Diet, Fecundity, and Use of Bromeliads by *Phyllodytes luteolus* (Anura: Hylidae) in Southeastern Brazil

Diet, Fecundity, and Use of Bromeliads by *Phyllodytes luteolus* (Anura: Hylidae) in Southeastern Brazil

Rodrigo B. Ferreira,[1,2,3] José A. P. Schineider,[2] and Rogério L. Teixeira[2]

[1]*Department of Wildland Resources and Ecology Center, Utah State University, Logan, Utah 84322–5230 USA*
[2]*Museu de Biologia Prof. Mello Leitão, Av. José Ruschi, 4, Centro, CEP 29650–000, Santa Teresa, Espírito Santo, Brazil*

Abstract.—This study explores the feeding ecology, habitat use, and fecundity of *Phyllodytes luteolus* inside bromeliads in the restinga of Regência (sandy coastal plain), Espírito Santo state, southeastern Brazil. Because bromeliads are harvested for commercial use, and frogs may be collected accidently, the ecology of this frog is of particular interest. We collected 363 individuals of *P. luteolus* (103 tadpoles, 74 juveniles, 64 males, and 122 females) from three species of bromeliads in a 4-km² area bimonthly from February to December of 1998. Ants and termites were the dominant food items in terms of number and mass over time. The percentage of prey items and the size of prey eaten by juveniles differed significantly from those of adults. Dominant prey items were relatively similar across the sampled bromeliad species and locations. *Phyllodytes luteolus* preferred *Vriesea procera*, the most-complex bromeliad in our study site. Half of the individuals were found in bromeliads located in transitional zones. Female *P. luteolus* were slightly larger than the males, which may have determined the strong sex ratio bias toward females. We found females with developed oocytes (range 11–15) in every sampled month, indicating a protracted spawning period. This frog can be considered an active forager and specialist, feeding preferentially on colonial insects. *Phyllodytes luteolus* uses several species of harvested bromeliads and possesses several attributes that could facilitate its success as an invasive species.

Phyllodytes luteolus occurs in hill and plain regions of Brazil from Minas Gerais and Espírito Santo to Paraíba (Feio and Caramaschi, 2002; Vrcibradic et al., 2006). Recently, Salles and Silva-Soares (2010) reported the introduction of this species to Rio de Janeiro municipality due to the trade of bromeliads. In the State of Espírito Santo, *P. luteolus* is considered a common species inside bromeliads (Weygoldt, 1981; Teixeira et al., 1997), but natural history information for this frog is scarce and no research has been conducted on its feeding habits. Without biological and ecological knowledge on *P. luteolus*, we are poorly equipped to identify causes for a potential population decline (Papp and Papp, 2000) or the possible impacts of this species on native species.

This hylid genus depends on bromeliad axils for refuge, breeding, egg laying, larval development (Teixeira et al., 1997; Caramaschi et al., 2004), and possibly foraging. Their dependence on bromeliads to complete their life cycle categorizes these species as bromeligenous (Peixoto, 1995). In this microhabitat, females of *P. luteolus* lay one to three eggs per axil, on multiple bromeliads, at intervals of a few days (Bokermann, 1966; Weygoldt, 1981). Fecundity is generally positively correlated with female size (Duellman and Trueb, 1994). In 90% of anurans, females are larger than males (Shine, 1979); in *P. luteolus*, however, the genders have similar body sizes (Giaretta, 1996), which may be due to territorial disputes for bromeliads.

Bromeliads are structurally complex plants that offer ideal microhabitats for their animal communities (Silva et al., 2010). Eterovick (1999) and Schineider and Teixeira (2001), however, reported no association of *P. luteolus* occupancy with bromeliad physical features such as height from the ground, axil width, pH, and water volume.

The microhabitat where a frog resides affects its diet, its foraging ability, prey palatability, and prey size (Duellman and Trueb, 1994; Giaretta et al., 1998; Attademo et al., 2005). Root (1967) suggested that there are three separate guilds of anurans in terms of feeding habits: ant specialists, nonant specialists, and generalists. Hylids are often recognized as generalists, which is common in frogs with a small feeding territory that base their diet on availability of prey (Houston, 1973; Blackith and Speight, 1974; Hirai and Matsui, 1999).

In this paper, we explore the following topics: (1) the feeding habits of *P. luteolus*; (2) the occurrence of seasonal ontogeny and sexual differences in diet; (3) the influences of vegetation zone on *P. luteolus* diet; (4) the spatial distribution of *P. luteolus*; and (5) the average fecundity of females.

Materials and Methods

Study Area.—Research was conducted in the restinga of Regência (sandy coastal plain), Linhares, northeastern Espírito Santo State (19°39′S, 39°51′W) near the Biological Station of Comboios, southeastern Brazil. The soil is sand of fluvial–marine origin (Suguio and Martin, 1982). The high permeability of the sandy soil, together with the proximity to the ocean, creates a xeric landscape where species of bromeliads, cacti, and shrubby vegetation dominate. The vegetation is organized in patches of different sizes encircled by open areas (Henriques et al., 1986; Araújo, 1992). The vegetation in the area is relatively preserved and open, similar to the open formation of *Clusia* described at the restinga of Setiba in the Municipality of Guarapari, Espírito Santo (Assis et al., 2004). The weather is hot and wet, with a dry season between April and October and a wet season between November and March (Panoso et al., 1978). Mean annual temperature ranges from 22°C to 24°C and mean annual precipitation varies between 1,000 and 1,250 mm (Nimer, 1989).

Samples.—Specimens of *P. luteolus* were collected bimonthly from February to December 1998, from 0800 to 1700 h. Because bromeliads occur in small islands (groups of several individuals) spread through the restinga habitat, our sampling effort was designed to collect a few plants in each small island within a selected 4-km² plot. Three of the most abundant bromeliad species were sampled in each island: *Aechmea blanchetiana* ($N = 303$), *Aechmea nudicaulis* ($N = 287$), and *Vriesea procera* ($N = 86$). Bromeliad zones were defined as open areas (totally exposed to the sun), transitional zones (between open areas and trees), under trees, and epiphytic plants. Bromeliads were cut off at the lowest possible point and immediately shaken upside-down over a plastic box to remove any frogs from the bromeliad axils. Collected frogs were then euthanized with 10% ethanol solution and transferred to 10% formalin for fixation. To interrupt further digestion of prey items, formalin was also injected into the body cavity. After a week, frogs were washed and preserved in 70% ethanol. Frogs were then dissected to determine sex and to extract the stomachs. Prey
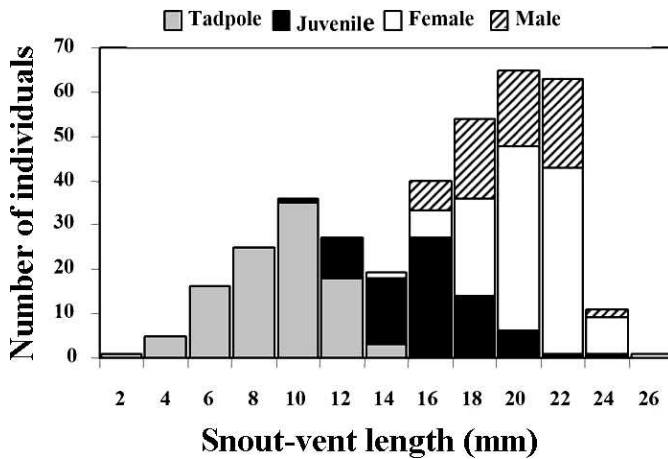
Fig. 1.   Snout–vent length distribution of *Phyllodytes luteolus*.

items were identified to order and counted. Prey were placed on absorbent paper to remove excess liquid and weighed to determine wet biomass (0.1 mg precision). Intact prey were measured with Vernier calipers (0.01-mm precision). Food items were quantified using frequency and number of prey.

Tadpoles collected were euthanized with 5% ethanol and preserved in the same solution. Tadpoles were not analyzed. Voucher specimens were deposited at the zoological section of the Museu de Biologia Prof. Mello Leitão (MBML 1322 and 4720–4732) located in Santa Teresa–ES, southeastern Brazil.

Statistical Procedures.—A chi–square test (χ^2) was used to compare the sex ratio to an expectation of 1 : 1. A Spearman rank correlation coefficient (r_s) was used to analyze similarity in abundance of the prey taxonomic classes compared (1) among sexes, (2) over time, (3) between bromeliad species, and (4) between bromeliad locations. Accidental, irregular food items, such as those representing less than 5% of total food, were not included in the analyses as suggested by Fritz (1974).

Prey sizes were compared separately for sexes and months using a one-way analysis of variance (ANOVA). Sex and month were the independent variables and size of the prey was the dependent variable. Bartlett's test was used a priori to

assess homogeneity of variances. The Kolmogorov-Smirnov test was used to assess normality. When there were significant differences between groups (e.g., months), the Schéffè test was used a posteriori because of unequal sample size (Neter et al., 1990). Cluster analyses (UPGMA) based on the Euclidian distances (Deza and Deza, 2009) were used to analyze trophic ontogeny. Means are given ±1 SD. All statistical procedures were performed with the software XLSTAT (Version 2006, Addinsoft Corp.) and Microsoft Excel (Version 2007, Microsoft Corp., Edmonds, WA).

RESULTS

We collected 363 *P. luteolus* and also detected the presence of eight *Scinax alter*, seven *Aparasphenodon brunoi*, one *Gastrotheca fissipis*, one *Leptodacylus fuscus*, and two *Rhinella granulosa*. Of the 363 specimens of *P. luteolus*, 103 were tadpoles (snout–vent length [SVL] range = 1.0 to 13.5 mm; mean = 8.3 ± 2.4 mm; Fig. 1), 74 were juveniles (SVL range = 10.0 to 22.0 mm; mean = 15.2 ± 2.4 mm), 64 were adult males (SVL range = 15.0 to 23.0 mm; mean = 18.9 ± 1.9 mm), and 122 were adult females (SVL range = 13.0 to 24.0 mm; mean = 19.7 ± 1.9 mm). The sex ratio was 1.0 : 1.9 with a strong female bias (χ^2_1 = 18.09, P < 0.001).

We found that 49.6% of *P. luteolus* specimens in bromeliads were located in transitional zones, 28.9% were in epiphytes, 17.7% were in open areas, and 3.8% were in bromeliads under trees. Of the 363 specimens, 104 were collected in *A. blanchetiana* (relative frequency of occurrence [FO] per bromeliad [% FO] = 47.5), 85 were in *V. procera* (% FO = 98.8), and 31 were in *A. nudicaulis* (% FO = 10.8).

We analyzed stomach contents from all 260 juveniles and adults. Of these, 243 stomachs contained food. Stomach contents were classified into three invertebrate groups (Insecta, Arachnida, and Mollusca) and 19 food categories (Table 1). Ants were the predominant prey in terms of number (61.7%) and mass (58.6%). Araneae, Diptera, and Odonata larvae were found in low numbers (Table 1).

The percentage of main and secondary prey items eaten by juveniles differed slightly from that of adult males and females (Table 1). There was no correlation in the type of prey items between juveniles and adult males (r_s = 0.31; df = 10; t_s = 1.04;

TABLE 1.   Percentage of ingested food of *Phyllodytes luteolus* for different genders and the total number of prey (% *N*) and prey wet weight (% W).

| Food items	Male	Female	Juvenile	% N	% W
Insecta					
Hymenoptera (Formicidae)	54.3	55.3	73.1	61.7	58.6
Isoptera	37.8	38.2	21.5	32.4	34.7
Coleoptera (Elateridae)	1.3	1.1	–	0.3	1.0
Coleoptera (Curculionidae)	1.3	0.2	–	0.2	0.5
Coleoptera (larvae)	–	<0.1	–	0.1	0.1
Other Coleoptera	2.5	3.3	1.6	2.0	2.7
Dyctioptera	1.0	0.1	–	0.1	0.4
Homoptera	0.4	0.1	0.1	0.2	0.2
Hemiptera	0.1	<0.1	0.1	0.1	0.1
Orthoptera	0.1	0.2	<0.1	0.2	0.1
Odonata (larvae)	–	0.1	<0.1	0.1	0.1
Diptera (adults)	0.1	–	0.2	0.1	0.1
Diptera (larvae)	–	<0.1	–	0.1	0.1
Lepidoptera (larvae)	–	0.1	0.9	0.1	0.2
Unidentified larvae	–	–	0.2	0.1	0.1
Arachnida					
Araneae	0.5	0.8	0.8	0.3	0.7
Pseudoscorpiones	0.3	0.1	–	0.2	0.1
Acarina	0.1	<0.1	0.6	1.5	0.1
Mollusca					
Gastropoda	–	–	<0.1	0.1	0.1
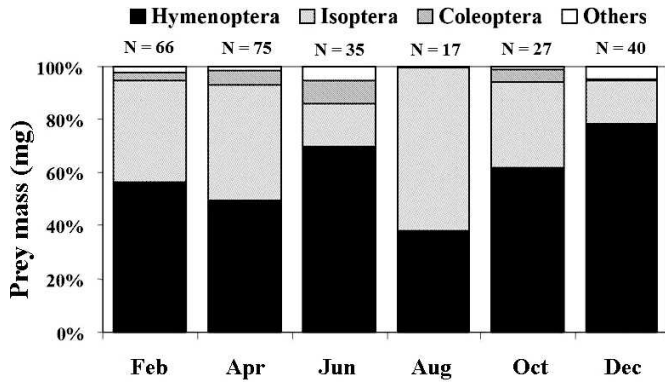
FIG. 2. Relative weight of main prey items of *Phyllodytes luteolus* over time.

$P = 0.32$) or between juveniles and adult females ($r_s = 0.49$; df $= 10$; $t_s = 1.80$; $P = 0.1020$). Males and females did not differ in their diets ($r_s = 0.83$; df $= 10$; $t_s = 4.74$; $P = 0.01$).

In terms of relative weight of the main prey items, ants were the dominant prey in most months but termites were the dominant prey in August (Fig. 2). There were no significant correlations in the type of prey of *P. luteolus* between most of the sampled months (Table 2).

Dominant prey items were relatively similar across the sampled bromeliad species (Table 3) and among bromeliad locations (Table 4).

There were significant differences in the diet composition according to SVL (Fig. 3). Cluster analysis suggested that two distinct size classes preyed on different food types. Specimens smaller than 18.0 mm fed mainly on ants, whereas larger specimens (>18.0 mm) fed mainly on termites.

Intact prey found in the stomach contents varied in size from 0.9 to 9.0 mm (mean = 2.96 mm; SD = 1.02). In juveniles, the length of prey varied from 0.9 to 5.2 mm (mean = 2.62 mm; SD = 0.96), in males from 0.9 to 7.8 mm (mean = 3.04 mm; SD = 0.96), and in females from 1.0 to 9.0 mm (mean = 3.13 mm; SD = 1.04). The size of prey eaten by juveniles differed significantly from that of adult males and females (ANOVA: $F_{2,997} = 23.37$; $P < 0.01$). Prey size did not differ between months (ANOVA: $F_{5,997} = 1.65$; $P = 0.14$). Prey size was positively correlated with frog SVL (Fig. 4). Mean size of prey differed significantly among some SVL classes (ANOVA: $F_{6,997} = 15.60$; $P < 0.01$), which is also evident using a posteriori Schéffè tests (Table 5). Mean size of prey did not differ among classes below 16 to 17.9 mm but increased strongly in larger SVL classes.

Females had ovaries with well-developed oocytes in every sampled month (Table 6). The mean number of oocytes found in the ovaries varied by month from 11 to 15 and, in total, from 4 to 28. However, the number of female specimens found in bromeliads decreased from winter to summer. Calling males and tadpoles were found throughout the year.

DISCUSSION

Phyllodytes luteolus can be classified as a specialist in feeding on colonial insects, based on the number and biomass of ants and termites in their stomachs throughout the sampled months. Additional evidence of specialized feeding is the presence of ants and termites as the main prey for juveniles, males, and females. In addition to ants, Coleoptera and Diptera are the most abundant fauna inside bromeliads in the Brazilian Atlantic Rainforest (Mestre et al., 2001; Juncá and Borges, 2002; Sepka, 2008). We found a higher abundance of ants in the diet of *P. luteolus* relative to these other studies. This contrast supports our inferences about the feeding habits of *P. luteolus*.

TABLE 2. Spearman rank correlation coefficient based on prey type of *Phyllodytes luteolus* in different months. r_s = Spearman rank correlation coefficient; t_s = statistic for the test of H_0; $r_s = 0$; df $= 10$ in each case; * denotes statistical significance; ** highly significant.

Months	February	April	June	August	October
April	$r_s = 0.57$; $t_s = 0.21$; $P = 0.0509$	–	–	–	–
June	$r_s = 0.79$; $t_s = 4.09$; $P = 0.0021^{**}$	$r_s = 0.71$; $t_s = 3.23$; $P = 0.0089^{**}$	–	–	–
August	$r_s = 0.59$; $t_s = 2.36$; $P = 0.0394^{*}$	$r_s = 0.68$; $t_s = 2.96$; $P = 0.0142^{**}$	$r_s = 0.59$; $t_s = 2.36$; $P = 0.3946$	–	–
October	$r_s = 0.64$; $t_s = 2.67$; $P = 0.0232^{*}$	$r_s = 0.80$; $t_s = 4.33$; $P = 0.0014^{**}$	$r_s = 0.56$; $t_s = 2.15$; $P = 0.0570$	$r_s = 0.84$; $t_s = 5.06$; $P = 0.0004^{**}$	–
December	$r_s = 0.24$; $t_s = 0.79$; $P = 0.4452$	$r_s = 0.74$; $t_s = 3.56$; $P = 0.0051^{**}$	$r_s = 0.43$; $t_s = 1.50$; $P = 0.1628$	$r_s = 0.54$; $t_s = 2.07$; $P = 0.0645$	$r_s = 0.45$; $t_s = 1.63$; $P = 0.1337$

TABLE 3. Spearman rank correlation coefficient based on the diet in different bromeliads used by *Phyllodytes luteolus*. r_s = Spearman rank correlation coefficient; t_s = statistic for the test of H$_0$: r_s = 0; df = 10 in each case; * denotes statistical significance.

Bromeliads	*A. blanchetiana*	*A. nudicaulis*
A. nudicaulis	r_s = 0.63; t_s = 2.63; P = 0.0251*	–
V. procera	r_s = 0.58; t_s = 2.30; P = 0.0436*	r_s = 0.49; t_s = 1.79; P = 0.1034

TABLE 4. Spearman rank correlation coefficient based on the diet in different places where bromeliads were collected having *Phyllodytes luteolus*. r_s = Spearman rank correlation coefficient; t_s = t statistic for the test of H$_0$: r_s= 0; df = 10 in each case; * denotes statistical significance; 1 = bromeliads in open areas; 2 = bromeliads in transitional zones (between open areas and under the trees); 3 = bromeliads under trees; 4 = epiphytic bromeliads.

Bromeliads	1	2	3
2	r_s = 0.70; t_s = 3.09; P = 0.0112*	–	–
3	r_s = 0.41; t_s = 1.43; P = 0.1819	r_s = 0.59; t_s = 2.34; P = 0.0406*	–
4	r_s = 0.66; t_s = 2.79; P = 0.0190*	r_s = 0.49; t_s = 1.81; P = 0.0999	r_s = 0.65; t_s = 2.72; P = 0.0212*

Ferreira and Teixeira (2009) suggested that specialization on colonial arthropods is a great advantage for anurans, primarily because these invertebrates comprise approximately 70% of the animal biomass in the tropical forests (Hölldobler and Wilson, 1990). Furthermore, ants are unpalatable to many predators because of formic acid (Zug and Zug, 1979), conferring certain advantages to ant specialists by reducing food competition with other insectivores (Ferreira and Teixeira, 2009).

Ecologically, *P. luteolus* fits well with Toft's (1980, 1981) characterization of an active predator: they eat preferentially small prey and have a high number and mass of ants in their stomach. Sit-and-wait foragers are rarely successful in capturing ants (Toft, 1980). The flat leaves of bromeliads are ineffective hiding spots for invertebrates; this may encourage the invertebrates to remain hidden inside axils and may favor the active habits of *P. luteolus*.

Phyllodytes luteolus most likely feeds exclusively on autochthonous prey; first, because this frog carries out its entire life cycle inside bromeliads (Teixeira et al., 1997; Eterovick, 1999), and second because the main prey category is largely encountered in bromeliads throughout the year (Wittman, 2000; Mestre et al., 2001; Sepka, 2008). Diptera, contrary to its reported abundance in bromeliads, was not significant in *P. luteolus*' stomach contents, indicating that this frog may not act as a biological control agent for diseases carried by this insect vector.

Due to the configuration of the axils, bromeliads may confer a certain advantage to their inhabitants in terms of protection against outside predators. On the other hand, the food web in this ecosystem does not ensure total safety for *P. luteolus* because common inhabitants of bromeliads, such as arachnids and odonate larvae, feed on frogs (see Hödl, 1990; Duellman and Trueb, 1994; Kwet, 1999). These predators may drastically affect the success of larval anurans (Menin et al., 2005). Because we found odonate larvae and arachnids in the *P. luteolus* diet, we suggest that the size and life stage of the individuals involved in this interaction determine which taxon will be the predator.

The interaction of *P. luteolus* with its prey and with outside predators might be driving this frog to choose *V. procera*, which possess the highest number of axils in our study site. A different *P. luteolus* population, approximately 65 km away from our study site, was also found more frequently inside *Vriesea* sp. than in *A. nudicaulis* or *A. blanchetiana* (Eterovick, 1999). Contrary to Babbitt and Jordan (1996), who stated that the effective success of the predator increases according to increases in habitat complexity, we suspect that in small ecosystems, such as bromeliads, the opposite process might be occurring where outside predators decrease their success according to increases in bromeliad complexity. A more-complex habitat, however, harbors a larger variety and abundance of organisms (Srivastava and Lawton, 1998), which also might favor the bromeligenous feeding specialist *P. luteolus* by encouraging a wide spectrum of potential prey.
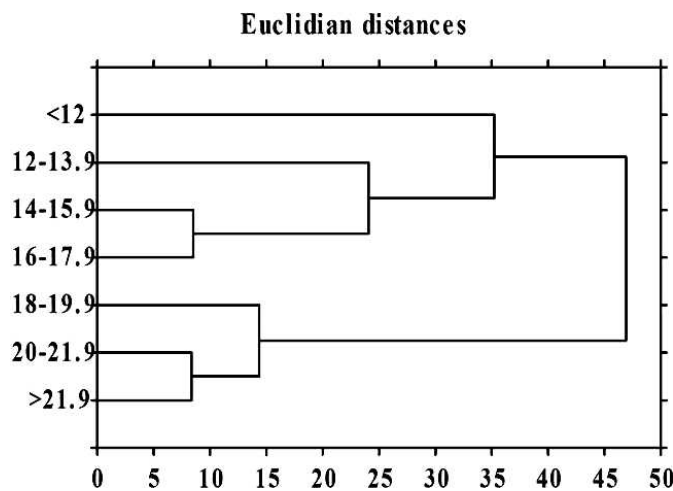

FIG. 3. Dendogram of similarities of main prey items according to size classes of *Phyllodytes luteolus*.
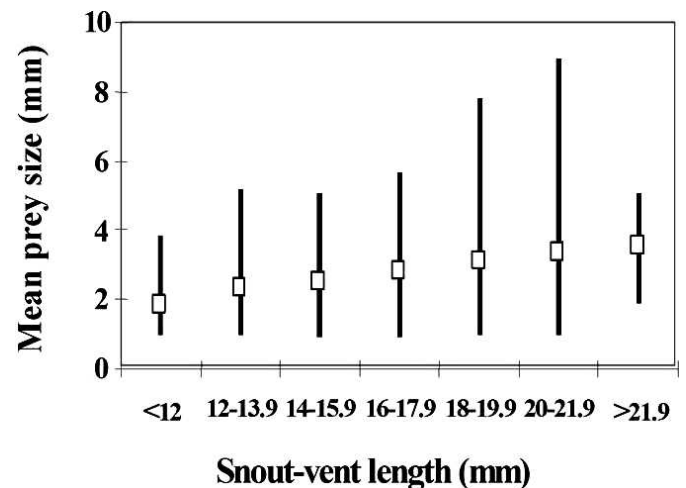

FIG. 4. Mean prey size according to size classes of *Phyllodytes luteolus*. Rectangle = mean prey size; vertical lines = prey size amplitudes.

TABLE 5. Probabilities of the Schéffè a posteriori test showing differences in prey size according to SVL classes of *Phyllodytes luteolus*. * significant; ** highly significant.

SVL	<12	12–13.9	14–15.9	16–17.9	18–19.9	20–21.9
12–13.9	0.9860	–	–	–	–	–
14–15.9	0.9380	0.9889	–	–	–	–
16–17.9	0.5632	0.0241*	0.0548	–	–	–
18–19.9	0.3704	0.0006**	0.0007**	0.7665	–	–
20–21.9	0.1430	0.0001**	0.0001**	0.0015**	0.2783	–
>21.9	0.0822	0.0001**	0.0001**	0.0633	0.3801	0.9751

TABLE 6. Mean fecundity of *Phyllodytes luteolus*. Min = minimum number of oocytes; Max = maximum number of oocytes; SD = standard deviation; MO = females having mature oocytes; IO = females having immature oocytes; N = total number of females.

Months	Mean	Min	Max	SD	MO	IO	N
February	14.4	4	28	6.91	25	12	37
April	14.5	8	22	3.80	27	30	57
June	12.7	6	16	4.57	4	11	15
August	12.0	12	12	–	1	1	2
October	11.0	9	12	1.41	4	1	5
December	15.0	15	15	–	1	5	6

Our results show differences in prey size according to the size classes of *P. luteolus*, suggesting resource partitioning between juveniles and adults. Such a process might be favoring coexistence in the same plant. Change in diet with ontogeny has been related to changes in selection for the type or size of prey (Simon and Toft, 1991; Lima, 1998). Another indication of resource partitioning is the fact that different stages of *P. luteolus* tend to segregate spatially inside the same plant (RBF, pers. obs.). Giaretta (1996) reported similar results by demonstrating that juveniles occupied only leaves at the base of bromeliads while adults, eggs, and tadpoles occurred at the central portion of the plant where water fills the axils.

The strong sex ratio bias toward females in our study site might have been influenced by the slightly larger size of females and suggests that intersexual dispute for access to bromeliads might occur in this frog. Wells (1978) predicted that territoriality is generally associated with similar mean size between males and females. Other studies on *P. luteolus* also found that males were nearly the same size as females (Giaretta, 1996; Teixeira et al., 1997; Eterovick, 1999). This type of interaction has been reported for different populations of *P. luteolus* males (Weygoldt, 1981). The fact that Teixeira et al. (1997) found that 65% of analyzed bromeliads were occupied by only one male or female presents additional evidence of intraspecific territorial competition. Therefore, resource partitioning does not seem to occur between adults of *P. luteolus*.

Larger females of *P. luteolus* had higher fecundity. Even so, as also noticed by Giaretta (1996), *P. luteolus* has a low fecundity compared to most hylid species (Prado and Haddad, 2005). Perhaps the investment in reproducing throughout the year might be the reason for reduced fecundity in *P. luteolus*. The adoption of long-term reproduction seems to be a successful strategy, based on the high abundance of *P. luteolus* in restingas. Although restinga habitat normally has little water, bromeliads are efficient in storing water, which allows this hylid frog to spawn at any time of the year. Another successful reproductive adaptation is the tendency of females to lay only one egg per bromeliad axil, reducing competition for food and space and cannibalistic oophagy by tadpoles (Weygoldt, 1981; Giaretta, 1996).

Phyllodytes luteolus is the most abundant anuran found in bromeliads of Regência. Several previous studies have demonstrated similar results in other restinga habitats (Giaretta, 1996; Teixeira et al., 1997; Eterovick, 1999). In Regência, *P. luteolus* was present mainly in bromeliads of transitional zones, e.g., between open areas and under trees. Vegetation of the restinga is related to temperature, salinity, and sun exposure (Ormond, 1960). These abiotic factors might be less intense in transitional zones, which might explain the preference for this zone by *P. luteolus*. This frog can also be encountered in other sun-exposure zones, being considered a species that can tolerate modified environments (Eterovick, 1999). Specialized feeding behavior on the most abundant invertebrates, and the protracted spawning period, are additional elements that contribute to the success of this bromeligenous frog. Because this species has several characteristics of successful invasive frogs, and uses a variety of harvested bromeliad species, we recommend that trade of bromeliads should be regulated to control the potential spread of *P. luteolus*.

LITERATURE CITED

ARAÚJO, D. S. D. 1992. Vegetation types of sandy coastal plains of tropical Brazil: a first approximation. *In* U. Seelinger (ed.), Coastal Plant Communities of Latin America, pp. 337–347. Academic Press, San Diego.

ASSIS, A. M., O. J. PEREIRA, AND L. D. THOMAZ. 2004. Fitossociologia de uma floresta de resting no Parque Estadual Paulo César Vinha, Setiba, município de Guarapari (ES). Revista Brasileira de Botânica 27:349–361.

ATTADEMO, A. M., P. M. PELTZER, AND R. C. LAJMNOVICH. 2005. Amphibians occurring in soybean and implications for biological control in Argentina. Agriculture, Ecosystems and Environment 106:389–394.

BABBITT, K. J., AND F. JORDAN. 1996. Predation on *Bufo terrestris* tadpoles: effects of cover and predator identity. Copeia 1996:485–488.

BLACKITH, R. M., AND M. C. D. SPEIGHT. 1974. Food and feeding habits of the frog *Rana temporaria* in bogland habitats in the west of Ireland. Journal of Zoology (London) 172:67–79.

BOKERMANN, W. C. A. 1966. O gênero *Phyllodytes* Wagler, 1830 (Anura, Hylidae). Anais da Academia Brasileira de Ciências 38:335–344.

CARAMASCHI, U., O. L. PEIXOTO, AND M. T. RODRIGUES. 2004. Revalidation and redescription of *Phyllodytes wuchereri* (Peters, 1873) (Amphibia, Anura, Hylidae). Arquivos do Museu Nacional Rio de Janeiro 62:185–191.

DEZA, E., AND M. M. DEZA. 2009. Encyclopedia of Distances. Springer-Verlag, Berlin.

DUELLMAN, W. E., AND L. TRUEB. 1994. Biology of Amphibians. Johns Hopkins University, Baltimore.

ETEROVICK, P. C. 1999. Use and sharing of calling and retreat sites by *Phyllodytes luteolus* in modified environment. Journal of Herpetology 33:17–22.

FEIO, R. N., AND U. CARAMASCHI. 2002. Contribuição ao conhecimento da herpetofauna do nordeste do estado de Minas Gerais, Brazil. Phyllomedusa 1:105–111.

FERREIRA, R. B., AND R. L. TEIXEIRA. 2009. Feeding patterns and use of reproductive habitat of the Striped Toad *Rhinella crucifer* (Anura: Bufonidae) from Southeastern Brazil. Acta Herpetologica 4:125–134.

FRITZ, E. S. 1974. Total diet comparison in fishes by Spearman rank correlation coefficient. Copeia 1974:210–214.

GIARETTA, A. A. 1996. Reproductive specializations of the bromeliad hylid frog *Phyllodytes luteolus*. Journal of Herpetology 30:96–97.

GIARETTA, A., M. S. ARAÚJO, H. F. MEDEIROS, AND K. G. FACURE. 1998. Food habits and ontogenetic diet shifts of the litter dwelling frog *Proceratophrys boiei* (Wied). Revista Brasileira de Zoologia 15:385–388.

HENRIQUES, R. P. B., D. S. D. ARAUJO, AND J. D. HAY. 1986. Descrição e classificação dos tipos de vegetação da restinga de Carapebus, Rio de Janeiro. Revista Brasileira de Botânica 9:173–189.

HIRAI, T., AND M. MATSUI. 1999. Feeding habits of the pond frog *Rana nigromaculata*, inhabiting rice fields in Kyoto, Japan. Copeia 1999:940–947.

HÖDL, W. 1990. Reproductive diversity in Amazonian lowland frogs. Fortschritte der Zoologie 38:41–60.

HÖLLDOBLER, B., AND E. O. WILSON. 1990. The Ants. Harvard University Press, Cambridge, Massachusetts.

HOUSTON, W. W. K. 1973. The food of the common frog, *Rana temporaria*, on high moorland in northern England. Journal of Zoology (London) 171:153–165.

JUNCÁ, F., AND C. L. S. BORGES. 2002. Fauna associada a bromélias terrícolas da Serra da Jibóia, Bahia. Sitientibus Série Ciências Biológicas 2:73–81.

KWET, A. 1999. Die Pfeiffrösche im Araukarienwald–schutzgebiet Pró–Mata. Elaphe 7:92–100.

LIMA, A. P. 1998. The effects of size on the diet of six sympatric species of postmetamorphic litter anurans in Central Amazonia. Journal of Herpetology 32:392–399.

MENIN, M., D. J. RODRIGUES, AND C. S. AZEVEDO. 2005. Predation on amphibians by spiders (Arachnida, Araneae) in the Neotropical region. Phyllomedusa 4:39–47.

MESTRE, L. A. M., J. M. R. ARANHA, AND M. L. P. ESPER. 2001. Macroinvertebrate fauna associated to bromeliad *Vriesea inflata* of the Atlantic Forest (Paraná State, south Brazil). Brazilian Archives of Biology and Technology 44:89–94.

NETER, J., W. WASSERMAN, AND M. H. KUTNER. 1990. Applied Linear Statistical Models: Regression, Analysis of Variance, and Experimental Designs. Irwin, Homewood, Illinois.

NIMER, E. 1989. Climatologia do Brasil. IBGE, Rio de Janeiro, Brasil.

ORMOND, W. T. 1960. Ecologia das restingas do sudeste do Brasil: comunidades vegetais das praias arenosas. Parte I. Arquivos do Museu Nacional Rio de Janeiro 50:185–236.

PANOSO, L. A., I. A. GOMES, A. M. PIRES–FILHO, AND S. BONELLI. 1978. Levantamento de reconhecimento dos solos do Estado do Espírito Santo. Embrapa Boletim Técnico 45:461.

PAPP, M. G., AND C. O. G. PAPP. 2000. Decline in a population of the treefrog *Phyllodytes luteolus* after fire. Herpetogical Review 3:93–95.

PEIXOTO, O. L. 1995. Associação de anuros a bromeliáceas na mata Atlântica. Revista da Universidade Rural Série Ciências da Vida 17:75–83.

PRADO, C., AND C. F. B. HADDAD. 2005. Size-relationships and reproductive investment in female frogs in the Pantanal, southwestern Brazil. Herpetological Journal 15:181–189.

ROOT, R. 1967. The niche exploitation pattern of the Blue-gray Gnatcatcher. Ecological Monographs 37:317–350.

SALLES, R. O. L., AND T. SILVA-SOARES. 2010. *Phyllodytes luteolus* (Anura, Hylidae) as an alien species in the Rio de Janeiro municipality, state of Rio de Janeiro, southeastern Brazil. Herpetology Notes 3:257–258.

SCHINEIDER, J. A. P., AND R. L. TEIXEIRA. 2001. Relacionamento entre anfíbios anuros e bromélias da restinga de regência, Linhares, Espírito Santo, Brasil. Iheringia Série Zoológica 91:41–48.

SEPKA, E. R. 2008. Estudo de macroinvertebrados associados a Bromeliaceae em uma área de mata atlântica no estado do Paraná, Brasil, com ênfase na família Syrphidae (Diptera). Unpubl. Master's Thesis, University Federal do Paraná, Brazil.

SHINE, R. 1979. Sexual selection and sexual dimorphism in the Amphibia. Copeia 1979:297–306.

SILVA, H. R., A. L. G. CARVALHO, AND G. B. BITTENCOURT-SILVA. 2010. Selecting a hiding place: anuran diversity and the use of bromeliads in a threatened coastal sand dune habitat in Brazil. Biotropica 42:1–10.

SIMON, M. P., AND C. A. TOFT. 1991. Diet specialization in small vertebrates: mite-eating in frogs. Oikos 61:263–278.

SRIVASTAVA, D. S., AND J. H. LAWTON. 1998. Why more productive sites have more species: an experimental test of theory using tree-hole communities. American Naturalist 152:510–529.

SUGUIO, K., AND L. MARTIN. 1982. Progress in research on quaternary sea-level changes and coastal evolution in Brazil. *In* Symposium on Holocene Sea-Level Fluctuations, Magnitude and Causes, pp. 166–181. Columbia University, South Carolina.

TEIXEIRA, R. L., C. ZAMPROGNO, G. I. ALMEIDA, AND J. A. P. SCHINEIDER. 1997. Tópicos ecológicos de *Phyllodytes luteolus* (Amphibia, Hylidae) da restinga de Guriri, São Mateus–ES. Revista Brasileira de Biologia 57:647–654.

TOFT, C. A. 1980. Seasonal variation in populations of Panamanian litter frogs and their prey: a comparison of wetter and drier sites. Oecologia 47:34–38.

———. 1981. Feeding ecology of Panamanian litter anurans: patterns in diet and foraging mode. Journal of Herpetology 15:139–144.

VRCIBRADIC, D., F. H. HATANO, C. F. ROCHA, AND M. VAN SLUYS. 2006. Geographic distribution. *Phyllodytes luteolus*. Herpetological Review 37:489–489.

WELLS, K. D. 1978. Courtship and parental behavior in a Panamanian poison-arrow frog (*Dendrobates auratus*). Herpetologica 34:148–155.

WEYGOLDT, P. 1981. Beobachtungen zur Fortpflanzungsbiologie von *Phyllodytes luteolus* (Wied, 1824) im Terrarium (Amphibia: Salientia: Hylidae). Salamandra 17:1–11.

WITTMAN, P. 2000. The animal community associated with canopy bromeliads of the lowland Peruvian Amazon rain forest. Selbyana 21:48–51.

ZUG, R. G., AND P. B. ZUG. 1979. The Marine Toad, *Bufo marinus*: a natural history resume of native populations. Smithsonian Contributions to Zoology 284:1–58.