Érica sena Neves

AVALIAÇÃO DE RISCO DE PREDAÇÃO E COMPORTAMENTO DE TAMBORILAR EM TRINOMYS YONENAGAE (RODENTIA: ECHIMYIDAE)

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Avaliação de risco de predação e comportamento de tamborilar em T*rinomys yonenagae* (Rodentia: Echimyidae)

Dissertação apresentada ao Instituto de Biologia da Universidade Federal da Bahia, para a obtenção de Título de Mestre em Ecologia e Biomonitoramento.
Orientador: Álvaro João Magalhães de Queiroz.
Co-Orientadores: Pedro Luís Bernardo da Rocha e Beatriz Monteiro Longo.

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Para minha querida tia-madrinha Maria Luísa.

In Memoriam.

“Never underestimate your own ignorance.”

Albert Einstein.

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INTRODUÇÃO GERAL

Trinomys yonenagae foi descrito por Rocha (1995) (Rodentia: Echimyidae, figura 1) e, desde então, é usado em estudos de autoecologia, ecofisiologia e comportamento (Manaf & Oliveira, 2000; Santos, 1999; Freitas *et al*, 2005). É uma espécie de roedor que se apresenta como interessante objeto de pesquisa por possuir características únicas que o diferenciam de outros membros de sua família. Enquanto todas as outras espécies conhecidas de *Trinomys e Proschimys* são habitantes de ambientes florestados, *T. yonenagae* é endêmico das dunas do Médio São Francisco, Bahia (figura 2), uma região de caatinga. O ambiente das dunas resultou na seleção, em *T. yonenagae*, de características morfológicas típicas de roedores de deserto, como bula timpânica aumentada, patas traseiras alongadas, cauda com tufo de pêlos, locomoção ricocheteante, coloração críptica e redução da massa corporal (Rocha, 1991,1995). As demais espécies do grupo aparentemente possuem comportamento solitário, mas *T. yonenagae* possui comportamento gregário, vivendo em tocas comunais (Rocha, 1991), nas quais formam grupos com vários machos e fêmeas adultas (Santos, 2004), e há indícios de que pode apresentar cuidado compartilhado dos filhotes pelas fêmeas (Manaf, 2000). Os dados existentes para as demais espécies do gênero *Trinomys* e *Proechimys* sugerem a existência de territorialidade entre fêmeas, que não apresentam sobreposição de área domiciliar (Bergallo, 1994, 1995; Fleming 1971; Emmons, 1982; Aguilera, 1999). Assim, é possível que as pressões seletivas do ambiente das dunas, semelhante às de deserto, tenham levado ao aumento da socialidade da espécie, de modo similar ao grupo de roedores africanos da família Bathyergidae (Bennett & Faulkes, 2000; Faulkes *et al*, 1997; Jarvis *et al,* 1994).

Os sistemas de comunicação se desenvolvem em variados hábitats e condições sociais, razão pela qual os sinais usados são produzidos, transmitidos e interpretados de diferentes maneiras (Randall, 1997). A comunicação sísmica, por meio da qual os animais transmitem informação através de sinais vibracionais, tem sido relatada para várias espécies de invertebrados e vertebrados (Randall, 1997). Tamborilar é um sinal sonoro não-vocal que contém componentes auditivos e sísmico, e que consiste em rápidas batidas das patas posteriores contra o substrato (Manaf, & Oliveira, 2000), sendo comum em roedores fossórios e semi-fossórios (Randall, 1994).

T. yonenagae apresenta um variado repertório sonoro vocal e não-vocal, e tamborilar tem sido observado, em laboratório, com os indivíduos mantidos em caixas separadas, bem como quando observado em colônias. Tal comportamento parece estar associado a reconhecimento individual e à defesa contra predadores. (Manaf & Oliveira, 2000). Entretanto, pouco se conhece sobre os eventos relacionados à sua comunicação a ao papel do tamborilamento nessa espécie, pois ainda não foi feito um estudo sistemático correlacionando conhecimento sobre aspectos sociais e as modalidades sonoras e sísmicas exibidas em eventos de comunicação.

Essa dissertação é composta por dois capítulos, que foram escritos de acordo com a formatação indicada pelos jornais que temos interesse em publicar, de forma que, depois que sejam feitas as correções e modificações após a defesa, sejam rapidamente encaminhados.

O primeiro capítulo foi resultado dos testes pilotos, no qual queríamos saber que tipo de estímulo faria com que o animal tamborilasse, e acabamos construindo um modelo de estudo sobre avaliação de risco de predação. Nosso objetivo foi comparar a resposta a dois tipos de estímulo (odor de uma serpente e a serpente viva), para verificarmos se existia uma modulação na resposta associada ao nível de risco.

No segundo capítulo nós avaliamos o contexto social do tamborilamento, as situações nas quais os animais tamborilam: se em situações de interação interespecífica, na presença de um predador, ou se quando havia um coespecífico presente. Analisamos se a freqüência e as características sonoras do sinal se modificavam a depender do contexto, o que poderia qualificar o tamborilamento como um provável sinal de alarme.

PREDATOR RISK ASSESSMENT BY RODENTS: CHANGES IN BEHAVIOURAL REPERTOIRE OF *TRINOMYS YONENAGAE* (ECHIMYIDAE) UPON EXPOSURE TO SNAKE STIMULI.

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ABSTRACTS

Changes in behavioral responses due to changes in the intensity of predation stimulus are indicative of risk assessment by prey. In order to evaluate if *T. yonenagae* performs risk assessment, we compared its behaviours among 4 experimental conditions (odor's stimulus, odor's control, living snake and living snake's control). Each individual was submitted to all treatments. Behaviour was represented by a synthetic axis built by reduction of 18 behavioural units to one dimension using the non-metric multidimensional scaling. Comparison among treatments was performed using a General Linear Model for repeated measures. Results showed that *T. yonenagae* only changed its behavioral response in the presence of the living snake. This difference of the living snake treatment is based mostly on the high frequency of the behavioural unit "footdrumming". We could not demonstrate that the risk assessment is modulated by the behaviors of the different predation stimulus, creating a gradient from the odor to the predator, but this study can be model to be used in studies about risk assessment, comparing different cues for the elucidation of antipredator behaviours and defensive responses.

KEYWORDS: risk assessment, behavioural repertoire, predation, rodents, *Trinomys yonenagae*.

INTRODUCTION

The threat of predation is an ecologically relevant stimulus (Carere *et al*, 1999), it's one of the most intensely investigated threats, and there are countless studies with prey animals exhibiting a variety of mechanisms to avoid capture and defend themselves from predators. Such mechanisms are critically important to animals as the cost of an inadequate defense may result in injury or death (Yang *et al*, 2004).

These defensive mechanisms may involve morphology, physiology, life history or behaviour, and in this last case, predator avoidance and antipredator behaviours (Kavaliers & Coleris, 2001). Defensive behaviour constitutes one of the most common sets of behaviours in mammals (Blanchard & Blanchard, 1989), including ultrasonic vocalizations (Holmes & Galea, 2002), flight/avoidance, crouching or freezing, defensive threat/attack, and risk assessment (Blanchard & Blanchard, 1989). The defensive response depends on the ability of a prey species to recognize its predators, and for many species, there is a very precise relationship between the specific stimuli and the response. In order to survive, they must identify and react appropriately to the presence of a predator (Hendrie *et al*, 1998).

Most defensive behaviors depend on environmental variables, mainly on the features of the threatening stimulus. For some species of rodents, the odor of a predator may be sufficient to trigger a response (Ylonen & Ronkainen, 1994). Bouskila (1995) examined the effect of sidewinder (*Crotalus cerastes*) scent on the foraging behaviour of two sympatric species, *Dipodomys deserti* and *D. merriami*. He demonstrated that both species reduced foraging in the presence of the sidewinder scent lending support to the notion that predation risk assessment via olfaction might be common in desert rodents. Many studies with different approaches (pharmacological, behavioral, ecological, etc) have shown that several rodents (laboratory and wild animals) use olfaction to assess predation risk, exhibiting a variety of behavioural responses to predator odors (e.g. Zangrossi & File, 1992; Dielemberg *et al*, 1999; Carere *et al*, 1999; Wallace & Rosen, 2000; McGregor *et al*, 2002; Masini *et al*, 2005). Species specific differences in reactivity to odor cues emanating from natural predators have been reported (Hendrie *et al.*, 1996).

In the presence of a living predator, we could expect an intensification of the response. Randall and King (2001) tested if two species of kangaroo rats (*Dipodomy ingens* and *D. deserti)* could assess the danger posed by snakes, displaying a different set of responses to the more dangerous stimulus of a real snake than to an artificial snake decoy. Foraging time decreased when a live snake was present compared with the decoy, and both species oriented towards, approached and footdrummed more in the presence of the live snake than the decoy. This snake-directed behaviour showed that the kangaroo rats could discriminate the difference in danger between the two stimuli.

Antipredator responses and defensive behaviour have been extensively dealt on ecological, pharmacological and ethological studies (see Dielenberg & McGregor, 2001). Nevertheless the assessment of the risk level, comparing different kinds of stimulus, have not been done. Behavioural response is a complex variable, and an analysis of the behavioral units, through the comparison of the repertories may provide rich information about changes. Behavioural studies that make use of repertories are an important method available to ethologists (Slater, 1973)

This work intends to evaluate the prediction that behavioral responses to predation stimulus by rodents are modulated by the assessment of the risk level. We predicted that if a rodent can assess the danger posed by predator, it should display a different set of behaviours to the more dangerous stimulus of a living predator than to an odor. To widen the generality level of the model, we studied a social rodent species distantly related to kangaroo rats: the torch-tail *Trinomys yonenagae* (Echimyidae). Rodents are usually prey for avian, reptilian, and mammalian predators. *T. yonenagae* may be also preyed upon by this variety of predators, including there owls, little tiger cats and snakes, such as *Crotalus durissus cascavella* (personal observation). The evaluation of the risk assessment was done through the comparison of the behavioural repertoires of T. *yonenagae* upon two predation stimulus: odor and the living snake.

Animals

Trinomys yonenagae is endemic to a desert-like dune habitat in the semiarid Brazilian caatinga and convergent with jumping rodents from several deserts of the world (Rocha 1995). While this psalmofile rodent inhabits a caatinga region, whose climate is characterized by irregular and scanty rainfall (Reis, 1976), the other species of equimyids inhabit forest environments. Data available for species of the genera *Trinomys* and the related genus *Proechimys* suggest that territoriality and intraspecific aggressive behaviors are quite common (Freitas *et al,* 2003). *T. yonenagae* seems to be the only well recorded exception to this general pattern of low level of sociability in the family. Rocha (1995) observed that individuals of this species dig burrows in the dunes and live in colonies. Manaf and Oliveira (2000) studied colonies of this species in the laboratory and detected low levels of aggressiveness, high levels of affiliation and bound formation among individuals within colonies. Freitas and colleagues (2003) studied dyadic interaction among adults in the laboratory and found that high affiliation and low aggressiveness occur between individuals who came both from the same and from different galleries.

We performed the capture of rodents for behavioural analysis in this study following governmental laws (IBAMA process 02006.004180/03-08). We collected the three females (144, 165 and 177 g) and two males (144 and 147g) used in this study on February to March 2004 in the dunes of the São Francisco River, Ibiraba village, municipality of Barra (10”48’S; 42”50’O). The village is around 480m above sea level and the local climate is semiarid, with rainfall unpredictable both in space and time (Reis, 1976). The plant cover in the sand dunes is dominated by clumped, short shrubs, and trees, and dunes valleys present high densities of terrestrial bromeliads and cactus (Rocha *et al*, 2004). Galleries are built and used by the rodents as a refuge to the epigeous conditions. Thereupon the capture, we transported the animals to the laboratory in the Biology Institute of the Federal University of Bahia. We housed them in same-sex pairs, in propylene boxes (34x40x16cm), with sawdust as substrate. The boxes were in air conditioned room (*T*_25±1°C) with a natural 12:12 h light:dark cycle (lights off from 18:00 to 06:00 h). Fruits, vegetables, seeds, pellet food and water were available ad libitum. The Regional Center of Ofiology and Poisonous Animals from Bahia located in the Biology Institute of the Federal University of Bahia, provided the *Crotalus durissus cascavella* snake (75cm and 390g).

Apparatus

In both experiments (odor and living snake) we used a rectangular arena with transparent perspex walls (80cm (L) x 40cm (W) x 30cm(H)), with a lateral entrance door, transparent Perspex cover and nine small holes (0.5 cm of diameter) placed on the bottom of one sides. We adapted the arena from Dielengerg and collaborators (1999) that built a similar one to be used in predatory odor experiments, where a rat was exposed to a cat's odor source. For the first kind of experiment (odor), we placed an opaque acrylic wall (25cm (L) x 30cm (H)) right in t middle of the arena, creating interconnected environments, of the same size. For the second experiment (live snake), we needed to readapt the arena; a transparent perspex wall covered with holes (1cm of diameter) was put in one of the sides of the arena, creating a bigger room (65cm (L)) and a smaller one (15cm (L)) (figure 1).

Procedure

We performed the experiments with the odor on June 2005, and the ones with the live snake on May and June 2006. We filmed all experiments under red light, at night, from 07:00 PM on, since we are dealing with a species with nocturnal habits (Marcomini & Spinelli Oliveira, 2003). The filming room had acoustic isolation, controlled temperature (*T*_25±1°C), and exhaustion system that continually renewed the air. In other to record the videos, we used four security cameras that were connected to a computer equipped with the recording video program EagleVision Pro®. Additionally, we recorded the sound with the sound design program Avisoft Pro®, using a Sennheiser® ME-67 microphone. After each filming, we carefully cleaned the arena with neutral liquid detergent and dries. The arena and all material used were always carefully handled by someone using procedure gloves, mask and laboratory coat in order to minimize interference of other odors.

There were four treatments, grouped in two tests, each one with stimulus itself and the control of the stimulus. The first stimulus tested was exposure to the odor, which was obtained from sterilized cotton kept in contact with a *Crotalus durissus cascavella* snake for one week. For the control we used only the sterilized cotton. This protocol was adapted from several tested predatory odor experiments (e.g., Carere *et al.*, 1999; Dielenberg *et al.*, 2001; De Paula *et al.*, 2005). All the animals passed through control and stimulus experiments; and there was an interval of at least 8 days between each. Both experiments had two phases of filming: (i) habituation, when we placed the animal in the arena through the lateral door and it remained there for 10 minutes; (ii) exposure, when after the habituation, we placed a plastic cup containing the cotton externally by the side holes, and continued filming for another 20 minutes. The second stimulus tested was the exposure to the live snake *Crotalus durissus cascavella.* For the control here we used a wood steak that was manipulated exactly like the snake was when it was put in the arena, with hooks. All the five animals passed through control and stimulus experiments, and there was an interval of at least 3 days between each. Both experiments had also two phases of filming: (i) habituation, when the animal was placed in the bigger side of the arena through the lateral door and it remained there for 10 minutes; (ii) exposure, when the snake or the steak was placed in the smaller side of the arena, and more 20min were filmed.

All experiments conducted in this study attained to ethical procedures and were attended by an observer in order to prevent any accident and injury to the rodents and snake.

Behavioural analysis

The records were watched, and we adopted the sampling *ad libitum* (Lehner, 1996) for construction of the behavioural repertoire. We used previously described behavioural units (Manaf & Oliveira, 2000; Neves, 2005, unpublished data) to build the repertoire, and also described new units. The units' nomenclature is based on classical ethological papers with rodents (*e.g.* Silverman, 1978; Eisenberg, 1967). Then, we watched all the records again, registering the frequency of the units in each treatment (odor's control, odor, living snake's control and living snake).

Hypothesis test

In order to test the hypotheses that rodents are able to perform risk assessment and modulate their behaviors based on intensities' difference of the predation stimulus, we compared the frequency of the behavioural units with frequency bigger than 100 occurrences among all the four treatments. We considered that since the dependent variable in this test was a multivariate descriptor of behaviours, based on frequency of behavioural units, we needed to reduce the dimensionality of it. For this, we used a non-metric multidimensional scaling (NMS), ordering the units of all the treatments on 1-dimension solution (with Euclidean distance, stability criteria of 0,005 and 99 runs), through the statistical program PC-ORD® (for Windows, version 4.25).

We performed a General Linear Model (GLM) test for repeated measures (0.05 as the significance level), using the NMS axis generated before, for each combination of treatments: odor's control x odor; living snake's control x living snake; odor x living snake; odor x living snake's control; living snake x odor's control; odor's control x living snake's control. For this tests we used the statistical program SPSS® 13.0. The GLM test provides an analysis of variance when the same measurement is made several times on each subject (Cramer & Bryman, 1999).

Finally, to visualize how the treatments were grouped in the multidimensional space, we reduced the units of all the treatments on 2-dimensions and plotted the axes. Also we used NMS (with Euclidean distance, stability criteria of 0,005 and 99 runs), through the statistical program PC-ORD® (for Windows, version 4.25).

RESULTS

The entire behavioral repertoire for both tests comprised of 19 behavioral units (table 1). The total number of behavior units exhibited was 1371 for the odor control and 1291 for the stimulus experiment. The behavior repertoire for the odor's test comprised of 14 different behaviour units, and because of obvious constraints of the experiment, the unit "explore the stimulus source with the snout" was exclusive for this particular experiment. The live snake control presented a total of 1364 behaviour units, and the ones with the snake itself had a total of 1167 units. The behavior repertoire for this test comprised of 18 different behaviour units, 13 identical to the odor stimulus and 5 new ones exclusive to this stimulus. The units "avert in reverse" and "footdrum" only appeared with the stimulus. The frequencies of each unit for the each individual are represented in the table 2.

The NMS ordination had final stress for one dimensional solution of 7.8, and a final instability of 0.005, with 26 iterations. The GLM test showed that there was no significant difference for odor's control x odor, odor's control x living snake's control and odor x living snake's control. The values of p for living snake's control x living snake, odor x living snake and living snake x odor's control were close to the significance level taken (= 0,05), so we decided to consider them significantly different (table_3). After this, we reduced the units of all the treatments on 2-dimensions (final stress of 4.3, final instability of 0.082 and 100 iterations) and plotted the axes (fig_3). We observed that the living snake's treatment is the most different, mainly because of three poin. So we went to the original table and ordered the units by the axis derived from the NMS based on the weighted mean. We can clearly detect that "footdrum" differs the most from the other units, and also had the highest frequencies of all units for three individuals.

We decided to make a rank transformation of the rows from the original data matrix. The rank transformation refers to the replacement of data by their ranks, which improves the relative power to detect active factors in the presence of outlying observations, normalizing effect on the data (McCune & Grace, 2002). Then, we reduced these data for a 1-dimension solution (stress of 23.7, final instability of 0.067 and 100 iterations), and again performed the GLM test, comparing the treatments (table_3). Now, we just found significant difference odor and living snake. In order to visualize how the treatments were now grouped, we also did again a reduction of the units of all the treatments for 2-dimensions (stress of 11.7, final instability of 0.075 and 100 iterations) and plotted the axes (fig_3).

DISCUSSION

Based on the results from the GLM tests between the treatments, we can not demonstrate that the risk assessment is modulated by the behaviors of the different predation stimulus. With the original data, there was significant difference between the living snake and all the other treatments, and with the ranked data, the only difference was for the living snake and the odor. By examining the proximity of each point on the graph (fig_2), it is evident that the individuals of the treatment with the living snake are more closely associated, and they are the only one evidently separated, while the rest are mixed. It is clear that for *Trinomys yonenagae,* in this laboratory experimental situation, individuals only change their behaviour when the snake itself is present.

This difference of the living snake treatment is based mostly on the high frequency of the behavioural unit "footdrumming", which also was exclusive for this situation. The same can be seen in the kangaroo rat (*Dipodomys spectabilis*), the tethered snake immediately induced high rates of footdrumming (Randall & Stevens, 1987). Footdrum, which involves striking the feet on the ground to create mechanical vibrations, is common in desert rodents and has evolved independently in several families of fossorial and semifossorial rodents around the world (Randall, 1994). It was often observed for *T. yonenagae* during laboratory's experiments, when individuals were kept in boxes and also in colonies and it seemed to be related to individual recognition and defense against predators (Manaf & Oliveira, 2000). Although in most cases antipredator defensive behaviours involve avoidance of predator, there is another category of antipredator responses that involve direct active signaling by the prey to the predator (Kavaliers & Choleris, 2001). Mammals prey species footdrum in response to predators, especially snakes, to communicate directly to the predator (Randall, 2001). The kangaroo rat approaches snakes to within striking distance, jumps back and footdrums. Randall & Matocq (1997) interpreted this behaviour to function in predator deterrence: the close approach informed the snake it was detected, and footdrum signaled the snake that the kangaroo rat was alert and would not be easy prey.

We could observe also a high frequency of units "raising the hind-quarter", "stretching the body", "shrinking the body" and "averting in reverse" in the living snake treatment comparing with the others. These units could be part of a ritualization of the individuals in presence of the snake. Randall (2001) discuss that footdrumming could be originally a displacement behaviour or an intention movement that may have developed in the presence of predators becoming ritualized. *T.*

yonenagae may have developed a whole specific ritual in the presence of an eminent threat like a snake. Also the exclusivity of "averting in reverse" for the living snake treatment, demonstrates that *T. yonenagae* also could have a specific pattern to avert from the living eminent threat, no turning its back to the predator. Many studies with antipredator defense using rodents suggest a very precise and apparently adaptive relation between the specific stimuli or situations and the defensive behaviour's elicitation (Blanchard & Blanchard, 1989). The california ground squirrels *(Spermophilus beecheyi),* for example, harass snakes in ways that evoke species specific displays (Carere *et al*, 1999). The same seems to be happening here: these are specific behaviours of the associated with the presence of the living predator.

Stretched attention postures is a well know behaviour described for wild rats (*Rattus rattus*) when they are submitted to different predator's odor (e.g. Kaesermann, 1986; Blanchard *et al*, 1998; Wallace & Rosen, 2000). The unit "stretch the body" had the highest frequencies in the living snake's experiments. It could indicates that for *T. yonenagae* only when there is a eminent predation's cue, "stretch the body" could be a cautiously way of trying to gain information about threat, which allows localization and evaluation of predatory threat, and through such evaluation, and the operation of specific learning processes (McGregor *et al*, 2002). Welton and colleagues (2003) discuss about the trade-off between gaining information about predation risk and survival: the more an animal exposes itself to possible predators, the greater the probability of death, but also the greater the information gained if it is still alive. *T. yonenagae* could be using this stereotyped behaviour to evaluate the risk and decides the next movement.

For rodents, mammalian predators are more likely to be detected via olfaction (Jedrzejewski *et al*, 1993; Ward *et al,* 1997). It seems likely that olfactory cues may also be important means of assessing mammalian predation risk (Ward et al. 1997). The results here indicate that for reptilian's predators, the most important cue may be the visual assessment. Another explanation for the lack of a milder form of defensive behaviour when exposed to the snake's odor is that there can be a rapid behavioral habituation to predator odors that are not reinforced by the presence of an actual predator (Kavaliers & Choleris, 2001).

The most remarkably result of this study is the begging of the function's understanding of the "footdrum". Studies about footdrumming of *D. spectabilis* to snakes (Randall & Stevens 1987; Randall et al. 1995; Randall & Matocq 1997) suggest that kangaroo rats respond to predation risk and interact with snakes to assess risk, as a pursuit deterrent to communicate to the snake its chances of ambush are no longer available. Nevertheless, Randall (2001) presented two others hypotheses why preys communicate to predators: to communicate that they are alert and continued pursuit is costly and to communicate that the preys are healthy and cannot be caught. Tests of these hypotheses require tests of responses of the predator to the behavior of the prey (Caro, 1995). Further research is required to understand the meaning of the “footdrum” in intra and interspecific contexts for *T. yonenagae*.

Conclusions here have to be restricted due to some shortcomings of the experimental design used in this study, in particular because of the small number of animals used. There is a considerably set of studies on behavioural responses to predation situation by kangaroo rats (Heteromyidae) and squirrels (Sciuridae) (e.g. Randall *et al*, 1995; Swaisgood *et al*, 1999; Herman & Valone, 2000; Randall & King, 2001; Leaver & Daly, 2003), but there was none previous studies using equimyids rodents. This also can be a model to be used in studies about risk assessment with rodents, comparing different cues (odor, sound or visual) for the elucidation of antipredator behaviours and defensive responses.

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Figure 1. Arenas made of transparent perspex walls. On the left side, the one used in the snake's odor experiments, and on the right the one used in the living snake's experiments.

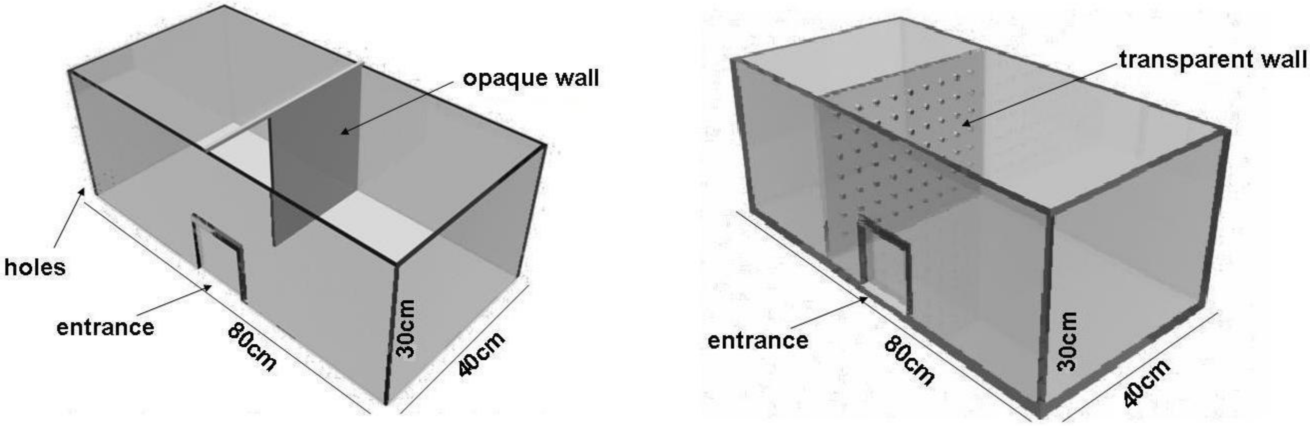

Figure 2. 2 dimensions' NMS reduction for original and ranked data. Treatments: odor's control (○), odor's (△), living snake's control (◇) and living snake(X).

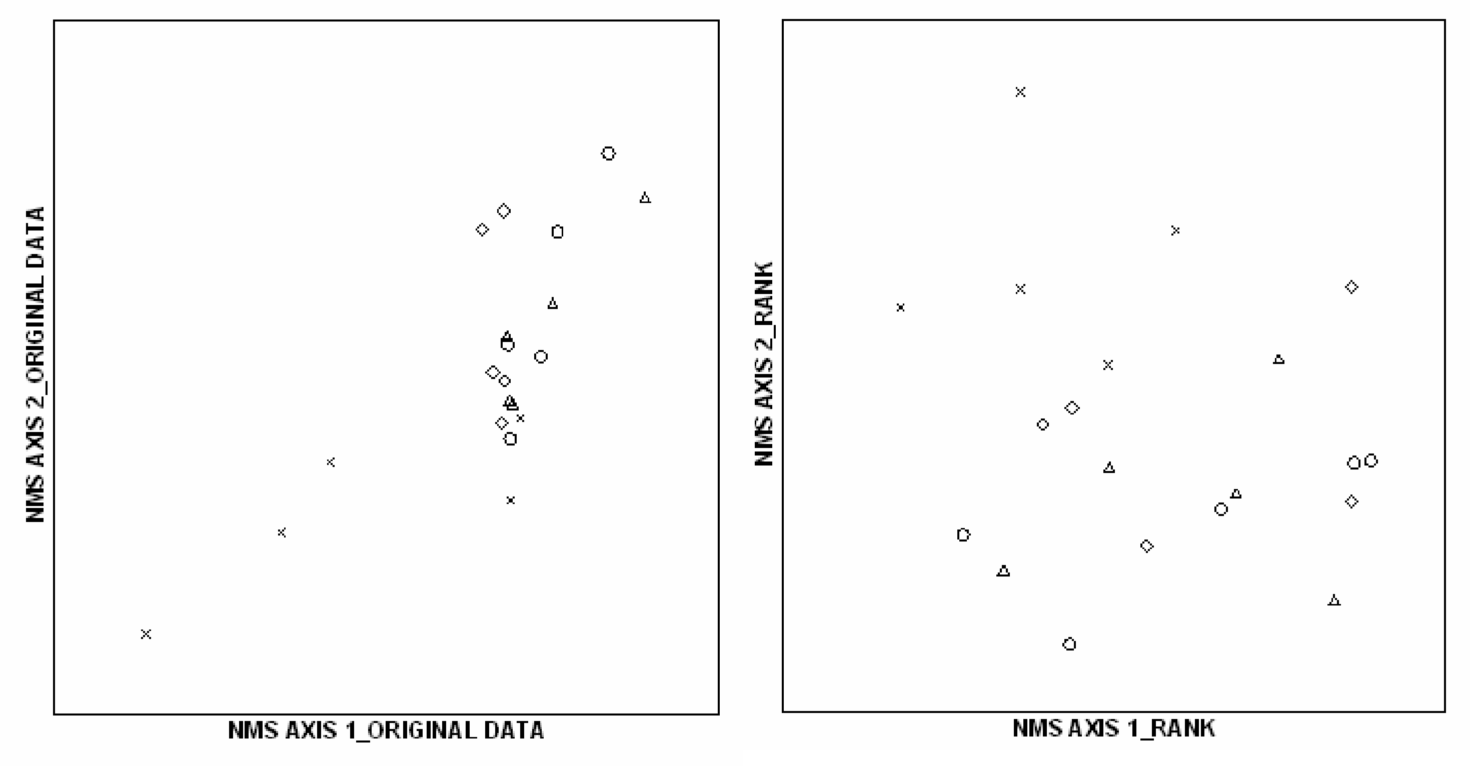

Table 1. Description of behavioural units, composing the repertoire of the four treatments.

Approaching	Approach the stimulus.
Averting	Move away from stimulus.
Averting in reverse	Slow locomotion in the reverse, moving away from the stimulus.
Erect position	Bipedal posture, totally extended spinal column, fore legs bent at the level of the shoulders and tail totally stretched.
Exploring air with the snout	Still quadruped or bipedal posture, supported with forefeet in a substratum or not. The animal lifts up the head or keeps it in line with the back stretched, and making short and fast movements of the snout, or long and slow movements, in different directions. It can remain, for some instants, completely still, except for the vibrissae that are always moving.
Exploring substratum with the snout	Approach the snout of the substratum (vertical or horizontal), with contact or not, and walking or not. The head moves, putting or not the vibrissae into motion.
Exploring the stimulus source with the snout	Approach the snout of the stimulus source (the wholes on the wall), with contact or not, and make random movements of the head, moving or not the vibrissae.
Footdrum	Fast beats of the hind feet against the substratum, producing characteristic sound.
Half-erect position	Fore legs bent, next to pectoral and tail stretched.
Jumping	Vigorous jump ahead or up.
Maintaining tail raised	Tail stay raised in form of arch or stretched.
Raising the hind-quarter	Lightly raise and lower the posterior region of the body one or repeated times.
Self-grooming	Wash the face, comb, lick the penis, scratch, clean the nails with the teeth or lick the foot.
Shrinking the body	Approach the head of the body bending the column.
Standing leant on substrate	Stand on hind feet, leaning fore feet on a vertical substrate.
Staying still	State of remaining motionless for more than five seconds, moving parts of the body in a discrete form or not.
Stretching the body	Keep the two posterior legs stop or stretched and at the same time it stretches the previous legs and the head, while it smells air or not.
Walking	Jump-like locomotion or not, with moderate or low speed.
Wet dog shake	Shake the head or the body, over a sequence from fast twisting of the head or body to right and left.

Table 2. Behavioural units' frequencies for each individual in the four treatments. They were from left to right, based on the weighted mean derived from the NMS axis for the behavioral units. The units marked in gray were the ones not used in the statistical analyses, because they had a total frequency under than 100.

TREATMENT	INDIVIDUALS	**Footdruming**	**Stretching the body**	**Raising the hind-quarter**	**Staying still**	**Exploring air with the snout**	**Approaching**	**Exploring substratum with the snout**	**Avert ing**	**Self-grooming**	**Walking**	**Half-erect position**	**Standing leant on substrate**	**Exploring the stimulus source**	**Shrinking the body**	**Averting in reverse**	**Erect position**	**Wet dog shake**	**Maintaining tail raised**	**Jumping**	**TOTAL/INDIVIDUAL**
ODOR'S CONTROL	1	0	0	0	14	23	7	43	11	0	72	65	1	8	0	0	0	0	0	0	236
	2	0	0	0	1	16	36	80	32	9	118	42	68	10	0	0	2	0	0	0	402
	3	0	0	0	4	5	17	70	18	11	57	34	33	7	0	0	6	2	0	0	249
	4	0	0	0	8	2	3	29	3	1	36	2	0	2	0	0	0	0	0	0	84
	5	0	1	0	3	7	36	76	37	13	192	42	45	9	0	0	1	2	0	1	452
ODOR	1	0	0	0	8	3	9	25	9	0	35	46	0	8	0	0	0	0	0	0	135
	2	0	24	0	4	7	26	33	26	0	95	66	37	9	0	0	3	0	0	0	318
	3	0	2	0	5	5	15	74	20	18	60	45	18	12	0	0	3	1	0	0	262
	4	0	3	0	14	6	11	40	13	8	48	9	3	5	0	0	3	2	0	0	155
	5	0	0	0	4	3	42	35	42	11	185	94	45	16	0	0	5	2	0	1	461
SNAKE'S CONTROL	1	0	0	0	5	9	73	90	67	10	85	73	19	0	0	0	3	2	0	0	431
	2	0	8	17	3	13	61	116	52	2	68	49	16	0	3	0	2	1	0	1	405
	3	0	0	0	15	3	12	60	16	14	45	20	11	0	0	0	0	7	0	0	196
	4	0	0	6	20	9	17	44	11	7	28	4	6	0	0	0	1	1	0	0	152
	5	0	0	14	21	4	25	69	23	5	31	33	2	0	0	0	1	1	0	0	227
SNAKE	1	164	0	9	16	9	29	36	16	0	57	2	0	0	1	21	0	0	11	0	338
	2	300	53	27	3	11	20	20	15	1	7	0	0	0	19	10	0	0	0	2	457
	3	23	0	37	21	26	11	9	7	1	11	0	2	0	15	4	1	0	2	1	148
	4	0	27	3	10	5	18	33	13	6	52	4	3	0	1	0	0	1	4	1	174
	5	202	38	1	6	1	40	42	29	7	35	15	11	0	8	2	1	0	0	0	427
TOTAL		689	156	114	185	167	508	1024	460	124	1317	645	320	86	47	37	32	22	17	7	

Table 3. Values of p for the GLM tests between the treatments. The white cells are the values for the original data, and the gray ones for the ranked data.

	odor’s control	**odor**	**living snake’s control**	**living snake**
odor’s control	**-**	**,681**	**,912**	**,173**
odor	**,416**	**-**	**,952**	**,072**
living snake’s control	**,475**	**,698**	**-**	**,153**
living snake	**,072**	**,068**	**,070**	**-**

IS FOOTDRUMMING AN ALARM SIGNAL? UNDERSTANDING THE FUNDAMENTALS OF FOOTDRUMMING IN *TRINOMYS YONENAGAE* (ECHIMYIDAE).

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ABSTRACTS

Alarm calls have been the main signal used in communication investigations. Calls may be directed to predators or to conspecifics to warn them about the presence of a potential predator. Footdrumming is the most common means of creating vibrational signals, and it involves striking the feet on the ground. They are grouped into short bursts called footrolls. Most rodents that drum are nocturnal and solitary, but this behavior is also seen in highly social rodents. Current known about vibrational communication in mammals is derived from solitary species, and more research on the rule of footdrumming in a social context is in need. *Trinomys yonenagae* is a rodent of the Echimyid family, and studies on social behavior have shown that they have low levels of aggressiveness and high levels of affiliation, what seems to be an exception in the family. Footdrumming in *T. yonenagae* has been observed both in laboratory conditions and in field, and one previous study has detected high rates of footdrumming in the presence of a snake. Our goal in this study was to evaluate if features of footdrumming in *T. yonenagae* facing a snake change when in the presence of a conspecific, and also if there is any modification of the footdrumming when this conspecific is known or unknown. In order to evaluate footdrumming features in 3 treatments (individual x snake, individual x known conspecific x snake, individual x unknown conspecific x snake), we analyzed the number of footdrums in the first, second and third footroll, the frequency and latency of the footdrumming. In the individual x snake situation, 4 animals out of the 9 (5 females and 4 males) footdrummed: 3 females and 1 male. In the individual x known conspecific x snake and individual x unknown conspecific x snake situation, only one animal footdrummed, the same female individual. The latency time varied from 23,4 to 993,6 seconds, and the number of footrolls in each experiment, from 5 to 107. The number of footdrummings in the 3 first footrolls varied among 1, 2 and 3. Three animals out of the 9 kept the same number of footdrummings in the 3 first footrolls in the individual x snake situation. Evidences in several species show that prey visually assess the relative risk of predation and only call when they are not subjected to excessive risk. But to footdrum when there is a conspecific around, the footdrummer could attract predator's attention to itself, increasing the risk. The larger number of females that footdrummed could demonstrate that there is a difference between sexes, and the same number of footdrummings in the two first footrolls could indicate that they have a footdrumming signature. Understanding the function of footdrumming in *T. yonenagae* is still unfolding, and more studies are necessary.

KEYWORDS: footdrumming, alarm signals, rodents, *Trinomys yonenagae*.

The alarm call communication has been investigated exhaustively along the last decades (see Shelley & Blumstein, 2004), and since Sherman's (1977) and Dunford's (1977) classic studies on calling in ground squirrels, others have studied alarm vocalizations in different species of rodents, including other species of ground squirrels (*Spermophilus* spp.) (Owings *et al*, 1986), tree squirrels (*Tamiasciurus hudsonicus*) (Greene & Meagher, 1998) and prairie dogs (*Cynomys gunnisoni*) (Placer & Slobodchikoff, 2000, 2001, 2004; Kiriazis & Slobodchikoff, 2006).

As the hunting success often requires an element of surprise, individuals may produce alarm call to alert the potential predator that it has been detected (Blumstein, 1999). Calls may be directed to predators (Hasson, 1991) or to conspecifics to warn them about the presence of a potential predator (Sherman, 1977). The reason why an individual incur the cost of attracting a predator's attention to itself is a question that puzzled evolutionary and behavioral ecologists for more than 50 years. Kinship is still the most used explanation in discussions; however recent studies have incorporated other factors like demography (Hoogland, 2007). Also a wide variety of evidences suggest that animals reduce risk to themselves when emitting alarm signals (Blumstein, 1999; Hasson, 1991).

This class of signal, alarm calls, has been the main signal used in communication investigations. Alarm calls are potentially rich sources for passing information to conspecifics (Sproul *et al*, 2006), and in the case of animals with functionally referential alarm calls, the call itself would elicit predator-specic defensive behaviour, rather than merely drawing the animal's attention to the presence of a possible threat (Seyfarth *et al.*, 1980).

In ethological and ecological studies, the signals have been grouped into four methods of communication: chemic, acoustic, visual and tactile (Poole, 1985), but the seismic method has not been frequently related. Footdrumming is the most common means of creating seismic signals (Randall, 1993), but mammals also communicate with vibrations by drumming other parts of the body. Footdrumming signals are unique because they can be transmitted through two channels, the air and the ground (Randall, 2001). It involves striking the feet on the ground, and they are grouped into short bursts called footrolls. Several footrolls can be combined to make a footdrumming sequence (Randall, 1989).

Randall (2001) mentioned five different intraspecific contexts why mammals footdrum: (1) as territorial advertisement, (2) during agonistic interactions in defense of territories and mates, (3) to coordinate mating interactions between males and females, (4) to communicate subordinance and an unwillingness to interact, and (5) to communicate danger from predators to family members. In interspecific communication, prey species footdrum in response to predators, especially snakes, to communicate directly to the predator. This is one of the more interesting aspects of footdrumming: when some prey species encounter a snake, instead of running away, they become active participants in an interaction with the predator, approach the snake and footdrum.

By far, the best studied footdrummer is the banner-tailed kangaroo rat (*Dipodomys spectabilis),* that has developed the footdrumming into a complex communication system that functions in both conspecific communication and in predator defense (Randall & Stevens, 1987; Randall, 1989). In conspecific communication, *D. pectabilis* footdrums to defende territory, and they can discriminate between footdrumming signatures of neighbours and strangers. The rats consistently footdrummed at higher rates to playbacks of strangers than to playbacks of neighbours. (Randall, 1994a). Two structural elements of footdrumming are known to account for most of the individual variation (signatures) in this species: the number of footdrums in the first footrolls and the number of footrolls in a sequence (Randall 1989).

Footdrumming is common in rodents and occurs in both fossorial and semi-fossorial species that inhabit open, arid environments (Randall, 1994a). This behavior is known from different lineages of both solitary and social species. Most of the rodents that drum are nocturnal and solitary, but this behavior is also seen in highly social rodents such as eusocial mole rats, *Crvptomvs damarensis* (Jarvis & Bennett, 1993)*,* and social gerbils, *Rhombomys opimus (*Randall *et al.,*2000). Most of the knowledge on seismic communication in mammals comes from solitary species and more research needs to be done on footdrumming role in social contexts (Randall, 2001).

Trinomys yonenagae (torch tail rat; Rocha, 1995) is a rodent of the Echimyid family, the group with the higher taxonomic, ecological, and morphologic diversity among hystricognaths. It is endemic to a desert-like dune habitat in the semiarid Brazilian caatinga and convergent with jumping rodents from several deserts of the world (Rocha, 1995). While this psalmofile rodent inhabits a caatinga region, whose climate is characterized by irregular and scanty rainfall (Reis, 1976), most species of equimyids inhabit forest environments. Data available for species of the genus *Trinomys* and *Proechimys* suggest that territoriality and intraspecific aggressive behaviors are quite common (Freitas *et al,* 2003). *T. yonenagae* seems to be the only well recorded exception to this general pattern of low level of sociability in the family. Rocha (1995) observed that individuals of this species dig burrows in the dunes and live in colonies. Manaf and Oliveira (2000) studied colonies of this species in the laboratory and detected low levels of aggressiveness, high levels of affiliation and bound formation among individuals within colonies. Freitas and colleagues (2003) studied dyadic interaction among adults in the laboratory and found that high affiliation and low aggressiveness occur between individuals who came both from the same and from different galleries.

T. yonenagae has a diverse vocal and non-vocal repertoire, and footdrumming has been observed in laboratory conditions, when the individuals are kept in separated boxes or in colonies (Manaf & Oliveira, 2000). It was also observed few times in field, where the animals drummed from inside of the burrows systems (unpublished data). Previous studies showed evidences for footdrumming in interspecific communication is strong for *T. yonenagae*, they footdrum at high rates in the presence of a snake (unpublished data). Nevertheless the question remains whether this semi-fossorial animal use this signal in intraspecific communication, as an alarm signal. We evaluated in this study, if the social rodent *T. yonenagae* increases the frequency of footdrumming or changes the signal's elements, in the presence of a conspecific, and if there is also any modification of the footdrumming when this conspecific is known or unknown.

Subjects

To develop as study, we used 22 wild-caught adults *T. yonenagae,* 13 females (137-170g) and 8 males (138-146g); 18 were the animals that we assumed that knew each other, each pair (9) was captured from the same gallery system, and 4 were captured from other different systems. They were trapped between 30 July and 17 August 2006 in the dunes of the São Francisco River, Ibiraba village, municipality of Barra (10"48'S; 42"50'O). The animals were transported to the Maintenance Laboratory for Animal Behavioural Study in the Biology Institute of the Federal University of Bahia. The Regional Center of Ofiology and Poisonous Animals from Bahia, located in the Biology Institute of the Federal University of Bahia, provided the *Crotalus durissus cascavella* snake (120cm and 2,5kg). Capture of rodents in this study was performed following governmental laws (IBAMA process n^0 02006.002120/2005-30)

Housing

Pairs of rodents of the same sex which were captured from the same gallery system were housed together, and the ones used in experiments with the unknown in individuals were housed solo. Housing occurred in propylene boxes (34x40x16cm) with sawdust as substrate. The boxes were keep in air conditioned room (*T*_25±1°C) with a natural 12:12 h light:dark cycle (lights off from 18:00 to 06:00 h). Fruits, vegetables, seeds, pellet food and water were available *ad libitum.*

Apparatus

In the three treatments (snake x individual, snake x individual x known conspecific, snake x individual x unknown conspecific) we used the same rectangular arena with transparent acrylic walls (80cm (L) x 40cm (W) x 30cm(H)), a lateral entrance door, and an acrylic cover. The arena was adapted from Dielengerg and collaborators (1999) that built a similar one to be used in predatory odor experiments, where a rat was exposed to a cat's odor source. Adjustments were made for each experiment: for the first kind of experiment (snake x individual), a transparent acrylic wall covered with wholes (1cm of diameter) was put in one of the sides, creating a bigger side (65cm (L)), where the rodent was placed, and a smaller one (15cm (L)), for the snake. For the others experiments (snake x individual x known conspecific, snake x individual x unknown conspecific), an additional room (30cm (L) x 30cm (W) x 30cm(H)) was plugged outside of the main arena, where the conspecific remained, and a wall was placed in the bigger side of the arena, that had an opaque side, as such one of the walls of the structure, in order to avoid visual contact of the conspecific (figure 1).

Procedure

Nine individuals (5 females and 4 males) passed through the 3 kinds of treatments: individual x snake, individual x known conspecific x snake, individual x unknown conspecific x snake. The rest of the individuals (11) were used as the conspecific, and because we didn't have enough animals, four of them were used more than one time. The experiments happened on October 2006, and the experiments with the same individual had an interval of at least 3 days between each. Because *T. yonenagae* is a species with nocturnal habits (Marcomini & Spinelli Oliveira, 2003), all data was filmed under red light, at night, from 7 o'clock pm. We recorded the experiments using 3 security cameras that were connected to a computer equipped with the recording video program EagleVision Pro®.The sound was recorded with the sound program Avisoft Pro®, using a Sennheiser® ME-67 microphone.

In the first experiment (individual x snake), the animal was carried from its home box to the testing room in a nest jar, and placed in the arena through the lateral door and remained there during 10 minutes (habituation). Then a person came into the room with a bucket containing the snake that was carried with hooks into the smaller side of the arena. We waited until the individual came out from freezing state, and recorded the experiment for 20 minutes.

In the second and third experiments (individual x known conspecific x snake; individual x unknown conspecific x snake), the individuals were carried individually from their home box to the testing room in a nest jar to arena. The first was placed in the bigger side of the arena, through the lateral door, and the second one was placed in the outside structure through the cover. The animals remained there for 10 minutes (habituation). Then a person came into the room, covered the arena with a piece of styrofoam, and brought a bucket containing the snake that was carried with hooks into the smaller side of the arena. We waited until the individual which had visual contact with the snaked came out from freezing state, and then they remained there for more 20 minutes.

After each experiment, the arena was carefully cleaned with neutral liquid detergent and dries. The arena and all material used was always carefully handled by someone using procedure gloves, mask and laboratory coat. All experiments conducted in this study attained to ethical procedures and were attended by an observer in order to prevent any accident and injury to the rodents and snake.

Data analysis

Five signal elements are known to account for individual variation in footdrumming: (1-3) the number of footdrums in the first, second and third footroll, (4) the number of footrolls in a sequence, and (5) the average footdrumming rate across footrolls in footdrums/s. (Randall, 1994a). In order to compare how footdrumming was varying in the treatments, we analyzed four of these elements (1-4), as well its frequency and latency of the footdrumming in each experiment where the individual that had visual contact with the snaked footdrummed.

We used only one snake for the tests, and this caused a problem of pseudoreplication. However, because of previous studies showed a strong and consistent response of *T. yonenagae* to an active snake (unpublished data), we considered the use of this large, active, snake was sufficient to elicit a normal range of responses.

RESULTS

In the individual x snake situation, four animals footdrummed: three females and one male. In the individual x known conspecific x snake and in individual x unknown conspecific x snake situation, only one animal footdrummed, the same female individual. The latency time varied from 23,4 to 993,6 seconds, and the number of footrolls in each experiment, from 5 to 107. The number of footdrummings in the 3 first footrolls varied from 1 to 3 (figure 1). Three animals produced the same number of footdrummings in the 3 first footrolls in the individual x snake situation, while just one had the same results in the individual x unknown conspecific x snake situation, varying the third footdrumming in the individual x snake situation and individual x known conspecific x snake (table 1). We were not able to calculate the number of footrolls in a sequence, because we couldn't identify any clear pattern of sequences. There was no persistent interval between footrolls that allowed us to label a sequence.

DISCUSSION

There was a decrease in the frequency of footdrumming when a conspecific was present. Only one individual footdrummed in the presence of a conspecific, while the same individual and three more footdrummed when they were alone with the snake.

One of the possible explanations for these results is that on the surface, footdrumming could be used only to communicate to predator, while inside the burrow system galleries it could have also a social function. In the social fossorial species, *Georychus capensis* for example, it provides information on the sex and reproductive condition of the neighbouring mole-rats (Bennett & Jarvis, 1988).

Randall (2001) listed three hypotheses that have been advanced to explain why a prey communicates to a predator: (1) to deter pursuit by informing the predator that has been detected and thus the chances of ambush are thwarted; (2) to communicate that the prey is alert and continued pursuit is costly and (3) to communicate that the prey is healthy and cannot be caught.

By deterring a predator's attack, the individual gains personal fitness benefits (Blumstein, 2007). If we assume that footdrumming evolved in *T. yonenagae* to communicate to predators, we would expect the individuals would try to minimize their risk while they footdrum. For animals that make use of alarm calls, Blumstein (2007) pointed that one way to do it, would be to vocalize only when it is possible to locate and track predators visually. There is evidence in several species that prey visually assess the relative risk of predation and only call when they are not subjected to excessive risk (Blumstein & Armitage, 1997). But to footdrum when there is a conspecific around, the footdrummer could attract predator's attention to itself, increasing the risk.

In our experiments a larger number of females that footdrummed, this could demonstrate that there is possible difference between the sexes. Banner-tailed kangaroo rat mothers in the presence of a tethered snake may footdrum to warn their offspring of danger (Randall & King, 2001). In *Dipodomys heermanni*, studies with captive colonies revealed that footdrumming occurs at a relatively low rate, and that rates are generally higher in females (Yoerg, 1999).

All the animals had the same number of footdrummings in the two first footrolls, but this number repeated between the individuals. This could indicate that they have a footdrumming signature, but it is repeated in the population, and it can refers to a status, age or sex difference, etc. Results from a study with *Dipodomys spectabilis* suggest that they can discriminate between footdrumming signatures of neighbors and strangers, and the main variation for the detection of these signatures were the number of footdrums in the first, second and third footroll and the number of footrolls in a sequence (Randall, 1994a).

Footdrumming may not be directed to conspecifics, but instead to the predators themselves. Whatever the mechanism for the evolution of footdrumming as an interspecific communication signal, the behavior may have became ritualized for communication because it benefited both the signal sender (*T. yonenagae*) and the signal receiver (snake). It would be an effective way for the drummer to convey information or to manipulate behavior of another animal (Krebs & Dawkins, 1984), avoiding pursuit or ambush situations.

Understanding the function of footdrumming in *T. yonenagae* is still unfolding, and communication by seismic vibrations has not yet been demonstrated. Conclusions have to be restricted due to some shortcomings of the experimental design used in this study, in particular because of the number of animals that footdrummed. More repetition should allow statistical analyses for significant differences between the treatments, and the signal elements. Also the conspecifics may be reacting to footdrumming by behavioral changes, and ethological analyses are necessary.

Footdrumming is one of the most complex communication signal, and this study was the first step for the understanding of the footdrumming contexts and its sound characterization in an equimyid rodent.

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Figure 1. Arenas made of transparent perspex walls. On the left side, the one used in the indivual x snake situation, and on the right the one used in the individual x known/unknow conspecific x snake treatments.

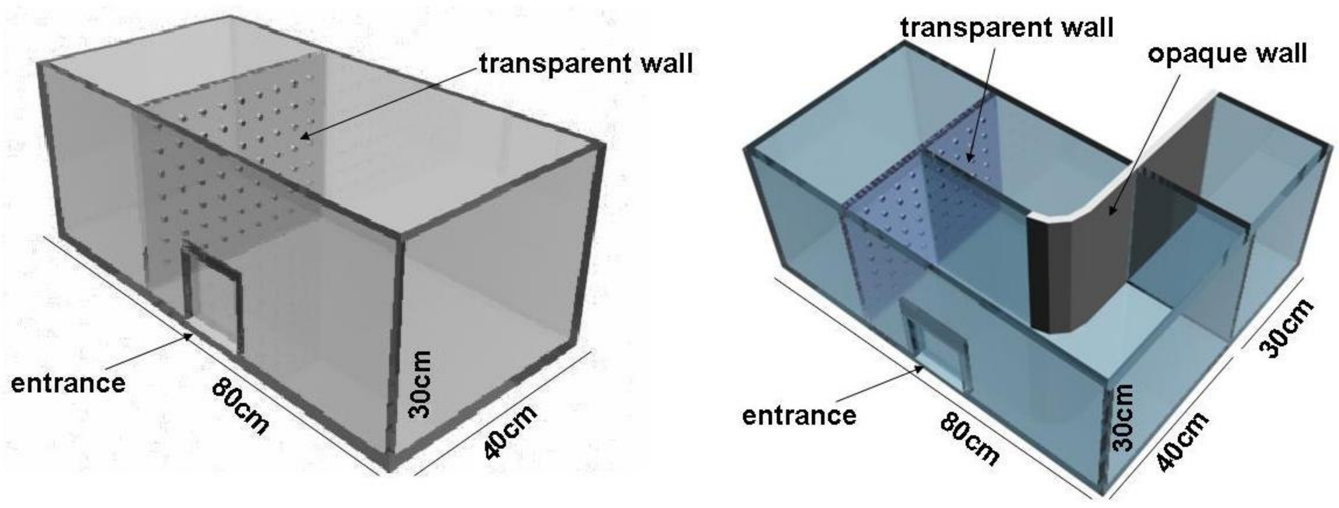

Figure 2. Examples of 3 footrolls with 1, 2 and 3 footdrummings, from left to right.

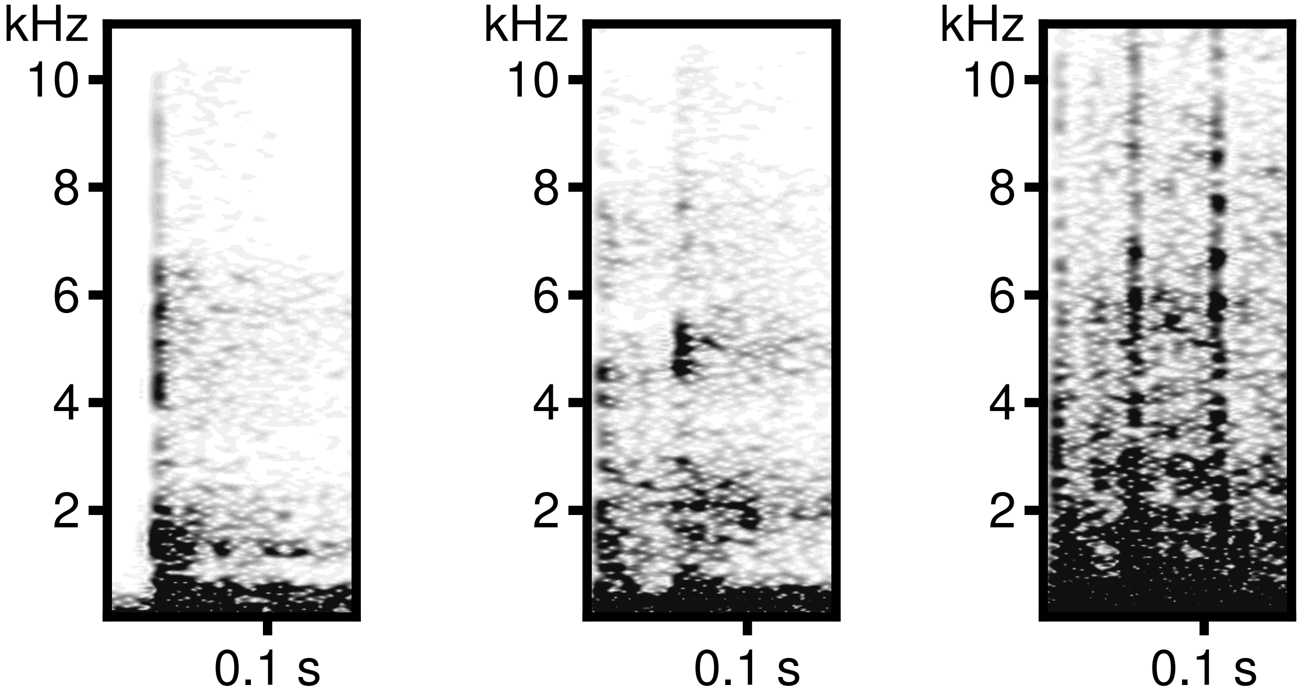

Table 1. Signal elements of footdrumming for each individual that footdrummed. *know conspecific and **unknown conspecific.

INDIVIDUAL	**SITUATION**	**LATENCY (sec)**	**# FOOTROLL**	**# FOOTDRUMMINGS IN FOOTROLLS**		
				1st	**2st**	**3st**
♀340	♀340 x Snake	347,7	107	3	3	1
♀340	♀340 x ♀344* x Snake	247,7	31	2	2	1
♀340	♀340 x ♀903** x Snake	993,6	5	1	1	1
♀348	♀348 x Snake	23,4	80	2	2	2
♀915	♀915 x Snake	119	86	1	1	1
♂930	♂930 x Snake	467,4	18	1	1	1

CONCLUSÕES

As principais conclusões do primeiro capítulo são:

- Os resultados indicaram que a avaliação de risco de predação não é modulada pelos comportamentos dos animais quando expostos aos dois tipos de estímulos testados.
- As analises estatísticas revelaram que o único tratamento que se diferenciou foi o da serpente viva. Essa diferença se deu principalmente pela alta freqüência de tamborilamento, unidade comportamental que foi exclusive desse tratamento.
- Altas freqüências das unidades comportamentais “levantar parte posterior do corpo”, “esticar o corpo” e “encolher o corpo” também foram encontradas quando a serpente viva era exposta, o que demonstra que existe um provável padrão comportamental específico quando um risco eminente.
- Este trabalho foi o primeiro passo para começarmos a entender o papel e os contextos de ocorrência do tamborilamento. No entanto, mais estudos devem ser feitos em contextos inter e intraespecíficos.
- Este trabalho também pode ser usado como um modelo de estudo sobre avaliação de risco de predação, comparando diferentes tipos de estímulos através de uma abordagem comportamental.

As principais conclusões do segundo capítulo são:

- Houve uma diminuição da freqüência de ocorrência de tamborilar quando um coespecífico estava presente. Possivelmente o indivíduo que tamborila deve evitar esse comportamento nessa situação para não chamar atenção pra si.
- Dos 4 indivíduos que tamborilaram, 3 eram fêmeas, o que pode demonstrar que existe uma diferença sexual.
- Todos os animais que tamborilaram tiveram o mesmo números de tamborilamentos nos dois primeiros “footrolls”, e esse número variou entre eles. Isso pode indicar que exista uma assinatura individual, mas que se repete na população.
- O tamborilamento parece ser um sinal para o predador, e não um sinal de alerta para coespecíficos. Esse mecanismo de comunicação inter-específica deve ser um importante mecanismo para evitar desperdício energético com perseguições, emboscadas, etc.

- Ainda estamos começando a entender a função do tamborilamento em *T. yonenagae,* e mais estudos precisam ser feitos.

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Figura 1. Foto do roedor psamófilo *Trinomys yonenagae,* espécie endêmica das dunas fósseis do Rio São Francisco, Bahia.

Figure 2. Mapa mostrando localização da área de estudo. O retângulo interno mostra a porção mais leste do Brasil e quatro cidades importantes como pontos de referência (1. Belém, Estado do Pará; 2. Salvador, Estado da Bahia; 3. Rio de Janeiro, Estado do Rio de Janeiro; 4. Brasília, Distrito Federal). A área diagonal mais escura limitada por áreas mais claras representa as matas arbustivas e secas da Caatinga limitada em sua porção oeste por áreas florestadas degradadas e em sua porção sul por áreas savânicas de Cerrado. A área delimitada pelo retângulo foi ampliada para mostrar os campos de dunas no banco oeste do rio São Francisco S.F.R. O campo de dunas está limitado em sua porção oeste pela Serra do Estreito (S. E) e em sua porção norte pelos pequenos triângulos. O rio Icatú (I.R., o único rio perene que cruza as dunas), o rio Grande (G.R.) e a lagoa de Itaparica (L. I), bem como os centros urbanos dos municípios de Barra (BA) e Xique-Xique (X.X.) são mostrados para referência geográfica. Os animais usados no presente estudo foram coletados nas dunas com morfologia nítida (faixa mais clara ao longo do rio São Francisco indicada pela seta preta) próximo da vila de Ibiraba (IB). As coordenadas do ponto central dessa imagem são 10°30'S 42°45'W.