Courtship, Nesting Behaviors, and Oviposition Site Selection of Malayan Flying Frog, *Zhangixalus prominanus* (Smith, 1924) at Sirindhorn Waterfall, Hala-Bala Wildlife Sanctuary, Narathiwat, Thailand

Hattaya Jaroensap

A Thesis Submitted in Partial Fulfillment of the Requirements for the Degree of
Master of Science in Biology (International Program)
Prince of Songkla University
2022

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I hereby certify that this work has not been accepted in substance for any degree, and is not being currently submitted in candidature for any degree.

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ชื่อวิทยานิพนธ์	พฤติกรรมการเกี้ยวพาราสี การสร้างรัง และการเลือกแหล่งวางไข่ของปาดเขียวตีนแดง (*Zhangixalus prominanus*) บริเวณน้ำตกสิรินธร สถานีวิจัยสัตว์ป่าป่าพรุ ป่าฮาลา-บาลา จังหวัดนราธิวาส ประเทศไทย
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ปีการศึกษา	2564

บทคัดย่อ

ศึกษาอิทธิพลของปัจจัยที่เกี่ยวกับช่วงเวลา สภาพภูมิอากาศ และลักษณะของแหล่งที่อยู่อาศัยต่อการใช้แหล่งสืบพันธุ์ การเลือกแหล่งวางไข่ และพฤติกรรมการสืบพันธุ์ ของประชากรปาดเขียวตีนแดง *Zhangixalus prominanus* บริเวณน้ำตกสิรินธร ในระหว่างเดือนมกราคม พ.ศ. 2561 ถึง เดือนมิถุนายน พ.ศ. 2562 โดยวิธีการติดตามและระบุตัวด้วยภาพถ่าย พบว่า [1] ปาดเขียวตีนแดงประชากรนี้สามารถสืบพันธุ์ได้ต่อเนื่องตลอดทั้งปี โดยสามารถพบปาดเพศผู้เต็มวัย ปาดเพศเมียกำลังอุ้มท้อง และการสร้างรังโฟมได้ตลอดระยะเวลาที่ศึกษา ซึ่งปัจจัยที่เกี่ยวกับสภาพภูมิอากาศที่มีผลต่อการปรากฏตัวของปาดเพศผู้เต็มวัย ปาดเพศเมียเต็มวัย และการวางไข่ ได้แก่ ฤดูกาล ค่าเฉลี่ยของอุณหภูมิในอากาศ และค่าเฉลี่ยของความชื้นสัมพัทธ์มีผลต่อจำนวนปาดเพศผู้ที่ปรากฏตัวในพื้นที่ ขณะที่ปริมาณน้ำฝนและการปรากฏตัวของปาดเพศผู้มีผลต่อการปรากฏตัวของปาดเพศเมีย และการปรากฏตัวของปาดเพศเมียมีผลต่อการปรากฏการวางไข่ [2] แม้ว่าปัจจัยที่เกี่ยวข้องกับสภาพอากาศและช่วงเวลา ไม่ได้มีผลโดยตรงต่อความน่าจะเป็นที่จะก่อให้เกิดพฤติกรรมการวางไข่ แต่ปัจจัยจากลักษณะของแอ่งน้ำที่ใช้สืบพันธุ์มีผลต่อความน่าจะเป็นของการเลือกแหล่งวางไข่ ประกอบด้วย ค่าความลึกของแอ่งน้ำ ค่าความเป็นกรดด่างของน้ำ ปริมาณออกซิเจนละลายในน้ำ และลักษณะที่จำเพาะของแอ่งน้ำ [3] อีกทั้งจากการเฝ้าติดตามปาดเขียวตีนแดงแต่ละตัวพบว่าพวกมันจะเข้ามาใช้พื้นที่นี้เพื่อการสืบพันธุ์เท่านั้น โดยปาดเพศผู้จะเข้ามาเพื่อปกป้องอาณาเขตสืบพันธุ์และครอบครองแอ่งน้ำสำหรับสืบพันธุ์เพียงตัวเดียว ขณะที่ปาดเพศเมียจะปรากฏตัวเฉพาะเมื่อต้องการวางไข่และเลือกเข้าคู่กับปาดเพศผู้ที่ครอบครองพื้นที่ขนาดใหญ่ใกล้แหล่งน้ำมากที่สุด พบรูปแบบการเข้าคู่สืบพันธุ์ 2 แบบ คือแบบเพศเมียสืบพันธุ์กับเพศผู้หนึ่งตัว (monandry) และกับเพศผู้หลายตัว (polyandry) และบ่งชี้ได้ว่ามีระบบการสืบพันธุ์แบบปกป้องทรัพยากร (resource defense mating system) คือบริเวณที่คู่สืบพันธุ์เลือกสร้างรังโฟมเป็นบริเวณเดียวกับที่ปาดเพศผู้ที่ถูกเลือกครอบครองซึ่งแตกต่างจากที่มีการรายงานในกลุ่มกบเขียดที่อาศัยอยู่บนต้นไม้ ข้อมูลจากการศึกษาในครั้งนี้จะเป็นประโยชน์ต่อการบริหารจัดการพื้นที่ปกปักษ์และการอนุรักษ์พันธุ์สัตว์ป่าต่อไป อีกทั้งยังนำไปสู่การประมวลองค์ความรู้และการศึกษาในแขนงสาขาที่หลากหลายทางชีววิทยา

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ABSTRACT

The breeding habitat use, oviposition site selection, and breeding behaviors of *Zhangixalus prominanus* at Sirindhorn Waterfall was studied from January 2018 to June 2019. The abiotic factors including temporal factors, climatic factors, and habitat characteristics were considered. The frogs were marked and monitored by photographic identification technique. The result shows that [1] the *Z. prominanus* was a prolonged breeder, the adult male, gravid female, and foam nests were found throughout the study. The climatic factors effected the appearance of males, females, and clutching. The seasons, an average of air temperature, also an average of relative humidity influenced the number of males occurring. The male occurrence and the rainfall affected females occurring, then the female occurrence affected clutches appearing. [2] Although the climatic and temporal factors did not impact the probability of clutching, the breeding pool characteristics affected the probability of oviposition selection including the water depth, pH, dissolved oxygen (DO), and pool characteristics. [3] Finally, the individual monitoring represented the population only use this site for breeding activities. The male arrived at the site for territorial defending and monopolize the breeding pool while female occurred for eggs laying by choosing the greater occupier male and as close to the water surface for mating. Moreover, it had two mating patterns (monandry and polyandry), with the resource defense mating system which was the defending site was the oviposition site, and unlike other arboreal anuran species that were reported. These pieces of information are helpful for protected area management and wildlife conservation, besides guiding research combining among diverse fields of biology.

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CHAPTER 1

INTRODUCTION

Amphibians are ectothermic vertebrates with biphasic life cycle. Typically, their larvae are aquatic, but adults are terrestrial (Pough et al., 2004; Wells, 2007). The interaction between physiological modification of matured males and females, also ecological conditions conduct reproductive activity display during the breeding period (Pough et al., 2004; Ten Eyck 2005; Wells, 2007; de Andrade, et al., 2017). The number of known amphibian species is approximately 8,000, of which nearly 90% are anuran (frog and toad) (The American Museum of Natural History; Frost, 2018). Recently, many amphibians have been threatened and rank on high risk of becoming extinct (Stuart et al., 2004, IUCN, 2018). The number of amphibian species is continually on decline due to human activities, including the introductions of exotic species, aquatic pollutions, habitat modifications, as well as the climate change (Collins and Storfer, 2003; Beebee and Griffiths, 2005). Thus, influence of abiotic factors (e.g., climate, season, habitat characteristics) on breeding habitat use, reproductive activities, and oviposition site selection are continually studied (Wells, 2007; Grant et al., 2009; Steen et al., 2013; de Andrade, et al., 2017).

The Anuran are highly diverse and unique in morphology, behavior, and ecology, they distribute in many locations but generally near a water source (Wells, 2007, Sridhar and Bickford, 2015; de Andrade, et al., 2017). Current evidence suggests that frog species have required specific habitat characters to breed (Wells, 2007; Brown et al., 2011; Barrett et al., 2016; Martha, 2017). The frogs can decide to choose the egg-laying duration and location (Anderson et al., 1999; Rodrigues et al., 2005; Wells, 2007; Li et al., 2018). The ecological condition such as rainfall, temperature, and humidity are usually reported that encourage the breeding activities of anuran species, but not absolute (Walther et al., 2002; Oseen and Wassersug, 2002; Saenz et al. 2006; Wells, 2007; Erdtmann and Lima, 2013). Some anuran species can not indicate the factors that influence breeding activities (Wells, 2007).

Mostly, the breeding activities of anuran were focused on courtship until egg-laying or types of parental care (if any). The breeding strategies of anurans impact the reproductive success and maximize fitness (Crump, 1974; Alcock, 2005; Wells, 2007). Furthermore, the oviposition site selection directly impacts the survival, growth, and development of offspring until species existence (Wilbur and Collins, 1973; Laurila, 1998; Newman 1992; Martha, 2017). Previous research mentioned that influence of environmental changing could modify or inhibit the breeding behavioral expression and oviposition decision (Ursprung et al., 2011; Toledo et al., 2012; Tumulty et al., 2014; Sridhar and Bickford, 2015; Luna-Gómez et al., 2017). The specific environmental conditions relate to the breeding activities of anuran, thus, studies of reproductive behavioral ecology are vital to future conservation management (Beebee, 1996; Rodrigues and Bertoluci, 2002; Wells, 2007; Hamer and McDonnell, 2008).

The gliding frogs in the family Rhacophoridae were interesting, this family contains 426 species in 19 genera (Frost, 2018) and are restricted distributed in a tropical zone such as Tropical Africa, China, Southeast Asia, and Greater Sunda Islands. They are easily recognized by their enlarged toe disc at the tip of the fingers and the extensive webbing used for gliding (Pough et al., 2004; Wells, 2007; Frost, 2016). They live mainly arboreal and stay close to the canopy and arrive at ground level to breed. Their spectral lifestyles have prevented herpetologists from understanding their ecology, especially from the perspective of reproduction biology (Sullivan et al., 1995; Halloy and Fiaño, 2000; Wells, 2007).

This study focused on the Malayan Flying Frog (*Zhangixalus prominanus*), the frog has a very limited distribution range since it can be found in the Thai-Malay Peninsula and on Sumatra Island (Harvey et al., 2002; Sukumaran et al., 2004). In Thailand, *Z. prominanus* were reported at two locations, which are Hala-Bala Wildlife Sanctuary, Narathiwat, and Khao Sok National Park (Thong-aree et al., 2011; Niyomwan et al., 2019). Since *Z. prominanus* is relatively rare and knowledge about the ecology, especially its breeding behavior is still limited. This study aimed to investigate the influence of abiotic factors on breeding habitat use, reproductive behaviors (including reproductive activity pattern, breeding activities, reproductive mode, mate choice, and mating system), as well as oviposition site selection of *Z. prominanus* at the Hala-Bala Wildlife Sanctuary.

1.1 Research questions

1. How is the influence of temporal and climate factors on the breeding habitat use of Malayan flying frog, *Zhangixalus prominanus* at Sirindhorn Waterfall, Hala-Bala Wildlife Sanctuary, Narathiwat, Thailand?

2. How is the oviposition site characteristic, and what abiotic factors influence the oviposition selection of *Z. prominanus* at Sirindhorn Waterfall, Hala-Bala Wildlife Sanctuary, Narathiwat, Thailand?

3. What are the reproductive activities and breeding behaviors of *Z. prominanus* at Sirindhorn Waterfall, Hala-Bala Wildlife Sanctuary, Narathiwat, Thailand?

1.2 Objectives

1. To investigate the effect of temporal and climatic parameters on the breeding habitat use of the Malayan flying frog, *Zhangixalus prominanus* at Sirindhorn Waterfall, Hala-Bala Wildlife Sanctuary, Narathiwat, Thailand.

2. To evaluate the abiotic parameters on oviposition site selection of *Z. prominanus* at Sirindhorn Waterfall, Hala-Bala Wildlife Sanctuary, Narathiwat, Thailand.

3. To describe reproductive activities and breeding behaviors of *Z. prominanus* at Sirindhorn Waterfall, Hala-Bala Wildlife Sanctuary, Narathiwat, Thailand.

1.3 Hypothesis

1. The breeding habitat use of the Malayan flying frog, *Zhangixalus prominanus* at Sirindhorn Waterfall, Hala-Bala Wildlife Sanctuary, Narathiwat, Thailand relates to the temporal and climatic parameters.

2. The oviposition site selection of *Z. prominanus* at Sirindhorn Waterfall, Hala-Bala Wildlife Sanctuary, Narathiwat, Thailand is influenced by the abiotic parameters.

3. Reproductive activities and breeding behaviors of *Z. prominanus* at Sirindhorn Waterfall, Hala-Bala Wildlife Sanctuary, Narathiwat, Thailand are not similar to members of the Family Rhacophoridae.

CHAPTER 2

LITERATURE REVIEW

2.1 Anurans (Class Amphibia)

The anurans are known as frogs and toads, they are vertebrate taxa with four legs and no tail. the anurans have the highest species diversity in Class Amphibia, containing about 7,000 frog species (Frost, 2018). The frogs are ectothermic animals with a double life, the juvenile (tadpole to froglet) are aquatic life meanwhile adults are terrestrial (Pough et al., 2004; Wells, 2007). Even though the distribution of frogs is generally near a water source, some species are quite specialized for terrestrial, fossorial, or arboreal life (Wells, 2007, Sridhar and Bickford, 2015; de Andrade, et al., 2017). The adaptation of frogs to survive in a variety of environments is an interaction between physiology and behavior (de Andrade, et al., 2017; Luna-Gómez et al., 2017). The differentiation of reproductive behavioral strategies between and within species represents the varieties of habitat use and oviposition sites that impact the reproductive success (Haddad and Pombal, 1998; Haddad and Prado, 2005; Wells, 2007; Toledo et al, 2012; de Andrade et al., 2017). Thus, they are often used as models in functional anatomy, behavioral ecology, and evolutionary biology of vertebrates (Beebee, 1996; Rodrigues and Bertoluci, 2002; Wells, 2007; Hamer and McDonnell, 2008).

2.2 Reproductive behaviors of anurans

The reproductive activities of matured males and females display during the breeding season, are influenced by the interplay between physiological modification and environmental conditions (Pough et al., 2004; Ten Eyck 2005; Wells, 2007; de Andrade, et al., 2017). The ecological factors that could affect frogs' reproductive behavior include biotic factors, such as competition and predation (Walther et al., 2002; Oseen and Wassersug, 2002), also the abiotic factors, such as photoperiod, rainfall, temperature, and humidity (Saenz et al. 2006; Grant et al., 2009; de Andrade, et al., 2017). Therefore, breeding habitat characteristics can influent their breeding behavior (Haddad and Prado, 2005; Toledo et al., 2012; Wells, 2007; Indermaur et al., 2010). The previous research suggests that specific environmental conditions relate to the breeding activities of anuran. So, the studies of reproductive behavioral ecology are necessary for future conservation management (Beebee, 1996; Rodrigues and Bertoluci, 2002; Wells, 2007; Hamer and McDonnell, 2008).

Previous studies about reproductive behaviors of the anurans reported a high competition between males in mating choice and continuous oviposition selection for reproductive success and to maximize fitness (Crump, 1974; Alcock, 2005; Wells, 2007). The reproductive behavioral study in frogs mostly focused on courtship, mating, until egg-laying, and types of parental care (Crump 1974; Sullivan et al., 1995; Kadadevaru and Kanamadi; 2000; Prado et al., 2005; Wells, 2007). Typically breeding behavior of frogs starts with courtship by the vocal calling of male frogs (Wells 1977; Duellman and Trueb, 1994). Then territory defense followed attractive females at terrestrial calling sites or aquatic breeding sites (Mitchell, 2002; Wells, 2007; Byrne and Roberts, 2012). Some species do not only display the advertisement call but also represent the physical fighting for territory defending (Ryan, 1986; Bastos and Haddad, 2002). The male frogs usually show courtship close to water sources, where they can increase mating and spawning opportunities (Vilaça et al., 2011; de Oliveira, 2017). When female approaches calling male, it suddenly grabs onto a female back, called amplexus (Pough et al., 2004; Wells, 2007) which is the one part of the mating process in externally fertilizing species (Kadadevaru and Kanamadi, 2000; Osikowski, 2001; Kraaijeveld et al., 2004; Sztatecsny et al., 2006). Finally, the amplexus deposits eggs close to water areas, and a few anuran species have parental care that male and/or female monitor and protect their offspring after egg laying (Pough et al., 2004; Wells, 2007).

2.2.1 Breeding habitat use (spatial and temporal patterns)

The spatial and temporal pattern of breeding habitat use is usually beneficial to wildlife management (Price et al., 2005; Wells, 2007; Yetman and Ferguson, 2011).

The previous studies show that these frogs used different aquatic features at different times for different purposes (Kato et al., 2010; Yetman and Ferguson, 2011; Pitt et al., 2017). Although some species of frogs could lay their eggs in the soil with high humidity (Wells, 2007, Sridhar and Bickford, 2015; de Andrade, et al., 2017), most frogs have a larval stage in water until metamorphosis, so the reproductive activities often occur near bodies of water (Crump 1974; Binckley and Resetarits, 2003). Components of the habitat are most important to specific age and sex of frog within a population (González-Bernal et al., 2015). Abiotic and biotic factors effected to habitat use, movement, and migration (Torres-Orozco et al., 2002; Wells, 2007). Because aquatic pollution, habitat modifications, as well as climate change, could have a negative effect on frog reproduction (Beebee, 1996; Collins and Storfer, 2003; Stuart et al., 2004; Beebee and Griffiths, 2005).

The abiotic factors such as climatic factors, season, and habitat characters affect the temporal location of anurans, they could stimulate or inhibit the reproductive activities of anuran (Wells, 2007; Steen et al., 2013). Generally, anurans in tropical regions breed throughout the year, having only rainfall as a major factor controlling reproduction. On the other hand, temperatures and rainfall are limiting factors of the breeding activity of anuran in the temperate area (Rodrigues and Bertoluci, 2002). However, reproductive activity in intraspecific could be modified by environmental factors changing during the breeding period (Luna-Gómez et al., 2017).

The statements of anuran reproductive activity patterns usually refer to advertisement calls and mating behavior and are classified by length of the active period (Wells, 1977; Duellman and Trueb, 1994; Arzabe, 1999; Rodrigues and Bertoluci, 2002; Wells, 2007). The reproductive activity patterns of anurans are classified into two types, including prolonged species, which continue breeding for more than three months, and explosive species, of which breeding activity lasts for only one or a few days (Wells, 1977; Duellman and Trueb, 1994). The breeding activities included male calling, female occurring, and nesting was continues monitored every month for a year (Prado et al., 2005; de Andrade et al., 2017).

2.2.2 Breeding activities of anurans

- *Mate choice*

The roles of male and female frogs in mating activities are usually focused on male tactics strategies and female choice (Emlen and Oring, 1977; Sullivan et al., 1995; Gerhardt and Huber, 2002; Wells, 2007). Pieces of research show that selected male mate often relates the body size to the decision of male-male combat for territorial defending in breeding sites (Arak, 1983; Woolbright, 1983; Wells, 2007). However, male tactics such as acoustic call, color, or physical displays were still reported (Summers et al., 1999; Wells, 2007; Gomez et al., 2011). Thus, mate choice behavior of frogs is diverse but consistent within species or population (Emlen and Oring, 1977; Wells, 2007).

- *Mating system*

Mating systems are classified according to levels of polygamy in a population (Emlen and Oring 1977; Wells 1977 Sullivan et al., 1995). However, the polygamy do not only exist in mating patterns of frogs, but also monogamy occur. The mating patterns have been divided into monandry, polygeny, polyandry, and polygynandry (Sullivan et al., 1995; Wells, 2007; Ursprung et al., 2011; Tumulty et al., 2014). The polyandry of mating pattern is most realized in Rhacophorids, which is a single female mate with multiple males. However, a female mate with a male frog is called a monandry is found (Jennions and Passmore, 1993; Kadadevaru and Kanamadi, 2000; Roberts and Byrne, 2011; Zhao et al., 2016). However, it could modify by effect of habitat environment on the intraspecific adaptation of anuran (Sullivan et al., 1995; Wells, 2007; Ursprung et al., 2011; Tumulty et al., 2014).

Following Wells (2007) Mating systems are categorized by courtship behaviors and oviposition site selection. The three major mating systems of anurans are consisting of scramble competition, resource defense, and the choruses and leks. First, the scramble competition often happens in explosive breeders, the activity of males' calling and spawning occurs in the same area. Second, the lek mating system which is most founded in frog species, male guides the female to a nesting site where is not same a suitable calling site (Sullivan et al., 1995; Wells, 2007). Third, the resource defense mating system had been reported in few anuran species, the oviposition site is the same as the calling site (Sullivan et al., 1995; Pröhl and Berke, 2001; Wells, 2007). Although, mating systems of most Rhacophorid' members are mentioned to being lek mating system and the oviposition was selected by female (Lank, 2002; Wells 2007; Liao and Lu, 2010; Khongwir, 2016; Niyomwan et al., 2019), some species are still obscures to determine (Sullivan et al., 1995; Halloy and Fiaño, 2000; Wells, 2007).

- *Reproductive mode*

The reproductive mode is a combination of oviposition site, ovum and clutch characteristics, rate and duration of development, stage and size of hatchling, and type of parental care (if there are any) (Duellman and Trueb, 1994). Frogs have most diverse reproductive modes among vertebrate taxa (Haddad and Pombal, 1998; Haddad and Prado, 2005). In 2005, Haddad and Prado identified the reproductive modes of anurans from 405 species, 56 genera, and 8 families in the Atlantic Forest of Brazil. They reported 39 reproductive modes, which are accountable for more than 34% of reproductive modes known for frogs worldwide (Haddad and Prado, 2005). The reproductive modes of frogs were discovered with the extension to many other groups from various locations (Iskandar et al., 2014; Santoro et al., 2014; Crump, 2015), the frogs can utilize various types of habitats such as tropical rainforests, grasslands, high-altitude heaths, and hot deserts (Wells, 2007). Furthermore, intraspecific differences in anuran reproductive mode could be exhibited as a result of ecological adaptations (Haddad and Pombal, 1998; Haddad and Prado, 2005; Toledo et al., 2012; Crump, 2015). For example, Toledo et al. (2012) reported that eggs *of Hypsiboas faber* were found in several modes and mentioned that environment around the breeding habitat could influent reproductive strategies or reproductive mode.

2.2.3 Oviposition selection

The characteristics of the breeding habitat affected to oviposition decision of the frog's parents (Anderson et al., 1999; Rodrigues et al., 2005; Wells, 2007; Li et al., 2018), these are differently required in each species for example types of nest substrate or plants, percent cover of canopy, and/or quality and quantity of water source, etc. (Anderson et al., 1999; Skelly, 2001; Sridhar and Bickford, 2015; Luna-Gómez et al., 2017). Current evidence suggests that the spawning habitat and substrates are various and indefinite, some species of frogs have required specific habitat characteristics (Wells, 2007; Brown et al., 2011; Barrett et al., 2016; Luna-Gómez et al., 2017).

The oviposition sites selection directly impacts the survival, growth, and development of offspring (Wilbur and Collins, 1973; Laurila, 1998; Newman 1992; Luna-Gómez et al., 2017), especially the lack of parental care and limited mobility of larva (Crump 1974, Skelly, 2001; Binckley and Resetarits, 2003). The environment of the closed space is unstable with a high risk of water evaporation, food limitation, and predation (Laurila, 1998; Adams, 2000; Binckley and Resetarits, 2003; Rodrigues et al., 2010). Therefore, the quality and quantity of temporary pools such as water depth, temperature, pH, and dissolved oxygen (DO) are limited conditions for oviposition selection and larva survival as well (Laurila, 1998; Skelly, 2001; Mitchell, 2002; Reading, 2003; Sridhar and Bickford, 2015).

Even the behavioral studies explored that some anuran species return to the breed in the site that they were hatching (natal philopatry) more than finding a new site (natal disperse) because this site was confirmed to be a good pond for egg-laying and decrease energy loss (Sinsch, 1992; Sjögren-Gulve, 1998a, 1998b; Wells, 2007). However, if the water source is not suitable or the pond is dried, so parent frogs will move to choose another pond around there (Sinsch, 1992; Halloy and Fiaño, 2000). The movement of frogs to breed in a new site could affect the distribution and abundance of the populations (Anderson et al., 1999; Skelly et al., 1999; Van Buskirk, 2005; Pitt et al., 2017). Hence, the influence of breeding habitat characteristics in anurans was continuously investigated. Not only give a benefit for studying and explaining the interaction between breeding behaviors with physiology, ecology, and /or evolution (Toledo et al, 2012; Indermaur et al., 2010; Crump, 2015; de Andrade, et al., 2017; Pitt et al., 2017) but also benefits to wildlife management and species conservation (Timm and Meretsky, 2004; Navas and Otani, 2007; Gaston et al., 2010; Landeiro et al., 2014).

2.3 Biology of Rhacophorid frog

Family Rhacophoridae contains 426 species of arboreal frogs from 19 genera (Frost, 2018) and is dominantly distributed in Tropical Africa, China, Southeast Asia, Japan, Taiwan, Philippines, Greater Sunda Islands. (Wells, 2007). Most members of the Rhacophorid frog exist in the tropical area where temperature and precipitation determine the frog's breeding activity (Wells, 2007; Sinsch and Dehling, 2017). The tropical anurans usually mature within their first or second year of life, earlier than temperate species, also the maximum lifespan of tropical anurans is about 2-3 years which is lower than temperate anurans (Sinsch and Dehling, 2017). Normally, the body size of a female is bigger than male, they have enlarged toe discs at the ends of the fingers (Pough et al., 2004; Wells, 2007). Some frogs have a supracloacal dermal ridge which is a key-character of the species (Chou et al., 2007). These features facilitate the frog on climbing or gliding, they can glide by extensive webbing between their digits (Wells, 2007; Frost, 2016).

After metamorphosis, the adult gliding frog lives on a high canopy for insect foraging as well as predation avoidance. They move down to the ground level only for spawning in the breeding season (Duellman and Trueb, 1994; Pough et al., 2004; Wells, 2007; Khongwir et al., 2016). The most of Rhacophoridae were found in the polyandrous mating pattern which is a female mates with two males or many males, so they can fertilize with the same clutch (Liao and Lu, 2010). Most rhacophorid frogs build foam nests on the water surface or objects over the water (Duellman and Trueb, 1994). The foam nests can protect their eggs and larvae from predators and desiccation (Pough et al., 2004; Khongwir et al., 2016). They have specific habitats by laying eggs in temporary water sources (Kadadevaru and Kanamadi, 2000; Liao and Lu, 2010). However, knowledge about the reproductive behavior of rhacophorid frogs is still limited due to their mysterious lifestyles and the difficulty of individual identification (Bourne, 1992; Lank et al., 2002; Wells, 2007; Liao and Lu; 2010; Khongwir et al., 2016; Abraham et al., 2018).

2.4 Study Species

The Malayan flying frog (*Zhangixalus prominanus*) is a gliding frog, and a native of Thai-Malay Peninsula, Sumatra Island, and Indonesia (Harvey et al., 2002; Sukumaran et al., 2004). All records of this species are from the closed-canopy rainforest at low to medium altitudes about 250 - 1,100 meters above sea level (Sukumaran et al., 2004; Marcus, 2017). This species was notified in both forest and artificial sites (Lim and Norsham, 2003; Kurniati, 2008). Like other members of the family, it builds foam nests was extended to any object above a shallow pool after sundown (Berry, 1972; Harvey et al., 2002; Ibrahim et al., 2011) and breeds in a tank or small forest rain pools and puddles, including the beds of intermittent streams (Berry, 1972; Sukumaran et al., 2004; Thong-aree et al., 2011; Niyomwan et al., 2019).

In Sumatra, Indonesia, the *Z. prominanus* was collected in vegetation above a shallow pool near a river at nighttime, some individuals were found along a stream in the forest and on the road (Harvey et al., 2002).

In Malaysia, the *Z. prominanus* were reported from an amplexus pair that their eggs were laid on thick vegetation and the eggs hatched in 3 days, one day later the most tadpoles occurred with external gills. Moreover, they described the morphological characteristics of tadpoles in various development stages until metamorphosed young (Berry, 1972).

In Thailand, there are two main populations of *Z. prominanus* reported; the first one is found near the Thai-Malay border (Yala, Narathiwat, and Pattani provinces) and the second one is at Khao Sok National Park, Surat Thani province (Sukumaran et al., 2004; Niyomwan et al., 2019) (Figure 1). In Hala-Bala Wildlife

Sanctuary, Narathiwat, the frogs were reported on many rock ponds surrounded by swamp forests and rain forests, on the other side that consist of canopy vegetation over a temporary pool such as a rock pool or animal wallows with water-filled or mud (Thong-aree et al., 2011; Niyomwan et al., 2019). Therefore, the population of *Z. prominanus* at Sirindhorn Waterfall, Hala-Bala Wildlife Sanctuary, Narathiwat province is large and healthy (Niyomwan et al., 2019), was chosen in this study.

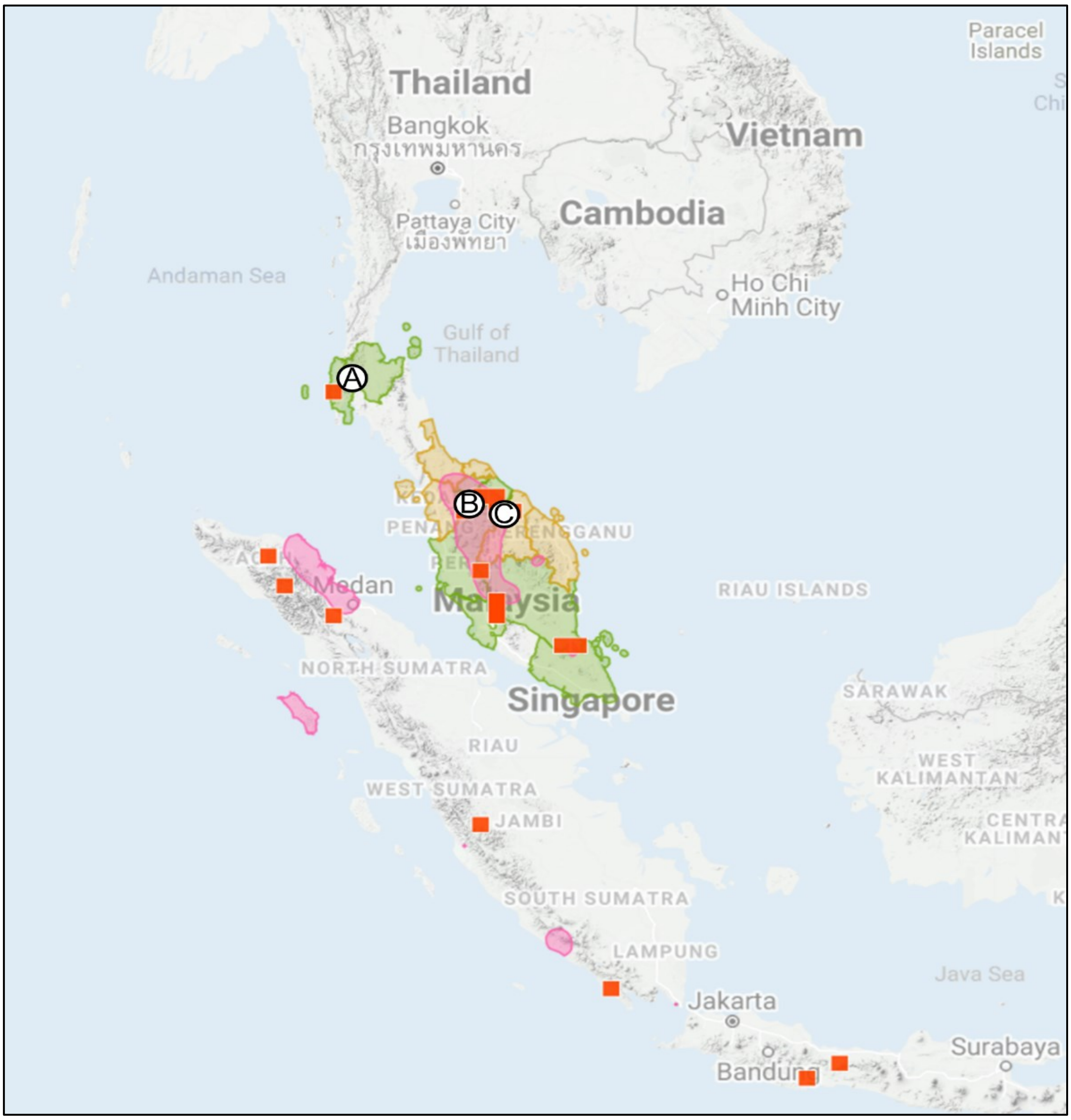

Figure 1. Rang distribution of *Zhangixalus prominanus* on worldwide, In Thailand have been reported in the Khao Sok National Park, Phanom, Surat Thani (A), Betong, Yala (B), and Hala-Bala Wildlife Sanctuary (C); data from Thai National Parks, 2022.

CHAPTER 3

MATERIALS AND METHODS

3.1 Preliminary study and research planning

Previous research reported that the Malayan flying frog, *Zhangixalus prominanus* are found in Hala-Bala Wildlife Sanctuary, Narathiwat province, and Khao Sok National Park, Surat Thani Province. This species was reported that they are found in rock pools and animal wallows with water, moreover, those places are usually nearby or covered by canopy vegetation.

We did preliminary study in nature trails at Hala-Bala Wildlife Sanctuary. Our pilot study was started in July 2017; the *Z. prominanus* are found around 50 individuals at the Sirindhorn Waterfall, while 2 individuals were found in the wallow pool beside the Bala road. We intensively started conducting the research in January 2018; the presented individual frogs were indicated by photo identification technique. Each frog was photographed on head dorsal surface followed Plăiaşu et al., 2005 and Lettink, 2012, the pictures were analyzed by using NaturePatternMatch version 1.00 to specify the individuals (Stoddard et al., 2014), and total number of frog individuals will be counted later. Furthermore, we continuously monitored those frogs in both sites from February to March 2018. During field survey in the Sirindhorn Waterfall the number of founded frog were increased, but in the wallow pool neither the individual nor nest were found. Eventually, we decided to focus and study only the reproductive behavior and ecology of *Z. prominanus* population at Sirindhorn Waterfall from 2018 to 2019.

During the frog survey at Sirindhorn Waterfall, in the 2019, we did the survey at Khao Sok, Surat Thani province as the *Z. prominanus* at was reported by Niyomwan et al., 2019, they mentioned that the population of *Z. prominanus* in the Khao Sok were found at a breeding site in a muddy temporary pool, covered by bush and climber tree. It is possible that they are an explosive breeder which has a short breeding period in May. Therefore, we observed the *Z. prominanus* population at Khao Sok from August to October 2019. However, the individual frogs and nests of this population were not found. Then, we decided to exclude this population from a study.

3.2 Study site

This research focused on *Zhangixalus prominanus* population at the Sirindhorn Waterfall (5.80°N 101.83°E: Google Earth Pro, 2014) locates at Hala-Bala Wildlife Sanctuary, Narathiwat province close to Thai-Malay border. The Bala forest is a lowland tropical rain forest, an elevation was reported from 50 to 960 meters above mean sea level (MSL) (Noon-Anant et al., 2005), with an average temperature of 28.0 °C, 2,098 mm of annual precipitation, and 60% of relative humidity (Niyomtham, 2000; Gale and Thongaree, 2006; Karapan, 2017). This area is classified as a monsoon zone of abundant rain throughout the year. The rain is influenced by afternoon thunderstorms (February-July), South-west monsoon (August-October), and South-east monsoon (November-January) (Niyomtham, 2000).

The population of *Z. prominanus* was found in the study site, there are many temporary rock pools surrounded by swamp forest and rainforest. This area next to the waterfall, on another side, is partly covered by canopy vegetation (Niyomtham, 2000; Thong-aree et al., 2011). The study area is about 12x40 m^2 (width x length) with 1-3 meters (m) deep slope rocks covered by leave, branches and root of plants such as Zingiberaceae, Fabaceae, Annonaceae, Lamiaceae, etc. The higher level of vegetation consisted of height trees, such as *Hellenia speciosa*, *Cananga* sp., *Premna* sp., etc. which were the 2-6 m in height. The trees that were higher than 10 m were also found at the study site such as *Premna* sp. On the west side of the study site is the running water from the waterfall, the stream is approximately 7 m in width (Figure 2A).

Beside the stream consisted of many temporary rock-pools. The pools contained plant components, algae, aquatic living such as insects, tadpoles, and fish in some pools (Figure 2B). There were ninety temporary rock-pools with various sizes:

range of diameter were 20 - 340 centimeters (cm), and range of maximum depth were 0.1- 35.0 cm. However, we were considered only the rock-pools that contained more than 5 cm water depth. Therefore, the 30 rock-pools were used to study according to the previous report mentioned that the water depth can influence breeding sites selection in anurans. The frog in family Rhacophoridae build the nest in the water that average depth was higher than 5 cm (Seale, 1982; Caldwell, 1986; Skelly, 2001; Van Buskirk, 2005; Sridhar and Bickford, 2015, Kato et al., 2010; Rowley et al., 2012).

Figure 2. The study site is at the creek of Sirindhorn Waterfall, Hala-Bala Wildlife Sanctuary, Narathiwat province. The temporary rock pool is indicated by arrow (A), and an example of water-pool components (B).

3.3 Overview of field work and data recording

We collected data in the study from January 2018 to June 2019 at Sirindhorn Waterfall, focusing on the flattening rock, with deep slope rocks covered by leaves, branches, and roots (Study area size: 12 x 40 m^2). The survey was conducted for one week per month. The rainfall periods in each sampling month were considered to be the data collecting periods (following the weather forecast website: AccuWeather, 2018) because the rainfall is the main factor in the reproductive induction of anuran (Duellman and Trueb, 1994; Saenz et al., 2006; Wells, 2007). The data were collected in the field at night from 18hr00 to 24hr00, which is reported as the most active time of anurans species (Wells, 2007). The dim and red light was used for reducing the disturbance of the frogs during the observations (Kadadevaru and Kanamadi, 2000; Liao and Lu, 2010; Khongwir et al., 2016).

We observed the frogs from the ground to the canopy at approximately 0 - 4 m height. Then, we rechecked the frogs every 10-15 minutes. The observers counted and recorded the frog number and clutch (Appendix 1A). The early clutches in each night were determined and recorded (the next morning, we rechecked and recorded whether a new clutch occurred after the previous observation). All the presented frogs were identified for sex by using the size of head and body, that males are smaller than females). Moreover, a female can identify by accumulated eggs while we can identify a male by advertisement calls. We also estimated presented individual positions, including height from the ground, distance from rock pools, and type of substrate. We recorded the activities present such as calling, fighting, grabbing position, spawning activity, mating system, etc. After the observation from 21hr00 to 24hr00, All the frogs were taken an individual photograph, and abiotic factors including the climatic factors of the breeding site, and physical and chemical factors of temporary rock pools were measured by research assistants (Appendix 1B), while some frogs were captured for marking by using the Photo-ID technique and measuring the body size. However, rock pools profile and some abiotic factors were also measured during the daytime.

3.4 Data collection and data analysis

3.4.1 Breeding habitat use (Temporal patterns)

The number of males, females, and clutches (New clutch) were counted. Also air temperature and relative humidity were measured in every 10-15 minuets; approximately 10 times per night. The air temperature and the relative humidity were measured by using a digital thermometer, while rainfall data was taken from the recording rainfall at Hala Bala Wildlife Sanctuary.

The maximum number of males, females, and clutches occurring in each night used for data analysis. The Kruskal-Wallis test was used to investigate the difference between the average counted number of males, females, and clutches per night among the observed months. Moreover, the tested factors consisting of the seasons, the rainfall, the air temperature, the relative humidity, and the number of males and females had analyzed for the effect of tested factors on the number of males, females, and clutches occurrence by using Generalized Linear Models (SPSS 27.0 for Windows, 2020).

3.4.2 Oviposition selection

The new clutches were recorded and noted for the presented position on every observed night at the study site. The temporal and climatic factors at the study site were recorded from January 2018 to June 2019. The air temperature and relative humidity were measured every 10-15 mins; approximately 10 times per night. The air temperature and relative humidity were measured by using a digital thermometer, while rainfall data was taken from recording precipitation dada at the Hala-Bala Wildlife Sanctuary. Moreover, to indicate the illuminance in the site on the observed nights, the ability of the observer's visual in the darkness (Moonlight Visual Distance: MVD) was used considering the distance between an observer and a white paper (15x10.5 cm) at the same point and position at night around 21hr00 to 24hr00.

The influence of habitat variables on oviposition site selection was tested by the rock-pool characteristics. The sixteen pools were chosen for this study. They could have contained water and the frog tadpole. The observed pools had various sizes, the eight pools were covered by hanging vegetation and the remaining were in open areas. The pool positions were mapped and drawn. Map ratio was correlated with the real measuring ratio measuring using. The pool shape was measured for 3 - dimensions, the pool depth was measured at the endpoint of the pool, length and width of the pool s were measured every 20 cm. All the data were used to make pool profile. Then the pool sizes were ranked by the maximum water volume.

Moreover, abiotic factors of the observed pools were measured and monitored along with the study. During the daytime, the distance between the center of the pool and hanging vegetation (DPH) was measured by a tapeline and a pole. Vegetation hanging over the pools (VH) was checked if it presented, so the percentage cover of shading over the water surface (%SH) was estimated by eyes and photos. At night, the water level in the pools was measured by a tapeline and a ruler, the water temperature was measured by using a Mercury-Filled Glass Thermometer, and pH was measured by using pH-indicator strips (MColorpHastTM: range pH 0 – 14) that were put in the middle of the pools and Dissolved Oxygen (DO) was tested by using Dissolved Oxygen Test kit (Vunique version v-color9780, Thailand: range 0.5-15.0 mg/l O_2) that were calculated by drop count titration.

In statistical analyzes, independent variables were tested for correlation with other factors for checking and cutting the multicollinearity which could affect the equation of the logistic regression (correlation value < 0.7; Schroeder, 1990). After that, the binary logistic regression was used to analyze the independent variables that effected the clutching appearance in the breeding site. The tested factors including the breeding period (seasons, and monthly), climatic factors (precipitation, air temperature, and relative humidity), and moonlight (moonlight visual distance) were tested whether they had influenced clutching appearances. Meanwhile, the characteristics of observed rock pools including the physical factors (DPH, %SH, Water Temperature, Water Depth, and Water Surface), the chemical factors (pH and DO of water), also the sixteen temporary rock pools were examined the influence of abiotic factors to oviposition site selection.

The Pearson correlation testing represented that most parameters were not high relation to each other (correlation value < 0.7), they were not multicollinearity. However, data were transformed by cutting off some parameters which were high relation. Therefore, both the presentation of vegetation hanging (VH) and water volume were cut off in statistical analysis, because VH was highly correlated with the distance between the center of the pool and hanging vegetation and the percentage of the percent cover of shading over water surface (%SH), as same as the water volume was highly related to water depth (SPSS 27.0 for Windows, 2020) (Appendix 2).

3.4.3 Reproductive activities and breeding behaviors

Every night, reproductive activities and breeding behaviors of *Z. prominanus* have focused in the study site where full of the flattening rock, covering by leaves, branches, and roots of plants. Those many rock pools contained water and varied in sizes, some of them were covered by canopy vegetations. In the fieldwork, the behaviors of frogs were monitored every 10-15 minutes. We recorded the position of the frogs' individuals and nests including the height and the distance of water source (temporary rock-pools), and the behavioral displays. The frogs on the ground level (approximately 0–4 m) were specially considered for their movement. During the survey, the monitored frogs were photographed and recognized using dorsal surface of the head. All the individuals were identified by the Photo-ID technique (Plăiaşu et al., 2005; Lettink, 2012). The courtship activity displays were detected on male's calling and physical fighting. The mating activities starting the females or amplexus pairs (a male grabbed on a female's back) were detected by active observing, then amplexus pairs were monitored until completing egg-laying and nested frogs left from the nest. Moreover, the tadpole stage was documented following Gosner, 1960, when the egg hatched. Then the data were indicated and classified the reproductive activity pattern, mate choice, mating system, and reproductive mode final.

- Reproductive activity pattern

The frog individuals were continuously monitored for 6 days per month throughout the year. the occurrence and the breeding activities (including male calling, female occurring, and nesting) occurred in the study site were observed and recorded. The breeding period was used to indicate the reproductive activity patterns of this population (Wells, 1977; Duellman and Trueb, 1994; Rodrigues and Bertoluci, 2002).

- Mate choice, and Mating system

The male tactics and female choices of this population were considered for their movement when courtship occurred until the male frog was chosen for mating. We hypothesized that the nearest males to the water source (breeding pools) had a high opportunity to be chosen by the females (Vilaça et al., 2011; de Oliveira, 2017). Therefore, mate choice was investigated. Moreover, the type of mating system in this species was analyzed considering the location of the male calling site and nesting site (Wells, 2007).

- Reproductive mode

In this study, the courtship, mating, and spawning activities as well as oviposition site selection were described in order of the events. The frequency of the frog activities appearing was also noted. Moreover, the reproductive modes were determined by using data from breeding activities followed Haddad and Prado, 2005 reporting.

3.5 Photographic identification (Photo-ID)

There are several methods used to determine a frog individual. However, it is difficult to monitor frogs' behavior in natural habitats. Capturing or handling frogs possibly harm them and change their behavior (Reaser 1995; Bradfield, 2004; Haigh et al., 2007). Many previous studies applied the mark-recapture method for individual identification, but some methods could injure or cause of dead (Plăiaşu et al., 2005; Hoffmann et al., 2008; Lettink, 2012). Recently, the photo identification method was introduced to use as it can decrease disturbance and injury which could interfere thefrogs' behavior (Lettink, 2012; Long and Azmi, 2017).

In this study, the individual frogs were identified by using the photographs ID technique and using NaturePatternMatch (NPM) program. The NPM currently consists of two program files including *npm_process*, which performs all image pre-processing including image enhancement, region-of-interest selection, and feature extraction, the second file called *npm_match*, this file was used to match an image or set of images against an existing dataset of images (Stoddard et al., 2014). In the first step, the frogs were taken one by one photo on the dorsal side with a clear focus. Then, the dorsal marks, lines, or spots of the frog were transformed into matrix data with the NaturePatternMatch program, version 1.00. For the frog photos identification, the program calculated a score ranking of photo-matching by the similarity of the pattern of analyzed marks, lines, and spots (Long and Azmi, 2017; Jaroensap et al., 2019) (Figure 3).

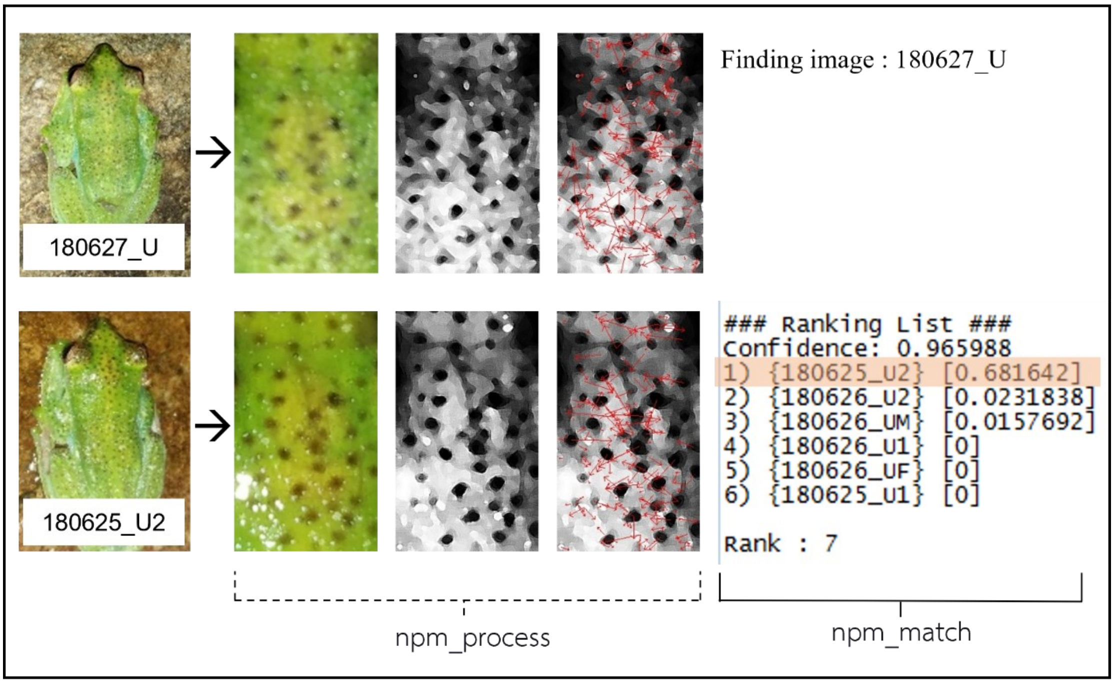

Figure 3. A sample of photo identification by NaturePatternMatch, version 1.00 program on the dorsal surface of *Zhangixalus prominanus*' head. The upper picture is the frog's individual on June 27, 2018, and the lower picture is the frog on June 25, 2018. The pictures were pre-processed by *npm_process* then each image was matched by *npm_match*, which provided a similarity score ranking and confidence score.

CHAPTER 4

RESULTS and DISCUSSION

4.1 Breeding habitat use (Temporal part) and Influence of abiotic factors

Results

The adult male, gravid female, and clutching of *Z. prominanus* at the study site (12 x 40 m^2) were detected along with the observation. The average number of counted males was high in June-2018, August-2018, and September-2018 (Mean ± SE: 24.25 ± 3.67, 17.50 ± 3.81, and 17.96 ± 6.72, respectively), which fewer in November-2018, February-2018, and June-2019 (Mean ± SE: 10 ± 1.10, 8.5 ± 6.22 and 8 ± 1.53 respectively). The average number of counted females were high in May-2018, September-2018, and February-2019 (Mean ± SE: 1.5 ± 0.62, 2.39 ± 0.98, and 1.5 ± 1.5, respectively), and the lower in June-2018, August-2018, and November-2018, which have the same values (Mean ± SE: 0.50 ± 0.25, 0.50 ± 0.34 and 0.5 ± 0.14, respectively). The average number of counted clutches were most high in September-2018, Mar-2018, and February-2019 (Mean ± SE: 2.04 ± 1.00, 1.5 ±1.5, and 1.03 ± 0.68, respectively) and the lower in February-2018, August-2018, and June-2019 (Mean ± SE: 0.17 ± 0.18, 0.33 ± 0.21, and 0.33 ± 0.21, respectively) (Figure 4 and Appendix 3). However, there are no data recorded on 2018, April, July, October, December and 2019, January, March, April, and May, by force majeure (There is an insurgency in the research area and the researcher was in an accident).

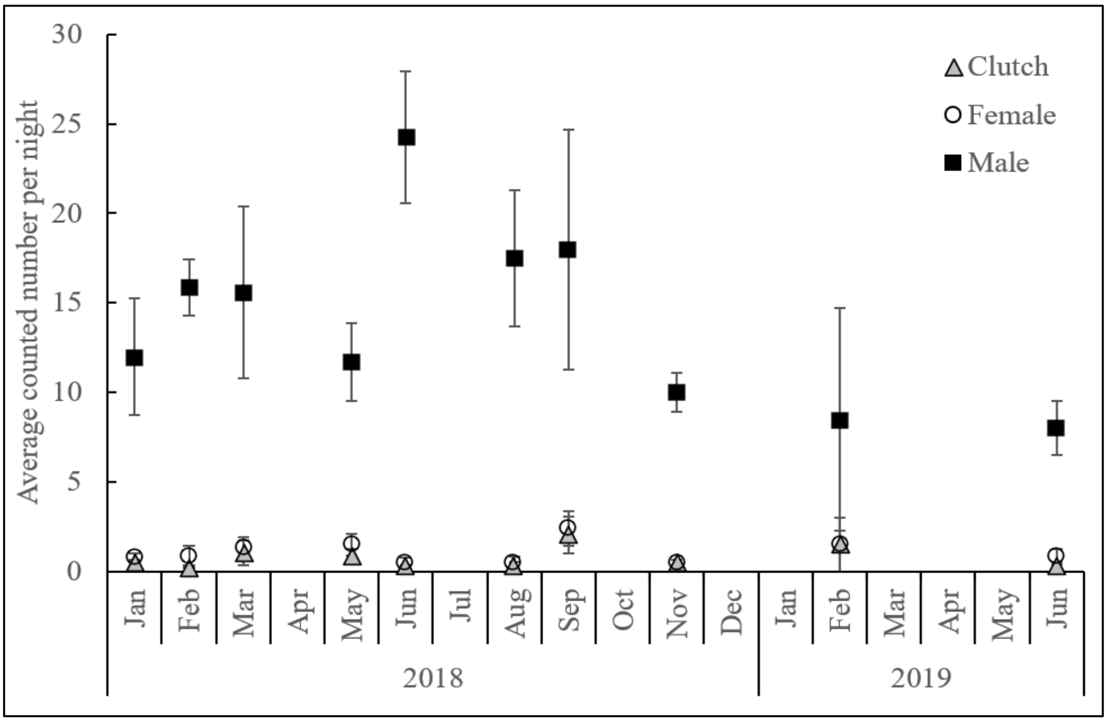

Figure 4. Average number of *Zhangixalus prominanus* divided in males, females, and clutches per night at Sirindhorn Waterfall during January 2018 and June 2019 for 10 sampled months.

The total of survey nights was 53, and the average number of counted males, females, and clutches in the breeding site during the survey month (n = 53) detail were 14.17 ± 10.58 (SD), while females and clutches were similarly lesser were 1.11 ± 1.73 (SD) and 0.79 ± 1.61 (SD), respectively. Result of Kruskal– Wallis nonparametric test show that the differentiation between survey month and number of male individuals ($K_{9,53}$ = 15.468, P = 0.079), female individuals ($K_{9,53}$ = 10.655, P = 0.300), and clutches ($K_{9,53}$ = 10.413, P = 0.318) did not differ significantly (Kruskal-Wallis, $P > 0.05$, Table 1).

Table 1. Descriptive Statistics and result of Kruskal– Wallis nonparametric test, mean counted individuals of male, female, and clutch (n = 53) at breeding site in the ten months during the 2018-2019. *P*-values were derived from Kruskal-Wallis tests and significant values ($P < 0.05$) were shown on table.

	N	Mean	Std. Deviation	Minimum	Maximum	Kruskal-Wallis H	df	*P*-Values
Male	53	14.1698	10.58798	0.00	39.00	15.468	9	0.079
Female	53	1.1132	1.72828	0.00	9.00	10.655	9	0.300
Nest	53	0.7925	1.60957	0.00	9.00	10.413	9	0.318

From the climatic factors analyzing shows an effect on the appearance of males, females, and clutching. Besides, the male occurrence is influence to female and also the nesting exist. The seasons, average of air temperature, and average of relative humidity had an effect on number of males occurring ($P < 0.05$). Meanwhile, the rainfall and male appearance have effect on number of females occurring ($P < 0.05$), seasons, average of air temperature, and average of relative humidity had not an effect ($P > 0.05$). The female occurring only influenced number of clutches appearing ($P < 0.05$) (Table 2).

Table 2. Statistical value of general linear model of climatic factors influenced to the appearance (n = 52) of mature male, gravid female and clutching in temporary rock pools (breeding site) at Sirindhorn Waterfall, Hala-Bala wildlife sanctuary, Narathiwat.

Tested variables	Male			Female			Clutch		
	Wald Chi-Square	df	Sig.	Wald Chi-Square	df	Sig.	Wald Chi-Square	df	Sig.
(Intercept)	0.930	1	0.335	0.678	1	0.410	0.122	1	0.727
Seasons	30.416	2	0.000*	1.509	2	0.470	0.410	2	0.815
Rainfall	0.632	1	0.427	11.797	1	0.001*	0.101	1	0.751
Air-temp.	5.236	1	0.022*	0.249	1	0.617	0.043	1	0.836
Humidity	15.684	1	0.000*	0.299	1	0.584	0.032	1	0.859
Male				23.548	1	0.000*			
Female							22.586	5	0.000*

Significant *p* values of tested variables are marked with asterisk (*)

Discussion

The tropical anurans usually mature within their first or second year of life, and the maximum lifespan is about 2-3 years (Sinsch and Dehling, 2017), which means the frog has a short time for producing the offspring in their population (Wells, 2007). This is the cause of most tropical anurans species being prolonged breeder and continuously breeding thought a year, which was influenced by temperature and precipitation (Wells, 2007; Sinsch and Dehling, 2017). Our results show that *Zhangixalus prominanus* at Sirindhorn Waterfall existed each month throughout the studying, which might be due to the regular rainfall at Bala wildlife sanctuary. It is the least rain during the hot season (February–July), the heavy rain is usually found as afternoon thunderstorms during the south-west monsoon (August–October), and the height of rainfall is recorded during the north-east monsoon (November–January) (Niyomtham, 2000; Kemp et al. 2011). These monsoons not only influence rainfall but also humidity and air temperature, it affects the humidity is consistently high, and varied inversely with temperature (Kemp et al., 2009), whence, it is an appropriate environment for the frogs doing any activities throughout the year.

The breeding area of this population had a mean annual relative humidity is 82 %, and a temperature is 27 °C in the Sukhirin district (The Bala Road) (*see* Kemp et al., 2009, 2011), where are high temperature and rainfall that suitable for the reproductive activity of frog during the breeding season. From the previous report, the spermatogenesis of male frogs could induce by high temperatures, then along the breeding period, the male frogs possibly have completely developed sperm in their testis (*see* Paniagua et al., 1990; Rastogi and Iela, 1992; Rastogi et al., 2005). In this study, the frog population also shows the gravid female occurrence was influenced by calling male and rainfall, which have an effect on the egg-laying behavior of females (Sullivan et al., 1995; Grafe, 2005; Wells, 2007; Rastogi et al., 2011; Byrne and Roberts, 2012). Generally, the rainfall has been identified as the stimulus for adult males and gravid females to generate their mating season and move to the breeding site (Oseen and Wassersug, 2002; Saenz et al., 2006; Wells, 2007; Schalk and Saenz, 2016). Thus, the environmental change in this area could be a negative effect on the reproductive behaviors of the anurans (Donnelly and Crump, 1998; Blaustein et al., 2001; Wells, 2007; Crump, 2015; Navas et al., 2017).

4.2 Oviposition site selection and Influence of abiotic factors

Results

Figure 5 shows the studying pools that exist on a 12x25 m^2 rock slope. It is between the creek of Sirindhorn Waterfall on the west side and the rocky slope with the vegetation on the east side. All pools have a water depth of 4 – 5 cm or more, the most aquatic living in pools is anuran tadpoles. The eight pools (number 5, 7, 8, 9, 10, 11, 13, and 14) were in the upper zone, which is 1-3 m in height from creek level. The eight pools (number 1, 2, 3, 4, 6, 12, 15, and 16) were in the lower zone at creek level. The shadow covering of each pool was ranked; six pools were more than 50% of shading, five pools were 1-50% of shading, and five pools were none-shading from any objects.

The cross-section of 16 rock pools was drawn at the deepest and widest (Figure 6). The slope profile pictures were organized into 2 groups of non-covered and vegetation covered. The depth of water in the open area pool is a range of 5 to 20 cm and in the vegetation-covered pool it varies since 4 cm to 40 cm.

The water capacity of pools was calculated from the average of maximum water depth and water surface area. The sizes of pools were ranked from lowest to highest volume into 3 groups. First is the water volume less than 1,000 cm^3 as a small pool (pool number 1, 2, 3, 4, 5, 6, 7, 8, 9, 10 and 11), and second group is the pool have water over than 1,000 cm^3 as a big pool (pool number 12, 13, 14, 15 and 16) (Figure 7).

We found that the five pools; number 8, 12, 14, 15, and 16, were selected for mating and nesting along the study. Meanwhile, the selected pools: number 12, 14, 15 and 16, are covered and categorized in the big size of the pool (>1,000 cm^2), except pool number 8 which is small size (approximately 300 cm^3) and far from vegetation covering, but it has an overhanging rock nearby (Figure 5, 6, and 7).

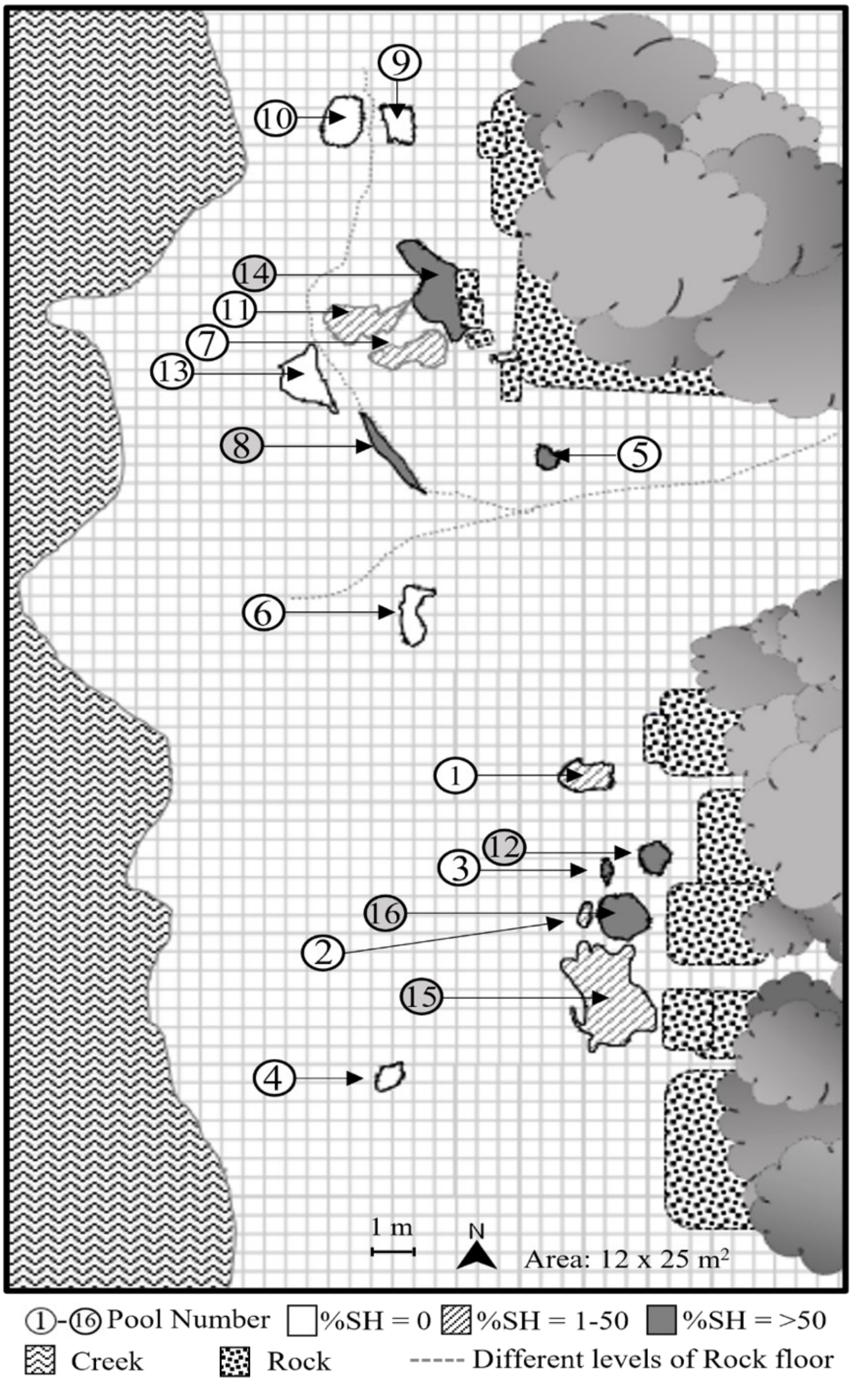

Figure 5. The map of study site shows top view of position, shape, size, and shading presence: white is 0% shaded, line is 1-50% shaded and gray is more than 50% shaded, of the pools number 1-16 during collecting years (2018-2019). The height level zonation was separated by dash line. The number in dark circle is the monitoring pools along the study.

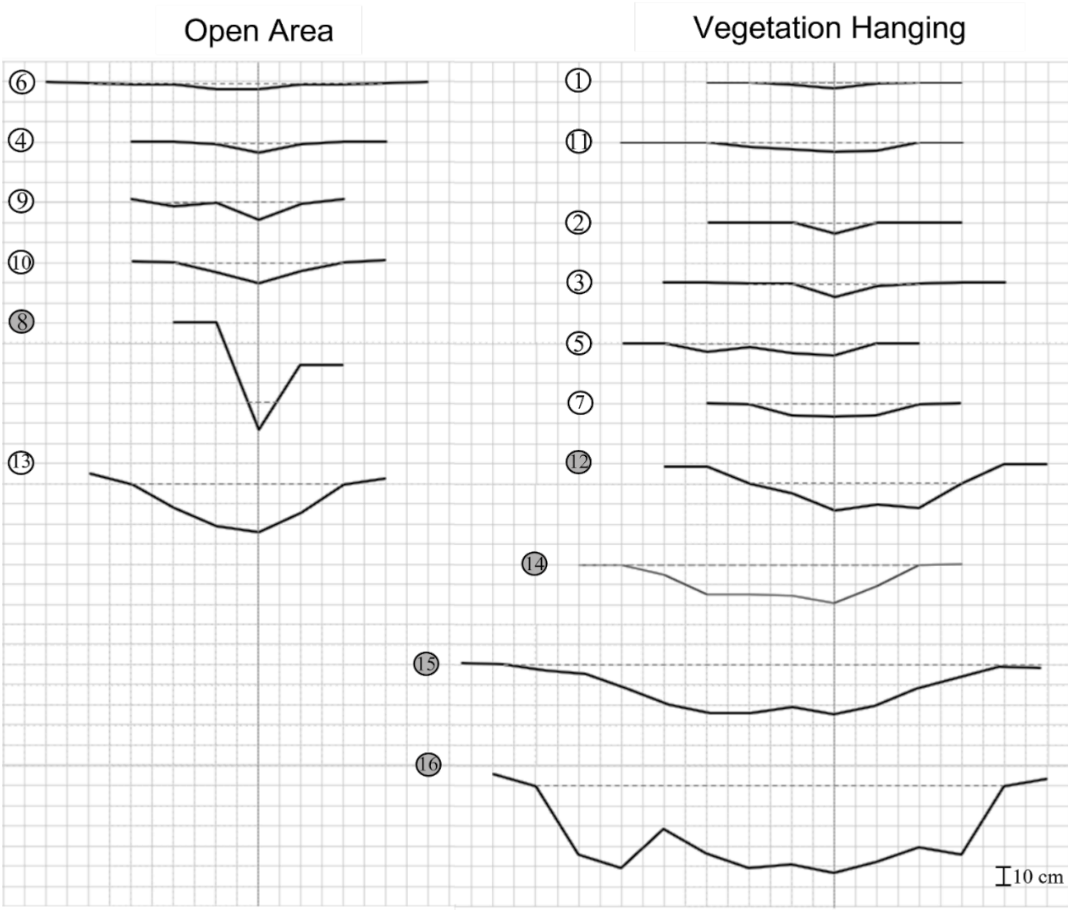

Figure 6. The slope profile of six exposed rock pool and ten covered rock pools were drawing at maximum depth and width. The pictures in row were sequenced by the average depth of water in pool (dash line) from lowest to deepest. The number in circles are pools number, and dark circle are the monitoring pools along the study.

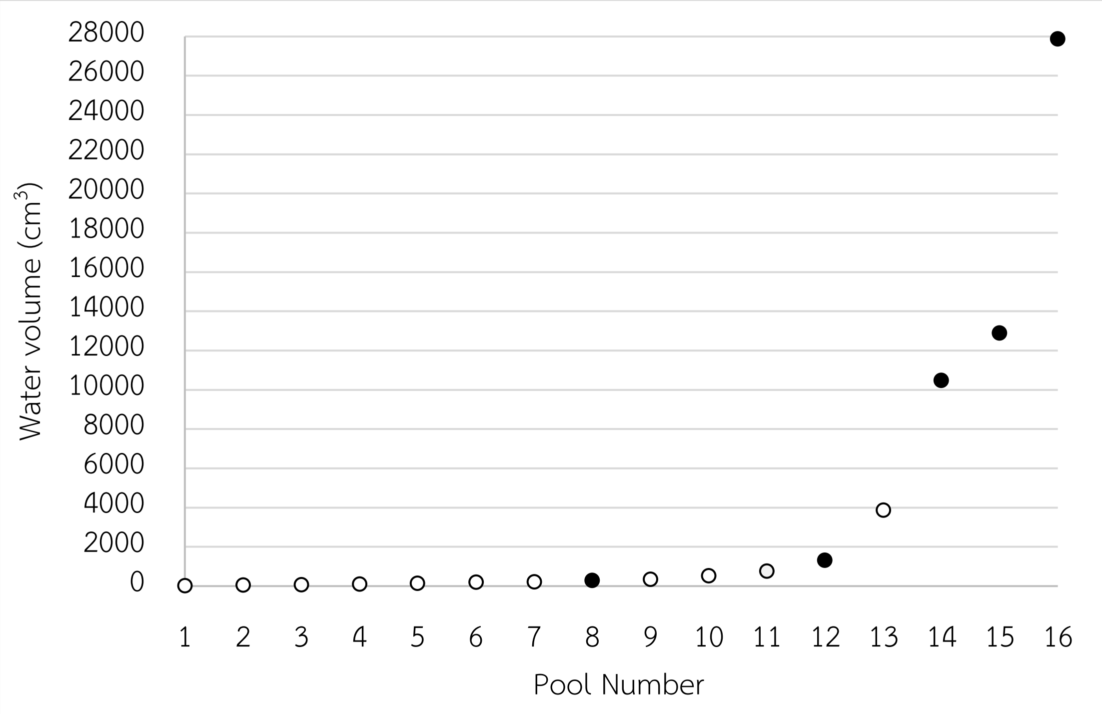

Figure 7. The graph shows a water volume of study rock – pools. The pools were arranged by water containing from smallest to largest sizes. The thick circles are monitoring pool along the study.

Logistic regression models revealed that the temporal climatic and factors including months, seasons, rainfall, average of air temperature, average of air humidity, and average of moonlight visual distance (n = 57) were not statistically significant (*P*-value > 0.05) (Table 3). Meanwhile, the habitat characteristics including the water depth, pH, dissolved oxygen (DO) of the study site are significantly influenced the probability of clutching appearance (independent binary variable: clutch present vs. clutch absent; logistic response function (logit): g(x) = - 21.272 + 0.287 (average water depth) + 1.462 (water pH) + 0.435 (DO); $P < 0.05$, percentage of corrected cases = 93.6 (*see* Appendix 4)). The other variables had no influence on the models (all variables had $P > 0.05$) (Table 4).

Table 3. Variables in the equation of binary logistic regression on the effects of the temporal and climatic factors on nested occurring (n^a = 57) by *Zhangixalus prominanus* at Sirindhorn Waterfall in Hala-Bala Wildlife Sanctuary, sampled during January 2018 and June 2019 (Indicate statistical significance in $P \leq 0.05$).

Variables [b]	B	S.E.	Wald	df	Sig.	Exp(B)
Months [c]			6.99	9	0.64	
Jan-18	-2.38	2.76	0.74	1	0.39	0.09
Feb-18	0.15	2.41	0	1	0.95	1.16
Mar-18	0.44	2.41	0.03	1	0.86	1.55
May-1	-0.81	2.21	0.14	1	0.71	0.44
Jul-18	-2.53	2.56	0.98	1	0.32	0.08
Aug-18	0.94	2.3	0.17	1	0.68	2.55
Nov-18	0.46	1.53	0.09	1	0.77	1.58
Feb-19	-2.41	2.51	0.92	1	0.34	0.09
Jun-19	-0.8	2.43	0.11	1	0.74	0.45
Seasons [d]			0.51	2	0.77	
ATS	1.35	2.07	0.43	1	0.51	3.86
SWM	0.1	2.05	0	1	0.96	1.11
Rainfall	-0.01	0.02	0.38	1	0.54	0.99
AT	-0.32	0.41	0.61	1	0.43	0.73
RH	-0.04	0.05	0.5	1	0.48	0.96
MVD	0.06	0.08	0.6	1	0.44	1.07
Constant	11.2	13.3	0.71	1	0.4	70405.94

[a] n is the total number of clutch recording (both present and absent) of *Z. prominanus* during 6 days per months in each abiotic variable.

[b] Variable(s) entered on step 1: Months, Seasons, ATs = Afternoon thunderstorms, SWM = South-west monsoon, Rainfall (mm.), AT = average of Air Temperature (°C), RH = average of Relative Humidity (%), MVD = average of Moonlight Visual Distance (m)

[c] June 2018 was used to being the reference group in Logistic regression with dummy variables

[d] South-east monsoon (SEM) was used to being the reference group in Logistic regression with dummy variables

Table 4. Variables in the equation of binary logistic regression on the effects of the habitat characteristics on nested occurring (n^a = 487) by *Zhangixalus prominanus* at Sirindhorn Waterfall in Hala-Bala Wildlife Sanctuary, sampled during January 2018 and June (Indicate statistical significance in $P \leq 0.05$). The statically significant variables (*)

Variables [b]	B	S.E.	Wald	df	Sig.	Exp(B)
Pools [c]			11.844	15	0.691	
Pool No. 1	-11.008	23564.239	0.000	1	1.000	0.000
Pool No. 2	-11.889	16151.669	0.000	1	0.999	0.000
Pool No. 3	-10.019	5838.585	0.000	1	0.999	0.000
Pool No. 4	-4.382	271984.173	0.000	1	1.000	0.013
Pool No. 5	-9.200	8762.104	0.000	1	0.999	0.000
Pool No. 6	-1.285	249331.945	0.000	1	1.000	0.277
Pool No. 7	-12.172	6066.514	0.000	1	0.998	0.000
Pool No. 8	10.570	113278.805	0.000	1	1.000	38955.313
Pool No. 9	-8.213	136078.282	0.000	1	1.000	0.000

Pool No. 10	-5.326	226720.543	0.000	1	1.000	0.005
Pool No. 11	-11.226	5646.594	0.000	1	0.998	0.000
Pool No. 12	6.966	3.176	4.809	1	0.028	1059.461
Pool No. 13	-9.299	158826.780	0.000	1	1.000	0.000
Pool No. 14	13.648	5.413	6.357	1	0.012	845480.714
Pool No. 15	12.681	6.330	4.014	1	0.045	321472.052
DPH	-1.599	45311.522	0.000	1	1.000	0.202
%SH	-0.043	0.048	0.791	1	0.374	0.958
WT	0.114	0.250	0.209	1	0.648	1.121
WD	0.287	0.141	4.143	1	0.042 *	1.333
WS	0.000	0.000	1.967	1	0.161	1.000
pH	1.462	0.544	7.224	1	0.007 *	4.315
DO	0.435	0.130	11.245	1	0.001 *	1.545
Constant	-21.272	9.512	5.002	1	0.025 *	0.000

[a] n is the total number of clutch recording (both present and absent) of *Z. prominanus* during 6 days per months in each abiotic variables from tested pools.

[b] Variable(s) entered on step 1: Pools, DPH = Distance of Pool's Center to hanging vegetation (m), %SH = Shading cover on water surface (%), WT = Water Temperature (°C), WD = average of Water Depth (m), WS = Water Surface (m^2), pH = pH of water, DO = Dissolved Oxygen of Water (mg/l O_2)

[c] Pool no. 16 was used to being the reference group in Logistic regression with dummy variables

Discussion

The previous research mentions that oviposition site selection of anuran is stimulated or exhibited by abiotic factors surrounding the breeding habitat (Spieler and Linsenmair, 1997; Anderson et al., 1999; Matsushima and Kawata, 2005; Wells, 2007; Wang et al., 2008). However, the data analysis of this study shows the breeding period (seasons, and monthly), climatic factors (precipitation, temperature, and humidity), and lighting in the breeding area (moonlight visible) did not influence to clutching appearance of *Zhangixalus prominanus* at Sirindhorn waterfall. These might cause the population is exist in a tropical rainforest, the environmental conditions such as rainfall humidity, and temperature are not greatly different in this area (Niyomtham, 2000; Gale and Thong-aree, 2006; Kemp et al., 2009, 2011), which is suitable condition throughout a year, that could stimuli a reproductive behavior of anuran (Rastogi et al., 2005; Wells, 2007; Rastogi et al., 2011, Luna-Gómez et al., 2017). Therefore, a slight fluctuation of abiotic factors surrounding the breeding area is not sufficiently impacting to male, female, and clutching (Halloy and Fiaño, 2000; McDonald et al., 2018).

The equation in this study showed the likelihood of oviposition was predicted by habitat characters, and the breeding habitat variables were significantly influenced and positively correlated with the appearance of egg-laying, which consisted of physical and chemical factors, including average depth, pH, and dissolved oxygen (DO) of water in a temporary rock pool. According to the previous studies reported that the conditions found in nesting pools could affect the tadpole survival (Moore and Townsend, 1998; Werner and Glennemeier, 1999; Adams and Saenz, 2012; Saenz and Adams, 2020), likewise, the water depth could influence oviposition selection, especially the temporary aquatic breeders' frog (Crump, 1991; Rodel et al., 2004; Rudolf and Rödel, 2005). Besides, the mature frogs are waiting until water is contained in pools with proper high to keep away from the desiccation of laying eggs (Spieler and Linsenmair, 1997; Laan and Verboom, 1990; Laurila, 1998; Skelly, 2001). Moreover, it has been reported that the frogs avoided eggs depositing in very high or very low pH values, and they usually choose the water pool with dissolved oxygen (DO) that was higher than 1 mg/l O_2 in water (Adams and Saenz, 2012).

Moreover, the shape of the water pool in terms of volume and water surface area is irrelevant to the water depth, pH, and DO as same as the temperature, leaf litter, also aquatic living in the water (Seymour and Loveridge, 1994; Werner and Glennemeier, 1999; Adams and Saenz, 2012; Saenz and Adams, 2020). The leaf little or secondary compounds in the water pond could regulate the water to high tannin concentrations and have the potential to create environments that are directly toxic to anuran tadpole performance, growth, and development (Maerz et al., 2005). The tannin could change in quality and quantity of tadpole food and direct toxicity by reducing the oxygen in the water (Brown et al., 2006; Earl and Semlitsch, 2015). Moreover, the optimistic correlation of water depth, pH, and DO values with the probability of clutching appearance in this study is possibly related to the heavy rain in the monsoon season, which attracts females to the breeding site. Then the rain filled the water in the pool, the pH changed from 5 to 6 or 7, and the DO is rising.

The oviposition site characteristics of this population were a water pool which consists of shading over the water surface covered by vegetation hanging, nearest to the resting habitat of the frog that they can hide from the predators. Moreover, the selected pools were high water depth and volume (over 1,000 cm3), which might affect the number of tadpoles living in the nursery pools. In this study, a clutch of *Zhangixalus* prominanus represented the number of eggs approximately 200 to 300 (n = 5, minimum and maximum = 166 and 331), and larva hatchling approximately 200 (n = 3, minimum and maximum = 100 and 251), they spend time around 72 hours after nesting until egg hatchling. Furthermore, all selected pools that were chosen for clutching were not ever dry out during the study period, from the monitoring of quality and quantity of water temperature between nighttime and daytime showed a more stable level of selected pool compared with non-selected pool (Appendix 5). It may be the big size of pools and shaded pools involved with the water temperature and the dissolved oxygen controlling (Anderson et al., 1999; Werner and Glennemeier, 1999), which directly affect the offspring's survival and the length of development time until completed metamorphosis (Newman, 1992; Laurila, 1998; Moore and Townsend, 1998; Skelly, 2001; Saenz and Adams, 2020).

In addition, the oviposition selection of *Zhangixalus prominanus* at Sirindhorn waterfall might be related to non-measured variables as well as other abiotic factors, or biotic factors such as competition and predation (Berven and Grudzien, 1990; Laurila and Aho, 1997; Halloy and Fiaño, 2000; Refsnider and Janzen, 2010; Buxton et al., 2017). Furthermore, the behavior studies found the reoccurrence of some anuran species to the natal philopatry; breeding site they were hatching, more than the natal disperse; a new breeding site, because the initial site confirmed to be a good pool for egg-laying and decrease energy loss. If the water source is not suitable, the parent frogs will move to the new pool around there (Sinsch, 1992; Sjögren-Gulve, 1998a; Wells, 2007; Halloy and Fiaño, 2000). However, there is still unclear evidence about oviposition behaviors of natal returning from the temporary pools of the *Z. prominanus* species.

4.3 Reproductive activities and breeding behaviors

4.3.1 Reproductive activities pattern and reproductive activities monitoring

Results

The 186 frog individuals were marked by Photo-ID technique, all of them were adult males and gravid females. Some of the marked frogs were measured the size of snout-vent length (SVL) and head width (HW) to indicate frog' sex and confirm the individuals. Although the SVL of males ($\bar{x}$ ± SD = 52.87 ± 2.62 cm, n = 100) and female ($\bar{x}$ ± SD = 58.40 ± 3.50 cm, n = 13) was not significantly different (*t*-test; $P > 0.05$), HW of males ($\bar{x}$ ± SD = 16.53 ± 0.55 cm, n = 100) show significantly (*t*-test; $P < 0.05$) smaller than females ($\bar{x}$ ± SD = 19.89 ± 1.08 cm, n = 13). We found that the calling male, gravid female, and clutching of *Zhangixalus prominanus* at the study site (12 x 40 m^2) were detected along with the observation (January 2018 to June 2019) and occurred continuously for more than three months (Figure 4 and Appendix 6). Thus, the reproductive activities pattern of this population at Sirindhorn Waterfall was classified to prolong breeding.

The number of males occurring in the breeding site was higher than female occurring (number of individuals: Male = 153, Female = 33), and after a night of nesting all nested female and nested male were not found again on the next night (number of events: Male = 17, Female = 15) (Appendix 6). Total of males and females which were found more than one time as 40 individuals, the males 36 individuals and female 4 individuals. The forty individuals were considered the frequency of repeating occurring in the breeding site during the study period. The frequency of males occurring in the breeding site was greater than females in terms of months and days. The male repeated occurring in the site was the highest to 6 months, 4 days in a week. Meanwhile, the highest of females occurring as 2 months, or a day before egg-laying. Moreover, we found that the shortest period of males and females appearing in the site after clutching was approximately one month (Appendix 7 and 8).

Discussion

The reproductive activity pattern of *Zhangixalus prominanus* at Sirindhorn Waterfall was prolonged breeding. We regularly observe the amount of calling male, gravid female, and foam nests throughout the study. It is consistent with previous reports from various locations on Thai-Malay Peninsula and Sumatra Island with extended reproduction cycles throughout a year (followed Sukumaran, 2004; Niyomwan et al., 2019). Because of constant warm temperatures with high humidity and precipitation, it is easy to induce the mature frog to develop their gamete (Harvey et al., 2002; Sukumaran et al., 2004; Ibrahim et al., 2011; Marcus, 2017).

In the monitoring of adult male and female occurrence in the study site, we could mention that the foraging site and breeding site of this population were different, and they use this study site for breeding activities only (Semlitsch, 2000; Wells, 2007; Khongwir et al., 2016; Abraham et al., 2018). Besides the gravid female was found only at this site, then after the date of clutch depositing the mated males and female were disappear until the next month. It might be this species is an arboreal living and insect-foraging, they are resting on high canopy vegetation to avoid the ground level predator (Duellman and Trueb, 1994; Pough et al., 2004; Wells, 2007; Khongwir et al., 2016). However, the frequency of adult males' reoccurrence in the site per night and month was higher than females because they arrive for ground defending (Mitchell, 2002; Vilaça et al., 2011; de Oliveira, 2017). Meanwhile, the frequency of reoccurrence in gravid females was lower, they appear a day before nesting and disappear afterward. For decreasing the risk of predation and energy, might be the female moving down for one purpose is egg-laying (Pough et al., 2004; Byrne and Roberts, 2012). Moreover, the research on germ cell histology shows a shorter period of sperm production in males than the follicle recovery in females, so the female spends more time for re-mating (Wells, 2007; Byrne and Roberts, 2012).

4.3.2 Breeding behaviors and Reproductive mode

Breeding behaviors of *Z. prominanus* was observed on courtship and mating (amplexus pair) until nesting activities are complete, thus the 99% similarity on activities were calculated from the couples. The breeding activity can be divided into six sequences, *see* Figure 8 beginning with [1] a male moving down from canopy vegetation and occurring in the breeding areas, then the courtship behavior over water pools or canopy level were shown (frequency of performance (F)/total observation (T); F/T = 50/54) and most calling with some fighting by a kick or jump up and sit on another male (Figure 8A). [2] The gravid females reach the breeding area (F/T = 24/54) (Figure 8B), [3] a male or many males would grab the female's back and clasping with the hand into the armpit called axially amplexus (number of couple's performance (n); n = 28) (Figure 8C). [4] After that amplexus pair moved (n = 17) to the breeding pool and [5] made foamy - nest over a water together (n = 50), preferably on rock substrates or hanging vegetations (Figure 8D - E). [6] Then the male moves out while the female shapes the foam nest into oval or eggs were completely covered by foam (Figure 8F). Finally, the female released the nest (n = 26) and moved to the canopy level. However, during the mating and foam nesting behavioral process, the selected males still called and aggressed all the time to prevent their spouse from other males and another organism confliction.

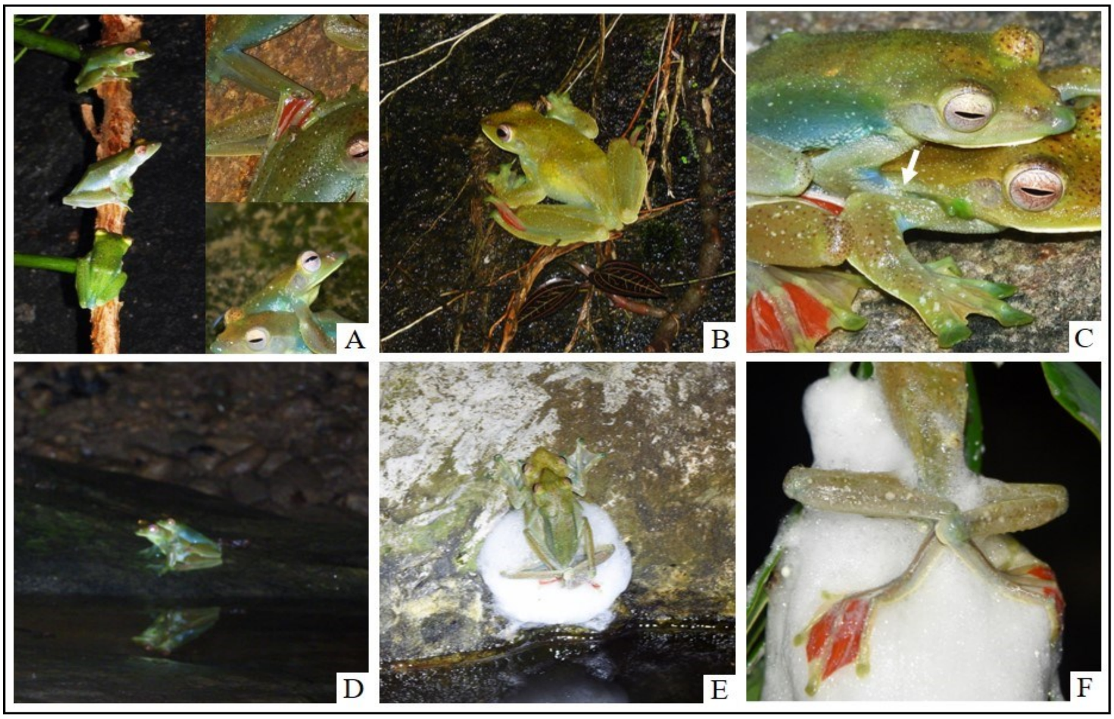

Figure 8. Breeding activity sequences of *Zhangixalus prominanus* at breeding area, Sirindhorn Waterfall; many male calling and fighting by a kick or jump up on another frog (A), gravid female appearing in the breeding site (B), axillary amplexus by a male grabbing on a female armpit at the white arrow (C), the amplexus pair moving over or near water pool (D), foam-nesting by both male and female (E), and foam shaping by the female (F), meanwhile male separating off.

The 28 amplexus pairs of *Z. prominanus* in observation showed two mating patterns. The monandry (n = 20), a female mate with one male (Figure 9A), was most observed. A few polyandric (n = 8) situations occurred when heavy rainfall, it is a group mate of one female with many males, the biggest group found 6 males in a mating (Figure 9B). The reproductive mode of this species was identified as mode 33 following Haddad and Prado (2005); the arboreal foam nest with eggs hence hatching tadpoles drop into pools. The corroboration was shown by the over temporary rock pools nested of mate monitored (n = 50). The clutches were white-foamy nest with oval or free shape, the green yellowish eggs were occupied inside. The distance between foam-nests and water surface was approximately 1 cm or less than 100 cm, but a situation of observer's interruption made the frog pair moved to nesting around 7 m from water surface. However, the nested position had without anything to obstruct the larva dropping into the water. The proportion of 50 foam nests substrate were 82% of rocks surface hanging (n = 41), 12% of one leaf hanging (n = 6), and 6% of many leaves hanging (n = 3) (Figure 9C-E). Therefore, the embryos developed within egg until a tail, external gills, and spiracle occurring (stage 25 followed Gosner, 1960). Then, the dropped hatchlings transitioned to exotrophic phase and metamorphosis in the pool (Figure 9F). The parental care behavior was not indicated in this population.

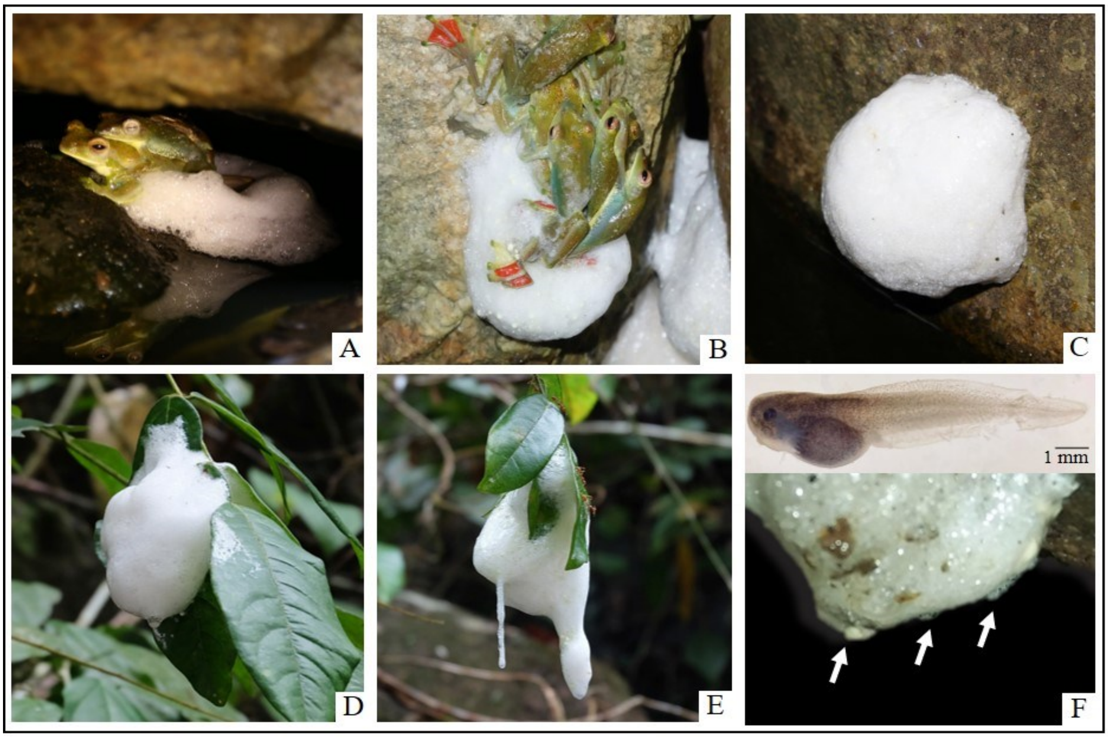

Figure 9. The mating patterns and the reproductive mode of *Zhangixalus prominanus* at Sirindhorn Waterfall. The detected two mating systems a monandry (A), and polyandry (B). The reproductive mode shows a foamy nest on the rocky surface (C), one leaf (D), and many leaves (E). The fully developed larva hatching (white arrow) and dropping into water pool (F).

Discussion

The series of *Zhangixalus prominanus* breeding activities at Sirindhorn Waterfall usually begins with male calling and combat, as the primary behavior of territory defense. Then the resulting behavioral pattern as axillary amplexus of the couple occurs and they will move to the intended places for nesting afterward (Johnson, 1968; Duellman and Trueb, 1994; Liao and Lu, 2010; Khongwir et al., 2016). The evolutionary studies on the reproduction of the family Rhacophoridae claim for the multipurpose of terrestrial foam nest, e.g., frog resource partitioning, predator avoidance, temperature buffer, and preventive desiccation. Additionally, the foam nest development could be evidence of historical climate oscillation as members of Rhacophoridae reportedly entered drier areas (Pough et al., 2004; Wells, 2007; Meegaskumbura et al., 2015; Khongwir et al., 2016; Pereira, et. al., 2017).

Due to the exploration at Sirindhorn Waterfall, the reproductive mode is classified as number 33 following Haddad and Prado (2005); directly pool dropped hatchling from foam nest. We also noted the different foam nest hanging substrates, which are preferably located on the rock. It might be the distance and slope of the rock are assisted to directly dropping into the water. It is supported by the previous report on many arboreal nests of anurans species, that live on an extended range of heights, but their oviposition site was significantly close to the water surface (Valencia-Aguilar et al., 2012; García et al., 2013). Due to those places, the foam nests are more concerned with temperature control, oxygen supply, solar radiation protection, predator avoidance and the most important is the accurate direction of larva slipping (Delia et al., 2010; Gould, 2021).

Generally, the mating patterns of animals were modified by environmental changing and the quality of a population (Wittenberger, 1979; Alcock, 2005; Adrian and Sachser, 2011). The monandry and polyandry of *Z. prominanus* found in observation are common mating systems in anurans, especially the family Rhacophoridae (Liao and Lu, 2010; Prado et al., 2005; Roberts and Byrne, 2011). However, the reasons for these mating patterns in *Z. prominanus* are ambiguous, where it might be related to environmental factors, meanwhile, the influence of the operational sex ratio of anurans population was also mentioned (Sullivan et al., 1995; Lodé et al., 2004; Sztatecsny et al., 2006; Kokko and Jennions, 2008; Matsuba et al., 2008). The sex ratio between male and female sexes of this population is not equal, seem the number of males is higher than female. Also, highly sufficient resources in the male population would possibly dominate a single female or many females. The limited resources could cause the population to the polyandrous mating pattern (Emlen and Oring, 1977; Brown et al., 2011; Ficetola et al. 2010; Ursprung et al., 2011; Byrne and Roberts, 2012; Hudson and Fu, 2013). In birds and mammals, females gain benefit when polyandry increases their access to resources or paternal care is provided by males (Lank et al., 2002; Reding, 2015; Auclair et al., 2014), but this is not explicit in the anuran. Moreover, the polyandrous system of anuran is increasing the reproductive success of males while harassment of females (Zhao et al., 2016).

4.3.3 Mate choice, mating patterns, and mating system

Results

From January 2018 to June 2019, the mating activities of this frog have been monitored completely for 12 events (n = 12). Each event was considered the breeding activities start with the male occurring until mating or complete nesting. The male frogs attempted to monopolize the breeding pool. Therefore, the territory was defended by physical fighting as kicking and jump over were shown, from the rock pools to the tree branches above (Figure 10A). We found that the greater occupier male and as close to the water surface would be more successful in mating (frequency of performance (F)/total observation(T); F/T = 11/12), while the non-selected male sneaked around and would shove in between selected male and female by chance (F/T = 4/12). Meanwhile, most females rarely indicated their position and activities, but when they reached the breeding pool, the selected male would approach anyway (Figure 10B). Nevertheless, the *Zhangixalus prominanus* amplexus pairs move to the male defending spot (F/T = 12/12), which is clearly that they mainly used a resource defense mating system. Then, the breeding process was initiated (Figure 10C). Normally, the level of foam nesting was chosen nearby the water surface first, the second level and the next would decide after the previous crowded (F/T = 4/12) (Figure 10D).

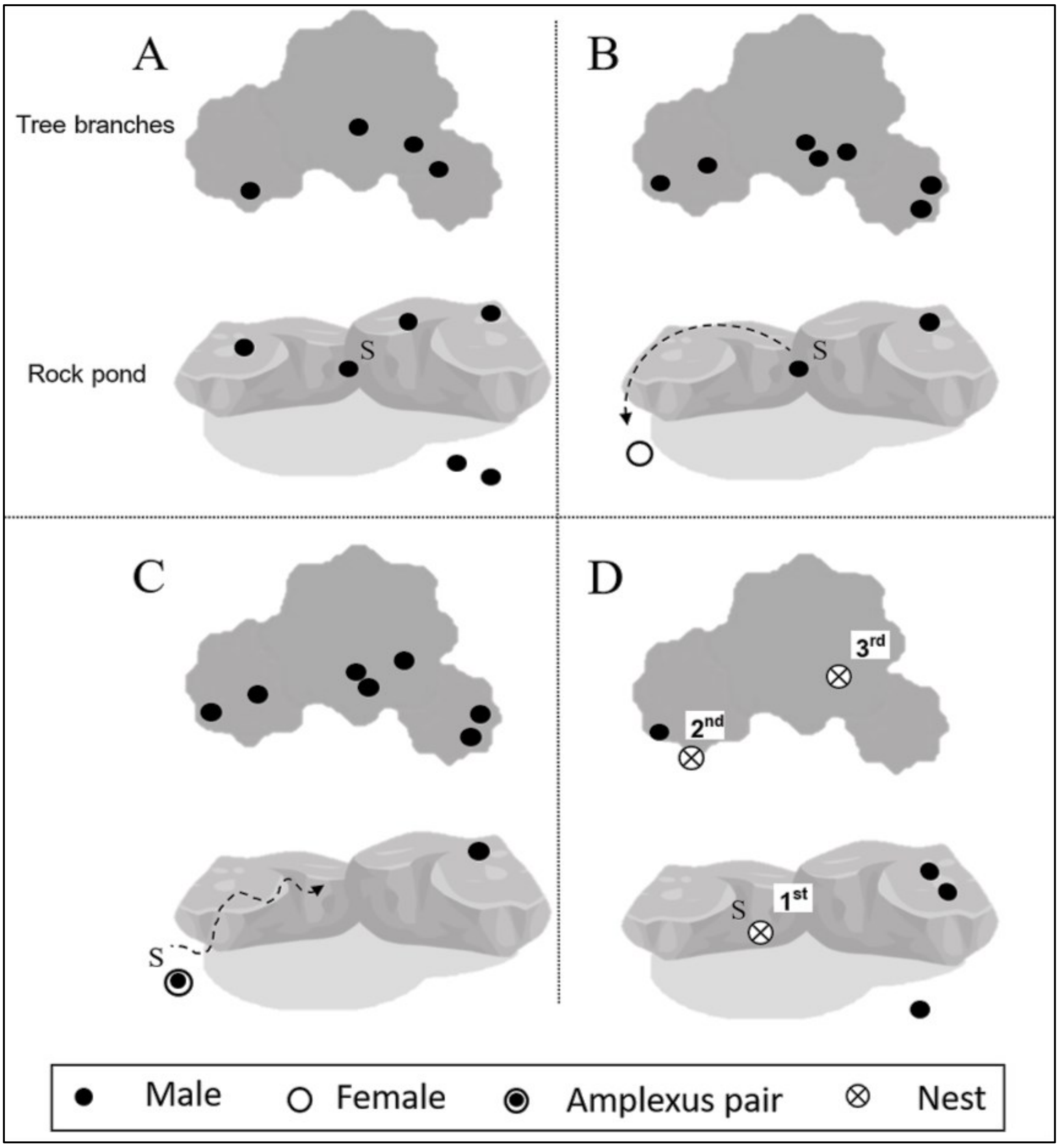

Figure 10. Diagram represented male and female activities of *Zhangixalus prominanus* around breeding rock pool and the bush above. The solid point substitute for male (●) and the selected male (●S). Male territory defending on a lek pool (A). The selected male was come and axillary amplexus with a female (O) (B), The amplexus pair (◉) moved to the occupied area of selected male (C). The nest (⊗) usually foaming close to water surface, another spouse might be nest higher later (D).

Discussion

The male tactics to a mating success of *Zhangixalus prominanus* at Sirindhorn waterfall were territorial defending site, the near to water source and large covering area have higher successful rely on the female choice. The male frogs attempted to monopolize the breeding pool. It is essential to increase the reproductive success of females and reduce the injured of either males or females during group activities (Sztatecsny et al., 2006; Wells, 2007; Zhao et al., 2016). The territory defending by physical fighting which their aggressive behavior might exhibit multiple amplexing (polyandry), or scramble-competition (Roberts and Byrne, 2011; Dias et al., 2017).

The male Rhacophoridae’s suitable calling sites are separated from oviposition sites. Thus, the role of females in the amplexus stage is not only in choosing the mated male but also conduct the males to oviposition places (Fukuyama, 1991; Gerhardt and Huber, 2002; Poelman and Dicke, 2008). However, we suggested that in this population the male defending site and oviposition site is the same place that both male and female choice for the advantage of the tadpole survival. These could be possible by following the mention of Llusia et al., 2013, they summarized environmental factors are critical to determining the mating system of intraspecific variation. Moreover, the selected oviposition place is directly affected the offspring's survival by increasing the efficiency of tadpoles dropping and fewer aquatic predators (Pröhl and Berke, 2001; Wells, 2007; Delia et al., 2010; Gould, 2021).

CHAPTER 5

CONCLUSIONS and RECOMMENDATIONS

Conclusions

The Malayan flying frog (*Zhangixalus prominanus*) population at Sirindhorn Waterfall, Hala-Bala Wildlife Sanctuary represent the unique breeding behaviors also specific habitats requiring. The data was observed and monitored during January 2018 to June 2019 for 10 months in study area with approximately size of 12 x 40 m^2 beside stream of Waterfall, Narathiwat. We investigated the temporal of breeding habitat use, oviposition selection, evaluated the influence of an abiotic factors to breeding activities, also describe breeding behavior including reproductive activity pattern, mating patterns, reproductive mode, mate choice, and mating system of this population at Sirindhorn Waterfall.

We found the *Z. prominanus* at Sirindhorn Waterfall appeared in the breeding site during the survey months. The number of males is always greater than females. In this population, the climatic factors are affecting the appearance of males, females, and clutching, also influencing the breeding habitat use of males and females. The number of males occurring is influenced by seasons, average air temperature, and average relative humidity ($P < 0.05$). Meanwhile, the rainfall and male occurrence affect the number of females occurring ($P < 0.05$). On the other hand, the female occurrence only influences the number of clutches appearing ($P < 0.05$). Then we could mention that the appearance of the member in the *Z. prominanus* population at Sirindhorn Waterfall is directly influenced by climate and environment, however, the tropical rainforest has suitable conditions throughout the year, so their alteration is not clearly monitored.

Consult of clutching monitoring during the study period the five pools were selected by frogs including pools number 8, 12, 14, 15, and 16. All of them were covered by shading over the water surface and most were covered by hanging vegetation. The pools were categorized as the big in size of the pool (over 1,000 cm^3), except pool number 8 which was small in size (an approximately 300 cm^3). The probability of nesting occurrence relied on the climatic and temporal factors including months, seasons, rainfall, average air temperature, average air humidity, and average moonlight visual distance was not statistically significant ($P > 0.05$). Meanwhile, the breeding pool characteristics including the water depth, pH, and dissolved oxygen (DO) affected the probability of oviposition selection. These data approve of the previous reports that the *Zhangixalus prominanus* species requires the specific habitats because they have a high impact on environment changing, then they need more concerned with protected area management.

The breeding strategies of this species could be transformable to fit with the environment for higher reproductive success. The reproductive activity pattern of *Z. prominanus* at Sirindhorn Waterfall was indicated as prolonged breeding, the adult male, gravid female, and foam nests were found throughout the study, and they use the repetitive site for breeding activities. The male was highly frequently reoccurring in the breeding site than the female. Anyway, both males and females could re-mating in a month after nest. The reproductive mode of *Z. prominanus* was identified as the arboreal foam nest with eggs, the complete stage development of hatching tadpoles will directly drop into ponds. The frogs laid their eggs on different kinds of substrates such as a leaf or many leaves, but the rock is favorite. The mate choice of *Z. prominanus* represented that the male frogs attempted to monopolize the breeding pond. Therefore, the territory defending by physical fighting as kicking and jumping over were shown, the greater occupier male and as close to the water surface would be more successful in mating. The mating system of *Z. prominanus* exhibit the resource defense, according to the defending site and oviposition site were the same place. From the study, *Z. prominanus* showed two mating patterns observed in 28 amplexus pairs are monandry (n = 20) and polyandry (n = 8), we suggest that it is for increasing the mating success opportunity.

Recommendations

These studies provide the understanding of the frog reproductive behavioral ecology is helpful to planning species conservation and an opportunity for research combining several fields such as behavioral ecology and evolutionary biology. Moreover, the photographic individual identification will be more used in the future for monitor and identify the frog without touching. However, any factors should be added to cover the potential and continued monitoring for making the data better complete. Moreover, we should increase the sample from many locations because a single population may not be sufficient.

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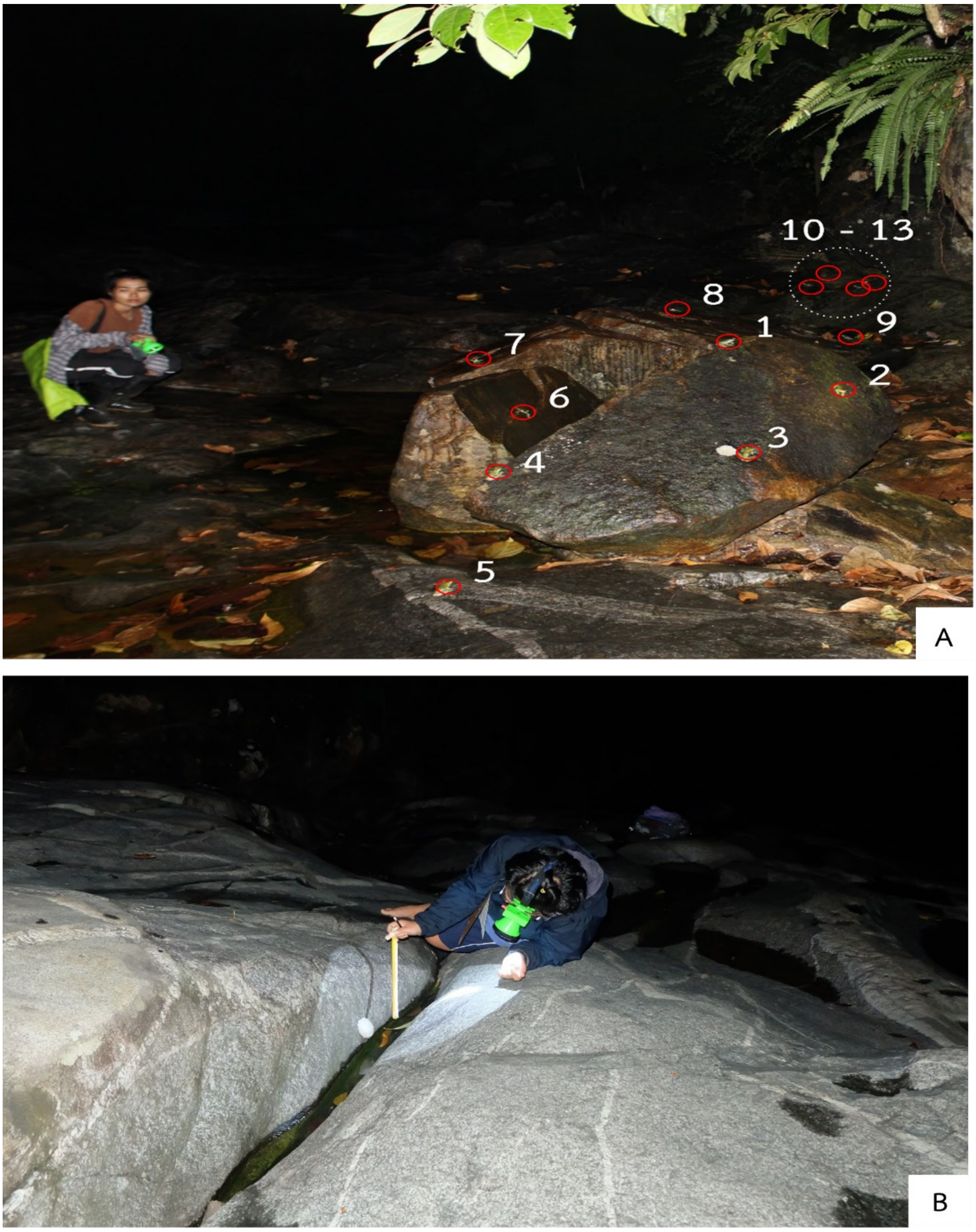
APPENDICES



Appendix 1. The number of frog individuals and clutches were counted (A), and the abiotic factors in a tested rock pool including water temperature, water depth, pH of water, and dissolved oxygen of water were measured (B) at the flattening rock beside the creek of the Sirindhorn Waterfall (study site).

Appendix 2. Correlations of independent variables that effect the clutching occurrence. The asterisk (*) tell the high correlation between tested variables (correlation value > 0.7; Schroeder, 1990)

		Clutch	VH	DPH	%SH	RF	AT	RH	MVD	WT	WD	WS	WV	pH	DO
Pearson Correlation	Clutch	1.000	0.182	-0.153	0.194	0.178	-0.027	0.116	0.036	0.030	0.133	0.216	0.170	0.085	0.053
	VH	0.182	1.000	-0.820*	0.777*	-0.011	0.105	0.044	0.091	0.141	0.335	0.361	0.400	0.283	0.018
	DPH	-0.153	-0.820*	1.000	-0.663	0.019	-0.109	-0.059	-0.050	-0.085	-0.260	-0.272	-0.321	-0.250	0.057
	%SH	0.194	0.777*	-0.663	1.000	0.019	0.027	0.073	0.062	0.135	0.300	0.228	0.249	0.218	-0.021
	RF	0.178	-0.011	0.019	0.019	1.000	-0.303	0.394	-0.037	0.026	0.062	0.043	0.044	-0.087	0.368
	AT	-0.027	0.105	-0.109	0.027	-0.303	1.000	-0.399	0.188	0.112	0.006	0.036	0.030	0.192	-0.196
	RH	0.116	0.044	-0.059	0.073	0.394	-0.399	1.000	0.031	0.013	0.096	0.032	0.071	0.023	0.154
	MVD	0.036	0.091	-0.050	0.062	-0.037	0.188	0.031	1.000	-0.094	0.047	0.037	0.033	0.097	-0.106
	WT	0.030	0.141	-0.085	0.135	0.026	0.112	0.013	-0.094	1.000	0.150	0.112	0.103	0.755	0.171
	WD	0.133	0.335	-0.260	0.300	0.062	0.006	0.096	0.047	0.150	1.000	0.231	0.820*	0.090	0.228
	WS	0.216	0.361	-0.272	0.228	0.043	0.036	0.032	0.037	0.112	0.231	1.000	0.686	0.091	0.141
	WV	0.170	0.400	-0.321	0.249	0.044	0.030	0.071	0.033	0.103	0.820*	0.686	1.000	0.059	0.203
	pH	0.085	0.283	-0.250	0.218	-0.087	0.192	0.023	0.097	0.755	0.090	0.091	0.059	1.000	-0.120
	DO	0.053	0.018	0.057	-0.021	0.368	-0.196	0.154	-0.106	0.171	0.228	0.141	0.203	-0.120	1.000
Sig. (1-tailed)	Clutch		0.000	0.000	0.000	0.000	0.274	0.005	0.212	0.255	0.002	0.000	0.000	0.031	0.121
	VH	0.000		0.000	0.000	0.403	0.010	0.169	0.022	0.001	0.000	0.000	0.000	0.000	0.349
	DPH	0.000	0.000		0.000	0.337	0.008	0.098	0.134	0.030	0.000	0.000	0.000	0.000	0.107
	%SH	0.000	0.000	0.000		0.338	0.275	0.054	0.086	0.001	0.000	0.000	0.000	0.000	0.326
	RF	0.000	0.403	0.337	0.338		0.000	0.000	0.206	0.281	0.085	0.171	0.168	0.028	0.000
	AT	0.274	0.010	0.008	0.275	0.000		0.000	0.000	0.007	0.446	0.213	0.256	0.000	0.000

		Clutch	VH	DPH	%SH	RF	AT	RH	MVD	WT	WD	WS	WV	pH	DO
	RH	0.005	0.169	0.098	0.054	0.000	0.000		0.247	0.387	0.017	0.238	0.059	0.306	0.000
	MVD	0.212	0.022	0.134	0.086	0.206	0.000	0.247		0.020	0.153	0.206	0.233	0.016	0.010
	WT	0.255	0.001	0.030	0.001	0.281	0.007	0.387	0.020		0.000	0.007	0.012	0.000	0.000
	WD	0.002	0.000	0.000	0.000	0.085	0.446	0.017	0.153	0.000		0.000	0.000	0.023	0.000
	WS	0.000	0.000	0.000	0.000	0.171	0.213	0.238	0.206	0.007	0.000		0.000	0.022	0.001
	WV	0.000	0.000	0.000	0.000	0.168	0.256	0.059	0.233	0.012	0.000	0.000		0.096	0.000
	pH	0.031	0.000	0.000	0.000	0.028	0.000	0.306	0.016	0.000	0.023	0.022	0.096		0.004
	DO	0.121	0.349	0.107	0.326	0.000	0.000	0.000	0.010	0.000	0.000	0.001	0.000	0.004	

Remark: VH = Vegetation Hanging, DPH = Distance of Pool's Center to Hanging vegetation (m), SH = Shading (%), RF = Rainfall (mm.), AT = average of Air Temperature (°C), RH = average of Air Humidity (%), MVD = average of Moonlight Visual Distance (m), WT = Water Temperature (°C), WD = average of Water Depth (m), WS = Water Surface (m^2), WV = Volume of water pool (m^3), pH = pH of water, DO = Dissolved Oxygen of Water (mg/l O_2)

Appendix 3. Average counted individuals at breeding site (SE) in each month during the 2018-2019.

	18-Jan	18-Feb	18-Mar	18-May	18-Jun	18-Aug	18-Sep	18-Nov	19-Feb	19-Jun
Male	12.00 (3.26)	15.83(1.56)	15.59(4.80)	11.67(2.17)	24.25(3.67)	17.50(3.81)	17.96(6.72)	10(1.10)	8.5(6.22)	8(1.53)
Female	0.75 (0.24)	0.83(0.59)	1.27(0.62)	1.5(0.62)	0.50(0.25)	0.50(0.34)	2.39(0.98)	0.5(0.14)	1.5(1.5)	0.83(0.40)
Clutch	0.5(0.14)	0.17(0.18)	1.03(0.68)	0.83(0.40)	0.25(0.13)	0.33(0.21)	2.04(1.00)	0.5(0.14)	1.5(1.5)	0.33(0.21)

Appendix 4. The consult of statistical analysis the oviposition site selection model

Table (1). Omnibus Tests of Model Coefficients

		Chi-square	df	Sig.
Step 1	Step	103.807	22	0.000
	Block	103.807	22	0.000
	Model	103.807	22	0.000

The three Chi-Square test statistic values are Step, Block and Model, respectively with the test hypothesis as

H0: **β**1 = **β**2 = **β**3 = ... = 0, the probability of clutching appearance is independent of all parameter variables.

H1: **β** ≠ 0, the probability of clutching appearance depends on at least one parameter variable, which is less than 0.05, H0 rejection accepts H1, which means there is a probability of clutching appearance depending on at least the independent variable at the *0.05* level of significance.

Table (2). Hosmer and Lemeshow Test

Step	Chi-square	df	Sig.
1	1.631	8	0.990

Homer and Lemeshow Test conducted a suitability test of the equation with test the hypothesis as

H0: Model is suitable

H1: Model is not suitable.

From the Chi-Square test, the value was 1.631 and the significant = 0.99, which is greater than 0.05, H0 is accepted, which means the model is fit at the *0.05* level of significance.

Table (3). Classification Table

Observed			Predicted		
			Clutch occurring		Percentage Correct
			.00	1.00	
Step 1	occur Clutch	.00	447	5	98.9
		1.00	26	9	25.7
	Overall Percentage				93.6
a. The cut value is .500					

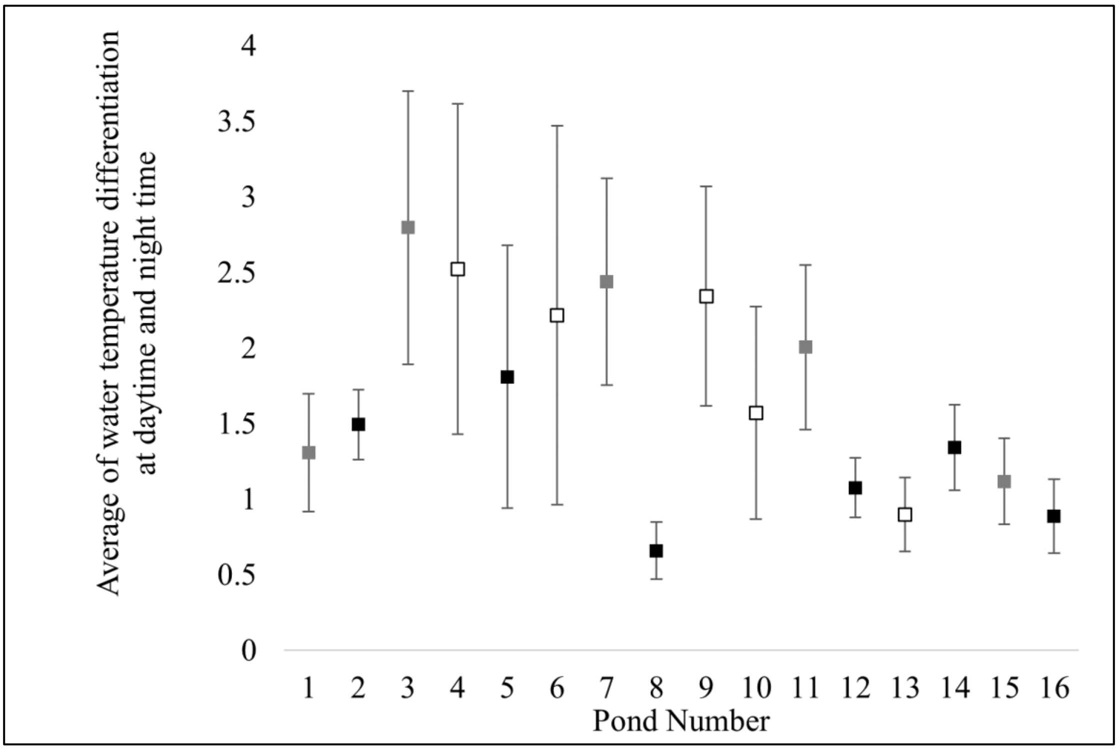
The predictive probability of the model (Predictive Efficiency) was calculated by the ratio between the predicted value and the observed value as a percentage corrected prediction. If it is high, the model has good accuracy. The results of the overall percentage calculation showed that the actual clutching appearing and non-clutching appearing data was 93.6% of clutching prediction.

Chi-Square test shown a probability of nesting that depended on at least one statistically significant independent variable (Table (1)). Furthermore, the model was fit (Table (2)) also the percentage of correct prediction could indicate that the data of nesting occurrence and non-nesting occurrence had a 93.6% accuracy (Table (3)).

The probability of clutching appearance was calculated by

Prob (Clutching) = $1/(1 + e^{-z})$ The coefficient (B) can be written as the equation for the probability of clutch appearance (*Z*-value) which is from all variables as:

Z = -21.272*+ 0.287 (Water Depth Average)* + 1.462 (Water pH)* + 0.435 (DO)* + 0.114 (Water Temperature) - 1.599 (Distance) - 0.043 (% Shading) + 6.966 (Pool No. 12)* + 13.648 (Pool No. 14)* + 12.681 (Pool No. 15)* + 10.570 (Pool No.8) - 11.008 (Pool No. 1) -11.889 (Pool No. 2) - 10.019 (Pool No. 3) - 4.382 (Pool No. 4) - 9.200 (Pool No. 5) - 1.285 (Pool No. 6) - 12.172 (Pool No. 7) – 8.213 (Pool No.9) -5.326 (Pool No. 10) -11.226 (Pool No. 11)



Appendix 5. The Average water temperature (°C) differentiation at daytime and nighttime in each pool. The black square is a pool that was more than 50 % of shading, the grey square is pools were more than 0 but less than 50 % of shading, and the white square was none-shading from any objects.

Appendix 6. Marked individuals occurring and their nesting activity in study area during January 2018 to June 2019: M = male, F = female, x = frog present, ☐ = nesting, Mo = Monandrous mating patterns, Pol = Polyandrous mating patterns, Unk = Unknow the mating patterns

ZP_No.	ZP_Code	Sex	2018/Jan						2018/Feb						2018/Mar						2018/May						2018/Jun					
			26	27	28	29	30	31	27	28	1	2	3	4	23	24	25	26	27	28	4	5	6	7	8	9	22	23	24	25	26	27
001	180126_B07	M	x										x			x																
002	180325_B04	M													x		x															
003	180302_T12	M									x	x	x					x														
004	180227_T08	M																											x			
005	180808_B01	M															x															
006	180929_T10	M																														
007	180928_T04	M																														
008	180228_B06	M								x																						
009	180807_B10	M																			x											
010	180804_T05	M																														
011	180804_B03	M																														
012	180624_T08	M																											x			
013	180301_T13	M									x		x		x																	
014	180302_B10	M										x																				
015	180127_UM	M		Mo								x																	x			
016	180302_T3T	M										x	x									x										
017	180303_T1T	M											x									x										
018	180301_B02	M									x						x				x											
019	180227_T08	M							x		x					x					x											
020	180808_B02	M																														
021	180806_B01	M																														
022	180806_T03	M																														
023	180807_T01	M																														
024	180324_B01	M														x																
025	180303_B05	M											x																			
026	180807_B08	M																														

ZP_No.	ZP_Code	Sex	2018/Aug						2018/Sep						2018/Nov						2019/Feb						2019/Jun						
			4	5	6	7	8	9	24	25	26	27	28	29	2	3	4	5	6	7	13	14	15	16	17	18	25	26	27	28	29	30	1
001	180126_B07	M	x		x	x								Pol			x																
002	180325_B04	M			x	x		Mo			x		Pol						x														
003	180302_T12	M																															
004	180227_T08	M																															
005	180808_B01	M					x							x																			
006	180929_T10	M												x																			
007	180928_T04	M											x																				
008	180228_B06	M																															
009	180807_B10	M				x																											
010	180804_T05	M	x																														
011	180804_B03	M	x											x					x														
012	180624_T08	M																	x														
013	180301_T13	M																															
014	180302_B10	M																															
015	180127_UM	M																															
016	180302_T3T	M																															
017	180303_T1T	M																															
018	180301_B02	M	x			x							x																				
019	180227_T08	M																															
020	180808_B02	M					x							x																			
021	180806_B01	M			x																												
022	180806_T03	M			x																												
023	180807_T01	M				x																											
024	180324_B01	M																															
025	180303_B05	M											Pol																				
026	180807_B08	M				x																											

Appendix 6. Marked individuals occurring and their nesting activity in study area during January 2018 to June 2019: M = male, F = female, x = frog present, □ = nesting, Mo = Monandrous mating patterns, Pol = Polyandrous mating patterns, Unk = Unknow the mating patterns (continued)

ZP_No.	ZP_Code	Sex	2018/Jan						2018/Feb						2018/Mar						2018/May						2018/Jun					
			26	27	28	29	30	31	27	28	1	2	3	4	23	24	25	26	27	28	4	5	6	7	8	9	22	23	24	25	26	27
027	180807_B02	M																														
028	180807_T04	M																														
029	180809_B01	M																														
030	180508_BM02	M																							Pol							
031	180929_B05	M																														
032	180924_TM	M																														
033	180929_B03	M																														
034	180926_T02	M																														
035	180928_B04	M																														
036	180624_B08	M																											x			
037	180504_B03	M																			x											
038	180624_T06	M																											x			
039	180928_TM4	M																														
040	180126_U02	M	x					x																								
041	180627_T01	M																														x
042	180806_B03	M																														
043	180326_TM	M																Mo														
044	180326_B01	M																x														
045	180228_Tunk	M								x																						
046	180626_T04	M																													x	
047	180624_B01	M																											x			
048	180624_B03	M																											x			
049	180127_UF	F		Mo																						Mo						
050	180928_B01	M																														
051	180228_T09	M								x																						
052	180131_T04	M						Mo		x																						
053	180506_B05	M																					x								x	

ZP_No.	ZP_Code	Sex	2018/Aug						2018/Sep						2018/Nov						2019/Feb						2019/Jun						
			4	5	6	7	8	9	24	25	26	27	28	29	2	3	4	5	6	7	13	14	15	16	17	18	25	26	27	28	29	30	1
027	180807_B02	M				x																											
028	180807_T04	M				x																											
029	180809_B01	M						x						x																			
030	180508_BM02	M						x																									
031	180929_B05	M	x											x								x											
032	180924_TM	M							Mo																								
033	180929_B03	M												x																			
034	180926_T02	M									x																						
035	180928_B04	M											x																				
036	180624_B08	M												x																			
037	180504_B03	M																															
038	180624_T06	M	x										Pol																				
039	180928_TM4	M											Pol																				
040	180126_U02	M																															
041	180627_T01	M																															
042	180806_B03	M			x	x																											
043	180326_TM	M																															
044	180326_B01	M																															
045	180228_Tunk	M																															
046	180626_T04	M																															
047	180624_B01	M																															
048	180624_B03	M																															
049	180127_UF	F																															
050	180928_B01	M											x																				
051	180228_T09	M																															
052	180131_T04	M																															
053	180506_B05	M				x	x							x																			

Appendix 6. Marked individuals occurring and their nesting activity in study area during January 2018 to June 2019: M = male, F = female, x = frog present, ☐ = nesting, Mo = Monandrous mating patterns, Pol = Polyandrous mating patterns, Unk = Unknow the mating patterns (continued)

ZP_No.	ZP_Code	Sex	2018/Jan						2018/Feb						2018/Mar						2018/May						2018/Jun						2018/Aug						2018/Sep						2018/Nov						2019/Feb						2019/Jun						
			26	27	28	29	30	31	27	28	1	2	3	4	23	24	25	26	27	28	4	5	6	7	8	9	22	23	24	25	26	27	4	5	6	7	8	9	24	25	26	27	28	29	2	3	4	5	6	7	13	14	15	16	17	18	25	26	27	28	29	30	1
054	180302_T1T	M										x																																																		
055	181103_T01	M																																												x			x														
056	180325_T03	M															x																																												
057	180323_B02	M													x																																														
058	180323_B03	M													x																																														
059	180323_T01	M													x	x																																													
060	180323_T02	M													x																																														
061	180326_T03	M																x																																											
062	180324_T01	M														x																																													
063	180326_TF	F																Mo																																												
064	180324_T06	M														x																																													
065	180327_T1177	M																	x																																										
066	180301_T07	M									x															Mo						x																															
067	180508_BM01	M																							Pol												x																										
068	180506_T02	M																					x																																							
069	180508_BF,Bfi	F																							Pol																																					
070	180505_B05	M																				x																																								
071	180128_U02	M			x												x																																												
072	190701_U	M																																																												x
073	180506_B02	M																					x																																							
074	180506_BM02	M																					x																																							
075	180509_BM	M																								Mo																																				
076	180624_B02	M																											x																																	
077	180327_B02	F																	x																																										
078	180624_B06	M																											x																																	
079	180624_B09	Unk																											x																																	
080	180624_B10	M																											x																																	

Appendix 6. Marked individuals occurring and their nesting activity in study area during January 2018 to June 2019: M = male, F = female, x = frog present, ☐ = nesting, Mo = Monandrous mating patterns, Pol = Polyandrous mating patterns, Unk = Unknow the mating patterns (continued)

ZP_No.	ZP_Code	Sex	2018/Jan						2018/Feb						2018/Mar						2018/May						2018/Jun					
			26	27	28	29	30	31	27	28	1	2	3	4	23	24	25	26	27	28	4	5	6	7	8	9	22	23	24	25	26	27
081	180624_T02	M																											x			
082	180626_B02	M																													x	
083	180131_B04	M						x																					x			
084	180624_T11	M																											x			
085	180505_B06	M																				x										Mo
086	180626_B04	M																													x	
087	180626_T01	M																													x	
088	180626_T02	M																													x	
089	180626_T03	M																													x	
090	180507_T(F)M	F																						Mo								x
091	180627_B03	M																														x
092	180627_FT	F																														Mo
093	180804_B01	M																														
094	180804_T03	M																														
095	180624_T05	M																											x			
096	180131_B02	M						x			x	x	x																			
097	180804_T01	M																														
098	180808_B04	M																														
099	180806_B02	M																														
100	180807_B05	M																														
101	180807_B06	M																														
102	180808_T01	M																														
103	180808_TM	M																														
104	180809_B03	M																														
105	180809_B05	M																														
106	180924_B01	M																														
107	180925_T01	M																														

ZP_No.	ZP_Code	Sex	2018/Aug						2018/Sep						2018/Nov						2019/Feb						2019/Jun						
			4	5	6	7	8	9	24	25	26	27	28	29	2	3	4	5	6	7	13	14	15	16	17	18	25	26	27	28	29	30	1
081	180624_T02	M																															
082	180626_B02	M																															
083	180131_B04	M																															
084	180624_T11	M																															
085	180505_B06	M																															
086	180626_B04	M																															
087	180626_T01	M																															
088	180626_T02	M																															
089	180626_T03	M																															
090	180507_T(F)M	F																															
091	180627_B03	M																															
092	180627_FT	F																															
093	180804_B01	M	x																														
094	180804_T03	M	x																														
095	180624_T05	M																															
096	180131_B02	M												x																			
097	180804_T01	M	x		x																												
098	180808_B04	M					x							Mo			x		Mo														
099	180806_B02	M			x																												
100	180807_B05	M				x																											
101	180807_B06	M				x																											
102	180808_T01	M					x																										
103	180808_TM	M					Mo																										
104	180809_B03	M						x																									
105	180809_B05	M						x																									
106	180924_B01	M							x																								
107	180925_T01	M								x																							

Appendix 6. Marked individuals occurring and their nesting activity in study area during January 2018 to June 2019: M = male, F = female, x = frog present, ☐ = nesting, Mo = Monandrous mating patterns, Pol = Polyandrous mating patterns, Unk = Unknow the mating patterns (continued)

ZP_No.	ZP_Code	Sex	2018/Jan						2018/Feb						2018/Mar						2018/May						2018/Jun						2018/Aug						2018/Sep						2018/Nov						2019/Feb						2019/Jun						
			26	27	28	29	30	31	27	28	1	2	3	4	23	24	25	26	27	28	4	5	6	7	8	9	22	23	24	25	26	27	4	5	6	7	8	9	24	25	26	27	28	29	2	3	4	5	6	7	13	14	15	16	17	18	25	26	27	28	29	30	1
108	180928_TM6	M																																								Pol																					
109	180928_TF	F																																								Mo																					
110	180929_B08	M																																									x																			
111	180929_T05	M																																									Pol																			
112	180929_T09	M																																									x																			
113	181103_B01	M																																											x																	
114	181106_B02	M																																														x														
115	180126_U01	M	x																																																										
116	180928_TF5	F																																								Mo																					
117	180128_U01	M			x																																																								
118	180128_U03	M			x																																																								
119	180131_T03	M						x																																																					
120	180131_B03	M						x																																																					
121	180131_T05	F						Mo																																																					
122	180131_T06	F						x																																																					
123	180217_Unk	M																																																			x								
124	180218_Unk	M																																																				x							
125	180323_B01	M													x																																														
126	180926_T01	M																																						x																						
127	180228_T11	M								x																																																			
128	180928_TM1	M																																								Pol																					
129	180301_B04	M									x																																																		
130	180323_UM3	M													x																																														
131	180928_B05	M																																								x																					
132	180928_B06	M																																								x																					
133	181106_T02	M																																														x														
134	180303_T10	M											x																																																

Appendix 6. Marked individuals occurring and their nesting activity in study area during January 2018 to June 2019: M = male, F = female, x = frog present, □ = nesting, Mo = Monandrous mating patterns, Pol = Polyandrous mating patterns, Unk = Unknow the mating patterns (continued)

ZP_No.	ZP_Code	Sex	2018/Jan						2018/Feb						2018/Mar						2018/May						2018/Jun						2018/Aug						2018/Sep						2018/Nov						2019/Feb						2019/Jun						
			26	27	28	29	30	31	27	28	1	2	3	4	23	24	25	26	27	28	4	5	6	7	8	9	22	23	24	25	26	27	4	5	6	7	8	9	24	25	26	27	28	29	2	3	4	5	6	7	13	14	15	16	17	18	25	26	27	28	29	30	1
135	180929_B07	M																																										x																			
136	180926_B01	F																																							x																						
137	180622_T01	M																									x																																				
138	180928_T02	M																																									x																				
139	180928_T01	F																																									x	Pol																			
140	180929_T07	M																																										x																			
141	180929_T08	M																																										x																			
142	181104_B01	M																																													x																
143	180508_T01	M																							x																																						
144	180509_BF	F																								Mo																																					
145	180301_T02	M									x																																																				
146	180301_T14	M									x																																																				
147	180227_B06	M							x																																																						
148	180303_T11	M											x																																																		
149	180807_B01	M																																		x																											
150	180807_B03	M																																		x																											
151	180925_B01	M																																						x																							
152	180928_B02	M																																									x																				
153	180929_B01	M																																										x																			
154	180507_BF	F																						x																																							
155	180507_TF(M)	M																						Mo																																							
156	180323_UM	M													Mo																																																
157	180626_B03	M																													x																																
158	180929_UF1	F																																										Mo																			
159	180929_F2	F																																										x																			
160	180929_F	F																																										Mo																			
161	181106_BF	F																																															Mo														

Appendix 6. Marked individuals occurring and their nesting activity in study area during January 2018 to June 2019: M = male, F = female, x = frog present, ☐ = nesting, Mo = Monandrous mating patterns, Pol = Polyandrous mating patterns, Unk = Unknow the mating patterns (continued)

ZP_No.	ZP_Code	Sex	2018/Jan						2018/Feb						2018/Mar						2018/May						2018/Jun						2018/Aug						2018/Sep						2018/Nov						2019/Feb						2019/Jun						
			26	27	28	29	30	31	27	28	1	2	3	4	23	24	25	26	27	28	4	5	6	7	8	9	22	23	24	25	26	27	4	5	6	7	8	9	24	25	26	27	28	29	2	3	4	5	6	7	13	14	15	16	17	18	25	26	27	28	29	30	1
162	180808_TF	F	`						`																												Mo																										
163	180323_UF2	F													x																																																
164	180323_UF	F													x																																																
165	180924_UF	F																																					Unk																								
166	180228_B10	M								x																																																					
167	190628_UF2	F																																																										x	Mo		
168	190626_UF	F																																																								Mo					
169	190625_U2	M																																																							x	x	x			x	
170	190625_U1	M																																																							x						
171	190626_U2+U2i	M																																																								x			x		
172	190626_UM	M																																																								Mo					
173	190629_U1	M																																																											x		
174	190629_UM	M																																																											Mo		
175	190629_U5	M																																																											x		
176	190629_U2	M																																																											x		
177	190629_UF	F																																																											x		
178	190213_190443 F	F																																																	Mo												
179	180228_MoF	F								Mo																																																					
180	180506_BF	F																					x																																								
181	180809_TF2	F																																				x																									
182	180928_TF4	F																																									Pol																				
183	181102_UM	M																																											x																		
184	181102_T(F)M	F																																											Unk																		
185	180324_BF1	F														x																																															
186	190628_UF1	F																																																										x			

Appendix 7. Frequency of Marked individuals occurring in the study area from January 2018 to June 2019. This diagram shows the forty frogs from 36 males and 4 females that were repeating detected in each night and each month along with observation: M = male, F = female, x = frog present, Mo = Monandrous mating patterns, Pol = Polyandrous mating patterns, Unk = Unknow the mating patterns.

No.	ZP_No.	Sex	2018/Jan						2018/Feb						2018/Mar						2018/May						2018/Jun						2018/Aug						2018/Sep						2018/Nov						2019/Feb						2019/Jun						
			26	27	28	29	30	31	27	28	01	02	03	04	23	24	25	26	27	28	04	05	06	07	08	09	22	23	24	25	26	27	04	05	06	07	08	09	24	25	26	27	28	29	02	03	04	05	06	07	13	14	15	16	17	18	25	26	27	28	29	30	01
1	001	M	x										x			x																	x		x	x								Pol			x																
2	018	M									x						x				x												x			x							x																				
3	002	M													x		x																		x	x		Mo			x		Pol						x														
4	053	M																					x								x					x	x							x																			
5	005	M															x																				x							x																			
6	011	M																															x											x					x														
7	015	M		Mo								x																	x																																
8	019	M							x		x					x					x																																								
9	038	M																											x				x										Pol																				
10	031	M																															x											x								x											
11	066	M									x															Mo						x																															
12	096	M						x			x	x	x																															x																			
13	098	M																																			x							Mo			x		Mo														
14	003	M									x	x	x					x																																													
15	009	M																			x															x																											
16	012	M																											x																				x														
17	013	M									x		x		x																																																
18	016	M										x	x									x																																									
19	017	M											x									x																																									
20	020	M																																			x							x																			

Appendix 7. Frequency of Marked individuals occurring in the study area from January 2018 to June 2019. This diagram shows the forty frogs from 36 males and 4 females that were repeating detected in each night and each month along with observation: M = male, F = female, x = frog present, Mo = Monandrous mating patterns, Pol = Polyandrous mating patterns, Unk = Unknow the mating patterns. (continued)

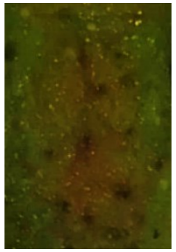
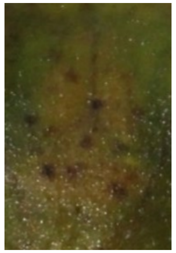
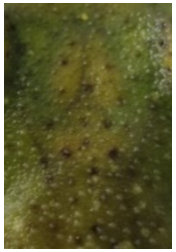
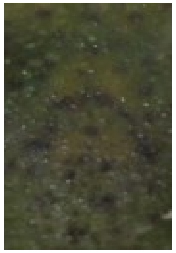
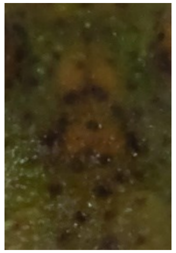
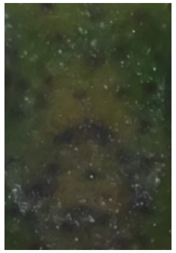
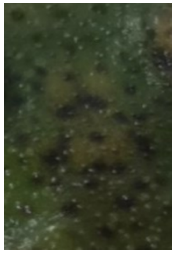
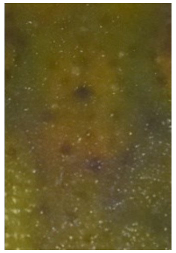
No.	ZP_No.	Sex	2018/Jan						2018/Feb						2018/Mar						2018/May					
			26	27	28	29	30	31	27	28	01	02	03	04	23	24	25	26	27	28	04	05	06	07	08	09
21	025	M											x													
22	029	M																								
23	030	M																							Pol	
24	036	M																								
25	052	M						Mo		x																
26	067	M																							Pol	
27	071	M			x												x									
28	083	M						x																		
29	085	M																				x				
30	040	M	x					x																		
31	042	M																								
32	055	M																								
33	059	M													x	x										
34	097	M																								
35	171	M																								
36	173	M																								
37	049	F		Mo																						Mo
38	090	F																						Mo		
39	141	F																								
40	169	F																								

No.	ZP_No.	Sex	2018/Jun						2018/Aug						2018/Sep						2018/Nov					
			22	23	24	25	26	27	04	05	06	07	08	09	24	25	26	27	28	29	02	03	04	05	06	07
21	025	M																	Pol							
22	029	M												x						x						
23	030	M												x												
24	036	M			x															x						
25	052	M																								
26	067	M											x													
27	071	M																								
28	083	M			x																					
29	085	M						Mo																		
30	040	M																								
31	042	M									x	x														
32	055	M																				x			x	
33	059	M																								
34	097	M							x		x															
35	171	M																								
36	173	M																								
37	049	F																								
38	090	F						x																		
39	141	F																	x	Pol						
40	169	F																								

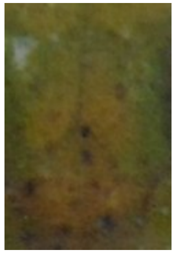
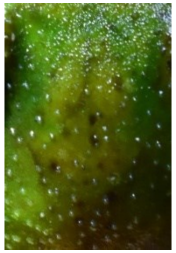
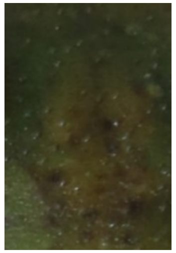
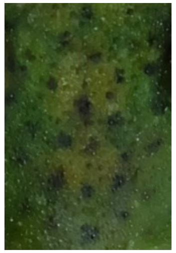
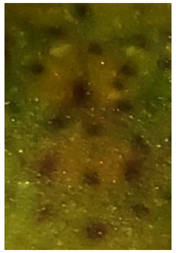
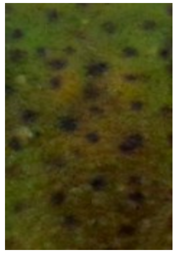
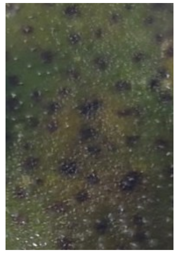
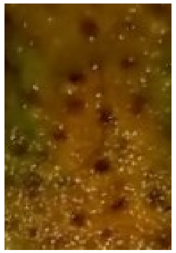
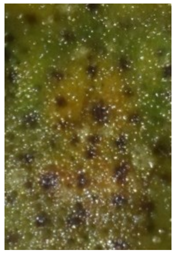
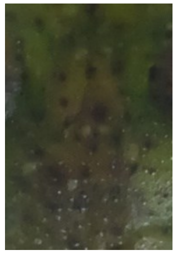
No.	ZP_No.	Sex	2019/Feb						2019/Jun						
			13	14	15	16	17	18	25	26	27	28	29	30	01
21	025	M													
22	029	M													
23	030	M													
24	036	M													
25	052	M													
26	067	M													
27	071	M													
28	083	M													
29	085	M													
30	040	M													
31	042	M													
32	055	M													
33	059	M													
34	097	M													
35	171	M							x	x	x			x	
36	173	M								x			x		
37	049	F													
38	090	F													
39	141	F													
40	169	F										x	Mo		

Appendix 8. The photos of surface forty frog individuals were marked and detected repeating occurrences in the breeding site.

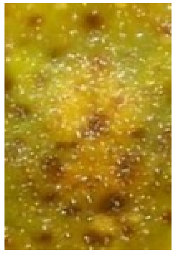
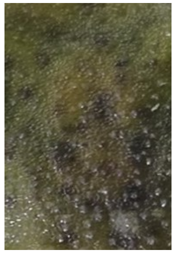
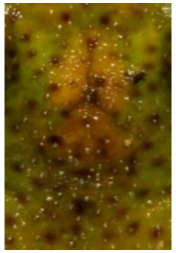
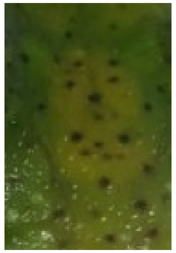
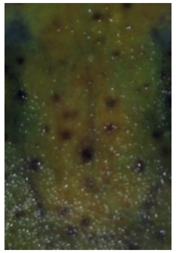
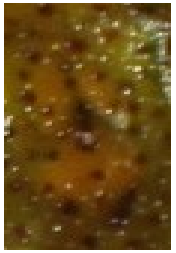
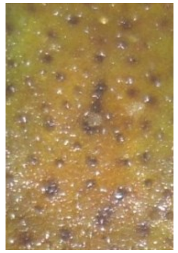
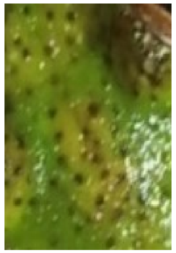
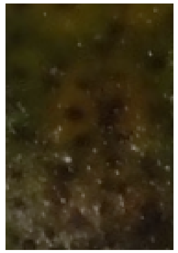
: a = number of marked frog individuals along the study, b = code number of captured frogs in each night (Date_code number)

ZP_001[a]	 180126_B07[b]	 180203_B02	 180324_T05	 180804_T04	 180806_B04	 180807_T02	 180929_T03	 181104_T01
ZP_002	 180323_UM2	 180325_B04	 180806_T02	 180807_T03	 180809_TM	 180926_T03	 180928_TM5	 181106_T04
ZP_018	 180301_B02	 180325_B01	 180504_B02	 180804_B02	 180807_B09	 180928_B03		

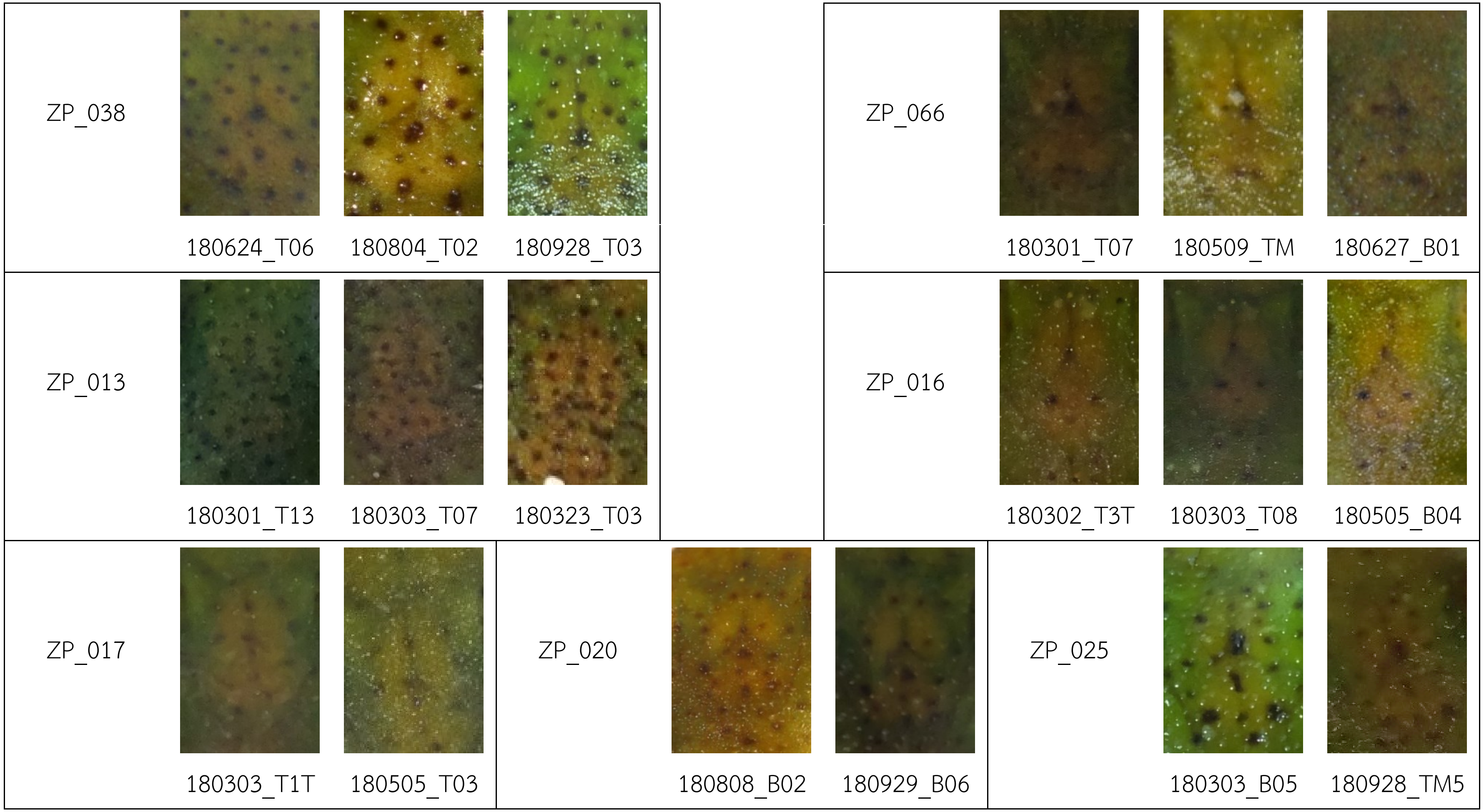
Appendix 8. The photos of surface forty frog individuals were marked and detected repeating occurrences in the breeding site. (continued)

ZP_053	 180506_B05  180626_B01  180807_B04  180808_B05  180929_B04
ZP_009	 180504_B01  180807_B10
ZP_096	 180131_B02  180301_B03  180302_T2T  180303_T3  180929_T06
ZP_012	 180624_T08  181106_T03
ZP_019	 180227_T08  180301_T21  180324_T02  180504_B04
ZP_011	 180804_B03  180929_T01  181106_B01

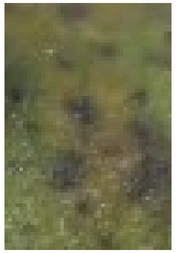
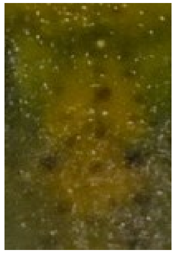
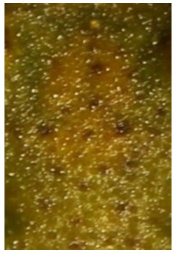
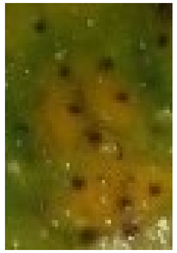
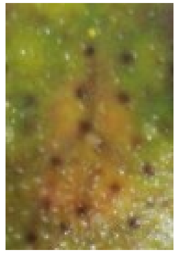
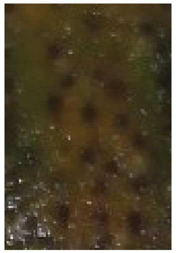
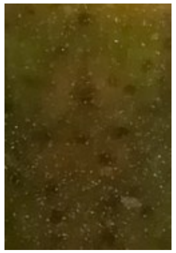
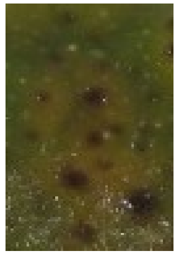
Appendix 8. The photos of surface forty frog individuals were marked and detected repeating occurrences in the breeding site. (continued)

ZP_098					ZP_005			
	180808_B04	180929_M	181104_T02	181106_BM		180325_T01	180808_B01	180929_T04
ZP_003					ZP_015			
	180301_T08	180302_T12	180303_T04	180326_B4		180127_UM	180302_B11	180624_B11
ZP_171					ZP_031			
	190625_U2	190626_U1	190627_U	190630_U		180804_B04	180929_B05	190214_Unk

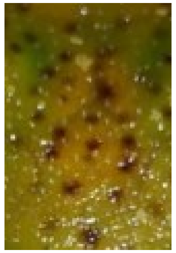
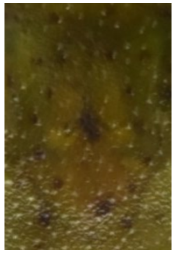
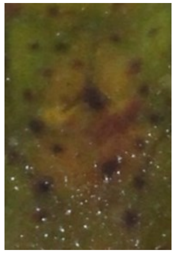
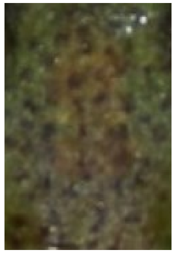
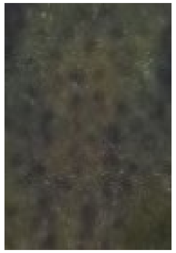
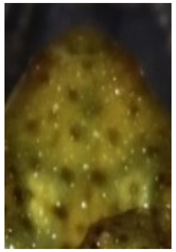
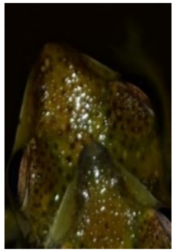
Appendix 8. The photos of surface forty frog individuals were marked and detected repeating occurrences in the breeding site. (continued)



Appendix 8. The photos of surface forty frog individuals were marked and detected repeating occurrences in the breeding site. (continued)

ZP_029			ZP_030			ZP_036		
	180809_B01	180929_T02		180508_BM2	180809_B02		180624_B08	180929_B02
ZP_052			ZP_067			ZP_071		
	180131_T04	180228_T14		180508_BM1	180808_B03		180128_U02	180325_T02
ZP_083			ZP_085			ZP_040		
	180131_B04	180624_T09		180505_B06	180627_MT		180126_U02	180131_T02

Appendix 8. The photos of surface forty frog individuals were marked and detected repeating occurrences in the breeding site. (continued)

ZP_042	 180806_B03	 180807_B07
ZP_055	 181103_T01	 181106_T01
ZP_059	 180323_T01	 180324_T07
ZP_097	 180804_T01	 180806_T01
ZP_173	 190626_U2i	 190629_U5
ZP_049	 180127_UF	 180509_TF
ZP_090	 180507_T(F)	 180627_B2F
ZP_141	 180928_T1F	 180929_PlyF
ZP_169	 190628_UF2	 190629_UF1

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Educational Attainment

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Scholarship Awards during Enrolment

Graduate School, Prince of Songkla University

List of Publications and Proceedings

Jaroensap, H., and Wangkulangkul, S. (2021, May 28). *Male Mating Tactics and Oviposition Site Selection of Zhangixalus prominanus Population at Sirindhorn Waterfall, Hala-Bala Wildlife Sanctuary, Narathiwat Province, Thailand* [Conference presentation]. The 52 National Graduate Research Conference, Chonburi, Thailand.

Jaroensap, H., Karapan, S. and Wangkulangkul, S. (2019, December 13). *Reproductive Activity Pattern of Malayan Flying Frog (Zhangixalus prominanus Smith, 1924) at Sirindhorn Waterfall, Hala-Bala Wildlife Sanctuary, Narathiwat* [Conference presentation abstract]. The 40th Thailand Wildlife Seminar 2019, Bangkok, Thailand.