DIET OF *LEPTODACTYLUS OCELLATUS* (ANURA; LEPTODACTYLIDAE) FROM COASTAL LAGOONS OF SOUTHEASTERN BRAZIL

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R e s u m o. — Estudamos a dieta de *Leptodactylus ocellatus* ao longo de três lagoas costeiras no Município de Anchieta, ES, sudeste do Brasil. Cinquenta e sete exemplares foram coletados, variando de 18,5 a 100,4 mm no comprimento rostro-uróstilo. *Leptodactylus ocellatus* consumiu uma grande variedade de itens alimentares. Besouros adultos foram as presas mais frequentes, seguidos por larvas de besouros e formigas. Cupins foram os itens predominantes em termos numéricos, enquanto ortópteros foram os ítens dominantes em termos de massa. Foi observada a presença de vertebrados na dieta de *L. ocellatus*, incluindo um jovem da mesma espécie. A dieta desta rã variou ontogeneticamente quanto ao tipo e ao tamanho das presas.

Palavras-chave: Leptodactylus ocellatus, dieta, lagoas costeiras, sudeste do Brasil.

A B S T R A C T. — We studied the diet of *Leptodactylus ocellatus* along three coastal lagoons in the Municipality of Anchieta, ES, Southeastern Brazil. Fifty-seven specimens were collected, ranging from 18.5 to 100.4 mm in snout-urostyle length. *Leptodactylus ocellatus* consumed a great variety of food items. Adult beetles were the most frequently consumed prey, followed by beetle larvae and ants. Termites were the numerically predominant food items, whereas orthopterans dominated the diet in terms of mass. The presence of vertebrates, including a conspecific individual, was observed in the diet of *L. ocellatus*. This frog's diet changed ontogenetically both in terms of prey type and prey size.

Key words: Leptodactylus ocellatus, diet, coastal lagoons, Southeastern Brazil.

INTRODUCTION

Most anurans are arthropodan generalists, and the composition of their diets depend mainly upon prey availability (Duellman and Trueb, 1994). Prey choice by anurans is usually much influenced by the size of species and/or individuals, and ontogenetic variations in diet composition within species are common (e.g. Woolbright and Stewart, 1987; Lima and Moreira, 1993; De Bruyn et al., 1996; Giaretta et al., 1998).

The family Leptodactylidae is the largest among the anurans with more than 800 species, in about 50 genera, including very small to very large species (Pough *et al.*, 1998). Leptodactylus ocellatus (L., 1758) is a relatively large leptodactylid (though of medium size for the genus) occurring throughout most of cisandean South America (Frost, 1985), usually near temporary or permanent ponds, streams, or marshes

(Heyer et al., 1990). In spite of its very wide distribution, relatively few ecological studies have been done regarding this species. Those studies have dealt mainly with aspects of reproduction and growth (Cei, 1948; Lima and Verani, 1984), behavior (Vaz-Ferreira and Gerhau, 1975), and food habits of tadpoles (Lajmanovich, 1994), juveniles (Lajmanovich, 1996) and adults (Strussmann et al., 1984). The latter two studies, carried out on an Argentinian floodplain and in Brazilian Amazonia, respectively, indicated that *L. ocellatus* has a very generalized diet, composed mainly by a wide variety of arthropodan taxa. Nevertheless, data on the food habits of this species are lacking for other South American biomes.

Herein some data is presented on the feeding habits and trophic ontogeny of *L. ocellatus* from three coastal lagoons in Espírito Santo state, Southeastern Brazil, within the Atlantic Forest biome.

MATERIAL AND METHODS

Fieldwork was carried out in three coastal lagoons in the municipality of Anchieta, Espírito Santo state, Southeastern Brazil: Barragem Norte, Lagoa de Mãe-Ba and Lagoa de Ubu, all located close to each other (20° 46'S, 40° 35'W). Lagoa de Mãe-Ba is the largest of the three, with the other two being about the same size. Barragem Norte is an artificial pond, built to receive iron ore powder from the locality of Germano, Minas Gerais state, through a water duct that stretches ca. 380 km. It has extensive vegetation at both the margins and inside (compared to the other two lagoons), which is repremainly by Typhadominguensis (Typhaceae), Nymphaea sp. (Nymphaeaceae), Eleocharis sp., and Lagenocarpus aff. rigidus (Cyperaceae). Typha aff. dominguensis is the domi-

nant species at both the Lagoa de Mãe-Ba and the Lagoa de Ubu. Those two lagoons, unlike Barragem Norte, are connected to the sea and formed by brackish water. The environment around the three lagoons is, for the most part, greatly disturbed and characterized by arbustive vegetation (locally called «capoeira») and Barragem Norte is also close to an eucalyptus plantation. Specific collection sites were the same throughout the study, each at the margin of one of the lagoons. Average monthly rainfall in the region of Anchieta is 1144 mm, with a monthly maximum of 194 mm and a monthly minimum of 43 mm (Moraes, 1974). Average monthly temperature during the period of study was 23.1°C.

Collections were conducted bimonthly, from November 1999 to September 2000. Frogs were collected by hand, mostly at the margins of the lagoons. Collections were made during one night each month, always between 20:00 and 22:00 h, with sampling effort being the same for each locality. Frogs collected were killed in 10% alcohol, and transferred to 10% formalin. After a week, the specimens were washed and preserved in 70% alcohol. Voucher specimens of *L. ocellatus* were deposited at the Museu de Biologia Prof. Mello Leitão (MBML 1241-2, 1245, 1942-3, 1946)

In the laboratory, frogs had their snout-urostyle length (SUL) measured with a caliper (to the nearest 0.1 mm). After those procedures, the animals were dissected and sexed. The stomachs of all frogs were removed, and all food items found were spread on a Petri dish and identified under a stereomicroscope. Prey were identified to Order, counted, and had their length measured with a caliper and their wet mass taken with a digital balance (0.1 mg precision). Frequency of occurrence, number of prey, and total prey mass were calculated for each prey category.

The relationship between the length of the largest prey item in the stomach and frog size (SUL) was tested using a simple regression analysis; for this analysis, we did not consider prey items that were too digested and/or fragmentary to have their original length estimated with reasonable accuracy. We also performed a cluster analysis (UPGMA; Krebs, 1989) based on the Euclidean distances in order to detect possible quantitative differences in the diet according to the size (SUL) range of frogs. Only the data on relative prey mass (log₁₀ transformed) were used in this analysis.

RESULTS

Fifty-seven specimens of *L. ocellatus* were collected, 44 of them at the Barragem Norte, seven at the Lagoa de Mãe-Ba and six at the Lagoa de Ubu. Frogs ranged from 18.5 to 100.4 mm in snout-urostyle length (SUL). Thirty-one specimens were males, 21 were females and five were juveniles whose sex could not be determined.

Of the 57 stomachs examined, only four (7.0%) were empty. Data on the diet of *L. ocellatus* at the study area are summarized in Table 1. *Leptodac*-

tylus ocellatus preyed upon a great variety of small animals, including vertebrates. The diet was dominated by arthropods, with adult beetles being the most frequently consumed food item, followed by beetle larvae, ants and cockroaches. Termites dominated the diet numerically (though only two frogs had eaten this prey type), followed by adult beetles. Crickets were the predominant items in terms of percentage of the total prey mass ingested. Among vertebrates, frogs, tadpoles and one small fish (Poecilia vivipara) were represented in the diet of L. ocellatus. The amphibians found in the stomachs were one Hyla albomarginata (SUL= 35.2 mm), one Physalaemus crombiei (SUL= 20.1 mm), a juvenile L. ocellatus (SUL= 23.1 mm), and three unidentified tadpoles. Number of individual prey per stomach varied from 1 to 25 (mean = 2.5 ± 3.8). Individual prey consumed varied in size from 1.5 to 35.2 mm. Maximum prey length was positively and significantly related to frog SUL ($R^2 = 0.59$, p < 0.05, N = 42).

The diet composition of L. occillatus varied among size (SUL) classes (Fig. 1). The smallest specimens (<30 mm; N = 32) fed on a wide variety of prey types, with beetle larvae, cockroaches and adult beetles comprising the bulk

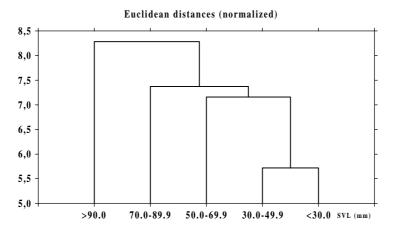


Fig. 1. Dendrogram representing the differences in diet composition (based on relative contribution in total prey mass for each prey category) among size classes of *Leptodactylus ocellatus* at Anchieta, Espírito Santo, Brazil.

of the diet. Diets of the remaining size classes were generally dominated (in terms of relative mass) by orthopterans, frogs and adult beetles.

DISCUSSION

Specimens of *L. ocellatus* representing a broad range of body sizes were collected throughout the period of study. Most individuals were collected at Barragem Norte, an artificial lagoon with a greater diversity of vegetation

than Lagoa de Mãe-Bá and Lagoa de Ubu. Probably, the denser vegetation around and within Barragem Norte provides a more adequate habitat for other anuran species and a variety of invertebrates, which are all potential prey for *L. ocellatus*, as well as a greater diversity of sheltering and reproducing sites for *L. ocellatus*. More importantly, Barragem Norte is a strictly freshwater «lagoon» whereas Lagoa de Mãe-Bá and Lagoa de Ubu contain brackish water. Considering the usual intolerance of salinity of

| PREY TYPE | F | %F | N | %N | M | %M |
|-------------------------|----|------|-----|-------|---------|-------|
| INSECTA | | | | | | |
| Blattodea | 8 | 14.8 | 9 | 8.3 | 685 | 3.8 |
| Coleoptera (adults) | 12 | 22.2 | 18 | 16.7 | 1890.1 | 10.5 |
| Diptera | 1 | 1.9 | 1 | 0.9 | 3.9 | < 0.1 |
| Hemiptera | | | | | | |
| Belostomatidae | 3 | 5.6 | 3 | 2.8 | 1236.7 | 6.8 |
| others | 1 | 1.9 | 1 | 0.9 | 9.2 | 0.1 |
| Hymenoptera (ants) | 9 | 16.7 | 12 | 11.1 | 61.8 | 0.3 |
| Isoptera | 2 | 3.7 | 22 | 20.4 | 1198.8 | 6.6 |
| Lepidopteran larvae | 1 | 1.9 | 5 | 4.6 | 1136.1 | 6.3 |
| Coleopteran larvae | 11 | 20.4 | 11 | 10.2 | 156 | 0.9 |
| Odonata | 1 | 1.9 | 1 | 0.9 | 595.8 | 3.3 |
| Orthoptera | 4 | 7.4 | 12 | 11.1 | 3906.3 | 21.6 |
| MYRIAPODA | | | | | | |
| Diplopoda | 2 | 3.7 | 2 | 1.9 | 1697.4 | 9.4 |
| ARACHNIDA | | | | | | |
| Araneae | 3 | 5.6 | 3 | 2.8 | 1370.7 | 7.6 |
| ANNELIDA | | | | | | |
| Oligochaeta | 1 | 1.9 | 1 | 0.9 | 217 | 1.2 |
| AMPHIBIA (ANURA) | | | | | | |
| Hyla albomarginata | 1 | 1.9 | 1 | 0.9 | 212.4 | 1.2 |
| Leptodactylus ocellatus | 1 | 1.9 | 1 | 0.9 | 1640.1 | 9.1 |
| Physalaemus crombiei | 1 | 1.9 | 1 | 0.9 | 1348.7 | 7.5 |
| Tadpoles | 2 | 3.7 | 3 | 2.8 | 165.6 | 0.9 |
| PISCES (TELEOSTEI) | | | | | | |
| Poecilia vivipara | 1 | 1.9 | 1 | 0.9 | 309 | 1.7 |
| OTHERS | | | | | | |
| Plant remains | 2 | 3.7 | - | - | 230.7 | 1.3 |
| Detritus | 5 | 9.3 | - | - | 10.8 | 0.1 |
| TOTAL | - | - | 108 | 100.0 | 18082.1 | 100.0 |

Table 1. Representativeness (in absolute numbers and percentages) of prey types found in the stomach contents of the frog *L. ocellatus* from three coastal lagoons of the Municipality of Anchieta, Espírito Santo, Brazil. F = frequency of occurrence; N = number of prey; M = mass of prey.

most amphibians, it is not surprising that *L. ocellatus* is much more abundant at Barragem Norte than at the other two lagoons.

Most of the food items ingested by L. ocellatus were terrestrial arthropods, especially insects, which are presumably captured by ambush at or near the margins of the lagoons. Aquatic insects such as belostomatid hemipterans were also present in the diet, but they could have been ingested on land (but see below). Terrestrial invertebrates usually dominate the diets of most anurans, and may be well represented even in the diets of some species which are largely aquatic in habits or are strongly associated with water (e.g. Stewart and Sandison, 1972; De Bruyn et al., 1996; Measey, 1998; Hirai and Matsui, 1999), which is the case of L. ocellatus. Diet of L. ocellatus from Anchieta was similar to that reported for conspecific populations studied by Lajmanovich (1996) and Strussmann et al. (1984); in those works, as in ours, diet was based on a wide variety of arthropods with beetles, orthopterans, spiders and ants generally comprising a significant part of it.

Like other large and medium-sized congeners (e.g. L. labyrinthicus - Cardoso & Sazima, 1977; L. pentadactylus and L. wagneri - Duellmann, 1978; L. chaquensis - Duré, 1999), L. ocellatus occasionally preys on smaller vertebrates, including anurans (Haddad and Sazima, 1992; this study). Curiously, among the anurans we found in the diet of L. ocellatus from Anchieta was Hyla albomarginata (Hylidae), an arboreal hylid. Since L. ocellatus is strictly ground-dwelling, the ingestion of arboreal frogs by this species may occur when they descend to the ground to mate and lay eggs. On a number of occasions, the senior author (pers. obs.) witnessed events of predation of H. albomarginata by L. ocellatus, all of them occurring when the hylid was on

the ground and approaching the margin of the lagoon, presumably for breeding purposes. A conspecific juvenile was also found among the stomach contents of *L. ocellatus*, indicating that cannibalism may not be uncommon in this species. Large leptodactylids are opportunistic feeders, and conspecific eggs and juveniles seem to represent just another available food source for such voracious predators (Crump, 1992; Duellman and Trueb, 1994).

It is interesting that L. ocellatus may include fully aquatic prey such as fishes and tadpoles in its diet, which suggests that it may occasionally forage on the water. During fieldwork, the senior author observed several dead Poecilia vivipara at the Barragem Norte, and many other specimens agonizing on the water surface (possibly due to iron ore contamination). We do not have evidence that L. ocellatus preys on dead fish (necrophagy), but agonizing fish may represent an easily obtainable food resource for opportunistic predators, and the senior author observed several specimens of waterbugs (Belostomatidae) feeding on dead fish.

In frog species for which there is an accentuated difference in size between juvenile and adult stages, trophic ontogeny becomes an important tool in promoting the partitioning of available food resources, since individuals in all developmental stages often share the same area. Metamorphosing L. ocellatus are detritivorous, whereas juveniles are arthropod generalists, and adults consume a broad spectrum of food items, including small vertebrates (Lajmanovich, 1994; 1996; this study). Diet composition of L. ocellatus varied with frog size both in terms of prey type and prey size, with maximum prey length being positively related to frog SUL. A positive relationship between prey size and frog body size or gape width has been reported for juvenile L. ocellatus in Argentina (Lajmanovich, 1996), as well as for many other frog species of various sizes (e.g. Duellman and Lizana, 1994; Giaretta et al., 1998; Hirai and Matsui, 1999; Duré and Kehr, 2001; Van Sluys et al., 2001). Frogs, in general, are gape-limited predators that swallow their prey whole, and such predators are expected to select prey mainly by size rather than by type (Toft, 1985). However, prey size selection may indirectly lead to prey type selection, since the mean size of individuals tend to differ among potential prey categories (Pengilley, 1971; Lima, 1998). In the present study, for instance, frogs and orthopterans (which tend to be relatively large prey items) were consumed only by L. ocellatus larger than 50 mm and larger than 30 mm, respectively. Conversely, ants (which are usually small prey items) were found only in the diet of specimens in the smallest size class (i.e. < 30 mm SUL). In his study of the diet of juvenile L. ocellatus in Argentina, Lajmanovich (1996) also found ants only in the stomachs of individuals under 30 mm, whereas the consumption of orthopterans was considerably greater in individuals over 30 mm. Thus, the ontogenetic shift in diet with regard to both prey type and prey size observed in our study is not surprising. In the study of Strussmann et al. (1984), on the other hand, ants were the most frequent and numerous items in the diet of L. ocellatus from an Amazonian locality, even though only frogs > 70 mm were examined; nevertheless, ants were not considerably more frequent in stomachs than other items such as coleopterans and orthopterans, and their consumption was less than expected considering their local availability in the habitat.

The present study evidences the opportunistic feeding behaviour of L. ocellatus which may partially account for the relative commonness of this species in anthropically altered envi-

ronments such as that of the Barragem Norte lagoon. Also, this voracious predator may have some negative impact on populations of other sympatric anurans.

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