ($\bar{x} = 17.1$ s), crickets ($\bar{x} = 17.0$ s), and wigglers ($\bar{x} = 7.7$ s; Fig. 3). The other variables that remained in the best model pertained to seasonality (including interaction terms for wigglers and chicken eggs) and number of trials. Duration of interest for wigglers changed seasonally ($\bar{x} = 8.2$ s during prebreeding season, 7.0 s during breeding season, and 15.1 s during postbreeding season), with significantly lower duration of interest than the 3 other most preferred materials during the prebreeding and breeding seasons. Duration of interest also changed seasonally for chicken eggs. It was higher than any other test material during prebreeding season (16.4 s), but dropped drastically thereafter and was, on average, lower overall than any of the other 4 most preferred test materials (1.9 s), and with significantly lower

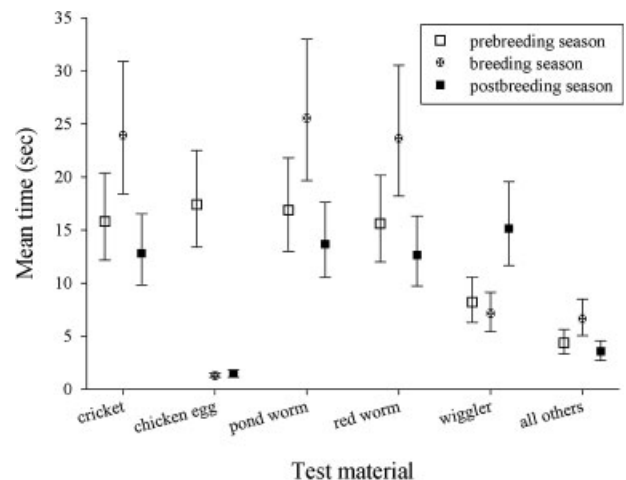


Figure 3. Mean duration of interest (no. of s captive nine-banded armadillos spent oriented toward each material when within 1 body length of that material) during the prebreeding (open square), breeding (cross), and postbreeding period (solid square) seasons, in experimental trials conducted in Florida, USA, 2008–2009. Error bars represent 95% confidence intervals.

duration of interest than the 4 other most preferred materials during the breeding and postbreeding seasons. Finally, duration of interest increased slightly with the number of trials an animal participated in ($\bar{x} = 0.1$ s/trial).

Palatability of invertebrates was highest for pond worms and crickets (96%), followed by wigglers (89%), red worms (80%), millipedes (*Diplopoda* spp.; 79%), glow worms (*E. hortensis*; 72%), big red worms (63%), and mealworms (0%).

Experiment 2

To assess the relative importance of olfactory and auditory (sound and vibration) cues that elicit armadillo attention, we used information from 21 individual animals collected over the course of 45 trials.

In the “prey presence” tests that compared armadillo attraction among bowls containing soil with live prey, soil with the olfactory cues of prey but no actual prey items, and empty bowls, the mean time to first contact of soil with live prey ($\bar{x} = 89.0$ s) was significantly less than that of bowls with odiferous soil ($\bar{x} = 108.0$ s) and less than that of empty bowls ($\bar{x} = 256.1$ s; Fig. 4). Time to first contact was not significantly influenced by the distance of test materials from the entrance door within the bioassay pens.

In the “prey mobility” tests that compared armadillo attraction among bowls with live prey, frozen prey, and empty bowls, the mean time to first contact of bowls with live prey ($\bar{x} = 32.7$ s) was significantly less than that of empty bowls or frozen prey (collective $\bar{x} = 91.7$ s; Fig. 4). Time to first contact was not significantly influenced by the distance of test materials from the entrance door within the bioassay pens.

Experiment 3

Measurements of sounds and vibrations produced by 4 invertebrate species highly attractive to armadillos (pond worms, crickets, red worms, and wigglers) and 2 species less attractive to armadillos (mealworms and big red worms)

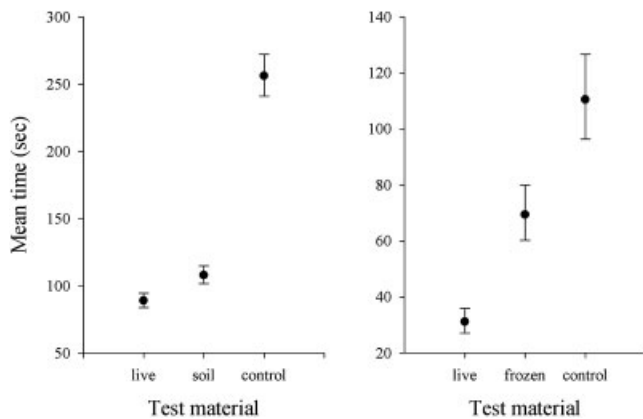


Figure 4. Mean time to first contact (amt of time elapsed between a captive nine-banded armadillo’s entrance to the bioassay pen and the first contact of that animal with each material), in experimental trials conducted in Florida, USA, 2008–2009. Left panel shows results from “prey presence” tests, which compared time to first contact among bowls containing soil with live prey, bowls containing soil that had recently contained the same prey, and empty bowls. Right panel shows results from “prey mobility” tests, which compared time to first contact among bowls containing live prey, bowls containing frozen prey, and empty bowls. Error bars represent 95% confidence intervals.

indicated that all prey species produced signals containing brief, 3–30 ms impulses or trains (bursts) of impulses of various amplitudes, similar to sounds and vibrations reported previously from various invertebrates (Mankin et al. 2000, 2011). Examples of 3-min vibrational and auditory records from an attractive species (i.e., red worms) and a less attractive species (i.e., big red worms) are shown in Fig. S1a–d, available online at <http://onlinelibrary.wiley.com/doi/10.1002/wsb.79/supinfo>. Overall, crickets produced the strongest vibrations and sounds, while red worms produced the weakest vibrations and wigglers the weakest sounds (Tables S1 and S2, available online at <http://onlinelibrary.wiley.com/doi/10.1002/wsb.79/supinfo>). However, due to the high level of variation in signal rates over time within species, there were no significant differences in the mean impulse-burst rates for either vibrations ($F = 1.48$, Df between species = 5, Df within species = 6, $P = 0.32$) or sounds ($F_{5,6} = 2.48$, $P = 0.15$). Wigglers, mealworms, and crickets produced vibrations with relatively high contributions at frequencies above 2,000 Hz (Fig. 5a), but the high-frequency components of sounds produced by wigglers and mealworms were not as readily transmitted to air (Fig. 5b). For this reason, crickets and pond worms produced sounds that were distinctly different from the sounds of

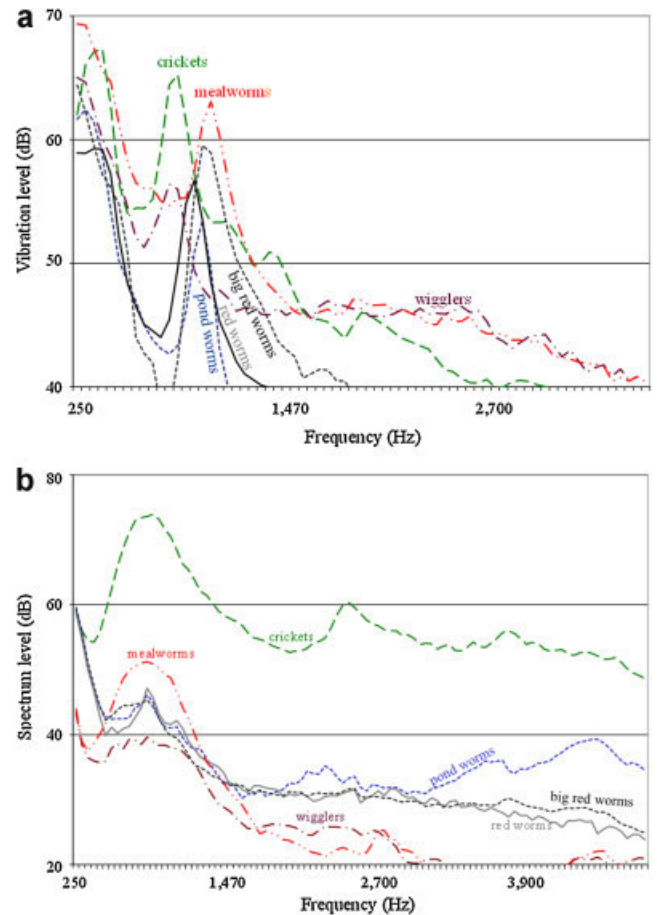


Figure 5. Mean vibration levels (dB) of vibration signals recorded by accelerometer from live prey (of nine-banded armadillos) in bowls (a) and mean spectrum levels (dB) of sound signals recorded by microphone from live prey in bowls (b). Experimental trials were conducted in Florida, USA, 2008–2009.

wigglers and mealworms to the human ear. Further investigation will be required to characterize the auditory and vibrational perception capabilities of armadillos.

DISCUSSION

Using 3 different metrics to assess the relative ability of a variety of substances to attract armadillos, we found that 4 commercially available materials consistently performed best: pond worms, crickets, red worms, and wigglers (Figs. 1–3). These 4 materials emitted cues that could be detected by more than 1 sensory modality (olfactory, auditory, and vibratory), whereas most of the other materials investigated emitted only olfactory cues (i.e., fruits, eggs, and odors from conspecifics). Our second round of behavioral experiments provided additional evidence that materials emitting auditory, vibrational, and olfactory cues elicited faster responses from armadillos than materials emitting only olfactory cues (Fig. 4).

Because armadillos feed mostly on organisms within the soil, and because they have unusually large olfactory organs (Pihlström et al. 2005), it has been assumed that olfaction is the primary sense these animals employ when locating food materials. Our results suggest that auditory and vibrational cues also play a role in prey detection, perhaps as a means of focusing attention once the armadillo has been attracted close to the prey by olfactory signals. Previous behavioral investigations of wild armadillos support this concept: short cessations of movement occur repeatedly during foraging bouts, which may enable multifunctional scanning of the environment for conspecifics, predators, and/or prey (McDonough and Loughry 1995). Given that there were few consistently distinctive differences in the vibrations and sounds produced by the invertebrates we tested (Fig. 5), the finding that only 4 of the 6 live prey (pond worms, crickets, wigglers, and red worms) were attractive to the armadillos suggests that olfactory cues and palatability play predominant roles in food selection once the prey is localized.

The response of armadillos to bait materials changed over the course of repeated trials with individual animals: time to first contact decreased, the number of attraction events increased, and duration of interest increased. These results suggest that individuals formed a search image during earlier trials, which reduced response times in later trials. The formation of olfactory search images has been demonstrated in a variety of other taxa, ranging from lobsters (*Homarus americanus*) to skunks (*Mephitis mephitis*) to dogs (*Canis lupus familiaris*; Derby and Atema 1979, Nams 1997, Gazit et al. 2005). For example, striped skunks (*M. mephitis*), which are similar to nine-banded armadillos in that they are nocturnal generalists that feed on patchily distributed prey materials using olfaction and audition, have been shown to form olfactory search images (Nams 1997). Switching lures seasonally to reflect the predominant materials in armadillo diets would be especially prudent if armadillos do, in fact, form search images.

Although nine-banded armadillos are known to consume eggs from northern bobwhite quail (*Colinus virginianus*),

domestic and wild turkeys (*Melagris gallopavo*), sea turtles (loggerhead, *Caretta caretta*; leatherback *Dermochelys coriacea*; and green *Chelonia mydas*), gopher tortoises (*Gopherus polyphemus*), lizards, and snakes in the wild (Kalmbach 1943, Fitch et al. 1952, Douglass and Winegarner 1977, Engeman et al. 2003, Staller et al. 2005), our research indicated that eggs from domestic bobwhite quail and chicken were less attractive than crickets and most worms. It may have been the case that without the full complement of cues from a typical nest in the wild, the armadillos did not identify the eggs we presented during trials as potential food items. Regardless, it appears that eggs from domestic birds have limited potential to serve as a lure for this species. It is interesting to note that although chicken eggs did not evoke interest from armadillos quickly (as quantified by time to first contact) and they did not elicit a strong response (as quantified by no. of attraction events), they did elicit long bouts of sustained interest (as quantified by duration of interest). Certain individual animals appeared to have a strong interest in eggs and spent long periods of time consuming them. Interest was particularly high during the prebreeding period, which interestingly coincides with the incubation period of wild turkey in the study region (Williams 1991; Fig. 3).

The relative ability of 2 materials to sustain the interest of armadillos changed seasonally: wigglers and chicken eggs. Wigglers were of maximum interest during the postbreeding period, of moderate interest during the prebreeding period, and of least interest during the breeding period. Evidence of seasonal changes in the relative proportion of wild armadillo diets comprised of Oligochaeta (earthworms) has previously been reported (reviewed in McDonough and Loughry 2008), with geographic variation in the timing of maximum consumption of these worms (Fitch et al. 1952, Nesbitt et al. 1977, Sikes et al. 1990). In general, oligochaetes are a more important part of an armadillo's diet in autumn and winter months. As mentioned previously, chicken eggs were only of great interest to armadillos during the period when wild turkey eggs are available in the wild. These patterns suggest that there may be some merit to switching among different bait materials seasonally when attempting to capture armadillos. However, it must be kept in mind that chicken eggs, on average, did not appear to be as attractive as most worms and crickets investigated.

A priori, we had expected odors from conspecifics to generate substantial interest from armadillos. The complex social systems of most mammal species necessitate the ability of animals to distinguish among individuals, with complex mixtures of molecules conveying information about sex, reproductive status, and identity (Brennan and Kendrick 2006). Although previous research has shown that nine-banded armadillos are capable of recognizing their own odor and discriminating the odors of kin from nonkin (Loughry and McDonough 1994), armadillos in our study exhibited little interest in conspecific odors. This may have been a function of the timing during which we collected odors: scent glands were swiped at the time animals were captured, which may have been a time during which animals were exuding odors that convey fear. If this were the case, it is

understandable that animals in captivity would be less interested in investigating the source of these odors than they were in investigating potential food materials. Also, auditory or contextual cues may be needed to prompt animals to investigate a conspecific's scent. Finally, because the test arena was on neutral territory (each test animal was new to the area), attraction or aggression toward another animal might not have been advantageous (McDonough 1994). Further investigation into the response of animals to odors collected from armadillos in some other manner than directly after capture may be fruitful.

We are unaware of any published attempts to quantify the perceptual range (Lima and Zollner 1996) of armadillos, although anecdotal evidence suggests the range is quite limited (Breece and Causey 1973). Other mammals with well-developed olfactory systems are known to detect specific odors above ground at distances ranging from 0.5 m to 60 m, depending on the environmental conditions and the magnitude of the odor source (Cablk et al. 2008, Hirsch 2010). Out of concern that relative levels of attraction to various materials might be influenced by the distance between the door of the bioassay pen and the test material, we structured our analyses to account for this distance. We found that the effect of distance between the door to the bioassay pen and the test materials on the relative ability of each test material to evoke a response from armadillos during the bait experiment was minimal, and no effect was apparent during the experiments involving auditory versus olfactory cues. Thus, it does not appear that the physical layout of materials during our experiments influenced animal response. It is worth noting that, on average, the most attractive materials investigated (pond worms) did not generate a response until >60 s after animals entered the bioassay pen. Given the short distances between the entry door and the station locations (the min. possible was approx. 0.3 m and the max. possible was 2.6 m), this long duration of time prior to animal response to food suggests that the perceptual range of the armadillo is quite limited, perhaps as short as 0.3 m. It is known from previous studies with insects (Mankin et al. 2011) that sounds and vibrations with the amplitudes and frequencies observed in this study attenuate rapidly within 0.1–0.3-m distances in soil. Although olfactory signals produced by these invertebrates may provide longer distance (see above) but less precise localization capability, the range of the olfactory cues of underground invertebrate prey would be somewhat diminished because the odors would need to diffuse to the soil surface before they became airborne.

MANAGEMENT IMPLICATIONS

It is convenient that several materials readily eaten by armadillos are commercially available from bait stores and pet stores. Each is, therefore, accessible to anyone interested in luring nuisance armadillos into traps. Our results suggest that live, active baits are preferable to other substances and that consideration should be given to changing baits seasonally in accordance with the predominant materials in the diets of local armadillos. However, during the course of our research it became apparent that armadillos have an extreme-

ly short perceptual range. For this reason, we believe there is limited potential for using naturally occurring materials as baits to effectively lure armadillos into traps over sizeable distances. This is particularly true if vibration is a relevant cue to armadillos because vibrations attenuate rapidly over short distances. Future research should be directed either toward development of repellents, toxicants, or other exclusion techniques, or else toward development of enhanced stimuli capable of travel over long distances.

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