

The recognition of *Dendropsophus minusculus* (Rivero, 1971) (Hylidae, Dendropsophini) as a highly polymorphic, multi-domain distributed species

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Abstract

Herein we present new occurrences of sites of *Dendropsophus minusculus* in Brazil adding information about reproductive biology and colour patterns of the species. Such information is fundamental for characterising the species that we believe has been neglected due to its morphological similarity with other congeneric species. *Dendropsophus minusculus* may be found in different morphoclimatic domains, being one of the most generalist species of the genus in this aspect. The species plasticity is not restricted to its occurrence, but also related to aspects of its reproductive biology, and we hypothesised that the latter feature could explain the wide geographical range of the species. We highlight the importance of further in-depth studies and the use of *D. minusculus* as a model to understand the historical events responsible for the current geographical distribution of the morphoclimatic domains in Brazil.

Keywords: reproductive plasticity, polymorphism, taxonomy, *Dendropsophus microcephalus* species group.

O reconhecimento de *Dendropsophus minusculus* (Rivero, 1971) (Hylidae, Dendropsophini) como espécie polimórfica e de ocorrência em distintos domínios morfoclimáticos

Resumo

No presente estudo relatamos novos locais de ocorrência para *Dendropsophus minusculus* no Brasil e acrescentamos informações sobre a biologia reprodutiva e padrões de coloração da espécie. Essas informações são de fundamental importância para a caracterização da espécie, que acreditamos ter sido negligenciada em virtude de sua semelhança morfológica com outras espécies congênicas. *Dendropsophus minusculus* pode ser encontrada em diversos domínios morfoclimáticos, sendo, neste aspecto, uma das espécies mais generalistas de seu gênero. A plasticidade da espécie não se restringe a sua ocupação territorial, mas também a aspectos relativos a sua biologia reprodutiva e especulamos que esta seja a razão de sua amplitude territorial. Destacamos ainda a importância de estudos mais aprofundados e o uso da espécie como modelo para o entendimento de eventos pretéritos responsáveis pela distribuição de domínios morfoclimáticos no Brasil.

Palavras-chave: plasticidade reprodutiva, polimorfismo, taxonomia, grupo de espécies de *Dendropsophus microcephalus*.

1. Introduction

Dendropsophus minusculus (Rivero, 1971) is a small-sized hylid (*sensu* Duellman, 1970) like its specific epithet suggests, reaching up to 24 mm SVL (females) (Langone and Basso, 1987; Duellman, 1997) and assigned to the species group of *D. microcephalus* (Cope, 1886) (*sensu* Faivovich et al., 2005), a group that includes 38 species

with unresolved phylogenetic relationships (Faivovich et al., 2005; Köhler et al., 2005; Moravec et al., 2006; 2008; Fouquet et al., 2011).

The taxonomy of species assigned to the *Dendropsophus microcephalus* group is complex and several reasons have contributed to the current taxonomical problems. For instance,

many species of the group are morphologically similar and need further revision [e.g. see comments about *D. nanus* (Boulenger, 1889) and *D. walfordi* (Bokermann, 1962) in Fouquet et al., 2007; 2011]. Some species that belong to the *D. microcephalus* species group, such *D. branneri* (Cochran, 1948), present polymorphic forms (see Lutz, 1973; Martins and Cardoso, 1987), and some considerable characteristic diagnostics are highly variable when a large series of specimens is examined (e.g. see comments about *D. branneri* in Lutz, 1973).

In Northeastern Brazil, in particular, this confusing scenario is even more dramatic due to the high species richness of the *Dendropsophus microcephalus* group. Currently, eight species of this species group have been recorded in Northeastern Brazil: *D. bipunctatus* (Spix, 1824), *D. branneri*, *D. decipiens* (Lutz, 1925), *D. haddadi* (Bastos and Pombal., 1996), *D. nanus*, *D. oliveirai* (Bokermann, 1963), *D. rubicundulus* (Reinhardt and Lütken, 1862), and *D. studerae* (Carvalho-e-Silva et al., 2003).

Data about polymorphic patterns, geographic distribution and habitat use by species of the *Dendropsophus microcephalus* group, even when anecdotal, are fundamental given that they provide valuable background for species identification; especially in the case of species with difficult taxonomy. Additionally, this data may provide support for phylogeographic studies, a field that has grown in the last two decades and deals with the spatial arrangements of genetic lineages in order to understand the demographic and historical nature of species or lineages evolution (Avisé, 2009).

In the present study, we record the occurrence of *Dendropsophus minusculus* for Northeastern Brazil, extending the species distribution for Caatinga, Cerrado and Atlantic Rainforest domains. Currently, the distribution of *D. minusculus* encompasses the region of Llanos in Colombia, lowland savannas of Venezuela, and eastward through Guianas to the state of Pará, Brazil (Knispel and Barros, 2008; Avila-Pires et al., 2010; Frost, 2011). A population on the extreme southwestern region of Trinidad island has also been recognised (Murphy, 1997). Additionally, we identify and describe the polymorphism in the dorsal colour pattern of some studied populations. We believe that the information provided here will be useful to elucidate the taxonomy of the *D. microcephalus* species group and the geographical distribution of *D. minusculus*, especially in Northeastern Brazil, where populations of this species have been historically confused with *D. branneri* or considered as a potentially undescribed species.

2. Material and Methods

We compiled data available in the literature and data from our surveys at the following localities in North/Northeastern Brazil: state of Maranhão: Municipality of Santana do Maranhão (03°06' S, 42°24' W, 33 m a.s.l.), state of Ceará: municipalities of Ubajara (03°49' S, 40°53' W – 03°52' S, 40°54' W; 860 m a.s.l.) and Viçosa do Ceará (03°21' S, 41°06' W; 88-129 m a.s.l.); state

of Piauí: municipalities of Ilha Grande de Santa Isabel (02°51' S, 41°48' W; 20 m a.s.l.) and Piracuruca (04°05' S, 41°32' W; 130 m a.s.l.); state of Roraima: municipality of Boa Vista (02°44' N, 60°30' W; 90 m a.s.l.); and state of Bahia: municipality of Ipiáú (14°07'S; 39°45'; 180 m a.s.l.). The identity of the specimens collected in the state of Piauí was confirmed through molecular analysis. The other specimens were identified as *Dendropsophus minusculus* through morphological confrontation with the specimens from Piauí.

We performed nocturnal expeditions in these localities when, through active and acoustic search, we located and collected the specimens. We monitored the populations of Ubajara and Viçosa do Ceará monthly, totalling 24 nights per locality between April/2007 and April/2009. Although both municipalities are relatively close to each other (ca. 60 km) they present pronounced different phytophysiognomies. Ubajara presents moist forest fragments of high altitude (ca. 800 m.a.s.l.) and permanent water bodies, while the area sampled at Viçosa do Ceará presents dry forests (Caatinga) and temporary water bodies.

Specimens collected were anaesthetised with xylocaine, fixed in formalin 10% and conserved in alcohol 70%. Voucher specimens are housed at three collections: Célio F. B. Haddad (CFBH) Amphibian Collection, Departamento de Zoologia da Universidade Estadual Paulista (UNESP), Rio Claro, São Paulo, Brazil; Zoological collection of the Universidade Estadual do Sudoeste da Bahia (UESB), Jequié, Bahia, Brazil; and Amphibian collection of the Universidade Estadual do Piauí (UESPI), Parnaíba, Piauí, Brazil. Collecting permits were issued by the Instituto Chico Mendes de Conservação da Biodiversidade (Permit numbers 13571-1, 12545-1; 23932-1; 12164).

3. Results

3.1. Geographic distribution and habitat use

Herein, we present the first records of *Dendropsophus minusculus* for the Brazilian states of Bahia, Ceará, Maranhão, Piauí, and Roraima (Figure 1) as well as for the Caatinga, Cerrado, and Atlantic Rainforest domains. The species showed high diversity regarding its morphoclimatic domains occurrence, being registered in areas of Atlantic Rain Forest (states of Piauí and Ceará), Cerrado (states of Piauí and Roraima), Caatinga (states of Ceará and Maranhão) and ecotonal areas of Caatinga and Atlantic Rainforest (in the state of Bahia). However, regarding the use of microhabitats as calling sites, the species was somewhat less plastic, being registered in shrubs at the margins of water bodies and grasses that emerged from the water either in temporary or permanent water bodies.

Males of *Dendropsophus minusculus* were registered in calling activity throughout the whole year in Ubajara in permanent water bodies, while in Viçosa do Ceará the species was recorded only during few months during the year (April to September) in temporary water bodies.

We were not able to observe courtship behaviour of *Dendropsophus minusculus*. However, it was possible to

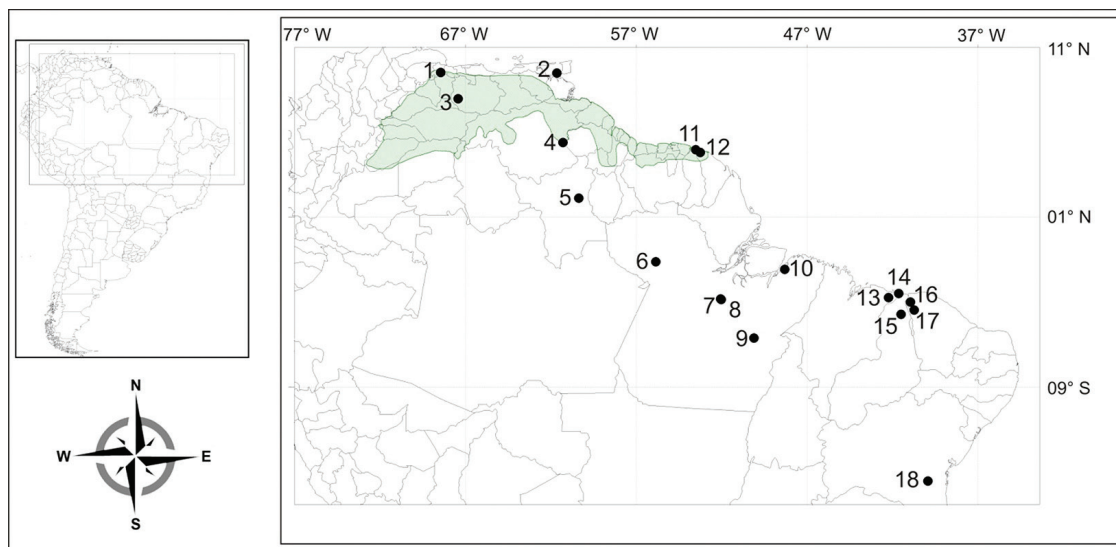


Figure 1. Distribution of *Dendropsophus minusculus* according to the IUCN Red List (greenish area) and compilation of updated records for species (black circles). 1- Municipality of Nirgua, state of Yaracuy, Venezuela (Type locality; Rivero, 1971); 2- Peninsula of Icaos, (Murphy, 1997); 3- Municipality of Calabozo, state of Guárico, Venezuela (Táranó, 2010); 4- Region of La Escalera, state of Bolívar, Venezuela (Duellman, 1997); 5- Municipality of Boa Vista, state of Roraima, Brazil (Present study); 6- Municipality of Óbidos, state of Pará, Brazil (Avila-Pires et al., 2010); 7- Municipality of Altamira, state of Pará, Brazil (Knispel and Barros, 2008); 8- Xingu river, state of Pará, Brazil (Caldwell and Araújo, 2005); 9- Reserva Biológica do Tapirapé, state of Pará, Brazil (as *Dendropsophus* aff. *branneri* in Bernardo et al., 2012); 10- Municipality of Belém, state of Pará, Brazil (Duellman and Pyles, 1983); 11 and 12- French Guyana (Lescure and Marty 2000); 13- Municipality of Santana do Maranhão, state of Maranhão, Brazil (Present study); 14- Municipality of Ilha Grande de Santa Isabel, state of Piauí, Brazil (as *Dendropsophus* gr. *microcephalus* in Loebmann and Mai, 2008); 15- Municipality of Piracuruca, state of Piauí, Brazil (Present study); 16- Municipality of Viçosa do Ceará, state of Ceará, Brazil (as *Dendropsophus* gr. *microcephalus* in Loebmann and Haddad, 2010); 17- Municipality of Ubajara, state of Ceará, Brazil (as *Dendropsophus* gr. *microcephalus* in Loebmann and Haddad, 2010); 18- Municipality of Ipiáú, state of Bahia, Brazil (Present study).

observe both aquatic and terrestrial ovipositions *in situ*. Under laboratorial conditions we also identified same plasticity in selection of oviposition site (Figures 2a and 2b).

In both sites studied at Ceará, *Dendropsophus minusculus* occurs sympatrically with the congeneric species *D. minutus*, *D. nanus* and *D. soaresi*. At the Caatinga of Viçosa do Ceará municipality, the species was recorded occurring syntopically with *D. nanus* and *D. rubicundulus*.

3.2. Patterns of dorsal colouration

We detected four main patterns of *Dendropsophus minusculus* dorsal colouration in life: pattern A individuals that present a relative wide light stripe contouring the dorsal region and forming a triangular area over the whole head (Figure 3A); pattern B individuals with small spots distributed uniformly along dorsal surface (Figure 3B); pattern C individuals with uniform dorsal colour pattern without spots or blotches, with a narrow light stripe present dorso-laterally (Figure 3C); pattern D individuals with asymmetrical light blotches distributed irregularly throughout dorsal region (Figure 3D). In some populations (e.g. Ilha Grande de Santa Isabel, Piauí) we could find all patterns syntopically.

4. Discussion

Dendropsophus minusculus has been reported occurring in Brazil since (at least) the 80s (see Duellman and Pyles, 1983). Nevertheless, until now, the most easterly records are from localities in the state of Pará: Xingu River (Caldwell and Araújo, 2005), municipalities of Altamira (Knispel and Barros, 2008) and Belém (Duellman and Pyles, 1983), all Amazonian localities.

The present study increases considerably the latitudinal distribution of *Dendropsophus minusculus* (i.e. extending to parallel 13° S, ca. 10 more latitudinal degrees than previously reported by Knispel and Barros, 2008, 3°S). The record from the state of Bahia is the southernmost record of species known so far; increasing species range distribution in ca. 1,800 km in a straight line from Altamira municipality, in the state of Pará (Knispel and Barros, 2008).

The absence of records in other Brazilian states east of Pará may be explained in part due to the confusion of this species with *Dendropsophus branneri*. Lutz (1973) defined *D. branneri* as a species widely distributed in Brazil, occurring on the Brazilian coast from the state of Rio de Janeiro to Pará, and westward through the state of Mato

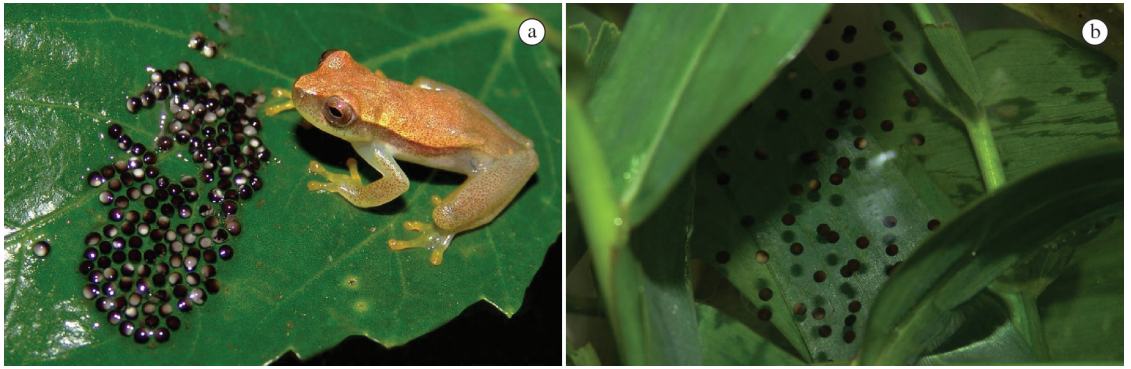


Figure 2. Aquatic and terrestrial oviposition by *Dendropsophus minusculus* and classification of reproductive mode according to Haddad and Prado (2005). a- Male of *Dendropsophus minusculus* next to clutch released in a leaf (reproductive mode 24); b- Entire clutch deposited in lentic water attached to vegetation (reproductive mode 1). Photographs were taken *ex situ* by Daniel Loebmann at the municipality of Ubajara, State of Ceará, Brazil.

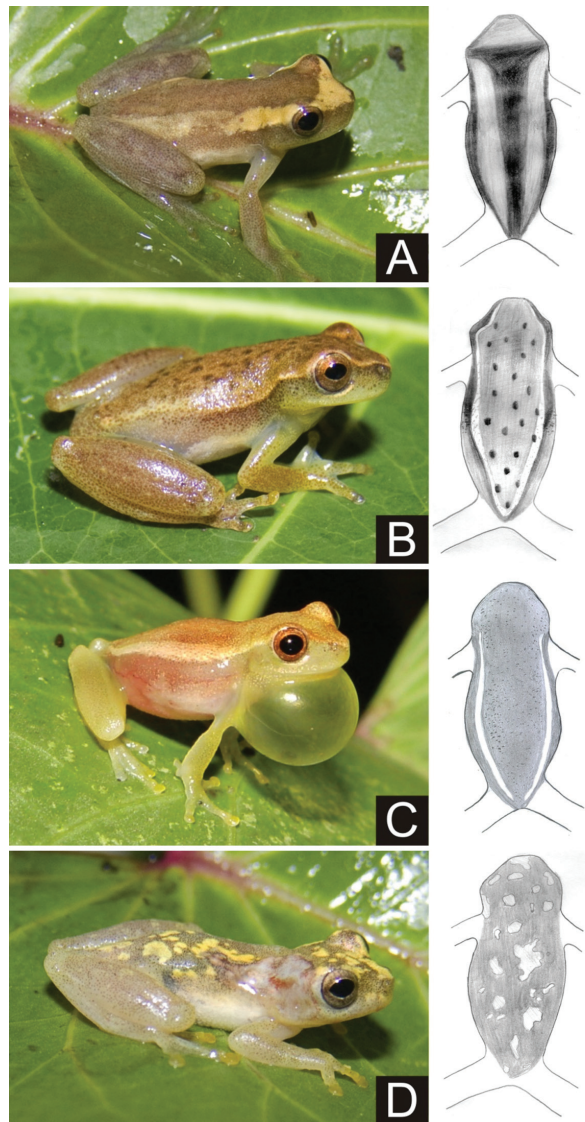


Figure 3. Photographs and schematic drawings of four patterns of dorsal colouration found in *Dendropsophus minusculus*. Photographs by Daniel Loebmann and drawings by Karine M. Pereira.

Grosso. The type locality of the species is in Northeastern Brazil, municipality of Bonito, state of Pernambuco. Lutz (1973) also suggested that the presence of a silvery white spot under the eye in *D. branneri*, defined as a diagnostic characteristic by Cochran (1948), should be treated as a variation, occurring only in some individuals. Topotypic specimens present the spot, as also do many other southern populations. However, the polymorphism in the presence of the spot is also present and some individuals may present spots only below one of the eyes.

It is important to remark that Lutz (1973) treated *Dendropsophus oliveirai* (Bokermann, 1963) as a junior synonym of *D. branneri*, although *D. branneri* and *D. oliveirai* are two rather distinct species with remarkably distinct advertisement calls (see Nunes et al., 2007 and Santana et al., 2011). Specimens from the state of Mato Grosso cited by Lutz (1973) as *D. branneri* were not checked for the present contribution.

Considering the large number of new records presented here, we hypothesised that individuals from Northeastern Brazil without the white spot under the eye may in fact be *Dendropsophus minusculus*. Population samples of *D. minusculus* from the states of Piauí and Ceará have been treated as a potential new species being designated as *Dendropsophus* gr. *microcephalus* (e.g. Loebmann and Mai, 2008; Loebmann and Haddad, 2010).

The lack of studies describing the variation limits of basic biological features of the species such as colour patterns, morphological, and bioacoustics parameters still continues to be a formidable task for herpetologists from the Neotropics. The fact that these data are basic for identifying many anuran species only highlights the importance of such studies. In polymorphic species, such as *Dendropsophus minusculus*, these studies may also bring insights relating to geographical gradients and ecological pressures, past and present, that shaped population dynamics in a given locality (Ohmer et al., 2009). Species can be considered as polymorphic when individuals of the same sex and age show variation in genetically inherited colour patterns and whose expression is minimally sensitive to bodily and environmental conditions (Roulin, 2004). In addition, a species can be considered as a colour polymorphic if a single interbreeding population should presents two or more distinct colour morphs (Huxley, 1955), a criteria covered by the studied species.

Polymorphism in colour have being described for some species of *Dendropsophus* [e.g. *D. anataliasiasi* (Bokermann, 1972), *D. cruzi* (Pombal-Junior and Bastos, 1998), *D. elianae* (Napoli and Caramaschi, 2000), *D. jimi* (Napoli and Caramaschi, 1999a), *D. pseudomeridianus* (Cruz et al., 2000), and *D. rubicundulus* (Reinhardt and Lütken, 1862)] (Pombal-Junior and Bastos, 1998; Napoli and Caramaschi, 1999a, b; Silveira et al., 2011). The geographic patterns of colour pattern polymorphism were determinate for *D. anataliasiasi*, *D. elianae*, *D. jimi*, and *D. rubicundulus* (see Napoli and Caramaschi, 1999a,b; Napoli and Caramaschi, 2000).

The colour pattern presented in the description of the species (type locality: Nirgua, Venezuela) (Rivero, 1971) and in Trinidad and Tobago (Murphy, 2011) and Xingu River-Pará-Brazil (Caldwell and Araújo, 2005) is similar to our pattern B. The colour pattern registered by Duellman (1997) is in accordance with our pattern C, which seems to be the most common colour pattern for species throughout its distribution or, at least, in Northeastern Brazil. However, we could not discard the possibility of further studies reveal the presence of more than one colour pattern in each sampled population, as observed in the Ilha Grande de Santa Isabel population in the present study.

Vicariant events, isolation of populations by distance and local adaptations may influence reproductive success and survival of a given population and, thus, contribute to the evolution of a particular phenotype (Lougheed et al., 2006). The patterns of colour polymorphism are hereditary characters and, therefore, they are predisposed to selection (Endler, 1992; Hoekstra et al. 2004; Hoffman et al., 2006). Although not rare in anurans populations, few studies describe polymorphism colour patterns and fewer aim to answer questions about the inheritance and selective maintenance of this variation (Hoffman and Blouin, 2000). Additionally, the maintenance of a colour polymorphism may be related to within population processes (e.g. predator selection, disruptive correlation selection, sexual selection leading females to choose rare masculine morphs) or between populations (divergent selection and gene flow) (Gray and McKinnon, 2007). Even though we did not test these hypotheses, we argue that *Dendropsophus minusculus* may be a model species not only to address these questions but also to examine the historical forces that maintain genetic variation in nature.

Although *Dendropsophus minusculus* was registered in a small variety of calling sites, the species presented high plasticity concerning the occurrence in different domains and sites used for oviposition. Different morphoclimatic domains exert different selective pressure that may modulate the community composition, richness and abundance of species. Semi-arid domains, such as the Caatinga, may limit the presence and reproduction of some species due to its low relative humidity, sparse vegetation, high day temperatures, and unpredictable seasonality of rains (Navas et al., 2004).

Dendropsophus minusculus is able to exhibit different reproductive modes, dealing with the constraints imposed by the Caatinga environment, where it has been registered in calling activity only during few months in the year and depositing eggs inside temporary water bodies attached in plants (reproductive mode number 1 *sensu* Haddad and Prado, 2005). On the other hand, it has also been registered in calling activity throughout the year depositing the clutches in leaves above permanent water bodies (reproductive mode number 24, *sensu* Haddad and Prado, 2005) in moist forests. Although it is well known that the reproductive season in anuran communities is related to climatic factors (see Vaira, 2005; Zina and Haddad, 2006; Zank et al., 2010), the present study shows that domain characteristics, that

are also associated with climatic factors, may not only be correlated to the duration of the reproductive season, but also act as a selective force on the reproductive mode exhibited by the species. This observation reinforces the ecological plasticity of *D. minusculus*.

Plasticity of choice for oviposition sites is not common among anurans, and sometimes results in a change in classification of reproductive mode exhibited by species. However, some species may show both a primary and an alternative reproductive mode [e.g. *Hypsiboas prasinus*, Haddad and Prado (2005), *Physalaemus spiniger* (Haddad and Pombal Junior, 1998)]. According to Haddad and Prado (2005), alternative reproductive modes are displayed when the species is in a specific social context (high male density on the chorus) or in the absence of the microhabitat needed for oviposition. Although the characteristics associated to different domains may be related to the presence or absence of a specific microhabitat, we argue that domain climatic factors may also be responsible for the reproductive plasticity exhibit by some anuran species.

Even though information about the reproductive mode of nearly half of the species assigned to *Dendropsophus* is lacking (Touchon and Warkentin, 2008), some species are known to lay eggs directly on the water or above it, perched on branches or leaves. Touchon and Warkentin (2008) were able to report and test plasticity in the choice for egg clutch deposit site of *Dendropsophus ebraccatus* (Cope, 1874). The ability to lay terrestrial clutches was proposed by Bastos and Pombal (1996) to be a diagnostic character of the *D. decipiens* species group. However, there are, at least, two more species of *Dendropsophus* [*D. elegans* (Wied-Neuwied, 1824) and *D. nanus*] that have been reported to place their clutches both in the water pond or perched above it, albeit not in the same contributions (Bokermann, 1963; Lescure and Marty, 2000; Izecksohn and Carvalho-e-Silva, 2001; Carvalho-e-Silva et al., 2008). It seems important to state that the nature of the egg clutch deposit site hinders comparisons and literature surveys. However, the exact identities of the *Dendropsophus nanus* in both contributions that describe its clutch are dubious. Langone and Basso (1987) stated that the specimens used by Bokermann (1963) would be in reality *D. sanborni* (Schmidt, 1944). The controversy around the status of French Guyana populations used by Lescure and Marty (2000) has its bases in phylogenetic studies. Previous molecular-based results raised the possibility that these populations could in fact belong to *D. walfordi* (e.g. Fouquet et al., 2011).

Herein, we have reported the second confirmed record for egg clutch deposit site plasticity for *Dendropsophus* and we argue that this characteristic allows *D. minusculus* to colonise and reproduce in a large amount of domains. Given the different physiological aspects of terrestrial and aquatic development, it seems obvious that egg and clutch structure could harbor significant variation and could be informative for phylogenetic studies. Unfortunately, these structures are almost unstudied in detail among amphibians

and nearly every facet of the field biology of amphibian eggs is poorly documented (Altig and McDiarmid, 2007).

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