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# Oviposition Site Selection and Conservation Insights of Two Tree Frogs (*Agalychnis moreletii* and *A. callidryas*)

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**Abstract.** Oviposition site selection directly affects biological fitness and is related to a large number of environmental factors. A conserved trait that constrains oviposition site selection in tree frogs is the laying of clutches in vegetation overhanging water bodies. Some factors that determine oviposition site selection in tree frogs are presence of predators, water temperature, desiccation risk, laying substrate, and the chemical traits of the water body. *Agalychnis moreletii* and *A. callidryas* are widespread throughout Central America, but their populations are declining due to deforestation, presence of pathogens, species smuggling, and changes in rainfall patterns caused by global warming. We studied the oviposition site selection of the aforementioned species in four sympatric sites in southern Mexico. We characterized the vegetation, pond area and depth, temperature, and precipitation of the four sites. Each site was visited three times per week for 4 mo to record clutch development and condition, the number of eggs, substrate species, distance to the pond, and sunlight incidence. We detected a total of 404 clutches of both species in all study sites. We used generalized linear models to explore the differences among sites and determine which variables most affected clutch condition. We found significant differences in vegetation structure and pond area and depth among sites. Oviposition site selection was observed at two different scales, and reproductive success was determined by precipitation, light incidence, and substrate availability. The non-random oviposition site selection suggests that both species rely on primary forest structure for a successful reproduction. This information emphasizes the prominent role of primary forest complexity in the reproductive success of these species.

**Keywords.** Amphibians; Clutch desiccation; Fungal predation; Global site factor; Phyllomedusinae; Reproductive success.

## INTRODUCTION

Oviposition site selection (OSS) is crucial to maintain demographic processes in oviparous species because it has a direct effect on their reproductive success (Resetarits, 1996; Refsnider and Janzen, 2010; Abbott and Dukas, 2016), which, in turn, is critical for threatened species. For amphibians in particular, knowledge of the OSS process is fundamental to develop successful, long-term conservation and management plans (Semlitsch, 2002).

Generally, reproduction is an energetically demanding process (Reznick et al., 2000) that can involve the acquisition and storage of resources for gamete production and maturation (Glazier, 2000; Reznick et al., 2000), mate selection (Watson et al., 1998; Gavrillets et al., 2001), territory and hatchling defense (Márquez-Luna et al., 2015), and OSS (Santos et al., 2010). OSS is considered to be critical for individual fitness and under intense selection pressures (Refsnider and Janzen, 2010); however, although OSS is under strong selection, it is highly dependent on environmental conditions (which can be highly variable

within and among years due to natural or induced factors) selecting for high phenotypic plasticity (Höbel, 2008). Therefore, OSS is a behavioral life history trait that varies widely within and among species (Resetarits, 1996; Madsen and Shine, 1999). Several non-mutually exclusive hypotheses have been proposed to explain why there is strong selection for oviposition site, including (1) to maximize embryo survival, (2) to maximize parental survival, (3) to modify offspring phenotype, (4) to provide suitable resources for offspring, (5) to maintain philopatry, and (6) as an indirect consequence of mate choice (Refsnider and Janzen, 2010). However, each hypothesis might involve several environmental factors that influence OSS (Refsnider and Janzen, 2010).

Among oviparous fishes and amphibians, reproduction is particularly complex because oviposition sites must be appropriate for external fertilization (Browne et al., 2015), embryonic development, hatching, and larval development (Bowcock et al., 2009). Furthermore, most amphibian life cycles have developmental stages that occur under highly divergent environmental condi-

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tions (e.g., aquatic egg and tadpole in water, terrestrial post-metamorphs; McDiarmid and Altig, 1999). These dissimilar conditions might act as differential selective pressures, but most amphibians have a strong dependence on water bodies. Hence, environmental humidity, precipitation, and unpolluted water bodies are critical to amphibian reproduction and development in order to maintain their populations (McDiarmid and Altig, 1999; Wells, 2010).

Offspring survival, which is closely related to suitable conditions for development, can be affected by several selective pressures that can act simultaneously on OSS, such as presence and abundance of predators, conspecific occurrence, temperature, and desiccation risk (Resetarits and Wilbur, 1989; Egan and Paton, 2004; Vredenburg, 2004). Specifically in hylid tree frogs, laying clutches on vegetation or surfaces overhanging water bodies is considered a relatively well-conserved trait that can be driven by phylogenetic inertia and also constrain OSS (Wells, 2010). However, the main factors identified in hylid OSS are tadpole predator presence, water temperature, desiccation risk, substrate, and water chemistry (Haramura, 2008; Doody, et al., 2009; Székely et al., 2010; Vilela et al., 2015; Mageski et al., 2016).

Evidence on the effect of predator presence is mixed. Some studies have shown that individuals select sites with conspecific egg clutches or tadpoles (Vaira, 2001; Abrunhosa and Wogel, 2004; Wogel et al., 2006; Doody et al., 2009), whereas other studies have shown that adults avoid laying clutches where conspecific tadpoles species occur to decrease competition or predation (cannibalism; Crump, 1983; Schiesari et al., 2003; Alves-Silva and da Silva, 2009). Water temperature affects growth rate and, ultimately, metamorph phenotype, leading adults to search for suitable sites for larval development (van Buskirk and Arioli, 2005; Székely et al., 2010; Tejedo et al., 2010). The effects of desiccation on hatchling survival are closely related to two non-exclusive selective forces, with desiccation risk being higher in ephemeral ponds, but risk of predation being higher in permanent ponds. Therefore, a trade-off between desiccation risk and predation risk is expected (Touchon and Warkentin, 2008; Touchon, 2012; Touchon and Worley, 2015; Cunha and Napoli, 2016; Mageski et al., 2016). The specific substrates on which the eggs are laid can affect clutch oxygenation, predator avoidance (Warkentin, 1995; Warkentin, 2000; Vonesh and Warkentin, 2006), desiccation risk (Dias et al., 2014; Vilela et al., 2015; Cunha and Napoli, 2016; Mageski et al., 2016), and chemical properties of the pond (when fallen leaves contain high concentrations of tannins or other compounds; Palen et al., 2005; Haramura, 2008).

Other important factors that affect the reproductive success of tree frogs are vegetation cover, height above the ponds where clutches are laid (Dias et al., 2014), and the specific substrate (Touchon and Warkentin, 2008;

Touchon, 2012; Dias et al., 2014; Touchon and Worley, 2015; Vilela et al., 2015), which are associated with high temperature avoidance (Touchon, 2012). However, there are few studies that consider more than one selective force on OSS, which prevents us from fully understanding if any process has a higher influence on this critical life history trait and from proposing good strategies for tree frog conservation.

Determining the factors involved in OSS in amphibians might be critical for threatened, geographically restricted, and rare species. This information can generate new proposals for population management and habitat conservation or restoration. Particularly, in the IUCN Red List (IUCN, 2017), amphibians have the highest number of species under a risk category among the vertebrates (32.4%), and several species are listed as data deficient (24%). Moreover, 173 species are listed in the Convention on International Trade of Endangered Species due to the risk associated with international pet trade (CITES, 2017). The humid-forests of northern Mesoamerica are recognized as a biodiversity reservoir for amphibians (Brooks et al., 2002; Lips et al., 2005; Pineda and Lobo, 2008) where more than 105 threatened species occur (Olivet and Asquith, 2004).

In the present study, we studied two species of tree frogs. The black-eyed tree frog (*Agalychnis moreletii* Duméril, 1853) is a critically endangered species (IUCN, 2017) that ranges from Mexico to Honduras; its populations have recently been reported as declining (Lawson et al., 2011). Red-eyed tree frogs (*Agalychnis callidryas* [Cope, 1862]) are listed as least concern, occurring from Mexico to Colombia. Nevertheless, their populations are also considered to be declining at a high rate (IUCN, 2017).

The main threats to these species are habitat loss, habitat degradation, the pathogenic fungus *Batrachochytrium dendrobatidis* (Bd; Longcore et al., 1999; although *Agalychnis callidryas* shows resistance to Bd infection due to gene expression inhibiting inflammatory processes and activating skin integrity processes; Ellison et al., 2015), and poaching for the illegal exotic pet trade; these are the most important factors contributing to the decline of their populations (Urbina-Cardona and Loyola, 2008). Both species co-occur along most of their distribution (Mexico, Guatemala, Belize, El Salvador, and Honduras; although *A. callidryas* has a wider distribution, from central Mexico to northern Colombia) and they are closely related; this may provide insights on similarities of factors associated with reproductive success (Duellman et al., 2016).

In this study, we analyzed OSS in *Agalychnis moreletii* and *A. callidryas* and its relationship with reproductive success in four sites with different vegetation structures, total light incidence, water body depth and area, and environmental temperature and humidity in order to identify the factors that are critical to both process.



**Table 1.** Study site locations and general characteristics.

Site	Geographic coordinates	Elevation (m)	Dominant vegetal species	Water body type	Predatory fish	Area (m <sup>2</sup> )	Distance to Site 1 (m)
1	16°57'48"N, 91°35'20"W	870	<i>Ficus</i> sp. <i>Ocotea</i> sp.	Permanent	Present	2,343	-
2	16°59'41"N, 91°35'44"W	837	<i>Eugenia</i> sp.	Ephemeral	Absent	1,717	3,523
3	16°58'23"N, 91°33'32"W	1,023	<i>Eugenia</i> sp. <i>Terminalia</i> sp.	Ephemeral	Absent	1,837	3,358
4	16°58'08"N, 91°35'10"W	919	<i>Inga</i> sp. <i>Ficus</i> sp.	Ephemeral	Absent	2,453	672

## MATERIALS AND METHODS

Our study was conducted in the Neotropical Natural Protected Area of Nahá, located in the Lacandona region of southern Mexico. The area consists of primary forests with a complex transitional vegetation structure between tropical rain forest and temperate cloud forest. Climate is tropical, wet, and humid with mild temperatures and a well-defined dry season (CONANP, 2006). We delimited four permanent plots around body waters or wetlands that differed in abundance of *Agalychnis moreletii* and *A. callidryas* (Fig. 1; Table 1).

## Study species

*Agalychnis moreletii* (Duméril, 1853) and *A. callidryas* (Cope, 1862) are species of Phyllomedusinae Günther, 1858, Hylidae Rafinesque, 1815 (Faivovich et al., 2010; for an alternative arrangement, see Duellman et al., 2016). Coloration varies from light to dark green depending on light conditions and activity patterns. Sometimes, the dorsal surface has white dots. The main difference between the species is observed in ventral (orange in *A. moreletii*; yellowish in *A. callidryas*) and flank (plain green in *A. moreletii*; green, yellow, and blue with white stripes in *A. callidryas*) coloration. Dur-

**Figure 1.** Representative images of each plot of the study region.



ing the dry season and daylight hours of the reproductive season, frogs seek shaded areas in the canopy (Duellman, 2001). Males congregate on vegetation over ponds and vocalize to attract females. Both species usually lay eggs on vegetation overhanging ponds (egg clutches are apparently indistinguishable in both species; Pyburn, 1970; Warkentin et al., 2001). Seven to ten days later, hatchlings fall into the water bodies, although there may be differences if mechanical disturbances occur (Warkentin 1995; Cohen et al., 2016; Warkentin et al., 2017). The mean snout–vent length (SVL) for *A. moreletii* is 65.7 mm for males and 82.9 mm for females (Köhler, 2011), whereas for *A. callidryas* it is 59 mm for males and 77 mm for females (Savage, 2002).

### Habitat characterization

The habitat characterization is based on a detailed description of the vegetation structure and water bodies of the four sites. Each site was characterized in terms of vegetation inside and outside of the flooded area. In particular, plant species were identified to genus, and their coverage and total height were measured to obtain canopy volume. To collect data, we used three circular plots, each consisting of a circle 5 m in diameter centered within a circle 10 m in diameter. From the outer circle, we measured tree total height, canopy coverage (from two perpendicular measurements), and minimum leaf height for every individual more than 10 cm diameter at 1.5 m above the ground). From the smaller circle, we took the same data for every individual shrub less than 10 cm of diameter at 1.5 m above the ground. Using both measurements, we calculated the canopy volume for trees and shrubs. Furthermore, we characterized light incidence using the global site factor (GSF; Anderson, 1964) with hemispherical photographs taken every 5 m (Canon 5D with a Sigma 4.5 mm lens, mode P, AF) at 1 m above the ground and north-oriented along two perpendicular 50 m transects covering most of the flooded area. GSF is the proportion of the global solar radiation light that is available and can take values from 0 (no light is available) to 1 (all of global solar radiation light is available). GSF was estimated using HemiView v.2.1 (Delta-T Devices, 1998) following the methods described in Halverston et al. (2003). We also measured pond area and depth weekly during the reproductive season (26 July–29 September 2016) as a measure of water availability of each site. We recorded precipitation every day at 09:00 with a graduated cylinder and temperature using a data logger (HOBO UA-001-64; measurements taken every 15 min) during the study.

### Oviposition site selection

We visited the study sites every 3 d between 26 July and 29 September 2016 to search for clutches of *Agalychnis*

*moreletii* and *A. callidryas*. For each clutch, we recorded the following data: number of eggs (validated through digital photographs), type of substrate on which the eggs were laid (leaf, roots, epiphytes, soil, branches), plant genus (when possible), the minimum linear distance to the pond (from the nearest portion of the pond to the clutch, considering that some clutches directly over the water body and others were not), light availability (measured by GSF using hemispherical photography next to the clutch and the same parameters described above), and status of eggs within each clutch (predated, desiccated, undeveloped, viable). For viable clutches, we differentiated between eggs that reached the tadpole stage and hatched but were not above water (hatched) and those that hatched over water (successful).

### Statistical analysis

Data are summarized as  $\bar{x} \pm SD$ . To explore differences in the physical and biological attributes between the sites, we constructed generalized linear models (GLM) with the Poisson distribution and log link function using the R program (R Core Team, 2017) and the RStudio (RStudio team, 2016) code editor. To evaluate the relationship between the response variables (OSS and reproductive success) and the environmental traits, we also used GLMs in a multi-model perspective (Burnham and Anderson, 2002), selecting the best fitting model using the Akaike information criterion (AIC; Akaike, 1973). We tested 92 models using the following five dependent variables: total egg number (TEN), number of hatched tadpoles (NHT), number of successful tadpoles (NST), number of desiccated eggs (NDE), and number of predated eggs by fungus or bacteria (NPE)—and eight independent variables—distance to the pond (D), area of the pond (A) and depth of the pond (DE) measured weekly, mean precipitation of five preceding days of hatching (S), and mean temperature precipitation of five preceding days of hatching (T), total light incidence measured with GSF—and two categorical variables—substrate (SC) and substrate species (SS). For each dependent variable, we fitted a simple model for each independent variable and for all possible second and third degree additive models (we did not test for fourth degree and further models as over-parametrizing models with non-informative variables did not improve their fit; Table S1). Considering that all dependent variables consisted on counts, we used a negative binomial distribution with the “logit” link function (RStudio, MASS package; Venables and Ripley, 2002), because the Poisson distribution has been proven to increase type II error (Gardner, 1995; Lindén, 2011). To explore more carefully the processes affecting clutches, we tested the effect of each independent variable mentioned above on the number of eggs affected by

desiccation and fungus predation (as these factors were the most common affecting egg survival). As both dependent variables consisted on counts, we used the same distribution and link function for GLMs as described above.

## RESULTS

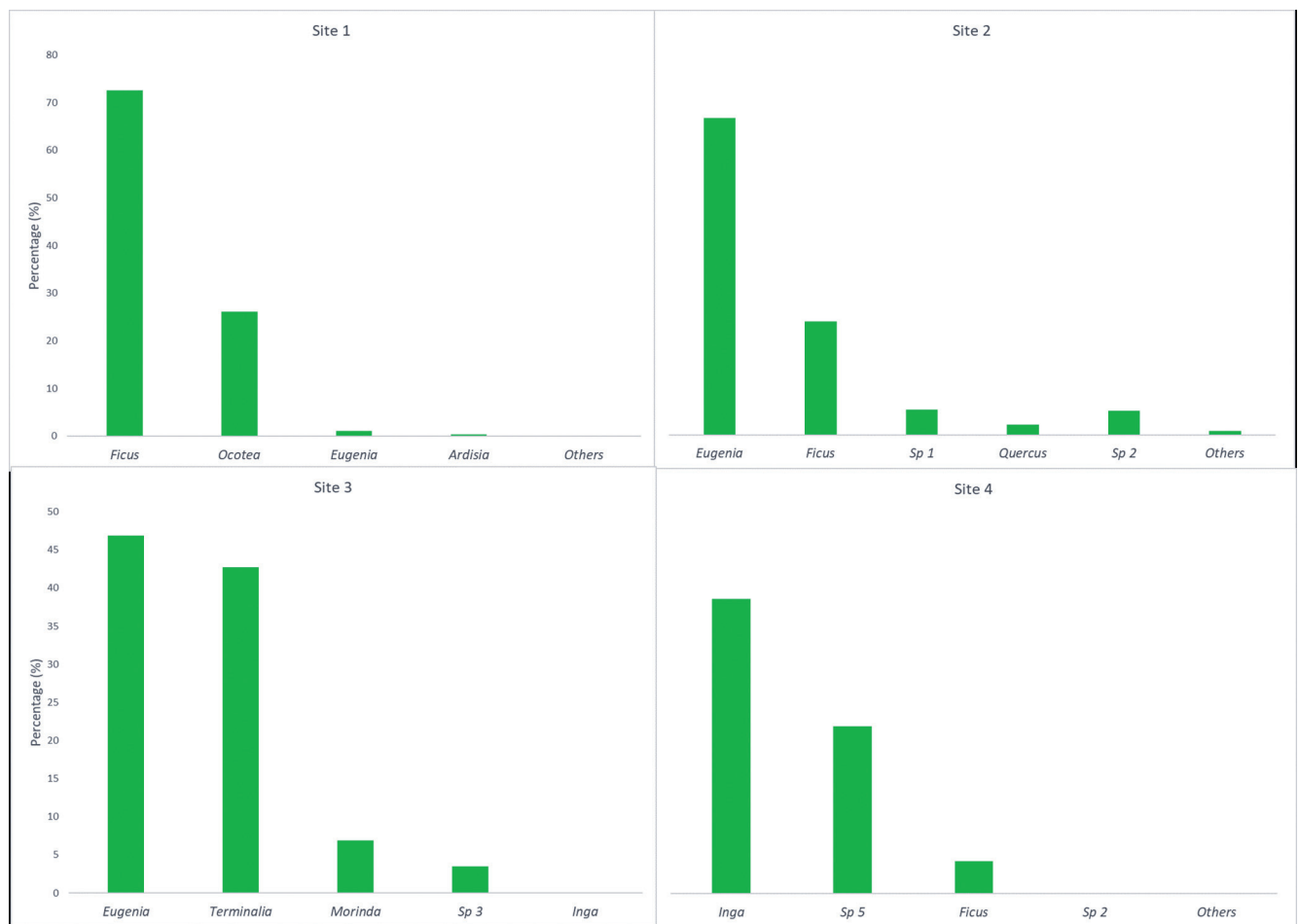
### Habitat characterization

For each site, the volume of canopy vegetation describes the availability of oviposition sites between vertical and horizontal structure. We found significant differences in canopy volume among sites ( $F = 7.77$ ,  $df = 205$ ,  $P < 0.01$ ), particularly between sites 1 and 2 ( $P < 0.01$ ), 1 and 3 ( $P < 0.01$ ), 2–4 ( $P = 0.04$ ), and 3 and 4 ( $P = 0.02$ ; Fig. 2). Nevertheless, vegetation structure heterogeneity was higher at site 4 than at site 1. The mean total light incidence among sites was  $0.33 \pm 0.15$  (0.12–0.88;  $n = 80$ ), and we did not find significant differences among sites. The area and depth of each site pond varied among sites ( $H = 48.87$ ,  $df = 3$ ,  $P < 0.01$ ;  $H = 47.94$ ,  $df = 3$ ,  $P < 0.01$ ;

respectively). For pond area, there were significant differences between sites 1 and 3 ( $P < 0.01$ ), 1 and 4 ( $P < 0.01$ ), 2 and 3 ( $P < 0.01$ ), 2 and 4 ( $P < 0.01$ ), and 3–4 ( $P = 0.02$ ). For pond depth, sites 1 and 2 ( $P < 0.01$ ), 1 and 3 ( $P < 0.02$ ), 1 and 4 ( $P < 0.01$ ), 2 and 3 ( $P < 0.01$ ), and 3 and 4 ( $P < 0.01$ ) were significantly different.

### Oviposition site selection

We found a total of 404 clutches for all study sites for both species, mostly at site 4 (94.8%). The total number of eggs considering all clutches and all sites was 22,626, each clutch having on average  $57.13 \pm 33.69$  eggs (12–297 eggs;  $n = 396$ ). Clutches were most commonly found on leaves of *Inga* sp. (48%), *Eugenia* sp. (3.5%), *Ficus* sp. (3%), *Terminalia* sp. (3%), several unidentified epiphytic species (14%), and other structures like branches, trunks, lianas, and roots (27%; Fig. 3B, C). Most clutches (91.75%) were affected by more than one factor; however, in most cases, these effects were partial (only on some eggs). The main factors affecting clutches were desiccation (42.5%) and predation (32%), but we also recorded unviable clutches



**Figure 2.** Histograms of canopy percentage per plant genus of each site.

(11%) and fallen leaves with clutches (6%). The mean clutch–pond distance was  $1.68 \pm 1.23$  m (0–12.5 m;  $n = 404$ ). The number of clutches fluctuated over the rainy season and was closely associated with rainfall, with four peaks of clutches observed (more than 29) following heavy rains (Fig. 3). The average total light for clutches was  $0.21 \pm 0.07$  GSF (0.04–0.53 GSF;  $n = 380$ ). The average temperature for clutches was  $21.75 \pm 0.62^\circ\text{C}$  (20.52–23.61°C;  $n = 383$ ). From the total number of eggs, only 40.6% (9,201 eggs) developed to tadpole stage; however, only 8.2% (1,870) of all tadpoles were successful (i.e., hatched over water).

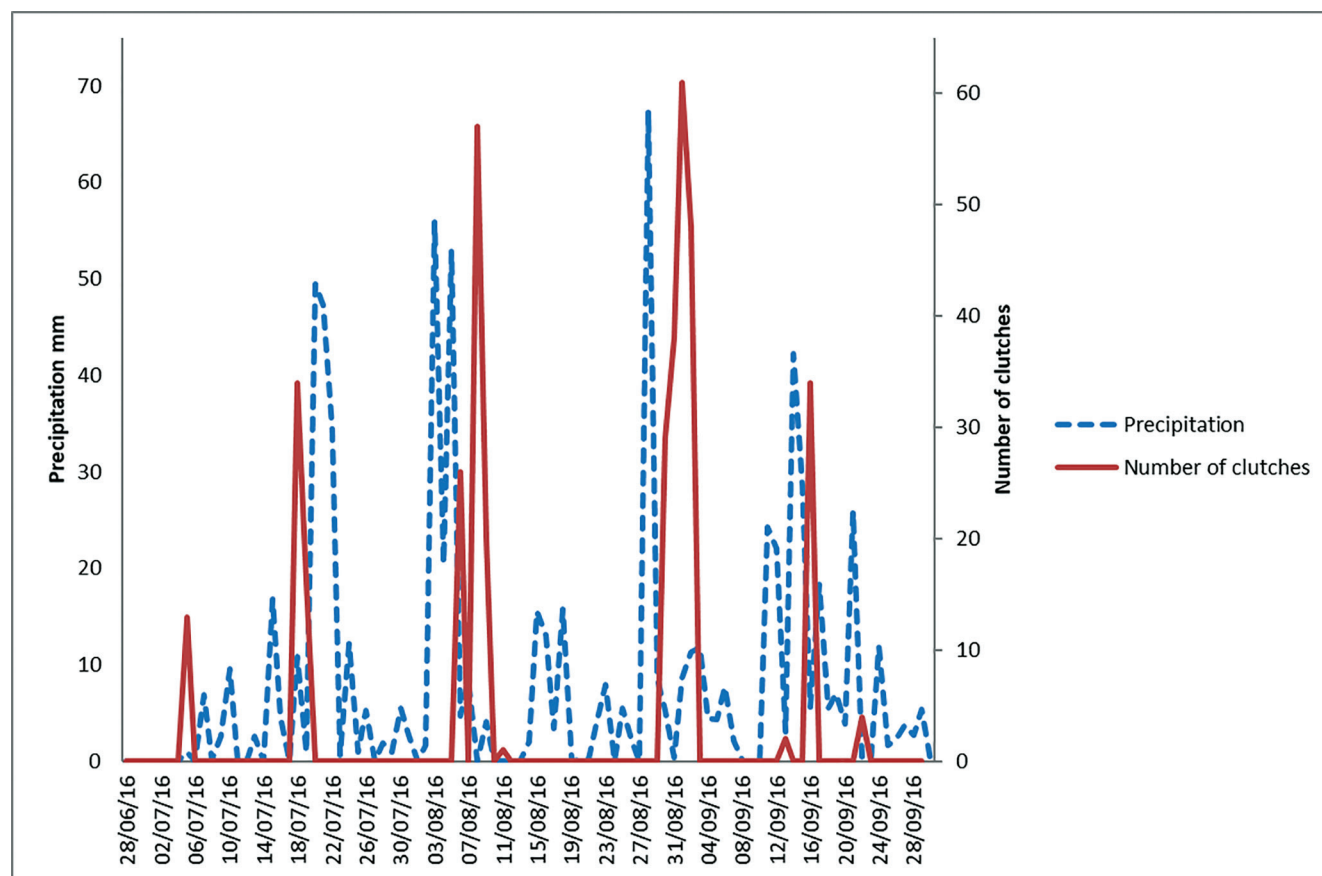
Regarding the GLMs for site selection and reproductive success, we found that TEN was best explained by the additive effects of GSF and substrate species (Fig. 4A, B). For NHT, the model with lowest AIC included the additive effects of precipitation, species, genus, and SC (Fig. 4C, D, E). For NST, the model with lowest AIC included precipitation, distance to the pond, and substrate (Fig. 4F, G, H). For NDE, the best model included the additive effects of precipitation, GSF, and substrate (Fig. 5A, B, C). Finally, for the number of predated eggs, two models had similar fit ( $\Delta\text{AIC} < 2$ ), one including only precipitation and the second including the additive effects of precipitation and GSF (Fig. 5D, E). The full models set

with their respective AICc,  $\Delta\text{AICc}$ , and freedom degrees are listed in Table S1.

## DISCUSSION

In *Agalychnis moreletii* and *A. callidryas*, OSS occurs at two different scales. First, there is a clear preference for site 4, which has a significantly greater canopy volume than sites 2 and 3, but it is similar to site 1. Site 4 also has a significantly smaller pond area and the pond is significantly shallower than at sites 1 and 3, but it is similar to site 2. This combination of factors seems to make this site the most suitable for oviposition.

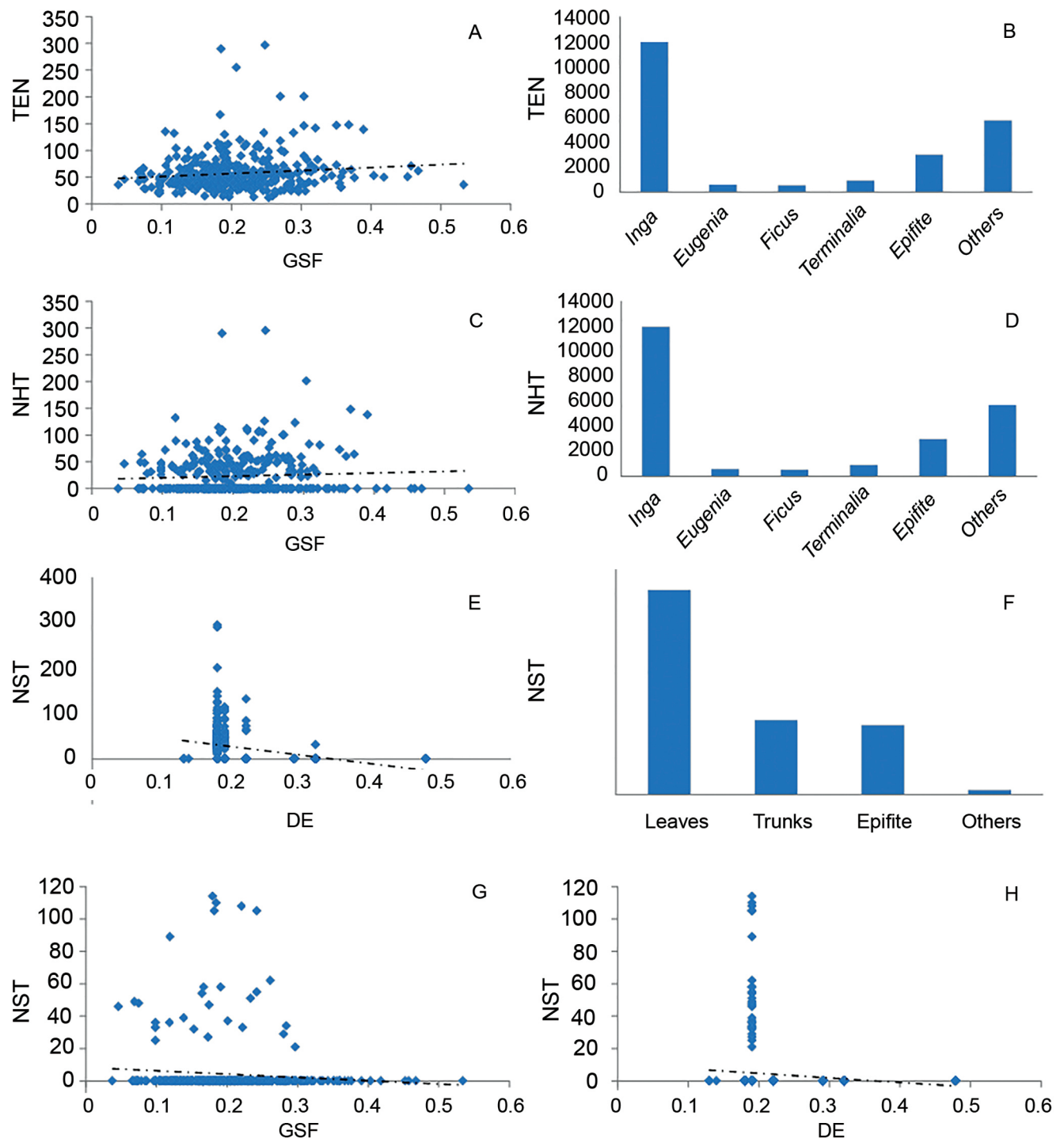
At a finer scale, several factors contribute to OSS. We observed a clear tendency regarding number of eggs in relation to substrate species and GSF, which are present in every model with  $\text{AIC} < 2$ . *Inga* sp. was the frequently used substrate species, and values of GSF were intermediate (0.14–0.53), although depth, distance, temperature, and area of the pond might also influence this trait. The observed trend might enhance egg development and hatching. The effect of vertical and horizontal vegetation structure on reproductive success in amphibians is not well understood (Shulze et al., 2012). Primary forest com-



**Figure 3.** Daily rainfall at the Protected Area of Nahá and number of *Agalychnis moreletii* and *A. callidryas* clutches recorded during the study.

plexity and annual floods are important to *Agalychnis moreletii* and *A. callidryas*, as in other amphibians (Donnelly and Guyer, 1994). Despite the similar availability of light in all our study sites, the overlapping of the canopy layers at site 4 provides the frogs with several sites for oviposition. Further, canopy volume might enhance adult sur-

vival, providing a higher number of covered areas for resting or reducing the probability of being seen by predators. The use of tree leaves, shrubs, herbs, roots, branches, and trunks near the ponds for oviposition is similar to observations for *Phyllomedusa boliviana* Boulenger, 1902 (Vaira, 2001), *Pithecopus azureus* (Cope, 1862) (Dias et al., 2014),



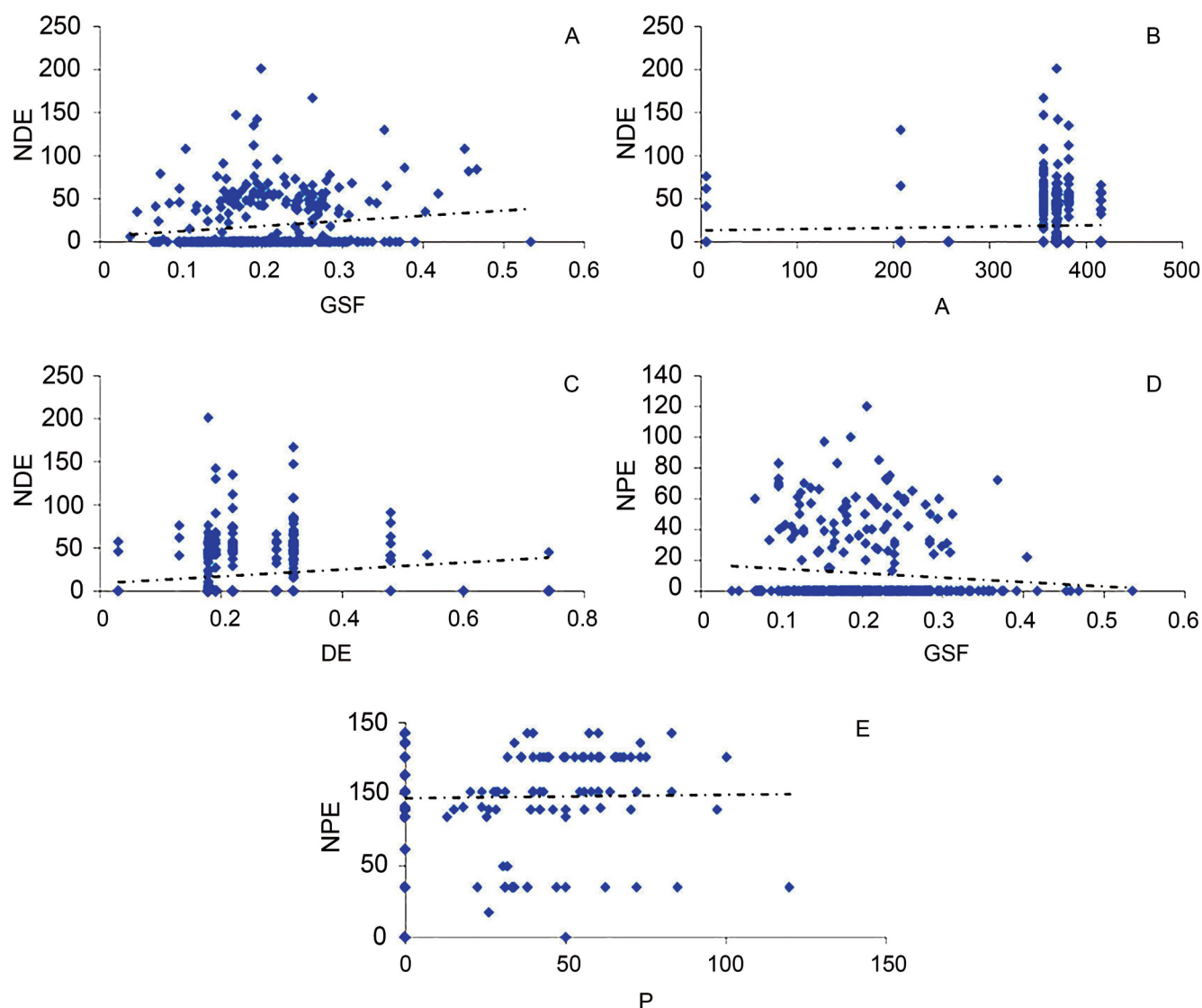
**Figure 4.** Relationship between the dependent and independent variables of the best fitted generalized linear models. (A–B) The two variables that affect TEN. (C–E) The three variables that affect NHT. (F–H) The three variables that affect NST. Abbreviations: DE = pond depth, GSF = global site factor (total light incidence), NHT = number of hatched tadpoles, NST = number of successful tadpoles, TEN = total egg number.



*Phyllomedusa burmeisteri* Boulenger, 1882 (Abrunhosa and Wogel, 2004), which suggests a highly conserved trait in phyllomedusines related to a high OSS plasticity that might vary among and within individuals throughout the life cycle (Mery and Burns, 2010).

Water availability is important for the development of most frog species, including our study species. Pond depth and area were among the most important variables in explaining the number of hatched and successful tadpoles and desiccated eggs. These variables were closely related to precipitation, and amphibian dependence on water availability has been reported in several studies of amphibian reproductive success (Cayuela et al., 2012; Walls et al., 2013); specifically, the persistence of water bodies is determinant for hatching. At our study sites, pond area varied drastically with rainfall, increasing after

heavy rains and decreasing with rain scarcity. If no heavy rain occurs before hatching, clutches laid at the periphery might result in tadpoles hatching out of the water. This might also explain why females lay their eggs near the water. Desiccation risk of the pond was reported as an important variable that influences reproductive success in other species, including *Lithobates sylvaticus* (Le Conte, 1825) (Gervasi and Foufopoulos, 2008), *Bombina variegata* (Linnaeus, 1758) (Barandun and Reyer, 1997), *Phrynobatrachus guineensis* Guibé and Lamotte, 1962 (Rudolf and Rödel, 2005), and *Bufo bufo* (Linnaeus, 1758) (Laurila, 1998). However, permanent ponds or water bodies have higher abundance and diversity of predators than temporary ponds, which inhibit amphibian colonization or reproduction (Touchon, 2012; Touchon and Worley, 2015). This might explain why we observed no clutches or



**Figure 5.** Relationship between the dependent and independent variables of the best fitted generalized linear models. **(A–C)** The three variables that affect NDE, **(D–E)** The two variables that affect NPE. Abbreviations: A = area of the pond, DE = depth of the pond, GSF = global site factor (total light incidence), NDE = number of desiccated eggs, NPE = number of predated eggs by fungus or bacteria, P = mean precipitation of five preceding days.

adults at site 1, where local community monitors reported *A. moreletii* to have been abundant before the introduction of cichlid fishes, and to have dramatically declined subsequently, as observed in other studies (Hecnar and M'Closkey, 1997; Semlitsch and Gibbons, 1988; Collins and Storfer, 2003; Kats and Ferrer, 2003).

Female selection of *Inga* sp. (a legume) to lay clutches and more eggs is poorly understood. It could be a spurious correlation because this tree represents a huge amount of the biomass of the site, but we also think that this tree might offer some protection to clutches. *Inga* sp. may produce repellent and antiherbivore defense to insects, as has been reported for species of same genus (Koptur, 1985; Coley et al., 2005; Kursar et al., 2009). Moreover, the flexibility that the leaves of legumes have because of *pulvinus* (a thickening at the base of the leaf; Rodrigues and Machado, 2008) might allow clutches to remain on trees despite wind or rain or even support larger, heavier clutches.

There is evidence that GSF affects developmental rate (Skelly, 2004; Hawley, 2010) and even the presence or abundance of amphibians in temperate regions (Halverson et al., 2003). Our results suggest that this trend also occurs in tropical areas and may influence OSS, and it is related with TEN, NHT, NST, NDE, and NPE. Indeed, total light incidence was the only factor present in every best fitted model for our dependent variables, which underscores its relevance for successful reproduction. The relationship of OSS and reproductive success to GSF might be mediated by a trade-off between developmental time and desiccation-predation risk. Clutches laid in open areas enhance the ability of eggs to reach larval stages because of higher temperatures (Saenz et al., 2003; Skelly, 2004; Székely et al., 2010); however, this increases desiccation risk (because of mucus layer decreasing) and clutch detectability for visual predators. In contrast, clutches laid in covered areas have lower desiccation risk but are more vulnerable to fungus, bacteria, and predators in general because the rate development is slower. Further, OSS in specific light exposure conditions indicates that females have good night vision under the canopy and can identify the gaps of sky in the matrix of vegetation. We do not know which mechanisms allow females to discriminate the total light incidence in each place at night, but this behavior has also been observed in other hylid frogs (Touchon and Warkentin, 2008). It is known that some tree frogs have good night vision (Gomez et al., 2010) and also that light incidence influences male calling activity (Grant et al., 2009; Vignoli and Luiselli, 2013). Furthermore, light exposure probably propitiates several trades-offs working together that increase or decrease the fitness of adult frogs.

Regarding our results on NDE and NPE, we think that predation might have less influence on OSS than desiccation risk. We found that most clutches were affected by variables associated with desiccation probability (total light incidence, area and depth of the pond, and

precipitation), concurring with previous observations on *Dendropsophus ebraccatus* (Cope, 1874) (Touchon, 2012). It is noteworthy that several studies consider predation to be the main factor promoting the evolution of reproductive models in amphibians (Magnusson and Hero, 1991; Blaustein, 1999; Refsnider and Janzen, 2010); however, this may not be the case for species that lay their clutches on overhanging vegetation, where predators might be a weak selective force compared to desiccation risk (at least in the time frame of this study).

## Conservation perspectives

Our results confirm that *Agalychnis moreletii* and *A. callidryas* oviposit nonrandomly, relying mostly on primary forest structure for successful reproduction. Both species had large distributional ranges that have been reduced to small areas as a result of land use conversion in southern Mexico (Ortiz-Espejel and Toledo, 1998; Díaz-Gallegos et al., 2008) and Central America (Laurance, 1999). Recently, forest degradation (particularly of flooding areas) and its conversion to grass- and crop-lands have highly reduced plant diversity and vegetation structure (both horizontally and vertically; Franklin and Van Pelt, 2004). Considering that hatchling success relies mainly on GSF and pond depth, primary forest conservation and restoration are critical for tree frog population maintenance. Our study represents a baseline to enhance amphibian monitoring in conserved areas, although data from fragmented areas are still needed. Finally, changes in rainfall patterns (Dore, 2005) associated with periodic events like “el Niño” increase both species' vulnerability, particularly in Central America, where rainfall patterns are changing (Touchon, 2012).

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## ONLINE SUPPORTING INFORMATION

The following Supporting Information is available for this article online:

**Table S1.** Fitted models for reproductive success variables, presenting all models with a  $\Delta\text{AIC} < 2$  and the first model with  $\Delta\text{AIC} > 2$ .