***LEPTODACTYLUS LABYRINTHICUS* (Pepper frog): REPERTOIRE OF DEFENSIVE BEHAVIOUR.** *Leptodactylus labyrinthicus* is a large sized terrestrial species that occurs in open biomes such as the Brazilian Cerrado and Caatinga (Heyer & Maxon, 1982; Machado *et al.*, 1999). Open habitats may expose frogs to visually oriented predators in a higher intensity when compared to frogs that live in forested habitats, where they may take advantage of a higher spatial heterogeneity (Martins *et al.*, 1993). Therefore, such conspicuous frogs may exploit different defensive tactics to avoid predators or, at least, reduce the risk of predation. Martins (1989) reported that individuals of *L. labyrinthicus* are able to perform a deimatic behaviour (puffing up the body, elevating the hind parts, and displaying aposematic marks on its inguinal region). However, no further information is available regarding to the defensive strategies of this species. Furthermore, the quantification of the frequency of occurrence of defensive behaviours is poorly documented (e.g., Hödl & Gollmann, 1986). Hence, we here describe and quantify unreported defensive strategies exhibited by adult males and females of *L. labyrinthicus*.

Most of the fieldwork was conducted at Itirapina Ecological Station (IES: 22°13'S, 47°54'W; approximately 700 m elevation), Municipality of Itirapina, State of São Paulo, southeastern Brazil, during two consecutive reproductive seasons of *L. labyrinthicus*, from February 2002 to February 2004. The IES is one of the last remnants of pristine Cerrado in the state of São Paulo. One single field expedition (November 2001) was made to an agricultural grassland site (IRC: 22°16'S, 47°42'W; approximately 650 m elevation) in the district of Itapé, Municipality of Rio Claro, State of São Paulo. The climate of both localities is mesothermic, with two well-defined seasons, a dry-cold season (April–August) and a wet-warm season (September–March).

We monitored individuals of *L. labyrinthicus* around flooded areas such as margins of streams and temporary ponds. When locating the individuals we recorded their defensive responses against the researcher approaching and during the subsequently handling. Distress calls were recorded with a Sony TCM 20 DC cassette recorder with a Leson MK2-Plus external microphone positioned at ca. 50 cm from the calling female. The sound analyses were made on a Macintosh computer, using the Canary 1.2.4 software, configured with 16 bits of resolution, 44.1 kHz of frequency sampling, FFT and frame length of 256 samples. The distress calls were recorded at IRC and the quantified data of the defensive strategies was obtained at IES.

Males and females combined exhibited nine different defensive strategies. Three of these were stimulated by human approach and eight by human handling (Figure 1). Motionlessness was the most common strategy in both situations. Body raising (observed as a complex of defensive mechanisms consisting of body lifting from the ground, puffing up the body, and displaying the bright reddish inguinal coloration), distress calls, and spine aggression were males-exclusive strategies at IES (distress call of a female was recorded at IRC); liquid cloacal discharge was female-exclusive. Aside from motionlessness, skin secretion and death feigning (thanatosis) were the most common defensive strategies among males and females during handling episodes, whereas body inflation and escape behaviour were quite scarce (Figure 1).

The distress call was emitted only when the individual frogs were handled. Two distress calls were recorded and analysed. Eight harmonic bands were identified with frequency varying from 0.3 to 9.37 kHz. The mean dominant frequency was 2.503 kHz on the third harmonic band. The call duration was 817.8 and 916.9 ms in both calls recorded (Figure 2).

Motionlessness was the most common performed defensive behaviour (both toward approach and handling) and may imply an avoidance of predator detection: a primary defence (Edmunds, 1974). Females showed themselves to be more skittish than males when approached; it may suggest that the presence of sexual spines on the chest and hands of the males, the only male-exclusive defence observed could be effective against predators (Villa, 1969). Besides the 10 defensive strategies observed, body tilting toward the direction of an external stimulus (e.g.,

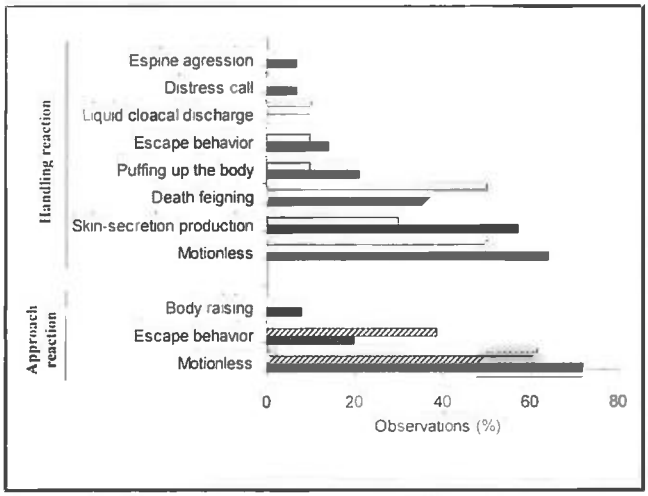

Figure 1. Human approach reaction (striped bars; *N*males = 25; *N*females = 18) and handling reaction (non-striped bars; *N*males = 14; *N*females = 10) of adult males (dark-grey bars) and adult females (white bars) of *Leptodactylus labyrinthicus* at the Itirapina Ecological Station, state of São Paulo, southeastern Brazil.

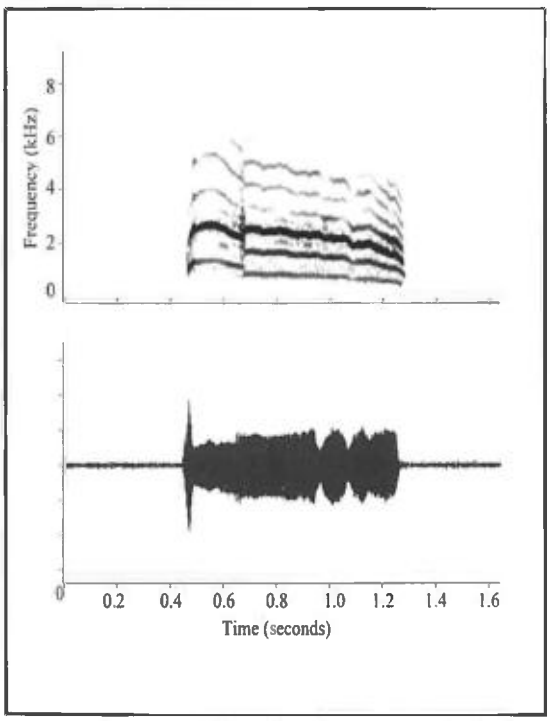

Figure 2. Sonogram (above) and oscilogram (below) of distress call emitted by an adult female *Leptodactylus labyrinthicus* recorded at the Municipality of Rio Claro; Air temperature = 20°C.

presence of predator or touching individuals' dorsum) was also exhibited by adults of *L. labyrinthicus* (C. F. B. Haddad, pers. comm.). It was not observed in the studied populations, probably due to lack of adequate stimuli experimentation.

Despite the large repertoire of defensive behaviours recorded, presence of toxic skin secretions, and large body size, adults of *L. labyrinthicus* are, at least, preyed upon by medium-to-large mammals at the IES (Prado *et al.*, in press). Therefore, the efficiency of any of the defensive strategies against natural predators still needs further investigation.

The complex of defensive repertoire might have originated due to the selective pressure of predation in open habitats, such as that occupied by *L. labyrinthicus* (Heyer & Maxon, 1982). Therefore, if environmental conditions (open or forested habitat) influences on the defensive strategies of the species of *L. pentadactylus* group (*sensu* Heyer, 1969), other species that inhabit forested habitats, such as *L. pentadactylus* and *L. flavopictus*, may exhibit fewer defensive strategies against predators.

Alternatively, defensive behaviours might be phylogenetically rather than ecologically dependent. In this case, individuals of closely related species may exhibit the same range of defensive strategies regardless of their habitat type (open or forested). In agreement with this hypothesis, *L. pentadactylus* was reported to exhibit eight defensive strategies out of the ten exhibited by *L. labyrinthicus* (Villa, 1969). In order to confirm whether or not the defensive behaviours are phylogenetic or ecologically dependent, however, more observations on the *Leptodactylus pentadactylus* species group (Heyer, 1969) are evidently required.

ACKNOWLEDGEMENTS

The authors are grateful to Célio F. B. Haddad, Lauren Chan, Cínthia A. Brasileiro, Cynthia P. A. Prado, Andrew Crawford, and Karen Akre for revising earlier versions of the manuscript. Field assistance was made especially by Victor Vetorazzo. Denise Zancheta conceded access authorization to the Ecological Station of Itirapina.

We also thank FAPESP, CNPq, and CAPES for grants received. This is publication number 23 of the project 'Ecologia dos Cerrados de Itirapina'.

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LUÍS FELIPE TOLEDO[1], ALEXANDRO MARQUES TOZETTI[2] and JULIANA ZINA[1]

[1] *Departamento de Zoologia, Instituto de Biociências, Universidade Estadual Paulista, Rio Claro, Estado de São Paulo, Brazil, Caixa Postal 199, CEP 13506-970.* E-mail: *toledolf@hotmail.com*

[2] *Departamento de Ecologia, Instituto de Biociências, Universidade de São Paulo, Estado de São Paulo, Brazil, Caixa Postal 11461, CEP 05422-970.* E-mail: *mtozetti@uol.com.br*

Corresponding author: LFT: *toledo@rc.unesp.br*