



**MURILO GUIMARÃES RODRIGUES**

**“ESTIMATING VITAL RATES WITH IMPERFECT DETECTION IN  
AMPHIBIAN AND REPTILE POPULATIONS”**

**“ESTIMANDO TAXAS VITAIS COM DETECÇÃO IMPERFEITA EM  
POPULAÇÕES DE ANFÍBIOS E RÉPTEIS”**

**CAMPINAS  
2013**





**UNIVERSIDADE ESTADUAL DE CAMPINAS**

**Instituto de Biologia**

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ESTE EXEMPLAR CORRESPONDE À VERSÃO FINAL DA TESE  
DEFENDIDA PELO ALUNO MURILO GUIMARÃES  
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Assinatura do Orientador

A handwritten signature in blue ink, appearing to read "Ricardo", written over a horizontal line.

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## ABSTRACT

Population ecology aims to search for factors that lead to variation in vital rates and consequently, in the number of individuals. This includes testing hypotheses about natural history traits and threats to populations. However, obtaining data to test hypotheses is challenging because following individuals in the field can be difficult, especially for amphibians and reptiles, where detection probabilities are often  $< 1$ . Mark-recapture methods are widely used to estimate detection probabilities and to test ecological hypothesis. Here we used mark-recapture methods to test hypotheses related to ecology and conservation of amphibian and reptile populations. We implemented open- and closed-population models in Program MARK, to account for detection probabilities and to calculate survival estimates and other population parameters. We organized this dissertation into four chapters. In the first chapter we emphasize the importance of considering detection probabilities besides simulating hypothetical scenarios to show the relationship between field effort, sample size and precision. In the second chapter we used a Cormack-Jolly-Seber model to compare the effect of two amphibian marking techniques, toe-clipping and PIT tagging, on survival in the blacksmith tree frog, *Hypsiboas faber*. In the third chapter our goal was to estimate survival and population growth of the golden lancehead, *Bothrops insularis* accounting for temporary emigration using Pollock's Robust Design. Besides the study of vital rates and population dynamics, energy allocation and its consequences for survival are testable with mark-recapture models. Thus, in the last chapter we used two traits from the lizard mating system, namely jaw size and courtship coloration, to compare survival estimates between males and females of the whiptail lizard, *Cnemidophorus cf. ocellifer*. In summary we observed that detection probability on the studied populations were low and similar to other vertebrate populations from the tropics. However, including covariates in estimation models of vital rates and detection is important to obtain more accurate results to explain population dynamics. Specifically we conclude that (i) return rates were biased low in relation to survival estimates that account for detectability, (ii) the estimates of survival were similar between toe-clipped and PIT tagged individuals of *Hypsiboas faber*, (iii) *Bothrops insularis* showed low survival probability and negative annual population growth. And (iv) larger *Cnemidophorus cf. ocellifer* males showed lower monthly survival probability than smaller males but the opposite was found for females.

## RESUMO

A ecologia de populações investiga os fatores que levam a variação das taxas vitais e, conseqüentemente, no número de indivíduos. Isso inclui testar hipóteses sobre aspectos da história de vida das espécies e entender os fatores que podem modular a dinâmica populacional. No entanto, a obtenção de dados para testar hipóteses pode ser difícil para populações que apresentam probabilidades de detecção  $< 1$ , como anfíbios e répteis. A marcação e recaptura é amplamente usada para estimar a detecção e inferir aspectos de dinâmica populacional e testar hipóteses ecológicas. Neste trabalho empregamos a teoria de marcação e recaptura para testar hipóteses relacionadas à ecologia e conservação de populações de anfíbios e répteis. Utilizamos o programa MARK para implementar modelos de populações abertas e fechadas incorporando a probabilidade de detecção dos indivíduos, para obter estimativas de sobrevivência, e outros

parâmetros populacionais usando máxima verossimilhança. Organizamos esta tese em quatro capítulos. Iniciamos enfatizando a importância da probabilidade de detecção, além de simular cenários hipotéticos para demonstrar a relação entre esforço de campo, tamanho ótimo amostral e viés amostral. Em seguida comparamos o efeito de duas técnicas de marcação, o corte de artelhos e o implante de *microchips*, sobre a sobrevivência individual do sapo ferreiro, *Hypsiboas faber*.

No terceiro capítulo estimamos a sobrevivência e o crescimento populacional da jararaca-ilhoa, *Bothrops insularis* incorporando emigração temporária aos modelos. Além do estudo de taxas vitais e de dinâmica nas populações, a alocação de energia e suas consequências na sobrevivência individual podem ser testadas com modelos de marcação e recaptura. Assim, no quarto e último capítulo consideramos dois caracteres sexuais presentes no sistema de acasalamento dos lagartos, o tamanho da mandíbula e a coloração chamativa, para comparar as estimativas de sobrevivência entre machos e fêmeas do lagarto cauda de chicote, *Cnemidophorus cf. ocellifer*.

. De forma geral, observamos que a probabilidade de detecção individual nos sistemas estudados foi baixa e condizente com a detecção de vertebrados em ambientes tropicais. Além disso, a inclusão de covariáveis na investigação de parâmetros vitais e no processo de detecção é fundamental para o melhor entendimento dos fatores que explicam a dinâmica de uma população. Especificamente observamos que: (i) demonstramos que as taxas que não incorporam a detecção são enviesadas em relação as estimativas que consideram a detecção, (ii) as estimativas de sobrevivência foram similares em indivíduos de *Hypsiboas faber* marcados com ablação de artelhos e microchips, (iii) *Bothrops insularis* apresentou baixa probabilidade de sobrevivência anual e crescimento populacional anual negativo. Por fim, (iv) machos maiores do lagarto *Cnemidophorus cf. ocellifer* apresentaram sobrevivência mensal menor do que machos menores, mas o oposto foi observado para as fêmeas.



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Celebrate the moment□  
As it turns into one more□  
Another chance at victory□  
Another chance to score

The measure of the moment  
Is a difference of degree  
Just one little victory  
A spirit breaking free  
One little victory  
The greatest act can be  
One little victory

A certain measure of righteousness  
A certain amount of force  
A certain degree of determination  
Daring on a different course

A certain amount of resistance  
To the forces of the light and love  
A certain measure of tolerance  
A willingness to rise above

One Little Victory

Rush



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## INTRODUÇÃO GERAL

A ecologia de populações se preocupa em investigar os fatores que controlam a dinâmica temporal e espacial de uma população, decorrentes de variações das taxas vitais, interações bióticas e abióticas (Godfray, 2009). A trajetória demográfica de uma população pode ser definida a partir da combinação de um conjunto de probabilidades de parâmetros, que ocorrem em diferentes escalas, culminando com alterações na abundância. Dentre os parâmetros vitais de uma população se destaca a probabilidade de sobrevivência, um fator chave na dinâmica populacional (Lebreton et al., 1992; Williams et al., 2002).

Caracterizar a sobrevivência é importante para que se possa identificar, por exemplo, a fragilidade de uma população frente ao declínio (Pollock, 1982). Entretanto, mensurar a sobrevivência de populações naturais é uma tarefa árdua, devido à dificuldade de acompanhar os indivíduos no campo (Lebreton et al., 1992), além da dificuldade de se amostrar determinadas populações em função da raridade de algumas espécies ou grupos (Thompson, 2004). Assim, frequentemente, dados de uma parcela da população são utilizados para realizar inferências sobre as estimativas de interesse para a população como um todo, e diferentes métodos são baseados neste tipo de rotina, incluindo a marcação e recaptura.

Com o avanço do ferramental analítico, os modelos de marcação e recaptura constituem-se em ferramentas eficientes e flexíveis que auxiliam a obtenção de estimativas de parâmetros populacionais (Williams et al., 2002; Nichols, 2005) e permitem o teste de hipóteses envolvendo aspectos da história de vida das espécies (Lebreton et al., 1992). Na marcação e recaptura, a partir de múltiplas amostragens, os indivíduos capturados não marcados recebem uma marca individual e os indivíduos capturados já marcados em amostragens anteriores tem sua recaptura registrada (Manly et al., 2005). A partir de uma variável categórica (capturado "1"/não capturado "0") são

construídos históricos de captura individual e a estimativa dos parâmetros é calculada com base na multiplicação das probabilidades (Doherty et al., 2010; Manly et al., 2005).

Para que sejam alcançados resultados acurados, as estimativas devem incorporar a probabilidade de detecção (Yoccoz et al., 2001), que é a probabilidade de encontrar um indivíduo ou espécie quando presente na área de estudo. No entanto, ainda hoje muitos artigos assumem detecção perfeita ou constante nos sistemas, o que gera estimativas subestimadas. O conhecimento do quão enviesada é a estimativa em questão permite obter melhores indicadores de resposta da população, facilitando os esforços de conservação (Ferraz et al., 2007). A probabilidade de detecção se faz importante principalmente em sistemas imprevisíveis, onde a chance de encontrar os indivíduos é variável e geralmente baixa, e pode estar relacionada, por exemplo, a habilidade dos investigadores em encontrar os indivíduos e ao clima. Tratando-se de estudos de vertebrados, existem indícios de que anfíbios e répteis apresentam baixa detectabilidade no campo (Dorcas & Willson, 2009).

De forma geral, anfíbios e répteis apresentam características comuns de história de vida, incluindo tamanho corporal geralmente pequeno, ocorrência em ambientes similares e hábitos elusivos. Devido a tais características, podem ser populações de difícil monitoramento em ambientes complexos e heterogêneos (McDonald, 2004). Além disso, esses grupos veem apresentando declínios significativos nas últimas décadas, sofrendo com a perda e a alteração de hábitat, introdução de espécies exóticas, além de doenças e alterações climáticas (Gibbons et al., 2000, Stuart et al., 2004).

Neste trabalho, aplicamos a teoria de marcação e recaptura em populações da herpetofauna para estimar parâmetros populacionais de interesse, considerando a detecção imperfeita dos indivíduos. Implementamos modelos de populações abertas e fechadas para

responder questões inerentes a cada sistema, utilizando a seleção de modelos. As análises foram realizadas no programa MARK 5.1 (White & Burnham, 1999).

Esta tese esta organizada em quatro capítulos independentes entre si, com objetivos específicos. O **primeiro capítulo** surgiu devido a escassez de trabalhos que incorporam a detectabilidade envolvendo estudos com a herpetofauna no Brasil e na América do Sul. Esse problema enfraquece o poder de previsão sobre os sistemas, com implicações diretas nas ações de conservação das espécies. Inicialmente, comparamos a estimativa de sobrevivência que incorpora a probabilidade de detecção com taxas de retorno, índices sem correção, para a rã-de-corredera, *Hylodes asper*. Em seguida, por meio de simulações, demonstramos a relação entre o esforço amostral e precisão, com o objetivo de fornecer elementos para auxiliar pesquisadores no campo

O **segundo capítulo** aborda a importância de se conhecer os efeitos das técnicas de marcação sobre os indivíduos, e conseqüentemente sobre a população. Para tanto comparamos os efeitos de duas técnicas amplamente empregadas em estudos com vertebrados, a ablação de artelhos e a aplicação de *microchips*, em uma população do sapo ferreiro, *Hypsiboas faber*.

O **terceiro capítulo** ilustra o primeiro estudo de dinâmica populacional para umas das espécies de serpentes ameaçadas do Brasil. Neste, empregamos o desenho robusto de Pollock para incorporar a migração temporária nas estimativas de sobrevivência e abundância. Além disso, investigamos possíveis respostas comportamentais oriundas do método de captura e provemos uma estimativa de crescimento populacional.

No **quarto capítulo** utilizamos a teoria de seleção sexual para testar o efeito de caracteres sexuais secundários sobre a sobrevivência individual em lagartos. Para tanto utilizamos o tamanho da mandíbula, empregado na luta entre machos, e a coloração de sinalização, para testar

a hipótese de que o maior investimento em caracteres sexuais tem efeito negativo sobre a sobrevivência de machos porém efeitos opostos em fêmeas do calango, *Cnemidophorus* cf. *ocellifer*.

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## **CAPÍTULO 1**

**STRENGTHING POPULATION INFERENCE IN HERPETOFAUNAL STUDIES BY  
ADDRESSING DETECTION PROBABILITY**

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ABSTRACT. Accounting for detection probability in population studies has been widely adopted. However, many Brazilian herpetological articles still report estimates without considering how detection can influence estimates of survival and other vital rates, assuming that detection probability is perfect (i.e. 100%). Using data from a population of the torrent frog, *Hylodes asper*, I calculated return rates and compared them with survival probability estimates adjusted for detection probability to show the discrepancies between the two metrics. Using power analysis, I also explored how survival is underestimated, considering different scenarios and sampling efforts, given low detectability. Finally, I provide information on the optimal number of surveys to achieve a 15% coefficient of variation, assuming a fixed number of individuals initially captured for a series of parameter values. Ignoring potential bias of uncorrected estimates may lead to weak inference and erroneous decisions for management and conservation. I suggest researchers consider detection probability in their studies to obtain more accurate estimates of population.

Key words: Mark-Recapture, Detectability, Amphibians, Reptiles, Vital Rates, Abundance, Survival Probability.

## INTRODUCTION

Conservation biology often focus on studies investigating population parameters, such as abundance, survival, or other vital rates. Estimating such measures without bias is imperative when dealing with population declines, which have been observed for amphibians and reptiles world-wide (Gibbons et al., 2000; Stuart et al., 2004; Bohm et al., 2013). Until about 10 years ago, most inferences made on herpetological populations were based on raw counts (Schmidt, 2003; Mazerolle et al., 2007), which may erroneously assume perfect or constant detection probability (the probability of seeing an individual or a species when present in the sampling area), through time and space. As such, many studies have overlooked potential biases in vital rate estimates associated with changes in detection probability due to individual and temporal variation (e.g. differences among sexes or size, behavioral responses, seasonal activity), as well as observer bias (Anderson, 2001; Bailey et al., 2004a). Assessments of species occurrence, colonization of fragmented areas, and species richness are also biased when detection probability is not accounted for (Williams et al., 2002; MacKenzie et al., 2006; Ruiz-Gutiérrez and Zipkin, 2011; Yackulic et al., 2012).

Using abundance as an example, consider  $y$  the number of animals observed in a survey,  $p$  as the detection probability associated with the survey and  $\tau$  as the true number of individuals. If we assume that (1) we see animals of a specific group with a certain probability  $p$ , and (2) one individual does not affect detectability of another (individuals are independent), then  $y$  can be model as binomial distribution, with the expected number of individuals observed after repeated counts being:

$$E(y) = \tau p \text{ (Thompson, 2012).}$$

When  $p$  is less than 1, the count statistic  $y$  must be adjusted by  $p$  in order to get an unbiased estimate of  $\tau$  (Williams et al., 2002; Thompson, 2012). If  $p$  varies in time or space, the variation in  $y$  could be due to variation in  $p$  (Williams et al., 2002; Schmidt and Pellet, 2010). Furthermore, because  $p$  can only take on values between 0 and 1 (because it is a probability), the simple count  $y$  will only be biased low (Schmidt and Pellet, 2010).

The probability of survival is another important life history parameter, directly related to fitness. Although critical to population dynamics, survival is difficult to obtain because time of death is usually unknown under natural conditions (Lebreton et al., 1992). In this way, inference may be based on marked animals and various robust models that account for detectability are available (Nichols et al., 1994, Schwarz and Arnason, 1996; Williams et al., 2002). However, survival is sometimes estimated through the return rate, a confounded index of survival which includes the probability of the individual surviving from the capture occasion  $t$  to  $t+1$ , and the probability of detecting the individual at  $t+1$ , given that the individual is alive and in the study area (Lebreton et al., 1992). Because detection probabilities are rarely 1, using return rate to infer patterns of survival may be erroneous (Martin et al., 1995).

Without adjusting for  $p$  (detectability), raw counts are referred as population indices when dealing with population sizes, trap rates when considering the number of individuals captured in traps, or as return rates with survival studies- all of which have been argued as being biased because they assume no random or systematic changes in detection (e.g. constant) over time (Anderson, 2001). The animal ecology literature is full of suggestions that detection probability needs to be addressed in conjunction with count statistics (Williams et al., 2002; MacKenzie et al., 2006), since obtaining a  $p = 1$  is difficult in most field situations. Besides that, ensuring high

detection probabilities help improving precision of estimates, such as survival or abundance (Otis et al., 1978; Pollock, 1982).

The importance of detection probability has been noted in European and North American herpetology journals (Schmidt et al., 2002; Dodd and Dorazio, 2004; Schmidt, 2004; Mazerolle et al., 2007), as well as in general ecology and zoology journals dealing with herpetofauna (Kéry, 2002; Schmidt, 2003; Bailey et al., 2004a; Bailey et al., 2004b; Willson et al., 2011). However, when considering south american and specially, Brazilian herpetological journals, many population and community articles still overlook this issue.

Here, using mark-recapture models, I intend to demonstrate the bias when using estimates uncorrected for detection probability and to make recommendations for study design in order to strength the inference in herpetofaunal studies. Specifically my goals are: (i) to show the discrepancy between estimates that account for detectability, with estimates that do not include detectability; (ii) to show the bias, through simulated scenarios, in estimates of survival probability when using different amounts of effort; and (iii) to provide recommendations of an optimum number of surveys based on given values, with a reasonable level of precision.

## METHODS

### General approach

In order to achieve my goals I organized this paper in three parts. First, I estimate survival probability, while accounting for detection probability, to contrast it with the return rate and show the bias when  $p$  is assumed to be 1. For that purpose, I used empirical data of a population of the torrent frog, *Hylodes asper* (Leptodactylidae). In the second part I use the estimates generated for the torrent frog population to plug into simulations to show the percentage of the simulated

scenarios that underestimate the true value of the apparent survival when different sampling efforts are used. In the third part I combine number of individuals initially released with survival and detection estimates to recommend sampling effort with reasonable precision (see Mackenzie et al., 2006).

*Survival probability and return rates in the torrent frog, *Hylodes asper**

I used a data set of a population of the torrent frog, *Hylodes asper* obtained in the Parque Estadual da Serra do Mar at Núcleo Picinguaba (23° 22'S; 45° 0'W), coast of São Paulo state, southeastern Brazil. Capture occurred in a 100-meter transect of a rocky stream during 43 consecutive months, from 2007 to 2010. Within each month, two to four trained investigators searched for frogs using visual and auditory cues while walking slowly upstream; this was done for one day on each month. Photographic mark-recapture was used to individually identify frogs and only adult frogs were considered.

I used maximum likelihood estimates to obtain apparent survival probability ( $\Phi$ ), a product of true survival and site fidelity of individuals from the sampling area (thus, emigration and death are confounded), and detection probability ( $p$ ) in the Comarck-Jolly-Seber open population model (CJS, Cormack, 1964; Jolly, 1965; Seber, 1965) in Program MARK (White and Burnham, 1999).

I fit four models on the data: a constant model, which considers no variation on  $\Phi$  and  $p$ , and three other models considering season (dry versus wet season) as a temporal covariate on one or both parameters. I used the Akaike Information Criterion adjusted for small sample sizes (AICc, Burnham and Anderson, 2002) to select and rank models. The AIC ranks models based on

the fit and on the number of parameters of each model. The model with the lowest AICc is the most parsimonious conditional on the data set (Burnham and Anderson, 2002).

After that, I calculated the return rate, which is defined as:

$$\sum_i^2 (m_{i+1}/R_i)/n \text{ (Martin et al., 1995)}$$

where  $R_i$  is the number of new individuals marked plus the number of individuals resighted in occasion  $i$ ,  $m_{i+1}$  represents the number of individuals resighted on occasion  $i + 1$ , and  $n$  is the number of field occasions (see Martin et al., 1995 and references therein). I calculated monthly return rates and then averaged within seasons to obtain estimates for both dry and wet seasons. Finally, I compare the estimates that unaccount for detectability (the return rates) with the apparent survival probability, which accounts for detectability.

### *Sampling effort and bias*

Here I set up two hypothetical situations, one called “dry season” and the other called “wet season”. Each situation was composed by an estimate of detection probability, obtained in the torrent frog population and used here, and an estimate of survival probability. Since no variation of survival probability was found between the dry and the wet season in the torrent frog population (see results), I chose two different but close values of apparent survival probability, similar to those obtained for the torrent frog population. Thus, the situation called “dry season”, had detection probability of 0.05 and apparent survival probability of 0.95. In the second situation, “wet season”, detection probability was 0.14 and apparent survival was 0.90. I considered these values the truth for my hypothetical population.

For each situation, I simulated 16 scenarios, representing four different sampling efforts (15, 30, 45 and 60 field occasions) and four different numbers of individual captures in the first



occasion (5, 10, 15 and 20 individuals) in all combinations. I set up the simulations in program MARK, using the CJS model. On each of the 32 scenarios (16 for each situation), I ran 500 simulations. The simulations were based on Bernoulli trials, where the probability of getting  $k$  successes (in this case the probability of surviving) is given by the Binomial probability function:

$$\text{Pr}(k|n, p) = f(k|n, p) = \binom{n}{k} p^k (1 - p)^{n-k}$$

where  $n$  is the number of surveys and  $p$  is the probability of detecting the individuals. To keep a simple design, I based all simulations on the constant model  $\{\Phi(\cdot) p(\cdot)\}$ , which means constant apparent survival and detection probabilities through time and space. To present the results, I calculated the relative number of simulations that presented survival estimates below the true value given by the wet and the dry scenarios.

#### *Optimum number of surveys*

In this simulation routine, I fixed the number of initial releases at 10, which means that 10 individuals were captured, marked and released in the population in the first occasion. In the following occasions, based on specific survival probability estimates, I caught/marked/released new individuals so that a similar number of marks was always present in the population. Then I made different combinations of the fixed number of initial releases with nine different parameter values of apparent survival (from 0.1 to 0.9) and nine different parameter values of detection probability (from 0.1 to 0.9) in all possible combinations, to establish 81 scenarios.

To make the results comparable, I used the coefficient of variation, defined as the standard deviation of a population mean divided by the mean estimate of a population parameter  $CV = \sigma/\mu$  (Thompson, 2012). I adopted a  $CV$  of 0.15 or 15% as goal. The coefficient of variation is

a useful metric, since it provides a measure of relative precision, which is comparable among studies (Thompson, 2012).

## RESULTS

### *Survival probability and return rates in the torrent frog, *Hylodes asper**

A total of 220 adult individuals were captured during the study period. The model that included season as a temporal covariate on  $\Phi$  and  $p$  ranked highly and had 0.99 of the AICc weight (Table 1). The constant model, with time constant on survival and detection probabilities had no support ( $\Delta$ AICc of 29.47, Table 1). Detection probability in the wet season was 0.14 (95% CI 0.10-0.18) and was higher than in the dry season, 0.05 (95% CI 0.03-0.07). Point estimates of apparent monthly survival were about three times higher than return rates in both seasons (Fig. 1).

### *Sampling effort and bias*

Among the 32 different simulated conditions, dry- and wet-season scenarios suggested gradual improvements with increased effort (Fig. 2). Simulations with 15 occasions performed poorly, with about 50% of the simulations resulting in biased apparent survival estimates, independent of the number of individuals initially released. With a 4-fold increase in the effort (60 occasions), the estimator underestimated 8.2% and 14.8% of the simulations in the dry and wet seasons, respectively. The larger the number of initial releases, the better the results achieved.

### *Optimum number of surveys*

If survival probability is high ( $> 0.8$ ), the investigator will need a few visits in the field, even if detection probability is low ( $< 0.3$ , Table 1). Considering apparent survival and detection probabilities of 0.9, the investigator will need only two occasions of effort in the field (Table 2), the minimum necessary for a mark-recapture study. However, when survival and detection are very low, close to 0.1, it will be necessary to increase the effort by at least 3 orders of magnitude to achieve the goal of 15% coefficient of variation (Table 1).

### DISCUSSION

In this paper, I revisited detection probability in an attempt to reinforce the importance of considering the issue. Addressing detectability in wildlife studies is unavoidable if we want to draw more accurate conclusions about the studied systems. Below, I discuss each section of this paper and important topics in each.

### *Survival probability and return rates in the torrent frog, *Hylodes asper**

Detection probability differed between the two seasons and was low, which is generally common in complex systems and occurs in different taxa (Ruiz-Gutierrez and Zipkin, 2011; Kajin and Grelle, 2012; Maritz and Alexander, 2012). Point estimates of monthly apparent survival probability for dry and wet seasons were high and very similar here. These estimates, may be plausible since they represent monthly survival, and may reflect the species' life history where individuals can live up to 3 years (Pato and Pie, 2001).

The return rates were lower than the estimates of apparent survival and the discrepancy usually occurs because return rates are uncorrected and confounded counts between survival and

detectability that assume constant or complete detection, disregarding any variation in space and time (Lebreton et al., 1993; Martin et al., 1995; Anderson, 2001). Despite the clear problem in using return rates, several articles, including, for instance, those comparing effects of marking techniques in amphibians (McCarthy and Parris, 2004), have based conclusions on return rates. Such estimates are generally biased low, leading to wrong answers and possible erroneous conservation decisions.

### *Sampling effort and bias*

I showed simulation scenarios that could represent many amphibian and reptile populations, which are characterized by high survival and low detection (Parker and Plummer, 1987). Using different combinations of survey schemes and effort, my results emphasize the importance of improving the detection process (i.e., increasing the detection probability) and obtaining large sample sizes. I kept simulations simple for demonstration purposes here, assuming no variation on each parameter. However, the literature shows that constancy is rarely achieved (Schmidt, 2003; Bailey et al., 2004a; Mazerolle et al., 2007; Schmidt and Pellet, 2010; Willson et al., 2011), and parameters fluctuate over time and space. Thus, one possible challenge is gathering data for amphibians and reptiles given their secretive life histories. The investigator must struggle to get good quality data of the target species whatsoever, always concerned in maximizing detectability.

### *Optimum number of surveys*

My goal here was to provide investigators the optimum number of surveys, which could be site visits or number of transects, necessary in the field, given specific population parameters

in order to achieve 15% of coefficient of variation. Although the results obtained here may be applied for different populations and species, each field survey may have a different cost and the investigator should be warned that achieving the conditions exemplified here might vary among systems.

Sometimes the level of effort necessary to achieve good precision may not be even possible. Thus, when dealing with an organism with low survival probability ( $<0.4$ ) the investigator will probably need to redesign the study such that the survival probability that will be estimated is higher ( $>0.5$ ). Besides that, the investigator will also need to ensure that detection probability is also around 0.5. A population with parameter values like those above cited may require multiple consecutive days/visits of effort.

Another key factor for the success of the study lies on the sample size. For simulation purposes here, I fixed the number of individuals captured in the first occasion; however, this is barely true in real studies dealing with amphibians and reptiles, since the number of captures usually does not represent the unit effort. More common measures of effort are time-constrained surveys, number of traps, transects and so on. Less effort will be necessary when detection probability is high, close to 1. However, low estimates of detectability will demand high sampling effort (MacKenzie et al., 2006).

#### Considerations and recommendations

Planning and designing the sampling scheme is a key step for the success of the study (Yoccoz et al., 2001), but unfortunately this is seldom done. Different approaches are available to incorporate detection probability in the sampling design. The multiple-observer sampling and the double sampling ratio estimator are two methods that encompass detection in design-based

studies. In model-based approaches, methods such as radio telemetry and distance sampling also account for detection (Thompson, 2012). Mark-recapture is another powerful technique used intensively in the wildlife for many decades to obtain robust estimates of detection, and other parameters of interest.

Detectability varies with field methods and populations, which means that even when applying searching standard methods, such as constrained searches by time or area, detection will vary (Mazerolle et al., 2007; Schmidt and Pellet, 2010). Tropical systems, such as rain forests, are generally characterized by high diversity and high complexity which may decrease detection when compared to simpler systems, where detection may be higher for small and elusive taxa such as amphibians and reptiles (Willson et al., 2011) and other groups (Ruiz-Gutierrez and Zipkin, 2011; Kajin and Grelle, 2012). Also, the use of temporal, spatial, and individual covariates may help to improve the estimates, and consequently all other parameters in the study (Williams et al., 2002). Detectability may be improved by increasing the number of site visits, as cited above, and trained observers. Besides that, increasing the number of traps and/or reducing the sampling area may also help.

The use of raw counts might be valuable if proved that detection does not vary over time and samples, as well as observers. In this case indices could be useful in monitoring population relative changes, such as abundance. However, detection is usually influenced by all these factors, and the use of raw counts is generally unadvisable (Anderson, 2001), since the proportion of variance explained by the raw counts can be very low (Pellet et al., 2007; Schmidt and Pellet, 2010). In all cases, estimates incorporating detection probability outperform raw counts (Schmidt and Pellet, 2010).

Imperfect detection is composed of two elements, easily discernible in theory, but not in practice (Schmidt and Pellet, 2010). To be detected, an individual must be available to be detected and must be found by the observer. If the population is closed and all individuals are available for detection, then availability is not a problem. However, sometimes individuals are not available because they have temporarily left the study site or because they are crossing a larger area and are captured just once, when crossing the study site, being characterized as transient individuals. Other times, such unavailability may be caused by inherent biology of the target species (e.g. females that are present in a breeding pond for only a few days). Unavailability may also be caused by weak study design when, for example, the investigator searches for the target species in different time or uses wrong capture method. Both transient individuals and temporary immigrants can be estimated using mark-recapture and other methods (see Schmidt and Pellet, 2010).

With a vast literature warning about the problem of unaccounted detection probability, why do researchers still rely upon indices, return rates, and trap rates? Mazerolle et al. (2007) and Schmidt and Pellet (2010) argue that investigators may be reticent to adopt a better approach because of misleading reasons, such as costly (energy, time and money) methodologies, unrealistic assumptions, no need to account for detection (since the investigator assumes his experience, and the fact that detection does not vary make this trait negligible), and that the use of standardized searching methods will make detection constant. Although this problem is not exclusive to herpetology, different solutions are available and imprecise corrected estimates are preferable to biased ones. Less costly methodologies such as distance sampling and occupancy modeling are good alternatives to mark-recapture (xxxx) allowing for robust estimates and reasonable assumptions that account for detectability.

I suggest researchers address detection probability. Also, thinking hard about hypotheses and predictions, pilot studies, power analysis and simulations are great tools that will assist and improve the sampling design in order to get estimates and reduce heterogeneity (Lebreton et al., 1993; Anderson, 2001; Anderson, 2008; Schmidt and Pellet, 2010). If uncorrected estimates are relied upon for population trends and dynamics, biased conclusions may lead to poor management and conservation decisions.

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TABLES

**Table 1.** Model selection results for the torrent frog population. Models included no variation (.) or seasonal variation between dry and wet seasons (season) on parameters.

Model	AICc	$\Delta AICc$	$w_i$	$K$	Deviance
$\Phi$ (season) $p$ (season)	868.64	0	0.99	4	612.67
$\Phi$ (.) $p$ (season)	881.34	12.70	0.01	3	627.43
$\Phi$ (season) $p$ (.)	893.60	24.95	0.00	3	639.68
$\Phi$ (.) $p$ (.)	898.11	29.47	0.00	2	646.24

AICc=Akaike's information criteria with small sample size correction,  $\Delta AICc$ =difference between top model and the current model,  $w_i$ =AICc weights,  $K$ =number of parameters, Deviance=difference of the current model and the saturated model.

**Table 2.** Number of field occasions to achieve a 15% coefficient of variation or less, given specific apparent survival and detection probability values. Number of initial individuals releases is 10.

		Survival probability ( $\Phi$ )								
		<b>0.1</b>	<b>0.2</b>	<b>0.3</b>	<b>0.4</b>	<b>0.5</b>	<b>0.6</b>	<b>0.7</b>	<b>0.8</b>	<b>0.9</b>
Detection probability (p)	<b>0.1</b>	> 360*	> 360*	> 360	152	58	21	12	10	7
	<b>0.2</b>	> 360*	> 360*	235	65	24	13	8	7	6
	<b>0.3</b>	> 360*	> 360*	177	48	16	10	7	6	4
	<b>0.4</b>	> 360*	> 360*	100	33	13	9	6	5	4
	<b>0.5</b>	> 360*	360	79	25	11	7	6	5	4
	<b>0.6</b>	> 360*	303	45	20	9	6	5	4	3
	<b>0.7</b>	> 360*	177	36	16	8	6	4	4	2
	<b>0.8</b>	> 360*	123	28	15	7	5	4	4	2
	<b>0.9</b>	> 360*	100	23	14	7	5	4	3	2

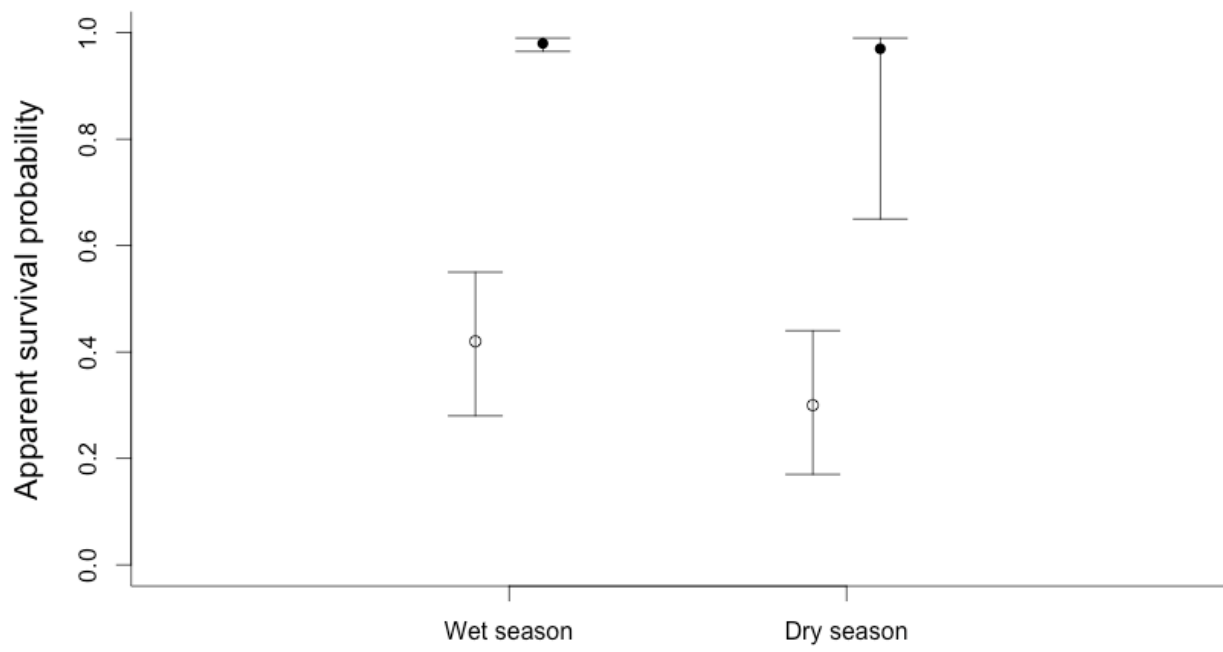
\*Program MARK capabilities allows for a maximum number of 360 encounter occasions.

## FIGURE CAPTIONS

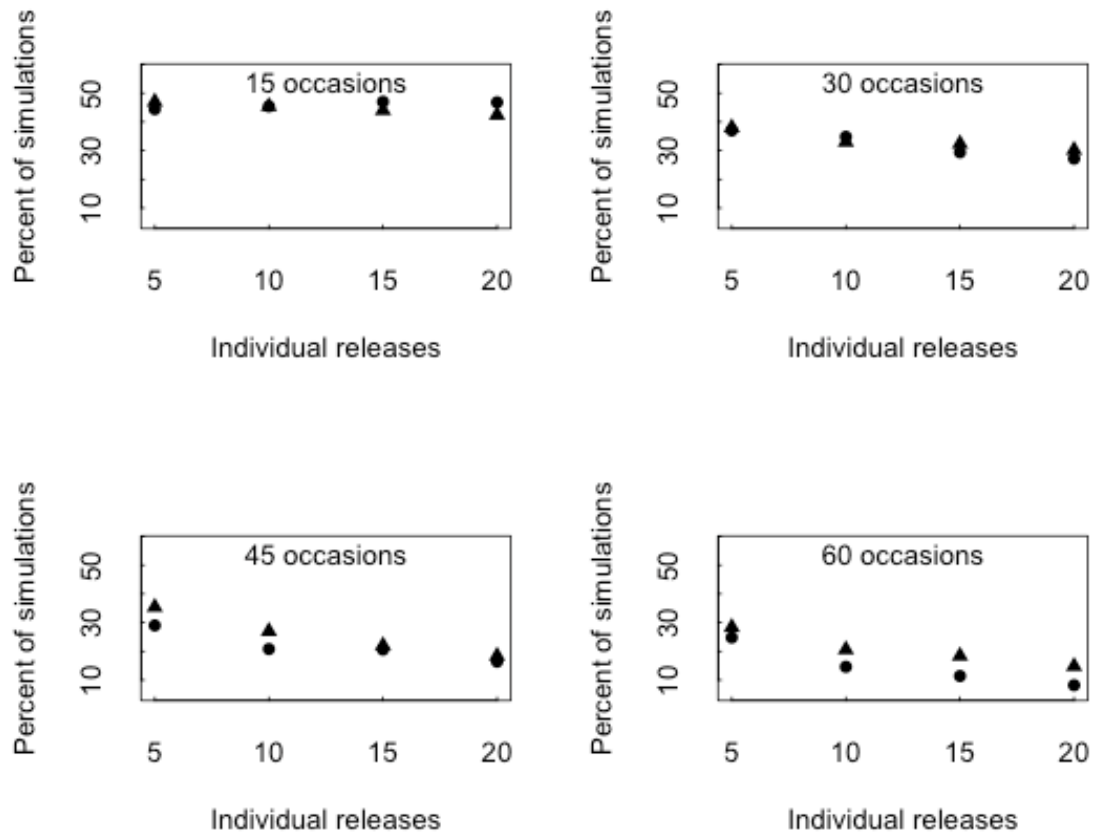
**Figure 1.** Apparent survival probabilities (closed circles) and return rates (open circles) in the wet season and in the dry season for the torrent frog population (95% confidence intervals are shown in the bars).

**Figure 2.** Percent of simulations that underestimated the true value of apparent survival within four scenarios of sampling effort and initial sample sizes for the dry season (circles) and wet season (triangles).

**Figure 1**



**Figure 2**



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## CAPÍTULO 2



**TOE CLIPPING AND PIT TAGGING HAVE SIMILAR EFFECTS ON FROG  
SURVIVAL AND RECAPTURE PROBABILITY**

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*Abstract.* Amphibians have been declining worldwide and the comprehension of the threats they face could be improved using mark-recapture studies to estimate vital rates of natural populations. Recently the consequences of marking amphibians have been under discussion and the effects of toe clipping, the most common technique for amphibian individualization, on survival are debatable. The passive integrated transponder (PIT tagging) is an alternative technique, but there has been no comparison between toe clipping and PIT tagging for free ranging populations. We compared these two marking methods using mark-recapture models to estimate apparent survival and recapture probability of a neotropical population of the blacksmith tree frog, *Hypsiboas faber*. We tested the effects of marking method and number of toe pads removed, while controlling for sex and rainfall. Survival was similar between toe-clipped and PIT-tagged frogs and did not vary by sex. Sex was the best predictor for recapture probability, with males being nearly five times more likely to be recaptured. In conclusion, we (i) recommend the use of covariates to better understand the effects of marking methods on frogs, and (ii) suggest the use of toe clipping, given the lack of comparisons with other alternative marking methods in the literature and logistical and cost issues associated with PIT tagging.

*Key words:* amphibians; detection probability; Hylidae; mark-recapture; multi-model inference, return rate.

## INTRODUCTION

With the current scenario of amphibian declines (Stuart et al., 2004), quantitative links between vital rates and explanatory covariates are fundamental to understand the dynamics of, and threats to populations (Biek et al., 2002). Among different strategies used to infer vital rates, mark-recapture constitutes an important tool, providing accurate information on population trends and demographic estimates (Manly et al., 2005) especially when population dynamics are poorly understood, such as occurs in the neotropics (Hiert et al., 2012).

Although field biologists strive to apply the least harmful marking technique to their study species, most techniques remain invasive and may affect behavior and survival (Lemckert, 1996; Bloch and Irschick, 2004; Schmidt and Schwarzkopf, 2010). Among the different methods used to mark anurans (Donnelly et al., 1994), the most common is the toe clipping (Bogert, 1947), which consists of removing different combinations of digits to give individuals a permanent mark.

However, the scientific community has recently been debating the impacts of marking individuals, especially toe clipping, with divergent opinions (May, 2004; Funk et al., 2005; Corrêa et al., 2013). Several recent papers have related the number of toes clipped to individual response of amphibians, including lower return or survival rates (Parris and McCarthy, 2001; McCarthy and Parris, 2004; Waddle et al., 2008). Although more research evaluating such impacts is needed, novel methods have been proposed to replace toe clipping but they remain to be tested (Brown, 1997; Hoffmann et al., 2008; Campbell et al., 2009, Kenyon et al., 2009).

The passive integrated transponder (PIT tag) is one such alternative to toe clipping, which consists of a glass-encapsulated electromagnetic coil with a unique alphanumeric code that is lodged under the skin or in the body cavity of an animal and read by a handheld scanner

(Gibbons and Andrews, 2004). Because of its low cost and the possibility to mark an unlimited number of individuals, PIT tags have been used in anurans as an alternative marking method (Christy, 1996; Jehle and Hödl, 1998). Nevertheless, negative effects on frog survival have already been reported (Scherer et al., 2005) and little is known on the impacts of PIT tags on anurans (e.g. Christy, 1996; Brown, 1997; Phillot et al., 2008). Behavioral and physiological deleterious effects from the injection of the tag may occur and frog response might be different from toe clipping. Overall, direct comparisons between different marking techniques are still lacking.

Another issue for studies that have attempted to quantify the effects of marking methods on frogs is the absence of statistical power, especially by toe clipping (Schmidt, 2003). Furthermore, past studies have been based on the return rate to infer survival (e.g. McCarthy and Parris, 2004), which consists of the proportion of marked individuals recaptured at least in one occasion (Lebreton et al., 1992). The return rate assumes a constant detection probability, which is unrealistic in natural systems, due to heterogeneity in behavior (e.g. between sexes) and climatic conditions, such as rainfall, which influences amphibian activity (Duellman, 1986). Despite the number of studies reporting decreased return rates with increasing number of toes removed, only a few studies have assessed the issue accounting for detection probability, which is likely less than one (e.g. Waddle et al., 2008; Grafe et al., 2011). Waddle et al. (2008) found different recapture probabilities for individuals with two, three and four toes removed in the squirrel treefrog, *Hyla squirella*, but survival was similar among the groups. The use of return rate in this case would lead to the erroneous conclusion that toe clipping reduces survival.

Here we contrasted the effects of toe clipping and PIT tagging on a free ranging neotropical tree frog population using mark-recapture models, which allowed us to disentangle

survival and recapture probabilities (Schmidt, 2003; Waddle et al., 2008). We specifically compared survival and recapture probabilities between marking techniques, while controlling for sex differences and climatic variability in rainfall. We hypothesized that individuals marked with PIT tags will present lower survival than individuals marked with toe clipping, and that the removal of more toes will linearly decrease individual survival.

## METHODS

### *Study site and study species*

We conducted this study in a 970-square meter permanent pond in Estação Ecológica de Jataí (21°30' S, 21°40' W), a conservation unit in the state of São Paulo, southeastern Brazil. The unit is located in a transitional area between the Atlantic Forest and the Cerrado biomes, composed of open grassy areas and semi-deciduous forests. Average temperature in the coldest months (June to August) is about 11° C, and about 30° C in the hottest months (December to February). Annual rainfall is about 1500 mm. Precipitation during the rainy season (October to March) typically exceeds 270 mm per month, but does not exceed 27 mm per month during the dry season (April to September) (CEPAGRI, 2011).

We sampled an adult population of the blacksmith tree frog *Hypsiboas faber* (Anura, Hylidae) (Fig. 1), a large tree frog (snout-vent length =  $92.3 \pm 4.8$  mm, N = 305; this population) distributed from northern Argentina to eastern Brazil (Martins, 1993). Males of this species occupy a pond and build nests at the beginning of the breeding season (generally from October to March; pers. obs), then begin to vocalize until a female approaches to inspect the nest. Males usually do not spend the whole reproductive season at the breeding site (Martins, 1993); females visit ponds only long enough to oviposit in the breeding site before leaving (Martins, 1993).

### *Data collection*

We collected data during two reproductive seasons, from November to March, in 2010-2011 and 2011-2012. We captured individuals during three nights per month and pooled nights within the same month together, resulting in 10 sampling occasions, five on each breeding season. On each capture occasion, three researchers systematically walked inside and in the margins of the pond capturing adult individuals by hand based on visual and acoustic cues in all accessible microhabitats.

We determined sex and randomly assigned one type of marking method to each individual, toe clipping or PIT tagging. We placed individuals in four different groups: group one (one toe clipped), group two (two toes clipped), group three (three toes clipped) and group four (PIT tag). We marked individuals in the toe clipping groups starting with the removal of one toe. When all combinations for removing one toe were used, we started removing two toes in unique combinations, and finally, three toe removal combinations, clipping up to two toes per limb. This sampling design generates uneven toe pad removal groups over the study period (see Grafe et al., 2010), which we accounted for by including a linear trend model in the parameter estimates (see Statistical analysis).

We adapted the marking method of Waichman (1992), removing only the toe pad ("toe tipping", *sensu* Phillot et al., 2007), which is enough for individual recognition as tissue regeneration is rarely observed (Luddecke and Amézquita, 1999; Phillot et al., 2007, Grafe et al., 2011). The PIT-tagging group received a 2.2 mm x 12.2 mm, 0.5 g internal transponder (Animall Tag company) implanted in a posterior laterally-dorsum position, using sterilized needles and followed by the use of surgical glue to help healing. The mass ratio PIT tag/tree frog never

reached 0.5%. To control for possible effects of the glue, all individuals from the toe clipping groups also received the same amount of glue on the same local.

The effects of marking technique and number of toes removed were assessed in three different ways: (i) by comparing the survival on individuals with one, two, three toe pads clipped and PIT tagged (hereafter ‘group effects’); (ii) by comparing the effects of toe pad clipping against PIT tagging, where we combined groups one, two and three and compared to group four (hereafter ‘marking method effects’); and finally (iii) by forcing a linear trend effect only on toe clipped groups (hereafter ‘linear trend effect’), to test the hypothesis that removal of more toes decreased survival. In addition, the inclusion of a linear trend in the recapture probability was used to account for the uneven toe pad removal groups over the study. Although the linear trend was applied only on the toe clipped groups, the PIT tag group was also included in the analysis. Sex was included in each analysis as an individual covariate. Total monthly rainfall during sampling periods was also included as a temporal covariate in both parameters in order to accommodate weather variability in the models (Table 1).

### *Statistical analysis*

We obtained maximum likelihood parameter estimates using a Cormack-Jolly-Seber (CJS) model (Cormack, 1964; Jolly, 1965; Seber, 1965) in Program MARK (White and Burnham, 1999). The CJS model estimates the parameters apparent survival probability ( $\Phi$ ), which is a combination of true survival and site fidelity, and recapture probability ( $p$ ). We constructed 577 different models representing hypotheses about the effects of marking methods, time, sex and rainfall, using the strategy proposed by Doherty et al. (2010) to run all possible

additive combinations of factors, except for combinations that did not make logical sense (e.g., different representations of marking effects, or temporal covariates and time effects in the same model).

Goodness-of-fit and a variance inflation factor (i.e., median  $\hat{c}$ ) were assessed using the general model ( $\Phi_{\text{group+time}} p_{\text{group+time}}$ ). We selected and ranked models using Akaike Information Criterion (Akaike, 1973) adjusted for small sample sizes ( $AIC_c$ , Burnham and Anderson, 2002). Survival and recapture probabilities were model averaged using all models, in order to include uncertainty in model selection (Burnham and Anderson, 2002). We then calculated the relative importance of each covariate through the cumulative  $AIC_c$  weights (Doherty et al., 2010) in order to determine the important covariates for each parameter. Following Barbieri and Berger (2004) we considered covariates with cumulative  $AIC_c$  weight above 0.5 to be important.

## RESULTS

In group one (one toe clipped) we marked 14 males and four females, in group two (two toes clipped) 110 males and 40 females, in group three (three toes clipped) 120 males and 30 females, and in group four (PIT tag) 177 males and 50 females. We recaptured 117 out of 545 individuals at least once. The goodness-of-fit test showed no problem with transient individuals or trap dependence effects and no extra binomial variation was detected ( $\hat{c}=0.96$ ).

The top model ( $AIC_c$  weight = 0.05) included constant apparent survival among groups and detection probability varying as an additive effect of linear trend on toe clipped groups, time variation and sex. However, many models had similar  $AIC_c$  weights, with considerable model selection uncertainty (Table 2). Considering all models averaged, apparent monthly survival



probability was very similar among the four marking techniques and sexes (Fig. 2), with none of the covariates having an important effect on apparent survival probability (Table 3), highlighting the importance of the constant survival among groups.

The best covariates predicting the recapture probability were sex and time (Table 3). Males presented higher averaged recapture probability than did females (Fig. 3), but no difference was detected among groups one, two, and three (toe clipped groups) when compared to group four (PIT tag). Groups presented monthly recapture estimates from 0.12 to 0.39.

## DISCUSSION

Our first hypothesis relating lower survival for PIT tagged individuals was not corroborated, since the apparent survival probability did not differ among groups and sexes. We also hypothesized that more toes clipped would reduce survival in toe clipped individuals, but no correlation between survival and the number of toes clipped was found. Based on the cumulative AICc weights, none of the covariates had a strong effect on the apparent survival probability in our model set. Two out of six covariates were important in describing the variation on the recapture probability. The most important was sex, which carried out the most cumulative AICc weight.

As mentioned before, males and females *H. faber* present clear behavioral differences (Duellman, 1986; Martins and Haddad, 1988; Martins 1993). Because females are more mobile, their recapture probabilities were lower, which indicates that pooling the sexes in the analysis would lead to biased results. Besides, if we had considered just the return rate as a survival estimate, estimates would be biased low (0.39 and 0.17, averaged among groups) for males and

females, respectively, leading to erroneous conclusions. As noted before, biased results may be obtained if not correctly accounting for the probability of detection (Mazzerole et al., 2005).

Effects of time were important on recapture probability. The substitution of individuals in the pond could account for this trend, since individuals stay at the breeding site for a limited amount of time, being substituted by new ones throughout the breeding season (Martins, 1993). Such permanent emigration will likely bias survival estimates low, since estimates of apparent survival are a product of true survival and site fidelity. In this study, groups presented similar apparent survival estimates, showing that emigration rates may be similar among groups. Accounting for permanent emigration in the field includes the use of radio telemetry and known fate models where fates of all marked individuals are known (Williams et al., 2002). On the other hand, if individuals of the population leave the site temporarily, the robust design approach is a good alternative to account for temporary emigration (Pollock, 1982; Kendall et al., 1997).

We included rainfall in the models as an attempt to account for the weather variability, since amphibians present a strict relation to water availability. However, in this study rainfall did not come up as an important covariate. Then, the substitution of individuals in the pond highlights the importance of considering time variation effects in the model set, besides other related covariates, whenever possible.

Invasive marking methods can cause negative effects for individuals, and toe clipping is a stressor for amphibians when compared to handling only (Narayan et al., 2011). Other studies have already reported negative or neutral effects of toe clipping on frog survival and capturing (Lemckert, 1996; Van Gelder and Strijbosch, 1996; McCarthy and Parris, 2004; Hartel and Nemes, 2006; Liner and Smith, 2007; Schmidt and Schwarzkopf, 2010; Grafe et al., 2011). In our study, the removal of toe pads was quicker than marking with the PIT tag, and bleeding usually

did not occur. The application of the PIT tag took from two to four times longer (pers. obs.), and possibly increased handling stress. Many males, especially from toe clipped groups, were seen in normal reproductive activities right after being manipulated and no inflammation was observed. Phillott et al. (2011) reported that 1.3% of individuals of four hylid species genus *Litoria* and *Nyctimystes* presented toe inflammation, which may suggest that toe clipping could be a safe method for marking hylids. Stress response should be included as an important trait to be measured in individuals, but few studies considered this characteristic when testing the impacts of different invasive marking techniques on amphibians.

However, despite its low cost and ease of use, the number of individuals to be marked using toe clipping is limited. In our study we failed to find evidence of toe regeneration, but in case it occurs, as described by Hoffmann et al. (2008), the important mark-recapture assumption of not losing the marks in the population will be violated, biasing survival estimates low (Lebreton et al., 1992; Williams et al., 2002). The use of PIT tag is not as common as toe clipping, but may be a reliable method and has not generally been demonstrated to cause serious problems for tagged anurans, such as detrimental effects on body condition or mortality (Christy, 1996; Brown, 1997; Jehle and Hodl, 1998; McAllister et al., 2004; but see Scherer et al., 2005). However, PIT tagging is more costly, increases handling time, requires more skill from the researcher to use, and may be unfeasible in small frogs. In addition, even being considered a permanent marking method (Gibbons and Andrews, 2004), PIT tags could be expelled from (Roark and Dorcas, 2000) or migrate to another location in the body (Tracy et al., 2011) causing tag loss.

In general, studies looking at the impacts of different marking methods on vital rates of wild populations are scarce. Works comparing toe clipping and PIT tagging have shown similar

effects on survival and growth rates of salamanders (Ott and Scott, 1999) and free-living naked mole rats (Braude and Ciszek, 1998). It is also important to note that the effects of marking methods vary by species, reproductive strategies, habitats (e.g. arboreal vs. fossorial), and behaviors (Liner and Smith, 2007). Frog species will respond in different ways to marking and investigators must consider the characteristics of each species, as well as the use of the most practical and least harmful method, evaluating all methods together, as suggested by Phillot et al. (2008). Additionally, we recommend using different temporal and individual covariates, depending on the motivation for the study, otherwise the results of the analysis may be biased.

Estimating the survival probability of a control group of non-marked individuals in the field would be ideal, as we did not have comparisons to survival of individuals that were not treated. Digital photography may be the best marking technique that might approach the condition of a control group for free ranging populations, but it also presents problems, like identifiable characteristics on the target species and obtaining good quality pictures without disturbing individuals. Controlled laboratory experiments may be useful for the inclusion of a non-marked group, for comparing survival (e.g. looking for inflammation) and for allowing estimation of tag loss (Brown, 1997). However, laboratory experiments are not a good solution to observe the effects of marking on species interactions (e.g. predation, competition) as well as the effects of weather variability on marked individuals.

In summary, both marking techniques tested performed equally well, with individuals showing similar survival responses. Thus, given the lack of comparisons among alternative marking techniques in the literature (e.g. visible implanted elastomer-VIE, natural marks), and logistical issues, such as budget and processing time, we recommend the use of toe clipping instead of PIT tagging.

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## TABLES

**Table 1.** Model notation and definition for the parameters apparent survival ( $\Phi$ ) and recapture probability ( $p$ ).

Model notation	Notation definition
(.)	parameter is constant
(t)	parameter varies with time
(g)	parameter varies with groups
(sex)	parameter varies with sex
(rain)	parameter varies with rainfall
(toe_chip)	parameter varies by marking method
(toe_lin)	parameter varies with linear trend effect on toe clipping

**Table 2.** Top 15 models of the candidate model set.  $AIC_c$ =Akaike’s information criteria with small sample size correction,  $\Delta AIC_c$ =difference between top model and the current model,  $w_i$ = $AIC_c$  weights,  $K$ =number of parameters, Deviance=difference of the current model and the saturated model.

Model	$AIC_c$	$\Delta AIC_c$	$w_i$	$K$	Deviance
Phi (.) p (toe_lin+time+sex)	847.40	0	0.05	12	822.90
Phi (.) p (toe_chip+time+sex)	847.71	0.31	0.04	12	823.22
Phi (toe_chip) p (time+sex)	847.90	0.50	0.04	12	823.40
Phi (.) p (time+sex)	848.06	0.66	0.04	11	825.64
Phi (toe_chip+sex) p (time+sex)	848.93	1.52	0.02	13	822.34
Phi (sex) p (toe_lin+time+sex)	849.00	1.58	0.02	13	822.40
Phi (toe_chip) p (toe_lin+time+sex)	849.01	1.60	0.02	13	822.42
Phi (toe_lin) p (time+sex)	849.03	1.63	0.02	12	824.53
Phi (rain) p (toe_lin+time+sex)	849.16	1.76	0.02	13	822.58
Phi (toe_chip) p (toe_chip+time+sex)	849.32	1.91	0.02	13	822.73
Phi (sex) p (toe_chip+time+sex)	849.32	1.92	0.02	13	822.74
Phi (rain) p (toe_chip+time+sex)	849.44	2.04	0.02	13	822.86
Phi (toe_lin) p (toe_lin+time+sex)	849.50	2.08	0.02	13	822.90
Phi (.) p (toe_lin+sex)	849.53	2.13	0.02	4	841.46
Phi (sex) p (time+sex)	849.64	2.24	0.02	12	825.14

**Table 3.** Cumulative  $AIC_c$  weights for the covariates used for apparent survival ( $\Phi$ ) and recapture probability (p). Values in bold are the most important (i.e. > 0.50).

Variable	$\Phi$	p
Group	0.08	0.05
Time	0.07	<b>0.66</b>
Sex	0.33	<b>1.00</b>
Rain	0.26	0.09
toe_chip	0.27	0.27
toe_lin	0.20	0.34

## FIGURE CAPTIONS

**Figure 1.** Adult male *Hypsiboas faber*. Foto: Décio T. Corrêa.

**Figure 2.** Model-averaged monthly apparent survival probability (and 95% confidence intervals) among groups and sexes.

**Figure 2.** Model-averaged monthly recapture probability (and 95% confidence intervals) among groups and sexes.

FIGURES

**Figure 1**



Figure 2

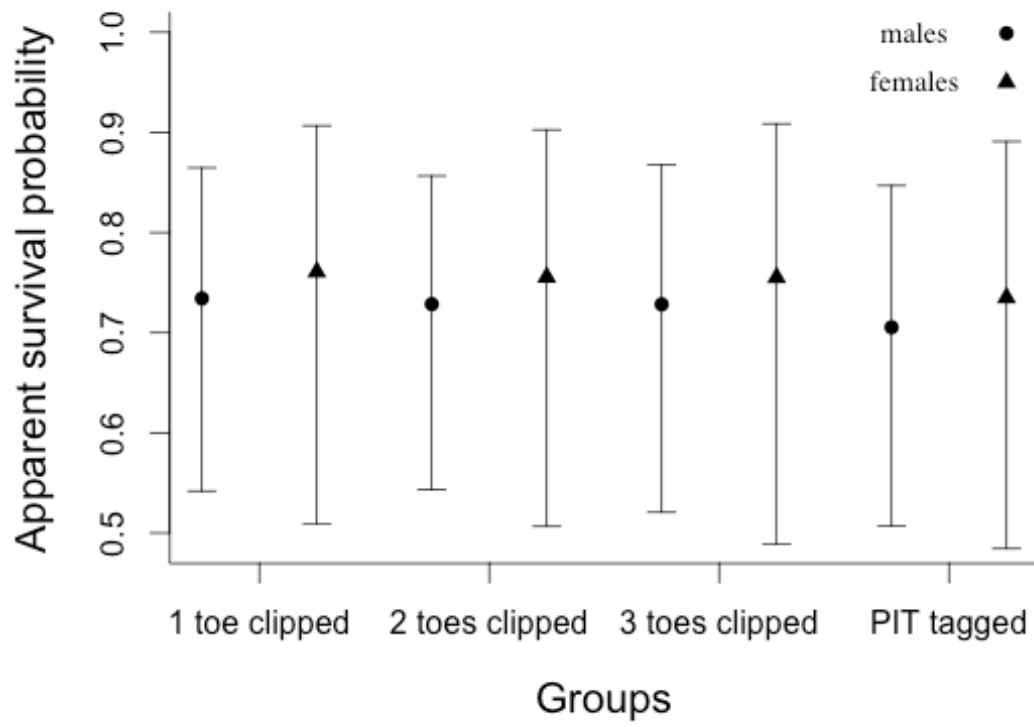
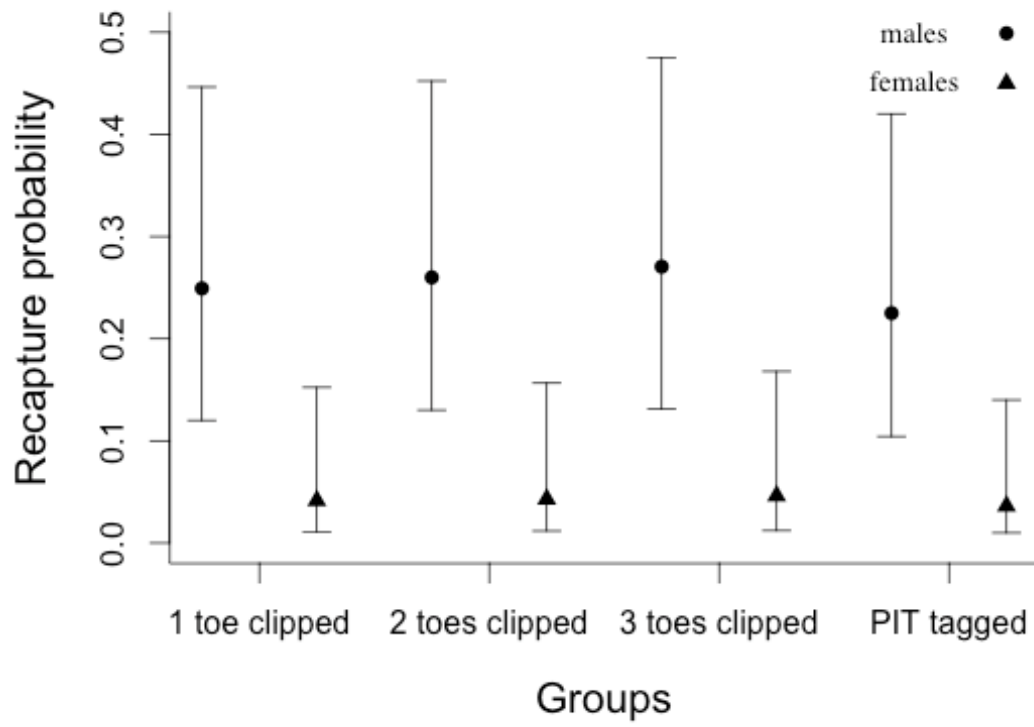


Figure 3



APPENDIX- Table of all model results.  $AIC_c$ =Akaike's information criteria with small sample size correction,  $\Delta AIC_c$ =difference between top model and the current model,  $w_i$ = $AIC_c$  weights,  $K$ =number of parameters, Deviance=difference of the current model and the saturated model.

Model	$AIC_c$	$\Delta AIC_c$	$w_i$	$K$	Deviance
Phi Int+p Int+p toe_lin+p t+p sex	847.4017	0	0.05272	12	822.9041
Phi Int+p Int+p toe_chip+p t+p sex	847.7157	0.314	0.04506	12	823.2181
Phi Int+Phi toe_chip+p Int+p t+p sex	847.8978	0.4961	0.04114	12	823.4002
Phi Int+p Int+p t+p sex	848.0598	0.6581	0.03794	11	825.6394
Phi Int+Phi toe_chip+p Int+Phi sex+p t+p sex	848.9292	1.5275	0.02457	13	822.3477
Phi Int+p Int+p toe_lin+Phi sex+p t+p sex	848.9779	1.5762	0.02397	13	822.3965
Phi Int+Phi toe_chip+p Int+p toe_lin+p t+p sex	849.007	1.6053	0.02363	13	822.4256
Phi Int+Phi toe_lin+p Int+p t+p sex	849.0295	1.6278	0.02336	12	824.5319
Phi Int+Phi rain+p Int+p toe_lin+p t+p sex	849.1599	1.7582	0.02189	13	822.5785
Phi Int+Phi toe_chip+p Int+p toe_chip+p t+p sex	849.3161	1.9144	0.02024	13	822.7347
Phi Int+p Int+p toe_chip+Phi sex+p t+p sex	849.3256	1.9239	0.02015	13	822.7441
Phi Int+Phi rain+p Int+p toe_chip+p t+p sex	849.4415	2.0398	0.01901	13	822.8601
Phi Int+Phi toe_lin+p Int+p toe_lin+p t+p sex	849.4846	2.0829	0.01861	13	822.9032
Phi Int+p Int+p toe_lin+p sex	849.5285	2.1268	0.0182	4	841.4655
Phi Int+p Int+Phi sex+p t+p sex	849.6411	2.2394	0.01721	12	825.1435
Phi Int+Phi toe_lin+p Int+p toe_chip+p t+p sex	849.7934	2.3917	0.01595	13	823.2119
Phi Int+Phi rain+p Int+p t+p sex	849.8144	2.4127	0.01578	12	825.3168
Phi Int+Phi rain+Phi toe_chip+p Int+p t+p sex	849.8451	2.4434	0.01554	13	823.2637
Phi Int+p Int+p toe_chip+p sex	850.2666	2.8649	0.01259	4	842.2036
Phi Int+Phi toe_lin+p Int+Phi sex+p t+p sex	850.2762	2.8745	0.01253	13	823.6947
Phi Int+Phi toe_chip+p Int+p toe_lin+Phi sex+p t+p sex	850.3004	2.8987	0.01238	14	821.6284
Phi Int+Phi toe_chip+p Int+p toe_chip+Phi sex+p t+p sex	850.6198	3.2181	0.01055	14	821.9478
Phi Int+p Int+Phi g+p t+p sex	850.7729	3.3712	0.00977	14	822.1009
Phi Int+Phi rain+p Int+p toe_lin+Phi sex+p t+p sex	850.8239	3.4222	0.00953	14	822.1519
Phi Int+Phi rain+Phi toe_lin+p Int+p t+p sex	850.824	3.4223	0.00953	13	824.2425
Phi Int+Phi rain+Phi toe_chip+p Int+p toe_lin+p t+p sex	850.892	3.4903	0.00921	14	822.22
Phi Int+Phi toe_chip+p Int+p sex	850.9107	3.509	0.00912	4	842.8477
Phi Int+p Int+p toe_lin+Phi sex+p sex	850.9345	3.5328	0.00901	5	840.8398
Phi Int+p Int+p sex	850.9484	3.5467	0.00895	3	844.9106
Phi Int+Phi rain+Phi toe_chip+p Int+Phi sex+p t+p sex	850.9863	3.5846	0.00878	14	822.3143
Phi Int+Phi toe_lin+p Int+p toe_lin+Phi sex+p t+p sex	851.0504	3.6487	0.00851	14	822.3784
Phi Int+p Int+p toe_lin+Phi g+p t+p sex	851.1358	3.7341	0.00815	15	820.3665
Phi Int+Phi rain+p Int+p toe_chip+Phi sex+p t+p sex	851.1445	3.7428	0.00811	14	822.4725
Phi Int+Phi rain+Phi toe_chip+p Int+p toe_chip+p t+p sex	851.1822	3.7805	0.00796	14	822.5102
Phi Int+Phi rain+Phi toe_lin+p Int+p toe_lin+p t+p sex	851.2478	3.8461	0.00771	14	822.5758
Phi Int+Phi toe_chip+p Int+p toe_lin+p sex	851.2872	3.8855	0.00756	5	841.1926



Phi Int+Phi toe_lin+p Int+p toe_chip+Phi sex+p t+p sex	851.3556	3.9539	0.0073	14	822.6836
Phi Int+Phi rain+p Int+p toe_lin+p sex	851.3876	3.9859	0.00719	5	841.293
Phi Int+p Int+p rain+p toe_lin+p sex	851.4063	4.0046	0.00712	5	841.3116
Phi Int+p Int+p toe_lin+Phi t+p sex	851.4514	4.0497	0.00696	11	829.031
Phi Int+Phi rain+p Int+Phi sex+p t+p sex	851.4786	4.0769	0.00687	13	824.8972
Phi Int+p Int+p toe_chip+Phi t+p sex	851.507	4.1053	0.00677	11	829.0866
Phi Int+Phi rain+Phi toe_lin+p Int+p toe_chip+p t+p sex	851.5291	4.1274	0.0067	14	822.8571
Phi Int+Phi toe_lin+p Int+p toe_lin+p sex	851.5544	4.1527	0.00661	5	841.4597
Phi Int+p Int+p g+p t+p sex	851.5737	4.172	0.00655	14	822.9017
Phi Int+Phi toe_lin+p Int+p sex	851.6622	4.2605	0.00626	4	843.5992
Phi Int+Phi toe_chip+p Int+Phi sex+p sex	851.6762	4.2745	0.00622	5	841.5816
Phi Int+p Int+p toe_chip+Phi sex+p sex	851.6995	4.2978	0.00615	5	841.6049
Phi Int+p Int+Phi g+Phi sex+p t+p sex	851.8262	4.4245	0.00577	15	821.0569
Phi Int+Phi toe_chip+p Int+p toe_chip+p sex	851.9845	4.5828	0.00533	5	841.8899
Phi Int+p Int+p toe_chip+Phi g+p t+p sex	852.0107	4.609	0.00526	15	821.2414
Phi Int+p Int+Phi t+p sex	852.1404	4.7387	0.00493	10	831.7906
Phi Int+Phi rain+Phi toe_lin+p Int+Phi sex+p t+p sex	852.1923	4.7906	0.00481	14	823.5203
Phi Int+Phi rain+p Int+p toe_chip+p sex	852.2208	4.8191	0.00474	5	842.1262
Phi Int+Phi toe_lin+p Int+p toe_chip+p sex	852.2702	4.8685	0.00462	5	842.1756
Phi Int+p Int+p rain+p toe_chip+p sex	852.2951	4.8934	0.00456	5	842.2005
Phi Int+Phi rain+Phi toe_chip+p Int+p toe_lin+Phi sex+p t+p sex	852.3077	4.906	0.00454	15	821.5385
Phi Int+p Int+Phi sex+p sex	852.328	4.9263	0.00449	4	844.265
Phi Int+Phi toe_chip+p Int+p toe_lin+Phi sex+p sex	852.4375	5.0358	0.00425	6	840.3048
Phi Int+p Int+p toe_lin+Phi g+Phi sex+p t+p sex	852.5756	5.1739	0.00397	16	819.7024
Phi Int+Phi rain+Phi toe_chip+p Int+p toe_chip+Phi sex+p t+p sex	852.6219	5.2202	0.00388	15	821.8526
Phi Int+Phi toe_lin+p Int+Phi sex+p sex	852.6226	5.2209	0.00388	5	842.5279
Phi Int+Phi rain+p Int+Phi g+p t+p sex	852.6676	5.2659	0.00379	15	821.8984
Phi Int+p Int+p rain+p toe_lin+Phi sex+p sex	852.8179	5.4162	0.00351	6	840.6852
Phi Int+Phi rain+p Int+p toe_lin+Phi sex+p sex	852.8725	5.4708	0.00342	6	840.7398
Phi Int+Phi rain+p Int+p sex	852.8817	5.48	0.0034	4	844.8187
Phi Int+Phi rain+Phi toe_lin+p Int+p toe_lin+Phi sex+p t+p sex	852.9113	5.5096	0.00335	15	822.1421
Phi Int+Phi rain+Phi toe_chip+p Int+p sex	852.9252	5.5235	0.00333	5	842.8305
Phi Int+Phi toe_chip+p Int+p rain+p sex	852.9254	5.5237	0.00333	5	842.8307
Phi Int+Phi toe_lin+p Int+p toe_lin+Phi sex+p sex	852.9589	5.5572	0.00328	6	840.8262
Phi Int+p Int+p rain+p sex	852.9598	5.5581	0.00327	4	844.8968
Phi Int+p Int+p toe_lin+Phi t+Phi sex+p sex	853.0458	5.6441	0.00314	12	828.5482
Phi Int+p Int+p toe_chip+Phi t+Phi sex+p sex	853.0713	5.6696	0.0031	12	828.5737
Phi Int+p Int+p toe_lin+Phi g+Phi t+p sex	853.0918	5.6901	0.00306	14	824.4198
Phi Int+Phi toe_chip+p Int+p toe_chip+Phi sex+p sex	853.116	5.7143	0.00303	6	840.9833
Phi Int+Phi toe_chip+p Int+p g+p t+p sex	853.1308	5.7291	0.00301	15	822.3616
Phi Int+Phi rain+p Int+p toe_lin+Phi g+p t+p sex	853.1559	5.7542	0.00297	16	820.2827
Phi Int+p Int+Phi sex+p g+p t+p sex	853.1578	5.7561	0.00297	15	822.3886

Phi Int+Phi rain+Phi toe_lin+p Int+p toe_chip+Phi sex+p t+p sex	853.1992	5.7975	0.0029	15	822.43
Phi Int+Phi toe_chip+p Int+p rain+p toe_lin+p sex	853.1999	5.7982	0.0029	6	841.0672
Phi Int+Phi rain+Phi toe_chip+p Int+p toe_lin+p sex	853.2217	5.82	0.00287	6	841.089
Phi Int+Phi toe_lin+p Int+p toe_lin+Phi t+p sex	853.307	5.9053	0.00275	12	828.8094
Phi Int+Phi toe_chip+p Int+p toe_lin+Phi t+p sex	853.3388	5.9371	0.00271	12	828.8412
Phi Int+Phi rain+p Int+p g+p t+p sex	853.3472	5.9455	0.0027	15	822.578
Phi Int+p Int+p g+p sex	853.3554	5.9537	0.00269	6	841.2227
Phi Int+Phi rain+p Int+p rain+p toe_lin+p sex	853.3641	5.9624	0.00267	6	841.2314
Phi Int+Phi toe_lin+p Int+p toe_chip+Phi t+p sex	853.3853	5.9836	0.00265	12	828.8877
Phi Int+p Int+p toe_chip+Phi g+Phi sex+p t+p sex	853.3879	5.9862	0.00264	16	820.5147
Phi Int+Phi rain+Phi toe_lin+p Int+p toe_lin+p sex	853.4193	6.0176	0.0026	6	841.2866
Phi Int+Phi toe_lin+p Int+p rain+p toe_lin+p sex	853.4408	6.0391	0.00257	6	841.3081
Phi Int+Phi toe_chip+p Int+p toe_chip+Phi t+p sex	853.454	6.0523	0.00256	12	828.9564
Phi Int+p Int+p rain+p toe_lin+Phi t+p sex	853.523	6.1213	0.00247	12	829.0254
Phi Int+p Int+p rain+p toe_chip+Phi t+p sex	853.5778	6.1761	0.0024	12	829.0802
Phi Int+Phi rain+Phi toe_lin+p Int+p sex	853.587	6.1853	0.00239	5	843.4924
Phi Int+Phi toe_lin+p Int+p toe_chip+Phi sex+p sex	853.606	6.2043	0.00237	6	841.4733
Phi Int+Phi toe_lin+p Int+p rain+p sex	853.6357	6.234	0.00234	5	843.5411
Phi Int+Phi toe_lin+p Int+p g+p t+p sex	853.6703	6.2686	0.0023	15	822.901
Phi Int+p Int+Phi t+Phi sex+p sex	853.6849	6.2832	0.00228	11	831.2645
Phi Int+Phi toe_chip+p Int+p rain+Phi sex+p sex	853.694	6.2923	0.00227	6	841.5613
Phi Int+Phi rain+Phi toe_chip+p Int+Phi sex+p sex	853.7031	6.3014	0.00226	6	841.5704
Phi Int+Phi rain+p Int+p toe_chip+Phi sex+p sex	853.7048	6.3031	0.00226	6	841.5721
Phi Int+p Int+p rain+p toe_chip+Phi sex+p sex	853.734	6.3323	0.00222	6	841.6013
Phi Int+p Int+p toe_lin+Phi g+p sex	853.749	6.3473	0.00221	7	839.5718
Phi Int+p Int+Phi g+p sex	853.7521	6.3504	0.0022	6	841.6194
Phi Int+Phi toe_lin+p Int+Phi t+p sex	853.7528	6.3511	0.0022	11	831.3324
Phi Int+Phi rain+p Int+Phi g+Phi sex+p t+p sex	853.8721	6.4704	0.00207	16	820.9989
Phi Int+Phi rain+p Int+p toe_chip+Phi g+p t+p sex	853.9151	6.5134	0.00203	16	821.0419
Phi Int+Phi rain+Phi toe_chip+p Int+p toe_chip+p sex	853.9826	6.5809	0.00196	6	841.8499
Phi Int+Phi toe_chip+p Int+p rain+p toe_chip+p sex	854.0165	6.6148	0.00193	6	841.8838
Phi Int+p Int+p rain+Phi t+p sex	854.211	6.8093	0.00175	11	831.7906
Phi Int+Phi rain+Phi toe_lin+p Int+p toe_chip+p sex	854.2258	6.8241	0.00174	6	842.0931
Phi Int+Phi rain+p Int+p rain+p toe_chip+p sex	854.2555	6.8538	0.00171	6	842.1228
Phi Int+Phi toe_lin+p Int+p rain+p toe_chip+p sex	854.3007	6.899	0.00167	6	842.168
Phi Int+Phi rain+p Int+Phi sex+p sex	854.3174	6.9157	0.00166	5	844.2228
Phi Int+p Int+p rain+Phi sex+p sex	854.3446	6.9429	0.00164	5	844.2499
Phi Int+Phi toe_chip+p Int+Phi sex+p g+p t+p sex	854.3458	6.9441	0.00164	16	821.4726
Phi Int+Phi toe_chip+p Int+p rain+p toe_lin+Phi sex+p sex	854.3678	6.9661	0.00162	7	840.1906
Phi Int+p Int+p toe_chip+Phi g+Phi t+p sex	854.3878	6.9861	0.0016	14	825.7158
Phi Int+Phi rain+Phi toe_chip+p Int+p toe_lin+Phi sex+p sex	854.4647	7.063	0.00154	7	840.2874
Phi Int+p Int+Phi g+Phi sex+p sex	854.5287	7.127	0.00149	7	840.3515

Phi Int+Phi toe_lin+p Int+p rain+Phi sex+p sex	854.5871	7.1854	0.00145	6	842.4544
Phi Int+Phi rain+Phi toe_lin+p Int+Phi sex+p sex	854.6318	7.2301	0.00142	6	842.4991
Phi Int+Phi rain+p Int+p toe_lin+Phi g+Phi sex+p t+p sex	854.662	7.2603	0.0014	17	819.6781
Phi Int+p Int+Phi g+p g+p t+p sex	854.7106	7.3089	0.00136	17	819.7267
Phi Int+Phi toe_chip+p Int+Phi t+p sex	854.7211	7.3194	0.00136	12	830.2235
Phi Int+Phi toe_chip+p Int+p toe_lin+Phi t+Phi sex+p sex	854.7224	7.3207	0.00136	13	828.1409
Phi Int+p Int+Phi sex+p g+p sex	854.7531	7.3514	0.00134	7	840.5759
Phi Int+Phi rain+p Int+p rain+p toe_lin+Phi sex+p sex	854.8317	7.43	0.00128	7	840.6545
Phi Int+Phi toe_chip+p Int+p toe_chip+Phi t+Phi sex+p sex	854.8372	7.4355	0.00128	13	828.2558
Phi Int+Phi toe_lin+p Int+p rain+p toe_lin+Phi sex+p sex	854.8445	7.4428	0.00128	7	840.6673
Phi Int+Phi rain+Phi toe_lin+p Int+p toe_lin+Phi sex+p sex	854.9074	7.5057	0.00124	7	840.7302
Phi Int+Phi rain+p Int+p rain+p sex	854.9134	7.5117	0.00123	5	844.8187
Phi Int+p Int+p toe_chip+Phi g+p sex	854.9222	7.5205	0.00123	7	840.745
Phi Int+Phi rain+Phi toe_chip+p Int+p rain+p sex	854.9561	7.5544	0.00121	6	842.8234
Phi Int+p Int+p rain+p g+p sex	854.9567	7.555	0.00121	7	840.7795
Phi Int+p Int+p toe_lin+Phi g+Phi sex+p sex	854.999	7.5973	0.00118	8	838.7708
Phi Int+Phi toe_chip+p Int+p g+p sex	855.0174	7.6157	0.00117	7	840.8402
Phi Int+Phi rain+p Int+Phi sex+p g+p t+p sex	855.0217	7.62	0.00117	16	822.1485
Phi Int+Phi toe_lin+p Int+p toe_lin+Phi t+Phi sex+p sex	855.0256	7.6239	0.00117	13	828.4441
Phi Int+Phi rain+Phi toe_chip+p Int+p g+p t+p sex	855.0566	7.6549	0.00115	16	822.1834
Phi Int+Phi toe_lin+p Int+p toe_chip+Phi t+Phi sex+p sex	855.0634	7.6617	0.00114	13	828.4819
Phi Int+p Int+p rain+p toe_lin+Phi t+Phi sex+p sex	855.119	7.7173	0.00111	13	828.5376
Phi Int+Phi toe_chip+p Int+p rain+p toe_chip+Phi sex+p sex	855.1514	7.7497	0.00109	7	840.9742
Phi Int+p Int+p rain+p toe_chip+Phi t+Phi sex+p sex	855.1527	7.751	0.00109	13	828.5712
Phi Int+Phi rain+p Int+p g+p sex	855.154	7.7523	0.00109	7	840.9768
Phi Int+Phi rain+Phi toe_chip+p Int+p toe_chip+Phi sex+p sex	855.1604	7.7587	0.00109	7	840.9832
Phi Int+p Int+p rain+p toe_lin+Phi g+Phi t+p sex	855.189	7.7873	0.00107	15	824.4198
Phi Int+Phi rain+Phi toe_chip+p Int+p rain+p toe_lin+p sex	855.205	7.8033	0.00107	7	841.0278
Phi Int+Phi toe_lin+p Int+Phi sex+p g+p t+p sex	855.2399	7.8382	0.00105	16	822.3667
Phi Int+Phi toe_lin+p Int+p rain+p toe_lin+Phi t+p sex	855.3887	7.987	0.00097	13	828.8072
Phi Int+Phi toe_lin+p Int+p g+p sex	855.3979	7.9962	0.00097	7	841.2207
Phi Int+Phi rain+Phi toe_lin+p Int+p rain+p toe_lin+p sex	855.4039	8.0022	0.00096	7	841.2267
Phi Int+Phi rain+p Int+p toe_chip+Phi g+Phi sex+p t+p sex	855.4137	8.012	0.00096	17	820.4298
Phi Int+Phi toe_chip+p Int+p rain+p toe_lin+Phi t+p sex	855.4157	8.014	0.00096	13	828.8342
Phi Int+p Int+Phi t+p g+p sex	855.4273	8.0256	0.00095	13	828.8459
Phi Int+Phi rain+Phi toe_lin+p Int+p g+p t+p sex	855.4485	8.0468	0.00094	16	822.5753
Phi Int+Phi toe_lin+p Int+p rain+p toe_chip+Phi t+p sex	855.4525	8.0508	0.00094	13	828.871
Phi Int+Phi toe_chip+p Int+p rain+p toe_chip+Phi t+p sex	855.5348	8.1331	0.0009	13	828.9533
Phi Int+Phi rain+p Int+Phi g+p sex	855.5974	8.1957	0.00088	7	841.4202
Phi Int+Phi rain+Phi toe_lin+p Int+p rain+p sex	855.6109	8.2092	0.00087	6	843.4782
Phi Int+Phi rain+Phi toe_lin+p Int+p toe_chip+Phi sex+p sex	855.6176	8.2159	0.00087	7	841.4404
Phi Int+Phi toe_lin+p Int+p rain+p toe_chip+Phi sex+p sex	855.634	8.2323	0.00086	7	841.4568

Phi Int+Phi rain+Phi toe_chip+p Int+p rain+Phi sex+p sex	855.7051	8.3034	0.00083	7	841.5279
Phi Int+Phi rain+p Int+p toe_lin+Phi g+p sex	855.7241	8.3224	0.00082	8	839.4959
Phi Int+Phi toe_chip+p Int+Phi t+Phi sex+p sex	855.7423	8.3406	0.00081	13	829.1609
Phi Int+p Int+p rain+Phi g+p sex	855.7466	8.3449	0.00081	7	841.5694
Phi Int+p Int+p rain+p toe_lin+Phi g+p sex	855.7479	8.3462	0.00081	8	839.5197
Phi Int+Phi rain+p Int+p rain+p toe_chip+Phi sex+p sex	855.7492	8.3475	0.00081	7	841.572
Phi Int+p Int+p rain+Phi t+Phi sex+p sex	855.7608	8.3591	0.00081	12	831.2632
Phi Int+Phi toe_lin+p Int+p rain+Phi t+p sex	855.83	8.4283	0.00078	12	831.3324
Phi Int+p Int+Phi g+Phi sex+p g+p t+p sex	855.9905	8.5888	0.00072	18	818.889
Phi Int+Phi rain+Phi toe_chip+p Int+p rain+p toe_chip+p sex	856.0271	8.6254	0.00071	7	841.8499
Phi Int+p Int+p toe_chip+Phi g+Phi sex+p sex	856.0498	8.6481	0.0007	8	839.8216
Phi Int+Phi toe_chip+p Int+Phi sex+p g+p sex	856.0536	8.6519	0.0007	8	839.8254
Phi Int+Phi rain+Phi toe_lin+p Int+p rain+p toe_chip+p sex	856.2695	8.8678	0.00063	7	842.0923
Phi Int+p Int+p rain+Phi sex+p g+p sex	856.338	8.9363	0.0006	8	840.1098
Phi Int+Phi rain+p Int+p rain+Phi sex+p sex	856.3534	8.9517	0.0006	6	844.2207
Phi Int+p Int+Phi g+Phi t+p sex	856.3935	8.9918	0.00059	14	827.7215
Phi Int+Phi rain+Phi toe_chip+p Int+Phi sex+p g+p t+p sex	856.4031	9.0014	0.00059	17	821.4192
Phi Int+Phi rain+Phi toe_chip+p Int+p rain+p toe_lin+Phi sex+p sex	856.4188	9.0171	0.00058	8	840.1906
Phi Int+p Int+p rain+p toe_chip+Phi g+Phi t+p sex	856.4556	9.0539	0.00057	15	825.6864
Phi Int+p Int+p rain+Phi g+Phi sex+p sex	856.5271	9.1254	0.00055	8	840.2989
Phi Int+Phi toe_chip+p Int+p rain+p g+p sex	856.5441	9.1424	0.00055	8	840.3159
Phi Int+Phi rain+p Int+Phi g+Phi sex+p sex	856.5465	9.1448	0.00054	8	840.3183
Phi Int+p Int+p toe_lin+Phi g+Phi t+Phi sex+p sex	856.5933	9.1916	0.00053	16	823.7201
Phi Int+Phi rain+Phi toe_lin+p Int+p rain+Phi sex+p sex	856.6277	9.226	0.00052	7	842.4505
Phi Int+Phi rain+p Int+Phi sex+p g+p sex	856.6448	9.2431	0.00052	8	840.4166
Phi Int+p Int+Phi g+Phi t+p g+p sex	856.7321	9.3304	0.0005	16	823.8589
Phi Int+Phi toe_lin+p Int+Phi sex+p g+p sex	856.7788	9.3771	0.00049	8	840.5506
Phi Int+Phi toe_chip+p Int+p rain+Phi t+p sex	856.8032	9.4015	0.00048	13	830.2217
Phi Int+Phi rain+p Int+p toe_chip+Phi g+p sex	856.8141	9.4124	0.00048	8	840.5859
Phi Int+Phi rain+p Int+Phi g+p g+p t+p sex	856.8152	9.4135	0.00048	18	819.7137
Phi Int+Phi rain+Phi toe_lin+p Int+p rain+p toe_lin+Phi sex+p sex	856.8687	9.467	0.00046	8	840.6405
Phi Int+Phi rain+Phi toe_chip+p Int+p g+p sex	856.8996	9.4979	0.00046	8	840.6714
Phi Int+Phi toe_chip+p Int+p rain+p toe_chip+Phi t+Phi sex+p sex	856.9278	9.5261	0.00045	14	828.2558
Phi Int+Phi rain+p Int+p rain+p g+p sex	856.9282	9.5265	0.00045	8	840.7
Phi Int+p Int+p rain+p toe_chip+Phi g+p sex	856.9661	9.5644	0.00044	8	840.7379
Phi Int+p Int+p rain+p toe_lin+Phi g+Phi sex+p sex	857.0004	9.5987	0.00043	9	838.7147
Phi Int+Phi toe_lin+p Int+p rain+p g+p sex	857.0073	9.6056	0.00043	8	840.7791
Phi Int+p Int+Phi t+Phi sex+p g+p sex	857.0277	9.626	0.00043	14	828.3557
Phi Int+Phi rain+p Int+p toe_lin+Phi g+Phi sex+p sex	857.0451	9.6434	0.00042	9	838.7594
Phi Int+p Int+Phi g+p g+p sex	857.0728	9.6711	0.00042	9	838.7871
Phi Int+Phi toe_lin+p Int+p rain+p toe_lin+Phi t+Phi sex+p sex	857.1098	9.7081	0.00041	14	828.4378
Phi Int+Phi rain+Phi toe_lin+p Int+Phi sex+p g+p t+p sex	857.121	9.7193	0.00041	17	822.1371

Phi Int+Phi toe_lin+p Int+p rain+p toe_chip+Phi t+Phi sex+p sex	857.1462	9.7445	0.0004	14	828.4742
Phi Int+Phi toe_lin+p Int+Phi t+Phi sex+p sex	857.1888	9.7871	0.0004	13	830.6074
Phi Int+Phi rain+Phi toe_chip+p Int+p rain+p toe_chip+Phi sex+p sex	857.2011	9.7994	0.00039	8	840.9729
Phi Int+Phi rain+Phi toe_lin+p Int+p g+p sex	857.2029	9.8012	0.00039	8	840.9747
Phi Int+Phi toe_lin+p Int+Phi t+p g+p sex	857.2913	9.8896	0.00038	14	828.6193
Phi Int+Phi toe_chip+p Int+Phi t+p g+p sex	857.3489	9.9472	0.00036	14	828.6769
Phi Int+p Int+Phi g+Phi t+Phi sex+p sex	857.3811	9.9794	0.00036	15	826.6118
Phi Int+p Int+p rain+Phi t+p g+p sex	857.4994	10.0977	0.00034	14	828.8274
Phi Int+Phi toe_chip+p Int+p rain+Phi sex+p g+p sex	857.5029	10.1012	0.00034	9	839.2172
Phi Int+Phi rain+p Int+p rain+Phi g+p sex	857.6403	10.2386	0.00032	8	841.4121
Phi Int+Phi rain+Phi toe_lin+p Int+p rain+p toe_chip+Phi sex+p sex	857.6651	10.2634	0.00031	8	841.4369
Phi Int+Phi rain+p Int+p rain+p toe_lin+Phi g+p sex	857.758	10.3563	0.0003	9	839.4722
Phi Int+Phi toe_chip+p Int+p rain+Phi t+Phi sex+p sex	857.7819	10.3802	0.00029	14	829.1099
Phi Int+p Int+p rain+p toe_chip+Phi g+Phi t+Phi sex+p sex	857.8385	10.4368	0.00029	16	824.9653
Phi Int+p Int+p toe_chip+Phi g+Phi t+Phi sex+p sex	857.8488	10.4471	0.00028	16	824.9756
Phi Int+p Int+p toe_lin+Phi t+p t+p sex	857.9989	10.5972	0.00026	18	820.8974
Phi Int+p Int+Phi g+Phi t+Phi sex+p g+p sex	858.0385	10.6368	0.00026	17	823.0546
Phi Int+Phi rain+p Int+p toe_chip+Phi g+Phi sex+p sex	858.0656	10.6639	0.00025	9	839.7799
Phi Int+Phi rain+Phi toe_chip+p Int+Phi sex+p g+p sex	858.0658	10.6641	0.00025	9	839.7801
Phi Int+p Int+p rain+p toe_chip+Phi g+Phi sex+p sex	858.093	10.6913	0.00025	9	839.8073
Phi Int+Phi rain+p Int+Phi g+Phi sex+p g+p t+p sex	858.0931	10.6914	0.00025	19	818.8673
Phi Int+p Int+Phi g+Phi sex+p g+p sex	858.1893	10.7876	0.00024	10	837.8396
Phi Int+p Int+p toe_chip+Phi t+p t+p sex	858.2691	10.8674	0.00023	18	821.1676
Phi Int+Phi toe_lin+p Int+p rain+Phi sex+p g+p sex	858.3395	10.9378	0.00022	9	840.0538
Phi Int+Phi rain+p Int+p rain+Phi sex+p g+p sex	858.3658	10.9641	0.00022	9	840.0801
Phi Int+p Int+p rain+Phi g+Phi t+p sex	858.4886	11.0869	0.00021	15	827.7194
Phi Int+Phi rain+p Int+p rain+Phi g+Phi sex+p sex	858.5713	11.1696	0.0002	9	840.2856
Phi Int+Phi rain+Phi toe_chip+p Int+p rain+p g+p sex	858.5791	11.1774	0.0002	9	840.2934
Phi Int+p Int+p rain+Phi g+p g+p sex	858.6812	11.2795	0.00019	10	838.3314
Phi Int+Phi rain+Phi toe_lin+p Int+Phi sex+p g+p sex	858.6831	11.2814	0.00019	9	840.3973
Phi Int+p Int+p rain+p toe_lin+Phi g+Phi t+Phi sex+p sex	858.6999	11.2982	0.00019	17	823.716
Phi Int+Phi toe_chip+p Int+Phi t+Phi sex+p g+p sex	858.7465	11.3448	0.00018	15	827.9772
Phi Int+Phi rain+p Int+p rain+p toe_chip+Phi g+p sex	858.8704	11.4687	0.00017	9	840.5847
Phi Int+Phi toe_chip+p Int+p rain+p toe_lin+Phi t+Phi sex+p sex	858.8888	11.4871	0.00017	15	828.1196
Phi Int+Phi rain+Phi toe_lin+p Int+p rain+p g+p sex	858.9857	11.584	0.00016	9	840.7
Phi Int+Phi toe_lin+p Int+Phi t+Phi sex+p g+p sex	859.0173	11.6156	0.00016	15	828.248
Phi Int+Phi rain+p Int+p rain+p toe_lin+Phi g+Phi sex+p sex	859.0631	11.6614	0.00015	10	838.7133
Phi Int+p Int+p rain+Phi t+Phi sex+p g+p sex	859.1006	11.6989	0.00015	15	828.3313
Phi Int+Phi rain+p Int+Phi g+p g+p sex	859.1247	11.723	0.00015	10	838.7749
Phi Int+Phi toe_lin+p Int+p rain+Phi t+Phi sex+p sex	859.2626	11.8609	0.00014	14	830.5906
Phi Int+Phi toe_lin+p Int+p rain+Phi t+p g+p sex	859.3825	11.9808	0.00013	15	828.6133
Phi Int+Phi toe_chip+p Int+p rain+Phi t+p g+p sex	859.4078	12.0061	0.00013	15	828.6386

Phi Int+p Int+p rain+Phi g+Phi t+Phi sex+p sex	859.4626	12.0609	0.00013	16	826.5894
Phi Int+Phi rain+Phi toe_chip+p Int+p rain+Phi sex+p g+p sex	859.5539	12.1522	0.00012	10	839.2042
Phi Int+p Int+p toe_lin+Phi t+Phi sex+p t+p sex	859.623	12.2213	0.00012	19	820.3972
Phi Int+p Int+p rain+Phi g+Phi sex+p g+p sex	859.7282	12.3265	0.00011	11	837.3079
Phi Int+p Int+p toe_chip+Phi t+Phi sex+p t+p sex	859.911	12.5093	0.0001	19	820.6852
Phi Int+Phi toe_lin+p Int+p toe_lin+Phi t+p t+p sex	860.0946	12.6929	0.00009	19	820.8688
Phi Int+Phi rain+p Int+p rain+p toe_chip+Phi g+Phi sex+p sex	860.1262	12.7245	0.00009	10	839.7764
Phi Int+Phi rain+p Int+Phi g+Phi sex+p g+p sex	860.2453	12.8436	0.00009	11	837.8249
Phi Int+Phi toe_lin+p Int+p toe_chip+Phi t+p t+p sex	860.3789	12.9772	0.00008	19	821.1531
Phi Int+Phi rain+Phi toe_lin+p Int+p rain+Phi sex+p g+p sex	860.3823	12.9806	0.00008	10	840.0325
Phi Int+p Int+Phi t+p t+p sex	860.3986	12.9969	0.00008	18	823.2972
Phi Int+Phi rain+p Int+p rain+Phi g+p g+p sex	860.6958	13.2941	0.00007	11	838.2754
Phi Int+p Int+p rain+Phi g+Phi t+p g+p sex	860.803	13.4013	0.00006	18	823.7015
Phi Int+Phi toe_lin+p Int+p rain+Phi t+Phi sex+p g+p sex	861.1089	13.7072	0.00006	16	828.2357
Phi Int+Phi rain+p Int+p rain+Phi g+Phi sex+p g+p sex	861.4375	14.0358	0.00005	12	836.9399
Phi Int+Phi toe_lin+p Int+p toe_lin+Phi t+Phi sex+p t+p sex	861.7511	14.3494	0.00004	20	820.3941
Phi Int+Phi toe_chip+p Int+p toe_lin+Phi t+p t+p sex	861.8267	14.425	0.00004	20	820.4697
Phi Int+p Int+p rain+Phi g+Phi t+Phi sex+p g+p sex	861.9084	14.5067	0.00004	19	822.6826
Phi Int+p Int+Phi t+Phi sex+p t+p sex	861.94	14.5383	0.00004	19	822.7142
Phi Int+p Int+p toe_lin+Phi g+Phi t+p t+p sex	861.9661	14.5644	0.00004	22	816.3259
Phi Int+Phi toe_lin+p Int+p toe_chip+Phi t+Phi sex+p t+p sex	862.0423	14.6406	0.00003	20	820.6852
Phi Int+p Int+Phi t+p g+p t+p sex	862.2397	14.838	0.00003	20	820.8827
Phi Int+Phi toe_chip+p Int+Phi t+p t+p sex	862.5158	15.1141	0.00003	20	821.1588
Phi Int+Phi toe_chip+p Int+p rain+Phi t+Phi sex+p g+p sex	862.8822	15.4805	0.00002	17	827.8983
Phi Int+Phi toe_chip+p Int+p toe_lin+Phi t+Phi sex+p t+p sex	863.0039	15.6022	0.00002	21	819.5087
Phi Int+Phi toe_lin+p Int+Phi t+Phi sex+p t+p sex	863.0406	15.6389	0.00002	20	821.6836
Phi Int+p Int+p toe_chip+Phi g+Phi t+p t+p sex	863.1496	15.7479	0.00002	22	817.5095
Phi Int+Phi toe_chip+p Int+p toe_chip+Phi t+Phi sex+p t+p sex	863.3265	15.9248	0.00002	21	819.8314
Phi Int+Phi toe_chip+p Int+Phi t+Phi sex+p t+p sex	863.4986	16.0969	0.00002	21	820.0035
Phi Int+p Int+Phi g+Phi t+p t+p sex	863.7175	16.3158	0.00002	22	818.0773
Phi Int+Phi toe_lin+p Int+Phi t+p t+p sex	863.8638	16.4621	0.00001	20	822.5068
Phi Int+Phi toe_chip+p Int+p toe_chip+Phi t+p t+p sex	864.2699	16.8682	0.00001	21	820.7747
Phi Int+Phi toe_lin+p Int+Phi t+p g+p t+p sex	864.3549	16.9532	0.00001	21	820.8598
Phi Int+p Int+Phi g+Phi t+Phi sex+p t+p sex	864.8666	17.4649	0.00001	23	817.0744
Phi Int+p Int+p toe_lin+Phi g+Phi t+Phi sex+p t+p sex	865.5397	18.138	0.00001	24	815.5885
Phi Int+p Int+Phi g+Phi t+Phi sex+p g+p t+p sex	865.8122	18.4105	0.00001	26	811.5218
Phi Int+p Int+Phi t+Phi sex+p g+p t+p sex	865.9532	18.5515	0	22	820.313
Phi Int+p Int+Phi g+Phi t+p g+p t+p sex	866.1083	18.7066	0	25	813.991
Phi Int+p Int+p toe_lin+Phi sex+p t	866.2426	18.8409	0	12	841.745
Phi Int+p Int+p toe_chip+Phi sex+p t	866.3221	18.9204	0	12	841.8245
Phi Int+Phi rain+p Int+p toe_lin+Phi sex+p t	866.6266	19.2249	0	13	840.0451
Phi Int+Phi toe_chip+p Int+Phi t+Phi sex+p g+p t+p sex	866.6347	19.233	0	23	818.8425

Phi Int+Phi rain+p Int+p toe_chip+Phi sex+p t	866.6706	19.2689	0	13	840.0891
Phi Int+p Int+p toe_chip+Phi g+Phi t+Phi sex+p t+p sex	866.691	19.2893	0	24	816.7398
Phi Int+p Int+Phi sex+p t	867.0834	19.6817	0	11	844.663
Phi Int+Phi toe_lin+p Int+p toe_lin+Phi sex+p t	867.369	19.9673	0	13	840.7875
Phi Int+Phi rain+p Int+Phi sex+p t	867.5557	20.154	0	12	843.0581
Phi Int+Phi toe_lin+p Int+p toe_chip+Phi sex+p t	867.6271	20.2254	0	13	841.0457
Phi Int+Phi rain+Phi toe_lin+p Int+p toe_lin+Phi sex+p t	867.9209	20.5192	0	14	839.2489
Phi Int+Phi toe_chip+p Int+Phi t+p g+p t+p sex	868.0818	20.6801	0	23	820.2896
Phi Int+Phi toe_lin+p Int+Phi t+Phi sex+p g+p t+p sex	868.1028	20.7011	0	23	820.3106
Phi Int+Phi rain+Phi toe_lin+p Int+p toe_chip+Phi sex+p t	868.1351	20.7334	0	14	839.4631
Phi Int+Phi toe_chip+p Int+Phi sex+p t	868.2997	20.898	0	12	843.8021
Phi Int+Phi toe_chip+p Int+p toe_lin+Phi sex+p t	868.319	20.9173	0	13	841.7375
Phi Int+Phi toe_chip+p Int+p toe_chip+Phi sex+p t	868.3794	20.9777	0	13	841.7979
Phi Int+Phi rain+Phi toe_chip+p Int+p toe_chip+Phi sex+p t	868.6536	21.2519	0	14	839.9816
Phi Int+Phi rain+Phi toe_chip+p Int+p toe_lin+Phi sex+p t	868.6552	21.2535	0	14	839.9832
Phi Int+Phi rain+Phi toe_chip+p Int+Phi sex+p t	868.9338	21.5321	0	13	842.3523
Phi Int+Phi toe_lin+p Int+Phi sex+p t	868.9852	21.5835	0	12	844.4876
Phi Int+p Int+p toe_lin+Phi g+Phi sex+p t	869.1498	21.7481	0	15	838.3806
Phi Int+Phi rain+Phi toe_lin+p Int+Phi sex+p t	869.4016	21.9999	0	13	842.8201
Phi Int+p Int+p toe_lin+Phi sex	870.1325	22.7308	0	4	862.0695
Phi Int+Phi rain+p Int+p toe_lin+Phi g+Phi sex+p t	870.2274	22.8257	0	16	837.3542
Phi Int+p Int+p toe_chip+Phi g+Phi sex+p t	870.2776	22.8759	0	15	839.5084
Phi Int+p Int+Phi sex+p g+p t	870.3717	22.97	0	14	841.6997
Phi Int+p Int+p toe_lin+Phi t+Phi sex	870.7512	23.3495	0	12	846.2536
Phi Int+Phi rain+p Int+Phi sex+p g+p t	870.7521	23.3504	0	15	839.9829
Phi Int+p Int+Phi g+Phi sex+p t	870.7619	23.3602	0	14	842.0899
Phi Int+Phi rain+p Int+p toe_chip+Phi g+Phi sex+p t	870.9245	23.5228	0	16	838.0513
Phi Int+p Int+p toe_chip+Phi sex	870.9409	23.5392	0	4	862.878
Phi Int+Phi toe_lin+p Int+p toe_lin+Phi sex	871.0718	23.6701	0	5	860.9771
Phi Int+Phi toe_lin+p Int+p toe_lin+Phi t+Phi sex	871.1166	23.7149	0	13	844.5351
Phi Int+p Int+p toe_chip+Phi t+Phi sex	871.1229	23.7212	0	12	846.6253
Phi Int+Phi rain+p Int+p toe_lin+Phi sex	871.2443	23.8426	0	5	861.1497
Phi Int+Phi rain+p Int+Phi g+Phi sex+p t	871.2964	23.8947	0	15	840.5272
Phi Int+Phi toe_lin+p Int+Phi sex+p g+p t	871.4886	24.0869	0	15	840.7193
Phi Int+p Int+p toe_lin+Phi g+Phi t+Phi sex	871.6948	24.2931	0	15	840.9255
Phi Int+Phi toe_lin+p Int+p toe_chip+Phi t+Phi sex	871.8069	24.4052	0	13	845.2255
Phi Int+p Int+Phi sex	871.9911	24.5894	0	3	865.9533
Phi Int+p Int+Phi t+Phi sex	871.9931	24.5914	0	11	849.5728
Phi Int+Phi rain+Phi toe_lin+p Int+Phi sex+p g+p t	872.0442	24.6425	0	16	839.171
Phi Int+Phi toe_chip+p Int+p toe_lin+Phi sex	872.0501	24.6484	0	5	861.9555
Phi Int+p Int+p rain+p toe_lin+Phi sex	872.1179	24.7162	0	5	862.0233
Phi Int+Phi rain+p Int+p toe_chip+Phi sex	872.3212	24.9195	0	5	862.2266

Phi Int+Phi rain+Phi toe_lin+p Int+p toe_lin+Phi sex	872.3617	24.96	0	6	860.229
Phi Int+Phi toe_lin+p Int+p toe_chip+Phi sex	872.4266	25.0249	0	5	862.332
Phi Int+Phi toe_chip+p Int+Phi sex+p g+p t	872.4469	25.0452	0	15	841.6777
Phi Int+Phi toe_chip+p Int+p toe_lin+Phi t+Phi sex	872.6915	25.2898	0	13	846.11
Phi Int+Phi toe_chip+p Int+p toe_lin+Phi t+Phi sex	872.6915	25.2898	0	13	846.11
Phi Int+Phi rain+Phi toe_chip+p Int+Phi sex+p g+p t	872.7494	25.3477	0	16	839.8762
Phi Int+p Int+p rain+p toe_lin+Phi t+Phi sex	872.8208	25.4191	0	13	846.2393
Phi Int+Phi toe_chip+p Int+p toe_chip+Phi sex	872.8494	25.4477	0	5	862.7548
Phi Int+p Int+p rain+p toe_chip+Phi sex	872.9545	25.5528	0	5	862.8599
Phi Int+Phi toe_chip+p Int+p toe_chip+Phi t+Phi sex	873.0438	25.6421	0	13	846.4623
Phi Int+Phi rain+Phi toe_chip+p Int+p toe_lin+Phi sex	873.0717	25.67	0	6	860.939
Phi Int+Phi toe_lin+p Int+p rain+p toe_lin+Phi sex	873.0772	25.6755	0	6	860.9445
Phi Int+p Int+Phi g+Phi sex+p g+p t	873.1036	25.7019	0	17	838.1196
Phi Int+p Int+p rain+p toe_chip+Phi t+Phi sex	873.1191	25.7174	0	13	846.5376
Phi Int+Phi toe_lin+p Int+p rain+p toe_lin+Phi t+Phi sex	873.1865	25.7848	0	14	844.5145
Phi Int+Phi rain+p Int+p rain+p toe_lin+Phi sex	873.2509	25.8492	0	6	861.1182
Phi Int+Phi toe_chip+p Int+Phi sex	873.3506	25.9489	0	4	865.2876
Phi Int+Phi rain+p Int+Phi sex	873.3881	25.9864	0	4	865.3251
Phi Int+Phi toe_chip+p Int+Phi t+Phi sex	873.4537	26.052	0	12	848.9561
Phi Int+p Int+p toe_lin+Phi g+Phi sex	873.6001	26.1984	0	7	859.4229
Phi Int+Phi toe_lin+p Int+Phi sex	873.7459	26.3442	0	4	865.6829
Phi Int+Phi toe_lin+p Int+p rain+p toe_chip+Phi t+Phi sex	873.7508	26.3491	0	14	845.0788
Phi Int+p Int+p rain+p toe_lin+Phi g+Phi t+Phi sex	873.7921	26.3904	0	16	840.9189
Phi Int+p Int+Phi sex+p g	873.8253	26.4236	0	6	861.6926
Phi Int+Phi rain+Phi toe_lin+p Int+p toe_chip+Phi sex	873.967	26.5653	0	6	861.8343
Phi Int+Phi toe_lin+p Int+Phi t+Phi sex	873.9896	26.5879	0	12	849.492
Phi Int+p Int+p rain+Phi sex	874.006	26.6043	0	4	865.943
Phi Int+Phi toe_chip+p Int+p rain+p toe_lin+Phi sex	874.0266	26.6249	0	6	861.8939
Phi Int+p Int+p rain+Phi t+Phi sex	874.0361	26.6344	0	12	849.5385
Phi Int+Phi rain+p Int+p rain+p toe_chip+Phi sex	874.1145	26.7128	0	6	861.9818
Phi Int+Phi rain+p Int+Phi g+Phi sex+p g+p t	874.1353	26.7336	0	18	837.0338
Phi Int+Phi rain+Phi toe_chip+p Int+p toe_chip+Phi sex	874.1911	26.7894	0	6	862.0584
Phi Int+Phi rain+Phi toe_lin+p Int+p rain+p toe_lin+Phi sex	874.3792	26.9775	0	7	860.202
Phi Int+Phi toe_lin+p Int+p rain+p toe_chip+Phi sex	874.3979	26.9962	0	6	862.2652
Phi Int+p Int+Phi t+Phi sex+p g	874.6264	27.2247	0	14	845.9544
Phi Int+Phi rain+p Int+Phi sex+p g	874.7405	27.3388	0	7	860.5633
Phi Int+p Int+Phi g+Phi t+Phi sex	874.7485	27.3468	0	14	846.0765
Phi Int+Phi toe_chip+p Int+p rain+p toe_lin+Phi t+Phi sex	874.7644	27.3627	0	14	846.0924
Phi Int+Phi rain+Phi toe_chip+p Int+Phi sex	874.8097	27.408	0	5	864.7151
Phi Int+p Int+Phi t+Phi sex+p t	874.8352	27.4335	0	18	837.7338
Phi Int+Phi toe_lin+p Int+Phi sex+p g	874.8467	27.445	0	7	860.6695
Phi Int+Phi toe_chip+p Int+p rain+p toe_chip+Phi sex	874.8677	27.466	0	6	862.735



Phi Int+Phi rain+p Int+p toe_lin+Phi g+Phi sex	874.9078	27.5061	0	8	858.6796
Phi Int+Phi toe_chip+p Int+p rain+p toe_chip+Phi t+Phi sex	875.0226	27.6209	0	14	846.3506
Phi Int+Phi rain+Phi toe_lin+p Int+Phi sex	875.0469	27.6452	0	5	864.9522
Phi Int+Phi toe_lin+p Int+Phi t+Phi sex+p g	875.0796	27.6779	0	15	844.3103
Phi Int+Phi rain+Phi toe_chip+p Int+p rain+p toe_lin+Phi sex	875.0929	27.6912	0	7	860.9156
Phi Int+Phi rain+p Int+p rain+Phi sex	875.2143	27.8126	0	5	865.1196
Phi Int+Phi toe_chip+p Int+p rain+Phi sex	875.3721	27.9704	0	5	865.2774
Phi Int+p Int+Phi g+Phi t+Phi sex+p g	875.3731	27.9714	0	17	840.3892
Phi Int+p Int+p toe_chip+Phi g+Phi sex	875.4934	28.0917	0	7	861.3162
Phi Int+Phi toe_chip+p Int+p rain+Phi t+Phi sex	875.5134	28.1117	0	13	848.9319
Phi Int+p Int+p rain+p toe_chip+Phi g+Phi t+Phi sex	875.5902	28.1885	0	16	842.717
Phi Int+p Int+p rain+Phi sex+p g	875.6303	28.2286	0	7	861.4531
Phi Int+p Int+p rain+p toe_lin+Phi g+Phi sex	875.6499	28.2482	0	8	859.4217
Phi Int+Phi rain+Phi toe_lin+p Int+p rain+p toe_chip+Phi sex	875.6935	28.2918	0	7	861.5163
Phi Int+Phi toe_lin+p Int+p rain+Phi sex	875.7752	28.3735	0	5	865.6805
Phi Int+Phi toe_chip+p Int+Phi sex+p g	875.7956	28.3939	0	7	861.6184
Phi Int+Phi toe_chip+p Int+Phi t+Phi sex+p t	875.8446	28.4429	0	19	836.6188
Phi Int+Phi rain+Phi toe_chip+p Int+p rain+p toe_chip+Phi sex	875.9708	28.5691	0	7	861.7936
Phi Int+Phi rain+Phi toe_lin+p Int+Phi sex+p g	875.9724	28.5707	0	8	859.7442
Phi Int+p Int+p toe_chip+p t	875.9918	28.5901	0	11	853.5714
Phi Int+p Int+p toe_lin+p t	876.0045	28.6028	0	11	853.5841
Phi Int+p Int+Phi g+Phi sex	876.0223	28.6206	0	6	863.8896
Phi Int+Phi toe_lin+p Int+p rain+Phi t+Phi sex	876.0422	28.6405	0	13	849.4608
Phi Int+p Int+p t	876.3859	28.9842	0	10	856.0362
Phi Int+Phi rain+p Int+p toe_chip+Phi g+Phi sex	876.5047	29.103	0	8	860.2765
Phi Int+Phi toe_lin+p Int+Phi t+Phi sex+p t	876.5282	29.1265	0	19	837.3024
Phi Int+Phi toe_chip+p Int+Phi t+Phi sex+p g	876.5966	29.1949	0	15	845.8274
Phi Int+Phi rain+Phi toe_chip+p Int+p rain+Phi sex	876.6563	29.2546	0	6	864.5236
Phi Int+Phi toe_chip+p Int+p t	876.6673	29.2656	0	11	854.2469
Phi Int+Phi rain+Phi toe_chip+p Int+Phi sex+p g	876.6712	29.2695	0	8	860.443
Phi Int+p Int+p rain+Phi t+Phi sex+p g	876.7231	29.3214	0	15	845.9538
Phi Int+Phi toe_lin+p Int+p rain+Phi sex+p g	876.7289	29.3272	0	8	860.5007
Phi Int+p Int+p toe_lin+Phi t+Phi sex+p t	876.7482	29.3465	0	20	835.3912
Phi Int+Phi rain+p Int+p rain+Phi sex+p g	876.7746	29.3729	0	8	860.5464
Phi Int+p Int+Phi g+Phi t+Phi sex+p t	876.797	29.3953	0	21	833.3018
Phi Int+p Int+p rain+Phi g+Phi t+Phi sex	876.8045	29.4028	0	15	846.0352
Phi Int+Phi rain+p Int+Phi g+Phi sex	876.8188	29.4171	0	7	862.6416
Phi Int+Phi rain+Phi toe_lin+p Int+p rain+Phi sex	876.9112	29.5095	0	6	864.7785
Phi Int+Phi rain+p Int+p rain+p toe_lin+Phi g+Phi sex	876.9146	29.5129	0	9	858.6289
Phi Int+p Int+Phi g+Phi sex+p g	877.0159	29.6142	0	9	858.7302
Phi Int+Phi toe_lin+p Int+p rain+Phi t+Phi sex+p g	877.1774	29.7757	0	16	844.3042
Phi Int+p Int+p toe_chip+Phi t+Phi sex+p t	877.194	29.7923	0	20	835.837

Phi Int+p Int+p toe_chip+Phi t	877.3032	29.9015	0	9	859.0175
Phi Int+p Int+p rain+Phi g+Phi t+Phi sex+p g	877.424	30.0223	0	18	840.3225
Phi Int+p Int+p rain+p toe_chip+Phi g+Phi sex	877.4955	30.0938	0	8	861.2673
Phi Int+Phi rain+p Int+p toe_chip+p t	877.5953	30.1936	0	12	853.0977
Phi Int+Phi toe_chip+p Int+p rain+Phi sex+p g	877.6244	30.2227	0	8	861.3962
Phi Int+Phi rain+p Int+p toe_lin+p t	877.646	30.2443	0	12	853.1484
Phi Int+Phi toe_chip+p Int+p toe_lin+p t	877.7727	30.371	0	12	853.2751
Phi Int+Phi toe_lin+p Int+p t	877.7729	30.3712	0	11	855.3525
Phi Int+Phi toe_chip+p Int+p toe_chip+p t	877.8286	30.4269	0	12	853.331
Phi Int+p Int+Phi t	877.937	30.5353	0	8	861.7088
Phi Int+Phi toe_lin+p Int+p toe_lin+p t	878.0113	30.6096	0	12	853.5137
Phi Int+Phi toe_lin+p Int+p toe_chip+p t	878.0175	30.6158	0	12	853.5199
Phi Int+Phi rain+Phi toe_lin+p Int+p rain+Phi sex+p g	878.02	30.6183	0	9	859.7343
Phi Int+Phi rain+p Int+p t	878.0517	30.65	0	11	855.6313
Phi Int+p Int+p rain+Phi g+Phi sex	878.0638	30.6621	0	7	863.8866
Phi Int+Phi rain+p Int+p rain+p toe_chip+Phi g+Phi sex	878.2836	30.8819	0	9	859.9979
Phi Int+Phi toe_lin+p Int+p toe_lin+Phi t+Phi sex+p t	878.3347	30.933	0	21	834.8395
Phi Int+Phi rain+Phi toe_chip+p Int+p t	878.5293	31.1276	0	12	854.0317
Phi Int+Phi rain+p Int+Phi g+Phi sex+p g	878.5667	31.165	0	10	858.2169
Phi Int+Phi toe_chip+p Int+p rain+Phi t+Phi sex+p g	878.6996	31.2979	0	16	845.8264
Phi Int+Phi rain+p Int+p rain+Phi g+Phi sex	878.7033	31.3016	0	8	862.4751
Phi Int+Phi rain+Phi toe_chip+p Int+p rain+Phi sex+p g	878.7191	31.3174	0	9	860.4334
Phi Int+Phi toe_chip+p Int+p toe_lin+Phi t+Phi sex+p t	878.8854	31.4837	0	21	835.3903
Phi Int+Phi toe_lin+p Int+p toe_chip+Phi t	878.8975	31.4958	0	10	858.5477
Phi Int+p Int+p rain+Phi g+Phi sex+p g	878.9029	31.5012	0	10	858.5532
Phi Int+p Int+p toe_lin+Phi g+Phi t+Phi sex+p t	878.962	31.5603	0	23	831.1698
Phi Int+Phi toe_lin+p Int+p toe_chip+Phi t+Phi sex+p t	878.9675	31.5658	0	21	835.4724
Phi(g+t+sex+rain+toe_chip+toe_lin) p(g+t+sex+rain+toe_chip+toe_lin)	879.0012	31.5995	0	32	811.5218
Phi Int+p Int+Phi g+p t	879.0697	31.668	0	13	852.4882
Phi Int+p Int+p toe_lin+Phi g+p t	879.1327	31.731	0	14	850.4607
Phi Int+Phi toe_chip+p Int+p toe_chip+Phi t+Phi sex+p t	879.3309	31.9292	0	21	835.8358
Phi Int+Phi toe_chip+p Int+p toe_chip+Phi t	879.3372	31.9355	0	10	858.9874
Phi Int+p Int+p toe_lin+Phi t	879.4519	32.0502	0	10	859.1021
Phi Int+Phi rain+Phi toe_lin+p Int+p t	879.4741	32.0724	0	12	854.9765
Phi Int+Phi rain+Phi toe_chip+p Int+p toe_lin+p t	879.537	32.1353	0	13	852.9555
Phi Int+Phi rain+Phi toe_chip+p Int+p toe_chip+p t	879.5501	32.1484	0	13	852.9686
Phi Int+Phi rain+Phi toe_lin+p Int+p toe_chip+p t	879.6108	32.2091	0	13	853.0294
Phi Int+Phi rain+Phi toe_lin+p Int+p toe_lin+p t	879.6403	32.2386	0	13	853.0588
Phi Int+p Int+p toe_chip+Phi g+p t	879.8721	32.4704	0	14	851.2001
Phi Int+p Int+p rain+Phi t	879.9921	32.5904	0	9	861.7064
Phi Int+p Int+p g+p t	880.0777	32.676	0	13	853.4963
Phi Int+p Int+p toe_lin+Phi g+Phi t	880.2566	32.8549	0	13	853.6752

Phi Int+p Int+p toe_chip+Phi g+Phi t+Phi sex+p t	880.3212	32.9195	0	23	832.529
Phi Int+p Int+p toe_lin	880.4071	33.0054	0	3	874.3694
Phi Int+Phi rain+p Int+p rain+Phi g+Phi sex+p g	880.6236	33.2219	0	11	858.2032
Phi Int+p Int+Phi t+Phi sex+p g+p t	880.8845	33.4828	0	22	835.2443
Phi Int+Phi rain+p Int+Phi g+p t	880.8905	33.4888	0	14	852.2185
Phi Int+Phi toe_lin+p Int+p toe_lin+Phi t	881.0672	33.6655	0	11	858.6468
Phi Int+Phi rain+p Int+p toe_lin+Phi g+p t	881.0974	33.6957	0	15	850.3281
Phi Int+p Int+p toe_chip	881.3276	33.9259	0	3	875.2899
Phi Int+Phi toe_chip+p Int+p rain+p toe_chip+Phi t	881.399	33.9973	0	11	858.9786
Phi Int+p Int+p rain+p toe_chip+Phi t	881.4117	34.01	0	11	858.9913
Phi Int+Phi toe_chip+p Int+p toe_lin+Phi t	881.4391	34.0374	0	11	859.0187
Phi Int+p Int+p rain+p toe_lin+Phi t	881.5225	34.1208	0	11	859.1021
Phi Int+p Int+Phi g+Phi t+Phi sex+p g+p t	881.5914	34.1897	0	25	829.4741
Phi Int+Phi rain+p Int+p toe_chip+Phi g+p t	881.6968	34.2951	0	15	850.9275
Phi Int+Phi rain+p Int+p g+p t	881.7169	34.3152	0	14	853.0449
Phi Int+Phi toe_lin+p Int+Phi t	881.8219	34.4202	0	10	861.4721
Phi Int+Phi toe_chip+p Int+p g+p t	881.9079	34.5062	0	14	853.2359
Phi Int+p Int	881.9592	34.5575	0	2	877.9404
Phi Int+Phi toe_lin+p Int+p g+p t	882.0911	34.6894	0	14	853.4191
Phi Int+Phi toe_chip+p Int+p toe_lin	882.3328	34.9311	0	4	874.2698
Phi Int+p Int+p rain+p toe_lin+Phi g+Phi t	882.3353	34.9336	0	14	853.6633
Phi Int+Phi toe_chip+p Int	882.3583	34.9566	0	3	876.3206
Phi Int+Phi toe_lin+p Int+p toe_lin	882.3628	34.9611	0	4	874.2999
Phi Int+Phi rain+p Int+p toe_lin	882.3726	34.9709	0	4	874.3096
Phi Int+p Int+p rain+p toe_lin	882.4289	35.0272	0	4	874.3659
Phi Int+Phi toe_lin+p Int+Phi t+Phi sex+p g+p t	882.569	35.1673	0	23	834.7768
Phi Int+Phi toe_chip+p Int+p rain+Phi t	882.9149	35.5132	0	11	860.4945
Phi Int+Phi toe_chip+p Int+Phi t	882.92	35.5183	0	11	860.4996
Phi Int+Phi toe_lin+p Int	882.9472	35.5455	0	3	876.9095
Phi Int+Phi toe_lin+p Int+p rain+p toe_chip+Phi t	882.9828	35.5811	0	12	858.4852
Phi Int+Phi toe_chip+p Int+Phi t+Phi sex+p g+p t	882.9902	35.5885	0	23	835.198
Phi Int+p Int+Phi g+p g+p t	883.0629	35.6612	0	16	850.1897
Phi Int+Phi toe_lin+p Int+p rain+p toe_lin+Phi t	883.141	35.7393	0	12	858.6434
Phi Int+p Int+Phi t+p g	883.1917	35.79	0	12	858.6941
Phi Int+p Int+p rain+p toe_chip	883.199	35.7973	0	4	875.136
Phi Int+Phi toe_chip+p Int+p toe_chip	883.2141	35.8124	0	4	875.1511
Phi Int+Phi rain+p Int+p toe_chip	883.3421	35.9404	0	4	875.2791
Phi Int+Phi toe_lin+p Int+p toe_chip	883.3524	35.9507	0	4	875.2894
Phi Int+Phi toe_chip+p Int+p rain+p toe_lin+Phi t	883.5163	36.1146	0	12	859.0187
Phi Int+p Int+p rain+p toe_chip+Phi g+Phi t	883.5553	36.1536	0	14	854.8833
Phi Int+p Int+p toe_chip+Phi g+Phi t	883.6251	36.2234	0	14	854.9531
Phi Int+Phi rain+Phi toe_chip+p Int+p g+p t	883.6738	36.2721	0	15	852.9045

Phi Int+Phi rain+Phi toe_lin+p Int+p g+p t	883.7162	36.3145	0	15	852.947
Phi Int+p Int+p g	883.7722	36.3705	0	5	873.6776
Phi Int+p Int+p rain	883.8464	36.4447	0	3	877.8086
Phi Int+p Int+Phi g+Phi t+p g	883.8531	36.4514	0	15	853.0839
Phi Int+Phi toe_lin+p Int+p rain+Phi t	883.887	36.4853	0	11	861.4666
Phi Int+Phi rain+p Int	883.9713	36.5696	0	3	877.9336
Phi Int+p Int+p rain+Phi g+Phi t	883.9979	36.5962	0	13	857.4165
Phi Int+p Int+Phi g+Phi t	884.0174	36.6157	0	13	857.4359
Phi Int+Phi toe_chip+p Int+p rain	884.2573	36.8556	0	4	876.1943
Phi Int+Phi rain+Phi toe_lin+p Int+p toe_lin	884.3295	36.9278	0	5	874.2348
Phi Int+Phi rain+Phi toe_chip+p Int+p toe_lin	884.3317	36.93	0	5	874.237
Phi Int+Phi toe_chip+p Int+p rain+p toe_lin	884.3568	36.9551	0	5	874.2622
Phi Int+Phi rain+p Int+p rain+p toe_lin	884.3751	36.9734	0	5	874.2805
Phi Int+Phi rain+Phi toe_chip+p Int	884.3786	36.9769	0	4	876.3156
Phi Int+Phi toe_lin+p Int+p rain+p toe_lin	884.3901	36.9884	0	5	874.2955
Phi Int+p Int+p toe_lin+Phi g	884.4729	37.0712	0	6	872.3402
Phi Int+p Int+Phi g	884.7233	37.3216	0	5	874.6287
Phi Int+Phi toe_lin+p Int+Phi t+p g	884.8181	37.4164	0	13	858.2366
Phi Int+Phi toe_lin+p Int+p rain	884.9056	37.5039	0	4	876.8426
Phi Int+Phi rain+Phi toe_lin+p Int	884.9613	37.5596	0	4	876.8983
Phi Int+Phi toe_chip+p Int+p rain+p toe_chip	885.0977	37.696	0	5	875.0031
Phi Int+Phi rain+p Int+Phi g+p g+p t	885.104	37.7023	0	17	850.1201
Phi Int+Phi rain+p Int+p rain+p toe_chip	885.1494	37.7477	0	5	875.0547
Phi Int+Phi toe_chip+p Int+Phi t+p g	885.2154	37.8137	0	13	858.6339
Phi Int+Phi toe_lin+p Int+p rain+p toe_chip	885.2289	37.8272	0	5	875.1343
Phi Int+Phi rain+Phi toe_chip+p Int+p toe_chip	885.2442	37.8425	0	5	875.1495
Phi Int+p Int+p rain+Phi t+p g	885.269	37.8673	0	13	858.6876
Phi Int+Phi rain+Phi toe_lin+p Int+p toe_chip	885.3732	37.9715	0	5	875.2785
Phi Int+Phi toe_chip+p Int+p g	885.5951	38.1934	0	6	873.4624
Phi Int+Phi rain+p Int+p g	885.675	38.2733	0	6	873.5423
Phi Int+p Int+p rain+p g	885.7229	38.3212	0	6	873.5902
Phi Int+Phi toe_lin+p Int+p g	885.7687	38.367	0	6	873.636
Phi Int+p Int+p toe_chip+Phi g	885.7719	38.3702	0	6	873.6392
Phi Int+Phi rain+p Int+p rain	885.8094	38.4077	0	4	877.7464
Phi Int+p Int+p rain+Phi g+Phi t+p g	885.8498	38.4481	0	16	852.9766
Phi Int+Phi rain+Phi toe_chip+p Int+p rain	886.282	38.8803	0	5	876.1874
Phi Int+Phi rain+Phi toe_lin+p Int+p rain+p toe_lin	886.3345	38.9328	0	6	874.2018
Phi Int+Phi rain+Phi toe_chip+p Int+p rain+p toe_lin	886.3401	38.9384	0	6	874.2074
Phi Int+p Int+p toe_chip+Phi t+p t	886.344	38.9423	0	17	851.36
Phi Int+Phi rain+p Int+p toe_lin+Phi g	886.4715	39.0698	0	7	872.2943
Phi Int+p Int+Phi t+p t	886.4757	39.074	0	16	853.6025
Phi Int+p Int+p rain+p toe_lin+Phi g	886.4812	39.0795	0	7	872.304

Phi Int+Phi rain+p Int+Phi g	886.6417	39.24	0	6	874.509
Phi Int+Phi toe_chip+p Int+Phi t+p t	886.6753	39.2736	0	17	851.6914
Phi Int+p Int+p rain+Phi g	886.7157	39.314	0	6	874.583
Phi Int+Phi rain+Phi toe_lin+p Int+p rain	886.8835	39.4818	0	5	876.7889
Phi Int+Phi toe_lin+p Int+p rain+Phi t+p g	886.9082	39.5065	0	14	858.2362
Phi Int+Phi rain+Phi toe_chip+p Int+p rain+p toe_chip	887.0879	39.6862	0	6	874.9552
Phi Int+p Int+Phi g+Phi t+p t	887.1209	39.7192	0	19	847.8951
Phi Int+Phi rain+Phi toe_lin+p Int+p rain+p toe_chip	887.1848	39.7831	0	6	875.0521
Phi Int+Phi toe_chip+p Int+p rain+Phi t+p g	887.2912	39.8895	0	14	858.6192
Phi Int+p Int+Phi g+p g	887.4613	40.0596	0	8	871.2331
Phi Int+Phi toe_chip+p Int+p rain+p g	887.5309	40.1292	0	7	873.3537
Phi Int+Phi rain+Phi toe_chip+p Int+p g	887.5542	40.1525	0	7	873.377
Phi Int+Phi rain+Phi toe_lin+p Int+p g	887.6725	40.2708	0	7	873.4953
Phi Int+Phi rain+p Int+p rain+p g	887.6883	40.2866	0	7	873.5111
Phi Int+p Int+p rain+p toe_chip+Phi g	887.6979	40.2962	0	7	873.5207
Phi Int+Phi rain+p Int+p toe_chip+Phi g	887.7071	40.3054	0	7	873.5299
Phi Int+Phi toe_lin+p Int+p rain+p g	887.7348	40.3331	0	7	873.5576
Phi Int+Phi toe_lin+p Int+Phi t+p t	887.9368	40.5351	0	17	852.9529
Phi Int+Phi toe_lin+p Int+p toe_chip+Phi t+p t	888.289	40.8873	0	18	851.1875
Phi Int+Phi rain+p Int+p rain+p toe_lin+Phi g	888.4526	41.0509	0	8	872.2244
Phi Int+p Int+p toe_lin+Phi t+p t	888.5173	41.1156	0	18	851.4159
Phi Int+Phi rain+p Int+p rain+Phi g	888.5724	41.1707	0	7	874.3952
Phi Int+p Int+p rain+Phi g+p g	889.4406	42.0389	0	9	871.1549
Phi Int+Phi rain+p Int+Phi g+p g	889.515	42.1133	0	9	871.2293
Phi Int+Phi rain+p Int+p rain+p toe_chip+Phi g	889.5448	42.1431	0	8	873.3166
Phi Int+Phi rain+Phi toe_chip+p Int+p rain+p g	889.5494	42.1477	0	8	873.3212
Phi Int+p Int+p toe_lin+Phi g+Phi t+p t	889.5876	42.1859	0	21	846.0925
Phi Int+Phi rain+Phi toe_lin+p Int+p rain+p g	889.6987	42.297	0	8	873.4705
Phi Int+Phi toe_chip+p Int+p toe_lin+Phi t+p t	890.3162	42.9145	0	19	851.0904
Phi Int+Phi toe_chip+p Int+p toe_chip+Phi t+p t	890.4155	43.0138	0	19	851.1897
Phi Int+Phi toe_lin+p Int+p toe_lin+Phi t+p t	890.4774	43.0757	0	19	851.2516
Phi Int+p Int+Phi t+p g+p t	890.5046	43.1029	0	19	851.2788
Phi Int+p Int+p toe_chip+Phi g+Phi t+p t	890.7148	43.3131	0	21	847.2197
Phi Int+Phi rain+p Int+p rain+Phi g+p g	891.4547	44.053	0	10	871.105
Phi Int+Phi toe_chip+p Int+Phi t+p g+p t	892.2329	44.8312	0	20	850.8759
Phi Int+Phi toe_lin+p Int+Phi t+p g+p t	894.6059	47.2042	0	21	851.1108
Phi Int+p Int+Phi g+Phi t+p g+p t	894.6563	47.2546	0	24	844.7051



**ESTIMATING VITAL RATES OF THE ENDANGERED GOLDEN LANCEHEAD  
PITVIPER, *BOTHROPS INSULARIS* USING ROBUST MARK-RECAPTURE DESIGN**

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ABSTRACT. Knowledge about many snake species' vital rates is lacking because of the difficulty in data collection. To provide guidelines for conservation efforts, we used a robust design mark-recapture model to estimate survival, behavioral effects on capture probability, temporary emigration, abundance and population growth rate for the golden lancehead pitviper, *Bothrops insularis*, an endemic and endangered species from southeastern Brazil. We collected data irregularly over ten occasions from 2002 to 2010. Annual survival was low and slightly positively correlated with average temperature. No behavioral effects were detected on capture probability. Temporal emigration was high, indicating the importance of accounting for this parameter both in the sampling design and modeling. On average, the population increased 9% per year during the study fluctuating between periods of increase and decrease, which might be attributed to natural oscillations, although illegal trade may also be responsible for declines.

*Key words:* endangered species, Huggins Closed Capture model, imperfect detection, pitviper population dynamics.



## INTRODUCTION

In the last decades efforts to understand and preserve natural populations have increased because diseases, climate change, and other human-induced threats have become more pervasive (Sala et al., 2000). Despite such efforts, information on the life history of most taxonomic groups is still lacking. This knowledge deficiency not only results in poor understanding of the impacts of anthropogenic and non-anthropogenic stressors, but also in possibly poor management actions (Greene, 2005).

Snake populations have been suffering great impacts and declines around the world (Gibbons et al., 2000; Reading et al., 2010; Bohm et al., 2013). For many decades, this group was thought to be difficult to study in the field and partly because of their natural history characteristics, which includes elusive habits, cryptic behaviors, and low densities (Parker and Plummer, 1987; Dorcas and Willson, 2009). Furthermore, habitat heterogeneity and complexity of some systems make species difficult to find and study. As a consequence, most information on snake population biology is anecdotal and characterized by basic descriptions of vital rates and relative abundance indices (Parker and Plummer, 1987). Robust quantitative estimates of population vital rates, such as survival, are generally difficult to obtain (Dorcas and Willson, 2009).

When considering studies that account for detection probability in the estimation of vital statistics, the scarcity of reliable information is even greater. Fortunately, in the last decade there has been a growing number of field studies and application of novel analytical techniques leading to robust estimates (Schmidt, 2003; Altwegg et al., 2005; Mazerolle et al., 2007; Dorcas and Willson, 2009; Christy et al., 2010; Durso et al., 2011; Breininger et al., 2012; Hyslop et al., 2012; Maritz and Alexander, 2012; Prival and Schroff, 2012). The improvement of detection

probability through good sampling designs and explanatory covariates (Parker and Plummer, 1987; Hyslop et al., 2012) is important because it will provide support for the evaluation of all other parameters, increasing precision and accuracy (Pollock et al., 1990). This, in turn, will enable effective guidelines for management actions on population dynamics to be implemented (Dorcas and Willson, 2009; Breininger et al., 2012).

In the face of the difficulty of sampling elusive species, model-based approaches are valuable tools that help improve quality of population ecology studies. Mark-recapture is a well-known technique used for the assessment of important population estimates such as survival and transition probabilities. Additionally, mark-recapture allows the estimation of temporary emigration, an important parameter that influences vital rates (Kendall et al., 1997) and whose effects on snake populations are still unknown (Parker and Plummer, 1987; Dorcas and Willson, 2009). Similarly, behavioral effects of marking individuals are still undescribed for snakes and should be investigated since marking techniques may disturb individuals.

As an attempt to further advance the knowledge of Neotropical snake population ecology, we sampled the population of the insular and endemic golden lancehead pitviper, *Bothrops insularis* (Fig. 1), a critically endangered species (IUCN, 2012). The golden lancehead is a semi-arboreal, medium-sized pitviper with ambush behavior that feeds upon migratory passerine birds as adults (Martins et al., 2001; Marques et al., 2002; Marques et al., 2012). *Bothrops insularis* is mostly diurnal, but presents nocturnal activity as well (Marques et al., 2002). In 2008, Martins et al. (2008) raised a concern about population decline based on raw counts and suspicion of illegal trading. Here, for the first time we provide estimates of survival, behavioral effects on detection probability, temporary emigration, abundance and growth estimates for *B. insularis*.

## METHODS

### *Study site*

*Bothrops insularis* is restricted to the Queimada Grande Island (24° 29'S, 46 ° 40'W), a small island (~ 43 ha) about 30 km south off the coast of São Paulo state, southeastern Brazil. The island consists of bare rocky areas, open grassy areas and lowland rainforest, which covers approximately 60% of the entire island, and is the habitat of the target species (Martins et al., 2008). Altitudinal variation in the island ranges from 0 to 200 m above sea level (Martins et al., 2008). The climate is subtropical with two prominent seasons; one rainy and warm (October to March) and the other dry and cold (April to September). Relative air humidity is always higher than 90%. The island serves as an important migration route for birds, which use the island to rest and feed and are preyed upon by the snakes (Marques et al., 2012).

### *Data collection*

We used visual encounter surveys (VES) on each sampling occasion, where four to six trained observers searched for snakes on the ground and on the trees, during daylight, in a single 1370 x 3-meters linear transect that crosses the island in the north-south direction. Due to weather and logistical restrictions, we visited the island 10 times (primary sampling occasions) irregularly from 2002 to 2010 in different periods of the year. Each visit varied from two to four days (secondary sampling occasions), resulting in 28 sampling occasions (Table 1). Because our samples were composed almost entirely by adults (juveniles are difficult to spot in the field), we decided to restrict our analysis only to this age class (snout-vent length of mature males > 505 mm, and mature females > 555 mm; Marques et al., in press).

Each individual sighted was hand-captured and marked using passive integrated transponders (PIT tags) injected in the latero-posterior region of the body with sterilized needles. We obtained sex and measured the snout-vent length (SVL) of each individual using a flexible tape (to the nearest cm). Afterwards, we released the individuals at the same place we sighted them. We also measured monthly air temperature to include in the analysis since temperature predicts ectothermic's activity, even in subtropical regions (Gibbons and Semlitsch, 1987; Lillywhite, 1987).

#### *Mark-recapture modeling*

To estimate the population vital rates, we used the Huggins closed capture model, (Huggins 1989, 1991) in a robust design, to obtain maximum likelihood estimates of apparent survival probability ( $\Phi$ ), temporary emigration ( $\gamma^t$ ), capture ( $p$ ) and recapture probability ( $c$ ) using program MARK (White and Burnham, 1999). We adjusted the time interval between visits because they were irregular.

The robust design incorporates aspects of closed models and open population models. In the former, the population is assumed to be biologically and geographically closed (neither births/deaths nor immigration/emigration are allowed) within primary sampling occasions and the model provides estimates of abundance and recapture probability. In the latter, the model relax the closure assumption between primary occasions and is used primarily to estimate survival (Pollock, 1982). The assumption of closure within each primary occasion is based on pitviper's biology, which are usually sedentary and sit-and-wait predators that remain in the same foraging and resting area for many days to weeks (Mushinsky, 1987; Sazima, 1992; Greene, 1997; pers.

obs. on radio-tagged *B. atrox* and *B. insularis*). Survival was assumed to be at or near 100% over the short period of the secondary sampling occasions.

Besides the estimation of  $\Phi$ , which is a product of true survival and permanent emigration (thus, permanent emigration and death are confounded), one great advantage of the robust design is the estimation of temporary emigration, the animal movement that leads to temporary unavailability of individuals for capture in the sampling area (Kendall et al., 1997). Since open and closed models assume that all animals are always available for capture, failing to meet this assumption may bias the estimates (Kendall et al., 1997). Temporary emigration is provided by two parameters,  $\gamma'$  and  $\gamma$ . The parameter  $\gamma'$  represents the probability that an individual is a temporary emigrant on primary occasion  $t$  given it was alive and available for capture on primary occasion  $t - 1$ . The parameter  $\gamma$  represents the probability of an individual that was a temporary emigrant on primary occasion  $t - 1$  remains as a temporary emigrant on primary occasion  $t$ . We used these parameters because we suspect that movement in and off the sampled area occurred during our study period.

The dissociation between capture ( $p$ ) and recapture ( $c$ ) probabilities allows for testing positive or negative behavioral responses to capturing and marking individuals (i.e., trap-shy and trap-happy effects, Nichols et al., 1984). Since we physically captured and marked individuals with PIT tags, the recapture probability could be lower (e.g., due to stress). Conversely, if  $p = c$ , no capture effect on behavior is assumed.

The Huggins closed capture robust design also provides an estimate of the population abundance for each primary occasion as a derived parameter, which means that the model does not contain abundance as an explicit parameter and calculates it based on the estimated capture

probabilities and obtained data. We used the estimates of the population abundance to obtain the finite population growth rate  $\lambda = N_{t+1}/N_t$  for each one of the primary occasions of the study, where  $\lambda$  is a positive number that measures the proportional population increase/decrease from  $N_t$  to  $N_{t+1}$ . To obtain sampling variances and derive standard errors and confidence intervals for the estimated  $\lambda$ , we used the delta method (Powell, 2007).

We constrained each parameter to be a logit-linear function of individual and temporal covariates. We kept a simple parameterization and did not include time effects on parameters because we anticipated poor support for complex models due to our limited data set. We modeled survival as a function of sex (SEX) because we suspected of differences between males and females, and monthly air temperature (TEMP) because of ectothermic activity. We also included a model that considered apparent survival as constant over time (.). We tested for a random emigration pattern of movement among individuals ( $\gamma^0 = \gamma^1$ ), meaning individuals move on and off the study area randomly. Conversely, we tested for a first-order Markov process of emigration, where the state of the individual at  $t - 1$  influences the state at  $t$ . For the detection process (capture and recapture probabilities) we tested for a positive effect of body size (snout-vent length, SVL), because larger snakes may be more detectable, monthly air temperature (TEMP), as well as no time variation (.).

We built 64 models representing hypotheses about the effects of the covariates on the parameters running all possible additive combinations of factors to obtain a balanced model set (Doherty et al., 2010). Our most parameterized model (i.e., the global model) assumed that apparent survival, initial capture probability and recapture probabilities were additive functions of temperature and sex, and allowed for Markovian time-constant temporary emigration,

$\Phi(\text{temp}+\text{sex}) \gamma''(\cdot) \gamma'(\cdot) p(\text{temp}+\text{svl}) c(\text{temp}+\text{svl})$ . We did not test for model fit, since the robust design has no standard goodness-of-fit test available. However, based on our experience about snake biology, we think we included important covariates for the parameters and we assume that the follow assumptions - same recapture probability within groups on  $t+1$  and same survival probability within groups on  $t+1$  - were respected.

We selected and ranked models using the principle of parsimony through the Akaike Information Criterion (Akaike, 1973) corrected for small sample sizes (AIC<sub>c</sub>, Burnham and Anderson, 2002). Estimates were model averaged in order to include model uncertainty (Burnham and Anderson, 2002) and all parameters are reported with the 95% unconditional variance confidence intervals. We then calculated the relative importance of each covariate through the cumulative AIC<sub>c</sub> weights (Burnham and Anderson, 2002). Following Berger and Barbieri (2004) we considered covariates with cumulative AIC<sub>c</sub> weight > 0.5 to be important.

## RESULTS

We marked 291 adult individuals (126 males, 165 females) and recaptured 46 of them at least once. In general, models presented similar weights resulting in high uncertainty in model selection (Table 2). Model averaged survival probability was slightly different among years based on temperature, but confidence intervals overlapped (Fig. 2). Air temperature had a marginal positive correlation with survival probability ( $\beta_{\text{temp}} = 0.29$ , CI = -0.04 - 0.62; cumulative AIC<sub>c</sub> weight of 0.50; Table 3). Sex was uncorrelated with survival ( $\beta_{\text{sex}} = 0.69$ , CI = -0.6 - 2.0; cumulative AIC<sub>c</sub> weight of 0.42; Table 3).

Model-averaged estimates suggested a slightly higher probability of being out of the study area (an emigrant) during period  $t$  if the individual was an emigrant during the previous period  $t - 1$  ( $\gamma' \geq \gamma''$ ), but the confidence intervals for these parameters overlapped (Fig. 3), and a random pattern of movement on and off the study area was most supported by the data (Table 2). Still, these estimates suggested there is a high probability that any marked snake may be outside of the sampled transect, and thus unavailable for detection, during a given sampling period.

Conditional on individuals being available for detection, the capture and recapture probabilities were constant and similar for all individuals and sampling occasions (Fig. 4), and therefore behavioral effects on recapturing individuals were not supported (Tables 2, 3). Similarly, air temperature and body size were not important predictors in the detection process, capture and recapture probabilities (Tables 2, 3).

The derived population abundance for the sampling area varied between sampling periods from 80 to 220 individuals (Table 4). From 2002 to 2010 the population showed an average annual finite population growth rate of 1.09 ranging from 0.4 to 2.1 (Fig. 5).

## DISCUSSION

Shine and Charnov (1992) suggested a high survival pattern for viperids, although most previous estimates of survival for other viperids did not account for detection probability (Turner, 1977; Parker and Plummer, 1987; Shine and Charnov, 1992). We found that *B. insularis*' annual adult apparent survival was relatively low, ranging from 0.27 to 0.50, similar to another tropical viper, the African namaqua dwarf adder *Bitis schneideri* (Maritz and Alexander, 2012).



The low annual survival observed here may be best explained by individuals that were captured just once, being outside the study area in the next occasions. Similarly, illegal removal of individuals, suggested by Martins et al. (2008), could cause the same pattern, characterizing permanent emigration, since the estimation of apparent survival makes no distinction between true survival and permanent emigration (Lebreton et al., 1992). Alternatively, if the illegal trade targets the largest individuals of the population, fewer snakes survive long enough to reach higher age classes and thus, the population will present higher proportion of younger snakes (e.g., Prival and Schroff, 2012, study on *Crotalus pricei*). Body size is usually positively related with fecundity in reptiles, including snakes (Seigel and Ford, 1987), and if larger individuals are removed from the population, the average population fecundity could also decrease. Although it has been hypothesized that the study population has declined from the 1990's to the 2000's, our population growth estimates do not support this hypothesis (2002-2010; see below).

Another potential cause to be considered for the low apparent survival is prey availability. As adults, the golden lancehead preys upon usually only two out of 50 migratory birds that are seasonally present on the island (Marques et al., 2012). Food shortages may depend on weather stochasticity and dynamics of migratory bird movement. In contrast to its mainland sister species, *B. jararaca*, the golden lancehead breeds biannually and produces a low number of viable vitellogenic follicles (Marques et al., in press). Such seasonal prey availability may impose a trade off between reproduction and survival.

Temperature slightly positively correlated with survival, an expected pattern since reptile activity usually correlates with weather variability (Gibbons and Semlitsch, 1987). Temperature and other weather covariates such as rainfall may affect age classes of a population in different ways, but the role of weather on age classes of ectothermic population demography is almost

unknown. Altwegg et al. (2005) showed that survival was lower during harsh winters for juvenile asp vipers in Switzerland, but did not affect adults. The ability of finding shelter or the level of body fat reserves may be crucial to determine survival.

Differential activity and behavioral patterns would be expected for males and females with impacts on survival (Gibbons and Semlitsch, 1987). Due to mate search, males move longer distances and may be more exposed to predation (Gibbons and Semlitsch, 1987; Andersson, 1994), while females may present decreased survival after parturition, because of the high amount of energy expended (Madsen and Shine, 1992; Andersson, 1994). Models that allowed for sex-specific differences in apparent survival were not strongly supported by our data (Table 2 and 3), still among models that included this covariate, males had higher apparent survival probabilities than females. This same pattern has been reported in the literature for adult viper populations, such as the asp viper *Vipera aspis* (Altwegg et al., 2005) and non-viper snakes such as the indigo eastern snake *Drymarchon couperi* (Breininger et al., 2012). *Bothrops insularis* may be prey of four raptors on the island (Marques et al., 2012), and juvenile individuals may be more vulnerable. However, if predation is not a strong pressure for the adult population, as suggested by Marques et al. (2002), females would pay a higher final cost to grow and breed than males. Then, this prediction would lead to a higher survival probability for males.

For most snakes, the importance of temporary emigration remains unknown, since no other studies have estimated the probability of temporary emigration (Dorcas and Willson, 2009). Maritz and Alexander (2012) recognized the importance of temporary movement when studying the namaqua dwarf adder and used a simulation method to estimate emigration, but they did not explicitly incorporate the movement probability in the model likelihood or provide a measure of error.

Temporary emigration was high in this study (~ 0.70) showing a high random probability of movement on and off the study area among primary occasions. The randomness of movement demonstrates sampling did not disturb animals. Additionally, this high temporary emigration might result from the small proportion of habitat we sampled, although movement even for sedentary vertebrates, such as pitvipers, is expected at some point. Without accounting for temporary emigration when it exists, the study will suffer with imprecise parameter estimates (Kendal et al., 1997) and investigators should be aware of that. Even if local conditions may difficult the use of alternative sampling designs, such as in the Queimada Grande island (Martins et al., 2008), we recommend hard thinking and planning to account for variability (Thompson, 2004).

Brown et al. (2007) reported trap-shyness in the rattlesnake *Crotalus horridus*, where snakes abandoned their shelters and became less prone to be recaptured. Prival and Schroff (2012) suggested that capture might disturb *C. pricei* individuals. The low detectability (0.05) of the aquatic viperid *Agkistrodon piscivorus* was partly attributed to the capture method used (Durso et al., 2011). Field procedures, such as marking or examining for prey or pregnancy information may reduce subsequent detection probability by means of altering normal activity, home ranges and increasing individual stress levels. Here, behavioral effects were negligible (AICc cumulative weight was 0.40) showing the species may be indifferent to our manipulation. Nonetheless, we are unaware of the effects of marking juveniles. Also, populations may respond differently and thus information on natural history is essential for the use of any marking method.

We did not observe any effect of temperature on detection probability. Since survival was marginally correlated with temperature, the same pattern could be expected for detection. Bovo et al. (2010) found no correlation of postprandial or gravid snakes and thermoregulatory behavior in

*B. insularis*. Snakes on the island are found almost exclusively inside the forest (Martins et al., 2008). Although reptile activity is related to temperature (Pough et al., 2004), the forest might lessen the heat gains and losses, protecting individuals from extreme temperatures and windy conditions of the grassy areas.

Body size did not correlate with detection probability, differently from other snake population studies (Koons et al., 2009; Maritz and Alexander, 2012). Adults may move at similar rates and detection of adult *B. insularis* may be unrelated with body size since they are relatively large (500-800 mm snout-vent length) and pale yellowish to brownish cream. Such traits would reduce heterogeneity in detectability among adult individuals. On the other hand, we are aware that newborns and juveniles are harder to detect because of their small size, potential reduced movement and elusive behavior, which may generate detection probability estimates close to 0 (Christy et al., 2010).

Detection probability only applies to individuals with a non-zero probability of being detected (available to be detected), which lead us to conclude that we did not sight all individuals available. Because of life history traits, snakes are difficult to find in the field, and different studies report relatively variable and low detection probabilities (Altwegg et al., 2005; Lind et al., 2005; Brown et al., 2007; Maritz and Alexander, 2012). *Bothrops insularis* occurs in relatively high densities (Marques et al., 2002) but detection, even with a relatively large and trained search team, was low. Christy et al. (2010) fenced a 5-ha area and obtained a detection probability estimate of 0.07 for the brown tree snake, *Boiga irregularis*. Similarities on habitat (tropical systems) and habit (arboreal) of both snakes, *B. insularis* and *B. irregularis* might preclude low detection since spotting individuals in 3-dimensional habitats could be challenging due to the complex architecture of the forest. Thus, we suggest reducing the studied area to the minimum

acceptable (depending on the species' biology), since detectability might be an inverse function of the size of the study area (Prival and Schroff, 2012), and also increase sampling effort as a strategy to increase detection in future studies.

We estimated that from 80 to 220 adult individuals were available to be captured on each primary occasion in the sampling area. The finite population growth rate of *B. insularis* was also variable among years, but on average we observed a slightly decrease in the abundance ( $\lambda = 0.94$ ) across years. Understanding the elements that contribute for population dynamics may clarify such patterns and reveal trends, allowing for precise management actions. As suggested, prey availability may influence the population growth and individuals in low body condition were seen in the island with certain frequency (pers. obs.). Similarly, weather stochasticity can restrict snake activity, affecting physiological processes and increasing mortality.

Illegal trade and, less importantly, habitat reductions were hypothesized to be the potential causes for *B. insularis* decline from 1995 to 2007 (Martins et al., 2008). However, natural oscillations such as those cited above or detectability issues might mask a real trend (Parker and Plummer, 1987) making the distinction between a real and an apparent decline hard. Such hypothesis decline were based on raw counts made in plots and pointed to a population size of about 2000 individuals (Martins et al., 2008), besides that speculations in a previous study based on counts in the same transect we used here varied from 2000 to 4000 individuals (Marques et al., 2002). Nevertheless, due to the habitat heterogeneity in the island, we believe that extrapolation methods, as used before (Martins et al., 2008), would provide naïve estimates of population size. Regardless of the methods used to estimate *B. insularis* population size before, we should be cautious that severe natural or man-induced oscillations in a potential small population could drive it rapidly to an extinction threshold.

We presented here the first population rates for an endangered Neotropical pitviper. Since snakes are among the least studied vertebrates in relation to population ecology (IUCN, 2012) it will take some time until we reach a good comprehension about Neotropical systems and be able to make good predictions about snake population dynamics in these habitats. Despite the biological difficulties in searching for such an elusive vertebrate, we believe we have taken the first step towards understanding neotropical pitviper populations.

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TABLES

**Table 1.** Date, number of secondary occasions, and air temperature of each of the 10 trips (primary occasions) between 2002 and 2010.

Primary occasion	Date	Secondary occasions	Air temperature <sup>a</sup>	Season <sup>b</sup>
1	Jan/2002	4	26.9	Summer (wet)
2	May/2002	2	22.2	Autumn (dry)
3	Dec/2004	3	27	Spring (wet)
4	Jun/2007	3	20.7	Autumn (dry)
5	Aug/2007	3	17.9	Winter (dry)
6	Mar/2008	3	26.3	Summer (wet)
7	Jul/2008	3	20	Winter (dry)
8	Oct/2009	3	21	Spring wet
9	Jan/2010	2	26.4	Summer (wet)
10	Mar/2010	2	26.2	Summer (wet)

<sup>a</sup> average monthly temperature (°C)

<sup>b</sup> Austral seasons

**Table 2.** Top 15 models of the model results. AICc=Akaike's information criteria with small sample size correction,  $\Delta AICc$ =difference between top model and the current model,  $w_i$ =AICc weights,  $K$ =number of parameters, Deviance=difference of the current model and the saturated model.

Model	AICc	$\Delta AICc$	$w$	$k$	Deviance
$\Phi(\text{temp}) \gamma''(\cdot) p(\cdot)$	1130.34	0.00	0.06	4	1122.22
$\Phi(\text{temp}) \gamma''(\cdot) p(\cdot) c(\cdot)$	1130.91	0.58	0.05	5	1120.74
$\Phi(\cdot) \gamma''(\cdot) \gamma'(\cdot) p(\cdot)$	1130.97	0.63	0.05	4	1122.85
$\Phi(\text{sex+temp}) \gamma''(\cdot) p(\cdot)$	1131.29	0.96	0.04	5	1121.12
$\Phi(\text{sex}) \gamma''(\cdot) \gamma'(\cdot) p(\cdot)$	1131.33	1.00	0.04	5	1121.16
$\Phi(\cdot) \gamma''(\cdot) p(\cdot)$	1131.42	1.09	0.04	3	1125.35
$\Phi(\text{temp}) \gamma''(\cdot) \gamma'(\cdot) p(\cdot)$	1131.70	1.37	0.03	5	1121.53
$\Phi \text{Int} \gamma''(\cdot) \gamma'(\cdot) p(\cdot) c(\cdot)$	1131.86	1.52	0.03	5	1121.68
$\Phi(\text{sex}) \gamma''(\cdot) p(\cdot)$	1131.87	1.54	0.03	4	1123.76
$\Phi(\text{sex+temp}) \gamma''(\cdot) p(\cdot) c(\cdot)$	1131.89	1.55	0.03	6	1119.64
$\Phi(\cdot) \gamma''(\cdot) p(\cdot) c(\cdot)$	1132.02	1.68	0.03	4	1123.90
$\Phi(\text{temp}) \gamma''(\cdot) p(\text{temp})$	1132.27	1.93	0.02	5	1122.09
$\Phi(\text{sex}) \gamma''(\cdot) \gamma'(\cdot) p(\cdot) c(\cdot)$	1132.29	1.95	0.02	6	1120.04
$\Phi(\text{temp}) \gamma''(\cdot) \gamma'(\cdot) p(\cdot) c(\cdot)$	1132.35	2.02	0.02	6	1120.11
$\Phi(\text{temp}) \gamma''(\cdot) p(\text{svl})$	1132.36	2.02	0.02	5	1122.18

**Table 3.** Cumulative AIC<sub>c</sub> weights of the covariates used to model apparent survival probability ( $\Phi$ ), temporary emigration ( $\gamma'$ ,  $\gamma$ ) and detection probability ( $p$ ,  $c$ ).

Variable	Cumulative AIC <sub>c</sub> weight
$\Phi$ (air temperature)	0.50
$\Phi$ (sex)	0.42
$\gamma'$ (markov process)	0.43
$p$ (air temperature)	0.28
$p$ (snout-vent length)	0.27
$c$ (behavioral effect)	0.40

**Table 4.** Model-averaged population estimates within each of the primary occasions. Unconditional standard errors (SE), lower 95% confidence limits (LCI), and upper 95% confidence intervals (UCI) are provided. All values are rounded.

Primary Occasion	Estimate	SE	LCI	UCI
(1) Jan/2002	163	58	50	277
(2) May/2002	80	35	13	149
(3) Dec/2004	165	63	42	288
(4) Jun/2007	116	43	31	202
(5) Aug/2007	122	46	21	212
(6) Mar/2008	88	35	19	156
(7) Jul/2008	138	50	39	273
(8) Oct/2009	109	41	29	190
(9) Jan/2010	220	88	47	393
(10) Mar/2010	88	39	12	163

## FIGURES CAPTIONS

**Figure 1.** Adult female *Bothrops insularis*.

**Figure 2.** Model-averaged apparent annual survival probability for the golden lancehead pitviper, *Bothrops insularis* on each primary occasion (95% confidence intervals are provided).

**Figure 3.** Model-averaged movement probability for the golden lancehead pitviper, *Bothrops insularis*. The probability of being off the study area on occasion  $t$  given it was alive and available for capture on primary occasion  $t - 1$  ( $\gamma''$ ), the probability of being off the study area on occasion  $t$  given it was alive and unavailable for capture on primary occasion  $t - 1$  ( $\gamma'$ ), and 95% confidence intervals are showed.

**Figure 4.** Model-averaged capture probability ( $p$ ) and recapture ( $c$ ) for the golden lancehead pitviper, *Bothrops insularis* during the study period (95% confidence intervals are also shown).

**Figure 5.** Finite population growth rate for the golden lancehead pitviper, *Bothrops insularis*. Each interval represents an estimate between primary occasions  $t$  and  $t+1$ . 95% confidence intervals are also showed.

FIGURES

**Figure 1**



**Figure 2**

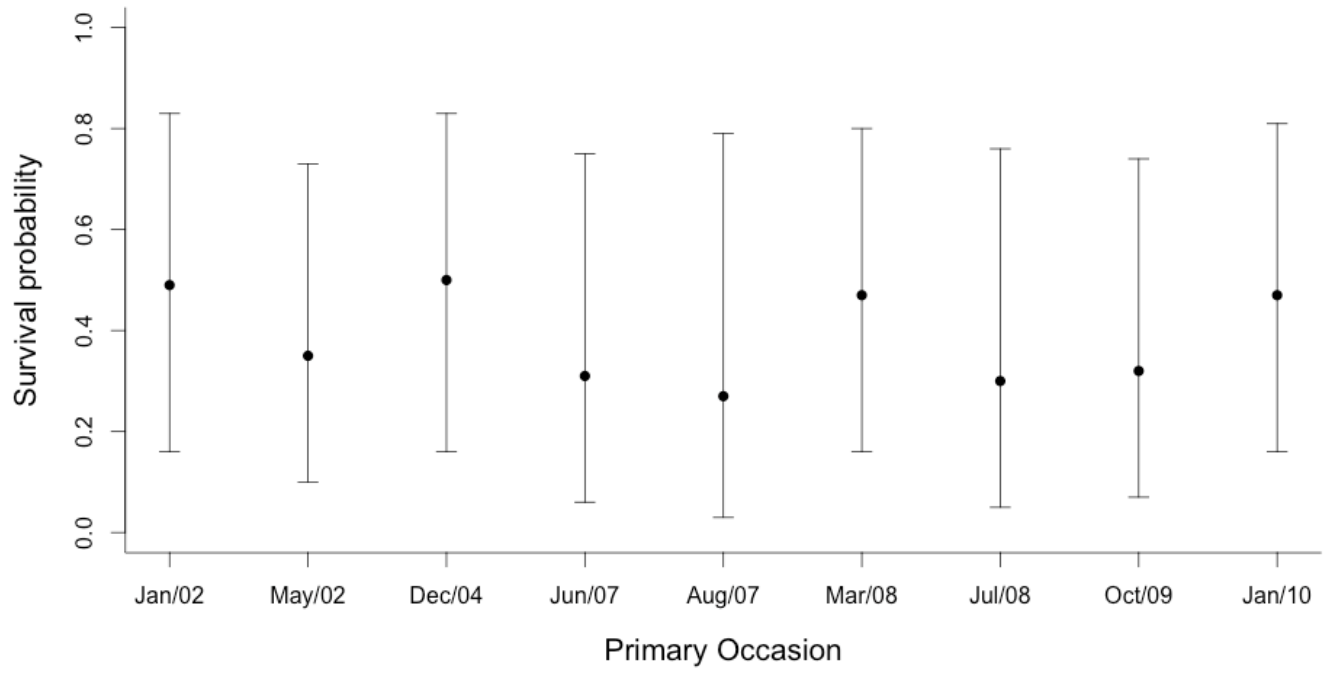
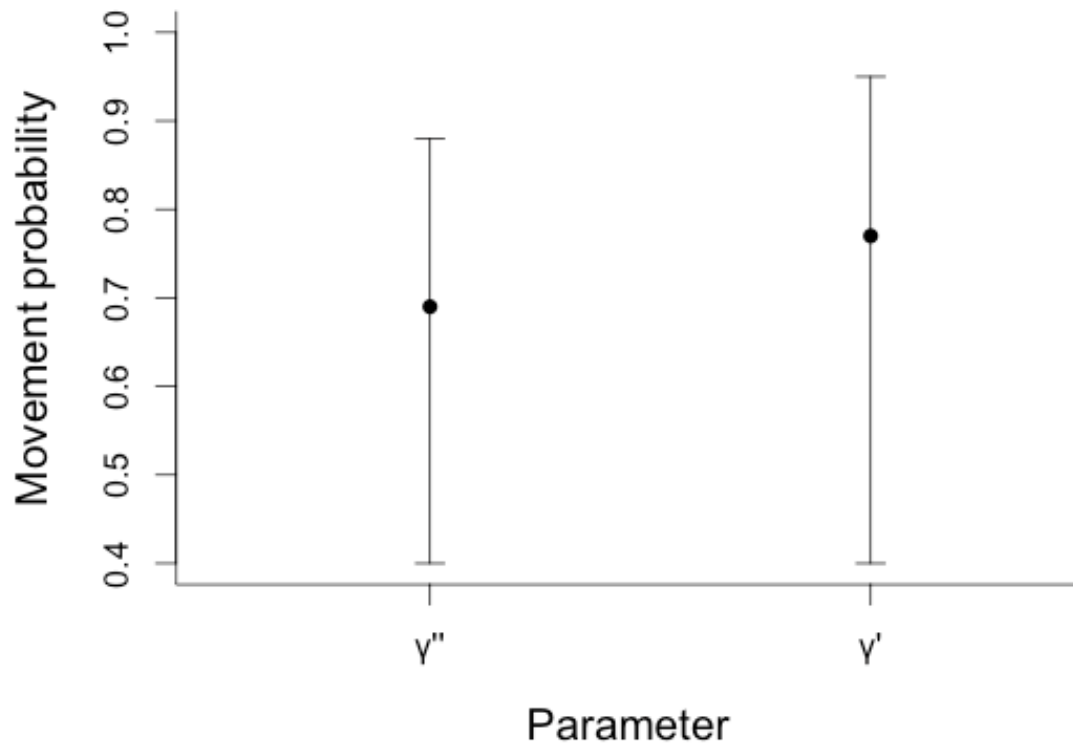
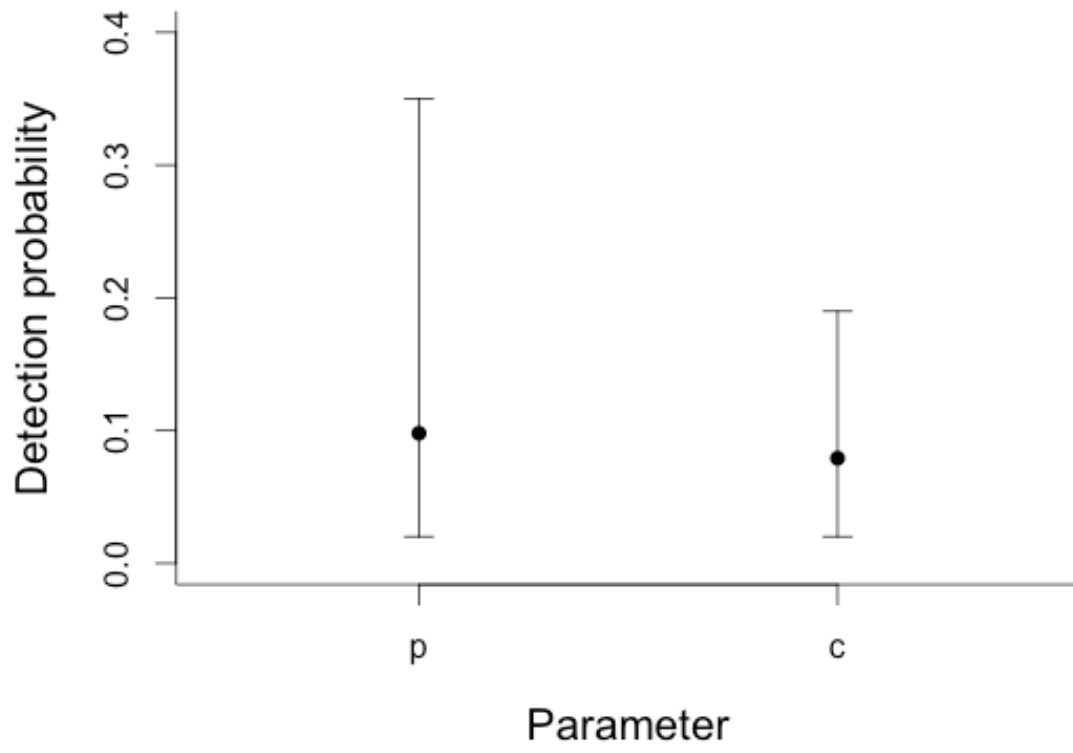


Figure 3

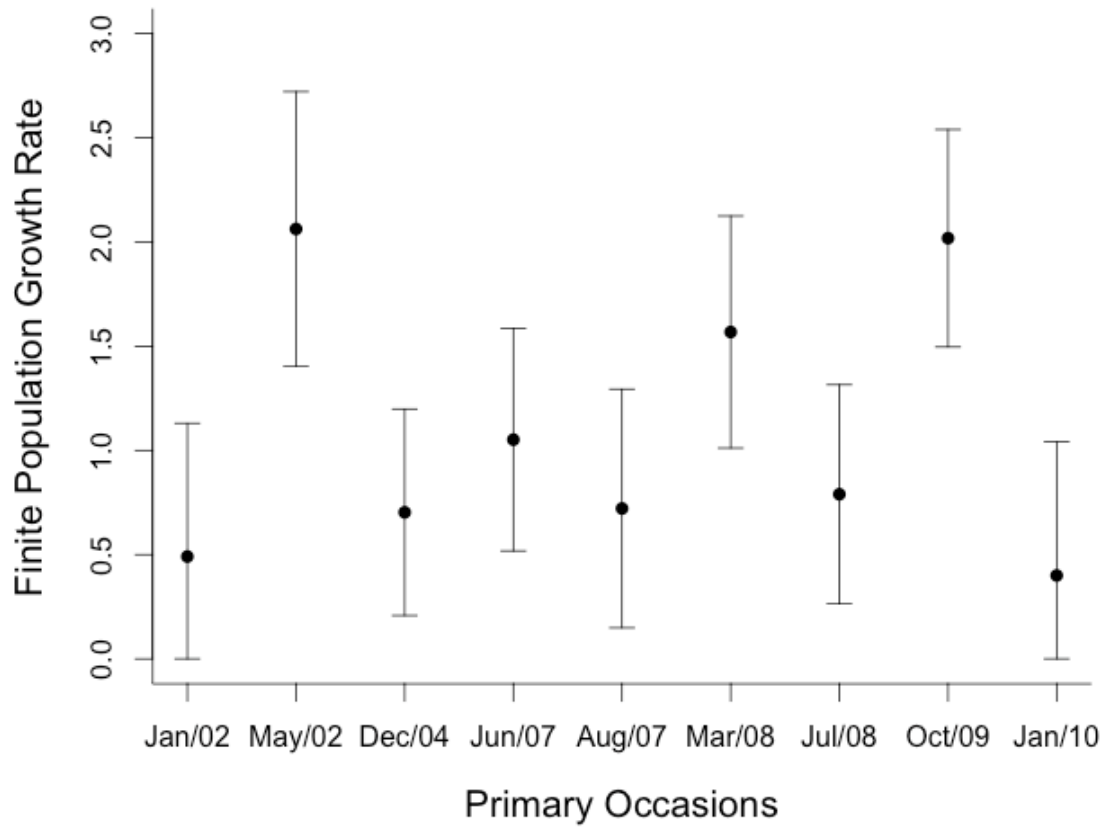




**Figure 4**



**Figure 5**



APPENDIX- Table of all model results. AICc=Akaike's information criteria with small sample size correction,  $\Delta AICc$ =difference between top model and the current model,  $w_i$ =AICc weights,  $K$ =number of parameters, Deviance=difference of the current model and the saturated model.

Model	AICc	$\Delta AICc$	$w_i$	$k$	Deviance
S Int+Gamma" Int+p Int+S temp	1130.34	0.00	0.06	4	1122.22
S Int+Gamma" Int+p Int+S temp+c	1130.91	0.58	0.05	5	1120.74
S Int+Gamma" Int+p Int+Gamma'	1130.97	0.63	0.04	4	1122.85
S Int+Gamma" Int+p Int+S sex+S temp	1131.29	0.96	0.04	5	1121.12
S Int+Gamma" Int+p Int+S sex+Gamma'	1131.33	1.00	0.04	5	1121.16
S Int+Gamma" Int+p Int	1131.42	1.09	0.04	3	1125.35
S Int+Gamma" Int+p Int+S temp+Gamma'	1131.70	1.37	0.03	5	1121.53
S Int+Gamma" Int+p Int+Gamma' +c	1131.86	1.52	0.03	5	1121.68
S Int+Gamma" Int+p Int+S sex	1131.87	1.54	0.03	4	1123.76
S Int+Gamma" Int+p Int+S sex+S temp+c	1131.89	1.55	0.03	6	1119.64
S Int+Gamma" Int+p Int+c	1132.02	1.68	0.03	4	1123.90
S Int+Gamma" Int+p Int+S temp+p temp	1132.27	1.93	0.02	5	1122.09
S Int+Gamma" Int+p Int+S sex+Gamma' +c	1132.29	1.95	0.02	6	1120.04
S Int+Gamma" Int+p Int+S temp+Gamma' +c	1132.35	2.02	0.02	6	1120.11
S Int+Gamma" Int+p Int+S temp+p svl	1132.36	2.02	0.02	5	1122.18
S Int+Gamma" Int+p Int+S sex+c	1132.49	2.15	0.02	5	1122.31
S Int+Gamma" Int+p Int+S sex+S temp+Gamma'	1132.66	2.32	0.02	6	1120.41
S Int+Gamma" Int+p Int+Gamma' +p temp	1132.72	2.38	0.02	5	1122.54
S Int+Gamma" Int+p Int+p temp	1132.92	2.59	0.02	4	1124.81
S Int+Gamma" Int+p Int+S temp+c +p temp	1132.93	2.59	0.02	6	1120.68
S Int+Gamma" Int+p Int+S temp+c +p svl	1132.96	2.63	0.02	6	1120.72
S Int+Gamma" Int+p Int+Gamma' +p svl	1133.01	2.67	0.02	5	1122.83
S Int+Gamma" Int+p Int+S sex+S temp+p svl	1133.03	2.70	0.02	6	1120.78
S Int+Gamma" Int+p Int+S sex+Gamma' +p svl	1133.06	2.73	0.02	6	1120.82
S Int+Gamma" Int+p Int+S sex+Gamma' +p temp	1133.10	2.76	0.02	6	1120.85
S Int+Gamma" Int+p Int+S sex+S temp+p temp	1133.21	2.87	0.01	6	1120.96
S Int+Gamma" Int+p Int+S sex+S temp+Gamma' +c	1133.35	3.01	0.01	7	1119.01
S Int+Gamma" Int+p Int+S sex+p temp	1133.39	3.05	0.01	5	1123.21
S Int+Gamma" Int+p Int+p svl	1133.45	3.11	0.01	4	1125.33
S Int+Gamma" Int+p Int+S sex+p svl	1133.58	3.25	0.01	5	1123.41
S Int+Gamma" Int+p Int+S temp+Gamma' +p temp	1133.65	3.31	0.01	6	1121.40
S Int+Gamma" Int+p Int+S temp+Gamma' +p svl	1133.74	3.40	0.01	6	1121.49
S Int+Gamma" Int+p Int+S sex+S temp+c +p svl	1133.75	3.41	0.01	7	1119.42
S Int+Gamma" Int+p Int+Gamma' +c +p svl	1133.91	3.58	0.01	6	1121.67
S Int+Gamma" Int+p Int+Gamma' +c +p temp	1133.93	3.59	0.01	6	1121.68
S Int+Gamma" Int+p Int+S sex+S temp+c +p temp	1133.94	3.60	0.01	7	1119.61

S Int+Gamma" Int+p Int+c +p temp	1134.05	3.72	0.01	5	1123.88
S Int+Gamma" Int+p Int+c +p svl	1134.07	3.73	0.01	5	1123.89
S Int+Gamma" Int+p Int+S sex+Gamma' +c +p svl	1134.12	3.79	0.01	7	1119.79
S Int+Gamma" Int+p Int+S temp+p temp+p svl	1134.32	3.98	0.01	6	1122.07
S Int+Gamma" Int+p Int+S sex+c +p svl	1134.32	3.98	0.01	6	1122.07
S Int+Gamma" Int+p Int+S sex+Gamma' +c +p temp	1134.37	4.03	0.01	7	1120.04
S Int+Gamma" Int+p Int+S temp+Gamma' +c +p temp	1134.38	4.05	0.01	7	1120.05
S Int+Gamma" Int+p Int+S temp+Gamma' +c +p svl	1134.42	4.08	0.01	7	1120.08
S Int+Gamma" Int+p Int+S sex+S temp+Gamma' +p svl	1134.43	4.09	0.01	7	1120.10
S Int+Gamma" Int+p Int+S sex+c +p temp	1134.53	4.19	0.01	6	1122.28
S Int+Gamma" Int+p Int+S sex+S temp+Gamma' +p temp	1134.58	4.24	0.01	7	1120.25
S Int+Gamma" Int+p Int+Gamma' +p temp+p svl	1134.78	4.44	0.01	6	1122.53
S Int+Gamma" Int+p Int+S sex+Gamma' +p temp+p svl	1134.89	4.55	0.01	7	1120.56
S Int+Gamma" Int+p Int+p temp+p svl	1134.98	4.64	0.01	5	1124.80
S Int+Gamma" Int+p Int+S temp+c +p temp+p svl	1134.99	4.65	0.01	7	1120.66
S Int+Gamma" Int+p Int+S sex+S temp+p temp+p svl	1134.99	4.66	0.01	7	1120.66
S Int+Gamma" Int+p Int+S sex+p temp+p svl	1135.18	4.84	0.01	6	1122.93
S Int+Gamma" Int+p Int+S sex+S temp+Gamma' +c +p svl	1135.22	4.89	0.01	8	1118.80
S Int+Gamma" Int+p Int+S sex+S temp+Gamma' +c +p temp	1135.41	5.07	0.00	8	1118.98
S Int+Gamma" Int+p Int+S temp+Gamma' +p temp+p svl	1135.71	5.37	0.00	7	1121.38
S Int+Gamma" Int+p Int+S sex+S temp+c +p temp+p svl	1135.80	5.47	0.00	8	1119.37
S Int+Gamma" Int+p Int+Gamma' +c +p temp+p svl	1136.00	5.66	0.00	7	1121.67
S Int+Gamma" Int+p Int+c +p temp+p svl	1136.12	5.78	0.00	6	1123.87
S Int+Gamma" Int+p Int+S sex+Gamma' +c +p temp+p svl	1136.22	5.88	0.00	8	1119.79
S Int+Gamma" Int+p Int+S sex+c +p temp+p svl	1136.38	6.05	0.00	7	1122.05
S Int+Gamma" Int+p Int+S sex+S temp+Gamma' +p temp+p svl	1136.39	6.06	0.00	8	1119.97
S Int+Gamma" Int+p Int+S temp+Gamma' +c +p temp+p svl	1136.45	6.12	0.00	8	1120.03
S(sex+temp) Gamma"(. ) Gamma'(. ) p(temp+svl) c(temp+svl)	1137.29	6.95	0.00	9	1118.76
S Int+Gamma" Int+p Int+S sex+S temp+Gamma' +c +p temp+p svl	1137.29	6.95	0.00	9	1118.76

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## CAPÍTULO 4

**WEAPON SIZE, NOT BADGE SIZE, PREDICTS SURVIVAL IN THE WHIPTAIL  
LIZARD, *CNEMIDOPHORUS* CF. *OCELLIFER***

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ABSTRACT. In many lizards, polygyny is the common mating system, and males guard females in order to prevent access of competitors. Males use biting as weapon and display status badges, in these guarding behaviors, presenting potential lower survival because of costs of reproduction. Females, in turn, take advantage of mate guarding presenting higher value as they grow. Here, we applied a mark-recapture study in the whiptail lizard to test for variations in male and female survival with respect to two important attributes for mating, head size and badge size, the latter defined here as the relative amount of bright coloration. Males with larger heads had lower survival than males with smaller heads, whereas female survival increased with head size. Badge size was not associated with survival of either males or females. We hypothesize that males with larger heads may be more vulnerable to sources of mortality, such as predation and fighting for females. On the other hand, females may become more attractive to males as they grow and hence survive better by benefitting from male guarding behavior.

*Key words:* mate guarding, mark-recapture, polygyny, sexual selection, survival probability.

## INTRODUCTION

One of the most striking features of animal species is the frequent difference in morphology, physiology and behavior between males and females known as sexual dimorphism (Andersson, 1994). Different hypotheses have been proposed to explain the occurrence of sexual dimorphism, including sexual selection (Darwin, 1859), which is the evolution of characters that confers advantage to one sex, usually males, in competition for mates (Andersson, 1994; Emlen, 2008). Under sexual selection, female preference may drive male traits to levels of exaggeration that are costly to maintain (Cotton et al., 2004). These traits settle where sexual selection is balanced by natural selection, and under this assumption, a cost for displaying honest signals of quality (Zahavi and Zahavi, 1997) would be expected for males with possible effects on fitness components, such as survival.

Resource defense polygyny is the most common mating system in lizards (Pianka and Vitt, 2003; Calsbeek and Sinervo, 2008), and mate guarding is common in non-territorial lineages, such as the Teiidae family where males, by limiting the chances of other males, mate with females increasing their confidence of paternity (Censky, 1997; Ancona et al., 2010). Sexually dimorphic traits such as head shape and conspicuous coloration, commonly present in lizards, are usually honest signals attributed to reproductive success (Zahavi and Zahavi, 1997; Lopez et al., 2003; Whiting et al., 2003; Molnar et al., 2012).

Head width is a good predictor of dominance in staged encounters because it is influenced by muscle size, which predicts bite force (Herrel et al., 2001; Lappin and Hussak, 2005; Cox et al., 2007). Bite force, a measure of weapon performance, is positively correlated with reproductive output and males may present serious injuries from same-sex aggressive



competition, sometimes resulting in death (Cooper and Vitt, 2002; Lappin and Husak, 2005). Other costs are attributed to mate guarding such as reduced foraging time (Anderson, 1993).

The extent of the body covered by the conspicuous coloration, or badges-of-status size, has been related to dominance, aggressiveness, and mate acquisition in lizards (Pianka and Vitt, 2003; Whiting et al., 2003; Huyghe et al., 2005). On the other hand, nuptial color also brings costs to males (Clutton-Brock and Isvaran, 2007), attracting a predator's attention (Andersson, 1994; Stuart-Fox et al., 2003) exposing individuals to higher mortality, as in the guppy *Poecilia reticulata* (Godin and McDonough, 2003), or because males tend to behave more risky, as in the house sparrow *Passer domesticus* (Reyer et al., 1998). Badges may act as a proxy of male quality and are used to decide conflicts (reviewed in Whiting et al., 2003). Females, in turn, may benefit in the presence of a large male, with increased foraging time, reduction of harassment by single smaller males and lower predation (Anderson, 1994; Zaldívar-Rae and Drummond, 2007).

Although some papers suggest opposite survival estimates for males and females due to sexual selection, survival is usually inferred indirectly using some related measure, such as body condition or number of females in a territory (Sinervo and Lively, 1996). Mark-recapture methods allow for testing hypotheses and making direct inferences about how morphological traits such as weapons and ornaments are associated with vital rates, including survival, while accounting for detection probability (Lebreton et al., 1992).

In this work, we assessed the effects of head size and badge size in adult male and female survival of the teiid whiptail lizard, *Cnemidophorus cf. ocellifer*. We used mark-recapture models to test the hypothesis that males with larger heads and displaying more conspicuous coloration over the body have lower survival than smaller males and females, since the allocation of energy

for these traits and guarding females might have negative consequences to individuals, accumulating with age.

## METHODS

### *Study site*

We conducted the study in Estação Ecológica de Jataí (21°30' S, 21°40' W), a conservation unit in the state of São Paulo, southeastern Brazil. The unit is located in a transitional area between the Atlantic forest and the Cerrado biomes, composed of open grassy areas and semi-deciduous forests. The area is characterized by an average temperature of 11° C in the coldest months (June to August), and 30° C in the hottest months (December to February). Annual rainfall is about 1500 mm, mostly concentrated in the rainy season (CEPAGRI, 2011).

### *Study species*

We tested the proposed hypothesis using mark-recapture methods for a population of the Brazilian whiptail lizard, *Cnemidophorus cf. ocellifer* (Fig. 1). This is a small (30-78 mm snout-vent length in the study population), fast moving, diurnal lizard that occurs throughout Brazil (Mesquita and Colli, 2003). Most species of *Cnemidophorus* are polygynous, with non-territorial behavior, where males compete directly for access to mates and show pre- and post-copulatory female accompaniment (Anderson and Vitt, 1990; Zaldívar-Rae and Drummond, 2007; Ancona et al., 2010). Males prefer larger females because they are able to oviposit a larger number of eggs (Vitt and Breitenbach, 1993). Females, in turn, prolong courtship, inciting contests and providing higher quality males the opportunity to displace pursuing males (Pianka and Vitt, 2003). Sexual dimorphism is present in body morphology (Mesquita and Colli, 2003), with males

having larger heads and more conspicuous coloration (bright green colored spots on flanks and tail).

### *Study design*

We set up a 250x250m trapping grid consisted of 121 pitfall traps. We captured adult males and females for seven consecutive days each month, from September 2010 through September 2011. Traps were opened early in the morning, before the species became active, and closed after the species became inactive, in late evening. We used digital photography as the primary method of individual identification but also batch marked individuals by toe clipping the third joint of the second toe of the right hand. On each capture we recorded weapon size, defined here as head width at the maximum lateral extent of the jaw adductor muscles (to the nearest 0.1 mm), total percentage of colored lateral area (badge size), snout-vent length and mass.

To identify individuals and measure badge size, we took four photographs of each lizard using a digital camera (Nikon Coolpix P6000, Nikon, Tokyo, Japan) that included the following views: dorsum, ventral, right and left flank. Pictures were always taken at the same distance from the lizard, using the macro mode and a circular external flash to standardize for light variation. The dorsum and ventral photographs were later used in the software Interactive Individual Identification System (I<sup>3</sup>S classic version 2.0, Van Tienhoven et al., 2007) for individual recognition.

Flank photographs were used to measure the badge size of the individuals using the software ImageJ (Abramoff et al., 2004). We quantified individual badges by calculating the relative percentage of pixels covered by the conspicuous (green) color over the right flank of individuals (see Olsson et al., 2000), accounting for body size (Berglund et al., 1996). The total

lateral area covered by the badge did not vary among the reproductive and non-reproductive seasons on individuals (data not shown). Badge size may be fixed at birth, implying heritability (Whiting et al., 2003).

Occasionally, we captured males and females together in the same trap during the mating season. Then we compared body size (snout-vent length), relative mass (mass standardized by body size) and head width of these males and females to the rest of male and female population, using t-tests with unequal variances, to check if those individuals were morphologically different from those caught alone - assuming males caught in the traps with females were guarding the respective females. Such comparison provides an opportunity of comparing traits of potential pairing individuals with traits of the whole population. Finally, we recorded minimum temperature and total rainfall during trapping activities as weather covariates because reptile activity, and thus detection probability, might be influenced by weather conditions. For the few occasions when these covariate data were missing (eight individual captures), we used averaged values of the data set.

#### *Survival analysis with imperfect detection*

We used the Cormack-Jolly-Seber model (CJS; Cormack, 1964; Jolly, 1965; Seber, 1965), implemented in program MARK (White and Burnham, 1999), to estimate apparent survival probability ( $\Phi$ ), which is the product of true survival and site fidelity, and recapture probability ( $p$ ) (Lebreton et al., 1992). We pooled the seven capture days each month to form encounter histories. Using these data, we constructed a set of 14 *a priori* models representing different hypotheses about the interaction effects of head size and badge size on male and female

apparent monthly survival probability. We also included a null model with no variation on monthly survival. For the recapture probability we constructed additive and interactive combinations of sex and time, and also included the weather covariates rainfall, minimum temperature, as well as a null model (being constant).

Goodness-of-fit and a variance inflation factor (i.e., median  $\hat{c}$ ) were assessed for our general model excluding individual covariates ( $\Phi_{\text{sex*time}} p_{\text{sex*time}}$ ) since there is currently no goodness-of-fit test for CJS models with individual covariates. Models were selected and ranked based on Akaike Information Criterion adjusted for small sample sizes and corrected for over dispersion (QAICc, Burnham and Anderson, 2002). We considered the model with the smallest QAICc value as the most parsimonious model (Burnham and Anderson, 2002).

## RESULTS

We captured a total of 162 adult males and 159 adult females during the study period. Males presented larger weapons ( $t = 10.19$ ,  $df = 276$ ,  $p < 0.01$ ; Fig. 2) and greater badge sizes ( $t = -27.35$ ,  $df = 284$ ,  $p < 0.01$ ; Fig. 2) than did females. We captured 12 couples together during the reproductive season. Companion males were larger ( $p < 0.01$ ) and heavier ( $p = 0.04$ ) but did not have larger heads ( $p = 0.29$ ) than unaccompanied adult males. Accompanied females were larger ( $p < 0.01$ ), but did not differ in relative mass ( $p = 0.12$ ) and head size ( $p = 0.26$ ) from unaccompanied females.

We adjusted the statistics due to some lack of fit of the general model to our data ( $\hat{c} = 1.13$ ). The top model in our analysis included an interaction effect between sex and weapon size for apparent survival probability (Table 1). Weapon was negatively and positively associated

with survival in males and females, respectively (Fig. 3). The second top model also included an interaction between sex and weapon size on apparent survival probability (Table 1). The third best model had QAICc weight of 0.14 and represents the interaction effect between sex and badge size (Table 1, Fig. 3). In this model survival and badge size were negatively correlated, however, the 95% confidence interval for the estimated interaction included zero ( $\beta_{\text{sex}*\text{color}} = -0.05$ , CI -0.35 to 0.24).

The top model included a time effect in recapture probability (Table 1) and indicated that it varied from 0 to 0.25 for males and from 0 to 0.20 for females (Fig. 4). In general, recapture probability was higher during the breeding season. The difference between the top-ranked model and the second top model was the inclusion of an extra parameter, sex as an additive effect on time, but Qdeviance was very similar suggesting that sex was an unimportant variable (Arnold, 2010). Recapture probability on the third model was again only a function of time.

## DISCUSSION

As expected for polygenic species, males presented larger heads and larger badges than females. When examining the individuals (i.e., pairs) captured together in the traps, males had a larger averaged body size and were heavier than males captured alone. Females captured with males in the traps also had larger body sizes than females captured alone. Larger and heavier males may present advantages because of the higher levels of testosterone and increased aggressiveness towards other males during mate guarding (Andersson, 1994; Zaldívar-Rae and Drummond, 2007). Males in turn, may target better-quality females, i.e., larger and older ones, since reptiles present indeterminate body growth and litter size is positively related to body size (Vitt and Caldwell, 2009).

We noted that the second and the fourth top models presented very similar QDeviance values when compared with the first and third top models, respectively. Structurally, the only difference among these models is the addition of sex as an additive effect to time in the recapture parameter. Although the second and fourth models encompassed 26% of the total variation in the candidate model set, the inclusion of sex did not improve the power of explanation, and consequently, sex should not be interpreted as having an important effect (Arnold, 2010), being considered a “pretending variable” (Anderson, 2008). Disregarding these two models, the top model (*i*) would have a three-fold evidence ratio in relation to the third top model (*j*) ( $QAICc\ weight_i/QAICc\ weight_j$ ), and more than 0.8 of weight.

In an attempt to model the recapture probability with weather covariates, we included rainfall and minimum temperature that are usually associated with reptile activity (Vitt and Caldwell, 2009). However, models containing weather covariates had low QAICc weights,  $w_i < 0.01$ . Time was the only important variable associated with recapture, with higher probabilities of capturing individuals in the breeding season (August to December). Weather variability may not be extreme and other covariates, such as reproductive activity already noticed or prey availability may be more related to recapture probability.

The lower survival of larger-headed males might be linked to the investment in reproduction, resulting in cumulative phenotypic damage over life. Weapons are generally used to defend critical resources, with its benefits usually outweighing potential costs (Andersson, 1994). The competing sex evolves in an intense and directional sexual selection for increased abilities, leading to the evolution of exaggerated structures, such as those seen in scarab beetles or cervid mammals (Emlen, 2008). Game theory predicts that conflicts will only escalate to fights when contestants are about the same size (Emlen, 2008), but individuals are constantly testing

opponents. Thus, despite the larger heads, individuals could often face pursuing rivals that are testing their abilities, and seeking sneaky copulations, which may increase conspicuousness to predators as well (Marler and Moore, 1988). All of these factors might increase energy expenditure and reduce survival.

On the other hand, smaller males may not present enough large and strong heads to win contests. In species where only a few individuals control all mating opportunities sneaky tactics, usually displayed by smaller individuals, are expected to take place (Andersson, 1994). Sneak behavior is known for teiid whiptail lizards, such as *Aspidoscelis costata*, where smaller males do not engage in fights; instead, they access females furtively and try to force copula, running away if the guarding male detects their presence (Zaldívar-Rae and Drummond, 2007). This strategy may ensure higher survival to individuals that present smaller weapons and has no other choice to mate but furtively. However, sneaky males may not sire many offspring. These two different strategies may occur along the male's reproductive life, investing in growth and trying furtive copula when low fighting ability is present (small weapon), and defending females aggressively when large and strong. Large males may sire more offspring, but with higher costs, translated in higher mortality probability (Ancona et al., 2010). This two-phased strategy may not generate a bimodal size of body or head size, because it would be just part of the development of individuals.

Contrary to our predictions, badge size uncorrelated with survival. This result leads us to refute the prediction that mortality increases with larger badges because of predation (Magnhagen, 1991), a pattern already showed for the collared lizard, *Crotaphytus collaris*. Extravagant characteristics such as badges of status are said to reduce longevity (Promislow, 2003; Preston et al., 2011) and leads to immunosuppression (Olsson et al., 2000; Preston et al.,



2011), being negatively correlated with survival. However, our data does not support this prediction and similar results were found for the lacertid lizard, *Psammmodromus algirus*, where testosterone, responsible for the conspicuous coloration, did not preclude body growth and body mass gain (Salvador and Veiga, 2000).

Badges of status are used by females to obtain information about male quality, and also may serve to signaling to other males. Females may choose males based on badges at first place and then expose these males to other competitors (Pianka and Vitt, 2003) in order to test the honesty of signaling (Jonhstone and Norris, 1993). A high risk of injury from fighting larger-headed individuals could be the cost of displaying a dishonest signal. Henningsem and Irschick (2011) experimentally reduced badge size (dewlap) in the anole, *Anolis carolinenses*, and found that smaller badges did not change the outcome of male-male interactions. Bite force, an intrinsically measure of performance, was the main factor to determine the winner in the conflicts.

Larger-headed females in turn presented higher survival. Larger-bodied females may be able to avoid predation, by means of increased experience and escaping behavior, and this holds true for both sexes. However, larger females are preferred as mates (Ancona et al., 2010), and this may reduce mortality through lower harassment (Zuk, 2011), since males generally display risky behaviors, presumably attracting more attention and giving females the opportunity to escape (Censky, 1997). Badges in females were not correlated with survival and their function is not clear. Female ornamentation might be related to resources, suggesting some sort of intrasexual competition (LeBas, 2006) or individual differences in fecundity, suggesting differences in female quality, as demonstrated for the striped plateau lizard *Sceloporus virgatus* (Weiss, 2006)

and for the collared lizard (Baird, 2004). The hypotheses surrounding female ornamentation must be further explored.

In summary, we partially corroborated our hypothesis since larger heads had opposite effects on male and female survival, but conspicuous coloration did not correlate with survival. Larger males, who may invest more in the acquisition of mates, may have reduced life span due to reproductive activity. Females may gain a higher value as they grow, having higher survival probability. Despite the higher mortality in larger males, the costs associated to reproduction might be worth it, with evolutionary advantages for high investment in sexual traits.

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TABLE

**Table 1.** Candidate model set. QAIC<sub>c</sub>=Akaike's information criteria with small sample size correction and corrected for overdispersion, ΔQAIC<sub>c</sub>=difference between top model and the current model, w<sub>i</sub>=QAIC<sub>c</sub> weights, k=number of parameters, QDeviance=difference of the current model and the saturated model.

Model	QAIC <sub>c</sub>	ΔQAIC <sub>c</sub>	w <sub>i</sub>	k	QDeviance
Φ(sex*weapon size) p(time)	579.99	0	0.61	16	546.40
Φ(sex*weapon size) p(sex+time)	582.12	2.13	0.21	17	546.33
Φ(sex*badge size) p(time)	582.97	2.98	0.14	16	549.38
Φ(sex*badge size) p(sex+time)	585.11	5.12	0.05	17	549.32
Φ(sex*weapon size) p(sex*time)	600.45	20.46	0.00	28	539.53
Φ(sex*badge size) p(sex*time)	603.05	23.06	0.00	28	542.13
Φ(sex*weapon size*badge size) p(sex*time)	605.74	25.74	0.00	31	537.67
Φ(sex*weapon size) p(rainfall)	611.45	31.46	0.00	6	599.21
Φ(sex*weapon size) p(mintemp)	613.22	33.23	0.00	6	600.98
Φ(sex*badge size) p(rainfall)	613.82	33.83	0.00	6	601.58
Φ(sex*badge size) p(mintemp)	615.30	35.31	0.00	6	603.06
Φ(.) p(.)	616.99	37.00	0.00	2	612.96
Φ(sex*weapon size) p(sex)	617.63	37.64	0.00	6	605.39
Φ(sex*badge size) p(sex)	620.05	40.06	0.00	6	607.81

## FIGURES CAPTIONS

**Figure 1.** Adult male (upper) and female (lower) *Cnemidophorus cf. ocellifer*.

**Figure 2.** Weapon size (head width) and badge size (percent relative colored area) in adult male and female *Cnemidophorus cf. ocellifer* (inside line = mean value, box = standard deviation, whiskers = minimum and maximum values).

**Figure 3.** Apparent survival probability of adult *Cnemidophorus cf. ocellifer* by head width and badge size (percent relative colored area) in males (upper panels) and females (lower panels). 95% confidence intervals are shown.

**Figure 4.** Monthly recapture probability during the study period based on the top model (time-varying only). 95% confidence intervals are shown

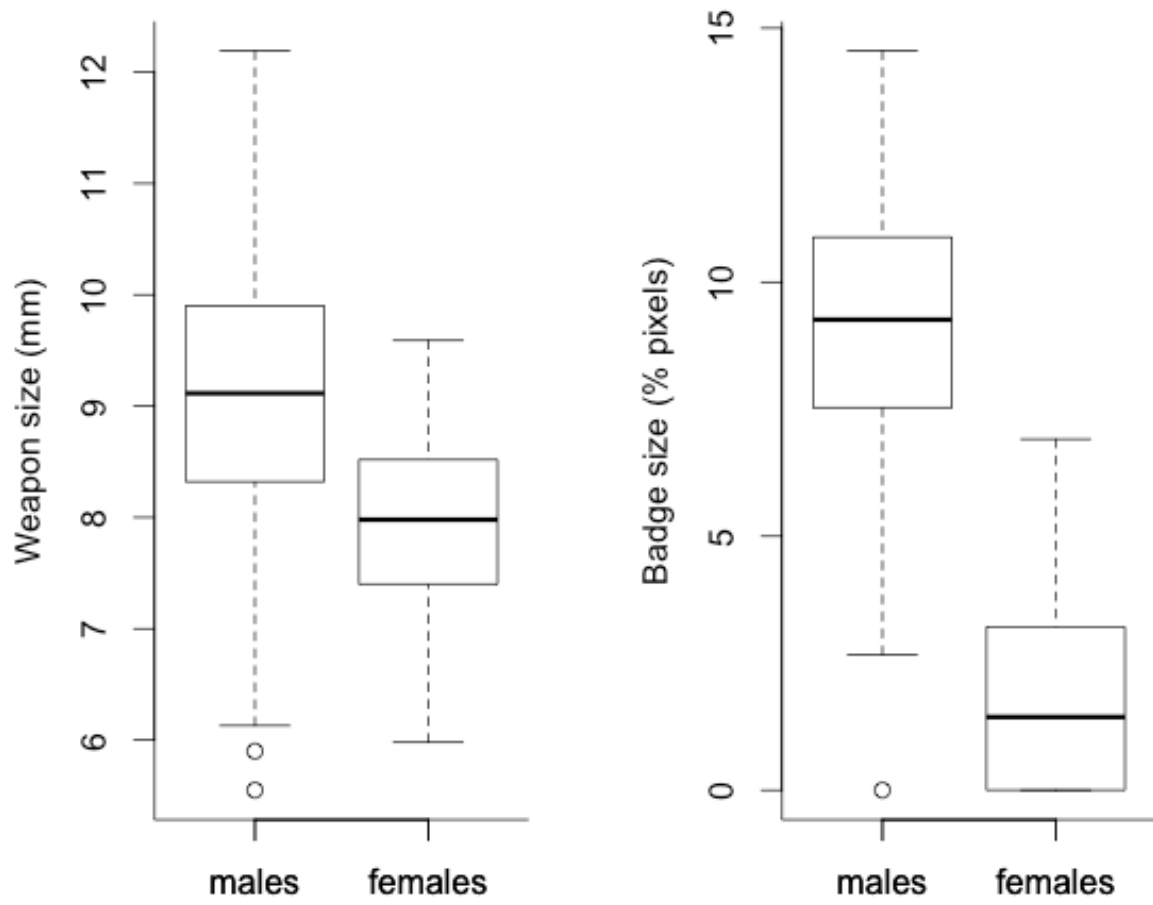


FIGURES

**Figure 1**



**Figure 2**



**Figure 3**

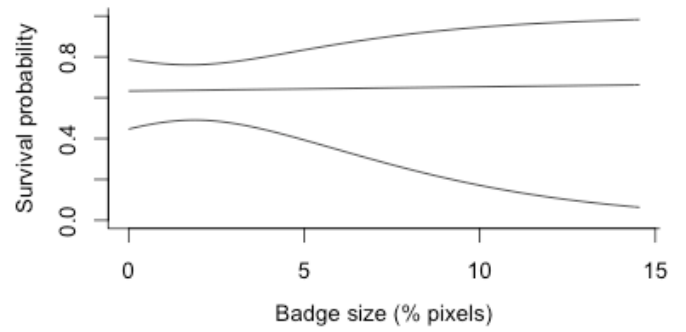
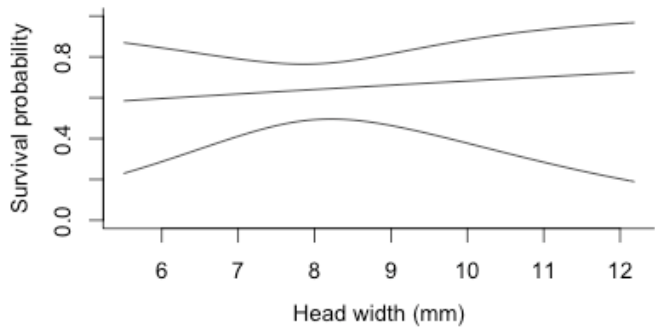
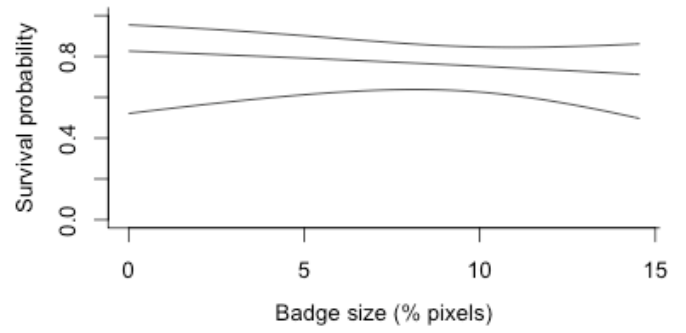
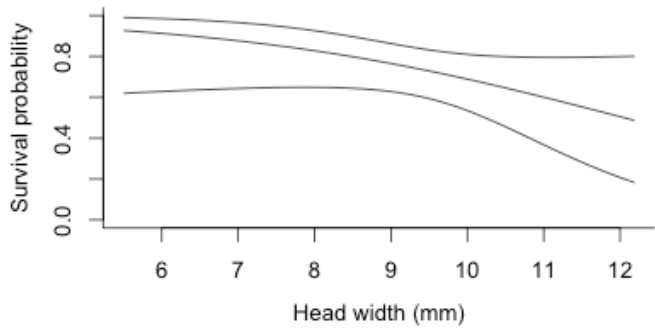
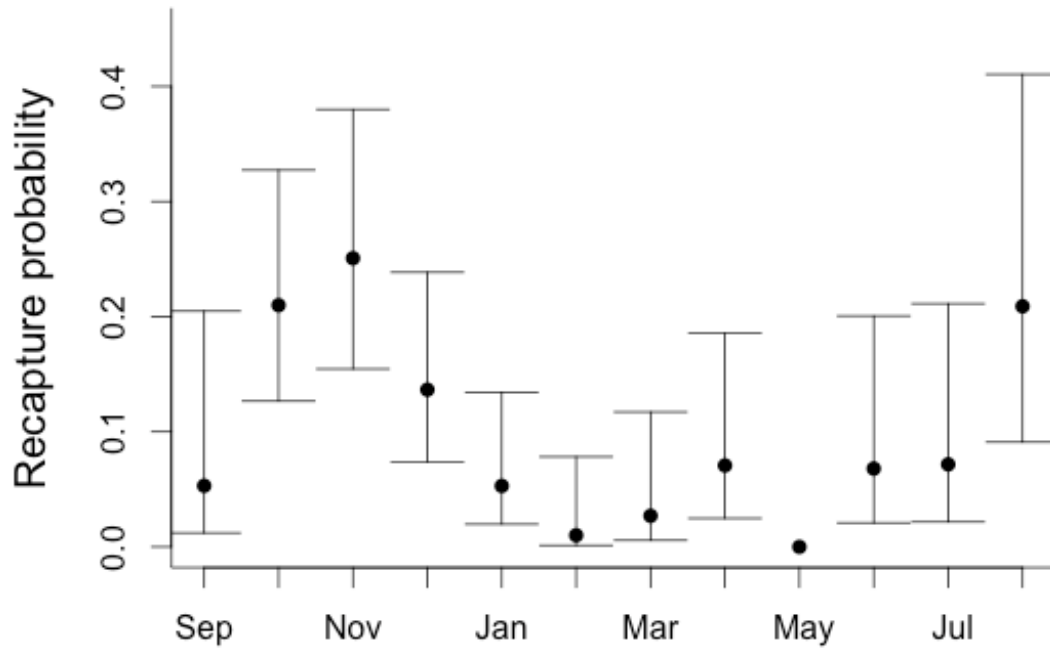


Figure 4



## SÍNTESE

Observamos que a probabilidade de detecção individual nos sistemas estudados foi baixa e condizente com a detecção de vertebrados em ambientes tropicais. O emprego de covariáveis individuais e temporais ajudará a aumentar a precisão das estimativas dos parâmetros vitais, incluindo a probabilidade de detecção.

No capítulo 1, concluímos que as taxas de retorno, índices brutos de sobrevivência, são subestimados em relação as estimativas de sobrevivência que incorporam a detecção imperfeita. Além disso, as estimativas de parâmetros populacionais resultantes do esforço de coleta no campo dependem da detecção.

Recomendamos o emprego da ablação de artelhos em vez da marcação por *microchip* para anfíbios anuros considerando os resultados obtidos, os custos e o tempo envolvidos na aplicação de ambas técnicas. Lembramos que as técnicas de marcação podem ser invasivas e os casos devem ser avaliados individualmente.

*Bothrops insularis* apresentou baixa probabilidade de sobrevivência anual e alta probabilidade de emigração temporária de nossa área de estudo. Detectamos um crescimento anual médio negativo da população adulta, salientando a importância da identificação das causas e do monitoramento da população.

No capítulo 4 observamos que os custos de sobrevivência foram mais elevados em machos adultos com maior tamanho de cabeça e concluímos que estes provavelmente investem mais energia na reprodução. Fêmeas, por sua vez, apresentaram sobrevivência maior conforme o aumento do tamanho da cabeça, e com isso concluímos que elas adquirem maior valor com a idade. Não encontramos relação entre ornamentação e sobrevivência.

Demonstramos aqui a eficiência do método de marcação e recaptura como uma abordagem eficiente na estimativa de parâmetros populacionais e questões relacionadas a história de vida das espécies. Consideramos que um bom desenho amostral deve ser prioritário no planejamento de um estudo pois permitirá captar todas as variações necessárias para responder as questões propostas, além de assegurar uma boa estimativa da probabilidade de detecção para a espécie/população. Caberá ao pesquisador que detêm o conhecimento sobre a história natural do grupo em questão, elevar a probabilidade de detecção, por meio do desenho amostral e esforço de campo, empregando métodos probabilísticos para a estimativa dos parâmetros.