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Animal behaviour

Grunting for worms: seismic vibrations cause *Diplocardia* earthworms to emerge from the soil

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Harvesting earthworms by a practice called 'worm grunting' is a widespread and profitable business in the southeastern USA. Although a variety of techniques are used, most involve rhythmically scraping a wooden stake driven into the ground, with a flat metal object. A common assumption is that vibrations cause the worms to surface, but this phenomenon has not been studied experimentally. We demonstrate that Diplocardia earthworms emerge from the soil within minutes following the onset of grunting. Broadband low frequency (below 500 Hz) pulsed vibrations were present in the soil throughout the area where worms were harvested, and the number of worms emerging decreased as the seismic signal decayed over distance. The findings are discussed in relation to two hypotheses: that worms are escaping vibrations caused by digging foragers and that worms are surfacing in response to vibrations caused by falling rain.

Keywords: earthworm; vibration; escape; rain; moles

1. INTRODUCTION

In the southeastern USA, worm 'grunting' is commonly practiced to collect earthworms for fish bait. A wooden stake is driven into the ground and typically scraped with a long metal object until worms come to the soil surface. Worm grunting is economically and ecologically important in localized regions. Appreciable income can be generated by collecting worms, but this can result in negative effects on earthworm populations and their associated benefits to plant nutrition (Hendrix et al. 1994; Callaham & Hendrix 1998). Hendrix et al. (1994) reported significant reductions in earthworm biomass due to bait harvest in Florida, while noting that during some seasons thousands of earthworms per hectare per day can be harvested via grunting. Similar practices are used to collect earthworms elsewhere, including England, where worms are 'charmed' out of the ground by 'twanging' the handle of a garden fork, the tongs of which are inserted into the soil (Edwards & Bohlen 1996).

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Despite their prevalence, worm grunting and similar techniques have not been examined experimentally. Vibrations have not been recorded, and the relationship between vibrations and worm emergence has not been documented. We record the vibrations being transmitted through the soil using a typical worm grunting technique, and test the hypothesis that earthworms surface in response to a vibration stimulus. The hypotheses explaining the adaptive significance of earthworms surfacing in response to vibrations are discussed.

2. MATERIAL AND METHODS

Experiments were conducted in the pine (*Pinus palustris* and *Pinus elliottii*)-dominated forests of Apalachicola National Forest, Liberty County, Florida (compartments 100 and 110) between 08.00 and 10.00, 14–15 April 2008. Both sites had recently undergone prescribed burning and had very little emergent vegetation or detritus obscuring the ground surface, making it easier to find worms. For this reason, burned areas are attractive to bait harvesters, and are preferentially used shortly after prescribed fires have been conducted (Hendrix *et al.* 1994).

Grunting vibrations were generated by one of the authors (M.A.C.), who had previously used this technique to survey earthworms (Hendrix et~al.~1994). Grunting was performed by first hammering a wooden stake into the soil to a depth of approximately 30 cm. The top end of the stake was then rubbed with a long (100×7 cm) flat metal object with a smooth surface (figure 1a; supplementary video in the electronic supplementary material). Specific locations within each site were evaluated for the presence or absence of earthworms, and if earthworms were observed to surface we moved a short distance away (approx. 20 m) to perform full trials. Visual inspection of the trial area prior to grunting indicated that no worms were visible on the soil surface.

Seismic vibrations were recorded using two set-ups: linear geophone arrays were used to examine the amplitude decay over distance, while equidistant arrays were used to examine the frequency composition of the vibrations. Linear arrays consisted of four identical vertical geophones (DT20DX 4.5 Hz, Dynamic Tech, Salt Lake City, Kolkata, India) buried at a depth of 10 cm, and placed at intervals of either 1.8 or 3 m from the wooden stake. Geophone signals were amplified (M-10MX, Edirol/Roland, Los Angeles, CA) and recorded onto data recorders (PMD671, Marantz, Kanagawa, Japan). The equidistant arrays consisted of four sensor types: three geophones including a DT20DX 4.5 Hz, a GS-20DM 28 Hz (Oyo Geospace, Houston, TX), a GS-100 100 Hz and a microphone (ATM10a, Audio Technica, Tokyo, Japan). Each was positioned either 0.9 or 3.6 m from the stake and buried 10 cm in the soil. All geophones were amplified and recorded as described above, while the microphone was connected directly to the data recorder. Data files were transferred to a laptop computer and analysed using Raven Bioacoustics Research Program (Cornell Laboratory of Ornithology, Ithaca, NY). Our objectives were to record the relative amplitudes and general frequency composition of vibrations. To do this, we used geophones that measure only the vertical component and velocity of vibrations.

Each trial consisted of a harvesting and recording phase. The harvesting phase preceded the recording phase, although all recording equipment was placed in position before the harvesting phase began. Five individuals searched for surfacing earthworms during the harvesting phase. The location of each worm was flagged, and the specimen was collected to prevent recounts. When worms ceased to surface, the recording phase began. A map was made, indicating the positions and distances between worm flags, sensors and the stake. All experiments were videotaped using a camcorder (DCR-TRV19, Sony, Tokyo, Japan).

3. RESULTS

Worm grunting generated a train of distinct seismic vibrations that proved to be successful in extracting *Diplocardia* worms (figure 1b) from the soil surrounding the stake. Individual strokes were 760.8 ± 99.8 ms in duration (n=25), repeated at a rate of one stroke every 1.2 ± 0.1 s (n=15). Each stroke consisted of an initial discreet noise (produced by the metal contacting the stake) followed by a broadband 'grunt'

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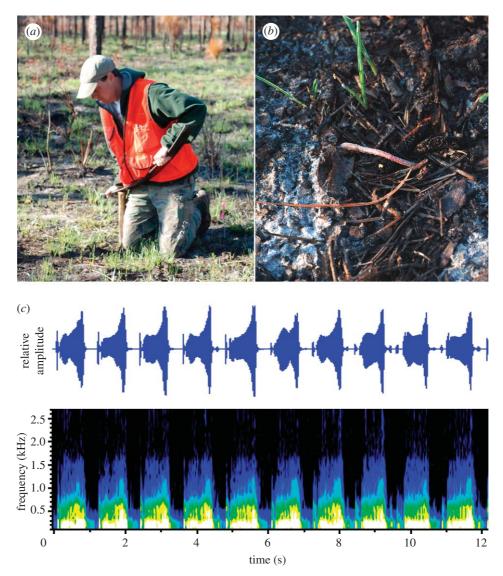


Figure 1. Worm grunting in the Apalachicola National Forest. (a) One of the authors demonstrating the worm grunting technique, whereby a wooden stake is vibrated using a flat metal object. (b) An earthworm emerging from its burrow. (c) Oscillogram and corresponding spectrogram of seismic vibrations recorded at 1.8 m from the stake during a linear array recording.

(caused by stroking the metal against the stake; figure 1c). Seismic signals were broadband, with all sensors indicating that most of the energy was concentrated below 500 Hz with a dominant frequency of $97.3 \pm 11.7 \text{ Hz } (n=15).$

Soil-borne vibrations were strong enough to be felt when standing several metres away from the stake. Vibrations were still detected by our farthest geophone placed 12 m away from the stake, but the relative amplitude decayed markedly beyond a few metres (figure 2a,b). Spectral changes were also apparent as the distance from the stake increased. Vibrations below 500 Hz were still prominent at our furthest recording distance (12 m), and frequencies above 1.5 kHz were typically attenuated beyond 7 m from the stake.

Worms began to emerge from their burrows within 54–131 (n=5) s following the onset of vibrations. Following emergence, they crawled across the soil surface and remained on the surface after vibrations ceased (at least until the specimens were collected). Surfaced worms did not show directional preferences, since they were observed moving both away from and towards the stake. The size of the worms that emerged ranged between 7 and 30 cm in length.

The largest number of worms surfacing in a single trial was 41, during 22 min of grunting in an area approximately 18 m in diameter centred on the stake (figure 2a). Data from the spatial distribution of surfaced worms from all trials show that the number of worms surfacing decreases as distance from the stake increases (figure 2c).

4. DISCUSSION

Our results demonstrate that the Diplocardia earthworms respond to the seismic vibrations generated by the worm grunting technique. Worms emerge from their burrows within a few minutes following the onset of vibrations, and the number of worms surfacing is positively correlated with the signal strength. Although the practice of grunting for harvesting fish bait is well known in the southern USA, there are few documented accounts of worms responding to vibrations. A few authors have briefly commented

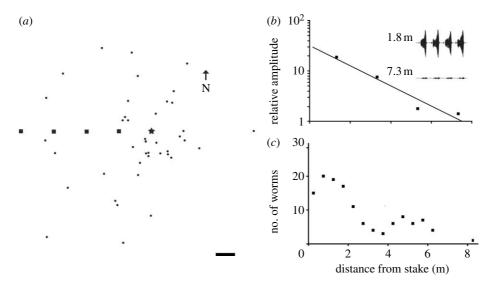


Figure 2. Distribution of recordings and worm emergence sites. (a) A map indicating the locations of surfaced worms (circles) during a single instance of grunting, geophones in a linear array (squares) and the wooden stake (star). The worm grunter is facing the linear array. Scale bar, 1 m. (b) Relative amplitude decay of vibrations recorded from a linear geophone array ($y=42.998 \, \mathrm{e}^{-0.3066x}$, $R^2=0.9406$). The inset shows the waveforms of four grunts recorded at 1.83 and 7.32 m. (c) The number of worms surfacing as a function of the distance from the stake. Data are plotted using sliding window comparisons (using 100 cm windows with 50 cm increments).

upon the worm grunting technique as a means of collecting Diplocardia mississipiensis, Diplocardia floridana or Pheretima diffringens (Vail 1972; Hendrix et al. 1994; Edwards & Bohlen 1996). It has also been reported that mechanical disturbances such as digging, power motors and even walking can cause worms to emerge (Darwin 1881; Kaufmann 1989; Edwards & Bohlen 1996). Interestingly, some animals have been noted to employ a similar technique to capture worms. Wood turtles (Clemmys insculpta) stomp their front feet at a rate of about once per second (similar to the grunting rate), which induces earthworms to surface (Kaufmann 1986, 1989). Similarly, different birds have been noted to 'paddle' the Earth with their feet, or peck hard on a rock to force earthworms to surface (Darwin 1881; Tinbergen 1960; Edwards & Bohlen 1996). Although in these reports it is implied that seismic vibrations cause the worms to surface, the vibrations were not recorded. Other reports of vibration-mediated behavioural responses mainly describe rapid escape reflexes, which do not resemble the locomotory response observed during our trials. Darwin (1881) observed that earthworms rapidly retreated into their burrows when presented with a vibration made by playing notes on a piano, upon which a worm within a container was placed. Herz et al. (1967) similarly describe the unconditioned response of Lumbricus terrestris to a 'mild vibratory stimulation' as 'an initial sharp contraction which appears to habituate upon repeated presentations', but also demonstrate that when the stimulus is 'more intense' the worm extends the anterior portion of its body. Perhaps this latter response more closely reflects the response to worm grunting.

Why do earthworms surface in the presence of seismic vibrations? One hypothesis is that the vibrations resemble those caused by rain, and the worms emerge from the soil to avoid drowning

(Kaufmann 1986), low oxygen levels (Minnich 1977) or to enhance dispersal (Butt & Nuutinen 2005). Preliminary recordings of light rainfall show that most energy falls below 500 Hz (O. Mitra 2008, unpublished data), corresponding to the same frequency range as grunting. A second hypothesis, first proposed by Darwin (1881) in response to indirect reports of worms surfacing in response to vibrations, and then by Tinbergen (1960) in relation to gull paddling, is that earthworms are responding to vibrations caused by the burrowing of predatory moles. Vibrations generated by digging moles have not been formally described as far as we know. However, other fossorial mammals produce vibrations (for orientation or communication purposes) that fall within the frequency range of worm grunting stimuli (Mason & Narins 2001). It should be noted that evidence for mole tunnelling was observed at our trial sites in Florida. Since other vertebrates and invertebrates use seismic cues to detect predators (Mason & Narins 2001; Cocroft & Rodríguez 2005), the hypothesis seems worthy of further testing.

We conclude that the Diplocardia earthworms can be induced to surface in response to seismic vibrations. Based on the available evidence, it is proposed that these vibrations are mimicking those of rain or predatory fossorial mammals, but these hypotheses remain to be formally tested by fully characterizing the natural vibrations and conducting playback studies. Additional studies on Diplocardia should adopt a neuroethological approach to elucidate the behavioural and physiological responses to vibrations the worms would experience in their natural environment. It should also be established whether this behaviour is observed in other earthworm species. The species reported to respond to worm grunting in Florida are almost exclusively Diplocardia mississippiensis or D. floridana (Vail 1972; Hendrix et al. 1994), while it has been noted that

L. terrestris does not respond similarly to such vibrations (Reynolds 1977). There are an estimated 7000 species of earthworms worldwide (Hendrix et al. 2008), but surprisingly little is known about the behaviour and life-history traits of any one species. Additional questions regarding how biotic (e.g. tunnelling habits, local predators, seasonal and diurnal rhythms) and abiotic (e.g. soil moisture, temperature, time of day) factors influence the sensitivity to vibrations in different species should be addressed in future studies.

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