

CALLING ACTIVITY AND AGONISTIC BEHAVIOR OF *PSEUDIS MINUTA* GÜNTHER, 1858 (ANURA, HYLIDAE, HYLINAE) IN THE RESERVA BIOLÓGICA DO LAMI, PORTO ALEGRE, BRAZIL

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ABSTRACT. The calling activity and agonistic behavior of *Pseudis minuta* Günther, 1858 were described based on observations made in the Reserva Biológica do Lami, Porto Alegre municipality, Brazil. Field work included bimonthly surveys in one semi-permanent pond, each lasting approximately two days and two nights, from August 2004 to July 2005. Males produced three distinct calls: the advertisement call and two aggressive calls. The dominant frequency of the advertisement call was not correlated with the mass or the snout-vent length of the recorded males. We observed two agonistic interactions between males: one involved acoustic interaction, and the other, acoustic and physical interactions. Calling activity was primarily nocturnal, and occasionally diurnal, with peak at about 2300 h. The number of calling males varied significantly through the year with a peak in September.

KEYWORDS. Hylinae, *Pseudis minuta*, calling activity, breeding behavior, Brazil.

INTRODUCTION

Vocalization, one of the most important aspects of the reproduction of anuran amphibians, plays a fundamental role in attracting females and in defending and keeping territories (Wells, 1977; Duellman and Trueb, 1994; Stebbins and Cohen, 1997). Many species of anurans have a complex call repertoire that is distinct, and each call type can be classified according to its function or circumstance when it is used (Langone, 1994; Wells and Schwartz, 2007). Some species use specific calls for territory defense, which may prevent the escalation to physical interactions among males (Bastos and Haddad, 1996; Abrunhosa and Wogel, 2004). Whereas the vocal behavior of many hylid species have been studied in detail, some genera such as *Pseudis* have been largely ignored.

In southwestern Rio Grande do Sul and in Uruguay, *Pseudis minuta* has seasonal prolonged reproduction concentrated in the hottest months of the year (Langone, 1994; Melchioris *et al.*, 2004). The reproductive success of males in anuran species with prolonged reproduction depends mainly on their capability of attracting females to their calling sites, and on their capability of avoiding interference with other males

by call competition, by maintenance of a minimum inter-male spacing or by defense of individual territories through physical interactions (Wells, 1977). Little is known about the reproductive behavior of *Pseudis* species. The first and only record of physical interaction for the genus was recently reported by Vaz-Silva *et al.* (2007), who observed in *Pseudis bolbodactyla* Lutz, 1925 physical combat, involving butting and pushing following all males encounters.

The objectives of this study were to document the call repertoire, to describe characteristics of reproductive behavior, especially those concerning temporal distribution (circadian and monthly), and to describe the agonistic behavior observed in a population of *Pseudis minuta* from middle-east Rio Grande do Sul.

MATERIALS AND METHODS

Field activities encompassed bimonthly trips to Reserva Biológica do Lami (30°14'S; 40°51'W), a protected area located in the south of Porto Alegre municipality, Rio Grande do Sul, Brazil, from August 2004 to July 2005. Each trip lasted for about two days and two nights. Observations were carried out at

a semi-permanent pond with approximately 818 m². Calling activity was identified by the presence and estimated number of calling males; observations occurred at two diurnal times (1200 h and 1500 h), five nocturnal times (2100 h, 2200 h, 2300 h, 2400 h and 0200 h), and at sunrise and sunset times. Auditory survey followed methods in Zimmerman (1994), that consist in an audio strip transect where all calling males along this transect are counted.

Captured individuals were sexed, weighed to the nearest 0.05 g with a Pesola scale and measured (snout-vent length, SVL) to the nearest 0.1 mm with digital calipers. Each specimen was marked by freeze-branding (Daugherty, 1976) and then released at the capture site. Individuals were considered mature with size parameters of SVL > 20.6 mm and mass > 1.3 g for males, and SVL > 32.0 mm and mass > 4.4 g for females (Melchioris *et al.*, 2004).

Agonistic encounters were observed during the observation periods using the focal-animal technique (Martin and Bateson, 1986). Water and air temperatures were recorded during each observation turn and at the moment of each recording with a mercury thermometer (to the nearest 0.1°C).

Vocalizations were recorded on metal cassette tapes with a Marantz PMD-222 recorder and Sony ECM-MS907 microphone held at a distance of 30 cm in front of the vocalizing male. The vocalizations were digitized in the laboratory with input frequency at 22 kHz and resolution 16 bits. Information about the dominant frequency was obtained using the software Cool Edit 96, by Fast Fourier Transformation (FFT, 1024 points). The spectrogram and oscillogram were obtained with the software Avisoft-SASLab. All recorded males were captured, weighted and measured (SVL).

RESULTS

Vocalizations

Males of *Pseudis minuta* use a variety of microhabitats as calling sites, although they were predominantly found in sites with abundant aquatic vegetation. During calling activity males usually were found floating horizontally on the water surface, generally anchored to the vegetation, holding themselves in bushes with their front limbs ($n = 64$). On several occasions they were found with the body completely out of the water, on leaves of water hyacinths ($n = 33$).

The call repertoire consisted of three kinds of calls (*sensu* Wells, 1977 and Duellman and Trueb, 1994): one advertisement call (Fig. 1A) and two aggressive calls. Aggressive call I has just one pulsed note (Fig. 1B), and aggressive call II (Fig. 1C) is composed of two distinct notes (Table 1). The mean snout-vent length (SVL) of the recorded males was 31.8 ± 1.6 mm (29.5–33.7 mm) and the mean mass was 3.4 ± 0.4 g (2.9–3.9 g). The mean dominant frequency of the advertisement call was not correlated to the SVL ($r = -0.26$; $n = 8$; $p > 0.05$) or to the mass ($r = -0.22$; $n = 8$; $p > 0.05$) of the recorded males. Finally, the air temperature during recording was 21°C on average and the water temperature was 18°C.

Calling Activity

Calling activity of *Pseudis minuta* was observed primarily at night and occasionally during the day. During the day, calling was recorded at sunrise, 1200 h and 1500 h for a small number of individuals ($n = 1$ –3). At sunset, the number of calling males increased, reaching a peak at around 2300 h. After this peak, the activity progressively decreased until sunrise (Fig. 2). Also, the number of calling males varied with the month. Calls were recorded from May ($n = 3$) to November ($n = 1$), and in September we recorded the highest number of calling males in activity ($n = 35$). From December to April no vocalizations were heard probably due to the drought that occurred during this period.

Agonistic Behavior

Two agonistic interactions between males of *Pseudis minuta* were observed on September 5 and 24, 2004. In both cases the residents were producing advertisement calls when an intruder approached, and this event caused the resident to change its call and posture. Both interactions occurred at around 2130 h, a time at which territories were probably still being defined. In the first sequence of interaction observed the resident was larger than the intruder (around 30 mm *versus* 20 mm), and both individuals interacted through advertisement and aggressive calls (Fig. 3). The resident emitted an advertisement call (Fig. 3A) and the intruder, at about 20 cm far from the resident, answered with an advertisement call (Fig. 3B). Right after that, the resident advanced toward the intruder (Fig. 3C), stopped close to it, and started to emit ag-

TABLE 1. Mean values, standard deviation and amplitude of parameters of recorded calls of *Pseudis minuta*, in the Reserva Biológica do Lami, Porto Alegre, Brazil.

| | Advertisement Call | Aggressive Call I | Aggressive Call II | |
|--------------------------|----------------------------------|-----------------------------------|-------------------------------------|-------------------------------------|
| Duration call (s) | 0.103 ± 0.019 0.074-0.149 | 0.024 ± 0.006 0.020-0.033 | 0.045 ± 0.007 0.036-0.056 | 0.023 ± 0.002 0.021-0.026 |
| Number of pulses | 10.67 ± 1.54 7-14 | 6.25 ± 0.5 6-7 | 13 ± 2.24 10-16 | 5.6 ± 0.55 5-6 |
| Duration pulses (s) | 0.007 ± 0.002 0.005-0.011 | 0.004 ± 0.0006 0.004-0.005 | 0.004 ± 0.0001 0.0042-0.0044 | 0.005 ± 0.0003 0.0044-0.0052 |
| Dominant frequency (kHz) | 2.69 ± 0.22 2.28-3.25 | 1.77 ± 0.38 1.36-2.28 | 2.16 ± 0.37 1.53-2.47 | 2.05 ± 0.43 1.4-2.57 |
| Analyzed calls (n) | 40 | 4 | 5 | 5 |

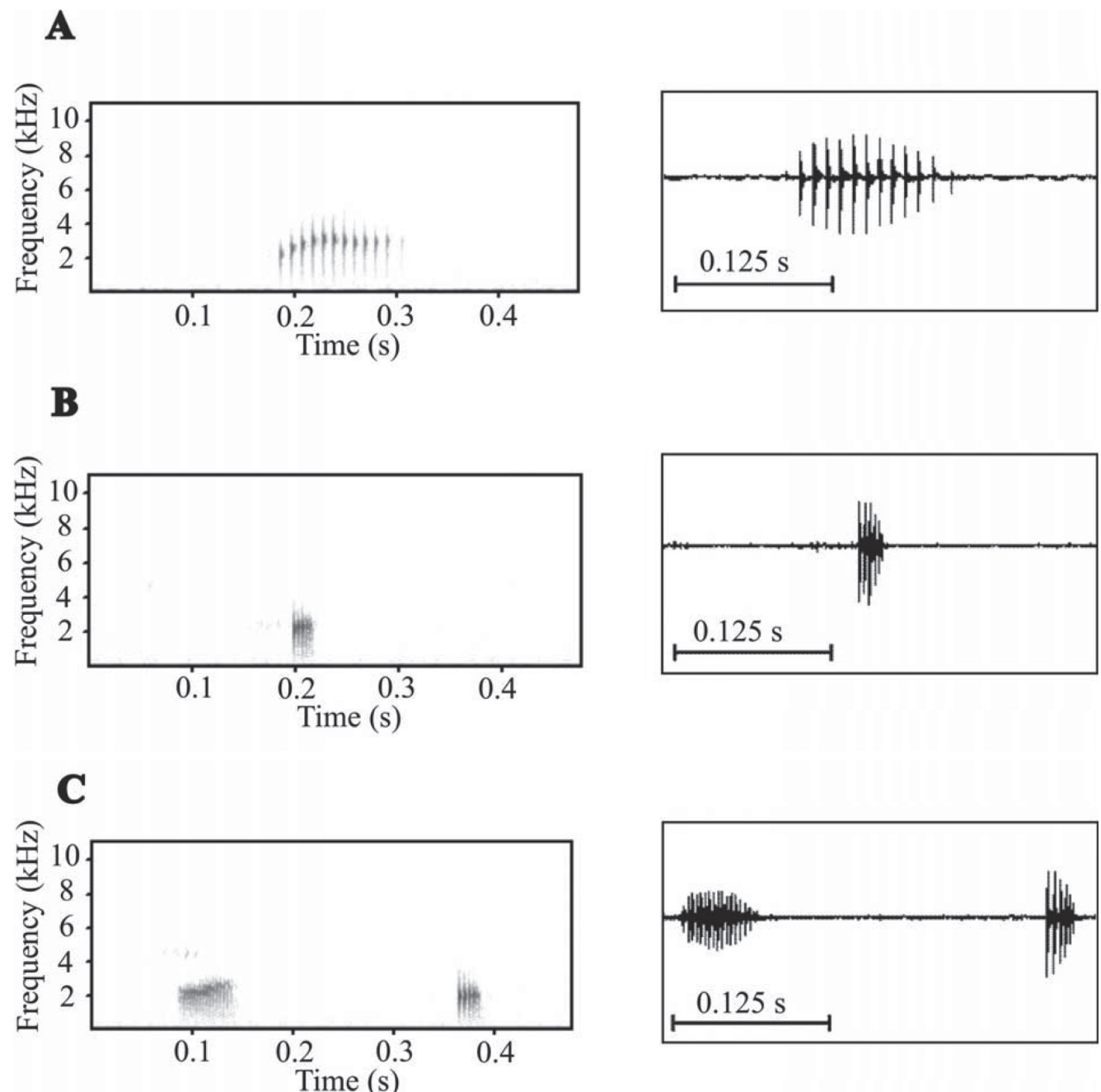


FIGURE 1. Spectrogram (left) and oscillogram (right) of advertisement call (A), aggressive call 1 (B) and aggressive call 2 (C) of *Pseudis minuta*, in the Reserva Biológica do Lami, Porto Alegre, Brazil. Air temperature 21°C and water temperature 18°C.

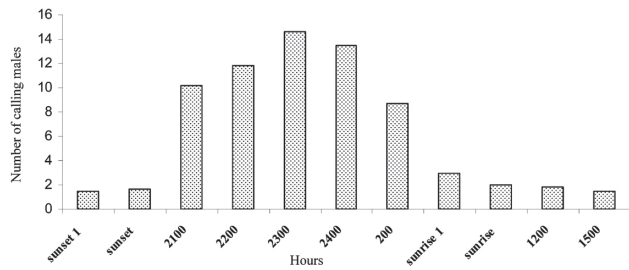


FIGURE 2. Daily vocalization activity of *Pseudis minuta* in a semi-permanent pond in the Reserva Biológica do Lami, Porto Alegre, Brazil. sunset 1 = one hour before sunset; sunrise 1 = one hour before sunrise.

gressive calls (Fig. 3D). The intruder fled (Fig. 3E) and the resident continued emitting aggressive calls and swam to the place where the intruder had been, and moved around as if searching for the other male (Fig. 3F).

In the second sequence of interactions, the resident and intruder had approximately the same body size (around 30 mm). There was acoustic interaction, characterized by production of advertisement and aggressive calls, and physical interaction with the males grasping each other during the wrestling bounds (Fig. 4). The resident emitted an advertisement call (Fig. 4A), then the intruder approached and remained at about 50 cm from the resident, and

emitted an aggressive call (Fig. 4B). The resident male emitted an aggressive call and turned to face the intruder (Fig. 4C) and emitted an advertisement call again. The intruder remained motionless for several seconds (Fig. 4D), but after that emitted aggressive calls, and then the two males swam toward each other (Figs. 4E, F). The males engaged in wrestling, holding each other around the head and grabbing each other with the forelimbs (Fig. 4G). After about a minute, the winner produced an advertisement call, but it was not possible to identify which male (resident or intruder) kept the territory (Fig. 4H).

DISCUSSION

The call repertoire observed in *Pseudis minuta* consisted of three calls: one advertisement call and two aggressive calls. The calling activity was primarily nocturnal and occasionally diurnal and calling males were predominantly found in sites with abundant aquatic vegetation. The number of calling males varied with the month with a peak in september. Furthermore, we reported for the first time agonistic interactions between males of *Pseudis minuta*.

The use of more than one kind of aggressive call by *P. minuta* is probably related to the different levels of aggressiveness of males, which has been suggested

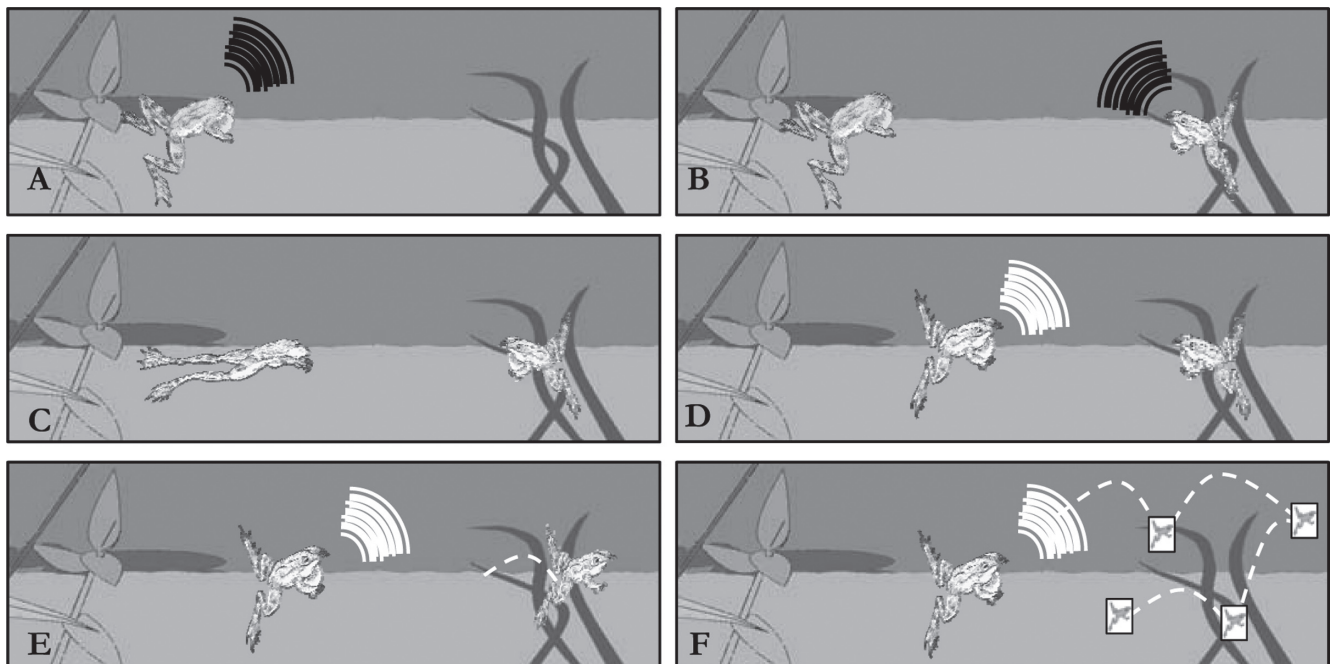


FIGURE 3. Agonistic behavior without physical interaction in *Pseudis minuta* in the Reserva Biológica do Lami, Porto Alegre, Brazil. Advertisement call = black; aggressive call = white; white stippling = trajectory of male.

for several hylid species (e.g. Schwartz, 1989; Bastos and Haddad, 1995; Martins *et al.*, 1998; Halloy and Espinoza, 2000). Aggressive calls seem to play a fundamental role in the maintenance of space between calling males (Brenowitz and Rose, 1999). The production of aggressive calls in *P. minuta* probably reduces the need of physical interaction, avoiding energetic and physical injury of the individuals involved, as suggested for other hylid species (Martins *et al.*, 1998; Abrunhosa and Wogel, 2004). On the other hand, agonistic interactions have been reported for several hylid species (e.g. Cardoso and Haddad, 1984; Bastos and Haddad, 1996; 2002; Martins *et al.*, 1998; Burmeister *et al.*, 1999; Abrunhosa and Wogel, 2004). Recently, Vaz-Silva *et al.* (2007) observed this behavior for *Pseudis bolbodactyla*, reporting the first record for the genus. Agonistic interactions are probably more common in *Pseudis* species than actually reported because descriptive studies are scarce.

In some anuran species correlations between some call parameters and the mass and/or SVL of males were detected. Larger and heavier males generally have calls with lower dominant frequency (Giacoma *et al.*, 1997; Bastos *et al.*, 2003; Guimarães and Bastos, 2003). The dominant frequency of calling males of *P. minuta* was not correlated with mass or SVL, ei-

ther because such a relationship does not exist within the population studied or is an artifact of the small number of individuals recorded ($n = 8$).

It is not yet clear if male anurans choose calling sites based on acoustic properties, but physical characteristics of some sites certainly affect propagation and direction of the sound (Wells and Schwartz, 1982). Some males of *P. minuta* used elevated sites during calling activity, and approximately 35% of the males were observed calling on water hyacinths, with the body completely outside the water. As previously reported for some species of amphibians, the vibration produced on water by the moving individuals or by the movement of the vocal sacs during calling attracts aquatic predators (Haddad and Bastos, 1997; Toledo, 2003). Maybe the utilization of these sites reduces the risk of predation, because most predators of *P. minuta* are aquatic, so that staying out of the water could reduce the chance of being located. In this case, the number of males calling on water hyacinths would be limited by the low availability of this kind of vegetation, which occurs only in a small portion of the pond.

The two kinds of agonistic behavior observed for *P. minuta* are very similar to those recorded by Bastos and Haddad (2002) for *Scinax rizibilis* (Bokermann,

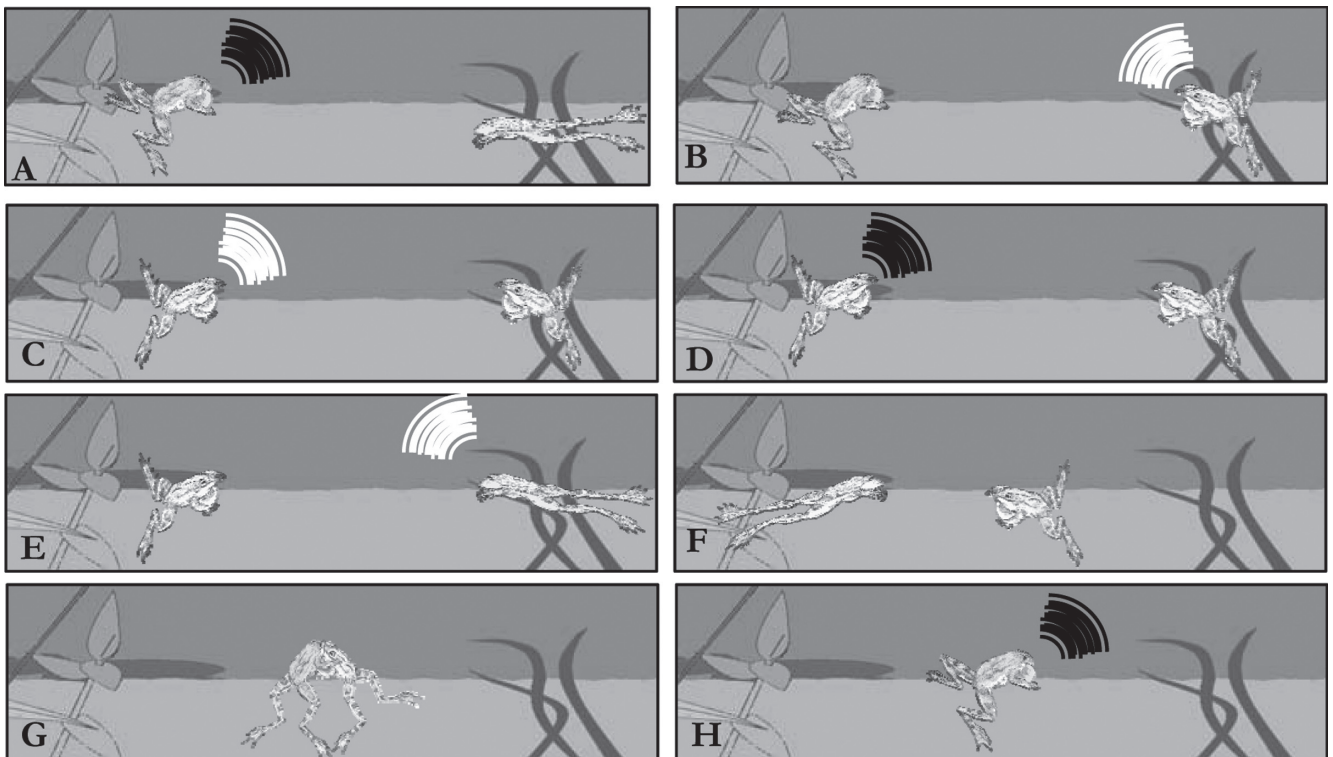


FIGURE 4. Agonistic behavior with physical interaction in *Pseudis minuta* in the Reserva Biológica do Lami, Porto Alegre, Brazil. Advertisement call = black; aggressive call = white.

1964). Maybe physical interactions occur when the difference in size between males is not evident and the characteristics of the call are not enough to indicate a weaker individual. However, it remains unclear why males of either species sometimes engage in physical interactions. Burmeister *et al.* (1999), on analyzing the reproductive behavior of *Acris crepitans* Baird, 1854, suggested that external influences play a fundamental role in the standard agonistic behavior. In *P. minuta* the agonistic interactions may be related to the density of males in the pond, considering that both observations occurred in the month when there was the greatest number of males calling. A similar pattern was recorded for other hylid species (e.g. Kluge, 1981; Martins *et al.*, 1998), and for the congeneric species *P. bolbodactyla* (Vaz-Silva *et al.*, 2007). However, the agonistic interactions of *P. minuta* and *P. bolbodactyla* include important differences; the intruder of *P. minuta* does not seem submissive to the resident, as recorded for the other species. In 11 observations of interactions between males of *P. bolbodactyla* the resident always kept the territory (Vaz-Silva *et al.*, 2007). Additional observations are necessary for *P. minuta* because it was possible to identify which male kept the territory in only one of two interactions observed.

Brandão *et al.* (2003) recorded diurnal and nocturnal activity for *P. bolbodactyla* and indicated this behavior as common for the genus since it was also recorded for *P. cardosoi* (Kwet, 2000), *P. paradoxa* (Dixon *et al.*, 1995), *P. tocantins* (Brandão and Peres Jr., 2001), and for a population of *P. minuta* in Argentina (Basso, 1990). In the Reserva Biológica do Lami, the calling period for *P. minuta* is long, as males were recorded in all months except during a drought. Activity also decreased in August, which was one of the coldest months of the year. The calling activity of *P. minuta* seems to be mainly influenced by abiotic factors (Zank, 2005), in a similar manner as for many other hylid species (Andrade and Cardoso, 1991; Moreira and Barreto, 1997; Bertoluci, 1998; Gottsberger and Gruber, 2004) and even members of other anuran families (Marsh, 2000; Bernarde and Machado, 2001; Oseen and Wassersug, 2002).

RESUMO

As vocalizações e o comportamento agonístico de *Pseudis minuta* Günther, 1858 foram descritos com base em observações realizadas na Reserva Biológica do Lami, município de Porto Alegre, Brasil. As ati-

vidades de campo compreenderam visitas bimensais com duração aproximada de dois dias e duas noites cada, entre agosto de 2004 e julho de 2005. Os machos apresentaram três vocalizações distintas: o canto de anúncio e dois cantos territoriais. A frequência dominante do canto de anúncio não apresentou correlação com a massa e o CRC dos machos gravados. Foram observados dois encontros agonísticos entre machos, sendo que em um houve apenas interação acústica entre os indivíduos, e no outro, interação acústica e física. Os machos apresentaram atividade de vocalização predominantemente noturna e ocasionalmente diurna, com pico de vocalização por volta das 23 horas. O número de machos vocalizando variou significativamente ao longo do ano, com pico em setembro.

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REFERENCES

- ABRUNHOSA, P. A. AND H. WOGEL. 2004. Breeding behaviour of the leaf-frog *Phyllomedusa burmeisteri* (Anura: Hylidae). *Amphibia-Reptilia*, 25:125-135.
- ANDRADE, G. V. AND A. J. CARDOSO. 1991. Descrição de larvas e biologia de quatro espécies de *Hyla* (Amphibia, Anura). *Revista Brasileira de Biologia*, 51:391-402.
- BASSO, N. G. 1990. Estrategias adaptativas en una comunidad subtropical de anuros. *Cuadernos de Herpetología – Serie Monografias*, 1:3-70.
- BASTOS, R. P. AND C. F. B. HADDAD. 1995. Vocalizações e interações acústicas de *Hyla elegans* (Anura: Hylidae) durante a atividade reprodutiva. *Naturalia*, 20:165-176.
- BASTOS, R. P. AND C. F. B. HADDAD. 1996. Breeding activity of the Neotropical treefrog *Hyla elegans* (Anura, Hylidae). *Journal of Herpetology*, 30:355-360.
- BASTOS, R. P. AND C. F. B. HADDAD. 2002. Acoustic and aggressive interactions in *Scinax rizibilis* (Anura: Hylidae) during the

- reproductive activity in southeastern Brazil. *Amphibia-Reptilia*, 23:97-104.
- BASTOS, R. P., M. A. F. BUENO, S. L. DUTRA, AND L. P. LIMA. 2003. Padrões de vocalização de anúncio em cinco espécies de Hylidae (Amphibia: Anura) do Brasil Central. *Comunicações do Museu Ciências e Tecnologia da PUCRS – Série Zoologia*, 16:39-51.
- BERNARDE, P. S. AND R. A. M. MACHADO. 2001. Riqueza de espécies, ambientes de reprodução e temporada de vocalização da anurofauna em Três Barras do Paraná, Brasil (Amphibia: Anura). *Cuadernos de Herpetología – Serie Monografías*, 14:93-104.
- BERTOLUCI, J. 1998. Annual patterns of breeding activity in Atlantic Rainforest anurans. *Journal of Herpetology*, 32:607-611.
- BRANDÃO, R. A. AND A. K. PÉRES JR. 2001. Levantamento da herpetofauna na área de influência do Aproveitamento Hidroelétrico da UHE Luís Eduardo Magalhães (Palmas, TO). *Humanitas*, 3:35-50.
- BRANDÃO, R. A., A. A. GARDA, V. BRAZ, AND B. FONSECA. 2003. Observations on the ecology of *Pseudis bolbodactyla* (Anura: Pseudidae) in central Brazil. *Phyllomedusa*, 2:3-8.
- BRENOVITZ, E. A. AND G. J. ROSE. 1999. Female choice and plasticity of male calling behaviour in the Pacific Treefrog. *Animal Behaviour*, 57:1337-1342.
- BURMEISTER, S., J. KONIECZKA, AND W. WILCZYNSKI. 1999. Agonistic encounters in a cricket frog (*Acris crepitans*) chorus: behavioral outcomes vary with local competition and within the breeding season. *Ethology*, 105:335-347.
- CARDOSO, A. J. AND C. F. B. HADDAD. 1984. Variabilidade acústica em diferentes populações e interações agressivas de *Hyla minuta* (Amphibia, Anura). *Ciência e Cultura* 36(8):1393-1399.
- DAUGHERTY, C. H. 1976. Freeze-branding as a technique for marking anurans. *Copeia*, 1976:836-838.
- DIXON, J. R., C. MERCOLLI, AND A. A. YANOSKY. 1995. Some aspects of the ecology of *Pseudis paradoxa* from northeastern Argentina. *Herpetological Review*, 26:183-185.
- DUELLMAN, W. E. AND L. TRUEB. 1994. *Biology of Amphibians*. The Johns Hopkins University Press, Maryland, 670 pp.
- GIACOMA, C., C. ZUGOLARO, AND L. BEANI. 1997. The advertisement calls of the green toad (*Bufo viridis*): variability and role in mate choice. *Herpetologica*, 53:454-464.
- GOTTSBERGER, B. AND E. GRUBER. 2004. Temporal partitioning of reproductive activity in a Neotropical anuran community. *Journal of Tropical Ecology*, 20:271-280.
- GUIMARÃES, L. D. AND R. P. BASTOS. 2003. Vocalizações e interações acústicas em *Hyla raniceps* (Anura: Hylidae) durante a atividade reprodutiva. *Iheringia – Série Zoologia*, 93:149-158.
- HADDAD, C. F. B. AND R. P. BASTOS. 1997. Predation on the toad *Bufo crucifer* during reproduction (Anura: Bufonidae). *Amphibia-Reptilia*, 18:295-298.
- HALLOY, M. AND R. E. ESPINOZA. 2000. Territorial encounters and threat displays in the Neotropical frog *Phyllomedusa sauvagii* (Anura: Hylidae). *Herpetological Natural History*, 7:175-180.
- KLUGE, A. G. 1981. The life history, social organization and parental behavior of *Hyla rosenbergi* Boulenger, a nest-building gladiator frog. *Miscellaneous Publications Museum of Zoology*, 160:1-170.
- KWET, A. 2000. The genus *Pseudis* (Anura: Pseudidae) in Rio Grande do Sul, southern Brazil, with description of a new species. *Amphibia-Reptilia*, 21:38-55.
- LANGONE, J. A. 1994. Ranas y sapos del Uruguay (Reconocimiento y aspectos biológicos). *Museo Damaso Antonio Larrañá – Serie Divulgación*, 5:1-123.
- MARSH, D. M. 2000. Variable responses to rainfall by breeding tungara frogs. *Copeia*, 2000:1104-1108.
- MARTIN, P. AND P. BATESON. 1986. *Measuring behaviour. An introductory guide*. Cambridge University, Cambridge, 199 pp.
- MARTINS, M., J. P. POMBAL JR., AND C. F. B. HADDAD. 1998. Escalated aggressive behaviour and facultative parental care in the nest building gladiator frog, *Hyla faber*. *Amphibia-Reptilia*, 19:65-73.
- MELCHIORI, J., M. DI-BERNARDO, G. M. F. PONTES, R. B. OLIVEIRA, M. SOLÉ, AND A. KWET. 2004. Reprodução de *Pseudis minuta* (Anura, Hylidae) no sul do Brasil. *Phyllomedusa*, 3:61-68.
- MOREIRA, G. AND L. BARRETO. 1997. Seasonal variation in nocturnal calling activity of a savanna anuran community in central Brazil. *Amphibia-Reptilia*, 18:49-57.
- OSEEN, K. L. AND R. J. WASSERSUG. 2002. Environmental factors influencing calling in sympatric anurans. *Oecologia*, 2002:616-625.
- SCHWARTZ, J. J. 1989. Graded aggressive calls of the spring peeper, *Pseudacris crucifer*. *Herpetologica*, 45:172-181.
- STEBBINS, R. C. AND N. W. COHEN. 1997. *A Natural History of Amphibians*. Princeton University Press, New Jersey, 316pp.
- TOLEDO, L. F. 2003. Predation on seven South American anuran species by water bugs (Belostomatidae). *Phyllomedusa*, 2:105-108.
- VAZ-SILVA, W., M. DI-BERNARDO, L. D. GUIMARÃES, AND R. P. BASTOS. 2007. Territoriality, agonistic behavior, and vocalization in *Pseudis bolbodactyla* A. Lutz, 1925 (Anura: Hylidae) from Central Brazil. *Salamandra*, 43:35-42.
- WELLS, K. D. 1977. The social behaviour of anuran amphibians. *Animal Behaviour*, 25:449-455.
- WELLS, K. D. AND J. J. SCHWARTZ. 1982. The effect of vegetation on the propagation of calls in the neotropical frog *Centrolenella fleischmanni*. *Herpetologica*, 38:449-455.
- WELLS, K. D. AND J. J. SCHWARTZ. 2007. The behavioral ecology of anuran communication: the vocal repertoires of frogs and toads; pp 44-86. In: Narins, P. M., A. S. Feng, R. R. Fay and A. N. Popper editors. *Hearing and sound communication in amphibians*. Springer Science Business Media, LLC, New York.
- ZANK, C. 2005. *Biologia reprodutiva de Pseudis minutus* Günther, 1858 (Anura, Hylidae, Hylineae) na Reserva Biológica do Lami, Porto Alegre, Brasil. *dissertation, Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre*, 58 pp.
- ZIMMERMAN, B. L. 1994. Standard techniques for inventory and monitoring: Audio strip transects; pp 92-97. In: Heyer, W. R., A. M. Donnelly, R. W. McDiarmid, L. C. Hayek and M. S. Foster editors. *Measuring and monitoring biological diversity. Standard methods for amphibians*. Smithsonian Institution Press, Washington.

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