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Semi-aquatic Snake Communities of the Central Plain Region of Thailand

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ABSTRACT.– **The Central Plain is one of the major natural regions of Thailand. It is a wide alluvial plain with little topographic relief consisting of multiple river basins. The many natural and anthropogenic wetland habitats in the region make it an ideal habitat for many aquatic and semi-aquatic species. We document the semi-aquatic snake communities associated with aquatic habitats in the Central Plain of Thailand. We surveyed a diversity of localities in the Central Plain and documented the occurrence of 10 species based on a sample of 786 snakes. The snake communities of the region are dominated by homalopsid snakes (7 species). *Enhydris enhydris*, the Rainbow Water Snake, was the dominant species at all sites surveyed and accounted for 80.2% of the snakes collected. We collected data on sexual dimorphism, sex ratios, reproduction, and diet. We found that all species examined, except *Homalopsis buccata*, exhibited female-biased sexual size dimorphism and we document significant differences in length and mass among Central Plain populations of *E. enhydris*. Sex ratios varied among populations, from male to female dominated. A large proportion of the *E. enhydris* examined were in reproductive condition (67.5%, n = 160). For *E. enhydris*, we documented clutch size based on vitellogenic follicles (mean = 16.7 ± 1.07) and oviducal eggs (mean = 11.4 ± 2.00), a positive relationship between female body length and clutch size, and a mean relative clutch mass of 0.37 ± 0.07. Diet analysis indicated that homalopsid species are piscivorous and species of the Cyprinidae were the most common diet item. Our data suggest homalopsids eat numerous, relatively small prey items. The Central Plain snake assemblage is similar in species composition to other semi-aquatic snake communities in Indochina. The populations of *E. enhydris* from the Central Plain are large in body size and exhibit high reproductive effort compared to other populations of *E. enhydris* for which information is available. The robustness of the Central Plain population may be related to the high productivity of the wetlands of the Central Plain. We discuss historical, biogeographical, biotic, and abiotic factors that may contribute to the differences observed among semi-aquatic snake communities in the region and the differences documented among populations of *E. enhydris*.**

KEY WORDS: **Homalopsidae, mud snakes, *Enhydris enhydris*, semi-aquatic snake communities, sexual dimorphism, sex ratios, reproduction, diet**

INTRODUCTION

Ecological communities are variable and change over time and distance in response to multiple historical and geographic factors. In a discussion of snake community ecology, Vitt (1987) notes that historical, biogeographic, abiotic, and biotic factors contribute to the particular assemblage of species found in a particular area. Karns et al. (2005) reported on semi-aquatic snake communities associated with the Khorat Basin (also referred to as the Khorat Plateau) in northeastern Thailand, a prominent geographic feature of Indochina. Karns et al. (2005) identified the Khorat Basin as a potentially important biogeographic feature that has likely influenced patterns of biological diversification in the region. We here report on a survey of semi-aquatic snake communities in the adjacent Central Plain region of Thailand (Fig. 1).

The semi-aquatic snake communities of Southeast Asia are dominated by the Homalopsidae, the Oriental-Australian Rear-fanged Water Snakes. This family currently includes ten genera and 37 species of snakes distributed from Pakistan across Southeast Asia to northern Australia and Micronesia (Murphy, 2007). Recent molecular phylogenetic analyses elevate the clade from subfamilial to familial status (Lawson et al., 2005), support the hypothesis that it is monophyletic (e.g. Voris et al., 2002; Alfaro et al., 2008), and robustly recover the Homalopsidae as the sister group to colubroids and elapoids *sensu* Vidal et al. 2007 (Vidal and Hedges, 2005, 2009; Kelly et al., 2003; Vidal et al., 2007; Wiens, 2008). Vidal et al. (2007) suggest the Homalopsidae be placed in the superfamily Homalopsoidea. The homalopsids are a relatively small, geologically old clade, that exhibit considerable morphological and ecological diversity (Alfaro et al., 2008).

All homalopsids are semi-aquatic, primarily nocturnal, and usually associated with mud substrates. Eight of the 37 species (22%) are coastal marine species living in mangrove forests, tidal mudflats, near-shore coastal waters, and estuarial habitats. The freshwater species are found in ponds, streams, wetlands, agricultural wetlands (e.g., rice paddies), and lakes (Murphy, 2007). Most homalopsids eat fish, frogs, or tadpoles, but feeding on crustaceans is well documented in three of the coastal marine species (Voris and Murphy, 2002). The Homalopsidae share several features that are frequently observed among semi-aquatic snakes, including dorsally placed valvular nostrils, relatively small eyes, and live birth. They are opisthoglyphous and have large venom glands with deeply grooved rear fangs for delivering haemotoxic and proteolytic venom (Fry et al., 2005). Homalopsids are relatively small in length (most species < 1 m adult snout-vent length).

FIGURE 1. Map showing the four primary collection localities in the Central Plain of Thailand (Bung Cho, Bung Ka Lo, Phetchabun, and Bung Boraphet) and two other areas sampled within Thailand: Kabin Buri (Southeastern Basin) and Ban Badan (Khorat Basin). Coordinates and other particulars for these localities are provided in Appendix 1.

Homalopsids thrive in the aquatic ecosystems of Thailand. The rivers, streams, lakes and wetlands of Thailand are found in six major river basins (Salween, Mae Klong, Southern Peninsula, Southeastern, Chao Phraya, and Mekong) with each river basin consisting of multiple sub-basins (Kitimasak et al., 2005). The Mun and Chi rivers of the Khorat Basin are part of the Mekong River

TABLE 1. Summary of semi-aquatic snakes collected from the Central Plain of Thailand (June 17 – July 14, 2007). Species are ordered by total abundance. Numbers in parentheses indicate the number of collecting nights at that site. The Nan and Pa Sak River sub-basins are two of the 8 sub-basins that form the Chao Phraya River Basin of the Central Plain of Thailand. We did not collect *Enhydris plumbea* during our study, but it is documented from the Central Plain, and we include it in our biogeographic analysis (see text and Table 2).

Species	Nan Sub-Basin Uttaradit Area		Nan Sub-Basin Bung Boraphet Area	Pa Sak Sub-Basin Phetchabun Area	Total number of snakes
	Bung Cho (11)	Bung Ka Lo (3)	Bung Boraphet (5)	Phetchabun (14)	
Homalopsidae					
Enhydris enhydris	91	196	180	163	630
Enhydris subtaeniata	0	0	54	0	54
Homalopsis buccata	5	29	3	0	37
Enhydris jagorii	0	26	0	0	26
Enhydris bocourti	0	3	0	0	3
Erpeton tentaculatus	0	0	3	0	3
Other Water Snakes					
Xenochrophis flavipunctatus	8	7	0	10	25
Cylindrophis ruffus	3	0	1	2	6
Xenopeltis unicolor	0	1	0	1	2
Total Snakes/Site	107	262	241	176	786
Number of Snakes/Night	9.7	87.3	48.2	12.6	23.8
Species Richness	4	6	5	4	10
Species Evenness	0.364	0.534	0.426	0.195	0.511

Basin and flow, ultimately, to the South China Sea. To the southwest of the Khorat Basin is the Southeastern River Basin consisting of three sub-basins. To the west is the Chao Phraya River Basin consisting of eight sub-basins that form the Central Plain of Thailand. The rivers of the Southeastern and Chao Phraya River Basins flow into the Gulf of Thailand. Our study took place in two of the sub-basins of the Central Plain, the Nan and Pa Sak.

The Central Plain of Thailand (the greater Chao Phraya River Basin) slopes southward from the mountainous northern, eastern, and western regions of Thailand to the Gulf of Thailand (UNESCO, 2003). The region can be divided into the Upper and Lower Central Plain. The Upper Central Plain is composed of the sub-basins of the Ping, Wang, Yom, and Nan rivers; these rivers, flowing from the north, combine to form the Chao Phraya River in Nakhon Sawan Province; the Pa Sak River, on the eastern edge of the Central Plain, joins the Chao Phraya further south, near Ayutthaya. The Lower Central Plain consists of a flat, featureless plain with the Chao Phraya River flowing into the Gulf of Thailand (UNESCO, 2003).

Today, over 90% of the area of the Central Plain is either used for agriculture or is forested (~50% of this area is dedicated to agriculture). The Central Plain is densely populated and heavily used for rice production. The complex irrigation system of the Central Plain has created an extensive agro-wetland that is suitable habitat for semi-aquatic snakes. The region faces conservation challenges from land degradation, dredging, erosion, pollution, and water availability (UNESCO, 2003).

In this report we document the semi-aquatic snake assemblages from three geographic areas in the Central Plain of Thailand and compare the Central Plain communities we studied to other semi-aquatic snake assemblages in Southeast Asia. We document species richness and species diversity among assemblages, compare population characteristics (sex ratio, sexual size dimorphism) among populations, and provide information on diet and reproduction.

MATERIALS AND METHODS

Study sites.– We collected the information presented in this report from June 17 to July 14, 2007 (Fig. 1 provides a map; see Appendix 1 for geographic details). For the purposes of this study we separated our nine sampling localities into three geographic areas (Fig. 1, Table 1): 1) Uttaradit Area consisting of two sites located in the vicinity of Uttaradit, Uttaradit Province (Bung Cho and Bung Ka Lo) in the central Nan River sub-basin; 2) Phetchabun Area consisting of five sites located in the vicinity of Phetchabun, Phetchabun Province (Nong Na Young, Nong Bua, Ban Pak Nam, Ban Subjampa, and the Phetchabun fisheries) in the Pa Sak River sub-basin; and 3) Bung Boraphet Area consisting of two sites located in the Bung Boraphet wetland near Nakon Sawan, Nakon Sawan Province (Khlong Khut, Ban Pra Non) in the southern Nan River sub-basin. Based on sample sizes and distance among the nine sampling localities, we will treat Bung Cho and Bung Ka Lo (Uttaradit Area) as separate sites, combine data from the five Phetchabun Area collecting sites, and combine the data from the two Bung Boraphet Area collecting sites for purposes of analysis; thus, we use four Central Plain locations for comparison (Fig. 1, Table 1).

Uttaradit area (14 collecting nights). The Bung Cho wetland (Fig. 2A) was visited on 11 nights and is located approximately 28 km southwest of the city of Uttaradit (straight-line distance). The wetland is approximately 1.4 sq km in area, 1.8 km in length, and 0.8 km at its widest point. It is a series of small ponds and canals surrounding a central shallow lake. Residents reported that, historically, Bung Cho was a natural wetland that flooded on an annual basis; however, the construction of a dam and perimeter road in the last 10 to 15 years has modified drainage patterns; lotus plants dominate the aquatic vegetation and the lotus fruit is harvested.

The Bung Ka Lo wetland (Fig. 2B) was visited on 3 collecting nights and is located approximately 3 km west of the city of Uttaradit (straight-line distance). The wetland is triangular in shape, approximately 10 sq km in area, 5.0 km in length, and 3.5 km at its widest point. It is a marshy wetland with a shallow, central lake. The wetland area is bordered by rice paddy. Bung Ka Lo was historically a natural wetland adjacent to the Nan River; however, the area has been modified in recent years by the construction of a perimeter road that created a canal around the wetland area and modified drainage patterns. An extensive area of rice paddy north of the perimeter road was originally part of the Bung Ka Lo wetland complex.

Phetchabun area (16 collecting nights). This locality differed from the other sites; there was no large lake/wetland complex. We collected snakes at five locations; four

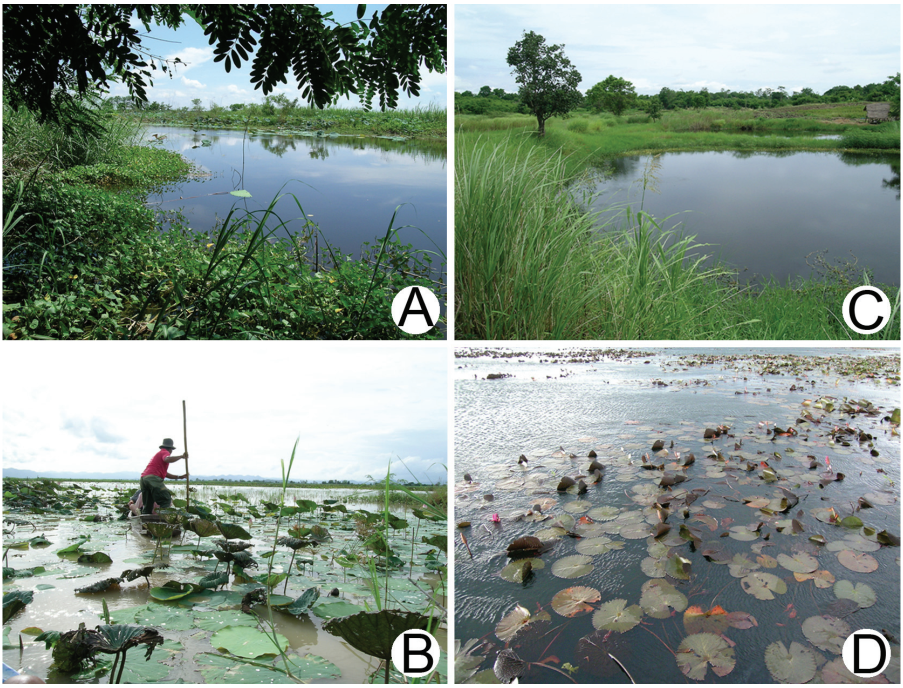


FIGURE 2. Central Plain snake collecting localities. (A) Bung Cho wetland, Uttaradit Province; a typical gill net site is shown. (B) Bung Ka Lo wetland, Uttaradit Province; the center of the wetland is a shallow lake dominated by lotus plants. (C) Nong Na Young, Phetchabun Province; a wetland area adjacent to the Nong Na Young reservoir is shown. (D) Bung Boraphet wetland, Nakon Sawan Province; Bung Boraphet is the largest wetland area in the Central Plain of Thailand. Photos by D. Karns.

of the five sites (two pond/reservoirs, a stream site, and government fishery ponds) were located within 5 km of the town of Phetchabun; the fourth site was located approximately 30 km south of Phetchabun. Nong Na Young (7 collecting nights) is a reservoir (Fig. 2C) surrounded by a paved road, marshy areas, and rice paddy; the reservoir is roughly rectangular and 0.07 sq km in area. Snakes were collected in the reservoir and in the adjacent wetland/rice paddy. We also collected at Nong Bua (1 collecting night), a small pond (rectangular, 5,600 sq m, located 1 km south of Nong Na Young) bordered by shrubby wetland adjacent to the Pa Sak River. Snakes were also obtained from a tributary of the Pa Sak River running through the town of Ban Pak Nam (6 collecting nights). We also collected at the government-operated fisheries facility immediately north of Phetchabun (1 collecting night). The station consists of an array of fish rearing ponds of various sizes. A fifth site, Ban Subjampa (1 collecting night), was located approximately 30 km south of Phetchabun in an upland site with paddy fields, corn fields, and cattle grazing. Snakes were collected in the small streams, canals, farm ponds, and paddy field ponds found there.

Bung Boraphet area (5 collecting nights). The Bung Boraphet wetland (Fig. 2D) is the largest freshwater wetland system in Thailand (Sriwongsitanon et al., 2007). Today, the center of the wetland is a large, shallow lake (mean depth of 2.0 m) with several islands bordered by rice paddies, marsh areas, and grassland. Large sedge beds and lotus swamps are found in the wetland. The wetland is approximately 20 km in length and 5 km at its widest point, depending on flood conditions. The catchment area of the central lake and wetland is approximately 4,300 sq km. The present surface area is 106 sq km, but this varies considerably due to water level fluctuations (up to 300 sq km during floods). Klong Tatako and Klong Bon are the two main tributaries of the lake. Historically the area was a natural wetland that annually flooded during the wet season and then became a grassy plain with scattered ponds and wetlands during the dry season. The current lake was created by a dam built in 1926-30 and further modified by later water level control structures and road construction. Portions of the Bung Boraphet wetland are protected as a non-hunting area and Bung Boraphet is internationally recognized for its diverse flora and fauna (Sriwongsitanon et al., 2007).

Collecting methods.– We employed hand-collecting and gill nets to obtain snakes. The majority of collecting effort went into the use of gill nets. Fishing with gill nets is a commonly employed practice and aquatic snakes are commonly caught as by-catch (organisms accidentally caught in the nets). We contracted with local fishers to set gill nets. Gill nets were usually deployed in the late afternoon and then checked once in the evening. Snakes drown in gill nets if they are not near the surface; checking in the early evening increases the capture of live snakes. The gill nets were removed the following morning, checked for snakes, and moved to another location. Mesh size of the gill nets employed varied from 2.5 to 4.0 cm, with 2.5 and 3.0 cm most commonly used. The typical gill net height of about 1.5 m exceeded the water depth under most circumstances; unweighted gill nets allowed snakes a better opportunity to surface for air. We recognize that gill nets are a size-biased sampling method (see Discussion). We attempted to monitor the number of net-nights, length of nets, and mesh size of nets in order to obtain some measure of collecting effort per site, but this proved difficult due to multiple fishers and conflicting information.

Dead snakes were quickly processed or frozen. Live snakes were euthanized, processed, and preserved with formalin. For all snakes we measured snout-vent length (SVL) and tail length to the nearest mm and weighed snakes to the nearest 0.1 gm. Tissue samples (liver and heart tissue) were typically taken from euthanized snakes. Snakes found dead in gill nets were usually dissected, examined for stomach contents, and the reproductive condition of females noted. We recorded females as reproductively mature when they contained enlarged vitellogenic follicles, oviducal eggs, or exhibited an obviously thickened and muscular oviduct (indicating that they were post-partum). We counted the number of vitellogenic follicles and oviducal eggs, and we categorized embryonic oviducal eggs according to Zehr (1962). The preserved collection of snakes was deposited with the National Science Museum of Thailand.

Statistical analysis.– We used regression analysis, t-tests, analysis of variance (ANOVA), analysis of covariance (ANCOVA), or chi-square analysis in statistical analyses. A Tukey HSD for unequal sample sizes post hoc test was used to test comparisons among means used in ANOVA and ANCOVA. We used the arcsine transformation to normalize proportional data. Statistical procedures were conducted using

STATISTICA (Version 6.01, StatSoft Inc., Tulsa, OK). Means are followed by ± 1 standard error (SE) except where otherwise noted; α was set at 0.05.

We calculated a sexual dimorphism index (SDI) for comparing populations and species of snakes. The SDI is calculated by dividing the mean SVL of the larger sex by the mean SVL of the smaller sex; a plus value is assigned if females are the larger sex and a minus sign if the males are the larger sex (Gibbons and Lovich, 1990). We calculated the relative clutch mass as the ratio of the clutch mass to the maternal mass minus the clutch mass. We determined species evenness (J) by dividing the Shannon-Wiener diversity index calculated for a locality by the natural log of the number of species found at that locality (Magurran, 1988). The Sorenson species overlap index was calculated as: species overlap between two assemblages = 2j/(a + b), where j = number of species common to the two samples, a = number species at one site, b = number of species at the other site (Magurran, 1988).

RESULTS

Snake community structure.– We collected a total of 786 snakes in June and July 2007 (Table 1). This includes dead snakes (by-catch), released snakes, and preserved snakes. We documented 10 species of semi-aquatic snakes. Seven of the 10 species recorded were homalopsids: *Enhydris enhydris* (Schneider), *Enhydris subtaeniata* (Bourret), *Enhydris bocourti* (Jan), *Enhydris jagorii* (Peters), *Homalopsis buccata* (Linnaeus), and *Erpeton tentaculatus* (Lacépede). We also collected three species of non-homalopsid, semi-aquatic snakes: one colubroid, the natricid *Xenochrophis flavipunctatus* (Hallowell); one xenopeltid, *Xenopeltis unicolor* (Reinwardt in Boie); and one cylindrophid, *Cylindrophis ruffus* (Schlegel). We did not collect *Enhydris plumbea* (Boie) in 2007; however, this species has been collected from the Central Plain. Tanya Chanard (personal communication), curator of Amphibians and Reptiles at the National Museum of Thailand, has collected *E. plumbea* from the Central Plain (THNMH 0071-74: Mae Wong Wildlife Sanctuary, Nakhon Sawan Province in 2004; THNMH 10304: Chiang Dao District, Chang Mai Province in 2006) and we include it in our community analysis. The taxonomy of the *X. piscator* complex is in the process of being revised; we followed Vogel and David (2006) and identified the *Xenochrophis* collected as *X. flavipunctatus*. Additionally, *E. subtaeniata* has been confused with *E. jagorii*; based on Murphy (2007) we differentiate between *E. subtaeniata* and *E. jagorii* in this report. In addition to semi-aquatic species, we incidentally collected a specimen of *Rhabdophis subminiatus* (Schlegel), a mostly terrestrial natricid species that prefers wet, lowland forest (Cox et al., 1998).

The four primary collection locations, Bung Cho, Bung Ka Lo, Phetchabun, and Bung Borpaphet, were similar in semi-aquatic species richness with 4 to 6 species recorded (Table 1). The number of snakes collected per night varied considerably, from 9.7 to 87.3 snakes per collecting night at the four primary collecting localities. These differences are a reflection of numerous factors, including the differences in collection effort (number of gill nets and collectors employed) among sites and the particular constellation of microhabitats at each site. Thus, in this case, the daily catch is not a reliable measure of comparative snake densities. The homalopsid *E. enhydris* was numerically dominant at all sites and

TABLE 2. Species richness and species overlap for Southeast Asian semi-aquatic snake assemblages. The Sorensen species overlap index is used (see text). The species richness data come from the following sources: Central Plain: Table 1, this study; Khorat Basin: Karns et al. (2005); Southeastern Basin: Karns et al. (2005); Tonle Sap: Brooks et al. (2007a,b); Lake Songkhla: Karns et al. (1999–2000); Sabah: Voris and Karns (1996).

	Number Species	Central Plain	Khorat Basin	SE Basin	Tonle Sap	Lake Songkhla	Sabah
Central Plain, Thailand	10	1.00	0.89	0.89	0.73	0.70	0.17
Khorat Basin, Thailand	8		1.00	0.88	0.70	0.67	0.20
SE Basin, Thailand	8			1.00	0.70	0.78	0.20
Tonle Sap, Cambodia	12				1.00	0.64	0.14
Lake Songkhla, Thailand	10					1.00	0.17
Sabah, Malaysia	2						1.00

accounted for 80.2% of the 786 total snakes collected, followed by the homalopsids *E. subtaeniata* (6.9%), *H. buccata* (4.7%), and *E. jagorii* (3.3%), and the natricid, *X. flavipunctatus* (3.2%).

Species overlap (Sorenson Index) among the Central Plain semi-aquatic snake assemblages varied between 0.36 and 0.75 (Bung Ka Lo compared to Bung Boraphet = 0.36; Bung Boraphet compared to Phetchabun = 0.44; Bung Ka Lo compared to both Bung Cho and Phetchabun = 0.60; Bung Cho compared to Phetchabun = 0.75; and Bung Cho compared to Bung Boraphet = 0.67). *Enhydris enhydris* was found at all sites, *E. subtaeniata* occurred only at Bung Boraphet, and *E. jagorii* occurred only at Bung Ka Lo. *Homalopsis buccata*, *X. flavipunctatus*, and *C. ruffus* were found at three of the four sites; *X. unicolor* at only two sites. Species evenness varied among sites, but was highest (0.534) at Bung Ka Lo and lowest (0.195) at Phetchabun (Table 1). Species evenness at all sites was heavily influenced by the numerical dominance of *E. enhydris*, and this was particularly true at Phetchabun where *E. enhydris* was the only homalopsid collected and accounted for 92.6% of the snakes collected (n = 176).

Table 2 compares the Central Plain assemblage to five other semi-aquatic snake assemblages from Southeast Asia. These species richness data show the localities of central Indochina ranging from 8 to 12 species, but dropping off to only 2 in Sabah, Malaysia (Borneo). *Enhydris enhydris*, *E. plumbea*, *Homalopsis buccata*, *X. flavipunctatus*, and *C. ruffus* are found in at least five of the six localities. The species overlap among localities in this table decreases with the geographic, straight-line distances between areas sampled: none of the Central Plain, Southeastern Basin, and Khorat Basin sites are more than 400 km apart (overlap of 0.88-0.89); the Central Plain/Khorat Basin region we sampled is approximately 600 km from Tonle Sap, Cambodia (0.70-0.73), 1000 km from Lake Songkhla, Thailand (0.64-0.78), and 2000 km from Sabah, Malaysia (0.17-0.20).

Sexual size dimorphism and sex ratios.– To examine sexual size dimorphism (SSD) we used snakes obtained from gill nets that could be reliably sexed using external morphology. We present the SSD comparison for *E. enhydris* (Table 3) from the four Central Plain populations and for two additional populations outside the

TABLE 3. Sex ratios and sexual dimorphism of populations of *Enhydris enhydris* from localities in central and northeastern Thailand. Data for Kabin Buri and Ban Badan are from Karns et al. (2005); data for Tonle Sap are from Brooks et al. (2009). *P* values for comparisons of sex ratios are from Chi-square tests, while *P* values for comparisons of snout-vent lengths (SVL), mass, and tail:SVL ratios are from two-tailed *t*-tests (NS = not significant; *** $P < 0.001$). For SVL, mass, and tail:SVL ratios, the mean ± 1 standard error (SE) are given, and for SVL and mass the ranges are given in parentheses; for Tonle Sap, only the maximum SVL is shown in parentheses. The sexual dimorphism index (SDI) is calculated by dividing the mean SVL of the larger sex by the mean SVL of the smaller sex; a plus value is assigned if females are the larger sex and a minus sign if the males are the larger sex (Gibbons and Lovich, 1990).

Locality	Sex ratio M:F	*P*	SVL (cm) mean ± SE (range)		*P*	Mass (gm) mean ± SE (range)		*P*	Tail:SVL Ratio mean ± SE		*P*	SDI
			female	male		female	male		female	male		
Central Plain Bung Cho	2.1 n = 90	***	54.9 ± 1.30 (44.1 - 69.6) n = 28	50.7 ± 0.52 (43.6 - 61) n = 61	***	156.0 ± 13.09 (58.3 - 325.0) n = 28	101.8 ± 2.62 (60.5 -154) n = 61	***	0.24 ± 0.003 n = 28	0.29 ± 0.002 n = 60	***	+1.08
Bung Ka Lo	0.47 n = 192	***	59 ± 0.45 (44.8 - 71.1) n = 131	54.4 ± 0.50 (43.5 - 66.5) n = 61	***	216.8 ± 4.97 (86.5 - 340.0) n = 131	130.1 ± 2.74 (89.5 - 183.4) n = 60	***	0.23 ± 0.002 n = 126	0.27 ± 0.002 n = 58	***	+1.08
Phetchabun	0.83 n = 162	NS	54.7 ± 0.66 (43 - 75.3) n = 89	51.4 ± 0.56 (42.4 - 63.0) n = 74	***	150.9 ± 8.39 (53.5 - 460.0) n = 89	109.1 ± 4.14 (54.9 - 242.0) n = 74	***	0.22 ± 0.002 n = 89	0.26 ± 0.004 n =70	***	+1.06
Bung Boraphet	1.33 n = 175	NS	60.2 ± 0.67 (49.3 - 78.8) n = 75	52.1 ± 0.30 (41.2 - 60.5) n = 100	***	205.7 ± 8.68 (95.6 - 490.0) n = 75	114.6 ± 2.38 (68.5 - 188.8) n = 100	***	0.23 ± 0.002 n = 67	0.27 ± 0.002 n = 92	***	+1.16
Kabin Buri (Southeast Basin)	1.01 n = 275	NS	55.3 ± 0.71 (35 - 73.5) n = 135	47.1 ± 0.38 (35.4 - 57.0) n = 140	***	133.0 ± 5.00 (27.6 - 325.0) n = 135	72.2 ± 1.96 (24.6 - 134.6) n = 140	***	0.22 ± 0.002 N=120	0.26 ± 0.002 N=138	***	+1.17
Ban Badan (Khorat Basin)	0.78 n = 28	NS	46.0 ± 1.58 (39.0 - 54.0) n = 17	44.9 ± 1.76 (36.5 - 61.8) n = 11	NS	85.2 ± 10.71 (40.2 - 182.3) n = 17	75.6 ± 7.78 (47.1 - 126.9) n = 11	NS	0.24 ± 0.005 N=17	0.28 ± 0.002 N=11	***	+1.02
Tonle Sap (Cambodia)	1.44	—	50.5 ± 0.2 (74.1) n = 1826	47.6 ± 0.1 (69.3) n = 2371	***	97.8 ± 1.2 (335) n = 1154	81.5 ± 0.5 (285) n = 2448	***	0.28 ± 0.001	0.32 ± 0.001	***	—

Central Plain (Karns et al., 2005): Ban Badan (Khorat Basin) and Kabin Buri (Southeastern Basin). All Central Plain populations of *E. enhydris* and the Kabin Buri population (Southeastern Basin) exhibited SSD with females significantly longer and heavier than males (Table 3). The Ban Badan population (Khorat Basin) did not exhibit SSD with respect to SVL and mass. Male *E. enhydris* from all localities had significantly longer tails, relative to SVL, compared to females (Table 3).

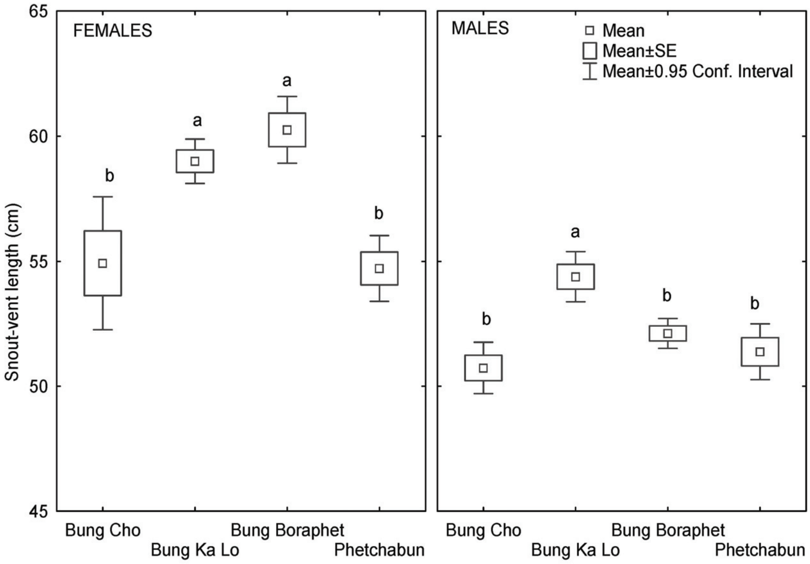
Central Plain populations of *E. subtaeniata*, *E. jagorii*, and *X. flavipunctatus* all exhibited SSD with females being longer and heavier than males (Table 4). Male *E. subtaeniata* and *E. jagorii*, but not *X. flavipunctatus*, had significantly greater tail : SVL ratios; only males with intact tails were used in these comparisons. The exception to the general pattern of female-biased sexual size dimorphism was *H. buccata*. Male *H. buccata* were significantly longer than females; male *H. buccata* were also heavier than females, but the difference was not significant.

We determined that SVL differed among the four Central Plain *E. enhydris* populations (Fig. 3) for both males ($F_{(3,292)} = 10.17$, $P < 0.001$) and females ($F_{(3,319)} = 17.32$, $P < 0.001$). We then did an ANCOVA on both male and female mass using SVL as the covariate (Fig. 3) and found a significant difference among localities for both males ($F_{(3, 290)} = 2.87$, $P < 0.05$) and females ($F_{(3, 318)} = 9.33$, $P < 0.001$). We used a Tukey HSD for unequal sample sizes post hoc test to determine specific differences in SVL and mass among populations shown in Figure 3.

The sexual dimorphism index (SDI: Gibbons and Lovich, 1990) varied from +1.06 to +1.16 for Central Plain *E. enhydris* populations sampled in 2007 (Table 3). For sites sampled in 2003-04 (Karns et al., 2005), the SDI varied from +1.02 (Ban Badan, Khorat Basin) to +1.17 (Kabin Buri, Southeastern Basin). All other species (Table 4), except for *H. buccata* (-0.90), exhibited female-biased SDI values (*E. subtaeniata* = +1.17; *E. jagorii* = +1.09; *X. flavipunctatus* = +1.29).

We calculated sex ratios for populations of snakes collected at the different sites for *E. enhydris* (where sample sizes were large) and combined from all sites for the other species (Tables 3 and 4). These ratios include all snakes that could be reliably sexed on the basis of external morphology. Sex ratios varied among localities for *E. enhydris* and among the other species; significant deviations from a 1:1 sex ratio were noted with Central Plain *E. enhydris* from Bung Cho and Bung Ka Lo, but not from Phetchabun or Bung Boraphet (Table 3). *Enhydris enhydris* populations from Kabin Burin (Southeastern Basin) and Ban Badan (Khorat Basin) were not significantly different from a 1:1 sex ratio. Sex ratios varied from being strongly male biased (Bung Cho: 2.10) to strongly female-biased (Bung Ka Lo: 0.47). The sex ratios for *E. subtaeniata*, *E. jagorii*, and *X. flavipunctatus* were not significantly different from 1:1 (Table 4); whereas, *H. buccata* was significantly male biased.

Reproductive biology.– Table 5 summarizes the reproductive characteristics for the *E. enhydris* we examined. A large percentage (67.5%) of the 160 female *E. enhydris* from the Central Plain localities were in reproductive condition (carrying vitellogenic follicles, oviducal eggs, or exhibiting enlarged, flattened oviducts, indicating recent birth); data from the four Central Plain sites are combined in Table 5.



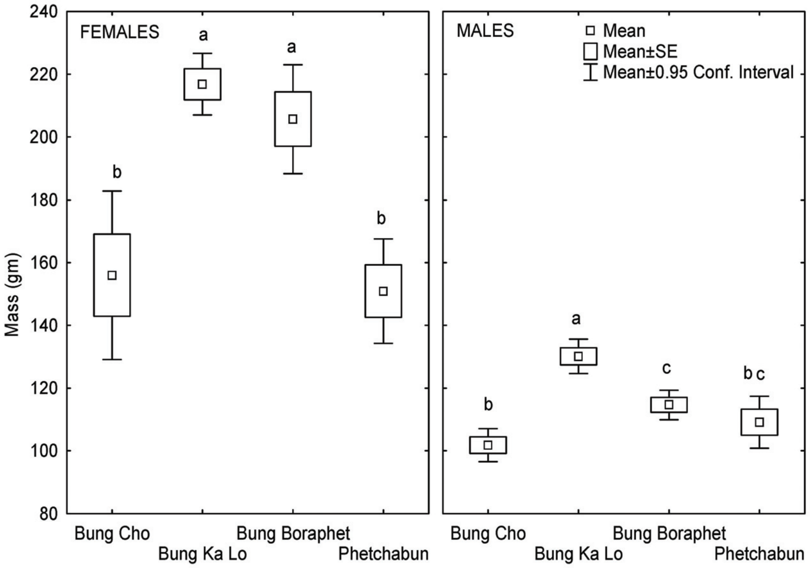


FIGURE 3. Geographic variation in snout-vent length (SVL) and mass among Central Plain populations of *Enhydris enhydris*. The mean SVL (± SE), mass (± SE), and 95 % confidence limits are shown for females and males from each population. Sample sizes for the four sites are given in Table 3. Different letters above the means indicate significant differences among means at $P \leq 0.05$ based on Tukey HSD unequal sample sizes post hoc test; letters in common indicate no difference. Comparison of male and female SVL and mass for each population shows the female-biased sexual size dimorphism observed in all populations (see Table 3 for statistical analysis).

The mean clutch size, based on the number of vitellogenic follicles was 16.7 ± 1.07 (n = 25); the mean clutch size based on the number of oviducal eggs was 11.4 ± 2.00 (n = 14). The mean relative clutch mass of seven *E. enhydris* was 0.37 (SE = ± 0.07; range = 0.14 – 0.60). We observed embryonic oviducal eggs in developmental stages 20-35 (Zehr, 1962). Female *E. enhydris* exhibited a strong positive relationship (n = 25, $r^2 = 0.5114$, $P < 0.001$; $y = -22.7784 + 0.6576*X$) between clutch size and SVL based on number of vitellogenic follicles; the relationship (n=14, $r^2 = 0.2760$, $P = 0.054$; $y = -30.82 + 0.7282*X$) between clutch size and SVL based on the number of oviducal eggs was close to significance (Fig. 4). For comparison, Table 5 also shows the mean SVL and mass of non-reproductive females (n = 52). Both the SVL (t = 2.00, df = 158, $P = 0.05$) and mass (t = 2.99, df = 158, $P < 0.01$) of reproductive and non-reproductive females were significantly different, although reproductive and non-reproductive SVL were similar and exhibited borderline significance.

Diet.– We obtained diet information from a total of 380 snakes that died in gill nets as incidental by-catch plus 14 preserved *E. subtaeniata*. Diet information is presented for four homalopsids (Table 6). All stomach contents were fish remains; the condition of most stomach contents made identification difficult. We identified fish from four families (Cyprinidae, *Puntius* [barb]; Osphronemidae, *Trichogaster* [gourami]; Anabantidae, *Anabas* [climbing perch]; Cichlidae, *Tilapia)* in the stomachs of the dissected sample. In female *E. enhydris*, the only sample with a sufficient number of measurable prey items to analyze, we found the mean prey-to-predator mass ratio to be 0.05 ± 0.01 (range = 0.01 - 0.19, n = 37) and the mean prey-to-predator SVL ratio to be 0.15 ± 0.01 (range = 0.08 - 0.23). Of 83 *E. enhydris* with vitellogenic follicles or oviducal eggs, 35 (42.2%) contained food. In snakes with relatively intact food in their stomach we observed multiple prey items in 5 of 64 *E. enhydris* with food (2 prey items in each, all females), in 2 of 6 *E. jagorii* with food (2 and 3 prey items respectively, all females), and in 1 male of 8 *H. buccata* with food (2 prey items).

We found significant differences in the frequency of feeding between males and females n = 274) in *E. enhydris* (39.5% of females contained food in their stomach, 18.8% of males; $\chi^2 = 9.27$, df = 1, $P < 0.01$), but not between *E. subtaeniata* (n = 39; 27.2% of males, 35.3% of females; $\chi^2 = 0.17$, df = 1, $P > 0.05$), or *H. buccata* (n = 21, 61.5% of males, 37.5% of females; $\chi^2 = 0.55$, df =1, $P > 0.05$). A large female *H. buccata* (86.5 cm SVL, 477.4 gm) ate an 82.6 gm *Tilapia* (17.3% of body weight) and a female *E. enhydris* (47.2 cm SVL, 85.2 gm) contained a 16.4 gm cyprinid (19.3% of body weight). In addition, a large *X. unicolor* (77.2 cm, 241.0 gm) regurgitated a partially digested *X. flavipunctatus* (20.6 cm). We found one unidentifiable fish in an *E. bocourti* (n =3 specimens examined) and one unidentifiable fish in a *X. flavipunctatus* (n = 5 specimens examined).

DISCUSSION

Differences in snake community structure.– This study documents basic attributes of snake assemblages collected from the Central Plain of Thailand during June and July, 2007. The overall species richness of semi-aquatic snakes documented in the Central Plain region (10 species) was comparable to the species richness (8 to 12

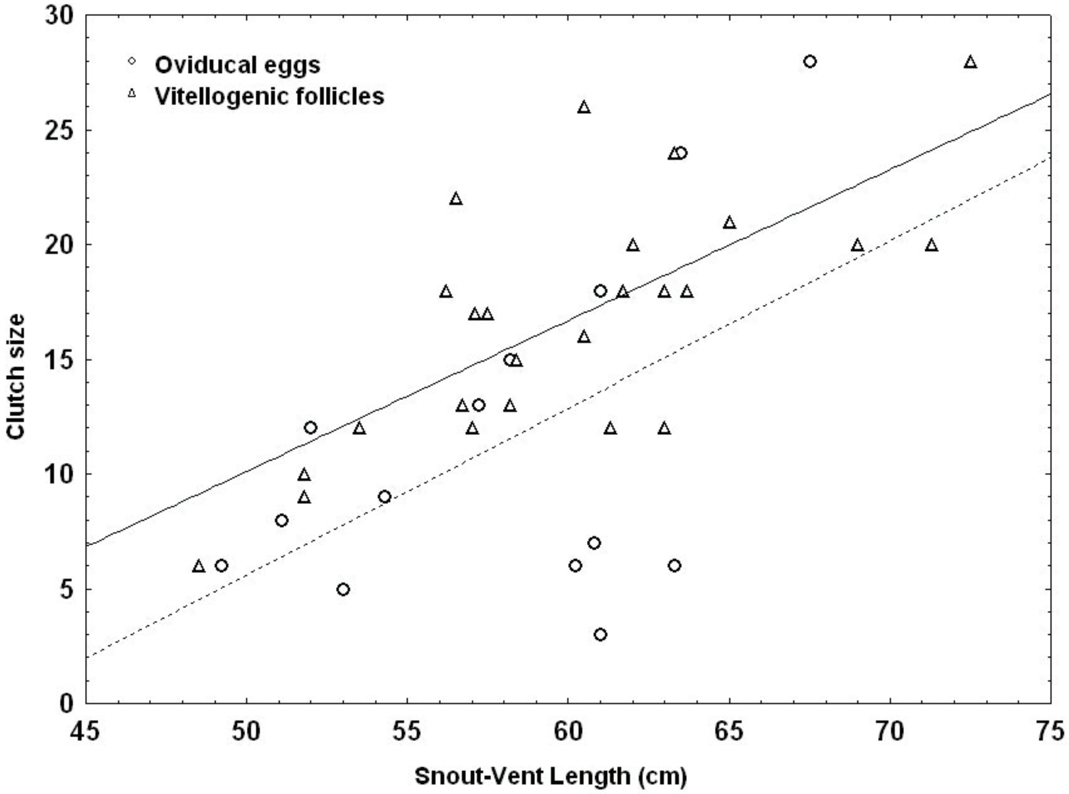


FIGURE 4. . Clutch size as a function of snout-vent length (SVL) in 39 *Enhydris enhydris* from the Central Plain. Clutch size is based on snakes with either enlarged vitellogenic follicles or oviducal eggs. The upper solid line represents the linear regression of the vitellogenic follicles ($n = 25$, $r^2 = 0.5114$, $P < 0.001$; $y = -22.7784 + 0.6576*X$) while the lower dashed line represents the linear regression of the oviducal eggs ($n = 14$, $r^2 = 0.2760$, $P = 0.054$; $y = -30.82 + 0.7282*X$). See text for details.

species) documented from elsewhere in Indochina. Note that the species richness shown in Table 2 indicates the cumulative number of species recorded from an entire geographic region; the number of species varied among the individual sites sampled in each geographic region due to the locality and collecting effort.

As indicated by the relatively high species overlap values (mean = 0.77, range = 0.64-0.89), the Indochinese snake assemblages share a common pool of species, with *E. enhydris* being numerically dominant at all the localities where it is found (see Voris and Karns, 1996; Karns et al., 1999-2000; Karns et al., 2005; and Brooks et al., 2007a, 2009 for more information on the Khorat Basin, Southeastern River Basin, Lake Songkhla, Tonle Sap, and Sabah sites). The dominant *E. enhydris* is widely distributed and abundant from eastern India across Indochina and southward into Indonesia from Sumatra to Sulawesi (Murphy, 2007). The species overlap of the snake assemblages decreases with distance to the south (Lake Songhkla on the Thai-Malay peninsula; mean = 0.70) and west (Sabah, Malaysia, Borneo; mean = 0.18) from Indochina.

As noted, *E. enhydris*, *E. plumbea*, *H. buccata*, X. *flavipunctatus*, *C. ruffus* have large geographic ranges and are found in at least five of the six localities. However, several of the species in the different assemblages exhibit restricted geographic distributions: *Enhydris subtaeniata* is largely restricted to the Lower Mekong River Basin, although it has been collected from Bung Boraphet in the Central Plain (lower Nan sub-basin of the Chao Phraya River Basin) of central Thailand. *Erpeton tentaculatus* is a species found in the southern Central Plain, the Southern Peninsula River Basin, and the Mekong River Basin of Thailand, and from Cambodia, but yet not reported from the Khorat Basin. *Enhydris jagorii* is known only from the upper and lower portions of the Central Plain and the Southeastern Basin. *Enhydris longicauda* is endemic to Tonle Sap in Cambodia.

Tectonic activity and the history of river drainage basins have been important in the faunal diversification of Indochina (e.g., Rainboth, 1996; Voris, 2000; Attwood and Johnson, 2001; Glaubrecht and Kohler, 2004) and provide insight into the observed patterns of snake community composition. River capture events, in which a river is diverted from its original course into another drainage system, (e.g., Waters et al., 2001; Glaubrecht and Kohler, 2004) may explain the close similarity of the Central Plain, Khorat Basin, and Southeastern River Basin snake assemblages.

The separation of the river drainages of the Khorat Basin from the Chao Phraya River Basin of the central plain of Thailand is relatively recent; rivers associated with the Khorat Basin today, and the Mekong River itself, were connected with the Chao Phraya River Basin until tectonic events of the late Cenozoic (Hutchison, 1989). Historically the expanded Mekong, incorporating the present day Salween and Chao Phraya Rivers Basins, flowed southward through the Central Plain of present-day Thailand helping to create the massive sedimentary basin found there today. In the Middle-Late Pleistocene, the expanded Mekong-Chao Phraya lost its headwaters and was diverted to form the present-day Mekong River course, flowing from China toward the southwest, turning abruptly eastward at ~20 ° north and then south, forming the border of present-day Thailand and Laos.

The Mun River, located in the southern half of the Khorat Basin, flows into the Mekong River at the present time; however, geological evidence suggests that it originally flowed into the Chao Phraya, until it was diverted to the Mekong drainage by the uplift that created the Khorat Basin in the Middle-Late Pleistocene (Rainboth, 1996). Another possible stream capture event involves the Loie River which today flows northward into the Mekong (headwaters in the Phrang Hoei mountains forming the northwestern rim of the Khorat Basin) and the Pa Sak River (same source as the Loie) which flows southward into the Chao Phraya River drainage (Rainboth, 1996). Both of these rivers may have flowed into the ancient, expanded Chao Phraya drainage.

The mountainous rim of the Khorat Basin is of Pleistocene origin; the rim of the Basin is well known for its abundance of waterfalls. The rocky, fast-flowing streams and waterfalls of the rim coupled with the upland forested landscape and lack of wet rice cultivation along the basin rim may be an important barrier for homalopsid snake dispersal and movement (Karns et al.,

TABLE 4. Sex ratios and sexual dimorphism of semi-aquatic snake species from the Central Plain. *P* values for comparisons of sex ratios are from Chi-square tests, while *P* values for comparisons of snout-vent lengths (SVL), mass, and tail:SVL ratios are from two-tailed *t*-tests (NS = not significant; * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$). For SVL, mass, and tail:SVL ratios the mean ± 1 standard error (SE) are given, and for SVL and mass the ranges are given in parentheses. The sexual dimorphism index (SDI) is calculated by dividing the mean SVL of the larger sex by the mean SVL of the smaller sex; a plus value is assigned if females are the larger sex and a minus sign if the males are the larger sex (Gibbons and Lovich, 1990).

Species Locality	Sex ratio M:F	*P*	SVL (cm) mean ± SE (range) female	male	*P*	Mass (gm) mean ± SE (range) female	male	*P*	Tail :SVL Ratio mean ± SE female	male	*P*	SDI
E. subtaeninata	0.50 n =54	NS	57.9 ± 1.07 (43.6 - 68.8) n = 27	49.6 ± 0.40 (46.8 - 55.7) n = 27	***	314.2 ± 18.93 (114.5 - 570.0) n = 27	150.3 ± 3.97 (116.0 - 202.0) n = 27	***	0.2 ± 0.002 n = 22	0.24 ± 0.002 n = 25	***	+1.17
E. jagorii	0.50 n = 24	NS	50.4 ± 0.76 (45.5 - 54.8) n = 16	46.4 ± 0.60 (44.0 - 49.0) n = 8	**	276.0 ± 12.44 (184.0 - 350.0) n = 16	214.9 ± 13.67 (167.3 - 266.0) n = 8	**	0.26 ± 0.005 n = 15	0.31 ± 0.013 n =8	**	+1.09
H. buccata	2.00 n = 36	*	68.2 ± 2.59 (56.3 - 86.5) n = 12	75.7 ± 2.03 (61.2 - 96.1) n = 24	*	321.0 ± 39.16 (179.7 - 560.0) n = 12	373.5 ± 24.17 (184.1 - 600.0) n = 24	NS	0.31 ± 0.005 n =12	0.34 ± 0.011 n = 23	*	-0.90
X. flavipunctatus	0.67 n = 25	NS	75.1 ± 2.38 (61.5 - 99.0) n = 15	58.4 ± 2.16 (51.3 - 74.1) n = 10	***	312.3 ± 28.44 (141.5 - 560.0) n = 15	189.1 ± 25.00 (122.9 - 400.0) n = 10	**	0.32 ± 0.024 n = 11	0.38 ± 0.028 n = 8	NS	+1.29

2005). Additionally, due to monsoonal weather patterns, the Khorat Basin exhibits a hotter, drier, and more seasonal climate than the rest of Thailand, and the geologically ancient basin has infertile soils. Thus, the basin has natural dispersal barriers and is separated from the humid climate and fertile soils of the Southeastern and Central Plain river basins. This combination of factors undoubtedly contributes to differences in community structure and in population characteristics among geographic regions (Karns et al., 2005).

Sexual size dimorphism and sex ratios.– Variation in body size and reproductive characteristics (clutch size, frequency of reproduction, and size at first reproduction) are well documented among squamates (Seigel and Ford, 1987; Zug et al., 2001). Body size, body condition, and associated reproductive characteristics may differ due to local genetic diversification or phenotypic effects influenced by food availability and other environmental factors (Madsen and Shine, 1993; Boback and Guyer, 2003). For example, Weatherhead et al. (1995) showed that female northern water snakes, *Nerodia sipedon*, grow faster than males and Brown and Weatherhead (2000) suggest that this may be a result of sexual differences in thermoregulatory behavior. Pearson et al. (2002) showed that the difference in SSD in an island population of *Morelia spilota*, the Australian Carpet Python, was due to cessation of growth and lowered feeding rates by male snakes.

All populations studied exhibited female-biased sexual dimorphism except the Ban Badan *E. enhydris* population (probably due to small sample size) and *H. buccata*. Similarly, Brooks et al. (2009) did not find SSD with *H. buccata* and attribute this to the insufficient sampling of larger body size snakes by gill nets. Comparable to Brooks et al. (2009), our result reflects a noticeable absence of large females with SVLs near or above one meter due, most likely, to size-selective gill net sampling. Murphy (2007) cites studies showing sexual dimorphism in *H. buccata*.

The abundant and widespread *E. enhydris* shows considerable geographic variation in body size and reproductive characteristics. With the exception of the Ban Badan population (Khorat Basin), all *E. enhydris* populations we have studied show female-biased sexual size dimorphism with respect to SVL and mass (Table 3, Fig. 3). The size statistics reported by Brooks et al. (2009) suggest that *E. enhydris* from Tonle Sap, Cambodia are smaller than the populations of *E. enhydris* from the Central Plain reported here (see Table 3). Brooks et al. (2009) used only non-reproductive females in their mass statistics; we included reproductive individuals in our analysis (Table 3); when we remove all reproductive individuals from our sample, there is still a considerable difference in female body mass between Tonle Sap and the Central Plain (Tonle Sap mean mass = 97.8 gm; Central Plain mean = 199.2 gm without reproductive females, n = 52; 233.4 gm with reproductive females included, n = 108). In contrast, the *E. enhydris* populations from the Khorat Basin (Karns et al., 2005; unpublished data) are smaller in SVL and mass than *E. enhydris* populations from Tonle Sap. The minimum SVL at maturity for *E. enhydris* recorded in this study was 48.5 cm. Brooks et al. (2009) reported that the minimum SVL at maturity of *E. enhydris* from Tonle Sap as 41.0 cm; she also employed a calculation employed by fisheries biologists and estimated the minimum size at maturity to be 48.7 cm. Brooks et al. (2009) also reported SSD in

TABLE 5. Summary of reproductive characteristics of *E. enhydris* from the Central Plain. The percent snakes in reproductive condition (last column) includes the total number of snakes with vitellogenic follicles, snakes with oviducal eggs, and the number of snakes that were obviously post-reproductive (based on enlarged, flaccid oviducts). For comparison, the SVL (snout-vent length) and mass of *Enhydris enhydris* that were not in reproductive condition are shown. Reproductive and non-reproductive snakes were significantly different with respect to SVL and mass (see text).

Species (examined)	SVL (cm) Mean ± 1 SE (range)	Mass (gm) Mean ± 1 SE (range)	Snakes with vitellogenic follicles	Clutch Size: Vitellogenic Mean ± 1 SE (range)	Snakes with oviducal eggs (post-reproductive)	Clutch Size: Oviducal eggs Mean ± 1 SE range	% Reproductive (min SVL at reproduction)
E. enhydris (reproductive) (n = 108)	60.1 ± 0.52 (48.5 – 72.5)	233.4 ± 6.76 (99.0 – 460.0)	72	16.7 ± 1.07 (6 – 28) n = 25	14 (22)	11.4 ± 2.00 (3 – 28) n =14	67.5 (48.5 cm)
E. enhydris (non-reproductive) (n = 52)	58.2 ± 2.00 (45.0 – 71.7)	199.2 ± 8.67 (74.8 – 340.0)	–	–	–	–	–

size, mass or relative tail length for seven species of water snakes from Tonle Sap.

Enhydris enhydris males exhibited significantly greater tail : SVL ratios in all Thailand population studied (mean male: 0.26 - 0.29; mean female: 0.22 - 0.24); Brooks et al. (2009) reported mean male tail : SVL ratios of 0.32 for males and 0.28 for females (Table 3). The ratio of tail length to SVL is a common sexually dimorphic trait in snakes. Shine et al. (1999) provided evidence that male snakes with longer tails achieve greater reproductive success.

We found considerable variation among our samples with respect to sex ratio, varying from strongly male-biased (M:F: 2.10 at Bung Cho) to strongly female-biased (0.47 at Bung Ka Lo). The majority of snakes show a 1:1 sex ratio at birth (Shine and Bull, 1977), but determination of sex ratios in natural populations is difficult (Shine, 1994). For example, we have observed that male *E. enhydris* are attracted to fishing traps containing females (Karns et al., 1999-2000) and this could produce male-biased ratios. The use of gill-nets can influence the size of snakes captured, an important factor in sex ratio determination if there is strong SSD. Thus, it is difficult to assess the biological significance of the variable patterns we observed.

Reproductive biology.– Information on reproductive characteristics for *E. enhydris* are available from Tonle Sap, Cambodia, Myanmar, Lake Songkhla, Thailand, the Khorat Basin, Thailand, and from this study (Murphy et al., 2002; Karns et al., 2005; Brooks et al., 2009). However, caution must be exercised in making comparisons among studies due to different methods of counting ova.

Murphy et al. (2002), Karns et al. (2005), and this study, using both the number of vitellogenic follicles (in ovaries before ovulation) and the number of oviducal eggs (vitellogenic or embryonic) to estimate clutch size, report mean clutch size for *E. enhydris* varying from 7.8 (Myanmar) to 20.3 (Tonle Sap) and total clutch sizes ranging from 2 to 39; in this study, we found a mean clutch size of Central Plain *E.*

enhydris of 16.7 (based on vitellogenic follicles) and 11.4 (based on oviducal eggs). Brooks et al. (2009) used only eggs found in the oviduct after ovulation (vittellogenic eggs or embryonic eggs) and reported a mean clutch size for *E. enhydris* of 13.5 (based on vittelogenic eggs) and 10.5 (based on oviducal eggs) from Tonle Sap, smaller than that reported from Tonle sap (20.3) by Murphy et al. 2002 .

Brooks et al. (2009) notes a reduction in clutch size based on counts of vitellogenic eggs compared to oviducal eggs; this may be due to lack of fertilization or post-fertilization abortion; there is no evidence that squamate reptiles actively reabsorb eggs (Brooks et al., 2009). Our study reported reduction in the number of vitellogenic follicles compared to the number of oviducal eggs and the difference is likely due to longer retention of some vitellogenic follicles or ovarian atresia (Kamosawa and Ota, 1996). The Central Plain RCM value reported here for *E. enhydris* (mean = 0.37 ± 0.07; range = 0.14 - 0.60, n = 7) is greater than that reported for *E. enhydris* from all other sites (Tonle Sap, Cambodia, Myanmar, Thale Noi, Thailand: mean = 0.12 to 0.20, range 0.03 - 0.35).

Ultimately, SSD is determined by allocation of resources to growth in each sex and associated costs and benefits of growth. There are size and fecundity benefits for females and size and competitive benefits (depending on mating system) for males (Shine, 1994). We demonstrated a positive size-fecundity relationship for *E. enhydris* from the Central Plain in this report and for *E. enhydris* from Kabin Buri, Thailand, Southeastern River Basin (Karns et al., 2005). Brooks et al. (2009) showed significant, positive, size-fecundity relationships in the seven species of water snakes, including *E. enhydris*, studied at Tonle Sap, Cambodia.

Our study lasted over a five-week period in June and July, at the beginning of the monsoonal wet season; thus, we cannot comment on annual breeding cycles. Brooks et al. (2009) and Pongcharoen et al. (2008) document that *E. enhydris* exhibits two distinct reproductive peaks corresponding to seasonal variation in rainfall and water level in Tonle Sap, Cambodia and in the Southeastern Basin in Thailand.

Geographic variation in body size and reproductive biology.– We have documentted geographic variation in body size and reproductive biology. What are possible factors contributing to observed differences? Stuart et al. (2000) and Brooks et al. (2007a,b) have documented the massive exploitation of snakes in the Tonle Sap system where an estimated 6.9 million snakes are taken annually, primarily for captive crocodile food and the skin trade. Homalopsids dominate this trade; *Enhydris enhydris* is the most heavily exploited species and accounted for 71.0%, 56.1%, and 71.6% of the catch in three provinces (Brooks et al., 2009). The primary harvesting of snakes coincides with the two breeding seasons of *E. enhydris*, indicating that it is particularly vulnerable. Brooks et al. (2009) also show that 56.1% of the *E. enhydris* sampled from the harvest were at or above the minimum length for sexual maturity; they estimate that if these snakes had reached their maximum size, their reproductive contribution to the system would have been doubled. Brooks et al. (2009) also suggest that there has been a decrease in the average size of *E. enhydris* since the report by Stuart et al. (2000). Thus, the available evidence indicates that the snake harvest is having a significant

Table 6. Dietary data for males and females of four species of homalopsid snake from the Central Plains of Thailand. No data are available for males of *Enhydris jagorii*. Means ± 1 standard error (SE) are given for prey length and weight. All observed prey were fish. Within the fish families the most common identifiable genera were as follows: Cyprinidae, *Puntius* (barb); Osphronemidae, *Trichogaster* (gourami); Anabantidae, *Anabas* (climbing perch); Cichlidae, *Tilapia*.

	E. enhydris		*E. subtaeniata*		*H. buccata*		*E. jagorii*
	Male	Female	Male	Female	Male	Female	Female
% containing food (n)	18.8 (112)	39.5 (162)	29.6 (27)	57.7 (26)	61.5 (13)	37.5 (8)	50.0 (12)
Number of measured prey	5	37	3	1	2	2	7
Mean ±1 SE prey length (cm)	7.5 ± 0.84	9.4 ± 0.40	5.7 ± 1.52	6.2	9.5 ± 4.5	13.9 ± 3.9	6.1 ± 0.82
Mean ±1 SE prey weight (g)	4.8 ±1.25	9.9 ± 0.85	2.5 ± 1.32	8	14.5 ± 11.5	44.2 ± 38.5	3.5 ± 0.83
# Prey identified to family	6	32	0	1	1	2	3
Cyprinidae	5	28	0	1	0	1	1
Osphronemidae	1	4	0	0	0	0	1
Anabantidae	0	0	0	0	1	0	1
Cichlidae	0	0	0	0	0	1	0

impact on *E. enhydris* and other species in the Tonle Sap system. The harvest of *E. enhydris* and other species in Tonle Sap may help explain the differences in population characteristics observed between Tonle Sap, the Central Plains and other sites. It should also be noted that changes in body size, litter size, and behavior in the Japanese mamushi snake (*Gloydius blomhoffii*) have been documented in hunted populations (Sasaki et al., 2008). Although incidental snake mortality is common due to standard fishing practices in Thailand, homalopsids are not the target of a commercial industry.

Brooks et al. (2009) noted a decrease in mean clutch size and relative clutch mass for *E. enhydris* between the 2002 Tonle Sap report (Murphy et al. 2002) and the 2009 Tonle Sap report; they suggest that this may reflect a reduction in fecundity between the sampling periods. However, both the Tonle Sap and the Central Plain clutch sizes and RCM values are relatively large compared to reports from Myanmar, Lake Songkhla, Thailand, and sites in the Khorat Basin and Southeastern Basin, Thailand (Murphy et al., 1999; Murphy et al., 2002; Karns et al., 2005; and unpublished data). Brooks et al. (2009) speculate that this may be related to the extremely high productivity of Tonle Sap. The Central Plain *E. enhydris* exhibit larger body size and greater reproductive effort than Tonle Sap, particularly *E. enhydris* from Bung Ka Lo and Bung Boraphet. Both Bung Ka Lo and Bung Boraphet are sites are extensive wetlands prone to flooding that are also highly productive. Stuart et al. (2000) suggested that human overfishing of larger fish species in Tonle Sap, and consequent increase in smaller prey fish species, may influence size and reproductive characteristics by increasing the food supply of homalopsids that eat relatively small prey items; this is also be true in the densely populated Central Plain. For example, Bung Boraphet supports an important fishery (Sriwongsitanon et al. 2007).

Diet.– Freshwater homalopsids are primarily piscivorous (Voris and Murphy, 2002). We found only fish in the stomachs of the snakes examined, except for the *Xenochrophis flavipunctatus* found in the stomach of the non-homalopsid *Xenopeltis unicolor*. The most common diet item found in the snakes examined were fish of the family Cyprinidae. The literature also reports that *H. buccata* and *E. enhydris* eat frogs and crustaceans (Voris and Murphy, 2002). We found fish and frogs remains in the stomach of *E. subtaeniata* from the Khorat Basin (Karns et al., 2005), but only fish in the snakes from the Central Plain. In a study of *E. plumbea* in Sabah, Malaysia (Voris and Karns, 1996), amphibian eggs, tadpoles, or adult frogs comprised the diet of the majority of snake stomachs examined. Fish species comprised the diet of homalopsids from Lake Songkhla in southern Thailand (Murphy et al., 1999).

Voris and Murphy (2002) suggested homalopsids frequently feed on numerous, small prey. Mean prey sizes reported here for *E. enhydris* (length: 7.5 cm for males and 9.4 cm for females; mass: 4.8 gm for males and 9.9 gm for females) were similar to those reported by Brooks et al. (2009) for *E. enhydris* from Tonle Sap (length: 6.9 cm for males and 8.2 cm for females; mass: 3.2 gm for males and 7.1 gm for females). Brooks et al. (2009) also found the prey-to-predator mass ratios of homalopsids to be lower (< 0.2) than that recorded for *X. piscator* and *C. ruffus* and for other snakes reported in the literature (Rodríguez-Robles et al., 1999); we also observed low predator-to-prey mass ratios (0.01 - 0.19) in female *E. enhydris* and observed multiple small prey items in the stomachs of some snakes. However, as documented, occasional large prey are taken. Contrary to reports of anorexia by snakes in reproductive condition (e.g., Gregory et al., 1999), we found that 42.2% of *E. enhydris* in reproductive condition contained food (n = 83). Brooks et al. (2009) reported that approximately 45% of their reproductive *E. enhydris* contained food. Similar to our study, fish of the family Cyprinidae were common diet items in Tonle Sap.

Radiotelemetry studies of homalopsids (Karns et al., 1999-2000) indicate that these snakes are passive thermoconformers living in thermally stable, aquatic microhabitats (body and microhabitat temperatures ~ 30° C). They also showed that *E. plumbea* and *E. enhydris* are equally active both day and night. Thus, homalopsids may forage frequently and process the small prey items that constitute the bulk of their diet in an energetically efficient manner resulting in increased levels of growth and reproduction. The fact that of 52.4% of male and 33.3% of female stomach contents were well-digested fish “mush” supports this contention.

Sampling issues.– Ecologists rely on demographic parameters, such as age structure, reproductive data, population density, and sex ratios, to study the population and community ecology of snakes. Demographic information is obtained via a number of sampling methods, including visual inspection, terrestrial or aquatic funnel trapping, and drift fences, but the biases inherent in these methods are seldom assessed (Willson et al., 2008). Using a variety of field and laboratory data with species of North American semi-aquatic snakes, Willson et al. (2008) found biases associated with aquatic funnel traps and suggested solutions. Gill net sampling also has inherent biases that must be considered.

Almost all of the snakes in this study were obtained from gill net capture; we contracted with local fishers to set and check the nets. Gill net success depends upon animals moving to the nets or being moved to the nets by currents. Thus, species differences in movement habits will strongly influence the probability of gill net encounters. For example, the highly sedentary and sit-and-wait predator, *E. tentaculatus*, is less likely to be caught in gill nets than the mobile *E. enhydris*. In past studies (Karns et al., 2005), we have found that a mesh-size of 2.5 or 3.0 cm works well for the semi-aquatic snakes we are collecting. We supplied fishers with gill nets of this mesh size or instructed them to use comparable gill nets. However, we know that 3.5 and 4.0 cm mesh nets were used at some sites.

Gill nets are obviously a size-selective sampling method that under-samples very small and very large individuals. This is especially true of the large, stout-bodied *H. buccata* and *E. bocourti* (circumference of large adults exceeds mesh size and they avoid entanglement) and very young, small snakes (who easily pass through the mesh), and these size classes are likely underrepresented in this study. For these two species, Brooks et al. (2009) used individuals obtained from baited hooks and traps to partially compensate for gill net bias. Brooks et al. (2009) considered the bias minimal for reproductive-aged individuals of most species because of the large range of sizes obtained in her samples. However, it is important to note that this has not been subjected to any kind of empirical test. Thus, we do not know to what degree variation in mesh size among collecting localities affected our results.

Future work.– This study documents basic attributes of snake assemblages found in the Central Plain of Thailand and compares the Central Plain assemblage to other sites in Southeast Asia. It contributes to a growing literature on the water snakes of Southeast Asia (e.g., Murphy, 2007; Brooks et al., 2007a,b; Brooks et al., 2009; Alfaro et al., 2008). These and other studies suggest a rich research agenda for the study of snake biology in the region. Year-round sampling needs to be done at more sites to provide much needed information on reproductive cycles, abundance, and activity patterns. Longer-term studies are needed in order to make well informed conservation decisions (Inger, 2003; Kupfer et al., 2005). Larger samples and better sampling procedures that would accurately reflect the population structure are required to verify the body size differences we found between populations. It would be valuable to sample prey availability at sites to determine if there are food resource differences that could affect population and community characteristics (Filippi et al., 2005).

In addition we are pursuing phylogeographic studies to determine how the biogeography and geological history of the region have influenced the evolutionary history of homalopsid species. Preliminary analysis of DNA sequence data indicates there is genetic divergence of populations of *E. enhydris*, *E. subtaeniata*, and *E. plumbea*; this divergence is likely correlated with the geological history of the Khorat Basin and with the history of changes in the river basins of the region. These processes, coupled with changes in climate and vegetation, have undoubtedly influenced patterns of speciation in the diverse semi-aquatic snake fauna of the region. Many significant ecological and evolutionary questions remain with respect to Southeast Asian water snakes.

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APPENDIX 1

Location details for the collecting localities discussed in this study. See text for more details.

Locality Name	GPS Coordinates	Province	District
Uttaradit Area (Nan Sub-Basin)			
Bung Cho	17° 23′ 01.3″ N 101° 03′ 69.1″ E	Uttaradit	Phichai
Bung Ka Lo	17° 36′ 99.4″ N 100° 10′ 35.7″ E	Uttaradit	Uttaradit
Phetchabun Area (Pa Sak Sub-Basin)			
Nong Na Young	16° 23′ 46.0″ N 101° 08′ 38.5″ E	Phetchabun	Mueang
Nong Bua	16° 22′ 95.6″ N 101° 08′ 53.0″ E	Phetchabun	Mueang
Ban Pak Nam	16° 23′ 61.0″ N 101° 10′ 39.5″ E	Phetchabun	Mueang
Phetchabun Fisheries	16° 26′ 06.6″ N 101° 09′ 72.0″ E	Phetchabun	Mueang
Ban Subjampa	16° 07′ 88.9″ N 101° 08′ 99.5″ E	Phetchabun	Nong Phai
Bung Boraphet Area (Nan Sub-Basin)			
Ban Klong Khut	15° 41′ 49.5″ N 101° 19′ 83.3″ E	Nakon Sawan	Tha Tako
Ban Pra Non	15° 40′ 31.9″ N 101° 14′ 21.8″ E	Nakon Sawan	Mueang Nakon Sawan