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Differences among Populations of the Mekong Mud Snake (*Enhydris subtaeniata*: Serpentes: Homalopsidae) in Indochina

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ABSTRACT.– This study examines between-population variation of the Mekong Mud Snake, *Enhydris subtaeniata* (Bourret, 1934) in Thailand, Cambodia, Laos, and Viet Nam, and relates the observed patterns to previously published patterns based on molecular data. *Enhydris subtaeniata* were collected from six representative locations throughout its range that encompassed three important river drainage basins: the Chao Phraya, the Middle Mekong and the Lower Mekong. Data on size, sexual size dimorphism, scalation, reproductive biology and diet were used to explore biogeographical patterns revealed by a previously published phylogenetic and population genetic analysis. In several cases the size and reproductive characteristics mirrored the genetic differences and habitat differences associated with the sampled locations.

KEY WORDS: **Freshwater snake, biogeography, sea levels, Mekong River, Chao Phraya River, Khorat Basin**

INTRODUCTION

Southeast Asia is a global bio-diversity hotspot with 20 – 25% of the planet's animal and plant species (Woodruff, 2010). Previous studies have identified various geographic features of the region that have likely influenced geographic variation in the distribution of terrestrial, freshwater and marine species of this region, as well as the patterns of intraspecific genetic diversity and population structure. In particular, Indochina has a complex geological history, with a number of potentially important physiographic events occurring in the Quaternary that certainly affected many taxa (see reviews in Rainboth, 1996; Inger and Voris, 2001; Glaubrecht and Köhler, 2004; Woodruff, 2010).

We have been conducting studies investigating the effects of geographical features on evolutionary and ecological processes in this region using homalopsid snakes, which dominate the semi-aquatic snake communities of Southeast Asia (e.g., Alfaro et al., 2004, 2008; Karns et al., 2005, 2010a; Murphy, 2007). The Homalopsidae (47 species currently recognized) are opisthoglyphous (rear-fanged), mildly venomous (Fry et al., 2006), and distributed from Pakistan and the Indian subcontinent across Southeast Asia to northern Australia (Murphy, 2007). Most homalopsids are semi-aquatic, primarily nocturnal, and usually associated with mud substrates. Semi-aquatic snakes are particularly interesting with respect to gene flow, dispersal, and speciation processes because of their intermediate ecological position

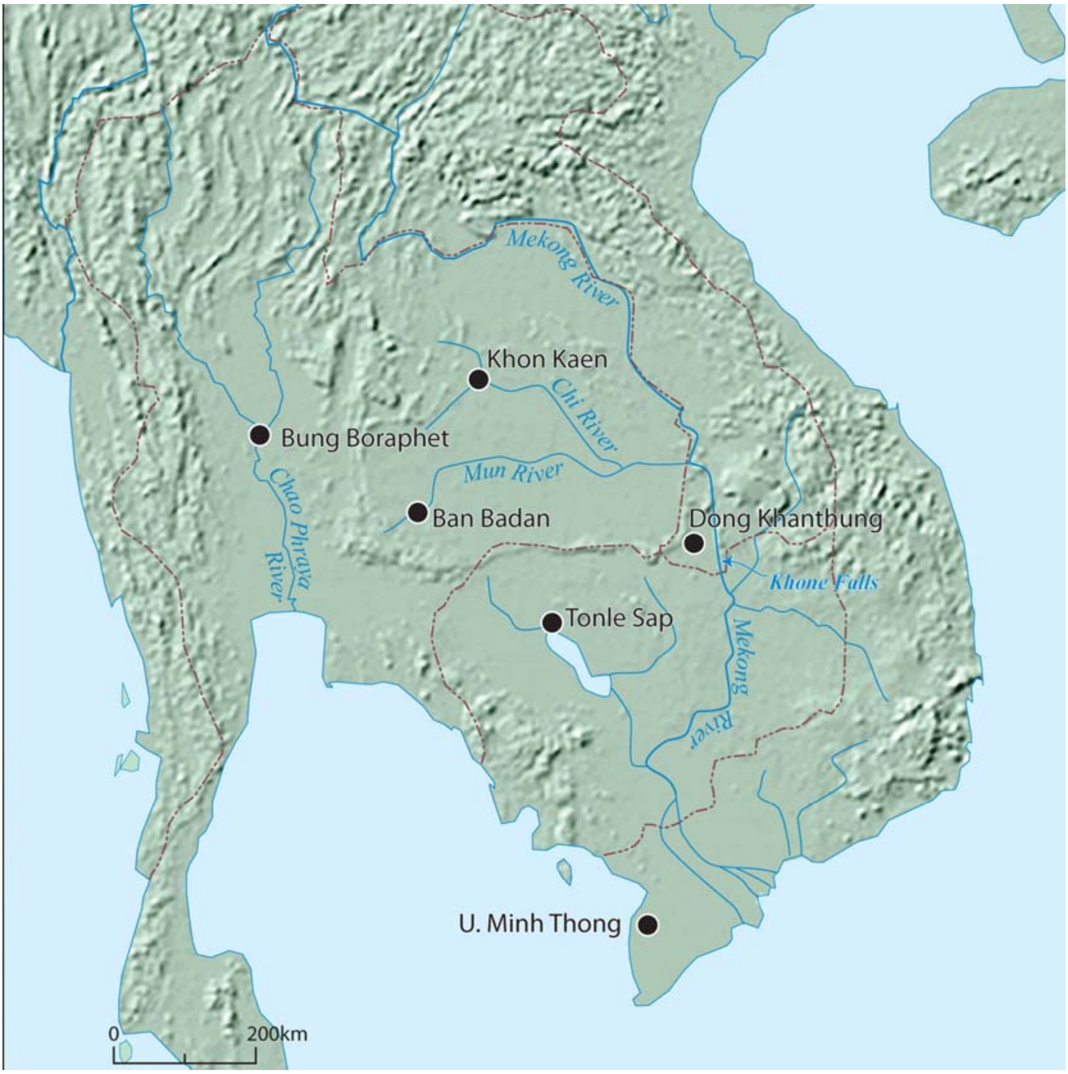

FIGURE 1. Map showing the six *E. subtaeniata* collection locations in Indochina. Bung Boraphet is in the Chao Phraya basin, located in the Central Plain of Thailand. Adjacent to the Middle Mekong and in the Khorat Basin is Khon Kaen (Ban Mai and Ban Nong Pueng sites) in the Chi River catchment and Ban Badan in the Mun River catchment (the Chi and Mun Rivers are tributaries of the Mekong). Dong Khanthung is in Laos above Khone Falls on the southern edge of the Middle Mekong. Tonle Sap and U. Minh Thong are in the Lower Mekong (See Lukoschek et al. 2011 for GPS coordinates and other details on sampling locations).

across the continuum of terrestrial-aquatic habitats. This study compares several populations of the Mekong Mud Snake, *Enhydris subtaeniata* (Bourret, 1934), a species known only from lowland regions of central Indochina (Fig. 1). This is a medium-sized, semi-aquatic piscivorous snake found in a variety of freshwater habitats with mud substrates, including rice paddies, streams, ponds, ditches, and canals (Karns et al., 2005, 2010a). It occurs primarily in the Middle and Lower Mekong

River basins from Laos, Thailand, Viet Nam, and Cambodia, although one population is known from Bung Boraphet in the Central Plain of Thailand (Karns et al., 2010a).

In this study we broaden our understanding of the biogeography of semi-aquatic taxa in Indochina by comparing the morphology (size, sexual size dimorphism, and scalation), habitat utilization, reproduction, and diet among populations of *E. subtaeniata* from six geographic localities in three major river basins in the region: the Middle Mekong (Mekong tributaries inside the Khorat Basin), the Lower Mekong (outside the Khorat Basin), and the Chao Phraya in the Central Plain of Thailand (Fig. 1). We evaluate our results in the context of the known biogeographical history of the region and the results of previous molecular studies (Lukoschek et al., 2011).

MATERIALS AND METHODS

Collecting.– *Enhydris subtaeniata* (Fig. 2) specimens used in this study came from collections obtained in 2003, 2004 and 2007 (Karns et al., 2005, 2010a) and from specimens collected by Stuart (Stuart et al., 2000; Stuart, 2004). We typically obtained adult and large subadult snakes collected as

FIGURE 2. *Enhydris subtaeniata* photographed in July of 2004 by J. C. Murphy at Bung Boraphet, Thailand.

incidental by-catch from local fishers. Young and small subadult snakes were rarely collected and were not included in the analysis. Dead snakes were quickly processed or frozen. Some dead snakes were partially decomposed and were not retained. Live snakes were euthanized, processed, and preserved with formalin. The preserved collection of snakes was deposited with the National Science Museum of Thailand.

Study sites.– We collected snakes from a total of 12 sites from the following river basins: the Chao Phraya River basin, Thailand; the Mun and Chi River basins in Thailand and Laos; and the Lower Mekong in Cambodia and Vietnam (Fig. 1; see Lukoschek et al., 2011 for detailed information about collection sites). Snakes from 12 sites were grouped into six locations (Fig. 1, Table 1) for analysis. Sites were combined if they were within several kilometers of each other and at the same elevation. The six locations were clustered into three geographic regions defined by river basins as follows: Chao Phraya River Basin – Bung Boraphet; Middle Mekong – Khon Kaen (Ban Mai and Ban Nong Pueng), Ban Badan, Dong Khanthung; Lower Mekong – Tonle Sap, U. Minh Thong.

Size, sexual dimorphism and sex ratios.– We examined sexual size dimorphism (SSD) using adult snakes obtained from gill nets that could be reliably sexed using tail morphology and the presence of hemipenes. For all snakes, we measured snout-vent length (SVL) and tail length to the nearest mm and weighed snakes to the nearest 0.1 g. We also measured the girth at the neck and mid-body for preserved specimens. A sexual dimorphism index (SDI) was calculated by dividing the mean SVL of the larger sex by the mean SVL of the smaller sex; a positive value is assigned if females are the larger sex and a negative value if the males are the larger sex (Gibbons and Lovich, 1990). We also calculated sex ratios for adult *E. subtaeniata* collected at the three Thailand locations with sufficient sample sizes (Bung Boraphet, n = 54; Khon Kaen area, n = 50; Ban Badan, n = 15).

Scalation, reproduction and diet. – We documented standard scalation characteristics for preserved specimens (nomenclature used follows Lillywhite, 2008) including the condition of the loreal and internasal, and the numbers of upper labials, lower labials, ventral, subcaudal, dorsal, and ocular ring scales. For this aspect of the study we examined 92 preserved specimens (54 females, 38 males) of *E. subtaeniata* (Khon Kaen area, n = 46; Ban Badan, n = 12; Bung Boraphet, n = 14; Dong Khanthung, n = 9; U. Minh Thong, n = 8; Tonle Sap, n = 3). Statistics on three variable characters (number of ventral scales, number of subcaudal scales, and number of anterior dorsal scales) are provided in Table 2.

TABLE 1. Sex ratios and sexual dimorphism of populations of Enhydris subtaeniata from localities in mainland Southeast Asia. Data for Thailand, Laos, and Vietnam are from specimens examined in this study; data for Tonle Sap (Siem Reap, Cambodia) 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; — = not tested). 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).

	Sex ratio		SVL (cm) mean ± SE (range)			Mass (g) mean ± SE (range)			Tail:SVL mean ± SE			
Locality	**M:F**	***P***	**female**	**male**	***P***	**female**	**male**	***P***	**female**	**male**	***P***	**SDI**
Bung Boraphet	0.5 n = 54	NS	57.9 ± 1.08 (43.6-68.8) n = 27	49.6 ± 0.40 (46.8-55.7) n = 27	<0.001	314.2 = 18.93 (114.5 ± 570.0) n = 27	150.3 ± 3.97 (116.0-202.0) n = 27	<0.001	0.2 = 0.002 n = 22	0.24 ± 0.002 n = 25	<0.001	+ 1.17
Khon Kaen ·Ban Mai and ·Ban Nong Pueng	0.34 n = 50	<0.05	44.4 ± 0.83 (33.2-56.7) n =33	39.2 ± 1.15 (31.0-46.7) n = 17	<0.001	93.5 = 5.2 (39.2-159.0) n =33	50.3 = 3.78 (27.2-78.1) n = 17	<0.001	0.23 = 0.002 n = 126	0.27 ± 0.002 n = 58	<0.001	+ 1.08
Ban Badan	0.27 n = 15	NS	42.3 ± 2.15 (30.0 - 53.3) n = 11	36.5 ± 0.63 (35.0-38.0) n = 4	NS	100.9 = 15.48 (30.0 - 182.7) n = 11	52.7 1 = 1.53 (49.3 - 56.1) n = 4	NS	0.22 = 0.002 n = 89	0.26 ± 0.004 n =70	<0.001	+ 1.06
Dong Khanthung Laos	0.33 n = 9	—	32.9 ± 3.23 (24.1-44.8) n = 6	38.6 ± 0.41 (38.0-39.4) n = 3	—	35.5 ± 7.3 (14.0-56.0) n = 6	42.7 = 0.50 (39.0-45.0) n = 3	—	0.2 ± 0.01 n = 6	0.23 ± 0.01 n = 3	—	-1.17
U. Minh Thong Vietnam	0.67 n = 6	—	33.4 = 5.6 (27.8-39.0) n = 2	50.2 ± 2.35 (46.0-54.8) n = 4	—	21.5 = 1.50 (20-23) n = 2	124.5 = 15.63 (79.0-150.0) n = 4	—	0.16 = 0.02 n = 2	0.21 ± 0.02 n = 4	—	-1.5
Siem Reap Cambodia	—	—	—	57.6 ± 0.65 (56.9-58.2) n = 2	—	—	172.0 ± 2.00 (170-174) n =2	—	—	0.21 ±0.01 n = 2	—	—

TABLE 2. Statistics on several scale counts made on Enhydris subtaeniata from six localities in mainland Southeast Asia. Data for Thailand, Laos, and Vietnam are from specimens examined in this study; data for Tonle Sap (Siem Reap, Cambodia) 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; — = not tested).

	Ventral scales mean ± SE (range)			Subcaudal scales (left) mean ± SE (range)			Dorsal scales (anterior) mean ± SE (range)		
Locality	**female**	**male**	***P***	**female**	**male**	***P***	**female**	**male**	***P***
Bung Boraphet	137.9 ± 0.62	145.0 ± 0.89	< 0.001	52.7 = 0.62	62.5 ± 0.29	< 0.001	22.8 ± 0.15	23 = 0.00	NS
	(135 - 141)	(143 - 147)		(53 - 54)	(62 - 63)		(22 - 23)	23	
	n = 9	n = 5		n = 6	n = 4		n = 9	n = 5	
Khon Kaen	140.8 ± 0.56	146.7 ± 0.74	< 0.001	45.4 ± 0.74	56.6 ± 1.00	< 0.001	21.9 ± 0.15	22.1 ± 0.19	NS
·Ban Mai and	(134 - 147)	(141 - 151)		(35-54)	(47-62)		(21 - 23)	(21 - 23)	
·Ban Nong Pueng	n = 29	n = 17		n = 25	n = 16		n = 29	n = 17	
Ban Badan	137.8 ± 1.80	144.8	< 0.05	47.0 = 0.87	54.5 ± 3.18	< 0.05	21.9 ± 0.23	22.8 ± 0.25	NS
	(134 - 150)	(142 - 146))		(44 - 50)	(45 - 58))		(21 - 23)	(22 - 23)	
	n = 8	n = 4		n =7	n = 4		n = 8	n = 4	
Dong Khanthung	145.3 ± 1.89	149.0 ± 1.00	—	55.4 ± 2.81	59. 7 = 1.76	—	22.0 ± 0.37	22.3 ± 0.33	—
Laos	(140 - 152)	(147 - 150)		(48 - 61)	(57 -63)		(21 - 23)	(22 - 23)	
	n = 6	n = 3		n = 5	n = 3		n = 6	n = 3	
U. Minh Thuong	142 ± 2.00	145.0 ± 2.07	—	63	63.4 ± 2.47	—	23	22.3 ± 0.33	—
Vietnam	(144 - 144)	(135 - 149)		—	(54 - 69)		—	(21 - 23)	
	n = 2	n = 6		n = 1	n = 5		n = 1	n = 6	
Siem Reap	—	149.0 ± 2.52	—	—	65.0 ± 0.56	—	—	22.0 ± 0.58	—
Cambodia		(146 - 154)			(64 - 66)			(21 - 23)	
		n = 3			n = 3			n = 3	

TABLE 3. Summary of reproductive characteristics of female *Enhydris subtaeniata* from central and northeastern Thailand.

Location (females examined)	SVL (cm) Mean (± 1 SE) (range)	Mass (g) Mean (± 1 SE) (range)	Clutch Size: Vitellogenic follicles Mean ± 1 SE (range)	Clutch Size: Oviducal eggs Mean ± 1 SE (range)	Number Post-Reproductive	Relative Clutch Mass	% Reproductive (min SVL at reproduction)
Bung Boraphet (26)	62.3 ± 1.53 (56.2 - 76.8) n = 15	328.1 ± 21.46 (200.0 - 468.0) n = 15	14.1 ± 1.41 (7 - 23) n = 14	15 n = 1	0	0.21 n = 1	63.0 (56.2)
Khon Kaen (29) ·Ban Mai & ·Ban Nong Pueng	45.3 ± 0.80 (39.0 - 56.7) n = 27	100.1 ± 5.00 (62.4 - 159.0) n = 27	9.2 ± 0.83 (3 - 14) n = 16	9.0 ± 0.93 (6 - 14) n = 8	3	0.16 ± 0.01 (0.12 - 0.20) n = 8	93.1 (39.0)
Ban Badan (8)	51.7 ± 0.88 (50.3 - 53.3) n = 3	170.5 ± 12.02 (146.5 - 182.7) n = 3	13.5 ± 0.50 (13 - 14) n = 2	—	1	—	37.5 (50.3)

Snakes were dissected in the field prior to preservation and the reproductive condition of females (n = 63) was documented. 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 calculated the relative clutch mass (RCM) as the ratio of the clutch mass to the maternal mass minus the clutch mass (Table 3). We also examined stomach contents in the field prior to preservation to determine diet for a total of 112 snakes, 66 females and 46 males (Khon Kaen area, n = 46; Bung Boraphet, n = 55; Ban Badan, n = 11).

RESULTS

Size, sexual dimorphism and sex ratios.– Snout-vent length (SVL) differed among three *E. subtaeniata* populations (Fig. 3A) for both males ($F_{(2,44)}$ = 67.45, $P < 0.001$) and females ($F_{(2,68)}$ = 55.43, $P < 0.001$). ANCOVAs on male and female SVL, using mass as the covariate, also demonstrated significant differences in slope among locations for both males ($F_{(2, 43)}$ = 5.35, $P < 0.01$) and females ($F_{(2, 67)}$ = 7.36, $P < 0.01$). Tukey HSD for unequal sample sizes post hoc test showed that males and females from Bung Boraphet were significantly longer in SVL and heavier than their counter-parts from Khon Kaen and Ban Badan (Fig. 3A and 3B).

The sampled populations of *E. subtaeniata* also exhibited sexual size dimorphism. Snakes from Bung Boraphet and Khon Kaen had an SDI with females significantly longer than males (Table 1, Fig. 3A) and heavier than males (Fig. 3B). Males and females from Ban Badan did not differ in SVL or mass (Figs. 3A and 3B, Table 1), but sample sizes were smaller. Male *E. subtaeniata* from all three localities had significantly longer tails, relative to SVL compared to females (Table 1).

Sex ratios (Table 1) varied among the three main localities sampled (Bung Boraphet, Khon Kaen and Ban Badan) with a significant deviation from a 1:1 sex ratio at Khon Kaen (M:F 0.34, n = 50), but not at Bung Boraphet (M:F 0.50, n = 54) or Ban Badan (M:F 0.27, n = 15).

Scalation.– Sixteen of the 20 scale characters examined were found to be invariant among locations for both males and females. However, the numbers of ventrals, subcaudals (left and right), and anterior dorsal scales showed some significant variation (Table 2). Specifi-cally, there was sexual dimorphism in ventral and

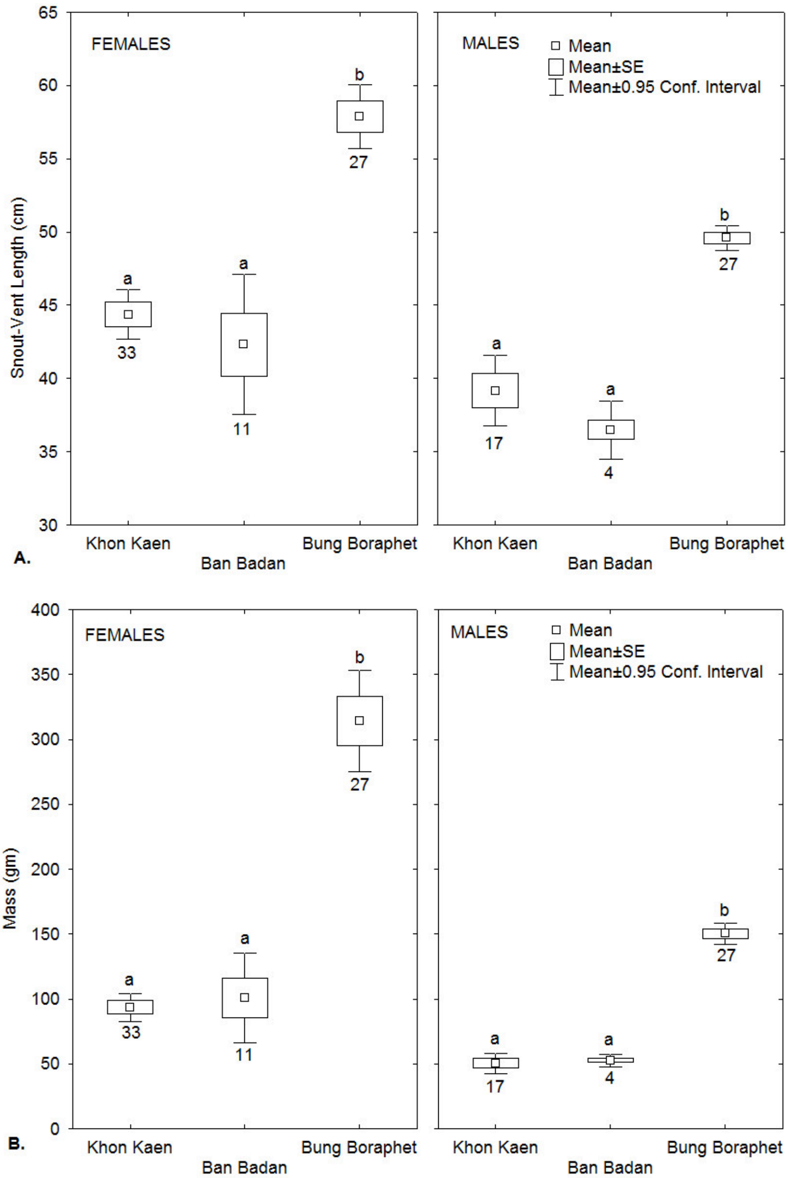

FIGURE 3. Geographic variation in snout-vent length and mass among three populations of *E. subtaeniata*. The mean SVL (± SE), mass (± SE), and 95 % confidence limits are shown for females and males from each population. The letters above the means indicate significant differences among means at $P \leq 0.05$ based on Tukey HSD unequal sample sizes post hoc test; letters in common indicate no difference.

subcaudal scale counts, with males having significantly ($P < 0.05$) more ventral scales than females at Bung Boraphet, Khon Kaen, and Ban Badan (Table 2, Fig. 4A and 4B). In addition, there were sex-specific geographic differences in the number of subcaucals, with females from Bung Boraphet having significantly higher numbers of subcaudals than females from Khon Kaen ($P < 0.05$), but not from Ban

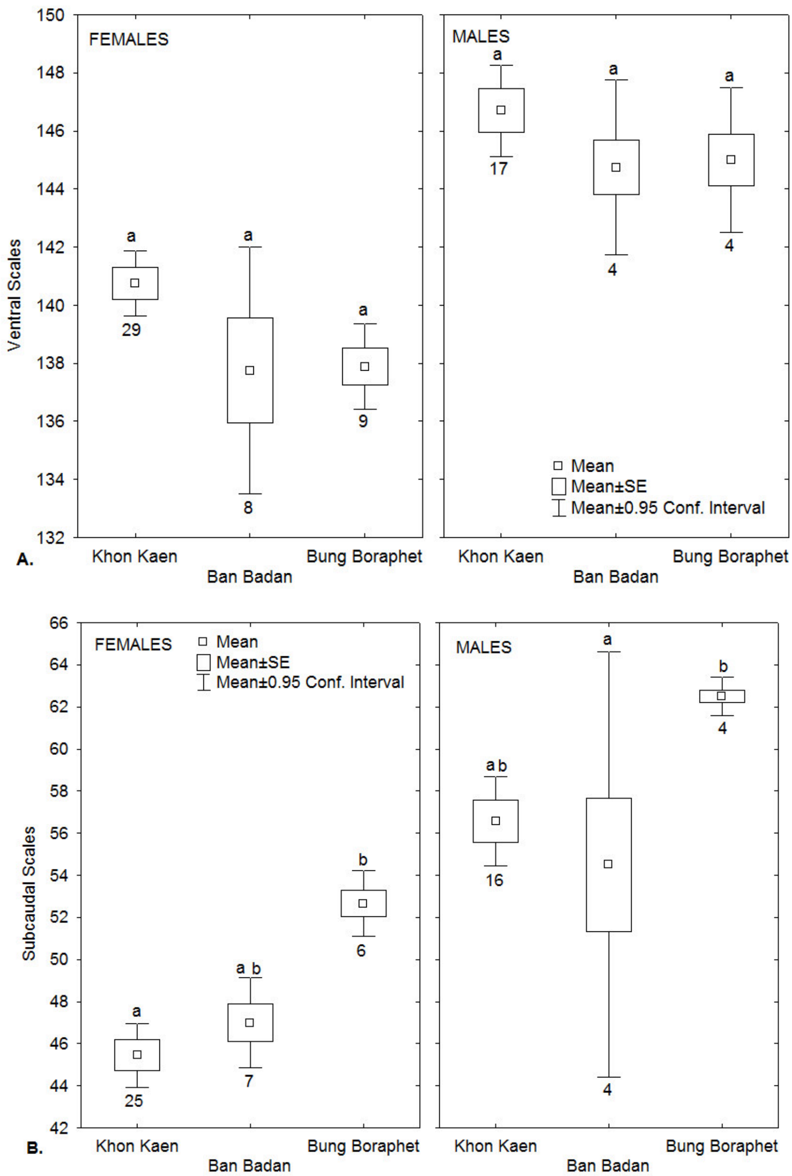

FIGURE 4. Geographic variation in the number of ventral and subcaudal scales among three populations of *E. subtaeniata*. The mean (± SE) and the 95 % confidence limits are shown for females and males from each population. The letters above the means indicate significant differences among means at $P \leq 0.05$ based on Tukey HSD unequal sample sizes post hoc test; letters in common indicate no difference.

Badan (Fig. 4B). By contrast, male subcaudal counts from Bung Boraphet were significantly higher than males from Ban Badan ($P < 0.05$), but not Khon Kaen (Fig. 4B). There were no sex-specific geographic differences in the numbers of ventrals (Fig. 4A).

Reproduction and diet.– The percentage of female *E. subtaeniata* in reproductive condition ranged from 37.5% to 93.1% in the three Thai samples; Bung Boraphet, Khon Kaen and Ban Badan (Table 3). The number of vitellogenic follicles ranged from 3 to 23 while the number of oviducal eggs ranged from 6 to 15 (Table 3). The larger Bung Boraphet females had significantly more vitellogenic follicles (mean = 14.1 ± 1.41) than the Khon Kaen females (mean = 9.2 ± 0.83) (t = 3.11, df = 28, P = 0.004). The RCM of nine *E. subtaeniata* ranged from 0.12 – 0.21. Female *E. subtaeniata* from Khon Kaen (Ban Mai + Ban Nong Pueng) exhibited a positive relationship between clutch size and SVL ($F_{(1,22)} = 18.092$, $r^2 = 0.451$, $P < 0.001$) (Fig. 5), however this was not the case for females from Bung Boraphet ($F_{(1,13)} = 3.011$, $r^2 = 0.19$, $P = 0.11$).

The majority of *E. subtaeniata* (61.6%) had stomach contents. There was a significant difference in the frequency of feeding between female (48 of 66 snakes with food: 72.7%) and male *E. subtaeniata* (21 of 46 with food: 45.6%) ($x^2 = 8.40$, df = 1, $P = 0.004$). Moreover, a large proportion

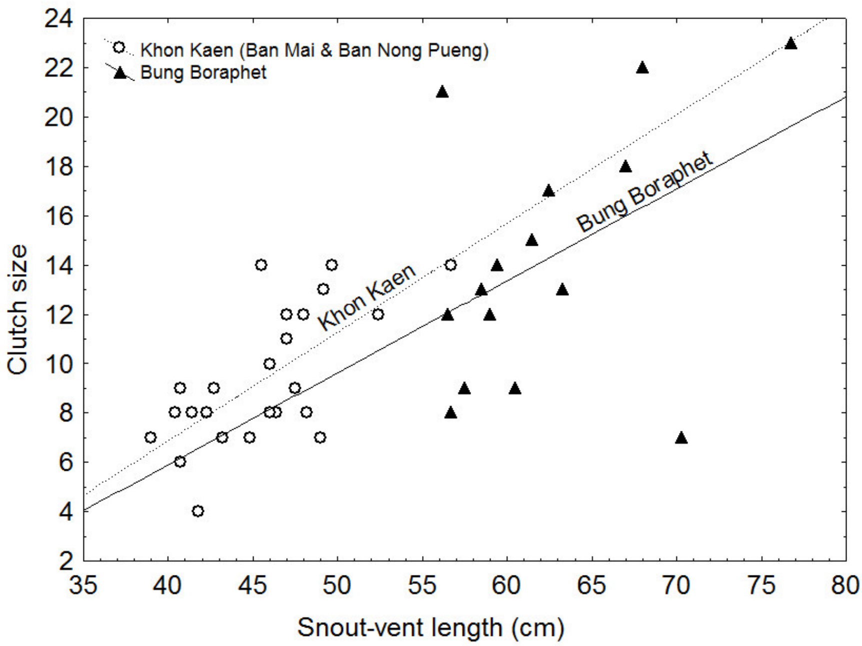

FIGURE 5. Comparison of clutch size as a function of snout-vent length for *E. subtaeniata* from Khon Kaen (Ban Mai + Ban Nong Pueng) vs. Bung Boraphet. Due to limited samples clutch size was calculated from snakes with either enlarged vitellogenic follicles or oviducal eggs. The upper dotted line (open circles) represents the linear regression for the Khon Kaen snakes (n=24, $r^2 = 0.4513$, $p < 0.001$; y = 0.4407*x - 10.7410) while the lower solid line (filled triangles) represents the linear regression for the Bung Boraphet snakes (n=15, $r^2 = 0.1881$, $p = 0.106$; y = 0.3730*x - 9.016).

of females in reproductive condition (32 of 43 snakes: 74.4%) contained food. Stomach contents invariably consisted of fish remains, although in most cases (75.4%) they were limited to unidentifiable scales, bone and undigested flesh. Identifiable fish included five *Puntius* (Cyprinidae), one *Esomus mettallicus* (Cyprinidae), and one *Trichopodus trichopterus* (Osphronemidae). Measurable prey length ranged from 6.2 to 8.1 cm and prey mass from 5.0 to 16.2 g, representing 2.1–17.1 % of snake body mass.

DISCUSSION

Morphology and ecology.– Variation in body size and reproductive characteristics (clutch size, frequency of reproduction, and size at first repro-duction) are well documented among squamates (Seigel and Ford, 1987; Zug et al., 2001) and 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; Weatherhead et al., 1995; Pearson et al., 2002). Males and females from Bung Boraphet were significantly larger in size (both SVL and mass) than *E. subtaeniata* from the Khorat Basin sites and Bung Boraphet females had larger clutch sizes (Table 3). These observed size differences may be a reflection of genetic differences shown in the maximum parsimony (MP) tree based on molecular data (Figure 2 in Lukoschek, et al., 2011). In this MP tree, snakes from Bung Boraphet were grouped with U. Minh Thong and Tonle Sap snakes from the Lower Mekong while the Middle Mekong snakes from the Khorat Basin grouped together. The observed size differences could also be due to the fact that Bung Boraphet is an extensive and highly productive wetland prone to flooding, whereas the Khorat Basin is relatively dry, with lower soil fertility (Parnwell, 1988). 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 repro-ductive characteristics by increasing the food supply of homalopsids that eat relatively small prey items. This mesopredator release (Ritchie and Johnson, 2009) may also be the case in the densely populated Central Plain where Bung Boraphet supports an important fishery (Sriwongsitanon et al. 2007). Similar to this study, Karns et al. (2010b) found that *E. enhydris*, a close relative of *E. subtaeniata* with similar ecology, collected from Bung Boraphet and Bung Ka Lo (another extensive wetland complex in the Chao Phraya basin) were significantly larger (SVL and mass) than other *E. enhydris* populations sampled in Thailand.

Despite moderate levels of genetic divergence observed among localities (1–2%, Lukoschek, et al., 2011), we did not find a suite of diagnostic morphological differences among populations using classical scale characters. *Enhydris subtaeniata* exhibited typical homalopsid female-biased sexual size dimorphism (Karns et al. 2005, 2010b) and males have longer tails and a greater number of subcaudal scales. The ratio of tail length to SVL is a common sexually dimorphic trait in snakes and male snakes of some species with longer tails achieve greater reproductive success (Shine et al., 1999).

Freshwater homalopsids are primarily piscivorous (Voris and Murphy, 2002) and *E. subtaeniata* is no exception. Voris and Murphy (2002) documented that homalopsids frequently feed on numerous, small prey. Brooks et al., (2009) found the prey-to-predator mass ratios of homalopsids to be lower (< 0.2) than that recorded for *Xenochrophis piscator*, *Cylindrophis ruffus* and other snakes reported in the literature (Rodríguez-Robles et al., 1999). We have limited data for *E. subtaeniata*, but we documented low prey-to-predator mass ratios (0.02 – 0.17) comparable to another small-headed homalopsid, *Enhydris enhydris* (0.01 – 0.19) (Karns et al., 2010b). The high percentage of stomachs with unidentifiable fish remains (scales, bone, tissue) also suggests a high rate of passage of small prey items. Contrary to reports of anorexia within snakes in reproductive condition (Lourdais et al., 2002), we found that 74.4% of female *E. subtaeniata* in reproductive condition contained food, whereas ~45% of reproductive *E. enhydris* contained food (Brooks et al., 2009; Karns et al., 2010b).

A recent paper by Lukoschek et al. (2011) revealed strong population subdivision for the Mekong Mud Snake, *E. subtaeniata*, throughout most of its range in Indochina, with each sampled location characterized by a unique suite of haplotypes, but with varying levels of genetic diversity. Relationships among phylogroups largely conformed to the geographic proximity of sampled locations and there was a strong relationship between genetic distance and geographic distances along suitable aquatic habitats, suggesting that the geographical configuration of river drainages may have significantly influenced the distribution of genetic diversity in this region.

The findings of the present study show that several aspects of the snakes' biology including size, sexual size dimorphism, scalation and female reproductive characteristics also differed between locations, further supporting a pattern of local differentiation. In addition, the differences observed in snake size and scalation between the Chao Phraya River Basin (Bung Boraphet) and the Middle Mekong (Khon Kaen and Ban Badan) lend further support to the notion that a barrier to gene flow exists for homalopsid snake species between the Khorat Basin and the Chao Phraya Basin.

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