VIBRATIONAL COMMUNICATION IN MAMMALS OF THE AFRICAN SAVANNAH

A literature study on vibrational communication in the context of predator-prey relationships

Elephant using its trunk and front foot to listen to seismic signals. Photo by O'Connell & Rodwell (2019)

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Abstract— **Animals communicate in various ways to each other which suits the situation they are in. Many species are known to communicate through sound, pheromones and with visual clues. However, probably the least known – but most commonly used – form of communication is through vibrations. Vibratory communication can be both airborne and substrate borne and is proven to have multiple forms of execution; head drumming, head dipping, foot drumming, trembulation, stridulation and bone conduction. In previous studies it was discovered that all arthropods use this form of communication to exchange information with family members, with possible mates and between predator-prey relationships. However, when in 1989 the first mammal to use bone conductive communication was discovered, a door opened to a whole new taxa of animal species that use vibrational communication. Various mammalian species were found to use this form of communication to find mates, avoid predators, detect and lure prey, warn competitors, find resources and demarcate territory. The largest mammal on the planet, the African elephant (*Loxodonta Africana*) uses vibrational communication to find water and detect predator presence. However, due to the difficulty in measuring and observing vibratory communication there is a lack of proper data on the subject. Even more so, since mammalian vibratory communication is not yet thoroughly studied, a lot of hypotheses remain just that; a theory. This paper provides some light on the previously executed studies on vibrational communication and elaborates on various communication forms and networks used by African mammals and the predator-prey relationships involved. Furthermore this paper lines up some of the gaps that still need to be filled.**

Keywords — **Africa, Savannah, predator-prey, evolution, adaptation, acoustic, seismic, waves, subterranean, networks, mimic, ear, ossicles**

I. INTRODUCTION

Intraspecific and heterospecific communication is proven to be important in various animal taxa. From fish to reptiles and mammals, communication within and between species is used for predator avoidance, prey detection, attracting a mate and navigation to name a few (O'connell-Rodwell *et al.*, 2001; Hill, 2008; Mason & Wenger, 2019). There are multiple forms of animal communication (Table 1). The most known is vocal or acoustic communication. This form of communication is noticeable for human beings and therefore easy to observe and study (Virant-Doberlet *et al.*, 2014; Yack, 2016). Other forms of communication are chemical signs such as pheromones to mark territory or attract mates, body language, visual clues and vibrational communication (Hill, 2008).

Vibrational communication is one of the most commonly used forms of communication, with over 230.000 arthropod species that use it (Virant-Doberlet *et al.*, 2014). Vibrational communication consists of both ground based (seismic) and airborne communication (Hill, 2008; Virant-Doberlet *et al.*, 2014). Both acoustic and seismic waves can experience disturbance from various environmental factors; wind, rain, soil type, temperature and anthropogenic noise (O'connell-Rodwell *et al.*, 2001; Randall, 2001; Virant-Doberlet *et al.*, 2014; Hager & Krausa, 2019). However, acoustic waves are most susceptible to these disturbances, plus airborne communication has an outer limit to its transmission (O'connell-Rodwell *et al.*, 2001). As a consequence, acoustic vibrations will not transfer as far as seismic vibrations. By using both acoustic and seismic waves simultaneously the signaler provides the receiver with almost the exact distance between them (Mason & Wenger, 2019; O'connell-Rodwell *et al.*, 2019). Vibrational communication consists of signals and cues, which can also be seen as active and passive vibrational communication (Yack, 2016). Vibrational signaling is an active communication. The individual is purposely making vibrations to communicate with other individuals. Vibrational cues are passive forms of communication. The individual is eating or walking, causing vibrations in the soil which can be picked up by other individuals (Virant-Doberlet *et al.*, 2014). In this paper I will refer to both signals and cues as vibrational communication.

Table 1: This table shows the distribution of various forms of communication in the animal kingdom. The animal species presented in this table are the most commonly studied African species for these types of communication.

Animal taxa	**Species**	**Form of communication**	**Production mechanism**	**Function**	**References**
ANURA	African clawed frog (*Xenopus laevis*)	Vocal	Pulsating the vocal sac	Showing fertility and attracting mates	(Kelley *et al.*, 2004)
	Banded rubber frog (*Phrynomantis bifasciatus*)	Visual	NA	Bright colours as a poisonous signal	(Van Der Walt *et al.*, 1992; Barnett *et al.*, 2018)
	Strawberry poison-dart frog (*Oophaga pumilio*)	Visual	NA	Bright colours as a poisonous signal	(Barnett *et al.*, 2018; University of Bristol, 2018)
ARANEAE	Jumping spider (*habronattus dossenus*)	Vibrational	Tremulation, stridulation and drumming	Mating calls, prey mimicry	(Hill, 2009; Randall, 2014)
	Tiger wandering spider (*Cupiennius salei)*	Vibrational	Tremulation, stridulation and drumming	Mating calls, species recognition	(Barth, 1997; Randall, 2014)
CARNIVORA	African lion (*Panthera leo*)	Chemical	Urinating, spraying and head rubbing	Marking territory	(Poddar-Sarkar *et al.*, 2008; Poddar-Sarkar & Brahmachary, 2014)
	Domesticated cat (*Felis catus*)	Vocal	Chirping, growling	Chirping; observing something desirable. Growling; territorial, distress	(Tavernier *et al.*, 2020)
	Tiger (*Panthera tigris*)	Chemical	Urinating, spraying	Marking territory	(Poddar-Sarkar & Brahmachary, 2014)
HYMENOPTERA	Acacia ant (*Pseudomyrmex ferruginea*)	Vibrational	Stridulation, tapping with antennae	Detection of herbivores eating their plant host	(Hager & Krausa, 2019)
	Western honey bee (*Apis mellifera*)	Vibrational	Stridulation (queen piping)	Encouraging work and establishing dominance	(Virant-Doberlet & Cokl, 2004)
ISOPTERA	Mound-building termites (*Macrotermes michaelseni*)	Vibrational	Head drumming	Alarming for predators	(Virant-Doberlet & Cokl, 2004; Geddes, 2013)

Vibrational communication is not yet fully understood. Research on this topic started relatively recent with the discovery that vibrational signals play a crucial role in various insect and spider groups (Virant-Doberlet & Cokl, 2004; Randall, 2014; Virant-Doberlet *et al.*, 2014; Hager & Krausa, 2019). Vibrational communication was found to be the least costly and most far reaching form of communication for small insects. The vibrations can extend up to several meters in small insects (Virant-Doberlet *et al.*, 2014). It was discovered that especially legs and feet play a crucial role in both signaling and receiving vibrations and that vibrational communication is commonly used for mate attraction, predator avoidance and territorial display (Randall, 2001; Bernal *et al.*, 2019; Mason & Wenger, 2019). However, predators learned to take advantage of this form of communication. For example spiders of the family Salticidae, of the genus *Portia*, commonly known as jumping spiders. These spiders capture their prey, which consists of other spider species, by placing themselves in their webs and mimicking the vibrational signals of distressed prey or willing mates, luring their prey towards them (Randall, 2014; Virant-Doberlet *et al.*, 2014). Nevertheless, there is still a lot unknown about the uses of vibrational communication in other taxa, how this form of communication is used, what the characteristics and mechanisms are and even how it evolved. Therefore this paper will answer the following questions: 1; is vibrational communication used in mammalian species on the African savannah? 2; if so, are there differences in use between predators and prey? And 3; how does vibrational communication influence predator-prey relationships on the African savannah? In this study I choose to look at mammals because there is very little known about vibrational communication in mammalian species. However, I found that the largest land mammal on this planet, the African elephant (*Loxodonta Africana*), uses vibrational communication in a wide range of context (Garstang *et al.*, 2014; O'connell-Rodwell *et al.*, 2019).This not only made me interested in vibrational communication in mammals, but especially mammals on the African savannah. I expect that if such a key species of that ecosystem uses vibratory signals to communicate both intraspecific and heterospecific, then this form of communication could very well exist in many more mammals in that ecosystem. Furthermore since vibrational communication is executed with low frequency noise, I suspect mammals to have much better vibratory senses then smaller taxa due to a larger middle ear (O'connell-Rodwell *et al.*, 2001; Mason, 2016). In addition I suspect that both predators and prey have adapted different ways of eavesdropping on each other. Virant-Doberlet *et al.*, (2014) already suspected that vibrational communication was not a private communication channel, but rather an open form of communication where competitors, predators and even prey could eavesdrop on the incidental cues that vibrations of the signaler deliver. For example a paper from Oberst *et al*., (2017) showed that the termite (*Coptotermes acinaciformis*) was able to eavesdrop on the footsteps of their main predator, the ant (*Iridomyrmex purpureus*), through wood and leaves. The vibrations of each footstep provided the termites with exact locations of their predator. On the other hand, the sand scorpion (*Paruroctonus utahensis*) uses its leg receptors to pick up subtle disruptions in the sand to hunt down its prey (Brownell & Leo Van Hemmen, 2001).

II. EVOLUTION OF VIBRATIONAL COMMUNICATION

How and when the form of vibrational communication evolved is still largely unknown. It is speculated that this form of communication evolved as a byproduct of behavioural responses to certain circumstances (Randall, 2014; Yack, 2016). For example a nervous foot stomping reaction when seeing predators coming close or an excitement body shake when a potential mate passes by. These incidental actions could catch the attention of potential mates or make individuals more alert (Randall, 2014; Virant-Doberlet *et al.*, 2014). Predation pressure is such a strong evolutionary force that it could drive prey species to evolve better strategies to successfully warn family members of close by predators (Randall, 2001). In addition, prey could even evolve strategies to alert the predator that they are aware of his presence. Hill (2009)

showed that the wandering spider (*Cupiennius salei*) is able to distinguish between the vibrations made by rain, wind, potential mates and prey. The prey, various species of grasshopper, evolved strategies to outsmart the ability of the wandering spider. Grasshoppers seem to be vibro-cryptic, meaning that they have the ability to stay unnoticed by creating vibratory signals that sound very similar to uninteresting vibrations such as wind (Barth *et al.*, 1988; Hill, 2009).
However, these studies show that there has to be a certain preference for these vibrational signals in order to evolve further from an incidental to a purposeful form of communication (Virant-Doberlet *et al.*, 2014). How this step came to be is still unclear, but due to the vast amount of animals species that use vibratory communication, it can be stated that this form of communication evolved separately in each lineage (Randall, 2014).

A. Costs and benefits of vibrational communication

As aforementioned, vibrational communication is not private and can be picked up by unwanted individuals. Therefore it is expected that vibrational communication is possibly costly for the signaler (Virant-Doberlet *et al.*, 2014; Bernal *et al.*, 2019). Predators can exploit this open form of communication by eavesdropping and locating prey. Especially during parenthood when youngsters often create not only more vocalization, but also more vibrations. For example in the oak treehopper (*Platycotis vittata*) where lots of offspring vibrations are produced during social interactions with the mother; providing food or protection. In these periods both the mother and the offspring are in great risk to attracting eavesdropping predators (Hill, 2009; Bernal *et al.*, 2019). Furthermore, vibrations can easily be misunderstood bringing the receiver in unnecessary danger. Biotic and abiotic noise can cause interpretation mistakes that might turn out costly for the receiver (Caldwell *et al.*, 2009; Virant-Doberlet *et al.*, 2014; Yack, 2016). With biotic noise most interpretation mistakes happen due to competition between vibrational signalers to get the receivers attention (Virant-Doberlet *et al.*, 2014). This competition between signalers gets most disturbing when both signalers communicate in the same time and frequency. Vibrational communication mostly happens in a frequency range below 2kHz, with some species being able to hear in the low-frequency range of below 3kHz (Virant-Doberlet *et al.*, 2014; Mason, 2016; O’connell-Rodwell *et al.*, 2019). When signalers communicate within this range at the same time receivers can experience difficulty in extracting the correct information from the right signaler, risking the probability of a false alarm or a missed opportunity to mate, find food or detect a predator (Virant-Doberlet *et al.*, 2014). With abiotic noise previous problems were mostly due to weather circumstances; wind, rain and thunder (Hill, 2009; Virant-Doberlet *et al.*, 2014). However, in more recent times anthropogenic noise is an increasing disturbance in vibrational communication. Animals living in urban places have continuous background vibrational noise such as airplanes, cars and other vehicles, construction work and loud places like amusement parks (O’connell-Rodwell *et al.*, 2001). The effects of anthropogenic noise also affect the studies done on vibrational communication in animal species that live in these urban settings, making it not possible to measure with certainty if these species still use vibratory communication as we know it (Virant-Doberlet *et al.*, 2014; O’connell-Rodwell *et al.*, 2019).
Vibrational communication thus appears to be quite costly and difficult to manage, but there must be something to it in order for it to become such a common form of communication. Hill (2009) showed some of the benefits by stating that vibrational communication can be used during both day- and nighttime and from greater distances. This makes it a more beneficial form of communication under some circumstances than visual communication. Hill also states that vibrational communication is a direct form of communication that is the most far reaching. Therefore this form of communication makes it easier to locate a mate or prey and thus saves time and energy. These findings were also stated in an earlier paper

by Virant-Doberlet & Cokl (2004) where they show that smaller insects use vibrational communication over airborne communication since it is the less costly and a far reaching form of communication. Another benefit of vibrational communication is competitor and predator avoidance and predator challenging (Randall, 2001, 2014; Yack, 2016; Mason & Wenger, 2019). The banner-tailed kangaroo rat (*Dipodomys spectabilis*) for example uses foot drumming to let snakes know that they are aware of their presence and show that they will not be an easy target (Randall, 2014). Foot drumming in kangaroo rats is also associated with attacking. Therefore they use this form of communication to keep intruders out of their territory and avoid costly interactions (Randall, 2001).

III. VIBRATIONAL COMMUNICATION NETWORKS

Most forms of communication between individuals can be distinguished in various networks (Peake, 2005; Virant-Doberlet *et al.*, 2014). Unfortunately, since vibratory communication is fairly new in research, vibrational communication networks have not received much attention over the years. However, the discovery that vibrational communication is not a common dyadic way of communication with one signaler and one receiver, but is open for other individuals within signaling and receiving range, resulted in an increase in studies on vibrational communication networks (Peake, 2005; Virant-Doberlet *et al.*, 2019).

Several basic network structures that can be recognized in animal communication are: broadcast networks (signals go from one signaler to multiple receivers), receiving networks (signals go from multiple signalers to one receiver), interactive networks (multiple signalers actively signal each other), eavesdropping/audience networks (obtaining information from signal-receiver interactions while you do not take part in the interaction) and incidental/bystander networks (a receiver notices the signals emitted between a signal-receiver interaction, but it is only background noise instead of useful information) (fig.1) (Burt & Vehrencamp, 2005; Peake, 2005; Virant-Doberlet *et al.*, 2014). How complex each network is, is fully dependable on the amount of individuals participating, both conscious and subconscious. As a consequence, multiple individuals can take advantage of both the signaler and receiver simultaneously. Virant-Doberlet et al., (2019) showed that due to these vast networks and diversity, various leafhopper species no longer distinguish between vibrations caused by different predator species or competitor movements. Instead leafhoppers tend to be more vigilant with any vibrational information that arrives from an unknown signaler. It appears that it is less costly to sound a false alarm multiple times than having to defend your territory, mate or life (Hill, 2009).

IV. VIBRATIONAL COMMUNICATION IN AFRICAN MAMMALS

The use of vibrational communication is commonly known in insect taxa and spiders. However, various mammalian species also use this form of communication to find mates, avoid predators, warn competitors and demarcate territory (Randall, 2001). As mentioned before, some papers explained vibrational communication in in the largest mammal on earth, the African Elephant (*L. africana*). Since vibratory communication can be both intra- and heterospecific African elephants could very well be communicating with various animal species on the African savannah when using vibrational communication, including other mammalian species (O'connell-Rodwell *et al.*, 2001; Hill, 2009; Mason & Wenger, 2019). However, not every animals species uses the same type of vibrational communication and some even use multiple forms simultaneously (Mason & Wenger, 2019). Various forms of vibrational communication used in mammals are foot drumming, head drumming/dipping, and bone conduction. In the following paragraphs

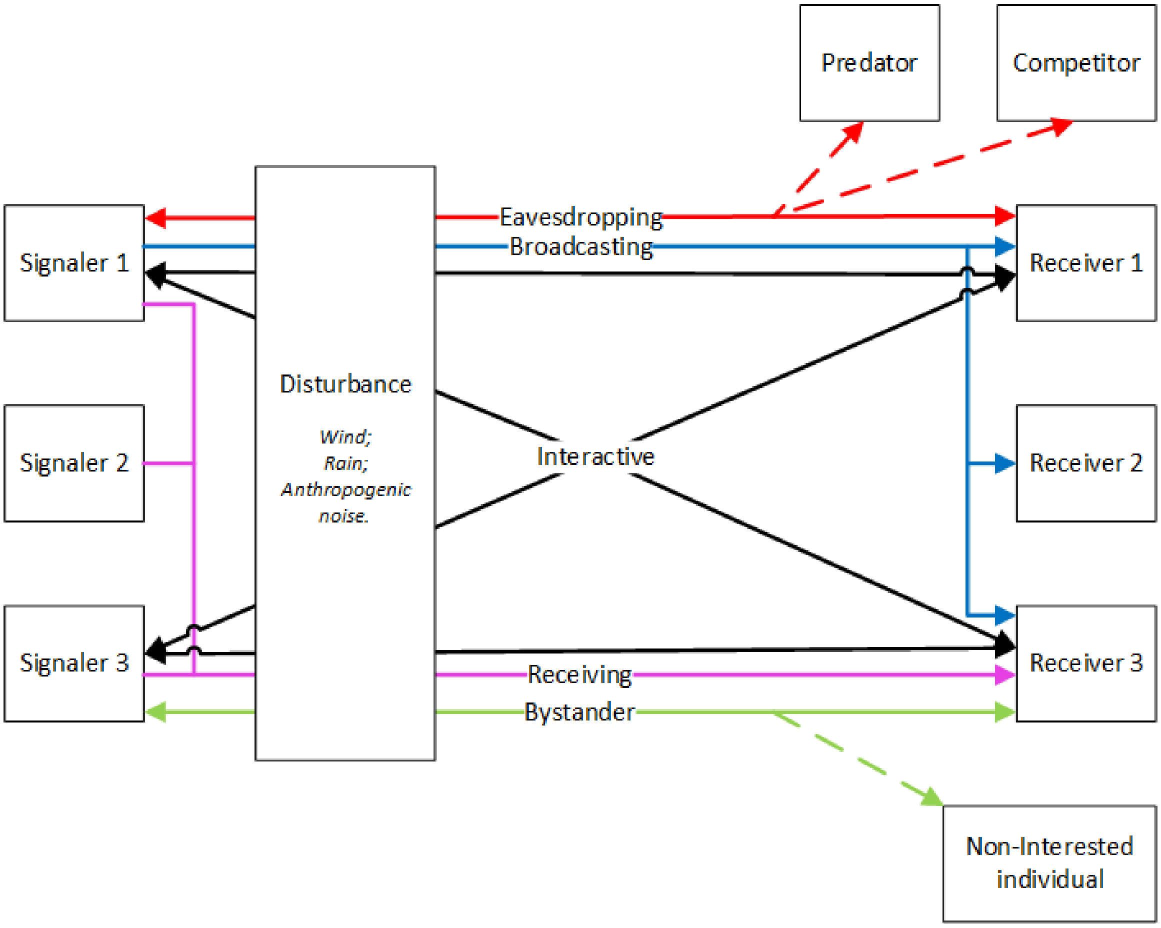

Figure 1: The various vibrational communication (VC) networks illustrated: 1) Eavesdropping (red), where other individuals such as predators and competitors can listen to and use VC in their advantage. 2) Broadcasting (blue), where one signaler reaches multiple receivers. 3) Interactive (black), where multiple signalers contact each other. 4) Receiving (pink), where multiple signalers reach one receiver and 5) bystander (green), where other individuals can pick up the VC, but do not use it. Every signal experiences some form of disturbance before it arrives at the receiver(s).

I will elaborate on each of these communication types and some African mammals that use this type of vibratory communication.

A. Foot drumming

Foot drumming is a type of vibrational communication that is the most likely to have evolved from incidental vibrational activity such as walking, running and stomping feet when feeling stressed (Randall, 2001; Mason & Wenger, 2019). Foot drumming in mammals evolved to be used in several occasions; demarcating and defending territory, agonistic behaviour to defend mates, communicating danger in the form of predators and competitors and communication between subordinates and superiors (Randall, 2001). In previous studies it was assumed that drumming causes close range vibrations and cannot be used for long range communication. O'Connell-Rodwell *et al*., (2001) provides evidence that foot drumming can not only be used for long distance communication, but it also achieves a larger communication range than airborne vibrations. Some terrestrial mammals use vibrational communication above ground. As a consequence these vibrations can also be perceived as airborne sound as well as substrate vibrations

(O'connell-Rodwell *et al.*, 2001; Sklíba *et al.*, 2008). Foot drumming however, is mostly used by subterranean rodents with sensitive low frequency hearing. They are able to transmit seismic signals underground, eliminating the presence of sound (Randall, 2001). One African mammal species that is particularly good at causing underground foot drumming vibrations is the banner-tailed kangaroo rat (*D. spectabilis)* (O'connell-Rodwell *et al.*, 2001; Randall, 2014; Virant-Doberlet *et al.*, 2019). These African rodents use individual, complex foot drumming rhythms to demarcate their territory. Their foot drumming patterns can be divided in four categories: 1) a certain number of separate drums together creating a so-called footroll; 2) a certain number of footrolls together; 3) the rate of the drumming and 4) the total amount of separate drums (fig.2) (Sklíba *et al.*, 2008; Randall, 2014). Kangaroo rats mostly use foot

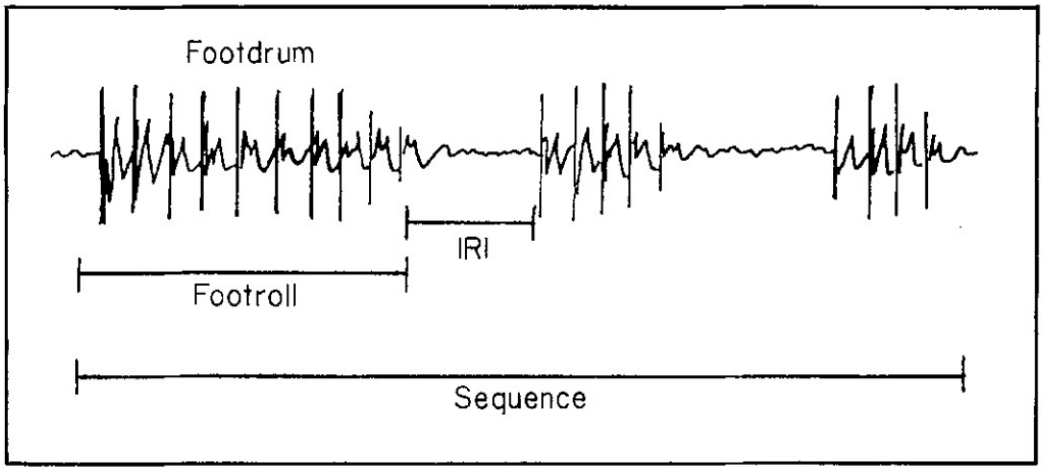

Figure 2: Individual foot drumming patterns in the banner-tailed kangaroo rat (*D. spectabilis*). A foot drum is a separate drum of the foot, a footroll is a group of foot drums together and a foot drumming sequence is a number of footrolls in a row. The time in between footrolls is called an Inter-Roll Interval (IRI). This figure is reprinted from J.A. Randall (1989), "Individual footdrumming signatures in banner-tailed kangaroo rats *Dipodomys spectabilis"*.

drumming to warn family members for predators, but they also use this type of vibrational communication to challenge predators. By using their feet to cause vibrations, they show incoming predators that they are aware of their presence and will not be an easy prey anymore (Randall, 1989; Mason & Wenger, 2019; Virant-Doberlet *et al.*, 2019).

Besides that feet can be used to signal vibrations, feet and legs are also commonly used as vibrational receptors. In most species the feet contain receptors that are able to rapidly adapt to vibrations in the ground. These receptors consist of Meissner's and Pacinian corpuscles (Pawson *et al.*, 2008; Randall, 2014; Mason & Wenger, 2019). Meissner's receptors are superficially located in the feet while the Pacinian corpuscles are mostly located in deeper locations of the body like joints (O'connell-Rodwell *et al.*, 2001; Pawson *et al.*, 2008). To make a sensitivity comparison, the human hand is the most sensitive part of the body with around 300 Pacinian corpuscles (Mason & Wenger, 2019). Humans barely make use of their hands in connection with vibrational communication. However, cats such as the African lion (*P. leo*) use the 660 Pacinian corpuscles in one foot to detect prey and even distinguish between prey (O'connell-Rodwell *et al.*, 2001; Mason & Wenger, 2019). By listening to the time in between vibrations of a walking individual a predator like the African lion can distinguish between different antelope species. However, this is based on lions being able to detect vibratory differences between elephant and gazelles, thus being able to distinguish between animal species that might provide almost the same vibrations is still just a theory (O'connell-Rodwell *et al.*, 2001).

B. Head drumming/dipping

Even though foot drumming is used more often, various mammals also use their head and teeth to cause drumming vibrations (Randall, 2001). Mammalian species that use head drumming to send signals bang their heads on a substrate which is usually the ground, but it can also involve obstacles like tree trunks and rocks . This head drumming is regularly used in the naked mole rat (*Heterocephalus glaber*). This African mammal is completely blind and uses a small flat part on its head to drum against the roof of its burrow to detect any obstacles along the way or to communicate with conspecifics (Hill, 2009; Randall, 2014; Virant-Doberlet *et al.*, 2019). A study of Sklíba *et al*., (2008) showed that the mole rats responded with head drumming after someone simulated a conspecific scratching noise near fresh mounds with their fingers. However, when someone opened a hole in the burrow the mole rats retreated far into the burrow, indicating that they can distinguish between both the sounds and vibrations made.

Head dipping is not a form of vibrational signaling, but it head dips are used to couple the head with the substrate vibrations and receive them (Mason & Wenger, 2019). The animal makes use of its middle ear with a technique called bone conduction, which I will elaborate on later. Head dipping is mostly used by fossorial species such as the Namib desert golden mole (*Eremitalpa granti namibensis*). This mole uses head dips during foraging. They run along the sandy surface and occasionally dip their head and shoulders into the ground to detect any vibrations caused by prey that is often hiding in isolated grassy tussocks (fig.3) (Narins *et al.*, 1997; Mason & Wenger, 2019). The actual detection of a tussock is not very hard. The wind blowing in the grass causes vibrations that are easily detectable by the moles, making the grass a clear guidepost (Narins *et al.*, 1997). When an individual gets closer to such a grassy tussock, the mole starts to make short clicking signals. These signals mimic the sounds of prey and are used to lure the prey towards them. Furthermore, the distance between head dipping positions got significantly smaller. This indicates that the mole is trying to get exact information of the location of the prey (Narins *et al.*, 1997; Hill, 2009; Mason & Wenger, 2019). This head dipping behaviour allows the desert golden mole to locate its prey on accurate information received from substrate vibrations created by prey (Hill, 2009).

Figure 3: A Namib desert golden mole (*E. g. namibensis*) dipping its head and shoulders under the sandy surface to detect prey vibrations, leaving its behind exposed (Narins *et al*., 1997)

C. Bone conduction

The typical route in mammals for receiving substrate borne vibrations is through the feet and legs (Rado *et al.*, 1989; Randall, 2014). However, as mentioned with the Namib desert golden mole (*E. g. namibensis*) some mammals use their head to receive ground vibrations. By taking the first step in bone conductive research in 1989, Rado *et al.*, discovered that the naked mole rat (*H. glaber*) was the first terrestrial mammal known to use "jaw hearing". By pressing its head against the ground, vibrations are transmitted through the lower jaw to the middle ear of an individual (Rado *et al.*, 1989; O'connell-Rodwell *et al.*, 2001). However, over the past years the use of bone conductive hearing has been discovered in many more

mammalian species. The jaw of mammals has a unique feature of being able to move both side to side and up and down. As a consequence the middle ear ossicles are more flexible than in other animal taxa which allows the ossicles to vibrate differently and pick up more vibrations (Rado *et al.*, 1989; Mason & Wenger, 2019). Since vibrational communication is performed with low frequency noise, the physiology of the ear needs to be adapted to have larger ossicles. Light middle ear ossicles are associated with high frequency hearing and would not be suitable for vibrational communication (Reuter *et al.*, 1998; O'connell-Rodwell *et al.*, 2001; Mason & Wenger, 2019). The Namib desert golden mole (*E. g. namibensis*) appears to have enlarged ossicles for its body size which have been hypothesized to have evolved specifically for vibrational hearing (fig.4) (Sumner-Rooney & Hutchinson, 2016; Mason & Wenger, 2019).
Besides jaw hearing there are many routes by which bone vibrations can reach the middle ear. African Elephants (*L. Africana*) and various species of rhinoceroses use the coupling of their feet with the earth to bring vibrations to their middle ear (Mason & Wenger, 2019; O'connell-Rodwell *et al.*, 2019). The

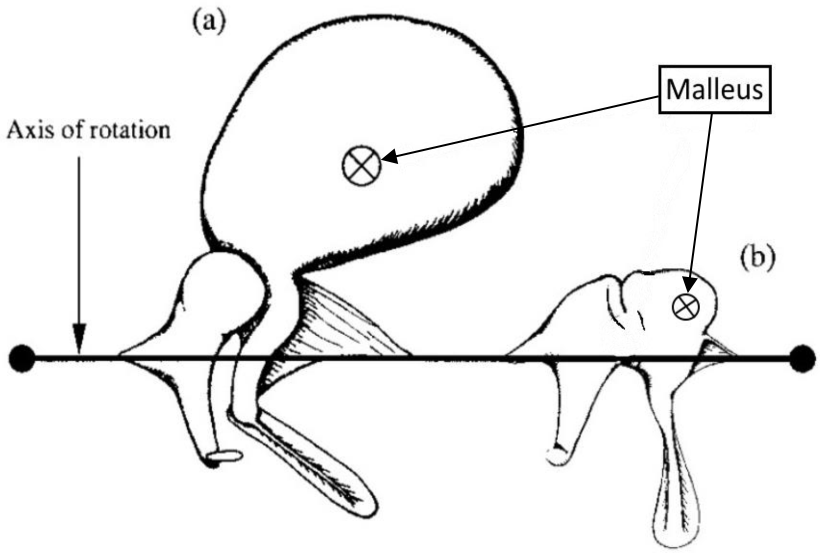

Figure 4: A comparison between the ossicles of the a) Namib desert golden mole (*E. g. namibensis*) and the b) Hottentot golden mole (*Amblysomus hottentotus*). Both from the golden mole family, *Chrysochloridae*. Note the enlarged size of the malleus in the Namib desert golden mole. As inspired by Sumner-Rooney & Hutchinson, 2016.

vibrations travel up from the feet through the legs and shoulders towards the middle ear ossicles. As mentioned before large middle ear ossicles are associated with better low frequency hearing and are therefore perfect for bone conduction. Since elephants have large ossicles, they are very well capable of receiving the low frequency vibrations through their feet (see front page) (O'connell-Rodwell *et al.*, 2001). The elephant uses both its trunk and front feet to detect substrate borne vibrations. Since these vibrations are in the ground, the ears are not used and thus in a relaxed position. Elephants turn their body approximately two or three times while listening to vibrational signals to establish its location (Mason & Wenger, 2019; O'connell-Rodwell *et al.*, 2019). However, enlarged ossicles seem to just be good at picking up low frequency noise, completely cancelling out high frequency noise. Massive ossicles therefore only seem to appear in animals that use bone conduction to receive vibrational signals (Reuter *et al.*, 1998; Mason & Wenger, 2019). The semi-aquatic mammal, the common hippo (*Hippopotamus amphibious*) has slightly smaller ossicles, enabling it to hear both high and low frequency noise. This benefits the hippo in underwater vibrational hearing (Reuter *et al.*, 1998). This indicates that various forms of vibrational communication are more suitable for different animal lifestyles.

V. DISCUSSION

Vibrational communication is probably the most commonly used form of communication in the animal kingdom. However, due to the difficulty of measuring and observing this form of communication it remained in the shadows of the more familiar forms of communication; visual, acoustic and chemical communication. Anthropogenic noise also affects the quality of the studies done on vibrational communication. Animal species that use vibrational communication in cities and other urban settings are very hard to study due to increased noise disturbance (Virant-Doberlet *et al.*, 2014; O'connell-Rodwell *et al.*, 2019). As a consequence, not only is vibrational communication not substantially researched, but the executed studies lack proper data. However, research on this form of communication spiked when it had been discovered that insects are not the only animal species using vibrational communication and that vibratory communication can come in many forms; foot drumming, head drumming, head dipping, stridulation, trembulation, bone conduction and maybe more undiscovered forms. The discovery that vibrational communication is not a simple dyadic form of communication with one signaler and one receiver, but can consist of very complex networks depending on the number of individuals participating in the communication helped increasing study interest and research even more (Burt & Vehrencamp, 2005; Peake, 2005; Virant-Doberlet *et al.*, 2014). This eventually resulted in the discovery of many more animal species that use vibrations to communicate with conspecifics, especially mammals (O'connell-Rodwell *et al.*, 2001). The use of vibratory communication in mammals is mostly used to navigate through the environment, to communicate with partners, family and possible mates, to localize food and water and to detect predators and prey. Predation pressure is such a strong evolutionary force that predator-prey relationships in the context of vibrational communication might be the main driver of these different vibrational communication methods. Elephants (*L. Africana*) and various species of rhinoceroses that use their feet to pick up substrate borne vibrations to detect water and predators and communicate with family members. The African lion (*P. leo*) is able to distinguish between the vibrations of different antelope species when they pass by in order to pick the easiest prey (O'connell-Rodwell *et al.*, 2001; Mason & Wenger, 2019). Prey species developed a way to fool predators by making vibrational signals that are similar to wind or rain vibrations in order to avoid them. In addition, predators fool prey by mimicking vibrations of a potential mate or food to lure them. It is yet unclear if predators and prey evolved these techniques around the same time or in response to one another. However, it is safe to say that many more mammalian species use both substrate borne and airborne vibrations to communicate with other individuals than it was previously thought.

Nevertheless, there is still a lot unknown about how this form of communication is used, what the characteristics and mechanisms are and even how it evolved. In order for vibrational communication to have evolved further from the incidental vibratory signals to a purposeful form of communication and persist, there has to be a certain preference for it. However, it is still largely unclear if certain vibratory patterns attract mates more than others and how individuals decide between vibrational communication trade-offs (Virant-Doberlet *et al.*, 2014). There is yet a lot to be discovered about the use of vibrational communication, especially in mammals. However since all mammals have ears and somatosensory receptors needed to pick up vibrations, all mammals could in theory be able to use vibrations to communicate both intra- and interspecific (Mason & Wenger, 2019). Nevertheless, despite the increase in interest and research on vibrational communication in mammals, a lot of these findings are not yet scientifically proven and still remain a mere theory.

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