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Allometry and Sexual Dimorphism in the Snail-eating Turtle Malayemys macrocephala from the Chao Phraya River Basin of Central Thailand

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Allometry and Sexual Dimorphism in the Snail-Eating Turtle *Malayemys macrocephala* from the Chao Phraya River Basin of Central Thailand

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ABSTRACT. – Allometric growth and sexual dimorphism of the shell is evident in *Malayemys macrocephala* from the Chao Phraya River Basin of central Thailand. Differences in allometric growth between males and females produce sexually dimorphic adults. Adult females exhibit larger sizes and have relatively wider and higher shells and longer plastra than males.

Brophy (2004) recently reviewed the systematics of the genus *Malayemys* (Testudines: Geoemydidae [Bataguridae]) and argued for the presence of two taxonomically distinct species. Analyses of head-stripe and shell characters revealed a clear pattern of geographic variation that was consistent with the topography of Southeast Asia and the poor dispersal abilities of these turtles. Turtles from the Mekong River Basin retained the name *M. subtrijuga* (Schlegel and Müller 1844), whereas those from the Chao

Phraya and Mae Klong river basins, coastal areas of southeastern Thailand, and the Malay Peninsula were assigned the name *M. macrocephala* (Gray 1859).

Malayemys macrocephala is a small geoemydid turtle reaching maximum sizes of 22 cm carapace length (Srinarumol 1995). This species has pronounced sexual dimorphism, with females exhibiting larger overall body sizes, proportionally wider carapaces, and shorter, narrower tails (Ernst and Barbour 1989; Srinarumol 1995; van Dijk and Thirakhupt, in press). Populations of *M. macrocephala* can be found in virtually all lowland areas of the Chao Phraya River Basin in central Thailand, where it is the most common turtle (van Dijk and Thirakhupt, in press).

Sexual dimorphism and allometry of the turtle shell have been studied extensively (reviews in Mosimann 1956; Berry and Shine 1980; Ernst and Lovich 1986; Gibbons and Lovich 1990). My research interest focused on geographic variation and the possibility of regional differentiation and speciation in *M. subtrijuga* (*sensu lato*). Studies of regional variation require the recognition and elimination of character variation due to factors such as sex, age, and ecology. Without such considerations, critical errors in taxonomic judgement are likely to occur.

Although M. macrocephala is a common turtle with high popularity in the pet trade, its biology is known only through an assortment of anecdotal reports. I discovered that despite the seeming abundance of *M. macrocephala* voucher specimens, few had precise locality data. I was able, however, to assemble a moderately large sample from the Chao Phraya River Basin. This sample permits the first published study to quantify allometry and sexual dimorphism in this species.

Methods. — I examined 97 museum specimens of M. macrocephala from the Chao Phraya River Basin of central Thailand. The geographic origin of each specimen was based on museum records, and the sample was divided by sex and life stage. Dial calipers (accurate to 0.1 mm) were used to take the following 29 straight-line measurements on the shell of each specimen: maximum carapace length (CL); carapace width at the level of the seam separating vertebral scutes 2 and 3 (CW); shell height at the level of the seam separating vertebral scutes 2 and 3 (SH); maximum plastron length (PL); maximum width (APLW and PPLW) and length (APLL and PPLL) of both plastral lobes; minimum bridge length (BrL); maximum width and length of vertebral scutes 1, 2, 3, and 5 (Vert1, 2, 3, 5W and L); maximum width and length of pleural scute 1 (Pleu1W and L); medial seam length of gular (GulL), humeral (HumL), pectoral (PecL), abdominal (AbdL), femoral (FemL), and anal (AnL) scutes; and maximum width of gular (GulW), humeral (HumW), femoral (FemW), and anal (AnW) scutes. One meristic character, RLatK, recorded the position (as a proportion) of the right lateral keel as it bisected pleural scute 2. Larger RLatK values corresponded to relatively greater distances from the median keel. The condition of bilateral characters was recorded from the right side of the carapace and the left side of the plastron unless damaged.

Tail morphology was the primary characteristic used for sexual identification in this study. Sexual dimorphism of this character is pronounced in both subadults and adults, with males having much longer and thicker tails (Ernst and Barbour 1989; Srinarumol 1995; van Dijk and Thirakhupt, in press). When tail morphology was not available (shell and skeletal material; some dried specimens), information from museum records formed the basis of sexual identification. Assignment of specimens to appropriate life stages (juvenile, subadult, adult) was based primarily on Srinarumol (1995), who distinguished adults from subadults based on the complete development of testes and ovaries, and subadults from juveniles based on tail morphology.

To test for allometric variation, CL was used as the independent variable for regression analyses (least squares method) of other shell characters. Nontransformed data (mm) were utilized for all specimens that had a determinable sex (juveniles, subadults, adults), and males and females were analyzed separately. The slope and intercept of each regression equation were tested for differences from zero using Student *t*-tests. Intercepts that were significantly different from zero ($\alpha = 0.05$) indicated differential growth (i.e., allometry) of the characters involved (Mosimann 1958; Stickel and Bunck 1989).

Sexual dimorphism of shell characters was examined using the regression analyses detailed above. The regression slopes of each bivariate relationship were compared for males and females using analysis of covariance (ANCOVA), with CL as covariate and sex as factor. Significantly different slopes ($\alpha = 0.05$) indicated sexual dimorphism in the characters regressed against CL (Mosimann and Bider 1960; Mouton et al. 2000). In addition, sexual differences in CL were tested using Student *t*-test and expressed by the sexual dimorphism index (SDI) proposed by Gibbons and Lovich (1990) and modified by Lovich and Gibbons (1992). Kolmogorov-Smirnov and *F*-tests were used to verify normality and homogeneity of variances, respectively.

Sexual dimorphism of shell characters was also examined using multivariate techniques. Twenty-eight mensural shell characters were divided by CL, and the resulting ratios comprised most of the data set. RLatK was not divided by CL because it was standardized upon measurement (expressed as a proportion). Using all 29 shell variables, stepwise selection (PROC STEPDISC; SAS, 1989; significance level for entry and removal = 0.30) was used to obtain a set of potential models that would classify turtles relative to their predetermined sex. Final selection of the best model was based on model size and classification accuracy. The best model gave the most accurate cross-validation results (PROC DISCRIM; SAS 1989) and had no more variables than the number of individuals in the smallest sample. This protocol was designed to select conservative models that had a low

number of variables and a high level of classification accuracy. Using the best model as defined above, the probability of correctly classifying each turtle relative to its predetermined sex was calculated using the cross-validation results of linear discriminant function analysis (PROC DISCRIM; SAS, 1989). To minimize the effects of allometric variation, only adult and larger subadult turtles of each sex (males $\geq$ 80 mm CL; females $\geq$ 100 mm CL) were compared.

Results and Discussion. — A frequency distribution of CL (Fig. 1) indicated that females were larger than males. Adult females averaged 148.60 $\pm$ 20.23 (mean $\pm$ 1 SD) mm CL (114.4–187.0 mm; $n = 21$), whereas adult males were considerably smaller and averaged 117.21 $\pm$ 9.55 mm CL (100.3–130.7 mm; $n = 15$). This difference in mean CL was statistically significant ($t = 5.6$, df = 34, $p < 0.0001$). Subadult females and males averaged 94.64 $\pm$ 9.56 (85.3–113.2 mm; $n = 11$) and 85.74 $\pm$ 7.68 mm CL (69.7–95.4 mm; $n = 24$), respectively. Juvenile females and juveniles of indeterminate sex averaged 75.75 $\pm$ 4.63 (68.1–83.4 mm; $n = 18$) and 57.33 $\pm$ 9.33 mm CL (42.7–67.9 mm; $n = 8$), respectively. Juvenile males could not be distinguished because all individuals $<$ 68 mm CL lacked sexual dimorphism of tail morphology.

Srinarumol (1995) reported that adult females and males from his study area averaged 155.48 $\pm$ 27.91 mm CL (116.5–220.0 mm; $n = 25$) and 112.20 $\pm$ 9.83 mm CL (100.8–133.0 mm; $n = 14$), respectively. Srinarumol (1995) also distinguished between subadults and juveniles and found that males could be identified at CL $\geq$ 80 mm and females at CL $\geq$ 86 mm.

Allometric growth of the shell was evident (Table 1). Among males, shell shape changed as CL increased proportionally more than shell width (CW, APLW, PPLW), shell height (SH), plastral length (PL and APLL), several scute widths (Pleu1W, Vert1W, Vert2W, Vert3W, HumW, FemW, and AnW), and a few scute lengths (Vert1L, BL, and AnL). For females, shell shape did not change as much because CL did not increase proportionally more than shell width or shell height but did increase proportionally more than plastral length (PL and PPLL) and a few scute widths (Vert1W, Vert3W, FemW, AnW) and lengths (BrL, AbdL, AnL).

Allometry of shell characters is a widespread phenomenon among turtles. Srinarumol (1995) performed regression analyses similar to those presented here, but he did not test for differential growth of shell characters. The allometric pattern that emerges for *M. macrocephala* is one where males grow proportionally longer than wider or higher, whereas females show proportional growth for most characters. This allometry yields adult males with relatively narrower, flatter shells and adult females with relatively wider and higher shells. It is critical to emphasize the interrelatedness of allometric growth and sexual dimorphism. The differences in allometric growth between male and female *M. macrocephala* produce the sexually dimorphic adults. Such a connection has been

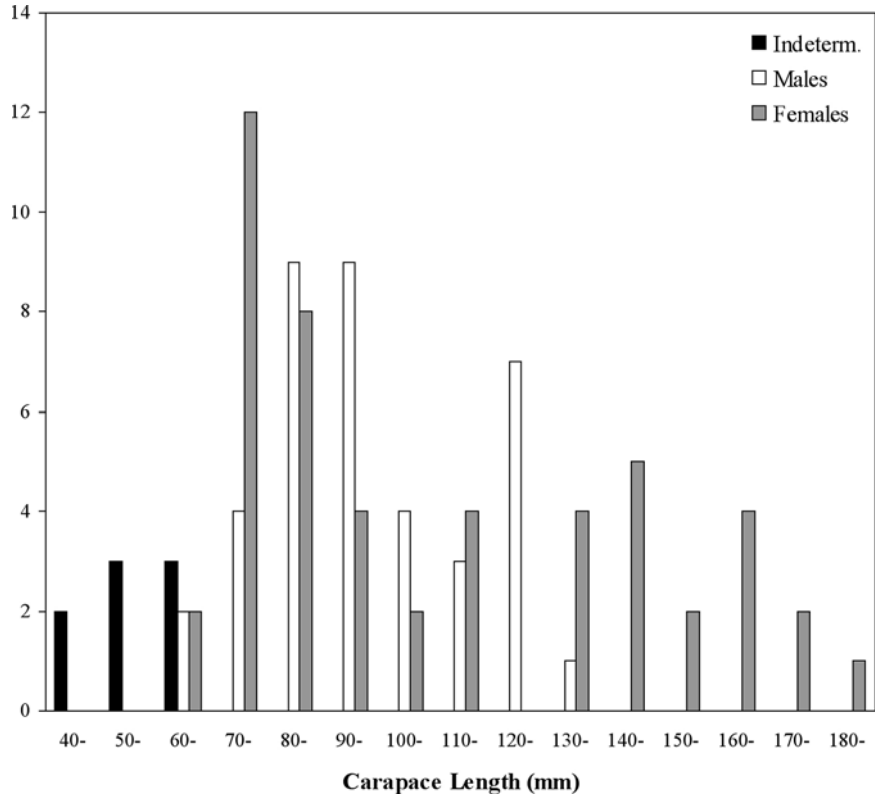

Figure 1. Frequency distribution of carapace length for *Malayemys macrocephala* from the Chao Phraya River Basin of central Thailand.

Table 1. Allometric relationships of shell characters to carapace length for *Malayemys macrocephala* from the Chao Phraya River Basin.

Character	Sex	*n*	Linear relation: y = a + bx (in mm)	R^2	Significance levels (*p*); intercept (a) (H_0: a = 0)
CW	F	48	CW = 2.43 + 0.75CL	0.98	ns
	M	38	CW = 14.77 + 0.58CL	0.94	<0.0001
SH	F	42	SH = 2.04 + 0.41CL	0.97	ns
	M	35	SH = 10.30 + 0.29CL	0.94	<0.0001
PL	F	43	PL = –4.43 + 0.92CL	0.99	0.0005
	M	36	PL = 4.89 + 0.80CL	0.99	0.0358
APLW	F	43	APLW = 0.02 + 0.45CL	0.99	ns
	M	36	APLW = 5.37 + 0.38CL	0.95	0.0015
APLL	F	43	APLL = –0.11 + 0.34CL	0.97	ns
	M	36	APLL = 3.97 + 0.29CL	0.92	0.0304
PPLW	F	43	PPLW = –0.67 + 0.45CL	0.98	ns
	M	36	PPLW = 7.21 + 0.35CL	0.94	0.0006
PPLL	F	43	PPLL = –6.71 + 0.61CL	0.99	<0.0001
	M	36	PPLL = 0.54 + 0.52CL	0.98	ns

[a] All slopes are significantly different from zero ($p < 0.0001$). For significance levels, ns = $p > 0.05$. CW, carapace width; SH, shell height; PL, plastron length; APLW and PPLW, maximum plastral lobe widths; and APLL and PPLL, maximum plastral lobe lengths.

demonstrated by other authors working with a variety of turtle species (Mosimann 1956, 1958; Mosimann and Bider 1960; Stickel and Bunck 1989; Ernst et al. 1998).

Sexual dimorphism of the shell was also evident. ANCOVA indicated that the regression slopes of males and females differed significantly ($p < 0.05$) in 22 of the 28 characters examined (Table 2). Among these, differences in relative shell width, shell height, and plastral length were most significant ($p < 0.0001$). Females had relatively wider carapaces (CW, Vert1W, Vert2W, Vert3W), higher shells (SH), and wider (PPLW, FemW, AnW) and longer (PL, PPLL, BL, AnL) plastra (Fig. 2). Srinarumol (1995), using a similar method, found females to have relatively wider carapaces, longer plastra, and longer midline gular and pectoral lengths. The SDI for *M. macrocephala* from this study was calculated as +0.27. This is comparable to the SDI of +0.39 derived from Srinarumol's (1995) data.

One character of particular interest was anal scute length (AnL). The present data showed that males had relatively shorter AnL than females (Table 2). Van Dijk and Thirakhupt (in press) stated that males are distinguished from females by the shape of their anal notches. Males have deeper, V-shaped notches whereas females have shallower, round ones. A deeper anal notch would correspond to a shorter AnL. The V-shaped anal notch and relatively shorter AnL allow for a longer precloacal distance in males (Mosimann and Bider 1960). This is significant because the precloacal region of the tail accommodates the male's penis (Mosimann and Bider 1960).

Sexual dimorphism of the shell was also demonstrated by multivariate techniques. The best model to classify turtles according to predetermined sex contained 6 of the original 29 shell character ratios. These were AnL/CL, PPLL/CL, RLatK, Vert3W/CL, FemL/CL, and PecL/CL. Mean values for these 6 shell character ratios are presented in Table 3. Using the 6-variable model, cross-validation

Table 2. Comparison of regression slopes (ANCOVA) of shell characters vs. carapace length among male and female *Malayemys macrocephala* from the Chao Phraya River Basin.[a]

	Male vs. female slopes (b) (H_0: $b_{males} = b_{females}$)		
Characters	*F*	df	*p*
CW	26.26	1, 82	<0.0001
SH	24.33	1, 73	<0.0001
Pleu1W	12.38	1, 82	0.0007
Pleu1L	5.61	1, 82	0.0202
Vert1W	21.44	1, 81	<0.0001
Vert1L	5.95	1, 80	0.0169
Vert2W	32.40	1, 78	<0.0001
Vert2L	6.21	1, 79	0.0148
Vert3W	30.40	1, 81	<0.0001
Vert3L	3.58	1, 78	ns
Vert5W	0.19	1, 79	ns
Vert5L	8.02	1, 76	0.0059
PL	22.17	1, 75	<0.0001
APLW	14.16	1, 75	0.0003
APLL	6.87	1, 75	0.0106
PPLW	20.02	1, 75	<0.0001
PPLL	22.94	1, 75	<0.0001
BrL	51.65	1, 74	<0.0001
GulW	0.00	1, 76	ns
GulL	2.40	1, 76	ns
HumW	5.10	1, 76	0.0269
HumL	0.68	1, 76	ns
PecL	5.19	1, 75	0.0255
AbdL	9.65	1, 75	0.0027
FemW	21.56	1, 76	<0.0001
FemL	0.03	1, 76	ns
AnW	18.63	1, 76	<0.0001
AnL	32.57	1, 76	<0.0001

[a] For significance levels, ns = $p > 0.05$. CW, carapace width; SH, shell weight; Pleu1W, maximum pleural scute 1 width; Pleu1L, maximum pleural scute 1 length; Vert1W, Vert2W, Vert3W, and Vert5W, width of vertebral scutes 1, 2, 3, and 5, respectively; PL, plastron length; APLW and PPLW, plastral lobe widths; APLL and PPLL, plastron lobe lengths; BrL, bride length; GulW, HumW, FemW, and AnW, width of gular, humeral, femoral, and anal scutes, respectively; and GulL, HumL, PecL, AbdL, FemL, and AnL, seam length of gular, humeral, pectoral, abdominal, femoral, and anal scutes, respectively.

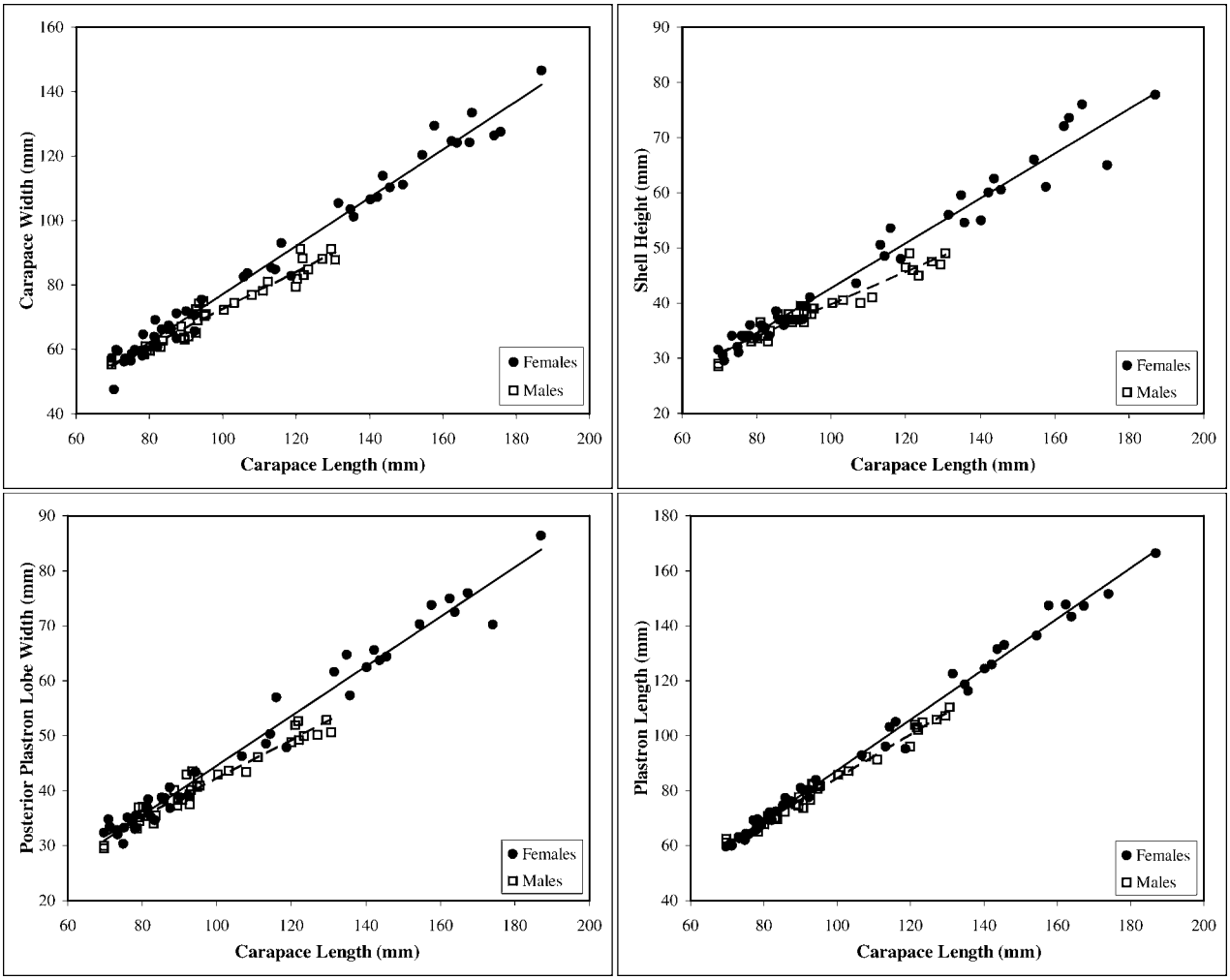

Figure 2. Allometry of carapace width, shell height, posterior plastron lobe width, and plastron length plotted as a function of carapace length and sex for *Malayemys macrocephala* from the Chao Phraya River Basin of central Thailand.

results of linear discriminant function analysis correctly classified 93.1% of males and 89.5% of females (Table 4).

Based on the preceding analyses, a clear pattern of sexual dimorphism emerges for *M. macrocephala*. Females attain larger sizes (Fig. 1) and have relatively wider and higher shells (carapace and plastron) and longer plastra than males (Fig. 2; Tables 2–4).

According to Gibbons and Lovich (1990), sexual size dimorphism (SSD) may be the result of a trade-off between the benefits of early maturity (increased matings leading to increased reproductive output) and the negative environmental consequences of small body size (increased risk of predation, desiccation, and thermal stress). Small body size may be favored in male *M. macrocephala* because the benefits of early maturity outweigh the risks of small body size.

Both Berry and Shine (1980) and Gibbons and Lovich (1990) recognized the importance of fecundity as a factor influencing body size in female turtles. Darwin's "fecundity advantage" hypothesis states that natural selection should favor large body size in females because this would allow them to produce more offspring. For turtles in general, larger female size generally results in more or larger eggs (Gibbons et al. 1982). Such a relationship has also been suggested for *M. macrocephala* specifically (van Dijk and Thirakhupt, in press). Although fecundity selection could induce an increase in overall female size, it should primarily act on the relative size of the abdominal cavity (Mouton et al. 2000). This helps to explain the many relatively wider, higher, and longer shell characters exhibited by female *M. macrocephala*.

Some authors (review in Gibbons and Lovich 1990) have suggested that SSD is a result of ecological forces or natural selection. The most frequently cited ecological cause is probably competitive displacement (Brown and Wilson 1956; Dunham et al. 1979). In this model, the sexes evolve to exploit different resources in the environment, thereby reducing competition between them. Large females of *M. macrocephala* consume freshwater mussels, whereas males and other small individuals feed almost exclusively on aquatic snails (Srinarumol 1995; van Dijk and Thirakhupt, in press). The weakness of the displace-

Table 3. Shell character ratios—mean ± 1 SE, (range), and [*n*]—used in discriminant function analysis to classify male and female *Malayemys macrocephala* from the Chao Phraya River Basin.

Character	Females	Males
AnL/CL	0.14 ± 0.002 (0.12–0.16) [19]	0.12 ± 0.002 (0.08–0.13) [30]
PPLL/CL	0.56 ± 0.006 (0.49–0.60) [19]	0.52 ± 0.003 (0.50–0.55) [30]
RLatK	0.22 ± 0.007 (0.13–0.25) [23]	0.24 ± 0.003 (0.20–0.25) [32]
Vert3W/CL	0.22 ± 0.003 (0.19–0.24) [23]	0.20 ± 0.002 (0.17–0.23) [31]
FemL/CL	0.14 ± 0.003 (0.12–0.17) [19]	0.15 ± 0.003 (0.12–0.18) [30]
PecL/CL	0.12 ± 0.003 (0.09–0.15) [19]	0.10 ± 0.003 (0.07–0.16) [30]

[a] AnL, anal scute length; CL, carapace length; PPLL; plastral lobe length; RLatK, right lateral keel (as it bisects pleural scute 2); Vert3W, width of vertebral scute 3; FemL, seam length of femoral scute; and PecL, seam length of pectoral scute.

ment model in explaining this situation is that it cannot predict which sex should be larger (Gibbons and Lovich 1990). Rather than ecological factors being the cause of SSD in *M. macrocephala*, it may be that ecological differences between the sexes are simply consequences of sexually selected dimorphism (Shine 1986).

Malayemys macrocephala has SDI values ranging from +0.27 to +0.39 (Srinarumol 1995 and current study). SDI values for turtles range from −0.45 to +1.75 (Gibbons and Lovich 1990). When compared to other species that have females as the larger sex (mean SDI = +0.36; median SDI = +0.23), *M. macrocephala* displays average SDI values (Gibbons and Lovich 1990). In summary, the SSD pattern exhibited by *M. macrocephala* may be the result of a combination of selective pressures. Selection for increased fecundity may produce larger females (Berry and Shine 1980; Gibbons and Lovich 1990), whereas selection for early maturity may result in smaller males (Gibbons and Lovich 1990).

Table 4. Cross-validation results for male and female *Malayemys macrocephala* from the Chao Phraya River Basin based on linear discriminant function analysis of shell character ratios (percentages in parentheses).

	Group classification		
Actual group	Males	Females	Total
Males	27 (93.1)	2 (6.9)	29
Females	2 (10.5)	17 (89.5)	19
Total	29	19	48

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Reproductive Trends in Captive *Heosemys grandis* (Geoemydidae)

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ABSTRACT. – A 20-year record of captive breeding of a female *Heosemys grandis* revealed a tradeoff between egg size and clutch size across the years when she produced 2 clutches per breeding season. First clutches had few large eggs and second clutches had a large number of smaller eggs. Four F1 progeny from this founder female began their reproductive years with much smaller eggs; however, their eggs increased in size over successive years until they were the same size as those of the long-term breeder.

Variation in egg size can be viewed as an adaptive form of bet-hedging (Kaplan and Cooper 1984). In this context, variation in egg size from a given female may be predictable within a short term, such as a year, but is at random in the long term. For instance, the growth of ovarian follicles to become eggs may occur during weather that is good or bad for ovarian growth, but the resultant hatchlings may face unrelated bad or good conditions for their type (e.g., large or small) because the weather has changed (Kaplan and Cooper 1984). Greater attention regarding turtles has focused on an energetic or space-limited reproductive tradeoff between egg size and clutch size (Elgar and Heaphy 1989). In natural populations, demonstration of a significant inverse correlation nearly always has required a statistical adjustment for female body size (Rowe 1994; Tucker et al. 1998), and even then, that correlation has not always been supported (Nieuwolt-Decanay 1997; Clark et al. 2001). Further, the statistical adjustment may confound interactions between female body size, age-related changes in the female reproductive system (Congdon et al. 2003), and a reversible, perhaps random tradeoff within fully mature females. Only one study has documented a significant egg size-clutch size tradeoff without adjustment for female body size and this tradeoff represented just one seasonal sample among three seasons (Roosenburg and Dunham 1997).

The world population of the Asian turtle *Heosemys grandis* (greater orange-headed earth turtle) is being