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The seismic wave motion camouflage of large carnivorous dinosaurs

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ABSTRACT

Living elephants produce seismic waves during vocalizations and locomotion that are potentially detectable at large distances. In the Mesozoic world, seismic waves were probably a very relevant source of information about the behavior of large dinosaurs. In this work, we study the relationship between foot shape and the directivity pattern of seismic waves generated during locomotion. For enlarged foot morphologies (based on a morphological index) of theropod dinosaurs, there is a marked effect of seismic wave directivity at 20 m. This effect is not important in the foot morphologies of other dinosaurs, including the foot shapes of herbivores and theropods such as therizinosaurids. This directivity produces a lower intensity in the forward direction that would slightly reduce the probability of detection of an ambush predator. Even more relevant is the fact that during the approach of a predator, the intensity of seismic waves detected by potential prey remains constant in the mentioned distance range. This effect hides the predator's approach, and we call this "seismic wave camouflage". We also discuss the potential relationship of this effect with enlarged fossil footprints assigned to metatarsal support.

1. Introduction

Physical models have been used to explore the bioacoustical capabilities of large dinosaurs in situations for which there are no good living analogues. Their results were used to speculate about the use of certain biological structures, such as the tails of sauropods (Christiansen, 1996; Myhrvold and Currie, 1997) or the crests of lambeosaurine hadrosaurids (Evans et al., 2009) to produce sounds used for defense, communication, intraspecific rivalry and courtship, among other purposes. Following these approaches, we used a physical model of seismic wave production to speculate about behavioral implications in predator-prey interactions.

During the Mesozoic period, the largest terrestrial vertebrates in the history of life thrived. Some representatives of the clade Sauropodomorpha, such as the titanosaurids, approached 100 tonnes in body mass, which is the biomechanical limit for a terrestrial vertebrate (Hokkanen, 1986).

Among theropods were the largest terrestrial carnivores that ever existed, and some reached body masses up to 10 tonnes (Mazzetta et al., 2004; Seebacher, 2001; Therrien and Henderson, 2007). Today, the largest terrestrial vertebrates are elephants. These mammals produce seismic waves during vocalizations and locomotion that are potentially detectable at distances up to 32 km (O'Connell-Rodwell et al., 2000). The signals detected at a large distance appear to predominantly have a low frequency (from approximately 10 Hz to 40 Hz) because absorption of seismic energy increases with increasing frequency (White, 1965). Airborne signal detection depends on weather, vegetation structure, height of the emitter and wind, among other factors (O'Connell-Rodwell et al., 2000 and references therein). Under certain conditions, signals through the ground are more reliable than signals through the air (O'Connell-Rodwell et al., 2000). Although seismic waves may not carry specific spectral information that air-borne signals contain, they could provide a general localizing mechanism based on time or phase differences (Aicher and Tautz, 1990). Seismic wave detection has been reported in arthropods (Aicher and Tautz, 1990; Cocroft, 1996; Sandeman et al., 1996; DeVries, 1990), amphibians (Narins, 1990), reptiles (Hartline, 1971; Hetherington, 1992), and mammals (O'Connell-Rodwell et al., 2000; Shipley et al., 1992; Narins et al., 1992; Narins et al., 1997), and it was also suggested that Pleistocene ground sloths used seismic waves for communication (Blanco and Rinderknecht, 2008,2012). In the Mesozoic world, the seismic waves were probably a very relevant source of information about the behavior of predators and prey.

There are several examples of camouflage strategies in the animal kingdom for both defensive and aggressive purposes (Stevens and Merilaita, 2011). Although most studies are related to

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visual camouflage, there is evidence for camouflage involving sensory systems other than vision (Ruxton, 2011). There are many examples for olfaction camouflage, particularly among insects (Cervo et al., 2008; Martin et al., 2008; Johnson et al., 2008; Kroiss et al., 2009; Silveira et al., 2010). Camouflage strategies based on the hydrodynamic disturbance generated by swimming speed are key to many predator-prey interactions in plankton (Munk and Kiørboe, 1985; Munk, 1992; Kiørboe, 2008; Holzman and Wainwright, 2009). There are many examples of organisms that are adaptively silent at times or in locations when or where predation risk is higher or in response to the detection of prey (Ryan et al., 1982; Miller and Surlykke, 2001; Barber and Conner, 2006; Digweed et al., 2005). Substrate-borne vibratory signals are utilized in a very diverse range of taxa, but this kind of signal and vibratory camouflage are understudied (Hill, 2008; for a review Hill, 2009). Motion camouflage is a stealth strategy employed by animals to achieve prey capture. In one type of motion camouflage, the predator approaches the prey such that from the point of view of the prey, the predator always appears to be at the same bearing (Srinivasan and Davey, 1995; Mizutani et al., 2003; Justh and Krishnaprasad, 2006). Several authors have stated that there is conclusive evidence that very large theropods, such as *Tyrannosaurus rex* or *Daspletosaurus* sp., were capable of active predation (Carpenter, 2013; Murphy et al., 2013). Possibly, seismic wave motion camouflage might have been useful to increase the probability of successful hunting.

Different suborders of dinosaurs are characterized by foot morphologies observed not only in their foot bones (Farlow et al., 2013,2014) but also in their ichnites (Lockley, 2009). There are noticeable differences in hind foot morphology, for example, between theropods and ornithopods (Farlow et al., 2013). In this study, we explore the length/width ratio of the ichnites assigned to different group of dinosaurs to look for some peculiarities in the feet of carnivorous theropods that could act as a seismic wave source compared to other groups of dinosaurs. We also use theoretical modeling to explore the spatial distribution of energy generated by a “foot stomp” depending on the overall shape of the footprint. We propose a possible effect of “seismic wave motion camouflage” in theropods.

2. Material and methods

2.1. Morphometric analysis

The criteria for sample categories were mainly based on inferred feeding habits, large size and preservation quality. We propose 5 groups that do not necessarily imply systematic significance based on previous studies (Lockley, 2009; Ellenberger, 1970; Lockley and Hunt, 1994; Harris et al., 1996; Calvo, 1999; Lockley et al., 2007; Weems, 2006; Li et al., 2008; Castanera et al., 2011; Fiorillo and Adams, 2012): *Carnivorous theropods* (17 ichnites): big-game-hunting predators with a flesh-eating diet (Paul, 2010), and this group includes a dromaeosaur footprint; *Ornithomimosaurs* (4 ichnites): possibly omnivorous with a diet consisting of small animals and insects with plant material (Osborn, 1917; Paul, 2010), although an in-depth study of the functional anatomy, paleoenvironmental and taphonomic evidence suggests that they have a herbivorous diet (Barrett, 2005); *Therizinosaurs* (2 ichnites): generally accepted to be browsing herbivores (Russell and Russell, 1993; Zhang et al., 2000; Kirkland et al., 2005) that may have picked up small animals on occasion (Paul, 2010); *Ornithopods* (24 ichnites): probably low- to medium-level browsers (Paul, 2010); and *Sauropods* (17 ichnites): a group predominantly composed of herbivorous browsers and grazers (Paul, 2010), and this group includes two prosauropod footprints. We selected hindfoot ichnites because the categories mentioned above include bipedal dinosaurs. We chose a relatively well-preserved footprint for ichnites that represents the total support area. We calculated the L/W ratio (where L is the maximum footprint length and W is the maximum footprint width), which is an index previously defined by Lockley (Lockley, 2009). We performed an ordinary least-squares regression of footprint length vs L/W ratio (Fig. 1). We then performed a one-way ANOVA analysis to differentiate the L/W mean ratios of select groups. The statistical analyses were performed with PAST 2.16 free software. We calculated the L/W ratio for elongated dinosaur tracks using a previously described method (Kuban, 1989), but these calculations were not included in the statistical analysis; these results will be analyzed in the Discussion section.

2.2. Theoretical model of seismic wave propagation

The seismic waves generated by a foot stomp were modeled using the Green’s function for Lamb’s problem (i.e., the problem of determining the elastic disturbance resulting from a point force acting normally to the free surface of an elastic half space). This Green’s function can be obtained using the Cagniard-de Hoop method (Johnson, 1974; Aki and Richards, 2002). The final expression for the vectorial displacement field is given in terms of integrals without an analytical solution, except for some special cases, e.g., the on-axis displacement and the surface displacement (Graff, 1991; Benech and Negreira, 2005). In this study, we are interested in the surface displacements for which closed form solutions exist. The contributions to surface displacement are determined by the compressional or P-wave, the shear or S-wave and the Rayleigh (surface) wave. Each of these waves arrives at a particular point of the surface at a specific time that depends on the compressional wave speed C_p and the shear wave speed C_s. The arrival times of the P and S waves are simply $t_i = r/C_i$, where $i = p$ or s and r is the distance between the source and the observation point. The arrival time of the Rayleigh wave depends on C_R, which is the surface wave speed and is given with good approximation by Viktorov’s formula (Royer and Dieulesaint, 2002)

$$C_R = C_s\left[0.718 - (C_s/C_p)^2\right]/\left[0.75 - (C_s/C_p)^2\right]$$

Therefore, the Rayleigh wave speed depends on the ratio C_s/C_p, which is intimately related to Poisson’s ratio ν of the half-space:

$$\nu = (1/2)\left[1 - 2(C_s/C_p)^2\right]/\left[1 - (C_s/C_p)^2\right]$$

Thus, depending on Poisson’s ratio, the Rayleigh wave speed varies from $0.87C_s$ ($\nu = 0$) to $0.96C_s$ ($\nu = 1/2$).

A detailed analysis of the surface wave reveals that the directivity pattern, as well as the energy distribution in each type of wave, depends on Poisson’s ratio of the half-space (Graff, 1991). In this work, we used a value of $\nu = 1/3$ to represent the soil value (Mavko and Nolen-Hoeksema, 1994). The surface displacements generated by the foot stomp at a given position were calculated by numerical integration of the point force over the surface of the foot. Although the Rayleigh surface wave is responsible for roughly 65% of the propagating energy (Graff, 1991), the integration takes into account all wave types. It is assumed that the whole plantar surface of the dinosaur is hitting the ground simultaneously. This seems to be a strong assumption that needs to be argued. In a human-like walking with a heel-sole-toe sequence, the shape of the ground contact surface is different at each stage of the support. The details of the process can be observed with high resolution plantar pressure distributions (Vereecke et al., 2003). Initially, at heel contact, the shape is almost circular ($L/W = 1$); at sole contact it is much more elongated ($L/W > 1$) and at toe stage it is wider ($L/W < 1$). In humans the whole sequence takes around 540 ms, the foot is progressively hitting the ground with a contact speed much slower than the seismic waves. In such case our assumption would be misleading. But the morphology and action of

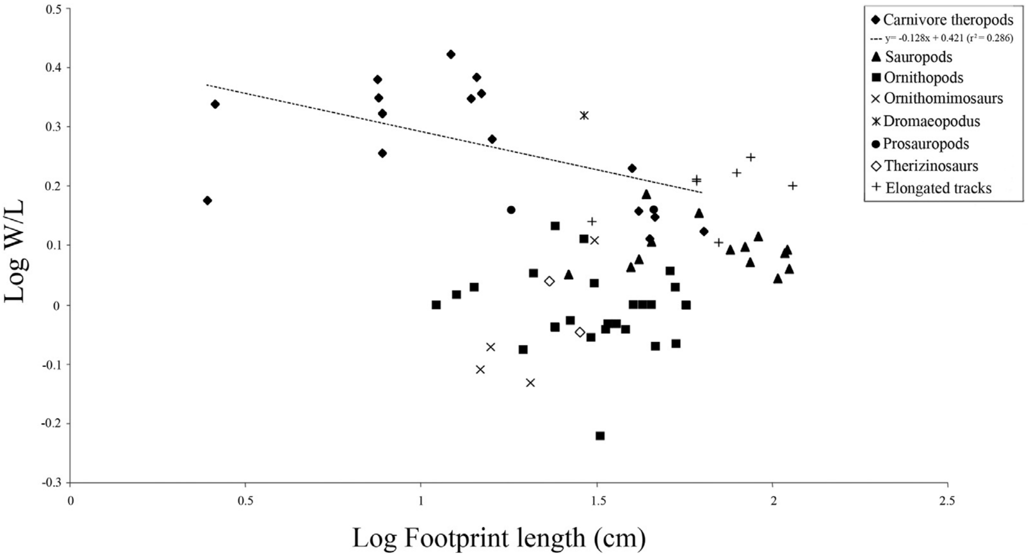

Fig. 1. Scatterplot for studied categories and the regression line for carnivore theropod footprints (linear equation and fit coefficient r^2) of the L/W index vs footprint length (L).

the human foot with a grounded heel behind a relatively distal ankle joint loaded early in stance and toes pushing off at the end of the stance (i.e. a heel-sole-toe stance) is very unusual outside the hominoidea. It is absent in the majority of cursors whether bipedal (e.g. ostrich, emu) or quadrupedal (Usherwood et al., 2012 and references therein). The best living analogues of theropods are large cursorial birds as ratites. In the case of ostrich the plantar pressure distribution during walking on solid ground was already studied (Zhang et al., 2017). Although the area of contact surface increases after touch down, the shape did not change significantly in the 782 ms of stance. This is enough to support the general conclusions of our model. Moreover, as carnivore theropods had between ten and hundred times the body mass of ratites, some allometric effects can be pointed. The peak plantar pressure scaled with the square root of body mass in a sample of 28 mammals with a range of mass from 4 to 3000 kg (Michilsens et al., 2009). Then for large vertebrates it is important to avoid hitting the ground in a way that could increase peak plantar pressure. The dynamics of the contacting components of the foot might determine the size of the load-bearing surface. Then in large dinosaurs it is even more important than in ostriches to hit the ground simultaneously with the whole foot. This gives good support to the assumptions in our model. Two geometric shapes were chosen for the footprints: an isosceles triangle with smooth corners to avoid artifacts related to sharp corners effect and a shape adapted from the ichnite of a large theropod in our sample. The triangle was modeled with L/W = 2.0 and the ichnite shape was based in *Eubrontes giganteus* type (Fig. 2A in Lockley, 2009, with L = 39.68 cm) with an L/W = 1.7.

3. Results

3.1. Numerical model results

The ratio between the length L and width W of the sources was chosen to approximately fit the real footprints of carnivore theropods, i.e., L/W = 2, as shown in Fig. 2(A). Fig. 2(B) displays the directivity pattern of the wave energy in dB scale for the triangular source at distances between 20 and 100 W. The distances are expressed in terms of the source width W. The figure clearly shows that at short distances (less than 60 times the W value), the energy is strongly directed to the sides (90° and 270°) of the triangle, with 0° being the direction of travel. With increasing radial distance, the pattern tends toward being isotropic. This is an expected behavior since at large distances, the source is viewed as a point one. An interesting result is the energy dependence on the distance to the source, which is displayed in Fig. 2(C). The computations show that the irradiated energy strongly depends on distance in lateral directions (90° and 270°) of the source but is almost constant for a wide distance range in the walk direction (0°). Since the variations in wave amplitude are a key factor for sensing the predator's approach, this result suggests that this kind of geometry is suitable for motion camouflage.

Fig. 3 shows the results for a shape adapted from the ichnite of *Eubrontes giganteus* (Lockley, 2009) with an L/W = 1.7. We can observe that the general results highlighted for the triangular source also apply in this case. The energy of the wave is almost constant with the distance to the source in the forward direction, which permits camouflage of the predator's approach. We also performed simulations with rectangular shapes with smooth and sharp corners and with shapes adapted from ichnites of smaller theropods. The general conclusions do not depend of those details. Thus, the ratio between the length and width seems to play a key role in the directivity of energy radiation independent of the particular shape of the source.

4. Discussion

The intensity of seismic waves generated by locomotion depends on the pressure exerted on the ground (wave amplitude) and the area of the foot (size of the source). Some estimations were already made from pressure on the ground and the foot area of dinosaurs compared to elephants, cattle, rhinoceros and giraffes (Alexander, 1985). For a sauropod about the size of *Apatosaurus* (34 tonnes), the total sole area (four feet) was 1.2 m^2, and the standing pressure was approximately 280 kPa. For a theropod about the size of *Tyrannosaurus* (8 tonnes), the total sole area (two feet) was 0.6 m^2, and the standing pressure was approximately 130 kPa. For an ornithopod the size of an *Iguanodon* (5 tonnes), the total sole area of the hind feet was 0.6 m^2, and the standing pressure was approximately 120 kPa. For elephants (4.5 tonnes), the total sole area (four feet) was estimated as 0.6 m^2, giving a standing pressure of approximately 80 kPa. Although the actual pressure values with all the weight supported on one foot during locomotion are probably higher than the values estimated statically (Falkingham et al.,

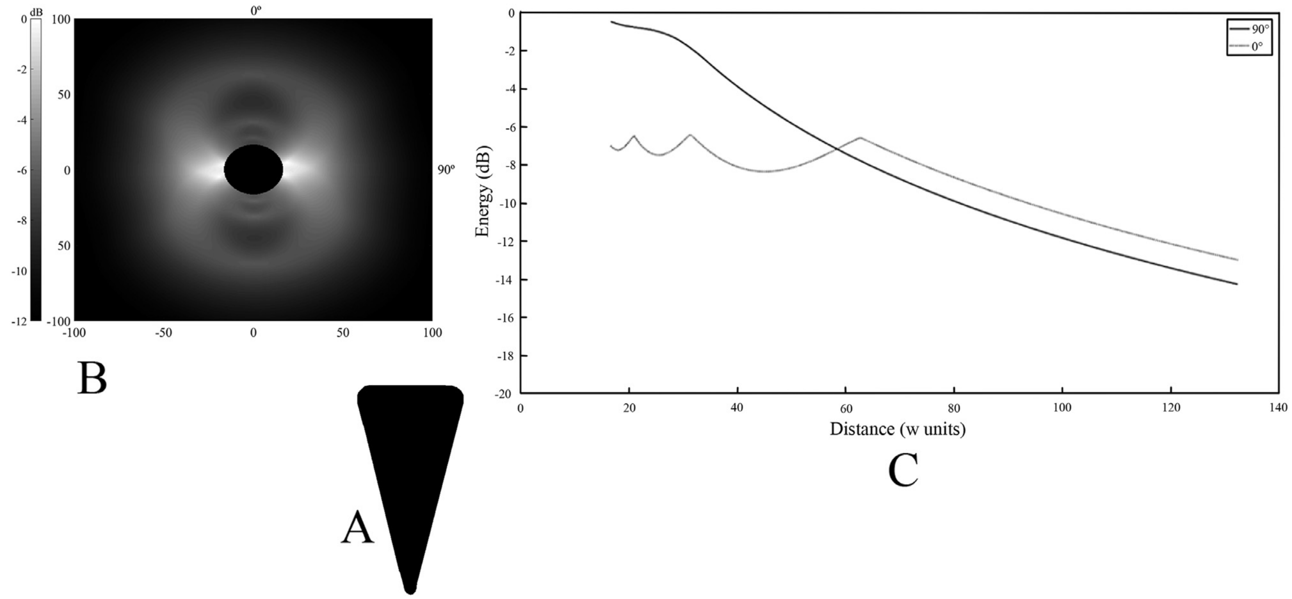

Fig. 2. (A) Triangular source geometry. (B) Directivity pattern of the wave energy at various distances from the source expressed in W units. (C) Energy as a function of distance to the source (expressed in W units) for 90° (dashed line) and 0° (full line).

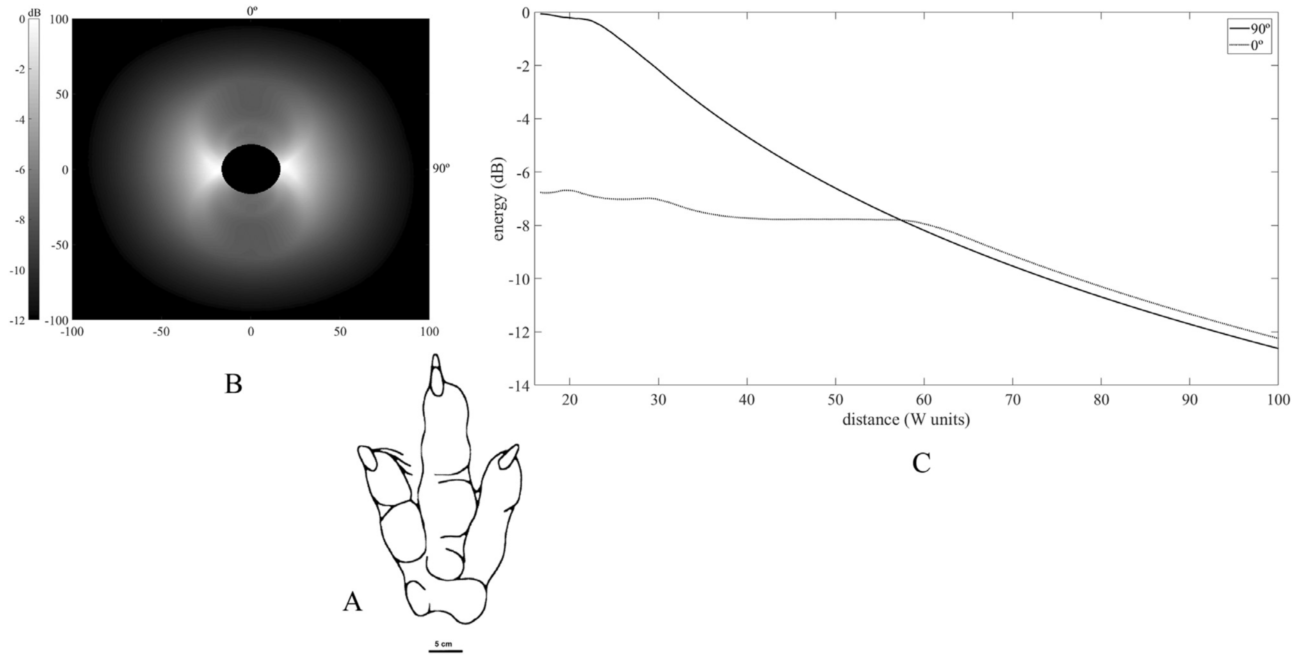

Fig. 3. (A) *Eubrontes giganteus* type (taken from Lockley, 2009 Fig. 2(A)) ichnite based geometry of the source. (B) Directivity pattern of the wave energy at various distances from the source (expressed in W units). (C) Energy as a function of distance to the source (expressed in W units) for 90° (dashed line) and 0° (full line).

2011), the estimation shown above is suitable for our comparative purposes. The total radiated energy is roughly proportional to the sole area, and the intensity is proportional to the square of the amplitude. If we also assume dynamic similarity, we can roughly estimate that the intensity of the seismic waves generated by a large sauropod were almost 25 times more intense, by a large theropod were 2.6 times more intense and by a large ornithopod were 2.3 times more intense compared to elephants. Therefore, the Mesozoic world was probably full of intense seismic signals generated by large dinosaurs.

Infrasonic and seismic detection in terrestrial vertebrates has been studied in a few groups, including amphibians, reptiles, birds and mammals (Randall, 2014; Narins et al., 2016). The mechanisms underlying infrasound and seismic wave detection in vertebrates are still poorly known. For elephants, the distribution, morphology and tissue density of Pacinian corpuscles, which are specialized mechanoreceptors, have been studied in the forefoot and hindfoot of Asian elephants. The results suggested that Pacinian corpuscles in the dermis of the foot are one possible anatomic mechanism used by elephants to detect seismic waves (Bouley et al., 2007). A similar distribution of Pacinian corpuscles is not exceptional among mammals and has also been described in the digits of humans, monkeys and raccoons (Bouley et al., 2007 and references therein). Other mechanisms accessible to other vertebrates, such as bone conduction, were also proposed (Reuter et al., 1998; Bouley et al., 2007). In birds, sensitivity to vibrations of low frequencies

Table 1
L/W means and standard deviations.

Group (N)	L/W mean	L/W standard deviation
Carnivorous theropods (17)[a]	1.94	0.43
Ornithomimosaurs (4)[b]	0.92	0.25
Therizinosaurs (2)[c]	1.00	0.14
Ornithopods (24)[d]	0.99	0.15
Sauropods (17)[e]	1.27	0.13

[a] Data from (Lockley, 2009; Lockley and Hunt, 1994; Li et al., 2008).
[b] Data from (Lockley, 2009),
[c] Data from (Harris et al., 1996; Fiorillo and Adams, 2012).
[d] Data from (Lockley, 2009).
[e] Data from (Ellenberger, 1970; Calvo, 1999; Weems, 2006; Lockley et al., 2007; Castanera et al., 2011).

has been documented many times. Herbst corpuscles were widely distributed in subcutaneous tissues in the legs, and close follicles of large flight feathers respond physically to small displacements (Narins et al., 2016 and references therein). Herbst corpuscles are mechanoreceptor analogs of Pacinian corpuscles and have been suggested to function as warning devices through detecting vibratory disturbances of the ground or other surfaces (Dorward and McIntyre, 1971) or as sensors in flight control (Hoerster, 1990). With the present knowledge, it seems highly plausible that dinosaurs could have mechanoreceptor analogs of Herbst or Pacinian corpuscles in their foot dermis or mechanisms of bone conduction with the sensitivity required to detect intense seismic waves produced during locomotion of other individuals. At same time, correlations obtained in living archosaurs have suggested that hearing in large dinosaurs was restricted to low frequencies with a high-frequency limit below 3 kHz (Gleich et al., 2005). Therefore, infrasound and seismic wave detection in large dinosaurs is plausible.

The ichnites of the hind feet of ornithopods, ornithomimosaurs and therizinosaurs have an almost equal length and width *sensu* (Lockley, 2009). The ichnites of sauropods are slightly longer than wider (see Table 1), and the ichnites of carnivorous theropods are almost two times longer than wider. One-way ANOVA shows that the mean index (L/W) for carnivorous theropods is significantly different compared to other groups (see Table 2). The allometric variation of this index for theropod tracks suggest a decreasing tendency with ichnite length (see Fig. 1), which implies that body size would have an influence on the foot morphology. However, the large index value of carnivorous theropods seems to be independent of biomechanical constraints related to body size because ornithopods and sauropods of similar (or even smaller) size have smaller index values (see Fig. 1). It is remarkable that the index values of therizinosaurs and ornithomimosaurs are different from those of carnivore theropods and almost indistinguishable from those of ornithopods (see Table 2). The pes of therizinosaurids are short and broad, and they are clearly different from those of any other theropod (Clark et al., 2004). Although the ornithomimosaur pes has a slender morphology, the three functional toes diverge quite widely (Thulborn, 1990), and this condition results in nearly equal width and length (Lockley, 2009). It is possible that this difference could be explained by the relevance of seismic wave camouflage to dinosaur behavior because the largest index values produce the largest effects.

The physics of the propagation of seismic waves implies that depending on the shape of the source, there will be differences in the energy radiated in different directions. Our results show that if the source length is larger than the source width, there is less energy emitted in the length direction. In the case of a typical theropod (L/W approximately 2), it is expected that surface seismic wave energy in the forward direction of motion will be lower than that in the lateral direction (Figs. 2, 3). This result suggests that a hunting theropod could avoid being detected by potential prey sensitive to seismic waves. However, there are other results from our physical model that could imply a more intriguing advantage. For a source with a relation of $L/W = 2$ (very close to the mean value for the carnivore theropod ichnites studied here, see Table 1), the intensity of seismic waves remains almost constant, even when the source is approaching (see Figs. 2(C), 3(C)). These results are independent of the source details and are mainly a consequence of the degree of asymmetry between the length and width (L/W index). In a paleobiological context, it might be expected that a typical theropod approaching a prey animal generated seismic waves that (due to the constant value of wave intensity) would be misinterpreted as a stationary or non-approaching source. With the parameters considered in our model, this masquerade effect would be relevant at distances between the predator and prey from approximately 25 m (see Figs. 2(C), 3(C)). Then, the theropod foot shape could be useful for producing seismic wave motion camouflage during the last stage of the approach to a prey animal.

There will be situations of low visibility, wind direction, and sound dispersion from vegetation, among others, in which the surface seismic waves could be the main source of information about predator behavior and be the stimuli that trigger initiation of prey flight. There are living analogues in vertebrates of this behavior such as the very specific response of the red-eyed tree frog to vibrations generated by egg-eating snakes (Warkentin, 2005), among other examples in animals (Randall, 2014 and references therein). For example, dense and high vegetation environments could conceal visual and acoustic clues that allow prey to detect a potential predator. Although airborne sound would be intense, high frequencies from the airborne sound would suffer scattering and attenuation in a dense environment. Otherwise, the low frequencies give not much information about source location making difficult to choose properly the escape direction. The lower frequency of sound that can be properly located depends of the distance between ears (limited by head size) but for seismic waves depends of the distance between the legs (limited by body size) as in elephants (Bouley et al., 2007; Blanco and Jones, 2014 and references therein). Even it is possible that hearing in large dinosaurs was restricted to low frequencies (Gleich et al., 2005) and had a poor ability to locate sound sources. Then it is possible that in some situations airborne sound cannot give enough information for initiating a proper defense. Additionally, wind direction can conceal the olfactory clues, and in some cases, the prey does not respond to a predator's odors (Schaller, 1972). The reduction of seismic wave intensity in the trail direction is significant only at distances less than 25 m (Figs. 2(C), 3(C)), and predator detection at this distance is relevant for the outcome of hunting. Field observations suggest that the distance covered in the final charge is a crucial variable for success. Several observations of hunting behavior in lions and leopards suggest that it is generally ineffective to launch attacks at distances larger than 20 m (Schaller 1972; Sunquist and Sunquist, 2009). At distances of 25 m or less, the seismic wave intensity is probably high enough to be easily detected by a prey. Then, the camouflage mechanism proposed here probably did not avoid the seismic wave detection at such distances but concealed the motion of the predator. In some situations, concealing the motion could be more relevant than avoiding detection (Griffin, 1992).

According to the economic hypothesis of prey flight distances (Ydenberg and Dill, 1986), prey may be aware of the predator well before it decides to flee. There are some features that can delay the escaping behavior of the prey. If other things are equal, the probability of prey flight initiation in a given encounter with a predator should increase with the approach velocity of the predator and the distance to effective cover, and it was proposed that it should decrease with the attainable escape velocity of the prey (Ydenberg and Dill, 1986). Prey flight distances have been shown to increase with predator approach velocity in a variety of species

Table 2
One-way ANOVA (post-hoc Tukey's pairwise comparison) probabilities.

Groups	Sauropods	Ornithopods	Ornithomimosaurs	Therizinosaurids
Carnivorous theropods	**0.0007405**	**0.0001342**	**0.0001338**	**0.0001344**
Sauropods	_	0.3869	0.1676	0.4243
Ornithopods	_	_	0.9888	1
Ornithomimosaurs	_	_	_	0.9821

Bold numbers significant difference ($p < 0.05$).

(Hurley and Hartline, 1974; Hutson, 1982). The seismic wave motion camouflage would be useful to hide actual approach velocity and could even produce the perception that the predator is not approaching. Predator size is also likely to be correlated with the probability of prey flight initiation and does influence flight distance (e.g., Hurley and Hartline, 1974; Dill, 1974). The reduction of the seismic wave intensity in the approaching direction can hide the actual body size of the predator, producing the delay of prey flight initiation. There are alternative defense tactics, such as crypsis, and defensive devices, such as spikes and armor, among others (see Ydenberg and Dill, 1986). Seismic camouflage could be useful to avoid these defensive devices. Seismic motion camouflage could have been a selective pressure for an active hunter adapted by macro-predaceous theropods, but body weight support and locomotion requirements could have imposed strong restrictions on the foot proportions.

There are also behavioral features that can improve seismic motion camouflage. For example, to touch the ground with metatarsals would reduce the seismic wave intensity and increase the L/W effective value for improving the seismic motion camouflage effect. The behavior of theropod dinosaurs that left metatarsal impressions has been discussed by G.J. Kuban, who suggested that the trackmakers may have been stalking or crouching as a part of their hunting behavior (Kuban, 1989; Thulborn and Wade, 1989; but see Lockley et al., 2003 for other interpretations). Seven of these elongated tracks show a mean L/W index of 1.6 and a standard deviation of 0.18. Five of these tracks show L/W values larger than expected for a theropod carnivore of such a footprint length (see Fig. 1). At the same time, this crouching locomotory behavior would produce a lower profile for visual detection.

The seismic wave motion camouflage concept proposed in this study could be applied to living animals and other fossil vertebrate groups. The theoretical approach presented in this study could be useful for understanding hunting strategies and depicting paleobiological scenarios.

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