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## Oviposition-site selection by *Phyllomedusa sauvagii* (Anura: Hylidae): An arboreal nester inhabiting arid environments



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### ARTICLE INFO

#### Article history:

Received 24 April 2013

Accepted 5 June 2013

Available online

#### Keywords:

Microhabitat features

Oviposition

Arid Chaco

Phyllomedusa

### ABSTRACT

Breeding biology in *Phyllomedusa sauvagii* is related to vegetation since the species encloses its eggs in leaves above water. Considering that arid environments may represent high risks of death by desiccation for amphibians with this reproductive mode, we evaluated plant characteristics associated with sites used for oviposition in semi-permanent ponds in the Arid Chaco region of Argentina. Plant characteristics were used to fit a statistical habitat selection model that allows the prediction of nest presence. Our results show that *P. sauvagii* needs substrate with specific features for oviposition that would help to reduce the probability of eggs and tadpoles desiccation.

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### 1. Introduction

Oviposition site selection is a type of habitat selection in which parental individuals, usually females, choose potential egg-laying sites depending on abundance and quality in order to maximize their reproductive success (Silva and Giarretta, 2008). Selection of breeding sites has been well documented in pond-breeding amphibians with many studies showing that microhabitat variables such as pond size, water temperature, water depth, vegetation cover, as well as the presence of predators or conspecifics, can influence the use of certain sites for reproduction (Goldberg et al., 2006; Pereyra et al., 2011; Resetarits and Wilbur, 1991). Despite the diversity of anuran reproductive modes and strategies, only a few studies have dealt with oviposition site selection of species that oviposit on vegetation outside water bodies (Kam et al., 1996; Oliveira and Navas, 2004). However, to our knowledge, studies on microhabitat selection of strictly arboreal nesters inhabiting arid environments are nonexistent.

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Arid regions are characterized by a negative water balance and unpredictable environmental stress (Vidal-Abarca et al., 1992). The major challenge faced by amphibians in these environments is evaporative water loss through the skin (Duellman and Trueb, 1986). Moreover, as the gelatinous outer capsule of amphibian eggs is almost completely permeable to water (Duellman and Trueb, 1986; Kam et al., 1998), arid environments may represent high risks of death by desiccation. On the other hand, the larvae of many amphibians are unable to leave the sites selected by their parents if conditions become unfavorable. Hence, there should be a strong selective pressure on the ability of reproducing individuals to discriminate between high and low-quality oviposition sites (Rudolf and Rödel, 2005).

The arboreal breeder *Phyllomedusa sauvagii* (Hylidae) is found along the entire Chaco biogeographical unit and it presents the southernmost distribution of the genus (Frost, 2011). This ecoregion is the second largest in South America, after Amazonia, and includes the largest seasonally dry forests in the continent (Bucher, 1982). Like other members of the Phyllomedusinae subfamily, pairs of *P. sauvagii* make a purse-like nest enclosing its eggs in plant leaves overhanging water (Duellman and Trueb, 1986; Shoemaker et al., 1972). The eggs are surrounded by gelatinous egg-less capsules that would help to protect the eggs from desiccation (Agar, 1909). Once hatched, larvae fall down into water where all the following developmental stages are accomplished until the

metamorphosis (Ceï, 1980). Arboreal microhabitat has been described in some species of the genus, although most of these studies have focused mainly on breeding behavior (Kenny, 1966; Vaira, 2001; Venâncio and Melo-Sampaio, 2010; Wogel et al., 2005).

The reproductive mode of *P. sauvagii*, along with the climatic conditions of the Chaco Arid subregion require that individuals find suitable habitat for offspring development. On this basis, the aim of this study was to identify microhabitat variables associated with the presence of nests of *P. sauvagii* in the Chaco Arid subregion of Argentina. Moreover we want to find out which combination of microhabitat variables are the most important for predicting the presence of nests of this species. We hypothesized that nest presence of *P. sauvagii* would be associated with: (1) substrate morphology: bigger plants with larger foliar area would allow the correct wrapping for the nests; (2) Spatial arrangement: plants closer to the water's edge and with their crowns projected above water would allow the fall of tadpoles once hatched.

## 2. Materials and methods

### 2.1. Study site

The study took place in a 13400 km<sup>2</sup> area situated in the Chacoan plains of northwestern Córdoba province (central Argentina) (longitude 64°34' to 65°46', latitude 29°38' to 31°30'). The area belongs to the Chaco Arid subregion (Morello et al., 1985). Original vegetation consists of a mosaic of open xerophytic forest with an arboreal stratum of 8–10 m dominated by *Aspidosperma quebracho blanco* inside a matrix of secondary forest, degraded scrubs and croplands. Succulent shrubs predominate the saline depressions (Cabido et al., 1992). The climate is subtropical with a mean annual temperature of 19.9 °C. Rainfall is about 450 mm yr<sup>-1</sup> and mainly concentrated in the warm season (Sayago, 1969; Zak and Cabido, 2002).

### 2.2. Field work

Field observations were conducted during two breeding seasons, from December 2009 to March 2010 and from December 2010 to February 2011. During these seasons, we surveyed 12 semi permanent farm ponds with the presence of reproductive activity of *P. sauvagii*. Farm ponds are field depressions used for storing rain water during the humid season and commonly serve as watering holes for cattle. The size of the farm ponds ranged from 450 to 2000 m<sup>2</sup> (mean ± SD = 1237 ± 659.41). Each farm pond was visited at a single occasion per season. During daylight hours, two people searched for nests present on every plant species surrounding each farm pond. Additionally, clutches were collected in order to quantify the number of leaves used for nest construction.

### 2.3. Microhabitat variables

Oviposition site characteristics concerning arboreal microhabitat were recorded including: (1) plant species, (2) plant height (cm), (3) trunk diameter at base height (DBH) (cm), (4) projection of the plants' crown measured as the linear distance from the waters' edge to the most internal branch overhanging the body of water (Projection) (cm), (5) distance from the base of the plant to the water's edge (Dist. Base-water) (cm), and (6) foliar area (cm<sup>2</sup>). Moreover, variables concerning spatial location of nests were also measured: (7) diameter of the branch containing a nest (Branch diam.) (cm), (8) nesting height (Height) (cm) and (9) horizontal distance from each nest to the waters' margin (Dist. margin) (cm). For the latter, we considered the waters' margin as "0". Distances from this point toward the center of the water body were

considered as negative values and those located outside the water were registered as positive.

Foliar area was quantified by analyzing two random samples containing five leaves each, obtained up to a maximum of 2 m height, which corresponds to the maximum vocalization and oviposition height cited for other members of the genus (Freitas et al., 2008; Vaira, 2001). Foliar area was measured using the software Hoja 1.1 (Verga, 2001). For simple leaves we calculated an average value for each plant whereas pinnately compound leaves received a different treatment in which leaflets were considered as the minimum surface area available for the frog to be used as substrate for oviposition. For this, we extracted 10 leaflets from 10 compound leaves and then estimated an average value of leaflet area per leaf. Finally, these values were averaged to obtain the mean foliar area per plant. Additionally, we measured the same arboreal microhabitat variables (variables 2–6) at random unused vegetation points taken from along the perimeter of the same pond.

### 2.4. Statistical analyses

Differences between sites used for oviposition and random unused sites were evaluated including variables 2 to 6 via the nonparametric Mann–Whitney rank sum test. In addition, oviposition site selection model using multiple logistic regressions with random effects was used to analyze the importance of the independent variables thought to be important in predicting the presence of oviposition sites, with the dependent variable being presence/absence of nests. Farm ponds and season were set as random effects and only noncorrelated variables (Pearson's coefficient  $r \leq 0.70$ ) were used in constructing the models. We used an information-theoretic approach (Burnham and Anderson, 2002; Mazerolle, 2006) to evaluate the relative support for the different hypotheses in explaining oviposition-site selection by *P. sauvagii*. First we formulated two a priori candidate models, each representing a biological hypothesis. The first model (substrate morphology model) included two independent variables: DBH and Foliar area. The second model (spatial arrangement model) also included two variables: Projection and Dist. Base-water. Finally, a combination of all variables from the two models were included for the analysis. The Akaike's Information Criterion (AIC) was then calculated to assess the strength of evidence for each model (Mazerolle, 2006). In addition, we calculated the Delta AIC ( $\Delta AIC$ ), which is a measure of each model relative to the best. We also estimated AIC weights ( $\omega_i$ ) which represents the probability that a model is the best in the whole set of candidate models. Another measure of the predictive efficiency of the models was calculated through Nagelkerke's  $R^2$  ( $R^2_N$ ). Statistical analyses were performed using the software InfoStat version 2012 (Di Rienzo et al., 2012).

## 3. Results

*P. sauvagii* used leaves of the following species for nest construction ( $n = 37$ ): *Celtis ehrenbergiana* (51%), *Vallesia glabra* ( $n = 30$ %), *Pithecoctenium cynanchoides* (8%), *Solanum argentinum* (8%) and *Senna* sp. ( $n = 3$ %). Mean number of leaves used were 11 ( $n = 7$  range = 6–14). Values of foliar area were variable ranging from 2.2 to 18.1 cm<sup>2</sup> (mean ± SD = 5.1 ± 2.9). Height of leaf nests reached a minimum of 6, 5 cm and a maximum of 225 cm (mean ± SD = 126.6 ± 68.6). They were placed with a mean distance to water margin of -137 cm (SD = 193 range: -650–74 cm) and on branches with a range diameter of 0.1–1.5 cm (mean ± SD = 0.2 ± 0.2 cm).

All microhabitat variables compared between used and unused sites differed significantly (Table 1). Nests were placed on higher vegetation with bigger DBH values and bigger leaf area. Distance

**Table 1**  
Comparison of arboreal microhabitat characteristics between sites with presence ( $n = 37$ ) and absence ( $n = 73$ ) of nests of *P. sauvagii* in the Arid Chaco. Plant height (cm); DBH: trunk diameter at base height (cm); Projection: projection of the plants' crown (cm); Dist. Base-water: distance from the base of the plant to the water's edge (cm); foliar area ( $\text{cm}^2$ ).

Variables	Nest present		Nest absent		W	p
	Mean $\pm$ SD	Range	Mean $\pm$ SD	Range		
Plant height	379.9 $\pm$ 133.2	25–700	232.16 $\pm$ 156.77	40–600	2739	<0.0001
DBH	31.4 $\pm$ 19.8	0.2–90	9.08 $\pm$ 10.89	0.3–42	2866	<0.0001
Projection	308.8 $\pm$ 237	0–825	27.46 $\pm$ 90.03	0–540	3201	<0.0001
Dist. base-water	103.8 $\pm$ 124.3	0–600	367.55 $\pm$ 268	0–1840	1093	<0.0001
Foliar area	5.1 $\pm$ 2.9	2.2–18	0.75 $\pm$ 1.02	0–4.8	3352	<0.0001

from the base of the plant to water's edge was significantly lower for used sites. Thus, leaf nests were found on plants closer to water, with more of 91% located at distances less than 200 cm from the edge. Likewise, values of crown projection were higher for sites with presence of nests. Most leaf nests were found on vegetation which had their crowns projected above water (Table 1). Moreover, 54% of the nests were registered on trees projected more than 300 cm over the water's edge, whereas only 5.4% of the nests were found on vegetation not projected.

The best model for oviposition included the variables of the substrate morphology model: DBH and foliar area (Table 2) and both variables were positively associated with the probability of oviposition, although foliar area was the only variable having a strong effect on the probability of oviposition, whereas DBH had no effect on it. ( $b_{\text{DBH}} = 1.11$ ,  $SE_{\text{DBH}} = 4.59$ ;  $b_{\text{foliar area}} = 17.35$ ;  $SE_{\text{foliar area}} = 41.2$ ). This model presented a probability of 0.87 of being the best model in explaining the presence of nests of *P. sauvagii* in the farm ponds studied. Alternative models had much lower support than the best model presented (Table 2).

#### 4. Discussion

Females of *P. sauvagii* showed a marked microhabitat selection that may favor the development of eggs and larvae by reducing the risks of desiccation in this arid sector. This behavior, coupled with the presence of gelatinous capsules and leaves enfolding the eggs, are essential to avoid desiccation of the embryos during the nonaquatic phase (Agar, 1909; Pyburn, 1980). Usage of trees and herbs for oviposition is similar to that registered in *Phyllomedusa azurea* (Freitas et al., 2008) and *Phyllomedusa boliviana* (Vaira, 2001). Usage of herbaceous vegetation to a lesser extent by *P. sauvagii* may be explained by the presence of cattle which continuously transit the farm ponds for feeding or drinking water, a situation that may reduce the amount of herbs surrounding the ponds (personal communication).

The average number of leaves per nest was greater than the records for other species of *Phyllomedusa* inhabiting higher rainfall environments such as the tropical forest of Trinidad, the Colombian plains, the Brazilian Cerrado, the subtropical mountain forests of Argentina and Amazonia (Kenny, 1966; Pyburn, 1980; Rodrigues

**Table 2**  
Habitat models obtained for oviposition, ranked according to Akaike's Information Criterion (AIC).  $k$ : number of parameters used in each model;  $\Delta\text{AIC}$ : Differences between AIC of a model and the best AIC.  $\omega_i$ : Akaike's weight of the model;  $R^2\text{N}$ : Nagelkerke's  $R^2$ ; DBH: trunk diameter at base height (cm); Projection: projection of the plants' crown (cm); Dist. Base-water: distance from the base of the plant to the water's edge (cm); foliar area ( $\text{cm}^2$ ).

Rank	Variables	$k$	$\Delta\text{AIC}$	$\omega_i$	$R^2\text{N}$
1	DBH + Foliar area	3	0	0.87	0.96
2	DBH + Foliar area + Projection + Dist. base-water	5	3.76	0.13	0.96
3	Projection + Dist. base-water	3	54.55	0	0.67

et al., 2007; Vaira, 2001; Venâncio and Melo-Sampaio, 2010). In these environments, records reached a maximum of 3 or 4 leaves per nest for *Phyllomedusa trinitatis* and *P. boliviana* (Kenny, 1966; Vaira, 2001), whereas nests constructed with only one leaf were commonly observed in species with smaller clutch sizes (*Phyllomedusa hypochondrialis* and *P. azurea*) (Pyburn, 1980; Rodrigues et al., 2007). This increase in the number of leaves used by *P. sauvagii* for wrapping the eggs can be explained by the high water deficit of the arid Chaco in which plants with small, strongly protected and persistent leaves are commonly present (Díaz et al., 1998). For this reason and because of the large size of its clutch, *P. sauvagii* can be compensating the lack of bigger leaves by incrementing the number of leaves of the plants available. Matos et al. (2000) observed that *P. azurea* used a higher number of leaves in their nests when they were too narrow. The same tendency was reported for *P. sauvagii* in the Cerrado, where the leaves of Asteraceae used for oviposition were of smaller size (Rodrigues et al., 2007). This fact suggests the existence of certain behavioral plasticity that depends on vegetation availability surrounding oviposition sites.

Variables regarding the morphology of the substrate were the most important in explaining the presence of nests, although foliar area appeared to be the only variable having an effect on the probability of oviposition. The use of plants with bigger leaves may again reflect the needs for the correct wrapping of the eggs. Although the spatial position model was less important in explaining nest presence, it is interesting to highlight that most leaf nests were found on vegetation which had their crowns projected above water. Moreover, most nests were placed toward the center of the farm ponds, directly above water. This arrangement may be suitable because it allows developing larvae to fall directly on water. At the same time, it may decrease the likelihood of embryo desiccation by enabling the direct reception of moisture released by the underlying water evaporation.

Our results indicate that *P. sauvagii* makes a nonrandom selection for both, the leaf material which will be used to envelop the egg mass and the plants overhanging standing water, as suggested by Kenny (1966). Thus, nests were placed mainly on trees closer to the farm ponds, with their crowns projected above water and with bigger leaves compared to those of unused sites.

The Chacoan forest of Córdoba province has suffered high rates of forest loss in the order of 2.8% per year<sup>-1</sup> (Zak et al., 2008). Forest degradation, stemming primarily from logging and overgrazing, has led to a simplification in the vertical structure of vegetation and in the diversity of tree species (Cabido and Zak, 1999). The lack of this type of vegetation and the simplification of the forest may have a negative impact on populations and the dynamics of the species by altering the availability of adequate vegetation for reproduction.

#### Acknowledgments

We thank the inhabitants of localities near Chancaní, Los Leones, La Patria, El Medanito, Las Toscas and El Tuscal for allowing us to

conduct research in their properties. We are especially grateful to José Gonzales and his family, Nicolás Maldonado, Nicolás Gutiérrez, Nicolás Flores and Sebastián Riera for their cooperation, kindness and hospitality in the field. The Secretaría de Ambiente de Córdoba allowed us to use the Chancaní provincial park. We also want to thank Silvana Burela and two anonymous reviewers who made valuable comments on the manuscript and María Eugenia Periago for her assistance with the english. JNL has a fellowship from Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET). This work was financially supported by Rufford Small Grant for Nature Conservation and MINCYT – PID 2010 (project n°000113/2011).

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