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Comparison of Semi-aquatic Snake Communities Associated with the Khorat Basin, Thailand

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ABSTRACT.– The Khorat Basin is a prominent geographic feature of Indochina, potentially important in the ecology and evolution of semi-aquatic snake communities. We compared community structure and population characteristics of semi-aquatic snakes (taxonomic focus on homalopsine snakes) from localities located in the Khorat Basin, on the mountainous rim of the Khorat Basin, and at lower elevation sites located outside of the Khorat Basin. Species richness of semi-aquatic snakes assemblages was comparable in and outside of the Khorat Basin (8 species). There was a high degree of species overlap between assemblages found in and out of the basin (coefficient of similarity = 0.88), but species diversity was higher in the Khorat Basin (evenness = 0.694). *Enhydris enhydris* was the strong dominant at sites located outside of the basin (evenness = 0.334). Homalopsine snakes were absent from the Khorat Basin rim sites. Snakes were over twice as abundant at sites located outside of the Khorat Basin compared to sites in the basin. We found size sexual dimorphism for *E. enhydris* outside of the Khorat Basin, but not in the basin. Female snakes (*E. enhydris* and *E. plumbea*) from sites outside the Khorat Basin were larger and heavier in comparison to Khorat Basin populations. We discuss historical, biogeographical, biotic, and abiotic factors that may contribute to the observed differences.

KEY WORDS: Homalopsinae; semi-aquatic snakes; snake ecology; *Enhydris enhydris*; *Enhydris plumbea*; Khorat Basin; Khorat Plateau; Thailand

INTRODUCTION

Multiple factors contribute to the composition of ecological communities in any given area (Brown & Lomolino, 1998). Vitt (1987) in his discussion of snake communities, notes that historical, biogeographic, abiotic, and biotic factors contribute to the assemblage of snakes found in a particular area. These factors will differentially affect snakes inhabiting different adaptive zones (e.g., arboreal vs. fossorial vs. aquatic). In this report we investigate how a prominent geographic feature in central and northeastern Thailand, the Khorat Basin, might influence the ecology and evolution of semi-aquatic snakes, especially the widely distributed

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and abundant Homalopsinae (Oriental-Australian Rear-fanged Water Snakes).

The colubrid subfamily Homalopsinae includes ten genera and 34 species of snakes distributed from Pakistan across Southeast Asia to northern Australia (Greene, 1997; Gyi, 1970; Murphy & Voris, 1994). All homalopsines are amphibious, primarily nocturnal, and usually associated with mud substrates. Eight of the 34 species (24%) are coastal marine species living in mangrove forests, tidal mudflats, nearshore coastal waters, and estuarial habitats (Heatwole, 1999). The freshwater species are found in ponds, streams, wetlands, agricultural wetlands (e.g., rice paddies), and lakes (Gyi, 1970). Most homalopsines eat fish, frogs, or tadpoles, but feeding on crustaceans is well documented in three of the coastal marine species (Voris & Murphy, 2002).

The Homalopsinae is characterized by a suite of features that adapt them for aquatic life (e.g., valvular nostrils). The species for which reproduction has been described are viviparous (Gyi, 1970). Homalopsines are opisthoglyphous (rear-fanged) and are considered mildly venomous (Minton, 1990). Homalopsines are relatively small in size (most species < 1 m adult snout-vent length). The homalopsines exhibit considerable morphological and ecological diversity for a small ophidian clade (Voris et al., 2002).

Despite their abundance and widespread distribution across the Oriental and Australian biogeographic regions, the homalopsines are a relatively understudied group of snakes. We have undertaken a series of ecological studies of homalopsine species in coastal peninsular Malaysia (Jayne et al., 1988, 1995), agricultural wetlands in Malaysian Borneo (Karns et al., 1996; Voris & Karns, 1996), in a lake/wetland complex in southern Thailand (Murphy et al., 1999; Karns et al., 1999-2000), in mangrove forests in Singapore (Karns et al., 2002) and in Tonle Sap, Cambodia (Stuart et al., 2000). The focus of this report is on snake populations in natural and agricultural wetlands associated with the Khorat Basin in central and northeastern Thailand.

The Khorat Basin is a prominent and ancient geographic feature in Indochina (Hutchison, 1989). It covers an area of about 155,000 km^2 and its geological origins can be traced back to the early Mesozoic. Although frequently referred to as a plateau, this geological feature is correctly a basin, not a plateau, and we shall refer to it as a basin in this report. Its plateau-like morphology is due to tectonic pressure along its southern and western margins, resulting in the uplifted, low mountainous margins that define its southern and western borders (Hutchison, 1989). The eastern border of the basin is formed by the Lower Mekong River, the southern border by the Phanom Dong Rak Mountains and the western border by the Phetchabun mountain range. These low mountain ranges together with the Truong Son Cordilliera in the northeast create a realatively low elevation (200-1100 m above sea level) rim. The basin tilts to the south and east with an average elevation of approximately 200 m. The mountainous rim weakens the effect of the monsoon rains, making the Khorat Basin the hottest, driest, and most seasonal (wet and dry seasons) region of Thailand (mean annual rainfall at Nakhon Ratchasima in the basin is about 1,150 mm, compared with 1,500 mm in central Thailand). The soils of the Khorat Basin are lateritic and known for their lack of fertility.

Vidthayanon et al. (1997) recognized six major river drainages in Thailand. The Mekong Drainage in the Khorat Basin consists of four major river basins. The Mun and Chi are major rivers of the Khorat Basin, and water in the basin flows into the Mekong and, ultimately, to the South China Sea. To the south of the Khorat Basin is the Southeastern Drainage consisting of three river basins. To the west is the Chao Phraya Drainage consisting of the river basins of the Central Plain of Thailand, dominated by the Chao Phraya basin. The Southeastern and Chao Phraya Drainages flow into the Gulf of Thailand.

There have been relatively few ecological studies of the herpetofauna of the Khorat Basin.

FIGURE 1. Map of region showing the northern portion of Thailand and the Khorat Basin. The sampling areas in the Khorat Basin (Khon Kaen and Ban Badan), on the south west rim of the basin (Khorat rim), and outside the Khorat Basin (Kabin Buri and Prachan Takham) are indicated. GPS coordinates and other details on the collecting localities are given in Appendix 1.

The classic study of Inger and Colwell (1977) examined the structure of herepetofaunal communities in evergreen and deciduous tropical forest and in agricultural areas. More recently, Kupfer et al. (2005) have investigated the habitat and community and population ecology of a caecilian (*Ichthyophis*) in the basin. We were particularly interested in the Khorat Basin because several features of the basin have important implications for the ecology and evolution of semi-aquatic snake assemblages: 1) The segregation of the Mekong Drainage of the Khorat Basin from the Chao Praya and Southeastern Drainages potentially isolates semi-aquatic and aquatic populations; 2) the mountainous southern and western rim of the Khorat Basin, although relatively low in elevation, may present barriers (e.g., waterfalls, topographic features, microclimates) to the movement and dispersal of semi-aquatic snakes; and 3) the hotter, drier, and more seasonal climate of the Khorat Basin coupled with infertile soils will affect the abotic and biotic environment, resulting in different selective pressures in the basin compared to adjacent areas. Taken together, these factors may influence the species composition of snake communities, affect gene flow among snake populations, and, ultimately, contribute to patterns of geographic variation and speciation.

In this report we present a comparison of the characteristics of semi-aquatic snake assemblages found in the Khorat Basin and assemblages located outside of the basin. We document differences in species richness, species diversity, species overlap, and population characteristics (snake density, sex ratio, body size, and sexual dimorphism). We also report information on diet and reproduction for some species.

MATERIALS AND METHODS

Study Sites

We collected the information presented in this report during two field seasons in Thailand (Fig. 1; see Appendix 1 for geographic details). In 2003 (June 12-July 30) we collected in five geographic localities; three of these localities are used in this study (Ban Badan area, Khon Kaen area, and Prachan Takham area). In 2004 (June14-July 3), we again collected in the Ban Badan area, along the Khorat Basin rim (three localities), and in the Kabin Buri area. Most of these sites consisted of multiple sampling localities located in a relatively small area (see Appendix 1). For the purposes of this study these sites can be separated into three geographic areas (Fig. 1): sites located in the Khorat Basin (Khon Kaen area and Ban Badan area), sites located on the elevated rim of the Khorat Basin (Forestry Reservoir, Thai Sammakit, and Bu Phram), and sites located to the south, outside of the Khorat Basin (Kabin Buri area and Prachan Takham area). The two sites located in the Khorat Basin are relatively far apart (Khon Kaen is approximately 250 km straight-line distance from Ban Badan); the next five sites, from Ban Badan to Kabin Buri, are located along a twisting 80 km segment of Highway 304 beginning at Ban Badan, crossing the Khorat Basin rim, and then to Kabin Buri in the lowlands outside the Khorat Basin. Prachan Takham is 20 km to the west of Kabin Buri, also outside of the Khorat Basin.

Sites Located in the Khorat Basin. Khon Kaen Area (5 collecting days in 2003): Two sites (Khon Kaen University Experimental Pond and Ban Huai Sun) were small pools and ponds located near/in the city of Khon Kaen. The remaining sites (Ban Wang Mueng, Ban Mai, Ban Tha Lad, and Ban Nong Pueng) were all located around the perimeter of Ubon Ratana Dam Reservoir to the northwest of Khon Kaen.

Ban Badan Area (6 collecting days in 2003; 20 collecting days in 2004): The area in and around Ban Badan is flat, agricultural country with a small reservoir, ditches, ponds, rice paddies, and streams (Fig. 2). One of the collecting localities was in a small reservoir, three localities in rice paddies and adjacent ditches, and two in small streams (Appendix 1). Elevations ranged from 225 to 239 m.

Sites Located on the Khorat Basin Rim. Good wetland habitat was less common in the rim highlands. We sampled at three medium to large reservoirs (19 collecting days in 2004): Forestry Station Reservoir (410 m elevation), Thai Sammakit Reservoir (408 m), and Bu Phram Reservoir (485 m).

Sites Located Outside of the Khorat Basin. The edge of the Khorat Basin drops off several hundred meters to the lowlands to the south. In the Kabin Buri Area (12 collecting days in 2004; 10 m elevation) we sampled small lakes, a reservoir, and rice paddies (Fig. 2). In the Prachan Takham area (3 collecting days in 2003) we sampled in small lakes, small ponds, ditches and rice paddies.

Collecting Methods

We employed hand-collecting, trapping, and gill nets to obtain snakes. Preliminary collecting by hand and with fish traps (using funnel traps we constructed or locally made fish-traps of different designs) did not prove to be as effective as gill nets, and the majority of

FIGURE 2. (**A**) Photograph of snake sampling locality at Kabin Buri, an extensive wetland site located at low elevation (10 m) outside of the Khorat Basin. (**B**) Photograph of a rice paddy at Ban Badan, a sampling locality in the Khorat Basin (elevation of 220 m). The fisherman in the photo, Pom Mongodjng, is deploying a gill net used in sampling snakes. (**C**) Two of the snakes commonly collected in the Khorat Basin. *Enhydris enhydris* is shown on the right and *Enhydris subtaeniata* on the left. *Enhydris subtaeniata* was found at sites in the Khorat Basin, but was not collected at sites outside the basin. The snakes in this picture are between 50 and 65 cm in SVL

collecting effort went into the use of gill nets (Fig. 2). Gill nets also lent themselves to quantification of effort (meters of gill net/nights at a site). The gill net height of about 1.5 m exceeded the water depth under most circumstances. We determined that gill net mesh-size was an important factor; a mesh opening of 2.5 cm worked best for semi-aquatic snakes, although biased against very small and very large snakes. In 2004 we recorded gill net effort; we had approximately 400 m of gill net deployed at each site over the course of the study. At Kabin Buri this effort was supplemented by local fishermen who deployed up to 2,000 m of gill net on some nights. The total linear meters of gill net per night deployed over the length of the study at each site in 2004 was: Ban Badan = 8,910 m (20 nights), Forestry Reservoir = 6,020 m (19 nights), Thai Sammakit = 6,020 m (19 nights), Bu Phram = 6,480 m (19 nights), and Kabin Buri = 10,600 m (12 nights). Gill net effort is not available for the 2003 sites (Ban Badan, Khon Kaen, Prachan Takham).

Fishing with gill nets is a commonly employed practice and aquatic snakes are commonly caught as by-catch in the nets. We contracted with local fishermen to set gill nets (Fig. 2). 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.

Dead snakes were quickly processed or frozen. Live snakes were euthanized and processed. 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 or tail snips) 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 checked. The preserved collection of snakes was deposited with the National Science Museum of Thailand.

We conducted night surveys at Ban Badan in 2004 (8 nights between June 15 and June 30, 2005, 19:30-21:30) by slowly walking on paddy dikes around flooded rice paddies and looking for snakes in the water/mud. Three to four observers visited the same two sites each survey night (approximately 30 minutes per site). We attempted to collect all snakes seen. We also did one visual inspection survey (four observers for one hour) near Kabin Buri in a disturbed wetland area (area of mounds and pools created by gold mining operations). We also searched for snakes on roadways by slowly driving along a predetermined route at Ban Badan; the route covered 6.4 km along a rural road through an area of rice paddies, water filled ditches, and small ponds.

Statistics

We used regression analysis, analysis of variance (ANOVA), or analysis of covariance (ANCOVA) in statistical analyses. We used ANCOVA to contrast the size dependent variable of mass using SVL as the covariate. We used an LSD post hoc test to make multiple comparisons among means used in ANOVA or ANCOVA. 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. Information on size at sexual maturity for most homalopsine snakes is limited. Based on available data (Voris & Karns, 1996; Murphy et al., 1999; Murphy et al., 2002; unpublished data from Field Museum collection) we used a SVL of 35 cm for both male and female *E. enhydris* and 28 cm SVL for *E. plumbea*. We calculated a sexual dimorphism index (SDI) for *E. enhydris*. 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 & Lovich, 1990). Relative litter mass (RLM) was calculated as the ratio of litter mass (without yolks) to female mass. We did not collect yolk mass data during field processing of snakes and thus our calculation of RLM, without the inclusion of yolk mass, underestimates female reproductive effort. Species evenness was calculated by dividing the Shannon-Wiener diversity index calculated for a particular locality by the square root of the number of species at that locality (Magurran, 1988). The Sorenson 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 Site A, b = number of species at Site B (Magurran, 1988).

RESULTS

Snake Community Structure

We collected a total of 668 snakes during the 2003-04 field seasons (Table 1). This includes dead snakes, released snakes, and preserved snakes. An additional 98 snakes were neonates removed from gravid females or born in captivity. We encountered 14 species of snakes, including nine species of semi-aquatic snakes and five species of incidental terrestrial snakes. We collected six species of the colubrid Homalopsinae: *Enhydris enhydris* (Schneider), *Enhydris plumbea* (Boie), *Enhydris subtaeniata* (Bourret), *Enhydris bocourti* (Jan), *Homalopsis buccata* (Linnaeus), and *Erpeton tentaculatum* (Lacépede). We also collected three species of non-homalopsine semi-aquatic snakes: Colubridae: Natracinae: *Xenochrophis piscator* (Schneider); Xenopeltidae: *Xenopeltis unicolor* Reinwardt in Boie; and Cylindrophidae: *Cylindrophis ruffus* (Schlegel). We identified

TABLE 1. Summary of snakes collected in and outside the Khorat Basin in central Thailand, June-July, 2003-04. Species are listed in overall order of abundance in each category. Numbers in parentheses under locality names indicate the number of collecting days at that site.

Species	In Basin		Basin Rim			Outside Basin		Total numbers of Snakes
	Khon Kaen (6)	Ban Badan (26)	Forestry Station (19)	Thai Sammaki (19)	Bu Phram (19)	Kabin Buri (12)	Prachan Takham (4)	
Homalopsinae								
Enhydris enhydris	64	34	0	0	0	290	28	416
Enhydris subtaeniata	57	15	0	0	0	0	0	72
Enhydris plumbea	3	30	0	0	0	14	0	47
Homalopsis buccata	1	11	0	0	0	12	0	24
Enhydris bocourti	0	1	0	0	0	2	0	3
Erpeton tentaculatum	0	0	0	0	0	0	1	1
Other semi-aquatic snakes								
Xenochrophis piscator	6	38	7	3	5	15	1	75
Cylindrophis ruffus	1	4	0	0	0	10	1	16
Xenopeltis unicolor	0	3	1	0	0	1	2	7
Terrestrial snakes								
Oligodon taeniatus	0	1	1	0	0	0	0	2
Ptyas korros	0	1	0	1	0	0	0	2
Pareas margaritophorus	0	0	0	0	1	0	0	1
Bungarus candidus	0	0	1	0	0	0	0	1
Elaphe flavolineata	0	0	0	0	1	0	0	1
Total /Site	132	138	10	4	7	344	33	668
No. Snakes/Day	22.0	5.3	0.5	0.2	0.4	28.7	8.3	6.4
Species Richness	6	10	4	2	3	7	5	14
Species Evenness	0.566	0.701	0.678	0.512	0.725	0.340	0.284	

the natracine as *X. piscator*; however, the systematic status of the species included in *Xenochrophis* is under investigation (P. Lawson, California Academy of Sciences, personal communication), and this identification should be treated as tentative. Additionally, *E. subtaeniata* has been confused with *Enhydris jagorii* (Peters); we use *E. subtaeniata* in this report (Murphy, In Press). We additionally collected a small number (7) of five species of terrestrial snakes caught in near-shore gill nets: Elapidae: *Bungarus candidus* (Linnaeus); Colubridae: Colubrinae: *Elaphe flaviolineata* (Schlegel), *Ptyas korros* (Schlegel), *Oligodon taeniatus* (Günther); Colubridae: Pareatinae: *Pareas margaritophorus* (Jan).

The number of collecting days and the emphasis on different collecting techniques varied among sites, accounting in part for the differences in numbers of snakes collected among sites (Table 1). Eight species of semi-aquatic snakes (of which five were homalopsines) were found at sites both in and outside of the Khorat Basin. No homalopsines were collected at the Khorat Basin rim sites (two non-homalopsine, semi-aquatic snake species, *X. piscator* and *X. unicolor*, were collected).

Among the seven collecting areas, Ban Badan (in the Khorat Basin) exhibited the greatest species richness (10 species, including 8 species of semi-aquatic snakes, of which 5 species were homalopsines) followed by Kabin Buri (outside the Khorat Basin: 8 species of semi-aquatic snakes; 5 species of homalopsines) and Khon Kaen (in the Khorat Basin; 6 species of semi-aquatic snakes; 4 species of homalopsine). In terms of snakes collected per day, Kabin Buri exhibited the greatest abundance of snakes (28.7 snakes/day) followed by Khon Kaen (22.0 snakes/day). The Khorat rim sites were low in both species richness and snake abundance (2 to 4 species recorded, 0.2-0.5 snakes/day). Overall, the Homalopsine *E. enhydris* accounted for 62.3% of the 668 total snakes collected, followed by the Natracine *X. piscator* (11.2%), and two homalopsines, *E. subtaeniata* (10.8%) and *E. plumbea* (7.0%).

Although homalopsines and other semi-aquatic snake species were frequently encountered in and outside of the Khorat Basin, they were uncommon on the Khorat rim despite considerable collecting effort at the three Khorat rim sites. No homalopsines were collected on the Khorat rim; only 15 *X. piscator* and one *X. unicolor* were collected at rim sites.

There was a high level of species overlap in the semi-aquatic snake assemblage between the sites located in and outside of the Khorat Basin (Sorenson similarity coefficient = 0.88). We did not collect *E. tentaculatum* from the Khorat Basin nor did we collect *E. subtaeniata* from sites outside of the Khorat Basin. These were the only differences in species composition between the two areas. Due to the absence of homalopsines from the Khorat rim sites, there was little overlap in semi-aquatic snake species between sites in or outside of the Khorat Basin and the rim sites (Sorenson similarity coefficient = 0.40).

Species diversity varied among sites. Species evenness indices for each site are shown in Table 1. Sites located outside the Khorat Basin were dominated by *E. enhydris* (84.4% of total snakes collected) and these sites exhibited the lowest overall species evenness (0.334). The sites in the Khorat Basin exhibited greater diversity (overall species evenness = 0.694); three homalopsine species, *E. enhydris* (36.3% of total), *E. subtaeniata* (26.7%), and *E. plumbea* (12.2%) were all relatively common. At Khon Kaen, *E. enhydris* (48.5% of total) and *E. subtaeniata* (43.2% of total) were similar in abundance. Relatively few snakes were collected at the Khorat rim sites (n = 21; *X. piscator* comprised 71.0% of the total). However, the species evenness index (0.571) at rim sites was relatively high due to the diversity of terrestrial snakes collected in the gill nets.

Snake Density

The number of snakes collected per day (Table 1) provides a crude measure of snake abundance that does not take into consideration different methods used or collecting effort. In

TABLE 2. Differences in SVL and body mass for *E. enhydris* males and females and *E. plumbea* females sampled from Ban Badan (in the Khorat Basin) and Kabin Buri (outside the Khorat Basin). Differences in SVL were tested using ANOVA. Differences in body mass were tested using ANCOVA. The post hoc analysis (LSD test) of the differences among means in each category is described in the text. The mean ± SE is shown with the range in parentheses.

Species, Locality, Sex	Snout-vent Length (cm)	Mass (gm)
E. enhydris		
Kabin Buri		
Female (n = 135)	55.3 ± 0.71	133.1 ± 5.00
	(35.0-73.5)	(27.6-325.0)
Male (n = 140)	47.1 ± 0.38	72.2 ± 1.96
	(35.4-57)	(24.6-134.6)
Ban Badan		
Female (n = 17)	44.9 ± 1.76	85.2 ± 10.71
	(36.5-61.8)	(40.2-182.3)
Male (n = 11)	46.0 ± 1.58	75.6 ± 7.78
	(39.0-54.0)	(47.1-126.9)
p-value	< 0.001	Locality: 0.011
		Sex: 0.001
E. plumbea		
Kabin Buri		
Female (n = 9)	42.4 ± 3.38	73.7 ± 9.08
	(28.8-65.0)	(29.6-114.0)
Ban Badan		
Female (n = 12)	35.4 ± 1.47	45.6 ± 5.07
	(28.2-43.0)	(22.8-75.2)
p-value	0.052	0.076

2004 we quantified collection effort by monitoring the number of nights and length of gill nets deployed at each site. At Ban Badan, in the Khorat Basin, we collected 94 snakes with 8,910 m of gill net in 20 nights (0.011 snakes per m/gill-net/night). A total of 18,250 m of gill net were deployed at the three Khorat rim sites for 19 nights (Forestry Station = 6,020, Thai Sammakit = 6,020, Bu Phram = 6,480) and we collected 21 snakes (0.001 snakes per meter of gill-net/night). At Kabin Buri, outside the Khorat Basin, we collected 269 snakes with 10,600 m of gill net over 12 nights (0.025 snakes per meter of gill-net/night). Thus, snakes were more than twice as abundant at Kabin Buri compared to Ban Badan and snakes were relatively rare at the Khorat rim sites.

Night Surveys

A total of 25 person-hours were spent in visual inspection surveys along rice paddy dikes at two sites in the Ban Badan area. We saw 12 *E. plumbea*, one *X. piscator*, one *H. buccata*, and two unidentified snakes (0.6 snakes/hour). Four person-hours of searching a wetland site near Kabin Buri produced one *E. plumbea* and one *E. bocourti* (0.5 snakes/hour). Snakes were usually seen in shallow water with most of the body submerged, although one *E. plumbea* and one *X. piscator* were caught hanging on vegetation above water. A total of 5.3 hours of nighttime road surveys (51.2 km total distance traveled) along a set route in the Ban Badan area produced one *E. plumbea* (0.02 snakes/hour).

Sex Ratios, Body Size, and Sexual Dimorphism

Sex Ratios: We calculated sex ratios for populations of snakes collected at different sites and in different years. These ratios include adults and larger subadults that could be reliably sexed on the basis of external morphology. Sex ratios varied among localities; significant differences from 1:1 were noted with *E. enhydris* from the Khon Kaen area in 2003 (0.46 M:F; χ^2 = 7.41, df = 1, p =0.006, n = 54), with *E. subtaeniata* from Khon Kaen in 2003 (0.48 M:F; χ^2 = 5.90, df = 1, p = 0.015, n = 49), and with *E. plumbea* from Ban Badan in 2004 (0.25 M:F; χ^2 = 5.40, df = 1, p = 0.020, n = 15). A comparison of sex ratios between geographic localities and between years showed that *E. enhydris* from Kabin Buri (n = 280) in 2004 differed significantly from *E. enhydris* from Khon Kaen (n =54) in 2003 (contingency table analysis, χ^2 = 5.74, df =3, p = 0.017). No other yearly or geographic differences were found.

Enhydris enhydris *Size and Mass*. Using 35 cm SVL as the size at maturity for both males and females, we collected 135 females and 140 males of *E. enhydris* from Kabin Buri and 17 females and 11 males of *E. enhydris* from Ban Badan (Table 2). There were significant differences in SVL among samples (ANOVA corrected for unequal sample sizes: F = 42.660, p < 0.001); post hoc LSD analysis indicated that females from Kabin Buri (mean SVL = 55.3 cm) were significantly different from males from Kabin Buri (47.1 cm) and from females (44.9 cm) and males (46.0 cm) from Ban Badan; the latter three sites were not significantly different. After correction for SVL using ANCOVA (2-way using locality and sex as factors), we found significant differences in mass for both locality (F = 6.600, p = 0.011) and sex (F = 11.372, p <0.001); post hoc LSD analysis showed that females from Kabin Buri (mean mass = 133.1 gm) were significantly different from males from Kabin Buri (72.2 gm) and females (85.2 gm) and males (75.6 gm) from Ban Badan. Females and males from Ban Badan were not significantly different. Males from Kabin Buri were significantly different from females, but not males, from Ban Badan. The sexual dimorphism index (SDI: Gibbons & Lovich, 1990) was 1.18 for the Kabin Buri population and -1.03 for the Ban Badan population. Thus, female *E. enhydris* from Kabin Buri were larger than males from Kabin Buri and from males and females from Ban Badan. The Kabin Buri snakes exhibited size sexual dimorphism whereas Ban Badan snakes did not.

Enhydris plumbea *Size and Mass*. Due to smaller sample sizes, only females were analyzed. Using 28 cm SVL as the size at maturity, we collected 9 female *E. plumbea* from Kabin Buri and 12 females from Ban Badan. The difference in SVL between females from Kabin Buri (mean SVL = 42.4 cm) and females (35.4 cm) from Ban Badan; was very close to significant (ANOVA: F = 4.282, p = 0.052). After correction for SVL using ANCOVA (F = 3.545, p = 0.076), we did not find a significant difference in mass between females from Kabin Buri (mean mass = 73.7 gm) and females from Ban Badan (45.6 gm). Thus, Kabin Buri females were generally larger and heavier than Ban Badan females, although not statistically different.

Reproduction

A total of 25 of the 78 female (32.1%) *E. enhydris* we dissected from Kabin Buri (outside the Khorat Basin) were in reproductive condition. Oviducal eggs were qualitatively ranked as small, medium, or large. The average litter size was 11.0 ± 1.0 (range = 2-20, n = 22). The mean SVL of gravid females was 56.8 cm ± 1.15 (range = 43.6-69.8). The mean mass of gravid females was 164.5 gm ± 7.85 (range = 94.0-250.0). We found a significant relationship between both female SVL and litter size (Fig. 3: r = 0.508, p = 0.016) and between female mass and litter size (r = 0.690; p < 0.001). The mean SVL of nonreproductive females (n =53) was 55.8 cm ± 1.28 (range = 29.5-73.5). The mean mass of nonreproductive females was 134.7 gm ± 8.73 (range = 13.7-325.0). Table 3 compares these data from Kabin Buri to *E. enhydris* reproductive data collected at other localities (Murphy et al., 2002).

One of the female *E. enhydris* we dissected (SVL = 53.3 cm, mass = 94 gm) contained six near full-term embryos (mean SVL = 16.1 cm

TABLE 3. Reproductive statistics from samples of gravid *E. enhydris* from four localities in Indochina. Data on snakes from Cambodia, Myanmar, and Lake Songkhla, Thailand are from Murphy et al., 2002.

Quantity	Statistic	Tonle Sap, Cambodia (n = 32)	Myanmar (n = 8)	Songkhla, Thailand (n = 18)	Kabin Buri, Thailand (n = 25)
SVL (mm)	Mean	56.4	42.8	42.6	56.8
	Range	47.5-64.7	38.7-47.2	37.5-50.9	43.6-69.8
	SD	4.1	2.6	3.5	5.7
Mass (gm)	Mean	179.0	66.9	81.9	164.5
	Range	165.4-194.1	52.9-85.6	55.9-122.3	94.0-250.0
	SD	39.80	11.35	18.97	38.47
Litter Size (gm)	Mean	20.3	7.8	8.1	11.0
	Range	6-39	6-11	5-16	2-20
	SD	6.96	2.41	2.48	4.87

± 0.14, range = 15.8-16.5; mean mass = 2.7 gm ± 0.05, range = 2.5-2.8; total embryo mass without yolks = 16.0 gm, RLM without yolks = 17.0%). In addition, we obtained 47 juvenile *E. enhydris* from snakes held for several days in captivity. Many of these had fresh yolk sac scars and were apparently born in captivity (mean SVL = 17.1 cm ± 0.13, range = 15.8-20.2; mean mass = 3.1 gm ± 0.06, range 2.7-5.0).

We also collected and dissected a gravid *E. bocourti* and *H. buccata* with well developed embryos. The *E. bocourti* from Ban Badan (SVL = 91 cm, mass = 1.25 kg) contained 28 near full-term embryos (mean SVL = 17.8 cm ± 0.17, range = 15.4-19.0; mean mass = 9.3 gm ± 0.25, range = 5.5–10.8; total embryo mass without yolks = 259.1 gm, RLM without yolks = 20.7%). The *H. buccata* from Kabin Buri (SVL = 81.7 cm, mass = 650.0 gm) contained 17 near full-term embryos (mean SVL = 23.8 ± 0.14, range = 23.2-25.0; mean mass = 11.3 gm ± 0.15, range = 10.0-12.3; total embryo mass without yolks = 191.5, RLM without yolks = 29.5%).

Diet

We dissected 141 *E. enhydris* (63 males; 78 females) that died in gill nets as by-catch (all from Kabin Buri). Prey items were found in 26 of these snakes (18.4%; 22 females, 4 males). All stomach contents were fish remains. Intact prey specimens were measured (mean = 10.4 cm ± 0.89, range = 7.0-4.5 cm, n = 9) and/or weighed (mean = 13.5 gm ± 5.31, range = 2.2–35.8 gm, n = 6) depending on condition. Two reproductive females (with 12 and 14 large oviducal eggs) had food in their stomachs. The condition of most specimens made identification difficult although one *Channa* spp. (Channidae) was identified. We found fish and frog remains in the stomachs of *E. subtaeniata* and observed a *C. ruffus* (SVL = 35.2 cm) regurgitate an *E. enhydris* (SVL = 16.8 cm).

DISCUSSION

Differences in Snake Community Structure

We found differences in both the community structure and population characteristics of semi-aquatic snake assemblages from sites sampled in the Khorat Basin, along the Khorat Basin rim, and from sites sampled outside of the basin. In terms of community parameters, species richness of semi-aquatic snakes was comparable in and outside of the Khorat Basin (8 species). There was a high degree of species overlap (0.89) between assemblages found in and outside of the basin region (but also some important differences in species composition, see below). Species diversity was higher at sites in the Khorat Basin (species evenness = 0.694) with *E. enhydris* the strong dominant at sites outside of the basin (species evenness = 0.334).

The most striking feature of this survey was the absence of homalopsines and the low abundance of other semi-aquatic snakes from

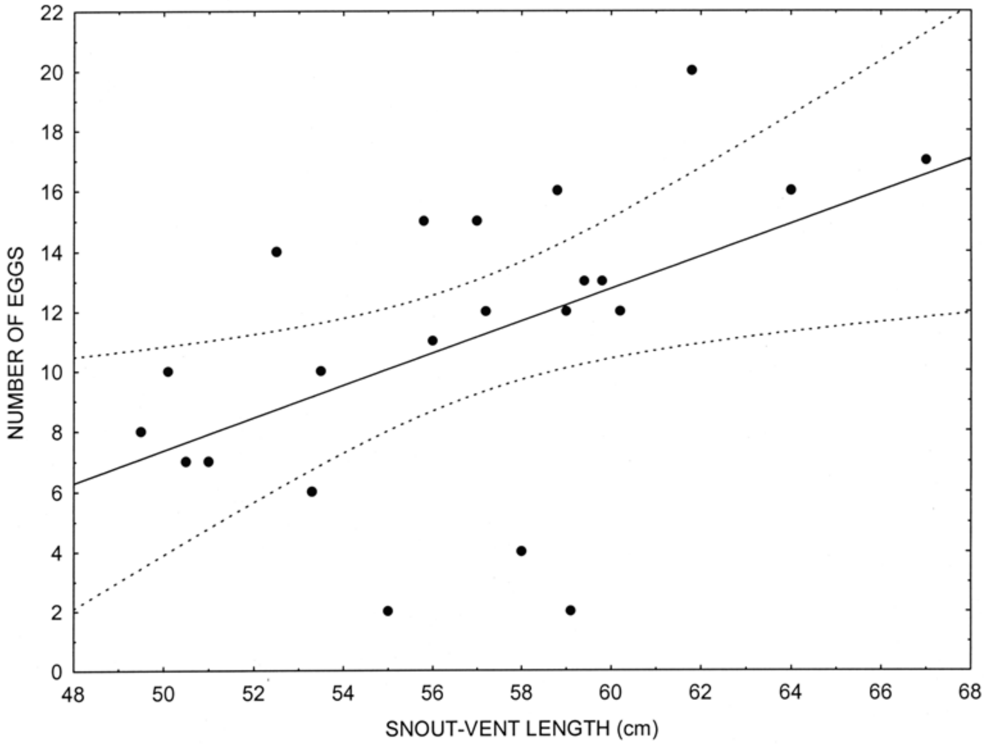

FIGURE 3. Scatter plot, regression and 95% confidence limits of the SVL of 22 female *Enhydris enhydris* from Kabin Buri (site outside the Khorat Basin) versus the litter size. The correlation is significant ($r = 0.508$, $p = 0.016$). The mean litter size was 11.0 ± 1.04.

the Khorat Basin rim sites. With respect to population characteristics, snakes were more than twice as abundant in the Kabin Buri area (outside the basin) as at Ban Badan (in the basin). We also found differences in size sexual dimorphism of *E. enhydris* in and outside of the basin (*E. enhydris* from Kabin Buri exhibited size sexual dimorphism, Ban Badan snakes did not). Female snakes (both *E. enhydris and E. plumbea*) from sites outside the basin were larger and heavier in comparison to Khorat Basin populations. What are the factors that contribute to these differences?

Historical and Biogeographical Factors

Indochina is the center of homalopsine species richness and abundance (Voris et al., 2002) and the Khorat Basin is an ancient feature of Indochina. The age and stability of this feature have likely contributed to the evolution of the rich assemblage of semi-aquatic snake species in this area. The separation of the Mekong drainage in the Khorat Basin from both the river basins of the Chao Phraya drainage of the central plain and the Southeastern drainage which flow into the Gulf of Thailand, coupled with the mountainous rim of the Khorat Basin, may promote isolation and speciation, thus helping to produce the observed species richness.

The composition of the assemblages found in and outside of the Khorat Basin are generally similar. However, *E. subtaeniata* is an example of a species largely restricted to the Lower Mekong Drainage, although it has been collected from Bung Borapet in the Chao Phraya River Basin of central Thailand. *Erpeton tentaculatum* is a species that appears to be largely confined to the southern Central Plain of Thailand, peninsular Thailand, and Cambodia, and not found in the Khorat Basin. Separation of river drainage basins may be a primary factor in explaining these geographic distributions.

Any consideration of the role of river drainages in the faunal diversification of Indochina must take into account the fact that the separation of the Mekong drainage of the Khorat region and the Chao Phraya drainage 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 drainage until tectonic events of the late Cenozoic (Hutchison, 1989). The impact of Pleistocene sea level changes is another historical factor that needs to be considered in understanding the evolution of the fauna of the region (Voris, 2000).

Why did we not find homalopsines at the Khorat rim sites? There is less aquatic habitat for semi-aquatic snakes in the rim areas we surveyed due to the topography, soils, and drainage of the Khorat rim. The rim has more forest cover, wet rice cultivation is not common in the area, and the only available sites for gill net collecting were reservoirs. Two species of semi-aquatic snakes, *X. piscator* (n = 15) and one *X. unicolor* were collected; five of the snakes collected were terrestrial snakes (5 different species) that were incidentally trapped in the gill nets. Only two terrestrial snakes were caught at sites in and outside of the Khorat Basin. It is unlikely that homalopsine snakes are actually absent from the Khorat rim, but our survey indicates that semi-aquatic snakes are certainly much less common than at adjacent sites located in and outside of the Khorat Basin. The mountainous rim of the Khorat Basin is well known for its abundance of waterfalls. The rocky, fast-flowing streams and waterfalls coming off the rim of the basin may be an important barrier for snake dispersal and movement. Thus, our survey results suggest that the Khorat Basin rim is a significant barrier for semi-aquatic snake populations located in and outside of the Khorat Basin.

Abiotic and Biotic Factors

The Khorat Basin is the hottest, driest, and most seasonal region of Thailand. The soils of the Khorat Basin are lateritic and infertile. In the Khorat Basin, irrigation and rice cultivation have created artificial wetlands where wetlands would not normally occur. In comparison to the wetter and more fertile Chao Phraya Drainage of the central plain and the Southeastern Drainage, the Khorat Basin can be considered environmentally stressed. Vitt (1987) notes that prey species density and diversity are major factors contributing to snake community characteristics. The poor nutrient status and lower habitat productivity of the Khorat Basin could influence prey availability and have important effects on top-order carnivores like snakes. We did not compare prey availability and quality at the sites we studied but this deserves further investigation. Differences in habitat quality may explain the differences we observed in body size, body mass, and population density between sites in and outside the basin. Filippi et al. (2005) found differences in food habits and body size (size sexual dimorphism) correlated with habitat variation in the Four-lined Snake (*Elaphe quatuorlineata*) in Europe. Differences in habitat quality may also account for the coexistence of several relatively abundant homalopsine species at Khorat Basin sites (or conversely, prevent one species of homalopsine from achieving numerical dominance, the pattern commonly observed in other Southeast Asian studies, see below).

In summary, we suggest that two sets of factors contribute to the patterns observed in this study. The history and biogeography of the area have produced a rich assemblage of species in the region, both in and outside of the Khorat Basin. The topography of the Khorat Basin rim and river basin drainage patterns of the region may restrict gene flow, lead to genetic variation among populations and, ultimately, to speciation in some cases. The abiotic characteristics of the Khorat Basin (hot, dry, seasonal, infertile soils) influence biotic characteristics of the basin (habitat productivity and trophic structure). Differences in the quality of the habitat and prey availability may help explain the lower density of snakes, differences in diversity, and body size differences observed in the Khorat Basin compared to outside the basin.

Diet

Freshwater homalopsines are primarily piscivorous (Voris & Murphy, 2002) and all the homalopsines reported in this study eat fish. *Homalopsis buccata* and *E. enhydris* are also reported to eat frogs and crustaceans, and in this study we documented that the poorly known *E. subtaeniata* eats fish and frogs. 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. Various fish species comprised the diet of homalopsines from Lake Songkhla in southern Thailand (Murphy et al., 1999). Although snakes are associated with feeding on large prey items, our observations with homalopsines (Voris and Murphy, 2002) suggest that they frequently feed on numerous, small prey. However, occasional large prey are certainly taken, as evidenced by a 62 cm SVL female containing a 37.8 gm unidentified fish (17.4% of body weight).

The reported diets (Cox et al., 1998) of two of the other semi-aquatic snakes encountered, *X. unicolor* (rodents, birds, mice, lizards, other snakes) and *X. piscator* (fish, frogs, and mice) reflect the semi-terrestrial habits of these species. *Cylindrophis ruffus* is reported to eat other snakes and eels (Cox et al., 1998); we documented snake feeding by *C. ruffus* in this study.

Reproduction

Variation in reproductive characteristics (litter size, frequency of reproduction, size at first reproduction) is well known among squamates (Seigel & Ford, 1987; Zug et al., 2001). Table 3 compares several reproductive variables for gravid *E. enhydris* from four Southeast Asian localities (Murphy et al., 2002). Note that the snakes from Kabin Buri and Cambodia are more "robust" in terms of size and mass, but the average litter size in the Cambodian sample is approximately twice as large as other sites. Multiple reasons can be advanced for this type of variation, including local environmental conditions and food availability (Seigel & Ford, 1987). Stuart et al. (2000) suggest that an increase in the small fish population in Tonle Sap due to human removal of larger species may be a causal factor in the relatively large reproductive effort documented for the Cambodian population.

The reproductive data reported here comes exclusively from the Kabin Buri site (outside the Khorat Basin). If it is true, as we suggest, that the Khorat Basin environment is a more resource-limited environment, we would predict a lower reproductive capacity in snake populations from Khorat Basin sites. Saint Girons and Pfeffer (1971) suggested that *E. enhydris* from Tonle Sap in Cambodia have two reproductive cycles per year. We predict that due to the climate and greater seasonality of the Khorat Basin, there will be differences in reproductive cycles in and outside of the Khorat Basin.

Comparison with Other Snake Assemblages

We recorded nine species of semi-aquatic snakes during the Khorat Basin study. Studies of other semi-aquatic snake communities provide a comparative context for the results presented here. In rice paddy and buffalo wallow environments in Sabah, Malaysia in Borneo (Voris & Karns, 1996), the snake assemblage consisted almost exclusively of *E. plumbea* (n = 351; one *Enhydris doriae* was collected). In a study of semi-aquatic snakes in Lake Songkhla in southern Thailand (Murphy et al., 1999; Karns et al., 1999-2000), a more diverse assemblage of ten species was recorded at the primary study site (three homalopsines: *Enhydris enhydris*, *E. plumbea*, and *H. buccata*; one natracine: *X. piscator*; one cylindrophiid: *C. ruffus*; one file snake: *Acrochordus granulatus*; and three elapids: *Naja kaouthia*, *Hydrophis brooki*, and *Bungarus fasciatus*. *Enhydris enhydris* overwhelmingly dominated this snake assemblage (96.4% of 752 snakes captured). With the exception of *E. subtaeniata*, all of the homalopsines found on the Khorat Basin have also been recorded from

Lake Songkhla. In a study of coastal marine homalopsines in Singapore (Karns et al., 2002), four species of homalopsines were found (*Cerberus rynchops*, *Fordonia leucobalia*, *Gerarda prevostiana*, and *Cantoria violacea*). *Cerberus rynchops* dominated this assemblage (72.2% of 220 snakes captured).

The sites located outside the Khorat Basin in this study (Kabin Buri and Prachan Takham) were similar to the snake communities noted above in that one species (*E. enhydris,* in this case) dominated the snake assemblage (84% of 377 snakes captured). The sites in the Khorat Basin were more diverse and three species (*E. enhydris*, 36.3%; *E. subtaeniata*, 26.7%; *E. plumbea* 12.2%; n = 270) were relatively common. At Khon Kaen, *E, enhydris* and *E. subtaeniata* were both common (*E. enhydris* = 48.5% of total; *E. subtaeniata* = 43.2% of total; n = 132). *Enhydris enhydris* and *E. subtaeniata* are similar in body size and form. *Enhydris enhydris* feeds primarily on small fish and *E. subtaeniata* feeds on fish and frogs. The ecology of these two sympatric species deserves further study. Gregory (1984) documented differences in the habitat, diet, and composition of snake assemblages (3 species of *Thamnophis*) on Vancouver Island, Canada. He found that the three species varied in local abundance (8 sites studied) and that snake diets showed the least overlap when the three species were relatively equal in abundance.

The tropics are notable for the greater species richness of many taxonomic groups, but temperate zone semi-aquatic snake assemblages can also be species rich and diverse (Gibbons & Dorcas, 2004). In the southeastern United States, natracine snakes (*Nerodia* and *Regina*) are ecological equivalents of the homalopsines. Mushinsky and colleagues (Mushinsky & Hebrard, 1977a; Mushinsky & Hebrard, 1977b; Hebrard & Mushinsky, 1978) studied a semi-aquatic snake community that consisted of four species of *Nerodia* and two species of *Regina*; they examined the use of food, space and time by these species. Similar to the more diverse snake assemblages found at sites on the Khorat Basin in this study, several species were abundant, with *N. cyclopion* and *N. rhombifer* accounting for > 50% of the water snake community.

The tropical semi-aquatic snake assemblages noted above consist of two to ten species. The Sakaerat Environmental Research Station, located about 3 km from Ban Badan, was the site of a classic year-long investigation of a tropical forest herpetofauna (Inger & Colwell, 1977). Their study provides a comparison between a snake species assemblage from tropical forest and the semi-aquatic assemblage described here. They recorded 29 species of snakes in evergreen forest and 27 species in deciduous forest representing five families of snakes.

Sampling Issues

This study must be considered preliminary because it is based on data collected over a relatively short period of time in two different years. It does not take into account interspecific variation in annual activity patterns and seasonal patterns in weather (Inger, 2003). However, because the collections were made at the same time of year (June-July), it can be argued that the data are comparable. Also, because we are studying snakes that live in water and water resources are available year-round at the study sites, it could be argued that seasonality would not be of great importance for water snakes in a tropical climate. However, we note that *E. plumbea* was not collected at Ban Badan at all in 2003, but frequently encountered in 2004. It was exceptionally dry in 2003. In 2004 we had a week of heavy rains in the area (June-July is the beginning of the southwest monsoon). Local residents commented that the number of semi-aquatic snakes they encountered was always higher in the wet season. Additionally, low sample sizes at some sites and differences in time and effort spent at different sites influence the results presented here.

Future Work

If, as suggested by this study, the Khorat Basin is an important biogeographic feature for semi-aquatic snakes, there may be genetic differences between snake populations found in and outside of the Khorat Basin. We are currently in the process of doing phylogeographic studies with mitochondrial DNA and corresponding morphological studies to test this hypothesis.

The work presented here suggests a rich research agenda for the study of snake biology in the region. Year-round sampling needs to be done in order to remove the bias caused by short-term sampling. Year-round sampling would also provide much needed information on reproductive cycles, abundance, and activity patterns. Longer-term studies are needed in order to make well informed biodiversity conservation decisions (Kupfer et al., 2005; Watling & Donnelly, 2002). Larger samples are required to verify the body size differences we found between populations. Sampling prey availability at sites located on and off of the Khorat Basin should be done to determine if there are food resource differences that would affect population and community characteristics (Filippi et al., 2005). The differences between the Khorat Basin and adjacent natural regions provide an ideal environment for the testing of different ecological and evolutionary hypotheses.

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Appendix 1.

Collecting localities used in this study. See text for more details.

Name	GPS Coordinates	Province	District	Subdistrict
IN KHORAT BASIN				
Khon Kaen Area				
Khon Kaen University	16º 27′ 31″ N 102º 48′ 29″ E	Khon Kaen	Mueang	
Ban Huai Sun		Khon Kaen	Mueang	Sila
Ban Wang Muan	17º 10′ 57″ N 102º 26′ 01″ E	Nong Bua Lam Phu	Mueang	Nong Bua Lam Phu
Ban Mai	17º 10′ 01″ N 102º 24′ 39″ E	Nong Bua Lam Phu	Mueang	Nong Bua Lam Phu
Ban Tha Lad	16º 48′ 32″ N 102º 28′ 09″ E	Nong Bua Lam Phu	Non Sang	Nong Bua Lam Phu
Ban Nong Pueng (Pieu)		Khon Kaen	Phu Wiang	Tung Chompu
Ban Badan Area				
Ban Badan Reservoir	14º 31′ 04″ N 101º 58′ 25″ E	Nakhon Ratchasima	Wang Nam Khieo	Udom Sap
Ban Badan Canal	14º 31′ 51″ N 101º 58′ 53″ E	Nakhon Ratchasima	Wang Nam Khieo	Udom Sap
Ban Badan Rice Paddies	14º 32′ 13″ N 101º 58′ 15″ E	Nakhon Ratchasima	Wang Nam Khieo	Udom Sap
Mr. Pom's Rice Paddies	14º 32′ 8″ N 101º 57′ 46″ E	Nakhon Ratchasima	Wang Nam Khieo	Udom Sap
Huey Bong Bridge	14º 32′ 27″ N 101º 58′ 11″ E	Nakhon Ratchasima	Wang Nam Khieo	Udom Sap
Huey Pae Bridge	14º 31′ 30″ N 101º 57′ 56″ E	Nakhon Ratchasima	Wang Nam Khieo	Udom Sap
KHORAT RIM SITES				
Forestry Reservoir	14º 27′ 55″ N 101º 54′ 11″ E	Nakhon Ratchasima	Wang Nam Khieo	Udom Sap
Thai Sammaki Reservoir	14º 26′ 13″ N 101º 52′ 35″ E	Nakhon Ratchasima	Wang Nam Khieo	Thai Sammaki
Bu Phram Reservoir	14º 20′ 30″ N 101º 49′ 35″ E	Prachin Buri	Na Di	Bu Phram
OUTSIDE KHORAT BASIN				
Kabin Buri Area				
Kabin Buri Lake	13º 59′ 15″ N 101º 44′ 58″ E	Prachin Buri	Prachan Takham	Meung Kow
Kabin Buri Gold Mine	13º 57′ 23″ N 101º 47′ 17″ E	Prachin Buri	Prachan Takham	Meung Kow
Kabin Buri Paddy	13º 57′ 59″ N 101º 48′ 01″ E	Prachin Buri	Prachan Takham	Meung Kow
Prachan Takham Area				
Klong Fai	14º 03′ 17″ N 101º 31′ 16″ E	Prachin Buri	Prachan Takham	Meung Kow
Koh Sur, Nong Ben	14º 02′ 40″ N 101º 30′ 26″ E	Prachin Buri	Prachan Takham	Meung Kow
Koh Sur, Nong Khe	14º 03′ 09″ N 101º 31′ 20″ E	Prachin Buri	Prachan Takham	Meung Kow