

Rafael dos Santos Henrique

Ecologia do movimento da rã-manteiga (*Leptodactylus latrans*)
e da rã-touro (*Lithobates catesbeianus*)

Movement ecology of the Butter Frog (*Leptodactylus latrans*)
and the Bullfrog (*Lithobates catesbeianus*)

São Paulo

2016

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Versão corrigida da dissertação apresentada ao Instituto de Biociências da Universidade de São Paulo, para a obtenção de Título de Mestre em Ciências, na Área de Zoologia. Versão original encontra-se disponível no mesmo instituto.

Orientador: Prof. Dr. Taran Grant

São Paulo

2016

Ficha Catalográfica

Henrique, Rafael dos Santos.

Ecologia do movimento da rã-manteiga (*Leptodactylus latrans*) e da rã-touro (*Lithobates catesbeianus*) / Rafael dos Santos Henrique ; orientador Taran Grant. -- São Paulo, 2016.

v, 81 f.

Dissertação (Mestrado) – Instituto de Biociências da Universidade de São Paulo. Departamento de Zoologia.

1. Anfíbios. 2. Movimento. 3. Radiotelemetria. I. Grant, Taran, orient. II. Universidade de São Paulo. Instituto de Biociências. Departamento de Zoologia. III. Título.

Comissão Julgadora:

Prof(a). Dr(a).

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Prof. Dr. Taran Grant
Orientador

Agradecimentos

Agradeço a Universidade de São Paulo e ao Instituto de Biociências pela oportunidade do conhecimento e crescimento acadêmico através da realização deste trabalho.

Agradeço a Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP) e ao Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) por financiar os equipamentos e saídas à campo (Processo FAPESP 2012-10000-5) e pela bolsa de estudo de pós-graduação (Processo CNPq 134324/2015-5)

Agradeço ao meu orientador, Prof. Dr. Taran Grant, pela orientação e pela oportunidade e confiança na execução do projeto de mestrado do qual este trabalho foi resultado.

Agradeço a Dra. Camila Both, pelos comentários e ajuda na elaboração do meu projeto de mestrado e durante o planejamento e execução das atividades com radiotelemetria de rã-touro. Agradeço também a Ma. Camila Ineu Medeiros por proporcionar minhas primeiras experiências práticas com a biologia da invasão da rã-touro, em seus experimentos em campo em que pude participar.

Agradeço a todos os queridos amigos do Laboratório de Anfíbios do IB-USP por toda a ajuda, conversas, discussões e momentos de distração que permearam nossas convivências durante o período em que estive no laboratório. Agradeço em especial ao Gabriel Jorgewich Cohen por toda a ajuda nos diversos campos, por todos os dias e noites que nos encharcamos em brejos e poças, por toda rã-touro que nos escapou pelos dedos e por toda a ajuda e risada em momentos de frustração.

Agradeço também as amigadas que construí no Departamento de Zoologia do IB-USP, no Museu de Zoologia da USP e na organização dos Cursos de Verão em Zoologia, que durante a execução deste trabalho me ajudaram em diversas situações.

Agradeço a minha família e aos meus amigos que, mesmo não compreendendo muito bem a vida acadêmica, me apoiaram e respeitaram as minhas escolhas.

Agradecimentos específicos encontram-se no final de cada capítulo.

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INTRODUÇÃO GERAL

O movimento dos animais desempenha papel importante na aptidão dos indivíduos, no fluxo gênico, na dinâmica de metapopulações e na persistência, a longo prazo, de espécies em um ambiente (Semlitsch, 2007; Pittman *et al.*, 2014). As diferentes estratégias de vida das espécies refletem-se em diferentes padrões de movimentos que exigem diferentes requerimentos ecológicos (Duellman & Trueb, 1994). Para a maioria das espécies, esses movimentos são fundamentais para forragear, reproduzir, evitar condições ambientais severas, e evitar ou escapar de predadores (Zug *et al.*, 2001).

A maioria dos anfíbios é conhecida por se mover relativamente pouco durante toda a vida quando comparados com outros vertebrados (Zug *et al.*, 2001). Da eclosão do ovo à morte, um anfíbio muda seu padrão de movimento em resposta a diferentes requerimentos ecológicos. Indivíduos recém metamorfoseados de espécies que se reproduzem em poças, por exemplo, emigram de suas poças natal para se instalarem em suas áreas de vida individuais.

A área de vida de um indivíduo pode ser definida como um mapa cognitivo estabelecido pela relação entre o meio ambiente e a percepção do mesmo pelo animal. Essa relação constrói uma área na memória do animal dos lugares que ele conhece, utiliza e atualiza para aumentar sua aptidão (Powell, 2000; Spencer, 2012; Powell & Mitchell, 2012). Indivíduos vão e voltam de suas áreas de vida para novas unidades espaciais (áreas para reprodução, áreas ricas em presas para nutrição e áreas para hibernação/estivação) em movimentos circulares conhecidos como migrações. Esses movimentos fornecem todos os recursos essenciais para sobreviver e reproduzir (Semlitsch, 2007; Sinsch, 2014; Pittman *et al.*, 2014).

Já foi demonstrado que alguns fatores podem influenciar o tamanho da área de vida de um animal e a extensão de suas migrações. O principal fator reportado como preditor da área de vida de um animal é o tamanho corpóreo do mesmo (Seton, 1909). Essa relação pode ser explicada pela abundância e distribuição de alimentos (Jenkins, 1981), pelo tipo de dieta (Schoener, 1968; Mysterud *et al.*, 2001) e pelo metabolismo (McNab, 1963). Apesar da relação entre tamanho corpóreo e tamanho de área de vida já ter sido reportada para mamíferos, aves e lagartos

(McNab, 1963; Schoener, 1968; Turner *et al.*, 1969), tal relação nunca foi testada para anfíbios.

Com relação as migrações de anfíbios, os principais atributos que tem sido testados como preditores do movimento são fatores ambientais relacionados a condições climáticas e fases da lua (FitzGerald & Bider 1974; Woolbright, 1985; Mazerolle & Vos, 2006; Phillips *et al.*, 2007). Fatores ambientais como chuva, temperatura e umidade relativa do ar atuam diferentemente entre as espécies de anfíbios e não há consenso de como esses fatores influenciam a extensão dos movimentos de anfíbios.

Existem diversas maneiras de se estudar o movimento de anfíbios na natureza, como por exemplo, através da captura-marcação-recaptura de indivíduos, instalando carretéis com linha nos animais, etiquetas radio ativadas, etiquetas com sistemas GPS e através de radiotelemetria (Heyer *et al.*, 1994). Esta última, foi primeiramente usada com anfíbios no início da década de 60 (Tester, 1963), e desde então vem sendo utilizada em diversos estudos (van Nuland & Claus, 1981; Seabrook & Dettman, 1996; McAllister *et al.*, 2004; Humphries & Sisson, 2012).

A radiotelemetria consiste em instalar um transmissor de ondas de rádio no corpo do animal e, então, rastreá-lo afim de responder alguma problemática. Para isso, um transmissor com uma frequência conhecida é instalado interna ou externamente ao corpo do animal. Externamente, o transmissor pode ser acoplado ao corpo do animal utilizando colares, colas, armaduras, “mochilas”, entre outros (Kenward, 2001; Millsbaugh & Marzluff, 2001). O rastreamento do animal é feito usando uma antena acoplada a um receptor de sinal, que vai captar o sinal de cada transmissor e retornar um sinal em forma de pulso, que é ouvido através de um fone de ouvido acoplado ao receptor. Cada transmissor trabalha em uma frequência específica, assim, é possível diferenciar cada indivíduo pela frequência emitida pelo transmissor. Ao se aproximar de um transmissor, o sinal fica cada vez mais forte, indicando a proximidade do animal (Kenward, 2001; Millsbaugh & Marzluff, 2001). Neste trabalho, a radiotelemetria foi a técnica escolhida para estudar questões relacionadas à ecologia do movimento de duas espécies de anuros.

A primeira delas, *Leptodactylus latrans* (Fig. 1A), popularmente conhecida como rã-manteiga, é uma espécie nativa (ou grupo de espécies; para comentários relacionados à taxonomia veja De Sá *et al.*, 2014) com ampla distribuição por todo o leste dos Andes da América do Sul (Frost, 2016). Os indivíduos dessa espécie são

terrestres, de tamanho corpóreo médio para grande, hábitos noturnos e usualmente habitam poças temporárias ou permanentes, córregos e alagados em áreas abertas ou florestadas (Heyer *et al.*, 1990; França *et al.*, 2004; Haddad *et al.*, 2013). Apesar da espécie ser relativamente abundante e estar distribuída em muitos países da América do Sul, há pouca informação em relação a aspectos ecológicos e nenhuma informação disponível em relação aos seus movimentos.

A segunda espécie, *Lithobates catesbeianus* (Fig. 1B), popularmente conhecida como rã-touro americana (*American Bullfrog*), é um anuro de porte grande (Durham & Bennett, 1963), predador generalista (Korschgen & Moyle, 1955; Raney & Ingram, 1941) e apresenta alta fecundidade (Howard, 1978). A distribuição original da espécie vai do sudeste do Canadá, leste dos Estados Unidos ao nordeste do México (Frost, 2016). Contudo, atualmente existem registros de ocorrência da espécie em quase 40 países, incluindo o Brasil (Kraus, 2009; Giovanelli *et al.*, 2007; Both *et al.*, 2011), devido a sua grande comercialização para consumo humano através da ranicultura.

A popularização da ranicultura no final da década de 90 (Ferreira *et al.*, 2002) foi responsável pelo aumento no número de ranários no país que, por sua vez, podem ter sido responsáveis por uma série de escapes da espécie para a natureza. Atualmente, a distribuição de *L. catesbeianus* encontra-se concentrada na região Sudeste e principalmente na região Sul do país (Giovanelli *et al.*, 2007; Both *et al.*, 2011). Porém, não é possível determinar o quanto da atual distribuição de rãs touro no Brasil é devido a maior concentração de ranários na região Sul e Sudeste e o subsequente escape de indivíduos de tais ranários, e o quanto, a partir de um evento de escape, a espécie migrou para novas localidades e ali se instalou. Como não existem informações sobre o histórico da invasão de cada local, não podemos diferenciar entre esses dois processos para determinar a contribuição de cada um deles para a expansão da espécie no Brasil. Para se entender a biologia da invasão desta espécie, sua relação com espécies nativas e o seu potencial de dispersão, é fundamental ter informações básicas sobre seus movimentos. Assim, adquirir conhecimento científico específico sobre como esses animais se locomovem em um ambiente invadido, é um dos primeiros passos para o manejo de áreas invadidas e para evitar que a espécie atinja regiões onde ainda não foram detectadas sua presença.



Figura 1. Espécies estudadas neste trabalho. (A) *Leptodactylus latrans*, (B) *Lithobates catesbeianus*. Ambos os indivíduos estão marcados com radiotransmissores.

Devido ao tamanho corpóreo grande e a elevada abundância nas regiões onde essas espécies ocorrem, tanto a rã-touro como a rã-manteiga, associadas a metodologias como a radiotelemetria, são excelentes modelos para se estudar aspectos da ecologia do movimento de anfíbios. Entender como esses animais se locomovem na natureza é fundamental para a conservação e entendimento de processos ecológicos e evolutivos relacionados as histórias de vidas dessas espécies. Para isso, esta dissertação está organizada em três capítulos que visam entender distintos aspectos da ecologia do movimento dessas espécies. Esses capítulos estão estruturados no formato de artigos científicos de diferentes periódicos. O primeiro capítulo, intitulado “**Intra and interspecific relationship of home range to body size in anurans**”, reporta a área de vida de indivíduos de *L. latrans* e testa a relação intraespecífica entre o tamanho corpóreo de indivíduos da espécie com o tamanho de suas áreas de vida. Ainda, esses dados são incluídos à informações de outras espécies de anuros, retiradas da literatura, para testar a relação interespecífica entre tamanho de área de vida e tamanho corpóreo em Anura. Este capítulo está estruturado para ser submetido para a revista *South American Journal of Herpetology*, que é uma revista especializada em herpetologia com amplo alcance na comunidade científica. O segundo capítulo, intitulado “**Shelter use and the influence of environmental factors on short-term movements of**

the Butter Frog, *Leptodactylus latras* (Anura, Leptodactylidae)”, descreve os abrigos diurnos de *L. latrans* e investiga a contribuição de fatores ambientais como chuva, temperatura, umidade relativa do ar, fases da lua, entre outros, na distância diária deslocada por indivíduos da espécie. Este capítulo será submetido para a revista *Journal of Herpetology*, outra revista de âmbito herpetológico amplamente difundida na comunidade científica. Por fim, o terceiro capítulo, “**Movements of new Bullfrog (*Lithobates catesbeianus*) propagules in an invaded area**”, investiga os movimentos de novos propágulos de rã-touro translocados para uma região já invadida pela espécie e busca entender se indivíduos recém introduzidos exploram mais o ambiente que indivíduos residentes por não terem territórios estabelecidos. Este capítulo, foi estruturado com as mesmas regras de formatação do segundo capítulo, contudo, não foi decidido para qual revista o mesmo será submetido. Por questões de estética, as formatações como margem, espaçamento de linhas, títulos e fontes serão as mesmas para todo o trabalho.

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CAPÍTULO 1

INTRA AND INTERSPECIFIC RELATIONSHIPS OF HOME RANGE TO BODY SIZE IN ANURANS

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ABSTRACT

Home range is the area traversed by an animal in its normal activities such as feeding, mating and caring for young. The size of the home range is influenced by the body size in lizards, birds, and mammals. No such correlation has been reported to amphibians. The aims of this study are to investigate the intra and interspecific relationships of home range to body size within *Leptodactylus latrans* individuals and among anuran species, respectively. Frogs were radio tagged and had their home range estimated by MCP and Kernel methods. To analyze home range size and body size of other anuran species, available literature data was used. The mean home range size of *L. latrans* was 2034.2 m². There was no correlation between home range size and body size within *L. latrans* but when analyzing other anuran species, larger species had larger home range sizes. The discordance in the home range–body size relationship at different taxonomic hierarchical levels shows that causal mechanisms operating within species should not be used to explain interspecific results because these relationships are not necessarily parallel. Metabolic rate, diet type and food abundance have been suggested as predictors of this relationship in endothermic vertebrates but not to exothermic vertebrates. Although there is no conclusion of what rules the relationship between body size and home range size in anuran species, population density, availability of shelter sites and food abundance should play an important role in this relationship.

Keywords. Amphibia; Body Length; Minimum Convex Polygon; Radiotelemetry; Space use; Spatial Ecology.

INTRODUCTION

Knowledge has been attributed to the definition of home range along the years. Burt (1943) set that home range is the area traversed by an animal in its normal activities such as feeding, mating and caring for young. A more statistical definition of home range is the one described by the utilization distribution (UD), in which home range is the relative frequency distribution of an individual in each point of space over time (Van Winkle Jr. et al., 1973; Worton, 1987). More recently, home range was defined as part of a cognitive map established by the relationship between the environment and the animal's perception of it. This relationship builds an area in the animal's memory of places it knows, maintains and updates, to increase fitness (Powell, 2000; Spencer, 2012; Powell and Mitchell, 2012). Although many studies have been published on home range, no conclusion has been taken on its definition.

The extension of home range might be influenced by the size of the animal (Seton, 1909). Such relationship has already been demonstrated for mammals (McNab, 1963; Harestad and Bunnell, 1979), birds (Armstrong, 1965; Schoener, 1968), and lizards (Turner et al., 1969). Although no global conclusion has been reported to what rules this relationship, it has been suggested to be determined by food abundance and distribution (Jenkins, 1981), diet type (Schoener, 1968; Myrnes et al., 2001), and metabolism (McNab, 1963). Despite being well reported in mammals, birds and lizards, the relationship of home range size to body size has never been tested for other vertebrate groups such as fishes or amphibians.

Mean home range sizes among anuran species vary widely, ranging from 0.6 m² in *Mannophryne trinitatis* (Wells, 1980) to 246,000.2 m² in *Anaxyrus boreas* (Muths, 2003). The difference in home range size between males and females also presents variations, being present in some cases (Muths, 2003; Poelman and Dicke, 2008), while absent in others (Ra et al., 2008; Werner et al., 2011; Valenzuela-Sánchez et al., 2014). Wells (2007) has suggested that small species of anurans have smaller home range sizes than bigger ones, although he did not test it empirically. While this relationship is present intraspecifically in some species (Currie and Bellis, 1969; Valenzuela-Sánchez et al., 2014) and absent in others (Forester et al., 2006; Ra et al., 2008), no test has been done with interspecific analysis.

Although Brazil is the richest country in anuran diversity, the study of anuran home range has been historically neglected in the Brazilian herpetological literature.

Hylodes dactylocinus is the only species with its home range estimated (Narvaes and Rodrigues, 2005). *Leptodactylus latrans*, a broadly distributed cis-Andean South American species (Frost, 2016), is a medium- to large-sized, nocturnal frog that usually inhabits temporary or permanent ponds, streams and marshes in open or forested areas (Heyer et al., 1990; França, Fecure and Giaretta, 2004; Haddad et al., 2013; de Sá et al., 2014) and is often found in strongly anthropogenic landscapes (Solé et al., 2009, Ferreira and Tonini, 2010). These attributes make the species a well suitable candidate for home range estimation. Therefore, the aims of this study are (1) to estimate the home range size of individuals of a Brazilian population of *L. latrans*; (2) to investigate the intraspecific relationship between home range size and body size of *L. latrans* and (3) to investigate the interspecific relationship between home range size and body size among anuran species.

MATERIALS AND METHODS

Study Site

The study was conducted from November 2015 to January 2016 in several permanent and temporary ponds, streams, and marshy areas of the Agronomic Experimental Station of the Federal University of Rio Grande do Sul (EEA-UFRGS) (30° 05.620' S; 51° 40.400' W, datum WGS 84), Eldorado do Sul city, Rio Grande do Sul state, Brazil. All water bodies were surrounded by pasture and underbrush matrices in a former Atlantic Rainforest area.

Marking Technique

Twenty-nine males of *Leptodactylus latrans* were captured by hand at night and sexed by the presence of nuptial spines and hypertrophied forearms in males (de Sá et al. 2014). Each frog was measured (snout–vent length, SVL) to nearest 0.05 mm and weighed to nearest 2.0 g. SVL and body mass are presented as mean \pm SD. Frogs were marked with 6-month lifespan radio transmitters (PD-2, Holohil Systems Ltd., Carp, Ontario, Canada) weighing 3.8 g each. The weight of the transmitters was less than 10% of each frog's mass, assuring that it would not negatively affect movements (Richards et al., 1994). The transmitters were attached on the waist of the frogs with satin ribbon, tested previously on captive *Lithobates catesbeianus* to ensure that the ribbon would not cause skin abrasions or otherwise

harm the frog. All frogs were released at the point of capture. All procedures were authorized by Instituto Chico Mendes de Conservação de Biodiversidade (SISBIO 44980-9) and the Institute of Biosciences Comissão de Ética no Uso de Animais (CEUA IB-USP 243/2016).

Radio Telemetry

Frogs were tracked daily with a handheld 3-Element Yagi antenna by morning and every other day by night. A minimum 12-hour interval was defined to avoid tracking individuals in the same moving period considering that individuals move only at night. Positions of the each frog were recorded with a Global Position System device (GPSmap 62sc, Garmin Ltd.) even when visual confirmation was not possible (triangulation was always $< 1 \text{ m}^2$). When frogs remained at the same place, previous geographical coordinates were used for the positioning as to avoid the GPS triangulation bias the relocation of the animals (wooden stack flags were placed during tracking to mark these spots). Frogs were not handled or disturbed until the end of the experiment in order to avoid interfering with or biasing their movements. At the end of the experiment, visual confirmation off all frogs was necessary to validate previously taken positions.

Home Range Estimation

Home range was estimated by Minimum Convex Polygon method (MCP; Mohr, 1947) and by Bivariate Normal Kernel method (Worton, 1989), utilizing the functions *mcp()* and *kernelUD()*, respectively, of the package *adehabitatHR* Version 0.4.12 (Calenge, 2015) in *R* 3.2.1 (R Core Team, 2015). Only frogs with more than 25 fixes (location points) were considered for the home range estimation to avoid small sample size bias (Schoener, 1981; Worton, 1987; Seaman *et al.*, 1999). Ninety-five percent of the fixes (contour level) was considered to estimate the home range sizes (Laver and Kelly, 2008). Plots were generated to each individual to check whether home range estimations have reached asymptotes. The smoothing parameter *href* (reference bandwidth) and a grid resolution of 100 were used in the Kernel method.

Literature Survey

In order to investigate the interspecific relationship between body length and home range size in anurans, four bibliographic scientific databases were searched (*Google Scholar*, *Scielo*, *Scopus* and *Web of Science*) to cover all the papers that have already published about home range in anurans. Only peer-reviewed publications were considered.

Search was made up to June 2016, and the following combination of key-terms in the title, abstract and keywords were taken into consideration: “home range” + “Anura” or “Amphibia” or “amphibian” or “anuran” or “frog” or “toad”. Corresponding Portuguese and Spanish terms of “home range” (“área de vida” and “ámbito de hogar”, respectively) were used with the corresponding terms of “frog” and “toad” (“rã”, “perereca” and “sapo”; Portuguese) (“rana” and “sapo”; Spanish).

The following data were recorded from each paper: year of publication, species name and family (as the current taxonomy), country of the study site, marking technique, data collection method, sampling duration, home range estimation method and minimum fixes considered to estimate home range. The sex of the individuals was taken into account to record sample size, mean home range size and mean body length (SVL). When the mean SVL of individuals was not mentioned, other studies were used to complete the mean body length of that species. When only minimum and maximum SVL was available, the mid SVL (maximum SVL + minimum SVL / 2) was used as proxy of the mean body length of that species. Only home range estimations of males were used due to little information on home range of females.

Statistical Analyses

To test if larger individuals of *L. latrans* have larger home range sizes, linear regression analyses were performed between $\log(n)$ transformations of (1) MCP ~ body mass; (2) MCP ~ SVL; (3) Kernel ~ body mass and (4) Kernel ~ SVL. The same analysis was used between (5) MCP ~ number of fixes and (6) Kernel ~ number of fixes, to test if individuals with more fixes would present larger home range areas.

To investigate the interspecific relationship between body length and home range size in anurans, the information extracted from the literature survey was used to achieve home range sizes and body lengths of other species. Linear regression analysis between $\log(n)$ transformations of (7) MCP ~ body lengths of the species,

was used to test if larger species have larger home range sizes. When information about both sexes was available, only the male was used. All the statistical analyzes were performed in R 3.2.1 (R Core Team, 2015), with a significance value of $\alpha=0.05$

The predictions are (a) with increasing body mass and SVL of *L. latrans* individuals, home range sizes will also increase; (b) individuals with more fixes collected should not have larger home range sizes since care was taken to avoid small sample size bias and (c) anuran species with larger body length will have larger home range sizes.

RESULTS

Among the 29 individuals of *Leptodactylus latrans*, only 11 were relocated more than 25 times for the home range estimation. SVL ranged from 84–97 mm (90.3 ± 4.1 mm), and mass from 77–134 g (94.1 ± 18.8 g). The mean number of fixes per frog was 39 (28–47). The Kernel method estimated larger home range sizes than MCP method (Wilcoxon test, $p= 0.001$). By the MCP estimation, the mean home range was 2034.2 ± 2238.4 m² (69.8–7196.9 m²). By the Kernel estimation, the mean home range was 9908.3 ± 10564 m² (722–33844.1 m²).

There was no increase in body length (SVL) with increasing home range size in *L. latrans* neither by MCP ($p= 0.262$) or Kernel ($p= 0.494$) estimation. The size of the home range was also independent of the body mass for both methods [MCP ($p= 0.6414$); Kernel ($p= 0.912$)]. The number of fixes also showed no influence in the home range estimation in both MCP ($p= 0.665$) and Kernel ($p= 0.657$) methods.

In the literature survey, 44 studies on home range of anuran species were found. Most studies are from North (n=16) and South (n=12) America (Figure 1), and there was an increase on these studies in the 2000s (Figure 2). The most common marking techniques were toe clipping (n=19) and radio transmitters (n=10). Regarding the data collection method, most studies used grids (n=19) to collect referenced spatial data of individuals (Table 1). Three studies were excluded for not mentioning the home range estimation method. Three other studies were excluded since they showed only movements or linear values of home range. Only studies of the MCP estimation method were selected, given that there were few studies (n=11) of Kernel estimation method of species with available body length data. Yet, two

studies of MCP estimation were excluded for lacking body length information in the literature. A summary of all studies is shown in Table 2.

In total, 29 species (from the available literature described above) plus the data registered for *L. latrans* were selected to investigate the relationship between SVL and home range size on anuran species. As a result, anuran species with larger SVL present larger home range sizes ($r^2= 0.35$; $p= 0.0003$; Figure 3).

DISCUSSION

The results revealed a disagreement between the intra and interspecific relationships of body size to home range size when comparing the analysis from *Leptodactylus latrans* data and the anuran species data. While there was no relationship within a *L. latrans* population, the literature analysis showed that with the increase in body size there is an increase in home range size among anuran species. The discordance in this relationship at different hierarchical levels shows that causal mechanisms operating within species should not be used to explain interspecific results because these relationships are not necessarily parallel (Gompper and Gittleman, 1991).

The mean home range size of *L. latrans* was much larger ($\bar{x}= 2034.2 \text{ m}^2$) than the mean home range size of all other species together of the literature analysis ($\bar{x}= 706.5 \text{ m}^2$). Only *Rana pretiosa* (Turner, 1960), *Babina subaspera* (Iwai, 2013) and *Pseudacris triseriata* (Kramer, 1974) had larger home range sizes than *L. latrans*. Still, the mean home range of *L. latrans* estimated by the MCP method may be underestimated given that not all estimation of home range have reached asymptote curves in relation to the number of fixes collected (eight out of eleven reached asymptote) representing a possible sample size bias in these cases (Worton, 1987; Seaman et al., 1999).

There was a large difference between the mean home range size estimated using MCP method and using Kernel method (2034.2 m^2 to 9908.3 m^2 , respectively). Differences between methods were also reported to other species (Qi et al., 2007; Brown et al., 2009). Anurans do not move often and use the same shelter or calling site multiple times during an active season. This can cause an autocorrelation of the position points (Row and Blouin-Demers, 2006). Statistical methods of home range estimation, such as Kernel methods, do not perform well with autocorrelated data

(Worton, 1987; Seaman and Powell, 1996), underestimating the size of the true home range (Swihart and Slade, 1985) while MCP is not affected by autocorrelation (Harris et al., 1990). Therefore, Kernel methods may estimate larger home range sizes than MCP for herpetofauna species (Row and Blouin-Demers, 2006). Still, the home range size of *L. latrans* could have been overestimated by Kernel method if there was a small sample size bias (Seaman et al., 1999). Therefore, MCP method must have estimated a more precise home range size for *L. latrans* than Kernel method.

When compared to other vertebrate groups, such as mammals and birds, little attention has been given to the study of anuran's home range even though the number of studies increased since 2000's (totalizing 44 studies in June, 2016). This scenario may reflect the limitations and the difficulties of marking and tracking amphibians. Toe clipping is the most usual marking technique applied in the study of anuran's home range (n = 19), even though this technique is highly time consuming. The difference in the amount of data collected in the same period of time with both toe clipping and radio tracking is huge. Yet, when considering movement studies of animals with little movement rate, such as most anurans species, handling an animal every time it is found or trapped would probably add a considerable bias on the next movement of the individual when it is released. On the other hand, radio tagging anuran species can be challenging since the animals could bruise their thin skin easily. Previous tagging tests, preferably in the field, are necessary to select the softest, but durable, tagging material to the species at issue. As a result, these disadvantages in both marking techniques, may limit the number of studies on amphibian's movements.

As in mammals (McNab, 1963), birds (Armstrong, 1965) and lizards (Turner et al., 1969), larger species of anurans showed larger home range sizes. But what drives the relationship between home range size and body size in anurans? Metabolic rate, diet type and food abundance have been suggested as predictors of this relationship in endothermic vertebrates (McNab, 1963; Schoener, 1968; Mysterud et al., 2001) but not to exothermic (e.g. lizards; Turner et al., 1969). Jenkins (1981) attributed this relationship to be associated to food abundance and distribution for birds and mammals. Although anurans show major differences in metabolism compared to endothermic animals, food abundance and distribution seems to be more explanatory of home range size to these animals than other causes. Actually,

the mode that anurans obtain food spatially distributed in the environment is probably a better predictor of home range size than body size itself (Wells, 2007). This conclusion, however, contradicts with the results described here since sit-and-wait predators usually are larger than active foragers (Wells, 2007). Thus, sit-and-wait predators, according to Wells (2007), would have smaller home range sizes since they move less than active foragers whereas our results suggest that sit-and-wait species would have larger home range sizes since they are larger. Unfortunately, foraging mode data of anurans is not always available for a more specific analysis.

Population density has also been reported to mammals (White, 1964) and to the plethodontid salamander, *Desmognathus monticola*, (Kleeberger, 1985) as the predictor of home range size. Although at high population density the size of home range is smaller in mammals, amphibians probably have to displace more to search for food and shelter at high population densities (Kleeberger, 1985) leading to larger home range sizes (Wells, 2007).

What rules the relationship between body size and home range size in anuran species is still unknown but probably population density, availability of shelter sites, and food abundance play important roles in this relationship. Investigating the intraspecific relationship of home range to body size within anuran species and its possible predictors could elucidate a bigger scenario in comparative studies. However, not all studies search for the intraspecific relationship when estimating home range sizes of anuran species. Although there was no correlation of home range to body size within *L. latrans* and to other species (Martof, 1953; Brown et al., 2009), within some others, bigger individuals have larger home ranges (Dole and Durant, 1974; Hutter et al., 2016). Researchers should be encouraged to estimate home range of amphibian species and to search for this relationship when publishing these studies. Taking into consideration species conservation programs, knowing the size of the home range of a species and its space utilization could be useful tools to achieve biological meaningful conservation boundaries areas.

ACKNOWLEDGMENTS

We thank J.R. do Desterro, C. Rossi, I.R.S. Cavalcanti, and G.J. Cohen for helping with fieldwork, C. Jared for providing the facilities for previous tagging tests, the crew from Estação Experimental Agronômica of Universidade Federal do Rio

Grande do Sul for logistical support, and A.M. Jeckel, A.Q. Bottallo, and D.O.V. Parajara for comments on the manuscript. This research was supported by Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP Process 2012/10000-5) and Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq Processes 305234/2014-5 and 134324/2015-5).

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TABLES

Table 1. Frequency distribution of marking techniques and data collection methods on available publications (n=38) on home range of anuran species.

	n	%
MARKING TECHNIQUE		
Toe clipping	19	39.6
Radio transmitter	10	20.8
Color pattern	7	14.6
PIT-tag	3	6.3
Thread bobbin	2	4.2
Radioactive tag	2	4.2
Beads	1	2.0
Lines and wires	1	2.0
Not mentioned	3	6.3
Total	48	100
DATA COLLECTION		
Grid	19	50.0
GPS	7	18.5
Landmarks	1	2.6
Polar coordinates	1	2.6
Not mentioned	10	26.3
Total	38	100

Table 2. Summary of available publications on home range of anuran species. Species names are listed alphabetically as in Frost, 2016.

SPECIES	SVL (mm)	MINIMUM SIGHTING	MCP (m ²)	KERNEL (m ²)	REFERENCE ^(A)
BUFONIDAE					
<i>Anaxyrus americanus</i>	-	-	-	687.9	Forester <i>et al.</i> , 2006
<i>Anaxyrus boreas</i>	65.4	5	-	58298.8	Muths, 2003
<i>Anaxyrus fowleri</i>	69.9 ⁽¹⁾	23	750	-	Clarke, 1974
<i>Atelopus carbonerensis</i>	44.1	4	56.2	-	Dole and Durant, 1974
<i>Atelopus hoogmoedi</i>	26.1	10	-	38.1	Luger, Hodl and Lotters, 2009
<i>Bufo bufo</i>	69.85 ⁽²⁾	-	1901	-	Sinsch, 1987
<i>Rhinella marina</i>	140 ⁽³⁾	-	167.8	-	Zug and Zug, 1979
CRAUGASTORIDAE					
<i>Craugastor augusti</i>	71,85 ⁽⁴⁾	-	-	1085.7	Goldberg and Scwalbe, 2004
<i>Pristimantis eremitus</i>	23.25 ⁽⁵⁾	3	26.14	-	Hutter <i>et al.</i> , 2016
DENDROBATIDAE					
<i>Allobates femoralis</i>	27.15	5	7.6	-	Roithmair, 1992
<i>Colostethus panamensis</i>	24.43 ⁽⁶⁾	-	2	-	Wells, 1980b
<i>Dendrobates auratus</i>	30.7 ⁽⁷⁾	-	3.15	-	Summers, 1989
<i>Dendrobates leucomelas</i>	33.8 ⁽⁷⁾	10	19.9	-	Summers, 1992
<i>Mannophryne trinitatis</i>	23 ⁽⁸⁾	-	0.6	-	Wells, 1980a
<i>Oophaga pumilio</i>	20.9 ⁽⁷⁾	20	18.2	20.7	Pröhl and Berke, 2001
<i>Oophaga sylvatica</i>	26.81 ⁽⁹⁾	10	3.9	-	Summers, 1992
<i>Ranitomeya amazonica</i>	16.23	5	2	1.8	Poelman and Dicke, 2008
<i>Ranitomeya imitator</i>	-	3	10.53	43.37	Brown, Morales and Summers, 2009
<i>Ranitomeya reticulata</i>	14.37 ⁽¹⁰⁾	4	26.03	55.35	Werner <i>et al.</i> , 2011
<i>Ranitomeya variabilis</i>	-	3	31.32	423.45	Brown, Morales and Summers, 2009
ELEUTHERODACTYLIDAE					
<i>Eleutherodactylus marnockii</i>	26.9 ⁽¹¹⁾	-	435	-	Jameson, 1955
HYLIDAE					
<i>Pseudacris triseriata</i>	26.5 ⁽¹²⁾	10	2117	-	Kramer, 1974
HYLODIDAE					

<i>Hylodes dactylocinus</i>	25.2 ⁽¹³⁾	3	6.62	-	Narvaes e Rodrigues, 2005
LEPTODACTYLIDAE					
<i>Leptodactylus latrans</i>	90.3	25	2034.2	9908.3	This study
<i>Leptodactylus macrosternum</i>	49.5	4	43.3	-	Dixon and Staton, 1976
RANIDAE					
<i>Babina subaspera</i>	116.5 ⁽¹⁴⁾	10	5300.4	-	Iwai, 2013
<i>Lithobates capito</i>	87.6	3	42.29	-	Blihovde, 2006
<i>Lithobates clamitans</i>	80.04 ⁽¹⁵⁾	-	64.8	-	Martof, 1953
<i>Lithobates heckscheri</i>	32.05	-	16	-	Hansen, 1957
<i>Lithobates pipiens</i>	77 ⁽¹⁶⁾	6	372	-	Dole, 1965
<i>Lithobates sylvaticus</i>	41.5	5	64.6	-	Bellis, 1965
<i>Pelophylax chosenicus</i>	50	3	-	713.8	Ra <i>et al.</i> , 2008
<i>Rana kukunoris</i>	57.3	-	157.9	796.2	Qi <i>et al.</i> , 2007
<i>Rana muscosa</i>	62.3	7	-	2381.7	Matthews and Pope, 1999
<i>Rana pretiosa</i>	46	5/10	8732.9	22000	Turner, 1960; Watson, McAllister and Pierce, 2003
<i>Rana sierrae</i>	59.5	5	139	-	Fellers <i>et al.</i> , 2013
RHINODERMATIDAE					
<i>Rhinoderma darwinii</i>	22.92	4	2.89	-	Velenzuela-Sánchez <i>et al.</i> , 2014
SCAPHIOPODIDAE					
<i>Scaphiopus holbrookii</i>	63 ⁽¹²⁾	6	8.5	-	Pearson, 1955

Supplementary references^(A): (1) Meacham, 1962; (2) Reading and Clarke, 1983; (3) Kenny, 1969; (4) Taylor, 1938; (5) Lynch, 1980; (6) Grant, 2004; (7) Silverstone, 1975; (8) La Marca, 1994; (9) Myers and Daly, 1976; (10) Myers, 1982; (11) Lynch, 1970; (12) Wright and Wright, 1933; (13) Pavan *et al.*, 2001; (14) Inger, 1947; (15) Martof, 1956; (16) Blomquist and Hunter Jr., 2007.

FIGURES

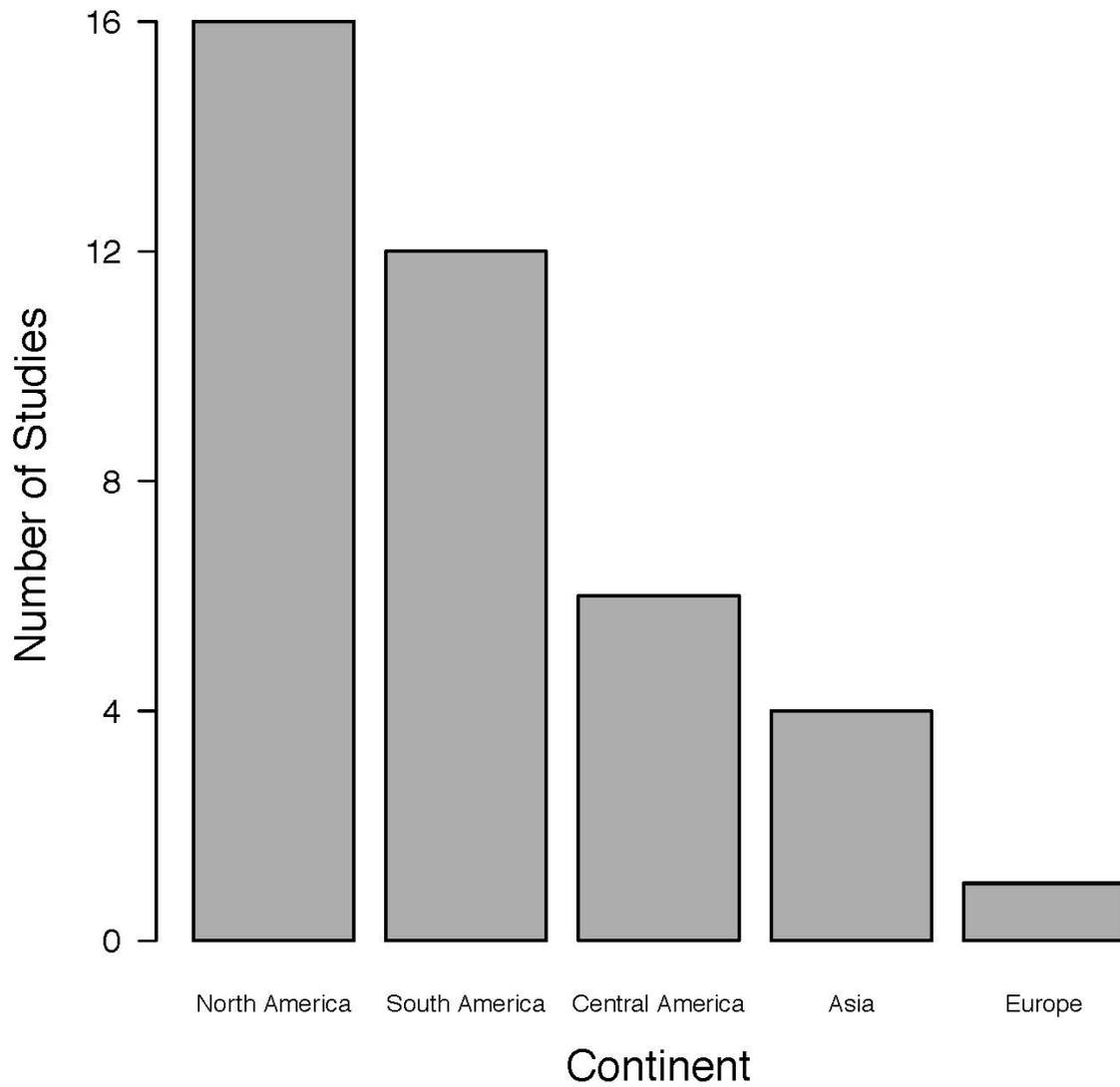


Figure 1. Distribution of available studies on home range of anuran species per continent.

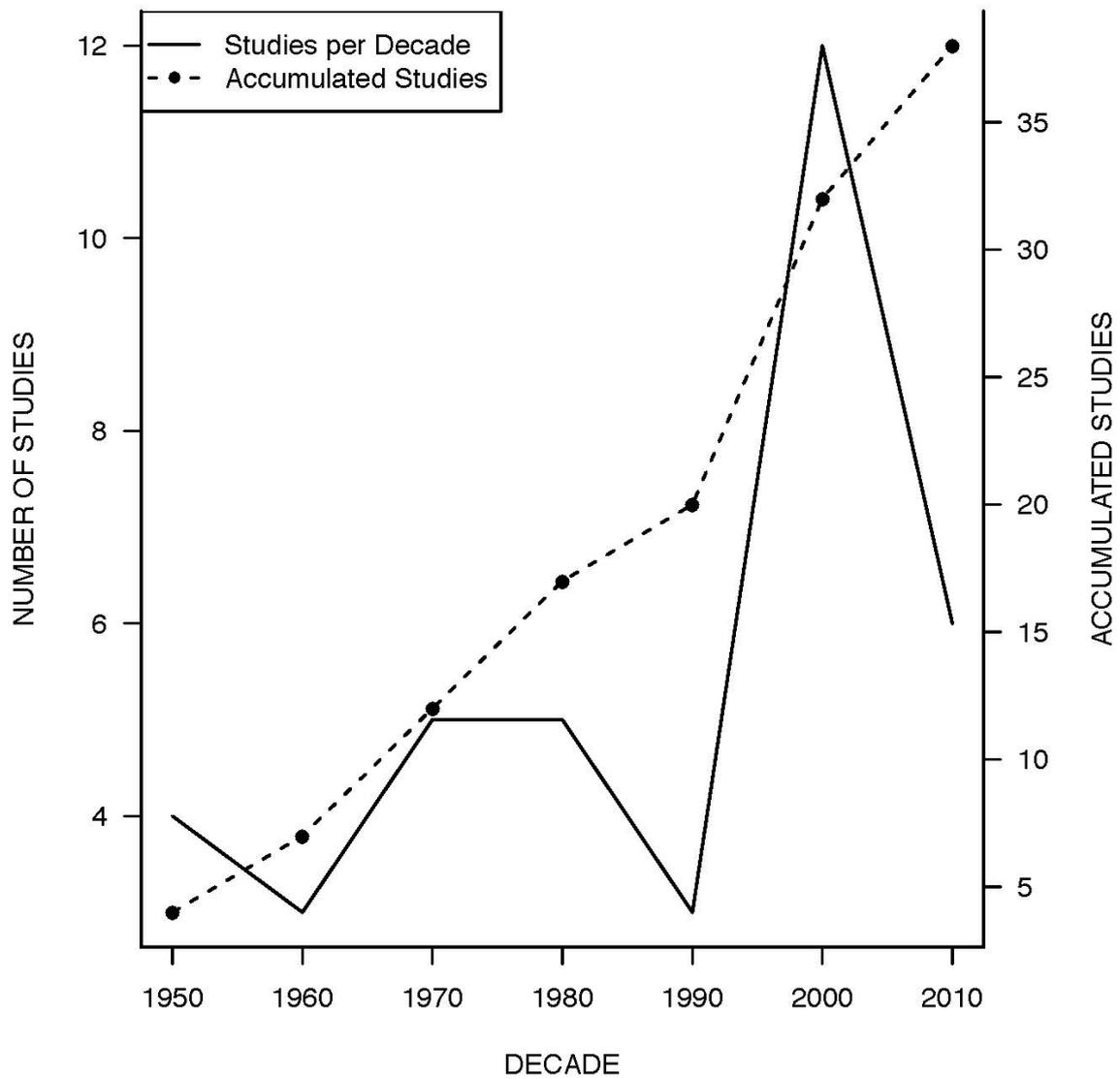


Figure 2. Absolut and accumulated frequency of studies on home range of anuran species per decade.

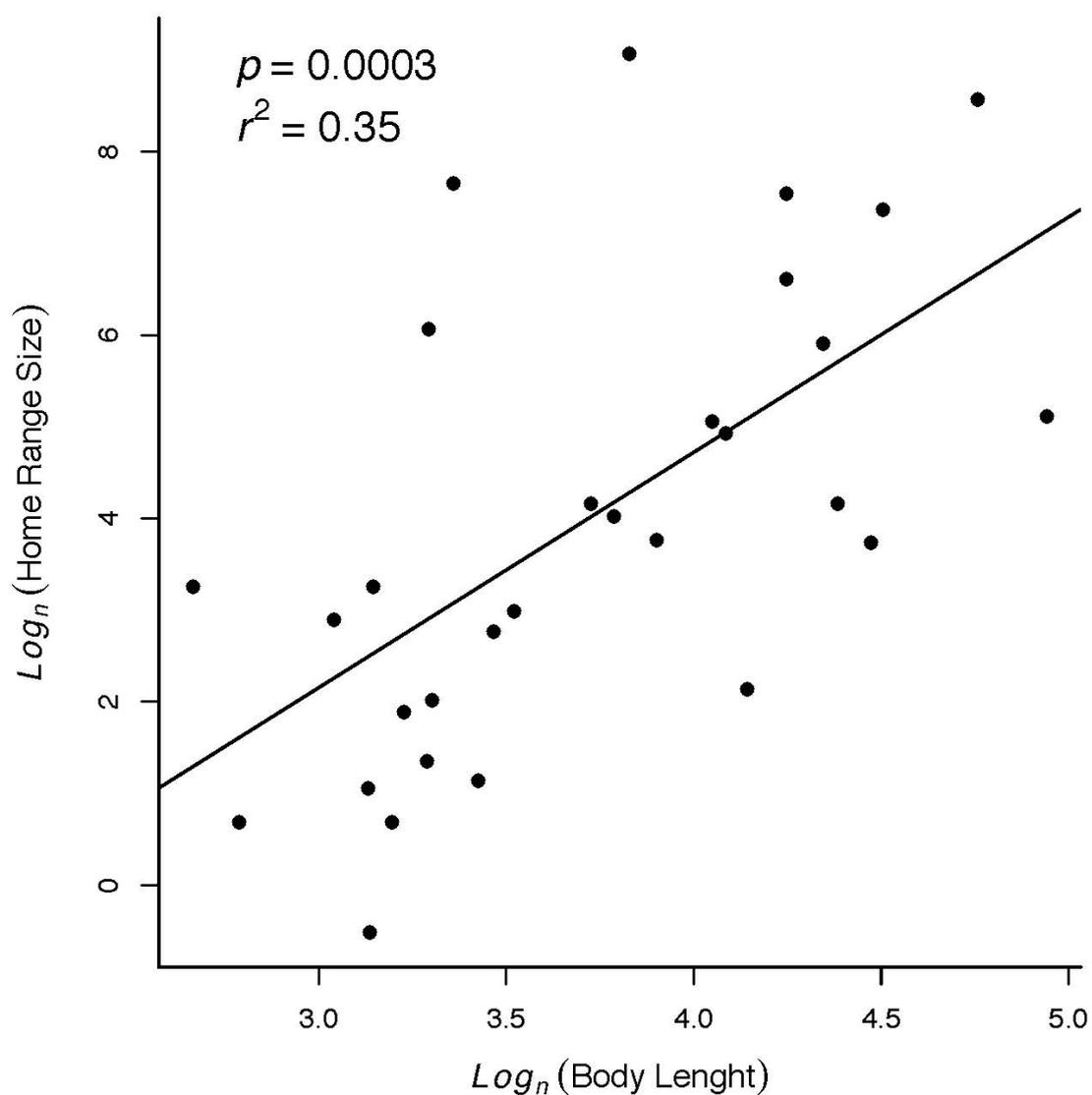


Figure 3. Relationship of mean home range size (MCP; m^2) to mean body length (mm) in anuran species. See Table 2 for details of species used in the analysis of regression.

CAPÍTULO 2

SHELTER USE AND THE INFLUENCE OF ENVIRONMENTAL FACTORS ON SHORT-TERM MOVEMENTS OF THE BUTTER FROG, *Leptodactylus latrans* (ANURA, LEPTODACTYLIDAE)

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ABSTRACT

For most pond-breeding amphibians, movements are fundamental for foraging, reproduction, avoidance of inclement environmental conditions, and to predator avoidance and escape. Although the influence of environmental factors on amphibian activity, such as temperature and rainfall, has been well reported, the role of these factors on amphibian movements is not clear. The aim of this study was to understand the influence of environmental factors on movement distances of *Leptodactylus latrans*. We radio-tracked 11 males during breeding season to collect data on their movements. We fit movement data as response variable and environmental factors as fixed effects in generalized linear models. We ran model selection and model averaging to understand the contribution of each variable on the species' movements. We were not able to clarify what triggers the movement in *L. latrans*, however, lunar phase, rainfall and temperature seem to play an important role in movement distances. Frogs moved three times more during dark nights of New Moon than in bright nights of Full Moon. The main reasons to amphibians' response to lunar cycle have been associated to predator avoidance and reproduction synchronization whereas rainfall and temperature are most associated to water balance and metabolism regulation.

Keywords. Amphibia; lunar phases; rainfall; temperature; model selection

RESUMO

Para a maioria dos anfíbios que se reproduzem em poças, movimentos são fundamentais para a alimentação, reprodução e para evitar predadores e condições ambientais extremas. Embora a influência de fatores ambientais na atividade de anfíbios, como temperatura e chuva, ser bastante reportada, o papel desses fatores no movimento de anfíbios não é claro. O objetivo deste estudo foi entender a influência de fatores ambientais na extensão dos movimentos de *Leptodactylus latrans*. Nós rastreamos 11 machos durante a estação reprodutiva para coletar informação de seus movimentos. Nós ajustamos esses dados como a variável resposta e fatores ambientais como fatores fixos em modelos lineares generalizados. Nós rodamos seleções de modelos e model averaging para entender a contribuição de cada variável no movimento da espécie. Nós não fomos capazes de esclarecer o que dispara o movimento em *L. latrans*, contudo, fases da lua, chuva e temperatura parecem exercer um papel importante na extensão do movimento. As rãs andaram três vezes mais durante as noites escuras da lua nova que durante as noites claras da lua cheia. As principais razões da resposta de anfíbios ao ciclo lunar tem sido associadas à evitar predadores e a sincronização da reprodução enquanto que chuva e temperatura estão mais associadas ao balanço hídrico e regulação do metabolismo.

Palavras-chave. Amphibia; fases da lua; chuva; temperatura; seleção de modelos

INTRODUCTION

Animal movements play a role in individual fitness, gene flow, population regulation, metapopulation dynamics and long-term persistence of species (Semlitsch, 2007; Pittman et al., 2014). Individuals present different age-regulated life strategies that result in different movement patterns and ecological requirements (Duellman and Trueb, 1994). For most species, these movements are fundamental for foraging, reproduction, avoidance of inclement environment conditions, and to predator avoidance and escape (Huey and Pianka, 1981; Zug, Vitt and Caldwell, 2001).

Most amphibians are known to move relatively little during their lifetime when compared with other vertebrates (Zug, Vitt and Caldwell, 2001). From hatching to death, an amphibian shifts its movement patterns to achieve different ecological requirements. Recently metamorphic individuals of pond-breeding species, for example, emigrate from their natal pond to settle in their individual home ranges. Round-trip movements (migrations) from their home range to other spatial units (breeding sites, prey-rich areas for nutrition, and hibernation/aestivation sites) provide all the essential resources to survive and reproduce (Semlitsch, 2007, Sinsch, 2014; Pittman et al., 2014).

Round-trip migrations of amphibians generally traverse several spatial units inside a single patch (patch-scale). However, in some species, all movements can occur within the same spatial unit (microhabitat scale; Sinsch, 1990), whereas in others, individuals can undertake long-distance interpatch, dispersive movements (regional scale; Sinsch, 2014). On a daily basis, amphibian movements generally take place at the microhabitat scale, inside a single spatial unit. These movements are mostly short-distance movements and are related to consumption of local resources, concealment from predators, and regulation of body moisture and temperature (Woolbright, 1985, Sinsch, 2014). As such, environmental factors are expected to play an important role in the daily movements of amphibian (Zug, Vitt and Caldwell, 2001).

The influence of environmental factors on amphibian activity has been well reported in literature. Air and water temperature (FitzGerald and Bider 1974b; Gilbert et al., 1994; Oseen and Wassersug, 2002), rainfall (Obert, 1975; Fukuyama and Kusano, 1992), wind velocity (Henzi et al., 1995), relative humidity (Bellis, 1962; Henzi et al., 1995), light intensity (Bellis, 1962), and lunar phases (Church, 1960; Ferguson, 1960; Kusano et al., 2015) are examples of environmental factors that influence amphibian's breeding activity, acting differently among anuran species (Salvador and Carrascal, 1990). However, the influence of environmental factors on amphibian movements is far from being clarified. For instance, temperature is the most common predictor of reproductive activity in anuran species, followed by rainfall (Oseen and Wassersug, 2002). However, no apparent relationship has been reported between temperature or rainfall and movement (Breckenridge and Tester, 1961; FitzGerald and Bider, 1974a; Woolbright, 1985; Tozetti and Toledo, 2005; Mazerolle and Vos, 2006). Relative humidity also plays some role in amphibian

activity but not in movement (Woolbright, 1985; Tozetti and Toledo, 2005). On the other hand, wind velocity, foliage, surface humidity and lunar phases have been reported as predictors of anuran's movements (FitzGerald and Bider 1974a; Woolbright, 1985; Mazerolle and Vos, 2006; Phillips et al., 2007).

Ambient light (e.g. dawn or dusk) seems to trigger and regulate movement and activity in most of the species on a daily basis (Zug, Vitt and Caldwell, 2001; Oseen and Wassersug, 2002) since most of amphibian species are nocturnal and tend to shelter in moist microhabitats during the day (Duellman and Trueb, 1994). This behavior allows individuals to reduce the effects of environmental stress and the risk of being attacked by visually oriented diurnal predators (Van Gelder, Aarts and Staal, 1986; Seebacher and Alford, 1999; Zug, Vitt and Caldwell, 2001; Oseen and Wassersug, 2002).

Therefore, the most common pattern in amphibian's daily movements is to move at night and shelter during the day. Since nocturnal microhabitats do not always suit diurnal requirements of sheltering, individuals use different microhabitats during the day and at night (Tozetti and Toledo, 2005). For some species, moving between diurnal shelters and nocturnal activity sites appears to be the main movement activity (Woolbright, 1985). Several types of microhabitats are used as diurnal shelters by anurans. In terrestrial species, rock crevices, fallen tree holes, dense or sparse ground vegetation and burrows constructed by other animals are usually used as shelters by frogs and toad (Seebacher and Alford, 1999; Stewart and Pough, 1983; Hoffman and Katz, 1989; Tozetti and Toledo, 2005; Wells, 2007).

Leptodactylus latrans is broadly distributed in cis-Andean South America (Frost, 2016). It is a ground-dwelling, medium- to large-sized nocturnal frog that usually inhabits temporary or permanent ponds, streams and marshes in open or forested areas (Heyer et al., 1990; França, Fecure and Giaretta, 2004; Haddad et al., 2013; de Sá et al., 2014) and is often found in strongly anthropogenic landscapes (Solé et al., 2009, Ferreira and Tonini, 2010). *Leptodactylus latrans* has a generalist diet comprising mostly arthropods such as Orthoptera, Dermaptera, Hemiptera, Hymenoptera, Coleoptera, Blattodea, Isoptera, insect larvae, and Aranea, as well as some vertebrates such as tadpoles and frogs (Teixeira and Vrcibradic, 2003; França, Fecure and Giaretta, 2004; Solé et al., 2009).

Despite being locally abundant and broadly distributed in many countries of South America, there is little information available on the ecology and microhabitat

use of *L. latrans* and none on movement. Thus, in this study we aimed to answer the following questions about *L. latrans* movement ecology: (1) what is the distance of daily movements of individuals of *L. latrans*? (2) How do environmental factors influence movement trigger in this species? (3) When moving, what is the contribution of environmental factors on movement distance? (4) How does this species use diurnal shelters? (5) Do individuals of *L. latrans* move long distances searching for nocturnal activity sites in the evening or diurnal shelters at dawn?

MATERIALS AND METHODS

Study Site and Environmental Data Collection

The study was conducted in November and December 2015 in several permanent and temporary ponds, streams, and marshy areas of the Agronomic Experimental Station of the Federal University of Rio Grande do Sul (EEA-UFRGS) (30° 05.620' S; 51° 40.400' W, datum WGS 84), Eldorado do Sul city, Rio Grande do Sul state, Brazil. All water bodies were surrounded by pasture and underbrush matrices in a former Atlantic Rainforest area.

Environmental data were collected every minute with an automated weather station data logger HOBO U30-NRC Weather Station (Onset Computer Corporation) placed near the study site lodge. The station was placed in an area where buildings and trees would not bias environmental data collection. The following environmental variables were collected: (1) air temperature, (2) relative air humidity, (3) wind velocity, (4) rainfall, and (5) solar radiation. Lunar phases were recorded and used as an index of moon luminosity.

Marking Technique

We captured 29 males of *Leptodactylus latrans* by hand at night and determined their sex by the presence of nuptial spines and hypertrophied forearms in males (de Sá et al., 2014). We marked the frogs with 6-month lifespan radio transmitters (PD-2, Holohil Systems Ltd.) weighing 3.8 g each. The weight of the transmitters was less than 10% of each frog's mass, assuring that it would not negatively affect movements (Richards et al., 1994). We attached the transmitters on the waist of the frogs with a satin ribbon, tested previously on captive *Lithobates*

catesbeianus to ensure that the ribbon would not cause skin abrasions or otherwise harm the frog, and released all frogs at the point of capture.

Daily Movements

We tracked frogs daily with a handheld 3-Element Yagi antenna by morning. We recorded the position of each frog with a Global Position System device (GPSmap 62sc, Garmin Ltd.) even when visual confirmation was not possible (triangulation was always $< 1 \text{ m}^2$), and we marked these diurnal shelter sites with a wood stake. To assess daily movement (DM), i.e., the distance a frog had moved on the previous night, we measured the shortest distance from the tracked location to the flag of the previous morning with a 40 m measuring tape or, when direct measurement was impossible due to obstacles or excessive distance, we assessed the distance using geographical coordinates. Minimum, maximum, mean and standard deviation values of DM from each individual were calculated and are presented as min-max (mean \pm SD). We also calculated the total DM for each individual as the sum of each individual's DM's over the course of the study. Following initial capture and marking, we did not handle or disturb the frogs until the end of the experiment in order to avoid interfering with or biasing their movements. At the end of the experiment, visual confirmation of all frogs was necessary to validate previously tracked positions.

Data Standardization

Statistical analyses were performed using *R* 3.2.1 (R Core Team, 2015). We categorized daily movement data into two datasets. In the first dataset, for each day we scored each frog as either stationary or moving as the binary variable MOV (i.e., 0 = no movement; 1 = moved any distance), which was used to test which environmental variables triggered movement. In the second dataset, we selected only the days in which the frogs moved and analyzed log-transformed daily movement distances (DIST).

We extracted means of the environmental variables: air temperature and relative air humidity from the periods (1) diurnal, (2) nocturnal and (3) 24-hour (daily) period. For rainfall, we extracted the total amount of rain in the same periods. We only considered the mean nocturnal wind velocity, due to the fact that, by being sheltered, diurnal wind velocity would not influence the frog's activity. We also only

considered diurnal solar radiation due to the lack of solar radiation at night. We standardized the environmental variables using the function *scale()* (mean = 0, variance = 1). We checked for collinearity by variance inflation factors (VIF's) using the function *vifstep()* of the package "usdm" (Naimi, 2015). We only consider variables with VIF < 3 (Zuur, Ieno and Elphick, 2010). Solar radiation was excluded from the set of environmental variables due to collinearity.

In order to decide which period to use, we ran a pre-variable selection based on the small sample-size corrected Akaike's Information Criterion (AIC_c; Burnham and Anderson, 2002; Symonds and Moussalli, 2011). We used maximum likelihood to fit general linear mixed models (GLMM) using DIST as the dependent variable, and each mean value of each period of the variables air temperature and relative air humidity and the total rainfall of each period, as the fixed effects in the set of candidate models. In all models we used each frog as a random effect (1|individual). We did not use body size as a random effect cause there was no correlation between body size (snout-vent length) and total DM (regression analyses, $p = 0.406$) or home range size (unpubl. data) in *L. latrans*. We used the function *AICcTab()* of the package "lme4" (Bates et al., 2016) to run the model selection. We ran one model selection analysis for each variable separately. The best-supported model (variable) was the one with the lowest AIC_c. The model selection analyses showed that daily values best predict movement over diurnal and nocturnal values (Table 1). The final set of variables is showed in Table 2.

Set of Candidate Models

In order to address how environmental factors trigger frog movement, we used maximum likelihood to fit GLMMs with binomial distribution and employed an all-subset model selection approach (Burnham and Anderson, 2002; Symonds and Moussalli, 2011), ranking the models based on AIC_c. We used the binary variable MOV as the response variable and built every possible combination models of the five fixed effects (TEMP, RH, RAIN, WIND, MOON), without interaction, using the function *dredge()* of the package "MuMIn" (Bartoń, 2015). In all models, we treat each individual frog as the random effect (1|individual). There were 31 models plus the null model in the final set of candidate models. We calculated the evidence ratio and performed a likelihood ratio test (Burnham and Anderson, 2002; Johnson and Omland, 2004) for the best-supported models (Table 3).

We were also interested in investigating how environmental factors predict the distance a frog moves in one night. We used maximum likelihood to fit general linear mixed models with Gaussian distribution to again run an all-subset model selection approach based on AIC_c . We used the continuous variable DIST as the response variable and built every possible combination models of the five fixed effects (TEMP, RH, RAIN, WIND, MOON), without interaction, using the function *dredge()*. In all models, we treated each individual frog as the random effect (1|individual). There were 31 models plus the null model in the final set of candidate models (Appendix 1). We calculated the evidence ratio for the best-supported models ($\Delta AIC < 6$; Table 4). No assumption of general or generalized linear mixed model analysis was broken.

Multimodel Inference

Since no single model was strongly supported (Akaike weight > 0.9 ; Burnham and Anderson, 2002; Symonds and Moussalli, 2011), we used multimodel inference (Burnham and Anderson, 2002; Johnson and Omland, 2004, Symonds and Moussalli, 2011) to address how environmental factors predict movement in *L. latrans*. We selected the six best-supported models (cumulative Akaike weight = 0.95; $\Delta AIC < 6$; Table 4) for model averaging and calculated the relative importance (Burnham and Anderson, 2002) of each predictor. We considered well-supported predictor variables those with relative importance > 0.8 and model averaged confidence intervals that did not include zero (Burnham and Anderson, 2002).

Movements Between Diurnal and Nocturnal Sites

To assess movements between diurnal shelter and sites used for nocturnal activities, we tracked frogs every other day at night, placing flags to mark the nocturnal sites. We measured the distance between each frog's diurnal shelter and its subsequent nocturnal site and used this measure as the distance moved by the frog in search of a nocturnal activity site (distance from shelter, DS). We also measured the distance between the nocturnal site to the frog's shelter site in the next morning and used this measure as the distance moved by the frog in search for diurnal shelter (distance from nocturnal site, DN). Minimum, maximum, mean, and standard deviation values of DS and DN were calculated. To investigate if individuals moved greater distances in search of diurnal shelters or nocturnal activity sites, we used restricted maximum likelihood to fit a general linear mixed model. We log-

transformed DS and DN values to achieve linearity and used these distances as the response variable (DSDNdist), predicted by the period in which the frog would search for shelter and the period in which the frog would search for a nocturnal site (DSDNperiod). In order to assure the non-independence of DS and DN collected on the same day (DS and DN collected on the same day were temporal dependent from each other), we treated each day as a random effect (1|day). We also treated each individual frog as a random effect (1|individual). We considered a significance value of $P = 0.05$.

Shelter Site Use

Every time we tracked a frog during daylight we recorded the characteristics of its shelter site, describing them according to (1) *Water body region* (outside, margin, inside), (2) *Humidity* (dry soil, moist soil, soaked soil, water), (3) *Vegetation* (leaf litter, grass, aquatic vegetation, no vegetation), and (4) *if the frog was unsheltered*.

RESULTS

General movements

Among the 29 marked frogs, only 11 were selected for analysis because 15 frogs escaped (probably due to loose transmitter belts) and three frogs did not provide enough data to analyze. We tracked frogs over 20–27 consecutive days (26.2 ± 2.1 days). Frog movements on a single night (DM) ranged from 0 – 245.9 meters (7.3 ± 20.8 m). Total DM range was 34.2 – 458.8 meters (190.8 ± 131.3 m).

Frogs inhabited temporary or permanent ponds, streams, and marshy areas. Three frogs moved from the same temporary pond to different spatial units when the temporary pond dried. Of these, two moved to different marshy areas and the third moved to a permanent pond. These three frogs crossed a dirt road and grassy matrix to reach these new areas. Six frogs remained at the original permanent pond during the entire study. Two frogs moved from the same temporary pond to the same small stream, one of which then one returned to the temporary pond while the other reached a new permanent pond.

Two frogs exhibited a peculiar movement behavior. Both frogs inhabited different shallow areas (< 0.5 m) of the same permanent pond. On the night of 19 November, the frogs moved relatively large distances (37.6 m and 31.3 m,

respectively) from the shallow areas at the margin to deeper areas (1.0–1.5 m depth) of the pond with dense vegetation. Both frogs remained in these areas for 15 days showing no or little movement (< 2 m). On the night of 4 December, the frogs moved 35.1 m and 43.5 m each from deeper areas to shallow areas. On the morning of 5 December, both frogs were submerged in shallow areas. One of them was concealed in aquatic vegetation beside an area of sparse vegetation that appeared to be a calling site. At this site, we heard calls twice during the study period, on 15 and 23 November, with foam nests appearing the next morning.

Influence of environmental factors on movement trigger

In the movement trigger model selection, of the 32 candidate models, 6 models had smaller AIC_c values than the null model (Table 3). Of these, only the first two best-supported models (MOON; MOON + RAIN, respectively) differed from the null model (likelihood ratio test; $P < 0.05$), and these two models together account for 26% of evidence in favor of the best models (cumulative Akaike weights). The best-supported model was 2.82 times better (evidence ratio) than the null model. The ΔAIC_c of the null model was 2.07 (Table 3).

Influence of environmental factors on movement distance

In the movement distance model selection, of the 32 candidate models, six were selected as best-supported ($\Delta AIC < 6$; Table 4). These models accounted for 95% of evidence in the data. The best-supported model (MOON + RAIN + TEMP + RH) account for only 34.5% of evidence, so we used the first six models ($\Delta AIC < 6$; cumulative Akaike weights = 0.95) to multimodel inference through model averaging (Table 5).

Lunar phase (MOON) was the most important factor predicting movement distance in *L. latrans*. Frogs moved more than three times further in the New Moon phase than in the Full Moon phase. Transitional moon phases (Waning and Waxing Moon) had intermediate values. The next most important factors were rainfall (RAIN) and air temperature (TEMP), which had similar relative importance values, with rainfall slightly a better predictor than air temperature (Fig. 1; Table 5). We did not consider relative humidity (RH) and wind velocity (WIND) predictors of movement in *L. latrans* because their relative importance values were low ($RI < 0.8$) and their confidence intervals included zero.

Diurnal shelter and nocturnal site use and movements

During the day, frogs were sheltered in the water body margin, submerged in the water, and concealed among aquatic vegetation in 90% of the encounters (Table 6). At night, frogs were not sheltered in 48.7% of the encounters but also used the margins of the water bodies in most of the cases. However, frogs used the outer margin (farther from water) of the water body margin more frequently (Table 6). Frogs 10 and 18 used the same microhabitat for diurnal shelter and nocturnal activity over at least four consecutive days (Fig. 2). These frogs were tracked in a concrete burrow between a dirt road and a marshy area. We cannot determine if they shared the site for longer because we found the transmitter of one of the frogs far from the burrow. Thus, we cannot surely assign that one of the remaining frog in the burrow was the one that escaped from the belt.

In searching for a nocturnal site (DS), movements ranged from 0–168 m ($4.3 \pm 16.2\text{m}$) and in searching for a diurnal shelter site (DN) movements ranged from 0–126 m ($3.6 \pm 12.2\text{m}$). There was no difference in the distance covered in the search for shelter sites or nocturnal sites by the frogs.

DISCUSSION

Information on *Leptodactylus latrans* movements is extremely limited. In the only previous study, based on only two individuals and few recaptures, Gallardo (1970) concluded that *L. latrans* is agile and presents fast movements but is quite a sedentary species. Our results suggested that some individuals can move long distances in a single night (e.g. 245.9 m) while others, besides not moving long distances, frequently undertake short daily movements ($\bar{x} = 7.3\text{ m}$).

Leptodactylus latrans daily movements appear to be shorter than *L. labyrinthicus* daily movements ($\bar{x} = 28.4\text{ m} \pm 47.6$; Tozetti and Toledo, 2005), the only other species of *Leptodactylus* for which movement has been studied. However, although Tozetti and Toledo (2005) did not report the duration of their study, in days, total daily movements during the entire study period were greater in *L. latrans* ($190.8 \pm 131.3\text{ m}$) than *L. labyrinthicus* ($30.9 \pm 48.6\text{ m}$). In both species, daily movements were in general short, with a few instances of individuals moving $> 100\text{ m}$ in a single night. The same behavior has also been reported to *Anaxyrus hemiophrys* (= *Bufo*

hemiophrys; Breckenridge and Tester, 1961). These daily short-distance movements generally occur at the microhabitat scale (Sinsch, 2014) within the same spatial unit, and when frogs moved greater distances some of them reached other spatial units within the same patch. These longer distance movements probably relate to the annual round-trip migrations of individuals searching for resources to survive and reproduce (Sinsch, 2014), such as prey-rich areas for nutrition, estivation sites to escape environmental extremes, and breeding sites for reproduction (Sinsch, 1990, 2014).

Round-trip migrations from one spatial unit to another could be seen when frogs 3, 4 and 5 moved from the same temporary breeding pond to different spatial units when the temporary pond dried. To reach these new areas, frogs were forced to cross dry dirt roads and open agricultural lands. These matrices represent hostile environments that are less permeable to frog movements (Mazerolle and Desrochers, 2005; Mazerolle and Vos, 2006). If given the choice, frogs would probably avoid these hostile environments (Mazerolle and Desrochers, 2005). Instead, individuals must have steered direct courses through these matrices to the new areas since these long distances movements were covered in a single night. This direct orientation to new areas is thought to reduce the risk of death and was probably based on previous experiences (Sinsch, 1990) in a combination of potential cues into a redundant orientation system (Sinsch, 2006). Weather conditions as well as the distance to the water body of destination are some other factors that contribute to the orientation system (Mazerolle and Vos, 2006). No interpatch movement was observed during the study period.

The great number of frogs that escaped from transmitter belts during the study might be explained by the foam nest building behavior. *Leptodactylus latrans*, as well as other leptodactylids, lays its eggs in a foam nest built by the amplexic pair (Heyer, 1969; Gallardo, 1970; De Sá et al, 2014). The albuminoid nest is built when the pair (mostly the male) beat their hind limbs increasing the foam volume (Gallardo, 1970). Almost all transmitters were found near the last place where the frog was tracked with no apparent sign of predation (blood, frog remains, near burrows). Only one frog was predated by an Argentine Giant Tegu (*Salvator merianae*) and the transmitter of another one was found near a possibly tegu burrow.

We were not able to elucidate the factors that trigger movement in *L. latrans*. The absence of daylight has been suggested as the most important factor of

movement trigger in some species of anurans due to the fact that frogs tend to avoid diurnal, visually oriented predators, like birds, by moving at night (Zug, Viit, and Caldwell, 2001, Oseen and Wassersug, 2002). We did not observe any *L. latrans* activity or movement during the day in the entire study period, which confirms that the frogs move only during the night. However, even when it is dark, frogs still must decide to move or to remain. This decision seems to be a multicausal, stage-dependent process in which the frog weighs the costs and benefits of exposing itself in a long-distance migration instead of remaining in a safe residency (Baguette et al., 2013; Pittman et al., 2014). Our analysis suggests that environmental factors might not contribute to this multicausal process. The six best-supported models together accounted for only 50.9% of the evidence in the data and the null model was the 7th best-supported model. Based on the likelihood ratio tests only the two best-supported models were statistically different from the null model. Yet, the null model had a ΔAIC_C of only 2.07, which includes it as an equally plausible model (Burnham and Anderson, 2002). Further, the evidence ratio of the null model was 2.82, which means that the best-supported model was only 2.82 times better than the null model. Together, the little cumulative weight of the six best-supported models, the rank of the null model relative to the other models, the little support from the likelihood ratio tests for all of the best-supported models, the ΔAIC_C , and the evidence ratio of the null model lead us to conclude that the environmental factors tested in this study were not important to trigger movement in *L. latrans*.

In contrast, once a frog is triggered to move, environmental factors seem to play an important role in affecting the distance moved. Lunar phase was the most important factor in explaining distance moved in this species. Frogs moved three times further during dark nights of New Moon than on brightly lit nights of the Full Moon, with transitional moon phases (waning and waxing) presenting intermediate effects on movement (Fig. 1). Greater activity at New Moon has been reported in several species (Church, 1960; Ferguson, 1960; FitzGerald and Bider, 1974a; Grant et al, 2012; Vignoli and Luiselli, 2013). The main explanations for amphibian's response to the lunar cycle are predator avoidance and reproduction synchronization (Church, 1960; Grant et al., 2012; Vignoli and Luiselli, 2013). There is a species-specific balance in the predator-prey relationships in which moonlight influences differentially the detectability of preys by anurans and the detectability of anurans by their predators. In anuran species that don't have visually oriented predators, such as

snakes and bats, moonlight might help anurans detect their predators before they detect the anurans (Grant et al, 2012). This hypothesis seems especially plausible given the recent finding that the two spectrally different kinds of rod photoreceptors (so-called red and green rods) in amphibians enable color vision at very low light levels (Yovanovich et al., in press). Still, reproductive success is maximized if conspecifics reach the same breeding area at the same period of time, minimizing energetic cost of reproduction and, predation risk by dissolution and increasing the number of available breeding adults (Grant et al, 2012; Vignoli and Luiselli, 2013).

Rainfall and temperature have been reported as the most important meteorological predictors of anuran activity (Zug et al., 2001; Oseen and Wassersug, 2002) due to their effect on the metabolism of ectothermic species (Bellis, 1962; Sinsch, 1988; Sanabria et al., 2003). Our results showed that both rainfall and temperature played important roles in the distances *L. latrans* moved. However, the specific relationship of these predictors to anuran movement is not clear. Magnitude of movement was positively associated with temperature and rainfall in *Bufo bufo* (Sinsch, 1988) and other salamander and anuran species (Todd and Winne, 2006). In contrast, the magnitude of movement in *Anaxyrus hemiophrys* (= *Bufo hemiophrys*, Breckenridge and Tester, 1961) is not related to temperature nor to rainfall, and movements in both *L. labyrinthicus* and *Eleutherodactylus coqui* were not correlated with temperature (Woolbright, 1985; Tozetti and Toledo, 2005).

When analyzing movements of frogs 12 and 15 we expected that something in common must have triggered that concomitant behavior. As reported for *A. hemiophrys* (Breckenridge and Tester, 1961), frogs 12 and 15 remained in a limited area for several days and then suddenly moved great distances on the same night, suggesting that something must have triggered this synchronous behavior. However, we could not find any plausible explanation to such behavior when looking at the environmental factors data itself. However, although not exactly tested, when we looked at rainfall dataset, we could see a strong tendency of rainfall to those larger displacements of both frogs. Nights of 4 and 19 November and 4 December were the ones with the largest amount of rainfall during the entire study (15.4, 22.4 and 12.0 mm, respectively). Those were the nights that frog 12 moved largest distances (17.1, 37.6 and 35.1 m, respectively) and frog 15 moved largest distances on 4 November and 4 December (245.9 and 43.5 m, respectively). These results evidence the importance of rainfall to movement in some anurans species and the existent

considerable variation in the response of amphibian movements and activity to environmental factors (Salvador and Carrascal, 1990; Todd and Winne, 2006).

Both relative air humidity and wind velocity showed no or little influence on *L. latrans* movements. These environmental factors have also been reported acting differently among anurans species (Woolbright, 1985; Henzi et al., 1995; Mazerolle and Vos, 2006; Phillips et al, 2007). Tozetti and Toledo (2005) also did not find any relation between relative humidity and movement in *L. labyrinthicus*. We expected that relative humidity would be an important predictor of *L. latrans* movements due to amphibian permeable skin characteristics. However, we speculate that relative humidity was not important for this species due to its close relation to water. Once individuals were in contact to water, relative air humidity would not be important to its water balance. A similar scenario was reported to *Eleutherodactylus coqui* in which movement was not correlated to relative humidity, but it was associated with foliage surface wetness (Woolbright, 1985). Although wind has already been reported as predictor of anurans movement and orientation (Tracy and Dole, 1969; Phillips et al, 2007), it is expected that it did not influence *L. latrans* movements, since increasing wind velocity increases the evaporatory rate of amphibians water balance (Bellis, 1962), so frogs would avoid moving on windy nights.

Another important aspect of water balance in nocturnal amphibians biology is to be sheltered during the extreme meteorological conditions of daytime. Besides avoiding environmental extremes, this behavior protects frogs from visually oriented, diurnal predators. In this study, frogs were found sheltered during the day in wet or humid microhabitats near water bodies' margins, rarely farther than one meter from water. On the other hand, it seems that *L. labyrinthicus* were able to retreat also to drier sites, exploring shelters both near and far from water (Tozetti and Toledo, 2005). In both species, frogs were almost always associated with dense or sparse vegetation. At night, although exploring farther microhabitats from water margins, frogs also did not go too far from water. This result agrees with what has been reported by França et al. (2004) for *L. latrans*. Although these authors reported that, at night, frogs used stream banks more frequently rather than margins of ponds and lakes, we could not find such preference. Most of the nights, frogs were active and unsheltered, the same pattern described to *L. labyrinthicus* (Tozetti and Toledo, 2005).

Frogs were tracked to the exact same site during the day and at night quite often during experiments. This might be attributed to the fact that frogs probably did not leave their shelter on those nights. Microhabitats from diurnal shelters to nocturnal sites did not differ spatially. This diurnal/nocturnal overlap in microhabitat use has already been reported to other species (Oliveira et al., 2016) and it is reflected by the short distances, in most of the cases, between diurnal shelters and nocturnal sites. In fact, no difference was found between the distances moved by the frogs from diurnal shelters to the nocturnal sites, and from nocturnal sites to subsequent diurnal shelters. This could be due to the fact that our radiotracking method provided only one point in space per night. Yet, the straight line distances between points could not reflected the actual movement of the frogs when searching for nocturnal sites and diurnal shelters, since straight lines distances might underestimate movement (Oliveira et al., 2016). Even so, frogs may use the most opportune site near where they emerge from shelter, or where they decide to shelter after an active night.

Some individuals used the same shelter and nocturnal site together for a couple of days. Although it was not tested, there seems to be no territoriality between males of *L. latrans* (Fig. 2). Laufer et al. (2014) have already reported satellite males of *L. latrans* sharing the same microhabitat with one calling male inside a foam nest with other non-calling males surrounding it with no apparently agonistic interactions.

Studying animal movements is fundamental for the understanding of basic ecological processes. It generates tools to other areas, such as, for conservation management of threatened species and in dealing with invasive processes of exotic species. In this study, we contribute to the understanding of the influence of environmental factors, especially lunar phases, in the movement of a pond-breeding amphibian species. Such studies could elucidate important aspects of an animal's ecology in a climatic changes context. We also highlight the deficit of studies on movement of tropical anuran species and encourage researchers to contribute on the understanding of such a fundamental aspect of an animal's life history.

ACKNOWLEDGMENTS

We thank J.R. do Desterro, C. Rossi and I.R.S. Cavalcanti for helping with fieldwork, C. Jared for providing the facilities for previous tagging tests, the crew from

Estação Experimental Agronômica of Universidade Federal do Rio Grande do Sul for logistical support, G. Requena, M. Leite, D. Melo, and especially G.L. Marin for helping with the statistics, and A.M. Jeckel, M. Targino and D.O.V. Parajara for comments on the manuscript. This research was supported by Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP Process 2012-10000-5) and Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq Processes 134324/2015-5 and 305234/2014-5) and was authorized by the Instituto Chico Mendes de Conservação da Biodiversidade (SISBIO 44980-9) and the Institute of Biosciences Comissão de Ética no Uso de Animais (CEUA IB-USP 243/2016).

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TABLES

Table 1. Variable selections of each period best predicts movement distance in *Leptodactylus latrans*.

Variables	AIC _c	Weight
Mean air temperature		
Daily	0.0	0.64
Nocturnal	2.4	0.19
Diurnal	2.7	0.17
Mean relative air humidity		
Daily	0.0	0.49
Diurnal	0.6	0.35
Nocturnal	2.0	0.18
Total rainfall		
Daily	0.0	0.56
Diurnal	0.5	0.43
Nocturnal	7.2	0.01

Table 2. Final set of candidate variables affecting movement in *Leptodactylus latrans*.

Variables	Unit	Abbreviation
Mean daily air temperature	(°C)	TEMP
Mean daily relative air humidity	(%)	RH
Total daily rainfall	(mm)	RAIN
Mean nocturnal wind velocity	(m/sec)	WIND

Table 3. Best supported models predicting movement trigger in *Leptodactylus latrans*.

Model	df	LogLik	AIC _c	ΔAIC _c	Weight	Evidence ratio	Likelihood ratio test (to null model)		
							χ ²	df	P
MOON	5	-138.921	288.1	0.00	0.152	-	8.244	3	0.041
MOON + RAIN	6	-138.217	288.7	0.68	0.108	1.41	9.651	4	0.048
MOON + RH	6	-138.589	289.5	1.42	0.075	2.03	8.908	4	0.063
MOON + TEMP	6	-138.759	289.8	1.76	0.063	2.41	8.568	4	0.073
RAIN	3	-141.982	290.0	1.99	0.056	2.70	2.123	1	0.145
MOON + WIND	6	-138.899	290.1	2.04	0.055	2.77	8.287	4	0.082
Null	2	-143.043	290.1	2.07	0.054	2.82	-	-	-

Table 4. Best supported models (ΔAIC < 6) predicting movement distance in *Leptodactylus latrans*.

Model	df	LogLik	AIC _c	ΔAIC _c	Weight	Evidence ratio
MOON + RAIN + TEMP + RH	9	-375.324	769.5	0.00	0.345	-
MOON + RAIN + TEMP	8	-376.551	769.8	0.29	0.299	1.16
MOON + RAIN + TEMP + RH + WIND	10	-375.130	771.3	1.80	0.140	2.26
MOON + RAIN + TEMP + WIND	9	-376.415	771.7	2.18	0.116	2.97
MOON + RAIN	7	-379.983	774.5	5.00	0.028	12.18
MOON + TEMP	7	-380.238	775.0	5.51	0.022	15.72

Table 5. Model averaged ($\Delta AIC < 6$; cumulative Akaike weight = 0.95) coefficients, adjusted SE, confidence intervals and relative importance for variables predicting movement distance in *L. latrans*. The predictors are sorted by the relative importance.

Predictor	Model averaged coefficients	Adjusted SE	Lower CI	Upper CI	Relative importance
MOON (new)	1.726	0.256	0.703	1.706	1.00
MOON (waning)	1.091	0.259	0.062	1.076	1.00
MOON (waxing)	0.912	0.249	-0.097	0.877	1.00
MOON (full)	0.522	0.241	0.050	0.994	1.00
RAIN	0.264	0.097	0.076	0.452	0.98
TEMP	0.261	0.094	0.076	0.446	0.97
RH	-0.179	0.114	-0.402	0.044	0.51
WIND	-0.051	0.089	-0.224	0.123	0.27

Table 6. Diurnal shelter and nocturnal site characteristics and its frequency distribution uses by *Leptodactylus latrans*.

Diurnal shelter characteristic	<i>n</i>	%	Nocturnal site characteristic	<i>n</i>	%
Water body region			Water body region		
<i>Outside</i>	46	14.2	<i>Outside</i>	13	14.4
<i>Margin</i>	185	57.3	<i>Margin</i>	48	53.4
<i>Inside</i>	92	28.5	<i>Inside</i>	29	32.2
Humidity			Humidity		
<i>Dry soil</i>	34	10.5	<i>Dry soil</i>	10	09.1
<i>Moist soil</i>	75	23.0	<i>Moist soil</i>	26	23.6
<i>Soaked soil</i>	85	26.2	<i>Soaked soil</i>	42	38.2
<i>In the water</i>	131	40.3	<i>In the water</i>	32	29.1
Vegetation			Vegetation		
<i>Leaf litter</i>	11	3.2	<i>Leaf litter</i>	2	01.8
<i>Grass</i>	132	40.0	<i>Grass</i>	62	55.4
<i>Aquatic vegetation</i>	183	55.3	<i>Aquatic vegetation</i>	44	39.2
<i>No vegetation</i>	5	1.5	<i>No vegetation</i>	4	03.6
Unsheltered			Unsheltered		
<i>Yes</i>	42	10.0	<i>Yes</i>	56	48.7
<i>No</i>	291	90.0	<i>No</i>	59	51.3

FIGURES

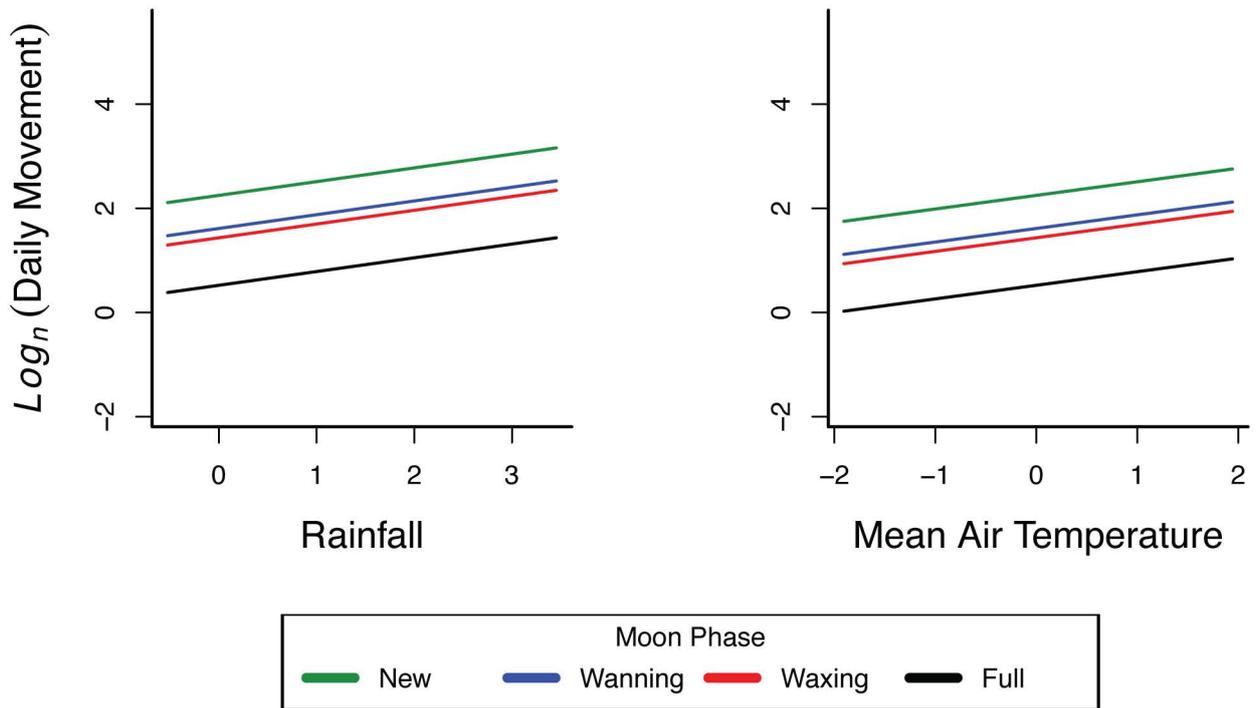


Fig. 1. Model averaged predictors of movement distance in *Leptodactylus latrans*.



Fig. 2. Two male frogs sharing the same concrete burrow between a dirt road and a marshy area as nocturnal activity site.

CAPÍTULO 3

MOVEMENTS OF NEW BULLFROG (*Lithobates catesbeianus*) PROPAGULES IN AN INVADED AREA

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ABSTRACT

The introduction of invasive species is one of the causes of biodiversity loss and ecosystem degradation. *Lithobates catesbeianus*, the American Bullfrog, is a North American species introduced in Brazil during the 1930's. Although some of the species' characteristics have been pointed out as important to establishment success, propagule pressure is the most important factor determining the establishment of non-native species. Increasing propagule pressure in an area increases the probability and the rate of geographical spread of a given population. Thereby, we hypothesized that, recently released bullfrogs would explore new habitats and, inside the releasing pond, they would move more than frogs from the established population. We radio tracked 18 local frogs and 20 propagule frogs and recorded their positions. Frogs of both groups equally explored the surrounding habitats and equally moved inside the pond. Although other aspects could have interfered in bullfrog movements, the input of bullfrog individuals to an already invaded area might not add to the spread of the species to new areas.

Keywords. Amphibia; invasion biology; propagule pressure; population establishment

INTRODUCTION

The introduction of invasive species has been contributing to biodiversity loss and ecosystem degradation (Pyšek and Richardson, 2010), and it is considered one of the five main causes of current biodiversity decline (Millenium Ecosystem Assessment, 2005). *Lithobates catesbeianus*, the American Bullfrog, is a large-sized anuran (Durham and

Bennett, 1963), generalist predator (Korschgen and Moyle, 1955; Silva et al., 2016), with high fecundity (Howard, 1978). The species is original from the east of the United States and Canada, and from the northeast of Mexico (Frost, 2016). It is widely used in frog farming and it was introduced in Brazil in the 1030's (Ferreira et al., 2002). In Brazil, the species is found in more than 240 cities (Henrique and Grant, not published; Giovanelli et al., 2007; Both et al., 2011) with greater occurrence in the South and Southeast regions, probably due to frog farming history, the following escapes from these frog farms, and dispersion. However, it is not possible to ascertain how much of the current distribution of bullfrog in Brazil is due to frog farm escapes and how much, from an escape event, the species dispersed to establish in new localities. Part of this uncertainty is due to the lack of knowledge on the species' movements in nature.

Although some of the species' characteristics described (e.g., large body size, generalist diet, and wide native range size) have been pointed out as important to establishment success of non-native species (Kolar and Lodge, 2001), comparative reviews have demonstrated that propagule pressure is the most important factor determining the establishment success of a non-native species in a new area (Lockwood et al., 2005; Colautti et al., 2006). Propagule pressure is a measure that incorporates the number of non-native individuals released into a habitat outside their natural range, and the number of release events occurred in a given population (Carlton, 1996). Increasing propagule pressure increases the probability of establishment and invasion success of a non-native species (Lockwood et al., 2005; Britton-Simmons and Abbott, 2008). Yet, once a non-native species is established in a given area, increasing propagule pressure in this area will increase the probability and the rate of geographical spread of that population (Brossenbroek et al., 2001; Rouget and Richardson, 2003).

The dispersion of bullfrogs occurs mainly through marshy areas acting as ecological stepping-stones between breeding sites, in which individuals from a non-native population would establish new populations in non-invaded areas (Peterson et al., 2013). Increasing bullfrog's propagules in an already invaded area would contribute to the spread of the species to new areas. Moreover, previous studies have shown that male bullfrogs are territorial and show homing behavior, which means that they tend to defend and remain in their territory (territory radius = 2.7m; Emlen, 1968) against intruder males and juveniles (Durham and Bennett, 1963; Emlen, 1968; Wiewandt, 1969; Howard, 1978).

Thereby, we raised the following question: would recently released bullfrogs explore

more the surrounding habitat than frogs from the established population? Due to increasing propagule pressure and territoriality of the established males, our hypotheses are that recently released bullfrogs would explore new habitats and, inside the releasing pond, they would move more than frogs from the established population.

MATERIALS AND METHODS

Study Site

The study was conducted from February to April 2016 in a permanent pond in Nova Palma city (29° 29.764' S; 53° 30.859' W, datum WGS 84), Rio Grande do Sul state, Brazil, in a former Atlantic Rainforest area (Fig. 1A). The pond was in an agricultural area, mainly surrounded by soybean plantation, pasture, and other ponds (Fig. 1B). There were aquatic grasses around the entire pond. The pond was almost circular and was about 1–1.5 m deep. We arbitrarily divided the pond in 20 slices by placing stakes every 5 meters (Fig. 2). There was an established bullfrog population in the area (Camila Both, pers. comm.).

Marking Technique and Tracking Design

We captured the frogs by hand at night and determined their sex by the diameter of the tympanum and by the pigmentation on throat and chest (Howard, 1981). We marked the frogs with radio transmitters (PD-2, Holohil Systems Ltd.) weighing 3.8 g each. The weight of the transmitters was less than 10% of each frog's mass, assuring that it would not negatively affect movements (Richards et al., 1994). We attached the transmitters on the waist of the frogs with a satin ribbon, tested on captive individuals to ensure that the ribbon would not cause skin abrasions or otherwise harm the frog.

For the control group, we captured nine frogs at the study site (local frogs), all at the same night, and released in randomly selected slices of the pond. At the same night we capture 10 other frogs at Faxinal do Soturno city (29° 33.474' S; 53° 25.199' W), 11.4 kilometers far from the study site (Fig. 1A). We kept the frogs in a large container, quickly transferred and released them in randomly selected slices of the study pond. This group was the propagule frogs, treated as the treatment group.

In the next morning, we tracked all frogs with a handheld 3-Element Yagi antenna and recorded their position inside the pond (slice number) or outside the pond (geographic

coordinates). We tracked the frogs for four consecutive days and tracked them again in one morning in a 14-day interval period. We recaptured all frogs, locals and propagules, and euthanized them with anesthetic.

The next night after recapturing all frogs, we repeated the procedure described above recapturing nine more local frogs and 10 more propagule frogs. The propagule frogs were also captured in another pond in Faxinal do Soturno city (29° 34.597' S; 53° 25.485' W), 12.4 kilometers from the study pond (Fig. 1), because there were not enough frogs in the first pond. We repeated the same tracking method in this second experiment. In total, we had, respectively, 18 and 20 frogs in control and treatment groups

Statistical Analysis

To assess if propagule frogs would explore the surrounding habitats more than the local ones, we recorded each time a frog was tracked in different habitats outside the study pond. To each frog, we also recorded the number of times it switched between the slices in the pond. We ran a Mann-Whitney test to test if propagule frogs move more than local ones inside the pond. The statistical analysis was performed using *R* 3.2.1 (R Core Team, 2015). We considered a significance value of $P = 0.05$.

RESULTS

In total, we had 18 frogs (8 males; 10 females) in the local group, and 20 frogs (14 males; 6 females) in the propagule group. Two frogs of the local group and three frogs of the propagule group left the study pond and explored the surrounding habitats. In the local group, one female frog was tracked in the first morning among the soybean plantation about 30 meters from the study pond. This frog stayed inside the soybean plantation for two more days and, in the fourth day, the frog returned to the study pond. Another frog of the local group went to shrubs and trees besides the same soybean plantation about 17 meters from the study pond in the first night. This male frog stayed one more day in the same area and then returned to the study pond.

In the propagule group, a female frog went to a pond 15 meters next to the study pond in the second night. No bullfrog activity was observed in this neighbor pond. In the two following mornings, the same frog was tracked in another soybean plantation 120 meters from the point where it was tracked in the last day. To reach this point, the frog was

probably forced to cross the study pond, a grassy matrix, and a dirty road. At some point in the 14 days after the last tracking, the frog returned to the study pond. On another case, a male propagule went to a soybean plantation on the first night and then returned to the study pond on the following night. Another propagule frog went to a bigger pond 216 meters from the study pond. This female frog was tracked inside the study pond during the first four mornings and, sometime during this 14-day interval, the frog moved to this farther pond. Considering that 2 frogs of the local group and 3 frogs of the propagule group explored the surrounding habitats, statistical analysis was not used due to the lack of evidence considering that both groups apparently explored the surrounding habitats equally.

When looking at movements inside the study pond, there was no difference in the number of times the propagule frogs switched between the slices in the pond in relation to local frogs ($P = 0.324$).

DISCUSSION

We were not able to corroborate neither of our hypothesis that recently released bullfrogs would explore more the surrounding habitats than local ones nor the hypothesis that, inside the releasing pond, propagule bullfrogs would move more than bullfrogs from the established population. Frogs of both groups explored the surrounding habitats and returned to the study pond (with the exception of the frog from the propagule group that did not returned to the study pond), and when looking at the movements inside the study pond, frogs of both groups also switched equally between slices of the pond.

A possible explanation to such results might be the number of females in the local groups. Between adult bullfrogs, dispersal is female-biased (Austin et al., 2003). Thus, local frogs would explore the habitat by the fact that the number of females in the local group was bigger than the number of males. Yet, it is known that juveniles and recent metamorphosed individuals are probably the most dispersers in *Lithobates catesbeianus* (Willis et al., 1956). However, difficulties in tracking a large number of bullfrogs at the same time, problems with tagging small individuals, and the available period of the study, precluded a larger sample size to do stage- and sex-based analyses.

The randomization of the release point of the local frogs might have forced the local frogs to establish new territories, what might elucidate the lack of difference between

groups in movements inside the pond. Still, given the apparent availability and the characteristics of microhabitats in the study pond, the propagule size (i.e., the number of released frogs) might have been too small to affect the established population dynamics. Thus, when propagule frogs were released in the pond, they might have found suitable available microhabitats (e.g., shallow and unshaded water, sand or gravel bottoms, and heavy growth of aquatic vegetation; Moyle, 1973; Minowa et al., 2008) without necessarily entering in any local frogs' territory. The importance of suitable microhabitats and availability of resources to establishment (Britton-Simmons and Abbott, 2008) could also be evidenced when a propagule frog went to a deeper and non-vegetated pond and returned to the study pond in the following nights, probably because there was no available and suitable microhabitat in that pond.

Also, the period to check for propagules establishment was small. We arbitrarily decided for the 14-day period between tracking due to logistic opportunities. At this period, one propagule frog did move to another pond, apparently suitable and with lower bullfrog's abundance. If a longer period would have been established, some other results could have emerged. When a longer period was established, Gahl et al. (2005) reported greater inter-pond movements in bullfrog individuals.

However, these results could exemplify a case where the increase in propagule pressure does not reflect an increase in the probability of geographical spread of a given population. Therefore, the input of bullfrog individuals to an already invaded area might not add to the spread of the species to new areas.

ACKNOWLEDGMENTS

We thank C. Jared for providing the facilities for previous tagging tests, the farmers from where the study was carried out for logistical support, A.M. Jeckel, P.H. Dias, M. Targino, and D.O.V. Parajara for comments on the manuscript, and P.G. Dias for helping with the map. This research was supported by Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP Process 2012-10000-5) and Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq Processes 134324/2015-5 and 305234/2014-5) and was authorized by the Instituto Chico Mendes de Conservação da Biodiversidade (SISBIO 44980-9) and the Institute of Biosciences Comissão de Ética no Uso de Animais (CEUA IB-USP 231/2015).

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FIGURES

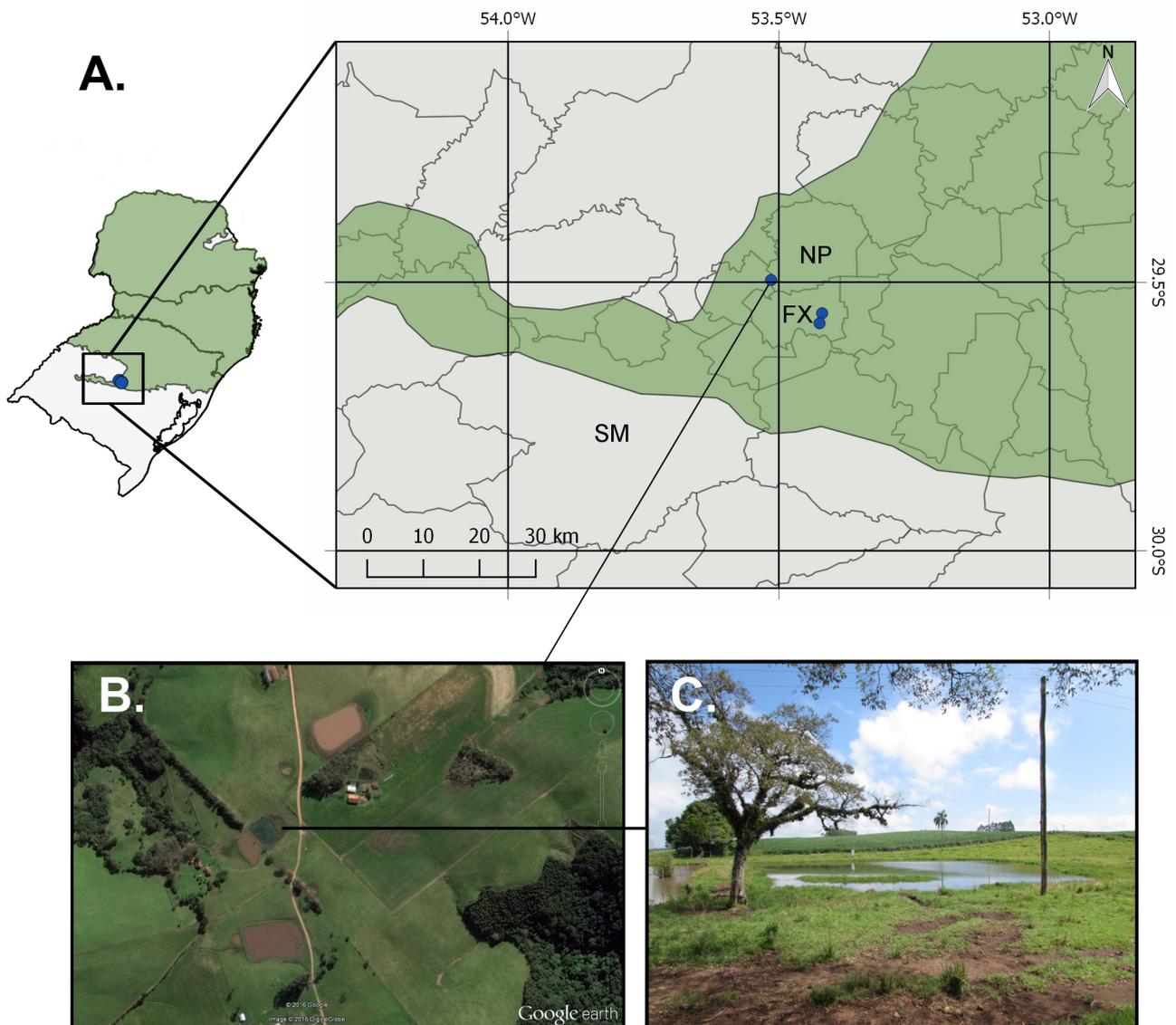


Figure 1. Study sites. (A) NP: Nova Palma city - study pond, FX: Faxinal do Soturno city – propagules' ponds, the cities are in the metropolitan region of Santa Maria city (SM); (B) Study pond from Google Earth view; (C) the study pond.

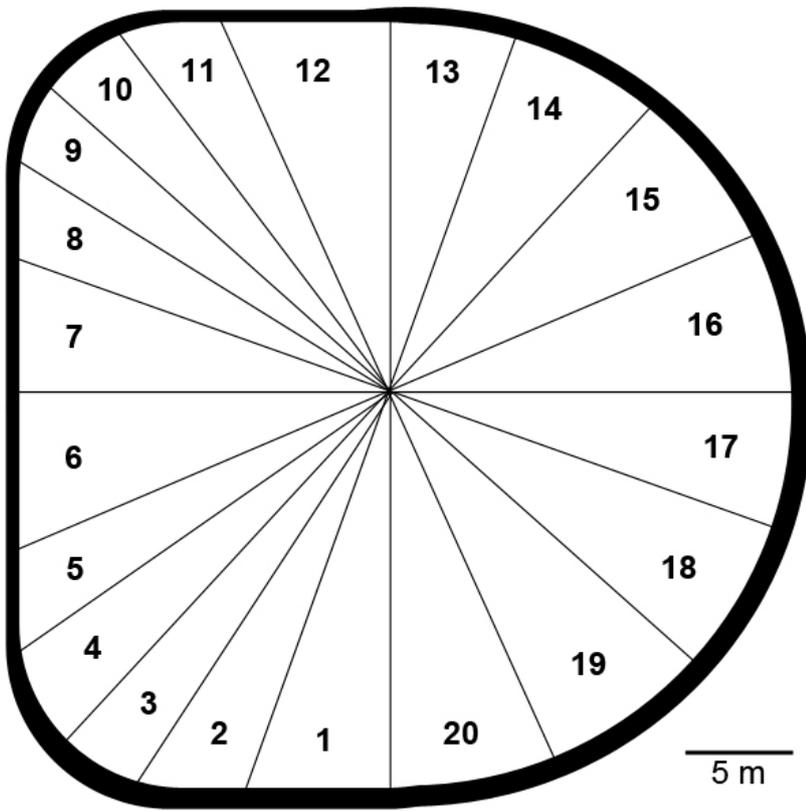


Figure 2. Scheme of the division of the study pond in 20 equally divided slices

CONCLUSÃO

A ecologia do movimento é uma área do conhecimento relativamente nova quando comparada à outras áreas de estudo em ecologia. Embora muitos trabalhos tenham sido publicados para outros grupos de vertebrados, o estudo do movimento em anfíbios não é muito difundido na comunidade científica. Com este trabalho, contribuimos para o entendimento sobre o movimento de duas espécies de anuros encontradas em território brasileiro, uma nativa (*Leptodactylus latrans*) e outra invasora (*Lithobates catesbeianus*), sendo que esta última pode oferecer potenciais prejuízos à fauna nativa.

O primeiro capítulo aqui apresentado foi o segundo estudo a estimar a área de vida de uma espécie brasileira de anfíbio. Levando-se em consideração que o Brasil é o país com maior diversidade de anfíbios, fica evidente a falta de conhecimento sobre a área de vida de espécies brasileiras e, acima de tudo, de espécies neotropicais. Adquirir conhecimento sobre como as diferentes espécies de anuros utilizam o espaço pode ser fundamental para elucidar questões sobre, por exemplo, as forças que regem a relação entre o tamanho corporal e o tamanho da área de vida em anuros, como foi mostrado nesse capítulo. Com isso, encorajamos pesquisadores a buscarem soluções para superar as dificuldades da marcação e do rastreamento de anfíbios e, assim, estimar a área de vida de espécies nativas, além de investigar a relação entre tamanho corpóreo e tamanho de área de vida nessas espécies. E, com relação à importância desse tipo de trabalho para programas de conservação, saber o tamanho da área de vida e a utilização do espaço por espécies de anfíbios pode ser fundamental para o estabelecimento de limites de áreas de conservação com significado biológico para essas espécies.

Outra ferramenta importante para a conservação e para o entendimento de processos ecológicos básicos é saber como os animais se movimentam na natureza. No segundo capítulo desta dissertação, contribuimos para o entendimento da influência de fatores ambientais, especialmente as fases da lua, chuva e temperatura, no movimento de uma espécie brasileira de anuro. Com este trabalho, mostramos que, durante a estação reprodutiva, indivíduos de *Leptodactylus latrans* se movimentam mais em noites escuras, chuvosas e quentes. Esse tipo de conhecimento pode elucidar aspectos importantes da ecologia de uma determinada espécie em um contexto de mudanças climáticas. O entendimento de como condições meteorológicas influenciam o movimento

de anfíbios é ainda mais escasso e deve ser melhor investigado, principalmente em estudos comparativos.

Por fim, no terceiro capítulo tentamos compreender a dinâmica da pressão de propágulos no risco de invasão de áreas adjacentes a uma área já invadida pela espécie *Lithobates catesbeianus*. Apesar de ajustes no delineamento experimental serem necessários para que maiores conclusões sejam tomadas, nossos resultados evidenciam um possível caso no qual o aumento da pressão de propágulos não reflete em uma maior probabilidade do aumento da distribuição geográfica da espécie. Contudo, são necessárias maiores informações a respeito do processo de invasão da rã-touro no Brasil, através do conhecimento de como esses animais se locomovem em um ambiente invadido. Entender a ecologia do movimento da espécie é um dos primeiros passos para que medidas de controle populacional e bloqueio do avanço da espécie para regiões onde ainda não foram detectadas sua presença possam ser tomadas.

RESUMO

O movimento dos animais desempenha papel importante na aptidão dos indivíduos, no fluxo gênico, na dinâmica de metapopulações e na persistência, a longo prazo, de espécies em um ambiente. Dessa forma, o objetivo deste estudo foi compreender aspectos relacionados à ecologia do movimento da rã-manteiga (*Leptodactylus latrans*) e da rã-touro (*Lithobates catesbeianus*). Para isso, indivíduos de ambas as espécies foram marcados com radiotransmissores e rastreados com o objetivo de coletar informações sobre seus movimentos. Ressaltamos os seguintes resultados deste trabalho: (1) a área de vida média de *L. latrans* é de 2034,2 m²; (2) com o aumento do tamanho corpóreo de anuros há o aumento do tamanho da área de vida; (3) indivíduos de *L. latrans* se locomovem mais em noites escuras, chuvosas e quentes; e (4) o aumento da pressão de propágulos não reflete uma maior probabilidade no aumento da distribuição geográfica de uma dada população de *L. catesbeianus*. Entender os padrões de locomoção dos anfíbios e como utilizam o espaço na natureza é fundamental para o entendimento de processos ecológicos e evolutivos relacionados às histórias de vida das espécies desse grupo. Além disso, esse conhecimento serve como uma ferramenta importante no estabelecimento de limites de áreas de conservação com significado biológico para espécies ameaçadas. Ainda, saber como espécies invasoras se locomovem é um dos primeiros passos para que se tomem medidas de controle populacional e para o bloqueio do avanço da distribuição de espécies exóticas.

Palavras-chave. Amphibia; radiotelemetria; área de vida; fatores ambientais; biologia da invasão; pressão de propágulo

ABSTRACT

The ability of animals to move plays an important role in individual fitness, gene flow, population regulation, metapopulation dynamics and long-term persistence of species. The aim of this study was to understand aspects related to the movement ecology of the Butter Frog (*Leptadactylus latrans*) and the Bullfrog (*Lithobates catesbeianus*). We collected movement data by radio tracking individuals of both species. Some of the most important results obtained were: (1) the mean home range of *L. latrans* is 2034.2 m²; (2) increasing body size increases home range size in anurans; (3) individuals of *L. latrans* are more likely to move larger distances in dark, rainy and warm nights; (4) the increase in propagule pressure does not reflect an increase in the probability of geographical spread of a given population of *L. catesbeianus*. Understanding how amphibians move and use the space in nature is fundamental for the understanding of basic ecological and evolutionary processes related to life history of the species. Moreover, this knowledge is a useful tool to establish biologically meaningful conservation boundary areas to threatened species. Yet, understanding how invasive species move in nature is one of the first steps to population control and to block the spread of geographical distribution of exotic species.

Keywords. Amphibia; radiotelemetry; home range; environmental factors; invasion biology; propagule pressure.

APÊNDICES

Capítulo 1 – Supplementary References

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Capítulo 2. Set of candidate models predicting movement distance in *Leptodactylus latrans*

Appendix 1. Set of candidate models predicting movement distance in *Leptodactylus latrans*.

Model Number	Dependent variable	Fixed Effects	Random Effect
1	DIST	MOON + RAIN + TEMP + RH + WIND	(1 individual)
2	-	MOON	-
3	-	RAIN	-
4	-	TEMP	-
5	-	RH	-
6	-	WIND	-
7	-	MOON + RAIN	-
8	-	MOON + TEMP	-
9	-	MOON + RH	-
10	-	MOON + WIND	-
11	-	RAIN + TEMP	-
12	-	RAIN + RH	-
13	-	RAIN + WIND	-
14	-	TEMP + RH	-
15	-	TEMP + WIND	-
16	-	RH + WIND	-
17	-	MOON + RAIN + TEMP	-
18	-	MOON + RAIN + RH	-
19	-	MOON + RAIN + WIND	-
20	-	MOON + TEMP + RH	-
21	-	MOON + TEMP + WIND	-
22	-	MOON + RH + WIND	-
23	-	RAIN + TEMP + RH	-
24	-	RAIN + TEMP + WIND	-
25	-	RAIN + RH + WIND	-
26	-	TEMP + RH + WIND	-
27	-	MOON + RAIN + TEMP + RH	-
28	-	MOON + RAIN + TEMP + WIND	-
29	-	MOON + RAIN + RH + WIND	-
30	-	MOON + TEMP + RH + WIND	-
31	-	RAIN + TEMP + RH + WIND	-
32	-	null	-