UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO
POSGRADO EN CIENCIAS BIOLÓGICAS
FACULTAD DE ESTUDIOS SUPERIORES IZTACALA
ECOLOGÍA

ELECCIÓN DEL SITIO DE PUESTA DE DOS RANAS ARBORÍCOLAS (*Agalychnis moreletii* y *Agalychnis callidryas*)

POR ARTÍCULO CIENTÍFICO TITULADO:

Oviposition site selection and conservation insights of two tree frogs

(*Agalychnis moreletii* (Duméril, 1853) and *A. callidryas* (Cope, 1862)

QUE PARA OPTAR POR EL GRADO DE:

MAESTRO EN CIENCIAS BIOLÓGICAS

PRESENTA:

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DR. PIERRE ALEXANDRE REMY ROBERT HENRI CHARRUAU
CENTRO DEL CAMBIO GLOBAL Y LA SUSTENTABILIDAD EN EL SURESTE, A.C.

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Lic. Ivonne Ramírez Wence
Directora General de Administración Escolar, UNAM
P r e s e n t e

Me permito informar a usted que en la reunión ordinaria del Comité Académico del Posgrado en Ciencias Biológicas, celebrada el día **26 de febrero de 2018** se aprobó el siguiente jurado para el examen de grado de **MAESTRO EN CIENCIAS BIOLÓGICAS** en el campo de conocimiento de **Ecología** del alumno **SANCHEZ OCHOA DANIEL JOAQUIN** con número de cuenta **307160847** por la modalidad de graduación de **tesis por artículo científico**, en el campo de conocimiento de **Ecología,** con la tesis titulada: **"Oviposition site selection and conservation insights of two tree frogs (***Agalychnis moreletii* **and A. callidryas)"**, producto del proyecto realizado en la maestría que lleva por título **"Elección del sitio de puesta de dos ranas arborícolas (***Agalychnis moreletti* **y** *Agalychnis callidryas***)** realizado bajo la dirección del **DR. HIBRAIM ADAN PÉREZ MENDOZA** quedando integrado de la siguiente manera:

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Sin otro particular, me es grato enviarle un cordial saludo.

A T E N T A M E N T E
"POR MI RAZA HABLARA EL ESPÍRITU"
Ciudad Universitaria, Cd. Mx., a 16 de abril de 2018

DR. ADOLFO GERARDO NAVARRO SIGÜENZA
COORDINADOR DEL PROGRAMA

POSGRADO EN CIENCIAS BIOLÓGICAS
COORDINACIÓN

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ÍNDICE

Resumen

La elección del sitio de puesta es un rasgo que afecta directamente la adecuación y se relaciona con una gran cantidad de factores ambientales. La elección de sitio de puesta es un rasgo conservado en ranas arborícolas y se ha demostrado que está restringida a los sitios cercanos a los cuerpos de agua. Algunos factores que determinan la elección del sitio de puesta en las ranas arborícolas son la presencia de depredadores, temperatura del agua, riesgo de desecación, tipo de sustrato y parámetros físico-químicos de los cuerpos de agua. *Agalychnis moreletii* y *A. callidryas* (Phillomedusidae) son especies con una amplia distribución en el continente americano, pero sus poblaciones han disminuido por la deforestación, la presencia de patógenos, el tráfico de especies y por los cambios en los patrones de lluvia causados por el calentamiento global. En este trabajo se estudió la elección del sitio de puesta de las dos especies, *A.* y *A. callidryas* en cuatro sitios en los que ambas especies ocurren al mismo tiempo en el sur de México. De la vegetación se caracterizó, la fluctuación del área y profundidad de los cuerpos de agua, así como la temperatura y la precipitación durante todo el estudio. Cada sitio fue visitado tres veces por semana durante cuatro meses en el periodo de mediados de junio a finales de septiembre. En cada visita se registró el número de huevos, la especie de la planta usada como sustrato, la distancia al cuerpo de agua, la incidencia de la luz solar y la condición de la puesta. Para los análisis estadísticos se realizaron pruebas paramétricas y no paramétricas para explorar las diferencias entre los sitios en términos de vegetación y características físicas del agua. Por otro lado se examinaron 92 modelos lineales generalizados (GLM) para determinar qué variables afectan la condición de las puestas. Encontramos diferencias significativas en la estructura de la vegetación, el área y la profundidad del estanque entre los sitios. La elección del sitio de puesta se determinó en dos escalas espaciales diferentes, el éxito reproductivo está determinado principalmente por la precipitación, la incidencia de la luz y la disponibilidad del sustrato. Que la elección de sitios de puesta no se deba al azar sugiere que ambas especies dependen de la estructura del bosque primario para que la reproducción sea exitosa. Esta información enfatiza la importancia de la complejidad del bosque primario inundable para el éxito reproductivo de estas especies.

Abstract

Oviposition site selection is a trait that directly affects the biological fitness and it is related to a large number of environmental factors. A conserved trait that restrains oviposition site selection in tree frogs is the laying of clutches overhanging water bodies. Some factors that

determine oviposition site selection in tree frogs are: presence of predators, water temperature, desiccation risk, laying substrate and some physicochemical properties of water body. *Agalychnis moreletii* and *A. callidryas* are widespread species throughout Central America; however, 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 at southern Mexico. We characterized the vegetation structure, area and depth fluctuation of the pond, temperature and precipitation of the four study sites. Every site was visited three times a week during four months to register the development of each clutch, the number of eggs, substrate species, distance to the pond, sunlight incidence, and their predated or desiccation condition. We performed parametric and non-parametric statistics to explore the differences among sites and a total of 92 GLMs to determine which variables affects the condition of the clutches. We found significant differences on the vegetation structure, the area and pond depth among sites. Oviposition site selection was observed at two different scales and the reproductive success was determined mainly by precipitation, light incidence and substrate availability. 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 for the reproductive success of these species.

Introducción

La reproducción es uno de los procesos en el que más energía se invierte a lo largo del ciclo de vida de los organismos (Reznick *et al*., 2000). Dicha energía se asigna primeramente, a la adquisición de recursos suficientes y de buena calidad, después a la búsqueda y elección de pareja, a la elección de un sitio de puesta y a la defensa y cuidado de las crías. La elección del sitio de puesta, es importante en los organismos que no tienen un cuidado parental, como la mayoría de los organismos ovíparos, ya que el éxito reproductivo depende en gran medida de dicha elección (Resetarits, 1996; Abbott y Dukas, 2011). De esta manera, este proceso está sujeto a presiones selectivas muy fuertes por su relación directa con la adecuación, al repercutir de manera directa en la supervivencia de los neonatos. Algunos autores consideran este proceso como un atributo de historia de vida, altamente plástico, definido por el comportamiento de los organismos (Höbel, 2008). De esta manera, la elección del sitio de puesta es un proceso complejo donde actúan distintas presiones selectivas de forma simultánea, e incluso en algunos casos opuestas entre sí, propiciando una variación y consecuentemente una evolución debido a los cambios en las frecuencias de este atributo de generación en generación. Se ha documentado que los procesos y factores que operan sobre la decisión de los padres en elegir el sitio de puesta, es diferente para cada grupo taxonómico (insectos, peces, anfibios, reptiles y aves, Refsnider y Jazen, 2010). Actualmente hay seis teorías evolutivas que sustentan que la elección del sitio de puesta no es se debe al azar: (1) aumento en la supervivencia de los huevos y neonatos; (2) aumento de la supervivencia de los padres; (3) diferenciación del fenotipo de los neonatos (*e.g.* manipulación de la proporción sexual, modificación en la tasa de desarrollo de larvas); (4) asegurar la disponibilidad de recursos para los neonatos; (5) propiciar la filopatría y (6) selección de pareja (Refsnider y Jazen, 2010).

De manera particular en los grupos de peces y anfibios, que tienen fertilización externa, propicia que la reproducción se convierta en un proceso relativamente más complejo que en otros grupos taxonómicos como aves y mamíferos. Los padres, deben buscar un sitio donde se pueda llevar a cabo la fertilización, el desarrollo del embrión y del subsecuente neonato (Warner y Dill, 2000; Bowcock et al. 2009). Aunado a esto, particularmente los anfibios con larvas de vida libre tienen un ciclo de vida más complejo, ya que en sus etapas de desarrollo están involucrados ambientes completamente diferentes (e.g. acuático y terrestre) y la elección del sitio de puesta es crucial para mantener a las poblaciones estables.

Uno de los principales factores que definen la elección de los sitios de puesta por las hembras es la reducción del riesgo de depredación (intra e interespecífica) que hay sobre las crías,

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(Seale, 1982; Resetarits y Wilbur, 1989; Egan y Paton, 2004; Vredenburg, 2004). La temperatura, es otro factor importante que incide en la supervivencia de los embriones y larvas ya que las temperaturas altas propician un desarrollo rápido en la fase embrionaria y larvaria (Seale, 1982; Pearl *et al.* 2007). Sin embargo al no tener una capa calcárea, los huevos son muy susceptibles a las temperaturas ambientales y en ocasiones las hembras prefieren los lugares más frescos para evitar la desecación de la puesta y de los cuerpos de agua. Otras especies tienen preferencias en el sustrato donde dejan a sus huevos. Por ejemplo, *Agalychnis granulosa* prefiere dejar la puesta en troncos, hojas y raíces que se ubican entre los cero a los 300 cm sobre el cuerpo de agua (Vilela *et al.*, 2015). En varias especies de *Phyllomedusa* (*P. tetraploidea*, *P. azurea, P. sauvagii*) las hembras suelen depositar sus huevos principalmente en hojas de plantas cercanas al cuerpo de agua y particularmente para *P. azurea* tiene una preferencia por las hojas con tricomas, ya que se cree que esto le brinda mayor protección, adhesión y oxigenación a la puesta (Dias *et al.*, 2014). Por otro lado, se ha observado que las hembras de *Phyllodytes melanomyxtax* prefieren sitios de alta abundancia de bromelias (Cuhna *et al.*, 2016), mientras que en *P. luteolus* la elección está sesgada a sitios con bromelias más frondosas, con mayor cantidad de agua almacenada y baja conductividad (Mageski *et al.*, 2016). En la rana *Scinax perpusillus*, la elección está sesgada hacia sitios con bromelias más grandes, cercanas al suelo y con pH ácidos en el agua almacenada (Wogel *et al.*, 2004). También, se ha observado que hay construcción de nidos por parte de los machos de *Hypsiboas faber* y ellos muestran preferencia por sitios con vegetación alta y abundante, agua somera y con poca materia orgánica en suspensión (Luza *et al.*, 2015). Finalmente, existe una situación más compleja a la hora de elegir un sitio de puesta en *Dendropsophus ebraccatus*, que, hasta donde se sabe, es el único vertebrado ovíparo que puede depositar sus huevos en el agua y fuera de ésta y en ambas situaciones ser exitosas. Esto sugiere que en la elección de sitio de puesta podría estar implicada una disyuntiva evolutiva. Por un lado, colocar los huevos en el agua los haría vulnerables a una mayor cantidad de depredadores, y por otro lado si la puesta es colocada fuera del agua los huevos recibirán mucha radiación. También, la elección de sitio, en ocasiones, puede estar determinada por la elección de una pareja con un territorio que ofrezca refugio y agua suficiente para la progenie (Wogel *et al.*, 2004; Mageski *et al.*, 2016).

Para proponer mejores planes de manejo y conservación de especies en riesgo es indispensable entender los procesos que están involucrados en la elección del sitio de puesta, ya que esta información permite entender las necesidades para que la reproducción sea exitosa. Esto permitiría evaluar si las áreas protegidas o los sistemas de corredores biológicos

cuentan con las condiciones necesarias para asegurar la viabilidad del proceso. Por otro lado, también puede servir para generar planes de erradicación o control de especies invasoras como *Rhinella marina*.

Agalychnis moreletii y *Agalychnis callidryas* son dos ranas arborícolas que tienen una amplia distribución en América. En época reproductiva, ambas especies suelen compartir pozas temporales para elegir los sitios de puesta y debido a que son especies cercanas filogenéticamente, sus puestas son indiferenciables entre ellas. *A. moreletii* es una rana que está en peligro crítico de extinción y *A. callidryas* tiene problemas con el decremento de sus poblaciones (Lawson, 2011; IUCN, 2016). Ambas especies tienen reportes de extinción local atribuidos a la presencia del hongo *Batrachochytrium dendrobatidis* a pesar de que solo existe un estudio que sustenta este supuesto (Lawson *et al.*, 2011). Sin embargo, el cambio de uso del suelo y todas las actividades humanas que esto conlleva, es una amenaza directa que podría actuar de la misma forma o incluso más rápido que el *B. dendrobatidis* sobre las poblaciones de estas dos especies (Urbina-Cardona y Loyola, 2008).

Conocer si hay diferencias en el microhábitat de los sitios donde las hembras depositan las puestas, nos podría dar información sobre los atributos que inciden en la elección del sitio de puesta en *Agalychnis moreletii* y *Agalychnis callidryas*. Así, esta investigación se plantea las siguientes preguntas: ¿Cuál variable podría estar implicada en la abundancia de puestas en un sitio? ¿Cuáles son las variables microambientales que determinan la elección del sitio de puesta? ¿Cuáles son las variables que determinan el éxito reproductivo de *A. moreletii* y *A. callidryas*? ¿Cuáles son las variables que determinan que las puestas se desarrollen?

El objetivo principal del trabajo es conocer cuáles variables son las que más efecto tienen en la elección del sitio de puesta. Los objetivos particulares son: conocer si hay diferencias significativas en la estructura de la vegetación y en las fluctuaciones de área y profundidad de las pozas. Conocer qué variables son las que más influyen en el desarrollo de los huevos, desecación, depredación por hongos y el éxito reproductivo de *A. moreletii* y *A. callidryas*.

HIPÓTESIS

Si el sobrelapamiento de los diferentes estratos del dosel propicia una mayor oferta en la disponibilidad de sustratos sobre el agua y una oferta de distancias e incidencias de luz, se esperaría una mayor abundancia de puestas en esos sitios. Por otro lado, si la lluvia es

constante y eso propicia que la temperaturas bajen, la tasa de desecación de los cuerpos de agua será menor, así que probablemente los sitios que tengan mayor disponibilidad de agua tendrán una mayor abundancia de puestas. Finalmente, si la incidencia de luz es mayor en un sitio, aumentará la temperatura y la evapo-transpiración, por lo tanto los adultos preferirán sitios con menor exposición a la luz para evitar que las puestas se desequen.

TITTLE PAGE

Title

Oviposition site selection and conservation insights of two tree frogs (*Agalychnis moreletii* (Duméril, 1853) and *A. callidryas* (Cope, 1862))

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ABSTRACT

Oviposition site selection is a trait that directly affects the biological fitness and it is related to a large number of environmental factors. A conserved trait that restrains oviposition site selection in tree frogs is the laying of clutches 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 species throughout 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 of southern Mexico. We characterized the vegetation, area and depth fluctuation of the pond, and temperature and precipitation of the four sites. Every site was visited three times a week during four months to register the development of each clutch, the number of eggs, substrate species, distance to the pond, sunlight incidence, and their condition. We performed parametric and non-parametric statistics to explore the differences among sites and a total of 92 GLMs to determine which variables affects the condition of the clutches. We found significant differences on the vegetation structure, the area and pond depth among sites. Oviposition site selection was observed at two different scales and the reproductive success was determined by precipitation, light incidence and substrate availability. 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 for the reproductive success of these species.

INTRODUCTION

It is known that oviposition site selection (OSS) for oviparous species is crucial to maintain demographic processes, because it has a direct effect on reproductive success (Resetarits 1996; Refsnider and Janzen 2010; Abbott and Dukas 2016) which in turn, is critical for threatened species. For amphibians in particular, OSS process is fundamental to develop successful conservation and management plans in the long term (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; Gavrilets et al. 2001), territory and hatchling defense (Márquez-Luna et al. 2014), and OSS (Santos et al., 2010). OSS is considered to be under intense selection pressures (Refsnider and Janzen 2010); therefore, is a behavioral life history trait that varies within and among species (Resetarits 1996; Madsen and Shine 1999) and can exhibits high phenotypic plasticity (Höbel 2008). Six non-mutually exclusive selective hypotheses have been proposed to explain why organisms might oviposit non-randomly: (1) to maximize embryo survival, (2) to maximize parental survival, (3) to modify offspring phenotype, (4) to provision suitable resources for offspring, (5) to maintain philopatry (6) indirectly by male choice (Refsnider and Janzen 2010). However, each hypothesis may involve several environmental factors that influences OSS (Refsnider and Jazen 2010).

In the oviparous vertebrates, fish and amphibian 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 of the amphibian´s life cycles have developmental stages that

occur under completely different environmental conditions (e.g. egg, tadpole on water, post metamorphic on ground; McDiarmid and Altig 1999). These dissimilar conditions may act as differential selective pressures but always amphibians have a strong dependence on water bodies. Hence, environmental humidity, precipitation and water body presence are critical to the amphibian reproduction and development life cycle stages to maintain their populations (Wells, 2010; McDiarmid and Altig 1999).

Concerning offspring survival, which is closely related to suitable conditions for developing, there are 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, lying clutches over vegetation or surfaces overhanging water bodies is considered a relatively well conserved trait which may be driven by phylogenetic inertia and also restrain oviposition site selection (Wells 2010). However the main factors identified in the OSS in hylids are: tadpole predator presence, water body temperature, desiccation risk, type of substrate and chemical traits of the water body (Haramura 2008; Doody et al. 2009: Székely et al. 2010; Vilela et al. 2015; Mageski et al. 2016).

Regarding predator presence, there is mixed evidence. Some studies have observed that individuals may select sites with conspecific egg clutches or tadpoles (Vaira 2001; Abrunhosa and Wogel 2004; Wogel et al. 2006; Doody et al. 2009). In contrast, other studies have showed that adults avoid lay clutches where conspecific tadpoles species occurs to decrease competition or predation (cannibalism; Crump 1983; Schiesari et al. 2003; Alves-Silva and da Silva 2009). Concerning water

temperature, adults search suitable sites for larvae development that affects the growth time and ultimately on metamorph's phenotype (van Buskirk and Arioli 2005; Tejedo et al. 2010; Székely et al. 2010). In addition, effects of desiccation risk on hatchling survival may be closely related to two non-mutually exclusive selective forces. Desiccation risk is higher on ephemeral ponds, however; permanent ponds have usually a higher abundance of predators. Therefore a trade-off between desiccation risk and predator presence is expected (Touchon and Warkentin 2008; Touchon 2012; Touchon and Worley 2015; Cuhna et al. 2016; Mageski et al. 2016). Lying eggs on specifically substrate may affect clutches oxygenation, predator avoidance, desiccation risk (Dias et al. 2014; Vilela et al. 2015; Cuhna et al. 2016; Mageski et al. 2016) and chemical properties of the pond (Palen et al. 2005; Haramura 2008). Other important factors that affect the reproductive success of tree frogs are vegetation cover, the 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) that are associated with high temperature avoidance (Touchon, 2012). However, there are few studies that consider more than one selective force on OSS, which prevent us from fully understanding if any process has a higher influence on this critical life history trait.

Determine the factors involved in the OSS, on amphibians, may be critical to threatened, geographically restricted and rare species. This information can generate new proposals for population management and habitats conservation or restoration. Particularly, in the red list, amphibians have the higher number of species under a risk category (32.4%) or data deficient (24%) among the vertebrates (IUCN, 2017) and in CITES are listed 173 species (2017). The humid-forests of North-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 worked with two tree frog species of Hylidae family and Phyllomedusinae subfamily (Duellman, 2001). Black-eyed tree frogs (*Agalychnis moreletii*; Duméril, 1853) is a critically endangered species according with IUCN (2017) that ranges from Mexico to Honduras; their populations have recently been reported as declining (Lawson 2011). Red-eyed tree frog (*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 treats to these species are the habitat loss, habitat degradation, the presence of a pathogenic fungus *Batrachochytrium dendrobatidis* (Longcore et al. 1999; Bd) and poaching for exotic illegal pet trade are the most important factors contributing to the decline of their populations (Urbina-Cardona and Loyola 2008). Both species (*A. moreletii* (Duméril, 1853) and *A. callidryas* (Cope, 1862)) co-occurs along their distribution (Mexico, Guatemala, Belize, El Salvador and Honduras) and they are closely related species, this may provide insights on similarities of factors associated with reproductive success.

In this study, we analyze OSS and its relationship between reproductive success of *A. moreletii* (Duméril, 1853) and *A. callidryas* (Cope, 1862) on four sites with different vegetation structure, total light incidence, water body depth and area, and environmental temperature and humidity in order to know which factors are critical on both process.

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 forest with complex transition vegetation structure between tropical rain forest and cloud temperate forest. Climate is tropical, wet, and humid with mild temperatures and a defined dry season (CONANP, 2006). We delimited four permanent plots around body waters or wetlands with differential abundances of *A. moreletii* (Duméril, 1853) and *A. callidryas* (Cope, 1862). Site 1 is located at 16°57′48′′N, 91°35′20′′W at 870 m of elevation, is a permanent pond dominated by *Ficus* sp. (Linnaeus, 1758) and *Ocotea* sp. (Aublet, 1775) trees; Site 2 is located at 16°59′41′′N, 91°35′44′′W at m 837 of elevation is a wetland dominated by *Eugenia* sp. (Linnaeus, 1753) shrubs; Site 3 is located at 16°58′23′′N, 91°33′32′′W at 1023 m of elevation is a temporary pond dominated by *Eugenia* sp. (Linnaeus, 1753) and *Inga* sp. (Miller, 1754); and Site 4 is located at 16°58′08′′N, 91°35′10′′W at 919 m of elevation is a temporary pond dominated by *Inga* sp. (Miller, 1754) and *Ficus* sp. (Linnaeus, 1758).

Study species

Agalychnis moreletii (Duméril, 1853) and *Agalychnis callidryas* (Cope, 1862) are members of the subfamily Phyllomedusinae, family Hylidae (although there is a taxonomic proposal to give Phyllomedusinae the family status (Köhler 2011), this change is not widely accepted, and we used the conservative classification). Coloration varies from light to dark green depending on light conditions and activity patterns. Sometimes the dorsal surface has white dots and the main difference between species is observed in ventral coloration (orange on *A. moreletii* (Duméril, 1853) and yellowish on *A. callidryas* (Cope, 1862)) and the pectoral girdle (*A. callidryas* (Cope, 1862) green, yellow with blue stripes). During the dry season and daylight hours on the reproductive

season, frogs seek for shaded areas on the canopy. Males congregate on vegetation over the ponds to attract females with vocalizations. Both species lay their eggs usually on overhanging vegetation over the pond (egg clutches are apparently identical in both species). Seven to ten days later hatchlings fall in the water bodies, although there may be differences if mechanical disturbances occur (Cohen et al. 2016). *Agalychnis moreletii* (Duméril, 1853) have a mean snout-vent-length (SVL) of 65.7 mm for males and 82.9 mm for females and *Agalychnis callidryas* (Cope, 1862) have a mean SVL of 56 mm for males and 71 mm for females (Köhler, 2011).

Habitat characterization

The habitat characterization considered 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 level and their coverage and total height were measured to obtain canopy volume. To collect data, we used three circular plots, 10 m in diameter; each plot was subdivided in a concentric circle of 5 m of diameter. On the outer circle, we measured trees' (every individual with more than 10 cm of diameter at 1.5 m of height) total height, canopy coverage (from two perpendicular measurements) and minimum leaf height. In the smaller circle we measured shrubs (every individual with less than 10 cm of diameter at 1.5 m of height) and took the same measurements as was taken for every tree individual. Using both measurements we calculated the canopy volume for trees and shrubs. Furthermore, we characterized the incidence of light trough the global site factor (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 can

take values from 0 when there is no light to 1 when light availability is total, GSF was estimated using HemiView software following the methods described in Halverston et al. (2003). We also measured pond area and depth weekly during the reproductive season (26 July to 29 September 2016) as a measure of water availability of each site. We registered precipitation and temperature every day at 09:00 using a data logger (HOBO UA-001-64, configured to take measurements every 15 minutes) during the study.

Oviposition site selection

We visited the study sites each three days between 26 July to 29 September 2016 to look for clutches of *A. moreletii* (Duméril, 1853) and *A. callidryas* (Cope, 1862). For each clutch, we counted the total number of eggs using three photographs from different angles in order to have a reliable counting, substrate (leafs, roots, epiphytes, soil, branches), substrate genus (when it consisted of identifiable plants), measured the minimum distance to the pond, a total light variable measured by the global site factor (GSF, measured with a hemispherical photography besides the clutch with same parameters as above), and the status of the clutch (predated, desiccated, undeveloped, viable). For viable clutches, we differentiated between those that reached tadpole stage and hatched but not on a water body (hatched) and those that hatched over water (successful).

Statistical analysis

To explore differences in the physical and biological attributes between the sites, we performed analysis of variance (ANOVA) for normal distributed factors on R program (R Core Team, 2017) using the code editor RStudio (RStudio team 2016), to

test for paired comparisons, Tukey tests were made using TukeyC package (Faria et al. 2015). For non-normal distributed factors Kruskal-Wallis tests were used and Dunn tests for paired comparisons using PMCMR package (Pohlert 2014). To look for preferences on OSS and reproductive success, we used generalized linear models (GLM), based on a multimodel perspective (Burnham and Anderson 2002), selecting the best fitting model using Akaike information criterion (AIC; Akaike 1973). We tested 92 models using 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 the global site factor (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 all possible second and third degree additive models (we did not test for fourth degree and further models as overparametrizing models with non-informative variables did not increase their fit; Apendix S1). Considering all dependent variables consisted on counts we used a negative binomial distribution with "logit" link function (RStudio, MASS package; Venables and Ripley 2002), because Poisson distribution has been proven to increase the possibility of type II error (Gardner 1995; Lindén 2011). To explore more carefully the processes affecting clutches, we test the effect of every 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 site between vertical and horizontal structure. We found significant differences on canopy volume among sites (F 7.77, df 205, $p < 0.01$), particularly among sites 1-2 ($p < 0.01$), 1-3($p < 0.01$), 2-4 (p 0.04), and 3-4 (p 0.02). Nevertheless, there is a higher heterogeneity in vegetation structure in site 4 than in the site 1 (Figure 1). The mean total light incidence among sites was 0.33 (N = 80; SD 0.15; Min 0.12; Max 0.88) and we did not find significant differences among sites. The area and depth of each site pond varies among sites (H 48.87, df 3, $p < 0.01$; H 47.94, df 3, $p < 0.01$; respectively). For pond area there are significant differences between sites 1-3 ($p < 0.01$), 1-4 ($p < 0.01$), 2-3 ($p < 0.01$), 2-4 ($p < 0.01$), and 3-4 (p 0.02). For pond depth sites 1-2 ($p < 0.01$), 1-3 (p 0.02), 1-4 ($p < 0.01$), 2-3 ($p < 0.01$), and 3-4 ($p < 0.01$).

Oviposition site selection

We found a total of 404 clutches for all study sites; most of them on site number 4 (94.8 %), which shows a strong preference for this site over the others. The total number of eggs considering all clutches all sites was 22,626, each clutch having on average 57.13 eggs (N 396, SD 33.69, Min 12, Max 297). Clutches were found most commonly on leafs of *Inga* sp. (Miller, 1754; 48%), *Eugenia* sp. (Linnaeus, 1753; 3.5%), *Ficus* sp. (Linnaeus, 1758; 3%), *Terminalia* sp. (3%), several unidentified epiphytic species (14%) and other structures like branches, trunks, lianas and roots

(27%; Figure 2 B and C). Most clutches (91.75%) were affected by different factors; however, in most cases affections were partial (only on some eggs). The main factors affecting clutches were desiccation (42.5%) and predation (32%), but we also registered unviable clutches (11%) and fallen leaves with clutches (6%). The mean distance between clutches and the pond was 1.68 m (N 404, SD 1.23, Min 0, Max 12.5). The number of clutches fluctuated along the rainy season and was closely associated with the rainfall patterns, registering four peaks of clutches laid (more than 29) following heavy rains. The average total light for clutches was 0.21 GSF (N 380; SD 0.07; Min 0.04; Max 0.53). The average temperature for clutches was 21.75 °C (N 383, SD 0.62, Min 20.52; Max 23.61). From the total number of eggs, only 40.6% (9,201) eggs developed to tadpole stage; however, only 8.2% (1,870) from all tadpoles were successful (hatched over water).

For GLMs for site selection and reproductive success, we found that TEN, is best explained by the additive effects of GSF and substrate species (SS; Figure 3 A and B). For NHT the model with lower AIC includes the additive effects of P, SS, and SC (Figure 3 C, D and E). For NST the model with lower AIC includes P, D, and SC (Figure 3 F, G and H). For NDE the best model includes the additive effects of precipitation, GSF and substrate (P+GSF+SC; Figure 4 A, B and C). Finally, for NPE, there are two models with similar fit (ΔAIC < 2) one including only precipitation (P), and the second including the additive effects of P and GSF (Figure 4 D and E). The full model set with their respective AICc, ΔAICc and freedom degrees are listed on Appendix S1.

There is OSS on *A. moreletii* (Duméril, 1853) and *A. callidryas* (Cope, 1862) at two different scales. First, there is a clear preference for site 4 among the others, this site has a significant higher canopy volume than sites 2 and 3, but similar to site 1. This site also has a significantly smaller pond area and the pond is significantly shallower than sites 1 and 3, but similar to site 2. This combination of factors seems to make this site the most suitable for oviposition. At a finer scale there are several factors contributing to OSS. We have observed a clear tendency on number of eggs in terms of substrate species and GSF, which are present in every model with AIC < 2. *Inga* sp. (Miller, 1754) was the most preferred substrate species and values of GSF were intermediate (from 0.14 to 0.53), although DE, D, T, and A may also have an influence on this trait. The observed trend may enhance egg development and hatching. Vertical and horizontal vegetation structure is poorly understood (Shulse et al. 2012), for reproductive success on amphibians. Primary forest complexity and annual floods are important to *A. moreletii* (Duméril, 1853) and *A. callidryas* (Cope, 1862). Despite the similar availability of light on all our studied sites, the overlapping of the canopy layers on site 4 provides the frogs several spots to lay their clutches. Besides, canopy volume may also enhance adult survival, providing a higher number of resting covered areas or reducing the sighting probability for predators. The use of tree leaves, shrubs, herbs, roots, branches and trunks near the ponds for oviposition was similar to those observed on *Phyllomedusa boliviana* (Boulenger, 1902; Vaira 2001*), Phyllomedusa azurea* (Cope, 1862; Dias et al. 2014), *Phyllomedusa brumeisteri* (Boulenger, 1882; Abrunhosa and Wogel 2004), which suggests a highly preserved trait on Phyllomedusines.

Water availability is very important to most frog species development, which is not different for our studied species. DE and A were one of the most important variables

explaining NHT, NST and NDE. These variables are closely related with P and amphibian dependence on water availability has been reported in several studies on amphibian reproductive success (Cayuela et al. 2012; Walls et al. 2013); specifically the persistence of water bodies is determinant for hatching. If the rain is not constant or periodic enough, the pond dries resulting in tadpoles hatching out the water. This may 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 on other species like *Lithobates sylvaticus* (Gervasi and Foufopoulos 2008), *Bombina variegata* (Barandun and Reyer 1997), *Phrynobatrachus guinensis* (Rudolf and Rödel 2005) and *Bufo bufo* (Laurila 1998), to name a few. 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 may explain why in study site 1 we had neither observed a clutch nor an adult. In contrast with the observations of the local community monitors, they used to be abundant and declined after cichlid fishes introduction, like has already observed in other studies (Hecnar and M´Closkey 1997; Semlitsch and Gibbons 1998; Kats and Ferrer 2003; Collins and Storfer 2003).

The females' selection of *Inga* (Miller, 1754; a leguminous) to lay clutches and more eggs it is poorly understood. It could be a spurious correlation because this tree represents a huge biomass on the site, but also we think that this tree may offer some protection to clutches. On one hand, *Inga* (Miller, 1754) may produce repellent and antiherbivore defense to insects like it has been reported for species of same genus (Koptur 1985; Coley et al. 2005; Kursar et al. 2009). Also, leaf flexibility that legumes have because of *pulvinus* (a thickening at the base of the leaf; Rodrigues and Machado

2008), may allow for clutches to stay on trees despite wind or rain or even support for larger clutches.

There is evidence that GSF affects developmental time (Skelly 2004; Hawley 2010) and even presence or abundance on amphibians in temperate regions (Halverston et al. 2003). Our results suggest that this trend also occurs in tropical areas and may influence OSS, and it is related with the TNE, NHT, NST, NDE and NPE. Actually, GSF was the only factor present on every best fitted model for our dependent variables, which underlines its relevance for successful reproduction. OSS and reproductive success relation with GSF may be mediated by a trade-off for developmental time and desiccation-predation risk. Clutches laid on open areas enhance egg development 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. On the other hand, clutches on covered areas have lower desiccation risk, but became more vulnerable to fungus bacteria and general predators because the time of development is longer. Besides, OSS on specific light exposure conditions indicates that females have good night vision under the canopy and also that they can distinguish the gaps of sky in the matrix of vegetation structure. We do not know which mechanisms allow females to discriminate the total light incidence on each place at night. It is known that some tree frogs have good night vision (Gomez et al. 2010) and also that light incidence influences males calling (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.

On view of our results on NDE and NPE, we think that predation may have a lower influence on OSS than desiccation risk. We found that most of the clutches were affected by variables associated with desiccation probability (GSF, A, DE, and P). It is noteworthy that several studies consider predation as the main factor promoting the evolution of reproductive models on amphibians (Magnusson and Hero 1991; Blaustein 1999; Refsnider and Janzen 2010); however, this may not be the case for species laying their clutches on overhanging vegetation, where predators may be a weakest selective force compared with desiccation risk (at least in the time frame of this study).

Conservation perspectives

Our results confirm that *A. moreletii* (Duméril, 1853) and *A. callidryas* (Cope, 1862) make a nonrandom oviposition, relaying mostly on primary forest structure for a successful reproduction. Both species had long distributional range that has been reduced to small areas due to land use conversion in Southern México (Ortiz-Espejel and Toledo 1998; Díaz-Gallegos et al. 2008) and Central America (Laurence 1999). Forest degradation (particularly flooding areas) and the conversion to grasslands and croplands, highly reduces plant diversity and vegetation structure (both, horizontally and vertically; Franklin and Van Pelt 2004). Having a negative impact on microhabitat availability for oviposition, with their consequent impacts on population dynamics. Besides, changes on rainfall patterns (Dore 2005) associated with periodic events like "el Niño" increases both species' vulnerability.

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Figure legends

Figure 1.- Vegetation structure of each site, the x only represents the area of the plots, the y represents each individual mean height of trees and shrubs, the diameter of the circle represents the canopy volume.
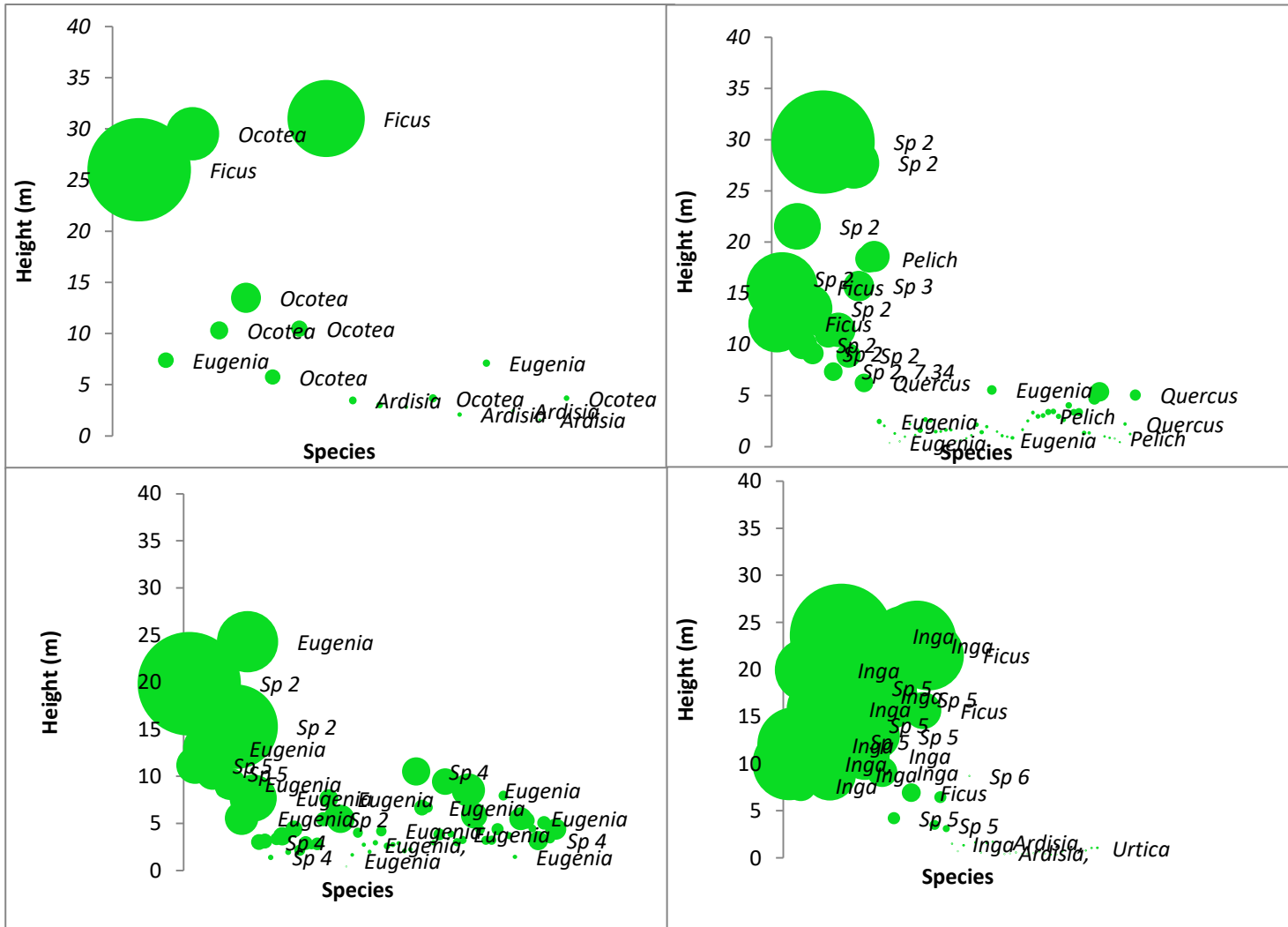
Figure 2.- Daily rainfall on Nahá's protected Area and number of *A. moreletii* and *A. callidryas* clutches registered during the study.
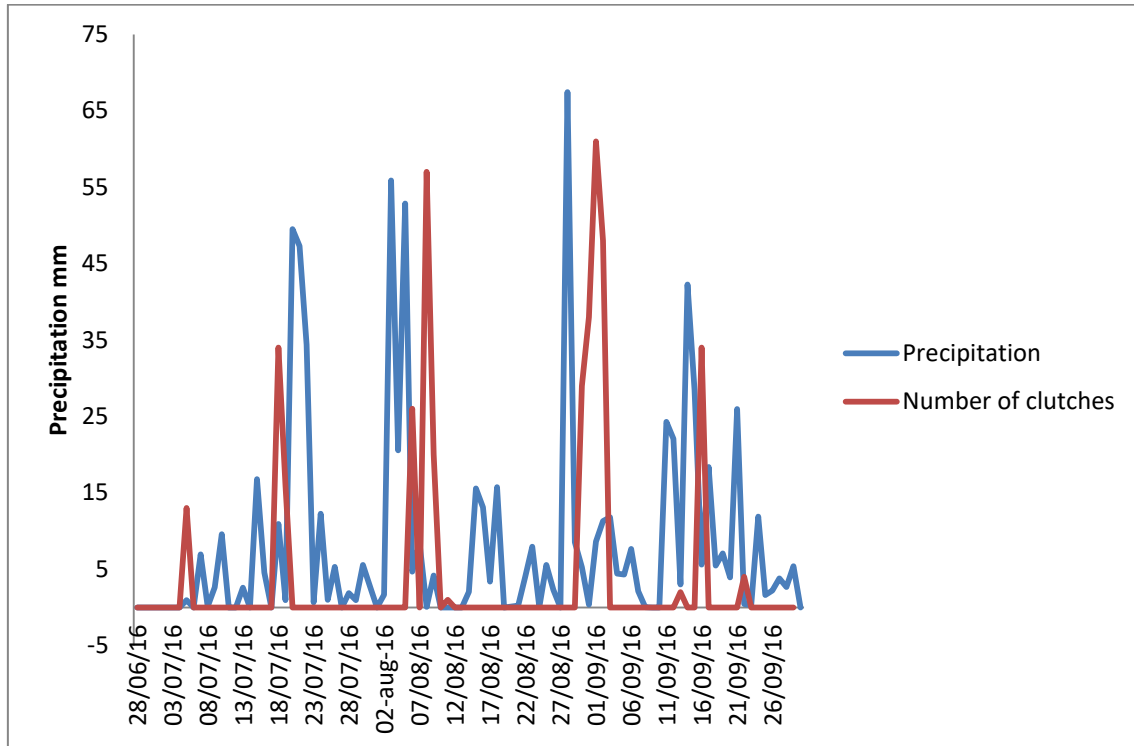
Figure 3.- Relation of dependent and independent variables of best fitted models of GLM. For dependent variables TEN = total egg number, NHT = number of hatched tadpoles, NST = number of successful tadpoles. For independent variables D = distance to the pond, A = area of the pond, DE = depth of the pond, P = mean precipitation of five preceding days, T = temperature, GSF = global site factor measured (total light incidence), SC = substrate (categorical) and SS substrate species (categorical).
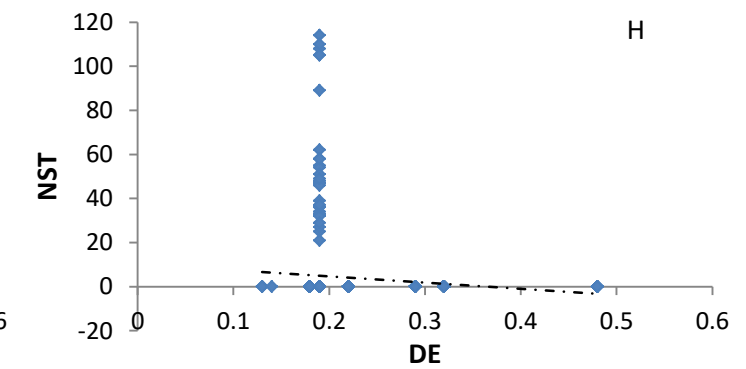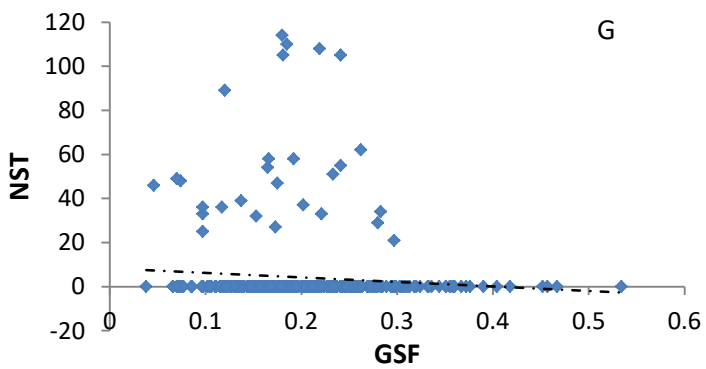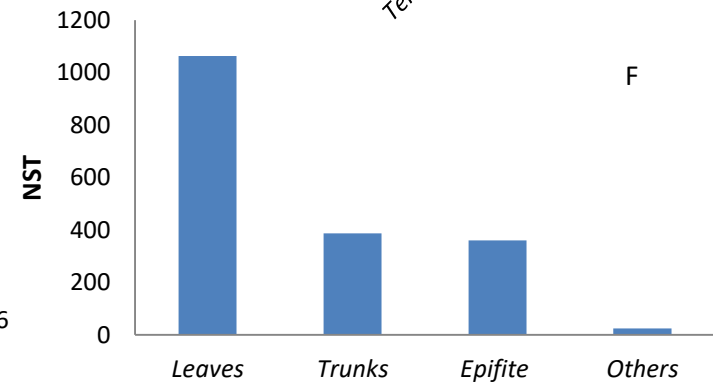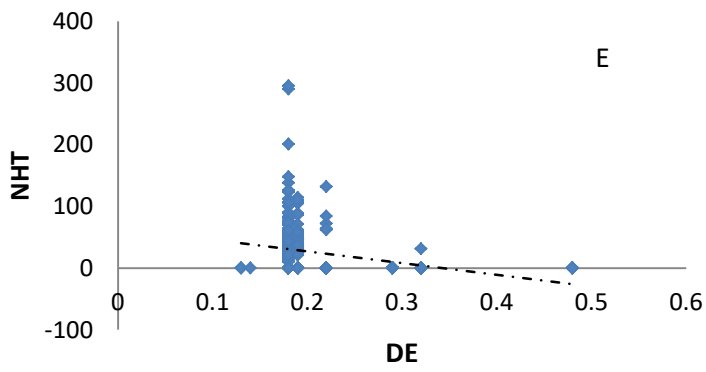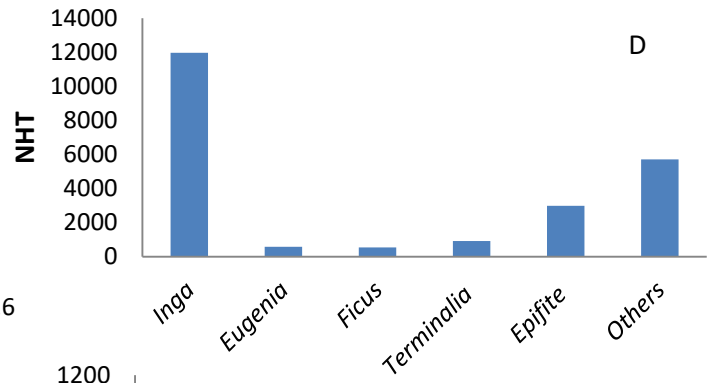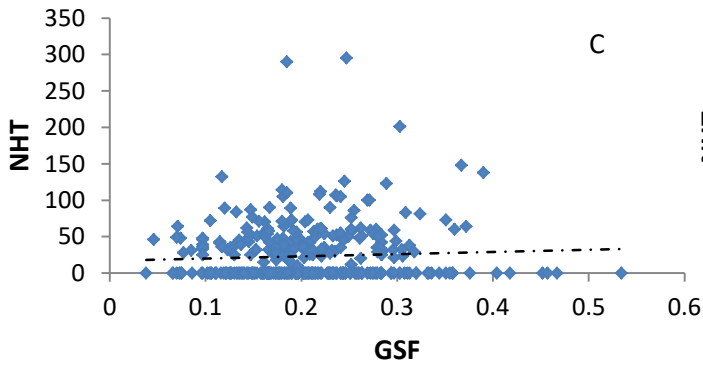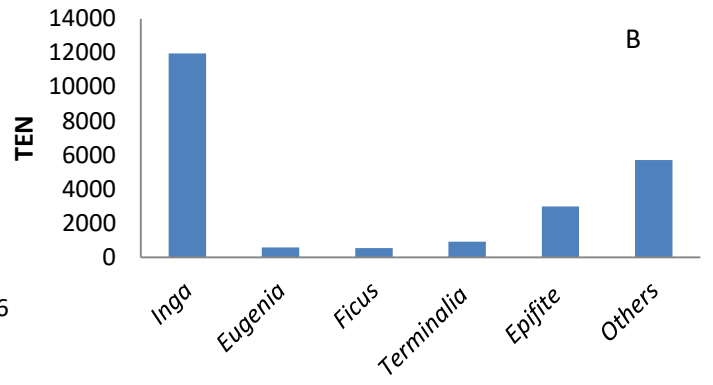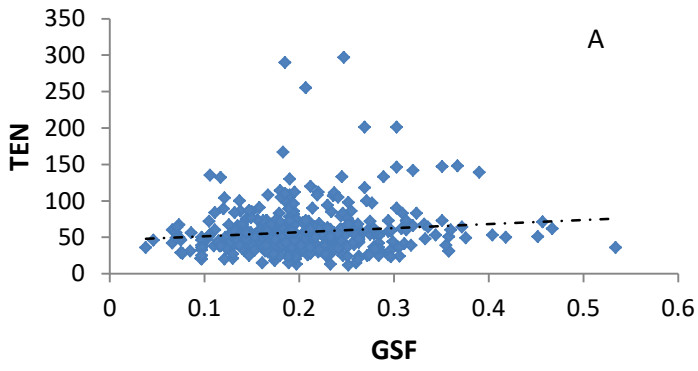
Figure 4.- Relation of dependent and independent variables of best fitted models of GLM. For dependent variables NDE = number of desiccated eggs, and NPE = number of predated eggs by fungus or bacteria. For independent variables A = area of the pond, DE = depth of the pond, P = mean precipitation of five preceding days and GSF = global site factor measured (total light incidence)
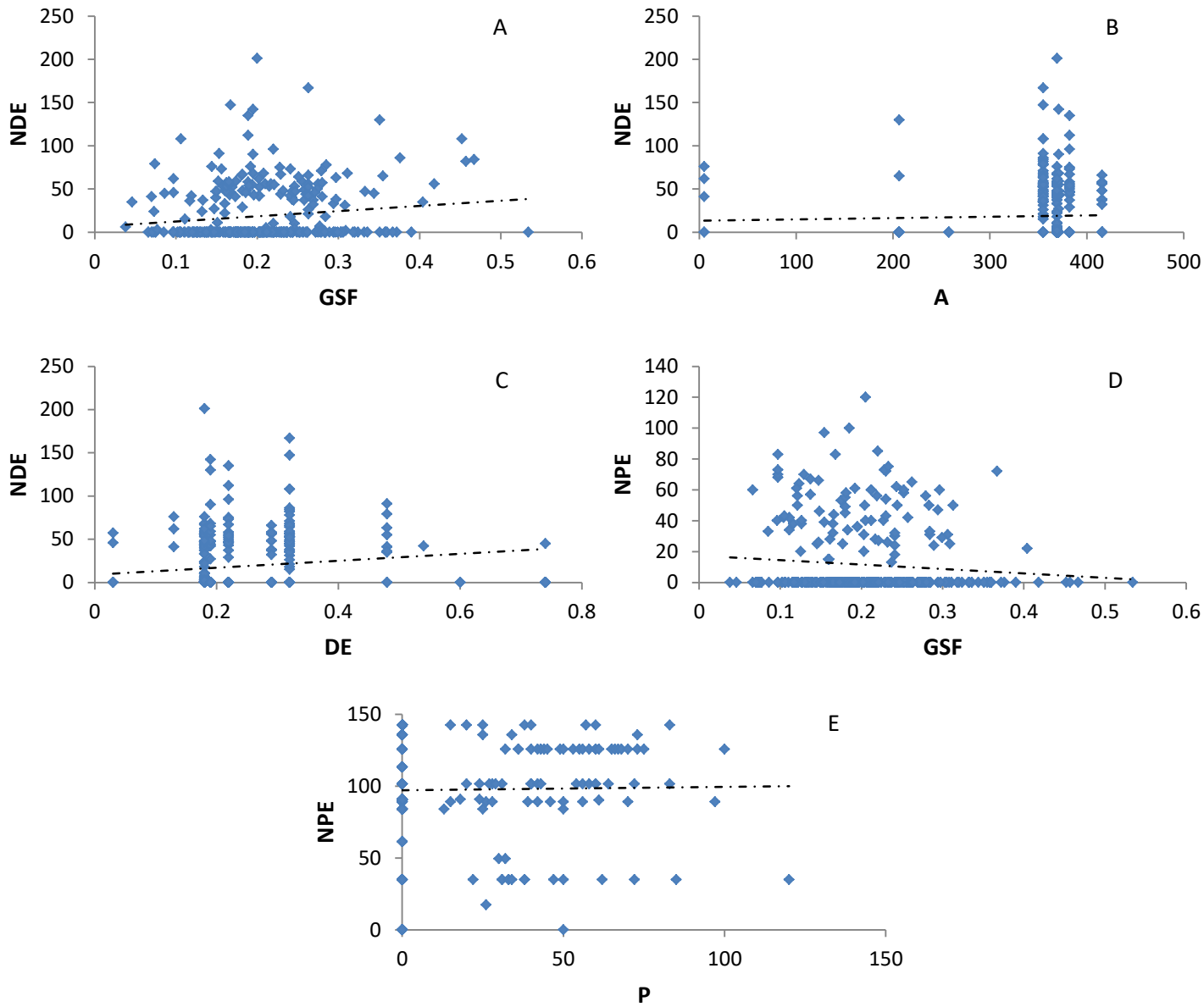
APPENDIX S1

Fitted models for reproductive success variables, presenting all models with a ΔAIC < 2 and the first model with ΔAIC > 2. For dependent variables TEN = total egg number, NHT = number of hatched tadpoles, NST = number of successful tadpoles, NDE = number of desiccated eggs, and NPE = number of predated eggs by fungus or bacteria. For independent variables D = distance to the pond, A = area of the pond, DE = depth of the pond, P = mean precipitation of five preceding days, T = temperature, GSF = global site factor measured (total light incidence), SC = substrate (categorical) and SS substrate species (categorical).

	Model	AIC	ΔAIC	df
TEN~	GSF+SS	3,527.5	0	402
	GSF+SS+DE	3,527.9	0.4	401
	GSF+D+SS	3,528	0.5	401
	T+GSF+SS	3,528.9	1.4	401
	GSF+A+SS	3,529.3	1.8	401
	P+GSF+SS	3,533.1	5.6	402
	GSF+SS+SC	3,533.2	5.7	401
	GSF+SC	3,536.5	9	402
	GSF+A+SC	3,538.1	10.6	401
	T+GSF+SC	3,538.3	10.8	401
	GSF+SC+DE	3,538.3	10.8	401
	P+GSF+SC	3,542.3	14.8	401
	GSF+D	3,550.7	23.2	402
	GSF+P	3,551.6	24.1	402
	GSF+D+A	3,552.7	25.2	401
	GSF+D+DE	3,552.7	25.2	401
	P+GSF+D	3,553	25.5	402
	GSF	3,553.1	25.6	401
	P+T+GSF	3,553.2	25.7	401
	P+GSF+A	3,553.2	25.7	401
	P+GSF+DE	3,553.2	25.7	401
	T+GSF	3,555.2	27.7	402
	GSF+A	3,555.2	27.7	402
	GSF+DE	3,555.2	27.7	402
	T+GSF+A	3,557.2	29.7	401
	GSF+A+DE	3,557.2	29.7	401
	A+SS	3,557.3	29.8	402
	T+SS	3,557.4	29.9	402
	A+SS+DE	3,557.7	30.2	401
	T+D+SS	3,557.8	30.3	401
	T+SS+DE	3,557.9	30.4	401
	T+A+SS	3,559.2	31.7	401

P+SS	3,562.9	35.4	402
T+SS+SC	3,564.4	36.9	401
P+T+SS	3,564.7	37.2	401
P+A+SS	3,564.7	37.2	401
P+SS+DE	3,564.7	37.2	401
P+D+SS	3,564.8	37.3	401
P+SS+SC	3,570.4	42.9	401
D+A+SC	3,571.5	44	401
T+D+SC	3,571.7	44.2	401
A+SC	3,571.8	44.3	402
T+SC	3,572.1	44.6	402
T+A+SC	3,573.8	46.3	401
A+SC+DE	3,573.8	46.3	401
T+SC+DE	3,574	46.5	401
P+SC	3,574.9	47.4	402
P+D+SC	3,576.7	49.2	401
P+T+SC	3,576.9	49.4	401
P+A+SC	3,576.9	49.4	401
P+SC+DE	3,576.9	49.4	401
P	3,581.9	54.4	401
D+P	3,583.4	55.9	402
T+P	3,583.8	56.3	402
P+A	3,583.8	56.3	402
P+DE	3,583.8	56.3	402
P+T+A	3,583.8	56.3	401
P+T+DE	3,583.8	56.3	401
P+A+DE	3,583.8	56.3	401
T+D	3,585	57.5	402
D+A	3,585.1	57.6	402
P+T+D	3,585.3	57.8	401
P+D+A	3,585.3	57.8	401
P+D+DE	3,585.3	57.8	401
T+D+DE	3,586.9	59.4	401
D+A+DE	3,586.9	59.4	401
D+SS+SC	3,586.9	59.4	401
T+D+A	3,587	59.5	401
T	3,587.7	60.2	401
A	3,587.8	60.3	401
T+DE	3,589.6	62.1	402
T+A	3,589.7	62.2	402
A+DE	3,589.7	62.2	402
T+A+DE	3,591.6	64.1	401
GSF+D+SC	3,596.5	69	401
SS+DE	3,680.2	152.7	402

	D+SS+DE	3,680.5	153	401
	SS	3,681	153.5	401
	D+SS	3,681.1	153.6	402
	SS+SC	3,688.1	160.6	402
	D+SC	3,697.7	170.2	402
	D+SC+DE	3,698.4	170.9	401
	SC	3,698.6	171.1	401
	SC+DE	3,699.1	171.6	402
	D	3,710.2	182.7	401
	D+DE	3,712	184.5	402
	DE	3,715.2	187.7	401
	T+GSF+D	*	*	*
	GSF+T+DE	*	*	*
	D+A+SS	*	*	*
	A+SS+SC	*	*	*
	DE+SS+SC	*	*	*
NHT~	GSF+SS+DE	2,205.8	0	401
	A+SS+DE	2,205.8	0	401
	GSF+SC+DE	2,207.4	1.6	401
	A+SC+DE	2,207.4	1.6	401
	T+SC+DE	2,209	3.2	401
	T+SS+DE	2,210	4.2	401
	T+A+DE	2,217.6	11.8	401
	GSF+D+DE	2,217.9	12.1	401
	GSF+A+DE	2,218.5	12.7	401
	D+A+DE	2,218.6	12.8	401
	GSF+T+DE	2,219.5	13.7	401
	T+D+DE	2,221.3	15.5	401
	D+SS+DE	2,403.9	198.1	401
	P+SS+SC	12,004	9,798	401
	P+GSF+SC	12,099	9,893	401
	P+GSF+SS	12,145	9,939	401
	P+SC	12,151	9,945	402
	P+T+SC	12,153	9,947	401
	P+D+SC	12,153	9,947	401
	P+A+SC	12,153	9,947	401
	P+SC+DE	12,153	9,947	401
	P+SS	12,192	9,986	402
	P+T+SS	12,194	9,988	401
	P+D+SS	12,194	9,988	401
	P+A+SS	12,194	9,988	401
	P+SS+DE	12,194	9,988	401
	GSF+P	12,471	10,265	402

P+T+GSF	12,473	10,267	401
P+GSF+D	12,473	10,267	401
P+GSF+A	12,473	10,267	401
P+GSF+DE	12,473	10,267	401
P	12,512	10,306	403
T+P	12,514	10,308	402
D+P	12,514	10,308	402
P+A	12,514	10,308	402
P+DE	12,514	10,308	402
P+T+A	12,514	10,308	401
P+T+DE	12,514	10,308	401
P+A+DE	12,514	10,308	401
P+T+D	12,516	10,310	401
P+D+A	12,516	10,310	401
P*D*DE	12,516	10,310	401
T+DE	15,198	12,992	402
A+DE	15,214	13,008	402
GSF+DE	15,215	13,009	402
GSF+SS+SC	18,117	15,911	401
GSF+A+SC	18,170	15,964	401
T+A+SS	18,274	16,068	401
T+A+SC	18,346	16,140	401
T+SS+SC	18,351	16,145	401
GSF+A+SS	18,404	16,198	401
T+GSF+SC	18,457	16,251	401
A+SC	18,534	16,328	402
D+A+SC	18,535	16,329	401
T+GSF+A	18,553	16,347	401
T+GSF+SS	18,590	16,384	401
A+SS	18,600	16,394	402
GSF+SC	18,792	16,586	402
GSF+D+SC	18,795	16,589	401
SC+DE	18,917	16,711	402
T+D+SS	18,950	16,744	401
T+D+SC	18,965	16,759	401
T+SC	18,974	16,768	402
T+D+A	18,998	16,792	401
T+A	19,012	16,806	402
T+SS	19,015	16,809	402
SS+DE	19,026	16,820	402
GSF+D+SS	19,032	16,826	401
GSF+SS	19,067	16,861	402
D+SS+SC	19,077	16,871	401
SS+SC	19,087	16,881	402

	GSF+D+A	19,191	16,985	401
	GSF+A	19,194	16,988	402
	T+GSF	19,258	17,052	402
	D+A	19,385	17,179	402
	A	19,390	17,184	403
	D+DE	19,633	17,427	402
	T+D	19,693	17,487	402
	DE	19,697	17,491	403
	T	19,700	17,494	403
	D+SC	19,729	17,523	402
	SC	19,749	17,543	403
	GSF	19,794	17,588	403
	GSF+D	19,794	17,588	402
	D+SS	19,922	17,716	402
	SS	19,932	17,726	403
	D	20,645	18,439	403
	T+GSF+D	*	*	*
	D+A+SS	*	*	*
	D+SC+DE	*	*	*
	A+SS+SC	*	*	*
	DE+SS+SC	*	*	*
NST~	GSF+SC+DE	510.35	0	401
	T+GSF+SC	521.95	11.6	401
	GSF+D+SC	522.1	11.75	401
	T+D+SC	522.74	12.39	401
	T+A+DE	588.04	77.69	401
	T+D+SS	824.3	314	401
	P+D+SC	1,166.6	656.3	401
	P+GSF+SC	1,181.7	671.4	401
	P+SC	1,197.9	687.6	402
	P+T+SC	1,199.9	689.6	401
	P+A+SC	1,199.9	689.6	401
	P+SC+DE	1,199.9	689.6	401
	P+D+SS	1,295.3	785	401
	P+GSF+SS	1,302.7	792.4	401
	P+SS	1,309.7	799.4	402
	P+T+SS	1,311.7	801.4	401
	P+A+SS	1,311.7	801.4	401
	P+SS+DE	1,311.7	801.4	401
	P+GSF+D	1,455.8	945.5	401
	D+P	1,457	946.7	402
	P+T+D	1,459	948.7	401
	P+D+A	1,459	948.7	401

P+D+DE	1,459	948.7	401
GSF+P	1,565.1	1,055	402
P+T+GSF	1,567.1	1,057	401
P+GSF+A	1,567.1	1,057	401
P+GSF+DE	1,567.1	1,057	401
P	1,567.3	1,057	403
T+P	1,569.3	1,059	402
P+A	1,569.3	1,059	402
P+DE	1,569.3	1,059	402
P+T+A	1,569.3	1,059	401
P+T+DE	1,569.3	1,059	401
P+A+DE	1,569.3	1,059	401
T+A+SC	2,509.8	1,999	401
GSF+A+SC	2,663.7	2,153	401
D+A+SC	2,679.6	2,169	401
A+SC+DE	2,709.5	2,199	401
A+SC	2,713.9	2,204	402
T+GSF+A	3,454	2,944	401
T+A+SS	3,665.9	3,156	401
T+D+A	3,705.9	3,196	401
GSF+A+SS	3,740.7	3,230	401
T+A	3,862	3,352	402
GSF+D+A	3,985.8	3,475	401
GSF+A	4,103.1	3,593	402
GSF+A+DE	4,106.1	3,596	401
A+SS+DE	4,372.2	3,862	401
A+SS	4,392.3	3,882	402
D+A	4,706.1	4,196	402
D+A+DE	4,709.1	4,199	401
A	4,820.1	4,310	403
A+DE	4,821.9	4,312	402
GSF+SC	7,036.9	6,527	402
T+SC	7,262	6,752	402
GSF+SS+DE	7,393.3	6,883	401
GSF+D+DE	7,740.1	7,230	401
T+SS+DE	7,743.3	7,233	401
GSF+DE	7,813.1	7,303	402
T+GSF+SS	7,990.1	7,480	401
GSF+D+SS	8,000.9	7,491	401
T+D+DE	8,018.5	7,508	401
GSF+SS	8,043	7,533	402
T+DE	8,054.2	7,544	402
T+SS	8,270.7	7,760	402
T+GSF	8,287.9	7,778	402

	GSF+D	8,308.4	7,798	402
	GSF	8,344.8	7,834	403
	SC+DE	8,373.4	7,863	402
	T+D	8,478.1	7,968	402
	T	8,516.5	8,006	403
	SC	8,778.1	8,268	403
	D+SC	8,780	8,270	402
	SS+DE	9,176.6	8,666	402
	D+SS+DE	9,179.1	8,669	401
	SS	9,386.5	8,876	403
	D+SS	9,386.8	8,876	402
	DE	9,433.8	8,923	403
	D+DE	9,435.6	8,925	402
	D	9,649.4	9,139	401
	T+SC+DE	18,663	18,153	401
	SS+SC	*	*	*
	P+SS+SC	*	*	*
	T+GSF+D	*	*	*
	T+SS+SC	*	*	*
	GSF+T+DE	*	*	*
	GSF+SS+SC	*	*	*
	D+A+SS	*	*	*
	D+SS+SC	*	*	*
	D+SC+DE	*	*	*
	A+SS+SC	*	*	*
	DE+SS+SC	*	*	*
NDE~	GSF+A+DE	2009.8	0	401
	GSF+T+DE	6597.8	4,588	401
	T+GSF+SS	6947	4,937	401
	GSF+A+SS	7,004.7	4,995	401
	GSF+D+A	7,121	5,111	401
	T+GSF+SC	7,121.3	5,112	401
	GSF+D+SS	7,404.9	5,395	401
	T+GSF+A	7,476.3	5,467	401
	GSF+SS+DE	7,661	5,651	401
	GSF+D+SC	7,663	5,653	401
	GSF+SC+DE	7,824.9	5,815	401
	GSF+D+DE	7,869.4	5,860	401
	P+GSF+SC	11,089	9,079	377
	P+D+SC	11,270	9,260	377
	P+GSF+SS	11,276	9,266	377
	P+D+SS	11,420	9,410	377
	P+T+SS	11,424	9,414	377

P+A+SS	11,424	9,414	377
P+A+SC	11,424	9,414	377
P+SS+DE	11,424	9,414	377
P+SC+DE	11,424	9,414	377
P+SS	11,427	9,417	378
P+GSF+D	11,558	9,548	377
P+T+GSF	11,568	9,558	377
P+GSF+A	11,568	9,558	377
P+GSF+DE	11,568	9,558	377
GSF+P	11,575	9,565	378
D+P	11,686	9,676	378
P+T+D	11,687	9,677	377
P+D+A	11,687	9,677	377
P+D+DE	11,687	9,677	377
P	11,693	9,683	379
T+P	11,694	9,684	378
P+A	11,694	9,684	378
P+DE	11,694	9,684	378
P+T+A	11,694	9,684	377
P+T+DE	11,694	9,684	377
P+A+DE	11,694	9,684	377
P+SS+SC	11,694	9,684	377
T+SS+DE	14,553	12,543	401
T+SC+DE	14,644	12,634	401
A+SS+DE	14,756	12,746	401
T+D+DE	14,915	12,905	401
T+A+DE	14,992	12,982	401
TDE	15,004	12,994	379
GSF+DE	15,122	13,112	378
D+A+DE	15,126	13,116	401
A+DE	15,262	13,252	378
GSF+SS	15,938	13,928	378
T+A+SS	15,999	13,989	401
T+D+SS	16,032	14,022	401
T+SS	16,043	14,033	378
A+SS	16,190	14,180	378
GSF+SC	16,409	14,399	378
D+SS+DE	16,518	14,508	401
SS+DE	16,550	14,540	378
T+GSF	16,628	14,618	378
D+A+SC	16,737	14,727	401
D+SS	16,774	14,764	378
A+SC	16,792	14,782	378
SS	16,794	14,784	379

	GSF+D	16,888	14,878	378
	T+D+A	16,921	14,911	401
	GSF+A	16,954	14,944	378
	T+A	17,017	15,007	378
	T+D	17,026	15,016	378
	GSF	17,056	15,046	379
	T	17,124	15,114	379
	D+A	17,257	15,247	378
	A	17,387	15,377	379
	D+DE	17,440	15,430	378
	SC	17,449	15,439	379
	DE	17,605	15,595	379
	D	17,905	15,895	379
	T+SC	*	*	*
	D+SC	*	*	*
	P+SC	*	*	*
	SS+SC	*	*	*
	SC+DE	*	*	*
	P+T+SC	*	*	*
	T+GSF+D	*	*	*
	T+D+SC	*	*	*
	T+A+SC	*	*	*
	T+SS+SC	*	*	*
	GSF+A+SC	*	*	*
	GSF+SS+SC	*	*	*
	D+A+SS	*	*	*
	D+SS+SC	*	*	*
	D+SC+DE	*	*	*
	A+SS+SC	*	*	*
	A+SC+DE	*	*	*
	DE+SS+SC	*	*	*
NPE~	GSF+P	1,388.3	0	378
	T+P	1,388.4	0.1	378
	P+DE	1,388.4	0.1	378
	P+T+A	1,388.7	0.4	377
	P+T+GSF	1,390.3	2	377
	P+GSF+A	1,390.3	2	377
	P+GSF+DE	1,390.3	2	377
	P+T+DE	1,390.4	2.1	377
	P+SS	1,392.7	4.4	378
	P+SC	1,392.9	4.6	378
	P+T+SS	1,394.7	6.4	377
	P+A+SS	1,394.7	6.4	377

P+SS+DE	1,394.7	6.4	377
P+T+SC	1,394.9	6.6	377
P+GSF+SC	1,394.9	6.6	377
P+A+SC	1,394.9	6.6	377
P+SC+DE	1,394.9	6.6	377
P+D+SS	1,395.5	7.2	377
P+GSF+SS	1,395.6	7.3	377
P+D+SC	1,396.9	8.6	377
P+SS+SC	1,398.6	10.3	377
A	1,400.9	12.6	401
T+A	1,400.9	12.6	378
GSF+A	1,401.1	12.8	378
A+SC	1,401.3	13	378
A+DE	1,401.9	13.6	378
T+A+DE	1,402.7	14.4	401
P+A	1,402.8	14.5	378
A+SC+DE	1,402.8	14.5	401
D+A	1,402.9	14.6	378
D+A+DE	1,403	14.7	401
T+A+SC	1,403.2	14.9	401
D+A+SC	1,403.5	15.2	401
T+D+A	1,404.6	16.3	401
A+SS+DE	1,406.2	17.9	401
A+SS	1,406.4	18.1	378
T+A+SS	1,407.3	19	401
T+SC+DE	1,412.5	24.2	401
P	1,431.7	43.4	379
SS+SC	1,454.5	66.2	378
GSF+A+SS	4,176	2,788	401
GSF+A+SC	4,294	2,906	401
T+GSF+A	4,354.8	2,967	401
T+GSF+SS	4,810.8	3,423	401
GSF+D+DE	5,193.5	3,805	401
GSF+DE	5,226	3,838	378
GSF+D	5,581	4,193	378
GSF	5,606	4,218	379
T+SS+SC	12,044	10,656	401
GSF+SC	12,254	10,866	378
T+D+SC	12,344	10,956	401
T+SC	12,354	10,966	379
D+SS+SC	12,481	11,093	401
D+SC+DE	12,770	11,382	401
SC+DE	12,782	11,394	378
D+SC	12,839	11,451	378

SC	12,856	11,468	379
T+SS+DE	12,931	11,543	401
GSF+SS	13,024	11,636	378
T+D+SS	13,049	11,661	401
T+D+DE	13,103	11,715	401
T+SS	13,114	11,726	378
T+DE	13,120	11,732	379
T+GSF	13,254	11,866	378
T+D	13,331	11,943	378
T	13,353	11,965	379
D+SS+DE	13,436	12,048	401
D+SS	13,502	12,114	378
SS+DE	13,509	12,121	378
SS	13,587	12,199	379
D+DE	13,697	12,309	378
DE	13,717	12,329	379
D	13,809	12,421	379
GSF+SS+DE	3E+08	3E+08	401
D+P	*	*	*
P+T+D	*	*	*
P+GSF+D	*	*	*
P+D+A	*	*	*
P+D+DE	*	*	*
P+A+DE	*	*	*
T+GSF+D	*	*	*
T+GSF+SC	*	*	*
GSF+T+DE	*	*	*
GSF+D+A	*	*	*
GSF+D+SS	*	*	*
GSF+D+SC	*	*	*
GSF+A+DE	*	*	*
GSF+SS+SC	*	*	*
GSF+SC+DE	*	*	*
D+A+SS	*	*	*
A+SS+SC	*	*	*
DE+SS+SC	*	*	*

Comprobante de requisitos de titulación por artículo

The South American Journal of Herpetology
Ovoposition site selection and conservation insights of two tree frogs (Agalychnis moreletii and A. callidryas)
--Manuscript Draft--

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Abstract:	Oviposition site selection is a trait that directly affects the biological fitness and it is related to a large number of environmental factors. A conserved trait that restrains oviposition site selection in tree frogs is the laying of clutches 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 species throughout 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 of southern Mexico. We characterized the vegetation, area and depth fluctuation of the pond, and temperature and precipitation of the four sites. Every site was visited three times a week during four months to register the development of each clutch, the number of eggs, substrate species, distance to the pond, sunlight incidence, and their condition. We performed parametric and non-parametric statistics to explore the differences among sites and a total of 92 GLMs to determine which variables affects the condition of the clutches. We found significant differences on the vegetation structure, the area and pond depth among sites. Oviposition site selection was observed at two different scales and the reproductive success was determined by precipitation, light incidence and substrate availability. 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 for the reproductive success of these species.

Dear Dr Hibraim Adan Perez-Mendoza,

Your submission entitled "Ovoposition site selection and conservation insights of two tree frogs (Agalychnis moreletii and A. callidryas)" has been been assigned the following manuscript number: SAJH-D-17-00103.

You will be able to check on the progress of your paper by logging on to http://sajh.edmgr.com/.

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Kind regards,

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The South American Journal of Herpetology

Discusión

En el estudio se observó que sí hay elección de sitio de puesta en *Agalychnis moreletii* y *A. callidryas*, en dos escalas espaciales diferentes. Primero, hay una clara preferencia por el sitio 4, este sitio tiene un volumen de dosel significativamente más alto que los sitios 2 y 3, pero similar al sitio 1. A pesar de que ambos sitios no tienen diferencias significativas, la dispersión de los valores del volumen de la copa es mayor en el sito 1, siendo el sitio 4 en el que el sobrelapamiento de los diferentes estratos del dosel es mayor. El sitio 4 también tiene un área de estanque significativamente más pequeña y el estanque es significativamente menos profundo que los sitios 1 y 3, pero similares al sitio 2. Esta combinación de factores parece hacer que este sitio sea el más adecuado y frecuente para la oviposición, siendo la disponibilidad de agua un factor necesario para este atributo como se ha visto en otros estudios (Dias *et al*., 2014; Vilela *et al*., 2015; Cuhna *et al,.* 2016; Mageski *et al*., 2016).

En una escala más fina, hay varios factores que afectan a la elección del sitio de puesta. Observamos que la luz es un factor importante en este atributo del comportamiento, encontramos que el número de huevos cambia con la cantidad de luz que recibe un sitio siendo los valores intermedios de luz los más elegidos (de 0.14 a 0.53). Esta variable está estrechamente relacionada a la estructura vertical y horizontal de la vegetación, sin embargo, hay pocos estudios donde se relacionen los atributos de la vegetación con la reproducción de los anfibios (Shulse *et al*., 2012). La complejidad de un bosque primario con inundación anual, es importante para *A. moreletii* y *A. callidryas*. En términos de la disponibilidad de luz, ésta fue similar en todos nuestros sitios estudiados, sin embargo, esta superposición de las copas de los árboles y arbustos en el sitio 4 proporciona a las ranas mayor cantidad de lugares para colocar sus huevos. Por otro lado, esto también puede mejorar la supervivencia de los adultos, proporcionando un mayor número de áreas de forrajeo y percha, lo que propicia que disminuya la vulnerabilidad a los depredadores. Colocar los huevos en las hojas, raíces, ramas y troncos cercanos a los estanques se ha registrado en otras especies del grupo como: *Phyllomedusa boliviana* (Vaira, 2001), *P. azurea* (Dias *et al*., 2014), *P. brumeisteri* (Abrunhosa y Wogel, 2004), sugiere un rasgo altamente preservado en el grupo de los Phyllomedusinos.

La disponibilidad de agua es muy importante para el desarrollo de los anfibios. La profundidad y el área de la poza fueron dos de las variables más importantes que explican el número de huevos que lograron desarrollarse, el número de huevos que fueron exitosos y el número de huevos que se desecaron. Estas variables están estrechamente relacionadas con la precipitación y es bien sabido que los anfibios dependen de la disponibilidad de agua y esto

está estrechamente relacionado con el éxito reproductivo (Cayuela *et al*., 2012; Walls *et al*., 2013); específicamente, la persistencia de los cuerpos de agua es determinante para que la eclosión sea adecuada. Si la lluvia no es constante, el estanque se seca y los renacuajos eclosionan sobre el sustrato. Esto explica que las hembras, en su mayoría, ponen sus huevos en distancias cercanas al agua. En otras especies, el riesgo de desecación de los cuerpos de agua es una variable importante que influye en el éxito reproductivo como sucede en *Lithobates sylvaticus* (Gervasi y Foufopoulos, 2008), *Bombina variegata* (Barandun y Reyer, 1997), *Phrynobatrachus guinensis* (Rudolf y Rödel, 2005) y *Bufo bufo* (Laurila, 1998), por nombrar algunos. Sin embargo, los estanques permanentes tienen mayor abundancia y diversidad de depredadores que los cuerpos de agua temporales, lo que evita la colonización o reproducción de anfibios (Touchon y Worley, 2015). Esto puede explicar por qué en el sitio 1 no se encontró ninguna puesta e incluso ningún adulto a pesar de que la gente local menciona que las ranas eran abundantes. Sin embargo este fenómeno se podría haber dado porque también hubo introducción de peces cíclidos (posiblemente *Petenia splenda)* en las últimas décadas. En otros estudios también se ha observado que la presencia de peces propicia que las poblaciones de anfibios decaigan o se extingan localmente (Hecnar y M'Closkey, 1997; Semlitsch y Gibbons, 1998; Kats y Ferrer, 2003; Collins y Storfer, 2003).

Por otro lado, se observó que las hembras tenían una preferencia por poner sus huevos en hojas del género *Inga* sp. (Leguminosae). Aunque, esto podría ser una correlación espuria ya que este árbol tiene una gran biomasa en el sitio y probablemente este árbol ofrece cierta protección a la radiación solar por su configuración de la copa que es ancha y larga. Por otro lado, se ha reportado que *Inga* sp. puede tener una defensa repelente y de anti herviboría contra los insectos (Koptur, 1985, Coley *et al*., 2005; Kursar *et al*., 2009). También, la flexibilidad de las hojas que tienen las leguminosas debido a pulvinus (un engrosamiento en la base de la hoja, Rodrigues y Machado, 2008), puede permitir que las puestas permanezcan en las hojas y que estas no se desprendan a pesar del viento, la lluvia o incluso depredadores grandes.

Existe evidencia de que la luz total que llega a un sitio afecta el tiempo de desarrollo embrionario (Skelly, 2004; Hawley, 2010) así como la presencia y ausencia de los anfibios en lugares templados (Halverston *et al*., 2003). Nuestros resultados sugieren que esto también ocurre en áreas tropicales y por lo tanto influye en la elección de sitio de puesta, en el desarrollo de los huevos, la desecación, la depredación y el éxito reproductivo. En realidad, la luz total fue el único factor presente en todos los modelos con menor AIC, de esta manera la luz total a la cual está expuesto cada uno de los sitios donde se colocaron las puestas, podrían

estar mediando el tiempo de desarrollo de los huevos, así como la desecación y la depredación por los hongos. Los huevos puestos en áreas abiertas tienen un desarrollo del huevo relativamente más rápido, lo que les permite alcanzar etapas larvarias en menor tiempo y caer al cuerpo del agua antes de que se seque (Saenz *et al*., 2003, Skelly, 2004, Székely *et al*., 2010); sin embargo, esto aumenta el riesgo de desecación de la puesta (debido a la pérdida de humedad). Por otro lado, las puestas colocadas en áreas cubiertas de la luz tienen una menor tasa de desarrollo y menor riesgo de desecación, pero son más vulnerables a las bacterias u hongos que dependen de la humedad. Que las hembras puedan escoger intervalos de luz específicos nos da indicios de que la especie podría tener buena visión bajo el dosel en condiciones de baja luz y probablemente pueden distinguir los claros que hay en la copa de los árboles durante la noche. Realmente no se sabe qué mecanismos están implicados a la hora de elegir sitios con diferente incidencia de luz en la obscuridad. Hay estudios que se demuestra que algunas ranas arborícolas tienen una buena visión nocturna (Gómez *et al*., 2010).

Perspectivas de conservación

Nuestros resultados confirman que existe elección de sitio de puesta de A. moreletii y A. callidryas y por tanto, los huevos no son puestos al azar. Es evidente también que se necesitan bosques con estructura vertical y horizontal compleja y que además se inunden una vez al año. Ambas especies tenían un amplio intervalo de distribución geográfica y se ha reducido a áreas pequeñas debido a la conversión del uso de suelo en el sur de México (Ortiz-Espejel y Toledo, 1998, Díaz-Gallegos *et al*., 2008) y América Central (Laurence, 1999). La degradación de los bosques y la conversión a pastizales y tierras de cultivo, reduce en gran medida la diversidad vegetal y la compleja estructura vertical y horizontal de la vegetación (Franklin y Van Pelt, 2004). Esto tiene un impacto negativo en la disponibilidad de microhábitats para el desove, afectando la dinámica poblacional. Aunado a estos problemas, los cambios en los patrones de lluvia (Dore, 2005) asociados con eventos periódicos como "El Niño" aumentan la vulnerabilidad de ambas especies.

Conclusiones

Hay elección de sitio de puesta de *A. moreletii* y *A. callidryas* en dos escalas diferentes.

La cantidad luz resultó ser el factor que afecta la elección de sitio de puesta, así como el éxito reproductivo, la depredación por hongos, el desarrollo y la desecación.

Las hojas de *Inga* sp. son los sitios preferidos para la elección del sitio de puesta por *A. moreletii* y *A. callidryas*.

La disponibilidad de agua en los sitios resultó ser fundamental para el éxito reproductivo de las puestas de *A. moreletii* y *A. callidryas*.

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