MORPHOLOGY AND SEXUAL DIMORPHISM OF THE JAGOR'S WATER SNAKE, *Enhydris jagorii* AT BUNG KA LOH WETLAND, UTTARADIT PROVINCE, THAILAND

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ABSTRACT

The Jagor's water snake, *Enhydris jagorii* is belonging to Family Homalopsidae is an endemic species restricted to the Chao Phraya - Ta Chin basin in the central plain of Thailand. This freshwater snake has been facing the population decline due to its freshwater habitats have been changed dramatically and disturbed by many human activities. In order to help protecting this little known endemic species from being threaten, the basic information regarding its biological aspects is needed. The aim of this research is to investigate the morphology and sexual dimorphism of this freshwater snake collected from Bung Ka Loh wetland located in the northern part of Chao Phraya - Ta Chin basin. In this study, 6 morphological characteristics were employed and measured and 5 characters of scale rows were counted and calculated from male and female specimens collected from this wetland during October, 2010 to August, 2012. The data of sexual dimorphism recorded in this study was the first report of this freshwater homalopsid species. The results indicated that females exhibited larger and heavier than males in term of overall body size and weight, but not tail length. Males showed the significant difference by longer in tail length at the same size of SVL than female one. Furthermore, morphological characteristics measurements were taken on neonates. This first attempt resulted in success in this study. This basic information is very important in term of setting up conservation and management procedures in order to help protecting this endemic species from threats by controling the mesh-size of trapping gill nets which is effected to population decline of Jagor's water snake in its habitat in this wetland.

Key words: Homalopsidae, morphology, scalation, sexual dimorphism, freshwater snake, *Enhydris jagorii*, neonate

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INTRODUCTION

The Oriental-Australian rear-fanged water snakes were classified into Subfamily Homalopsinae in Family Colubridae but recent evidences on molecular phylogenetic analyses elevate this clade from subfamilies to familial status. They are opisthroglyphous and have venom glands with deeply grooved rear fangs for delivering hemotoxic and proteolytic venom to their prey. Therefore, 53 species of homalopsid snakes in 27 genera are classified into Family Homalopsidae, sister group to Family Colubridae and Elapidae. Homalopsid snakes are relatively small in length, snout-vented length (SVL) usually less than 1 meter. These snakes have a widely distribution range along northeast -southwest axis from Pakistan's Indus river of Pakistan and Indian subcontinent across Southeast Asia upward to China and eastward to Micronesia and Queensland of Australia (Gyi, 1970; Cox, 1991; Murphy *et al*., 1999; Karns *et al*., 2005; Murphy & Voris, 2005; Fry *et al*., 2006; Murphy, 2007; Pongcharoen, 2008[a,b] ; Karns *et al*., 2010; Cox *et al*., 2013; Murphy & Voris, 2014). This monophyletic group is semi-aquatic snakes, primarily nocturnal and usually associated with mud substrates. They can be separated into 2 groups according to their different habitats which are marine and freshwater species. Marine species live in mangrove forests, tidal mudflats, near-shored coastal waters and estuarine habitats. They feed mainly on fish and crustaceans. Freshwater species are piscivorous but tadpoles and frogs were reported as prey items. This group of snakes can be found in ponds, wallows, canals, streams, rivers, lakes, wetlands and agricultural areas. According to lifestyle, they spend most of their life time in aquatic habitats. Homalopsid snakes are viviparous and distinguished from other snakes by a suite of shared anatomical characteristics related to their habitats including crescent-shaped valvular nostrils, relatively small and dorsally oriented eyes, tightly fitting rostral and labial scales and some have slightly compressed tails (Voris & Murphy, 2002; Murphy, 2007, Pongcharoen, 2008; Karns *et al*., 2010). Nevertheless, while the anatomy, taxonomy and geographic distribution of these snakes have been studied in certain aspects, few has been done on their natural history, consisting primarily of ecological notes and anecdotes. Hence, information on morphology, diets, reproduction and population biology are virtually unknown. (Murphy *et al*., 1999).

Since the widespread of freshwater resources occur throughout Thailand, high biodiversity of aquatic fauna and flora are existed in this country, especially at the Chao Phraya - Ta Chin basin. Sixteen species in 10 genera of homalopsid snakes were reported from Thailand, of which 10 species in 5 genera live in freshwater habitats (Gyi, 1970; Cox, 1991; Karns *et al*., 2005; Murphy & Voris, 2005; Murphy, 2007; Pongcharoen, 2008; Karns *et al*., 2010; Cox *et al*., 2013; Murphy & Voris, 2014). These snakes are recognized as important indicator species serve for measured the health of environment and as important predators for maintaining biodiversity of the wetlands. They may comprise a significant proportion of the vertebrate biomass and occupy important role in trophic dynamics of wetland ecosystems in the Southeast Asia (Karns *et al*., 1999; Murphy, 2007; Karns *et al*., 2010).

However, some freshwater homalopsid snakes have extremely restricted distribution and being endemic to specific drainage systems (Murphy, 2007). Information on natural history of these restricted species is usually poorly known and still unclear. For example, all of freshwater homalopsid snakes found in Thailand, the Jagor's water snake, *Enhydris jagorii* is one of the excellent example for threatened species (Murphy, 2007) (Figure 1). According to Murphy & Voris (2014), This freshwater species belongs to the "*Enhydris* group" that includes a total of six species belonging to the genus *Enhydris*, a species which has been reported as an endemic species restricted to the Chao Phraya - Ta Chin basin inside the central plain of Thailand (Murphy, 2007; Karns *et al*., 2010; Cox *et al*., 2013; Murphy & Voris, 2014). Holotype of this freshwater snake was first described by Peters in 1863. Type locality of this species was documented as "Siam" which might be restricted to

the vicinity of Bangkok, Thailand. Later in the 19th century, this freshwater snake was documented in some reports but there is confusion with other related species. The only information of this mysterious freshwater snake is its distribution which is widely scattered in literatures. Until Karns *et al.* (2010) updated the new localities of this freshwater homalopsid snake at the Bung Ka Loh wetland at Uttaradit Province (Figure 2). Unfortunately, a large area of this wetland is disturbed by many human activities. Uncontrolled fishery is the main problem affected to this freshwater snake population, as well as habitat change and destruction in this wetland. Trapping fish with various mesh-sizes of gill nets is one of the serious treats to population of this freshwater snake. In order to prevent the decline in this freshwater population, investigation on the basic information of this freshwater snake is necessary. In this study, morphology of the Jagor's water snake, *Enhydris jagorii* is described based on specimens collected from this wetland. Morphological characteristics of males and females were investigated by taking measurements and calculations. Sexual dimorphism is also determined. Furthermore, information on morphological characteristics of neonates from gravid females is first described and reported in this study.

Figure 1 Photographs of the Jagor's water snake, *Enhydris jagorii*, an endemic species in Chao Phraya - Ta Chin basin in the central plain of Thailand. (a.) whole body and (b.) head from side view.

Figure 2 Photographs of Bung ka Loh wetland, Pa Sao and Khung Taphao Subdistrict, Meuang District, Uttaradit Province, Thailand. (a.) Arial view of Bung Ka Loh wetland location, close to the 11th highway, Nan River and the downtown of Meuang Uttaradit (Google Earth, 2013) and (b.) Photograph of the wetland during preliminary survey in 2008.

METHODOLOGY

Investigation on morphology of the Jagor's water snake, *Enhydris jagorii* was conducted at the Bung Ka Loh wetland in the period between October 2010 and August 2012 (for the duration of 23 months). Specimens were obtained from those that were regularly trapped in local fishermen's fishing gears, including multiple size of gill nets and funnel traps. Fish traps were regularly set and checked for everyday by local fishermen during the period of investigation. Collected specimens (dead or live) from fish traps were subject to sex determination. Data on morphology were obtained only from mature specimens. Mature females were considered based on the presence of vitellogenic eggs, oviducal eggs, embryos or exhibited an obviously thickened and muscular oviducts. As for males, size of mature specimens were considered based on the same length of SVL of the smallest gravid females found during thiss investigation (Karns *et al.*, 2010 and Voris *et al.*, 2012). Five morphological characteristics; snout-vented length (SVL), tail length (TL), neck girth (NG), body girth (BG) and body mass (BM) were

measured and weighed (Figure 3.1). All the length measurements were conducted using 1 meter measuring tape to the nearest 0.1 centimeter and specimen body mass was weighed using digital balance to the nearest 1 gram. Proportion between TL and SVL (TL/SVL) was also calculated and compared between sexes. Sexual dimorphism Index (SDI) was also calculated for this species. The SDI was calculated by dividing the mean SVL of the larger sex by the mean SVL of smaller sex; a plus was assigned if females were the larger sex whereas a minus was assigned if males were the larger sex (Gibbon and Lovich, 1990). Likewise, 3 characters of scale rows were counted form specimens with completed body scales; dorsal scale rows, ventral scale rows and subcaudal scale rows followed Dowling (1951). For dorsal scale rows, scales were counted at 3 parts; at 10th ventral scales behind the jawbone, at the mid-body of specimens and at 10th ventral scales before the opening of the cloaca (Figure 3.2). Furthermore, 3 morphological characteristics; SVL, TL and body mass of neonates born from live females were also measured and recorded in this study. However, sex determination of these offspring did not conducted because of incompatible size between the sexing probes and the body size of neonates. Three replications of each morphological measurements and scalations were conducted and mean values (±1SD) had been used for statistical analysis. Differences in morphological characteristics and scalations between sexes were calculated and compared the obtained data by using T-test and Man-Whitney U-test ($p \leq 0.05$). Statistical analyses were performed on Laptop computer using the SPSS program version 21.0 for MacOSX operating system version10.9.3. Afterwards, live specimens were released at the site where they were collected inside the area of wetland. For dead specimens, 95% alcohol is used in order to preserve these specimens and later were deposited into the collection of Chulalongkorn University Museum of Zoology (CUMZ) of the Museum of Natural History of Chulalongkorn University.

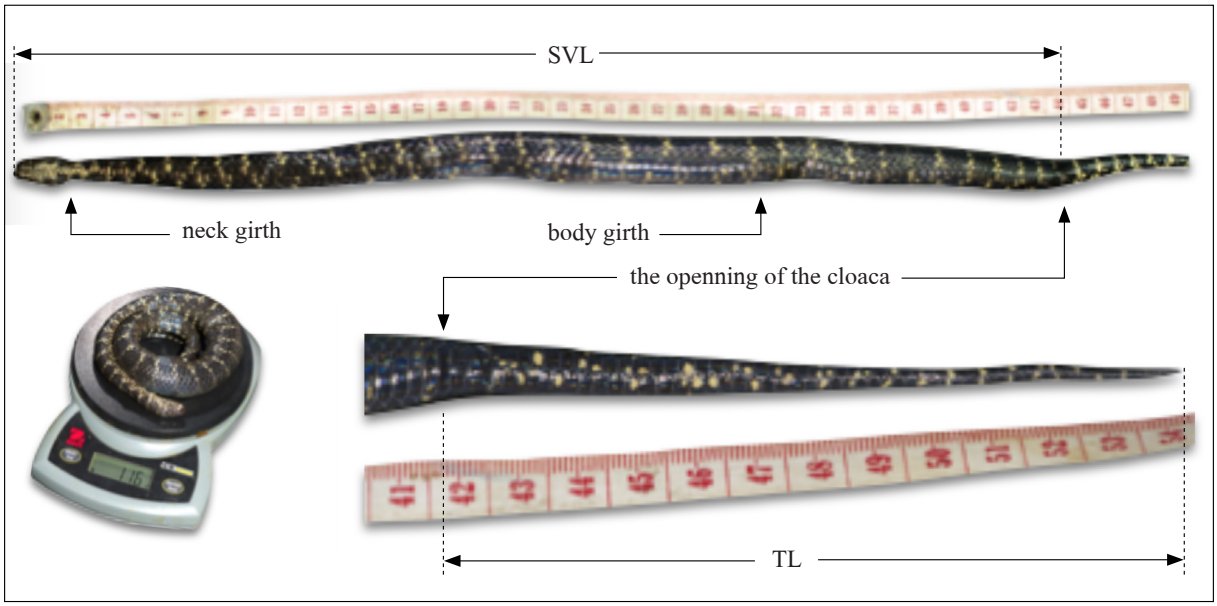

Figure 3.1 Five morphological measurements undertaken on specimens of the Jagor's water snake, *Enhydris jagorii* collected from Bung Ka Loh, Uttaradit Province, Thailand; snout-vent length (SVL), tail length (TL), neck girth, body girth and body mass. The measurements were conducted using 1meter tapeline to the nearest 0.1 centimeter for the length measurements and digital balance to the nearest 1 gram for the weight.

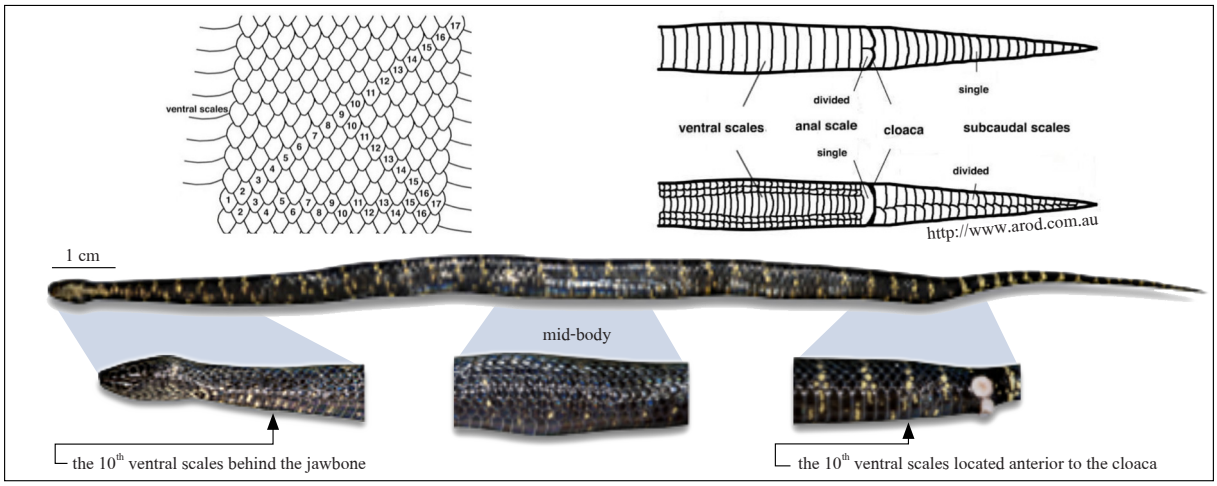

Figure 3.2 Body scale counts of the Jagor's water snake, *Enhydris jagorii* specimens collected from the Bung Ka Loh, Uttaradit Province, Thailand. (a) Three scale rows along different parts of the body were counted; dorsal, ventral and subcaudal scale rows (Dowling, 1951). (b) Dorsal scale rows were counted at three different parts of the body; first at the 10th ventral scales behind the jawbone, secondly at the middle of the specimen body and thirdly at the 10th ventral scales located anterior to the cloaca.

RESULT

The total number of one hundred and eight specimens of the Jagor's water snakes, *Enhydris jagorii* were collected from Bung Ka Loh wetland. Among these, forty eight were mature males and fifty mature females. All specimens were subject to measurements for morphological analysis and sexual dimorphism investigations (Table 1). In this study, the smallest gravid female of this species found in the wetland was 34.0 centimeters in SVL. Thus, male and female specimens with SVL equal to or greater than this length were considered as a mature snake.

Morphological characteristics of 48 males were measured and calculated. The mean SVL was 47.64 ±4.82 centimeters ranged from 34.0 to 53.0 centimeters. The mean TL was 15.27 ±1.97 centimeters ranged from 9.5 to 18.0 centimeters. The mean NG was 3.57 ±0.47 centimeters ranged from 2.3 to 4.5 centimeters. The mean BG was 7.55 ±1.05 centimeters ranged from 5.0 to 9.7 centimeters. The mean body mass was 210.59 ±58.97 grams ranged from 63.0 to 302.0 grams. For females, 50 specimens were measured and calculated. The mean SVL was 50.30 ±7.24 centimeters ranged from 34.0 to 65.0 centimeters. The mean TL was 13.16 ±1.87 centimeters ranged from 10.0 to 16.1 centimeters. The mean neck girth was 4.31 ±0.86 centimeters ranged from 3.0 to 6.7 centimeters. The mean body girth was 9.66 ±2.07 centimeters ranged from 6.2 to 14.5 centimeters. The mean body mass was 323.08 ±152.18 grams ranged from 94.0 to 707.0 grams. The proportion between TL/SVL of both sexes were also calculated. The mean value of the proportion between TL and SVL was 0.32 ± 0.02 in males and 0.26 ± 0.02 in females. The SDI of this species was 1.07.

In this study, 3 characteristics of body scale rows were counted from 24 males and 26 females (Table 2). The 25 - 26 scale rows at the 10th ventral scales behind the jaw, 21 - 23 scale rows at mid-body and 19 - 21 at the 10th ventral scales before the opening of the cloaca were found in males whereas 24 - 26 scale rows at the 10th ventral scales behind the jaw, 21- 23 scale rows at mid-body and 19 - 21 at the 10th ventral scales before the opening of the cloaca were found in females. 117 - 124 scales of ventral scale row and 106 - 136 scales of subcaudal scale row were found in males whereas 116 - 124 scales of

Table 1 A comparison between males and females morphological characteristics of the Jagor's water snake, *Enhydris jagorii* collected from Bung Ka Loh wetland, Uttaradit Province, Thailand. In each column, the mean (±SD) and range (minimum and maximum) values for 5 morphological characteristics; SVL, TL, neck girth, body girth and body mass, and the proportion between TL and SVL are present. Statistical analyses were performed by using T-test and Man - Whitney U-Test ($p \leq 0.05$).

Species	Sex	Morphological characteristics (mean values ± SD)					
		SVL (cm)	TL (cm)	Neck girth (cm)	Body girth (cm)	Body mass (grams)	TL/SVL
	M	47.64 ±4.82	15.27 ±1.97	3.75 ±0.47	7.55 ±1.05	210.59 ±58.97	0.32 ±0.02
	(n=48)	(34.0 - 53.0)	(9.5 - 18.0)	(2.3 - 4.5)	(5.0 - 9.7)	(63.0 - 302.0)	(0.26 - 0.37)
E. jagorii	F	50.30 ±7.24	13.16 ±1.87	4.31 ±0.86	9.66 ±2.07	323.08 ±152.18	0.26 ±0.02
	(n=50)	(34.0 - 65.0)	(10.0 - 16.1)	(3.0 - 6.7)	(6.2 - 14.5)	(94.0 - 707.0)	(0.23 - 0.30)
	p - value	0.021	0.000	0.002	0.000	0.002	0.000

ventral scale row and 97 - 127 scales of subcaudal scale row were found in females. Significant differences of all morphological characteristics of the Jagor's water snakes, *Enhydris jagorii* were observed among males and female specimens collected from the wetland ($p \leq 0.05$). Comparison of the mean values of all morphological characteristics showed that females exhibited significantly larger than males in term of body size based on 4 following morphological characteristics; SVL, Neck girth, body girth and body mass with an exception of tail length (TL). Results from the proportion between TL and SVL showed that males had significantly longer in tail length than females of the same length of SVL (Figure 4). For scalations, the number

Table 2 A comparison between male and female scalations of the Jagor's water snake, *Enhydris jagorii*, collected from Bung Ka Loh wetland, Uttaradit Province, Thailand. In each column; the ranges of each body scale rows (minimum and maximum values) along with the mean value (±SD) are present. Statistical analysis was performed by using Man-Whitney U-Test ($p \leq 0.05$).

Species	Sex	Dorsal scale rows			Ventral scale row	Subcaudal scale row
		10^{th} ventrals behind the jaw	Mid-body	10^{th} ventrals before cloaca		
	M	25 - 26	21 - 23	19 - 21	117 - 124	106 - 136
	(n=24)	(25.25 ±0.44)	(21.17 ±0.48)	(19.79 ±0.66)	(121.65 ±1.56)	(128.65 ±6.95)
E. jagorii	F	24 - 26	21 - 23	19 - 21	116 - 124	96 - 127
	(n=26)	(25.23 ±0.51)	(21.08 ±0.38)	(19.73 ±0.72)	(120.54 ±1.68)	(112.52 ±8.45)
	p-value	0.329	0.153	0.885	0.03	0.000

of dorsal scale rows counted at 3 parts on the specimen body was not significantly different between sexes ($p > 0.05$). The significant differences of number of ventral scale row and subcaudal scale row were found between males and females ($p \leq 0.05$). The mean value (±SD) of ventral scale row was 121.65 ±1.56 scales in males and was 120.54 ±1.68 scales in females. The mean value (±SD) of subcaudal scale row was 126.85 ±6.95 scales in males and 112.52 ±8.45 scales in females. These results indicated that males exhibited greater in number of ventral scale row and subcaudal scale row than females.

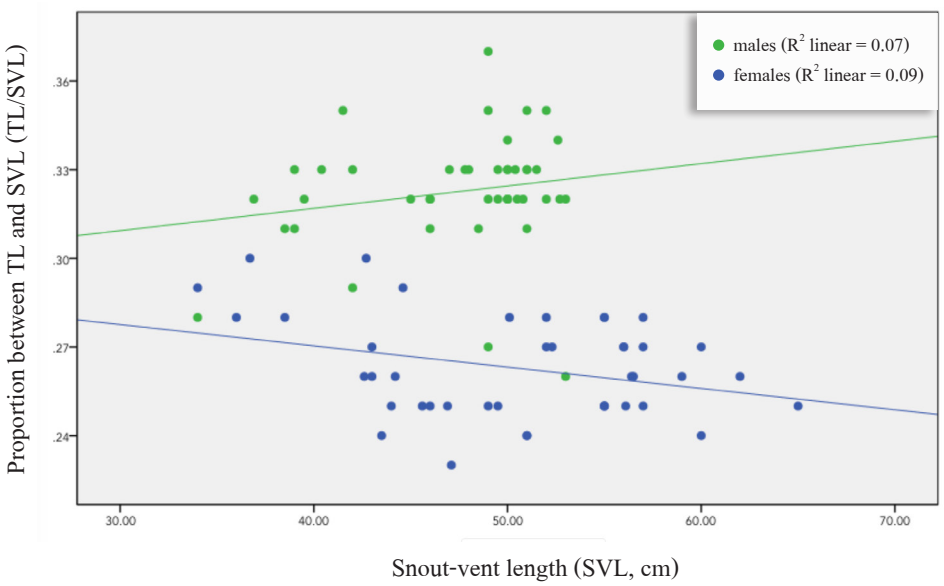

Figure 4 Graph of scattered plots and linear regression of SVL versus the proportion between TL/SVL of males and females of the Jagor's water snake, *Enhydris jagorii* collected from the Bung Ka Loh wetland, Uttaradit Province, Thailand during October 2010 to August 2013 (23 months). Males exhibited longer in tail length than females at the same size of SVL.

Figure 5 Neonates of the Jagor's water snake, *Enhydris jagorii* taken from gravid females from Bung Ka Loh wetland, Uttaradit Province, Thailand.

Moreover, 48 neonates born from live females collected during the period of study were brought for investigation (Figure 5). Five morphological characters consisting of SVL, TL, neck girth, body girth and body mass were measured and calculated (Table 3). Unfortunately, sex determination was not performed on these neonates due to the over size of the equipment. The mean values (±SD) of 5 morphological characteristics of neonates were 14.90 ±0.92 centimeters in SVL, 4.65 ±0.45 centimeters in TL, 1.44 ±0.16 centimeters in neck girth, 1.90 ±0.28 centimeters in body girth and 4.56 ±0.45 grams in body mass. Beside, neonates could swim and feed by themselves immediately after birth.

Table 3 Morphological characteristics of neonates of the Jagor's water snake, *Enhydris jagorii* collected from Bung Ka Loh wetland, Uttaradit Province, Thailand. In each column; the mean (±SD) and the range (minimum and maximum) values of 5 morphological characteristics such as SVL, TL, neck girth, body girth and body mass are present.

Species	**Morphological characteristics (mean values±SD)**				
	SVL (cm)	**TL (cm)**	**Neck girth (cm)**	**Body girth (cm)**	**Mass (grams)**
neonates of *Enhydris jagorii* (n = 48)	14.90 ±0.92 (12.0 - 16.3)	4.56 ±0.45 (3.6 - 5.3)	1.44 ±0.16 (1.2 - 1.8)	1.90 ±0.28 (1.4 - 2.5)	4.56 ±0.83 (2.74 - 8.14)

DISCUSSION

The differences in morphological characteristics between males and females in several species of snakes were documented and reported (Cox, 1991; Mattison, 1995; Shine *et al.*, 1999; Rivas & Burghardt, 2001; Zug *et al.*, 2001; Mattison, 2002; Tomovic *et al.*, 2002; Bertona & Chiaraviglio, 2003; Mattison, 2007; Kings, 2008; Hendry *et al.*, 2014). Likewise, morphology, scalations and sexual dimorphism of some species of freshwater snakes in family Homalopsidae were studied and reported by previous researches. However, these researches are focused on the very common and widely distributed species such as the rainbow water snake, *Enhydris enhydris*, the Mekong water snake, *Enhydris subtaeniata*, the plumbeous water snake, *Enhydris plumbea* are very common and widely distributed species (Murphy *et al.*, 1999; Karns *et al.*, 2002; Karns *et al.*, 2005; Brooks *et al.*, 2007; Murphy, 2007; Pongcharoen, 2008[b]; Karns *et al.*, 2010; Voris *et al.*, 2012). In this study, morphology and sexual dimorphism of the endemic freshwater snake, the Jagor's water snake, *Enhydris jagorii* were revealed (Figure 6).

The significant differences in morphology between sexes of this freshwater snake were observed. In this study, 4 morphological characteristics namely SVL, neck girth, body girth and body mass indicated that females had a significantly larger and heavier body than males ($p < 0.05$). On the contrary, the tail length and the proportion between TL/SVL indicated that males had a significantly longer in tail length than females at the same SVL ($p < 0.05$). Males of this freshwater species had a significantly longer in tail length than females which was strongly supported by their scalations counted from collected specimens. Subcaudal scale rows counted from males had significantly outnumbered those females. Moreover, SDI value also indicated that this freshwater snake exhibited the female-biased sexual size dimorphism. This information were supported

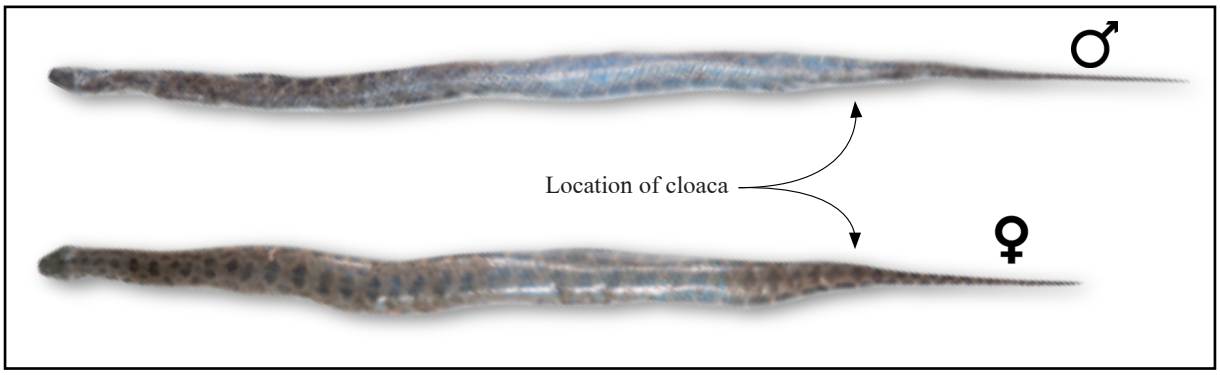

Figure 6 Photograph of male and female of the Jagor's water snakes, *Enhydris jagorii* collected from theBung Ka Loh wetland, Uttaradit Province, Thailand. The significant differences in morphology were observed between sexes; females being larger and heavier in overall body size while males exhibited longer in tail length at the same size of SVL.

by short-term study by Karns *et al.* (2010). Despite their small size sample (n [females] =16 and n [male] =8), females in their study showed larger and heavier in SVL and body mass whereas males showed longer in tail length. Additional to this, information on morphology of neonates was first reported in this study suggesting that gravid females of this freshwater snake reproduced quite a large size of newborns (29.62% of female size). Nevertheless, neonates of this freshwater snake could feed by themselves immediately after birth.

Exhibition of female-biased sexual size dimorphism with a longer in tail length and greater in the number of subcaudal scales of males was a common sexually dimorphic trait in snakes (Karns *et al.*, 2010; Voris *et al.*, 2012). The origin and maintenance of this dimorphism have been proposed and clarified by several researches into 3 primary categories such as sexual selection on male size through mechanism of male-male competition, selection related to fecundity on females such as relationship between reproductive biology and female size and ecological divergence in size mediated by intraspecific competition due to niche partitioning (Cox *et al.*, 2003; Shine, 1989 cited in Hendry *et al.*, 2014). Nevertheless, the benefit of the larger in body size of females was related to their reproductive biology. Many studies reported that the larger females reproduced the larger clutch size and clutch mass which were great for reproductive success (Seigel & Ford, 1987; Bonnet *et al.*, 2000; Aubret *et al.*, 2002; Murphy *et al.*, 2002; Bertona & Chiaraviglio, 2003; Wangkulangkul, 2004; Pongcharoen, 2008[a,b]; Brooks *et al.*, 2009). For males, the benefit of the longer tails was suggested by Shine *et al.* (1999) that males with the longer tails achieve greater reproductive success. Furthermore, the significant information for conservation and management procedures of this freshwater snake habited in the wetland was proposed in this study based on their overall morphological characteristics. Two to 5.0 centimeters in mesh-sized of gill nets are commonly used by local fishermen for fishing in the wetland which are exactly matched to the size of morphological characteristics such as neck girth and body girth of males and females of this freshwater snake. Thus, these snakes would undoubtedly be trapped and could not escape from these mesh-sized gill nets. This due to their body could not pass through these fish traps. According to current situation of these fish traps and uncontrolled fishery, a large number of freshwater snakes were accidentally trapped and drowned to death inside this wetland. In oder to reduce such risk, the control on the mesh-sized of gill nets should be conducted. Gill nets that are used in this wetland should be larger than 4.62 centimeters or approximately larger than 5.0 centimeters, in mesh-size which is

thediameter of the largest collected females in this study. However, the same fish trap has no effect on neonates of this freshwater snake. Since the Jagor's water snake is an endemic species and is restricted Thailand, the conservation and management procedures in order to help protecting the species should be conducted and taken seriously. Nevertheless, their biology, ecology, population and natural history are truly unknown. Hence, further studies on life of the Jagor's water snake, *Enhydris jagorii* which still remains unknown should be undertaken.

ACKNOWLEDGEMENTS

This work was supported by the The 90TH Anniversary of Chulalongkorn University Fund (Ratchadaphiseksomphot Endowment Fund) (16/2011) and the Center of Excellence in Biodiversity under the Research Program on Conservation and Utilization of Biodiversity (CEB_D_27_2011), Department of Biology, Faculty of Science, Chulalongkorn University. The authors would like to thank all contacted local fishermen at Bung Ka Loh wetland for their field assistance during this study period. This paper is dedicated to the memory of Dr. Daryl Ralph Karns who discovered the Jagor's water snake, *Enhydris jagorii* at Bung Ka Loh wetland in 2007. Dr. Daryl Ralph Karns was a biologist and specialist on Oriental-Australian rear-fanged water snakes in Family Homalopsidae whom passed away in 2011.

REFERENCES

Aubret, F., X. Bonnet, R. Shine & O. Lourdais. 2002. Fat is sexy for females but not males: the influence of body reserves on reproduction in snakes (*Vipera aspis*). **Hormones and Behavior** 42: 135 - 147.

Bertona, M. & M. Chiaraviglio. 2003. Reproductive biology, mating aggregations and sexual dimorphism of the Argentine boa constrictor (*Boa constrictor occidentalis*). **Journal of Herpetol**ogy 37: 510-516.

Bonnet, X., G. Naulleau, R. Shine & O. Lourdais. 2000. Reproductive versus ecological advantages to larger body size in female snakes, *Vipera aspis*. **OIKOS** 89: 509-518.

Brooks, S. E., E. A. Allison & J. D. Reynold. 2007. Vulnerability of Cambodian water snakes: initial assessment of the impact of hunting at Tonle Sap Lake. **Biological Conservation** 139: 401-414.

Brooks, S. E., E. H. Allison, J. A. Gill & J. D. Reynold. 2009. Reproductive and trophic ecology of an assemblages of aquatic and semi-aquatic snakes in Tonle Sap, Cambodia. **Copeia** 2009: 7-20.

Cox, M. J. 1991. **The Snakes of Thailand and their Husbandry**. Kriger Cundall Publishing, Florida.

Cox, M. J., M. F. Hoover, K. Thirakhupt & L. Chanhome, L. 2013. **The Snakes of Thailand**. Sirabutr Printing Co., Ltd., Bangkok.

Dowling, H. G. 1951. A proposed standard system of counting ventrals in snakes. **British Journal of Herpetology** 1(5): 97-99.

Fry, B. G., N. Vidal, J. A. Norman, F. J. Vonk, H. Scheib, S. F. R. Romjan, S. Kuruppu, K. Fung, S. B. Hedges, M. K. Richardson, W. C. Hodgson, V. Ignjatovic, R. Summerhayes & E. Kochva. 2005. Early evolution of the venom system in lizards and snakes. **Nature** 439 (7076): 584-588.

Gibbons, J. W. & J. E. Lovich. 1990. Sexual dimorphism in turtles with emphasis on the Slider turtle (*Trachemys scripta*).

Herpetological Monographs 4: 1–29.

Gyi, K. K. 1970. A revision of colubrid snakes of the subfamily Homalopsinae. **University of Kansas Publication, Museum of Natural History** 20: 47-223.

Hendry, C. R., T. J. Guiher & R. A. Pyron. 2014. Ecological divergence and sexual selection drive sexual size dimorphism in new world pitvipers (Serpentes: Viperidae). **Journal of Evolution and Biology** 27 (2014): 760–771.

King, R. B. 2008. Sexual dimorphism in snake tail length: sexual selection, natural selection, or morphological constraint? **Biological Journal of the Linnean Society** 38(2): 133-154

Karns, D. R., H. K. Voris, T. Charn-ard & J. C. Murphy. 1999. The spatial ecology of the rainbow water snakes, *Enhydris enhydris* (Homalopsinae) in southern Thailand. **Herpetological Natural History** 7(2): 97-115.

Karns, D. R., H. K. Voris & T. G. Goowin. 2002. Ecology of Oriental - Australian rear - fanged water snakes (Colubridae : Homalopsinae) in the Pasir Ris Park Mangrove Forest, Singapore. **The Raffles Bulletin of Zoology** 50(2): 487 - 498.

Karns, D. R., J. C. Murphy, H. K. Voris & J. S. Suddeth. 2005. Comparison of semi-aquatic snake communities associated with the Khorat Basin, Thailand. T**he Natural History Journal of Chulalongkorn University** 5(2): 73-900.

Karns, D. R., J. C. Murphy & H. K. Voris. 2010. Semi-aquatic snake communities of the Central Plain Region of Thailand. **Tropical Natural History** 10: 1-25.

Mattison, C. 1995. **The Encyclopedia of Snakes**. Blandford Press, London.

Mattison, C. 2002. **The Encyclopedia of Snakes.** Cassell Paperbacks, London.

Mattison, C. 2007. **The Encyclopedia of Snakes.** Octopus Publishing Group, London.

Murphy, J. C., H. K. Voris, D. R. Karns, T. Chan-ard & K. Suvunrat. 1999. The ecology of the water snakes of Ban Tha Hin, Songkhla Province, Thailand. **Natural History Bulletin of Siam Society** 47: 129-147.

Murphy, J. C., H. K. Voris, B. L. Stuart & S. G. Paltt. 2002. Female reproduction in the Rainbow water snakes, *Enhydris enhydris* (Serpentes, Colubridae, Homalopsinae). **The Natural History Journal of Chulalongkorn University** 2(1): 31 - 37.

Murphy, J. C. 2007. **Homalopsid Snakes: Evolution in the Mud**. Krieger Publishing, Florida.

Murphy, J. C. & H. K. Voris. 2005. A new Thai *Enhydris* (Serpentes: Colubridae: Colubrinae). **The Raffles Bulletin of Zoology** 53(1): 143-147.

Murphy, J. C. & H. K. Voris. 2014. A checklist and key to the homalopsid snakes (Reptilia, Squamata, Serpentes), with the description of new genera. **Fieldiana, Life and Earth Sciences** 8: 1-43.

Pongcharoen, C., K. Thirakhupt & H. K. Voris. 2008a. **Life history patterns of homalopsinae snakes inside and outside the Khorat Basin, Thailand**. M.Sc. Thesis, Chulalongkorn University.

Pongcharoen, C., K. Thirakhupt, & H. K. Voris. 2008b. Reproductive cycle of the rainbow water snake, *Enhydris enhydris*, Prachinburi Province, Thailand. **Journal of Wildlife in Thailand** 15(1): 49-53.

Rival, J. & G. M. Burghardt. 2001. Understanding sexual size dimorphism in snakes: wearing the snake's shoes. **Animal Behaviour** 62(3): F1–F6

Seigel, R. A., N. B. Ford & S. S. Novak. 1987. **Snake: Ecology and Evolutionary Biology**. McGraw-Hill, New York.

Shine, R., M. M. Olsson, I. T. Moore, M. P. LeMaster & R. T. Mason. 1999. Why do male snakes have longer tails than

females? **Proceedings of the Royal Society** 266(1434): 2147-2151.

Stuart, B. L., K. J. Smith, P. D. Davey & S. G. Platt. 2000. Homalopsine water snakes the harvest and trade Tonle Sap, Cambodia. **TRAFFIC** 18: 115-122.

Tomovic, L., J. Radojicic, G. Dzukic & M. L. Kalezic. 2002. Sexual dimorphism of the Sand viper (*Vipera ammodytes* L.) from the Central Part of Balkan Peninsula. **Russian Journal of Herpetology** 9(1): 69-76.

Voris, H. K. & J. C. Murphy. 2002. The prey and predators of homalopsine snakes. **Journal of Herpetology** 36: 1621-1632.

Voris. H. K., J. C. Murphy, D. R. Karns, E. Kremer & K. O'Connell. 2012. Differences among populations of the Mekong mud snake (*Enhydris subtaeniata*: Serpentes: Homalopsidae) in Indochina. **Tropical Natural History** 12: 175-188.

Zug, G. R., L. J. Vitt & J. P. Caldwell. 2001. **Herpetology: An Introductory Biology of Amphibians and Reptiles**. Academic Press, San Diego.

Wangkulangkul, S., K. Thirakupt & H. K. Voris. 2005. Sexual size dimorphism and reproductive cycle of the little file snake *Acrochordus granulatus* in Phangnga Bay. **Science Asia** 31: 257-263.