Sexual Dimorphism in Body Size and Shape of Beal's Eyed Turtle (*Sacalia bealei*)

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Abstract. – We studied the sexual dimorphism in body size and shape of Beal's eyed turtle, *Sacalia bealei*, by measuring 15 morphological characteristics of 68 adult individuals (40 females, 28 males) collected from Fujian Province, China. Females were slightly larger than males in carapace length with a sexual dimorphism index of 0.09. This translated into greater absolute values of females for all the traits we measured except for tail length, preanal tail length, and analia to supracaudal junction length. Comparisons between the sexes of size-corrected morphological traits indicated that females exhibited a longer plastron and higher carapace relative to carapace length, thereby providing a larger internal volume. Females also exhibited relatively wider heads. In males, the plastron was smaller and more indented than in females and the openings between the plastron and the carapace were also more developed. Overall, females were larger in size and displayed a more voluminous shell than did males while males had longer tails and larger spaces available to move the legs, head, and tail.

Key Words. – adaptive evolution; Fujian Province; morphological characteristics

Sexual dimorphism of size or shape is widespread in animals and has attracted considerable interest from biologists (Kolata 1977; Hedrick and Temeles 1989; Bonnet et al. 2010). It is assumed that sexual dimorphism results from the interactions between natural selection and sexual selection: natural selection favors morphological traits that maximize survival and juvenile growth rates while sexual selection influences morphological characteristics in ways that directly increase reproductive success (Lande and Arnold 1985; Shine 1990; Rivera 2008). Sexual selection and natural selection can interact in opposition or in synergy, depending upon various factors (Hedrick and Temeles 1989; Shine 1989, 1990; Arnold 1994; Djordjevic et al. 2011). Examining the size and shape of traits together provides a much-more complete quantification of sexual dimorphism, as the 2 components are inherently related to one another (Travis 1994; Willemsen and Hailey 2003; Mann et al. 2006; Kuo et al. 2009; Bonnet et al. 2010).

Turtles are an excellent group in which to test the selective forces of sexual dimorphism. First, they exhibit a diversity of ecologies (strictly terrestrial to highly aquatic), mating strategies (female choice, combat, and/or forced insemination), and types of sexual dimorphism (males larger than females to females larger than males). Second, the absence of parental care in turtles could minimize the overlap between the male and female roles and favor multiple mating systems (Bonnet et al. 2001). Third, their body shape can be assessed via measurements of the shell geometry because feeding and reproductive statuses do not modify shell dimensions (Bonnet et al. 2010). Therefore, extensive and profound research on turtle sexual dimorphism has been conducted worldwide, ranging in scope from one focal species (Gibbons and Lovich 1990; Bonnet et al. 2001) to multiple species (Willemsen and Hailey 2003; Kaddour et al. 2008; Barros et al. 2012) or different geographical populations (Iverson 1985; Stillwell et al. 2007; Lovich et al. 2010; Lefebvre et al. 2011).

Beal's eyed turtle *Sacalia bealei* is endemic to China and has been listed as a Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES 2017) Appendix II species. However, data on sexual dimorphism in size and shape of *S. bealei* are lacking except for a few studies with limited data on size measurements (Chen 1991; Zhang et al. 1998), and no quantitative analysis has been done. We studied the sexual dimorphism of *S. bealei* by analyzing various morphological characteristics and used these analyses to provide plausible explanations for the adaptive evolution of sexual dimorphism in *S. bealei*.

METHODS

Study Species. — *Sacalia bealei* is a small aquatic turtle species inhabiting mountainous streams of southern China including in Fujian, Guangdong, Hunan, and Jiangxi provinces and in Hongkong. Adult *S. bealei* exhibit obvious sexual dimorphism in coloration (Zhang et

al. 1998; Shi 2013). Both sexes have two pairs of different-colored ocelli on the head, with the posterior pair being brown in males and yellow in females. Male adult *S. bealei* exhibit numerous tiny black dots on the head, bright-red stripes on the neck, and plentiful small black spots on the peripheral area of the plastron. In contrast, female adults have fewer black dots on the head, faint yellow stripes on the neck, and fewer and larger black patches on the plastron (Shi 2013).

Sampling. — Sixty-eight adult individuals (40 females, 28 males) were collected at Fujian Province of China and measured in this study. Nineteen turtles were caught at Huboliao National Nature Reserve. Turtles were marked on their marginal scutes, fixed with a radio transmitter after measurements, and released to the wild. The other turtles came from local turtle households; most of them came from the wild and had been kept less than 2 yrs. We identified adult females by size, as the smallest females with eggs were 117–120 mm in carapace length (*n* = 3), and we only selected those females larger than 120 mm in this study. We identified adult males by their bright-red neck stripes.

Measurements. — The size and shape of the main morphologic characteristics of each individual were recorded as follows. Carapace length (CL): maximal anteroposterior carapace length; carapace width (CW): maximal width at the level of the eighth marginal scutes; curved carapace length (CCL): the curvilinear dorsal length of the carapace from the anterior tip of the shell to the end of the anal scute; curved carapace width (CCW): taken from the same point as for CW but following the curvature of the carapace; carapace height (CH): maximal height of the shell; plastron length (PL): the maximal anteroposterior length of the plastron; midline plastron length (MPL): the minimal midline length of the plastron; plastron width (PW): the maximal width of the 4th intermediate plastral scutes; anal notch width (ANW): the width between the tips of the 2 anal scutes; analia to supracaudal junction (ASJ): length between the rear parts of the plastron and the supracaudal scute; bridge length (BL): minimum length of the bridge; tail length (TL): tail length along its ventral edge, from the base of the external portion of the tail to the tip; preanal tail length (PTL): length from the midline anal notch of the plastron to the anterior border of the cloaca; and head length (HL) and width (HW): the maximal external cranial length (from the base of the skull to the tip of the snout) and the widest part of the head, respectively. Comprehensive measurements were not recorded on all individuals to avoid injury owing to the difficulty of taking some measurements (e.g., measuring the head).

Analyses. — We used the sexual dimorphism index (SDI) to estimate sexual size dimorphism (SSD; Lovich and Gibbons 1992), where SDI = [(mean size of the larger sex/ mean size of the smaller sex) − 1]. This index has the best statistical properties of all dimorphism indices that have been proposed (Smith 1999; Stillwell et al. 2007).

Comparisons of the body size and shape variables between the sexes were performed by using analyses of variance (ANOVA) or covariance (ANCOVAs), with CL as the covariate, depending on whether the variables were significantly correlated with CL. Although we had unequal sample sizes of males and females due to sample acquisition difficulty, the single factor ANOVA or ANCOVA includes an assumption of variance homogeneity across groups regardless of sample size. In our study, all variables showed normal distribution (Kolmogorov-Smirov Test) and variance homogeneity (Levene Test). ANW was compared by calculating the regression residuals as adjusted values because of the interactive effect between sex and CL. Previous studies have found that the relative width of the head was better characterized relative to head length and, similarly, the relative depth of the notches in the plastron was better characterized relative to plastron length (Kaddour et al. 2008). Thus, we performed another ANCOVA analysis for HW with HL as the covariate and for MPL, with PL as the covariate. We performed all statistical analyses using SPSS (v19.0, SPSS Inc., Chicago, IL) and determined statistical significance at the level of *p* = 0.05.

RESULTS

In this study, the SDI for CL was (139.4/127.8) − 1 = 0.09, indicating that females were slightly larger than males. The comparisons between the sexes of the size-corrected morphological traits (body proportions or body shape) are summarized in Table 1. On average, females attained larger maximal and mean sizes than did males. This translated into greater absolute values for all the traits we measured except for PTL (more distally located cloaca in males), ASJ (more space available to move the tail in males), and TL (longer tail in males).

Females displayed a more voluminous shell than did males. Notably, they exhibited a longer plastron (PL, MPL) and higher carapace (CH, CCW) relative to CL, thereby providing a larger internal volume. Females also exhibited a relatively wider head (HW relative to CL; HW relative to HL). In males, the openings between the plastron and the carapace (BL and ASJ) were more developed. Overall, the spaces available to move the legs, the head, and the tail were relatively larger in males.

DISCUSSION

Turtle species vary greatly in the degree of SDI, with the larger sex ranging from 1% to 158% larger than the smaller sex (Ernst et al. 1994). Our results showed, when compared with other species that have females as the larger sex, that *S. bealei* displayed relatively small SDI values (0.09 compared with mean SDI = 0.36; median SDI = 0.23; Gibbons and Lovich 1990).

Female-biased SSD is thought to be driven by both sexual selection and natural selection. According to the sexual selection hypothesis, SSD would contribute to

Table 1. Sexual dimorphism of body size and shape in adult *S. bealei* from Fujian Province of China. Results for CL and PTL are means, and statistics are from ANOVA by sex, while other variables are adjusted means and statistics are from ANCOVA by sex with CL, PL, or HL used as a covariate (see text).[a]

Variable	Covariate	*n*	Females Mean ± SE (mm) Original	Females Mean ± SE (mm) Adjusted	*n*	Males Mean ± SE (mm) Original	Males Mean ± SE (mm) Adjusted	Results
CL		40	139.36 ± 2.04		28	127.82 ± 1.58		$F_{1,66} = 17.229, p < 0.001*$
PTL		40	7.45 ± 0.49		28	14.79 ± 0.79		$F_{1,66} = 68.942, p < 0.001*$
CCL	CL	40	153.83 ± 2.32	148.58 ± 0.45	28	140.20 ± 1.74	147.69 ± 0.55	$F_{1,65} = 1.390, p = 0.243$
CW	CL	40	95.92 ± 1.43	92.87 ± 0.488	28	88.67 ± 1.04	93.02 ± 0.60	$F_{1,65} = 0.036, p = 0.851$
CCW	CL	40	152.92 ± 2.17	148.15 ± 0.83	28	138.43 ± 1.82	144.93 ± 1.21	$F_{1,65} = 4.865, p = 0.031*$
CH	CL	40	51.67 ± 0.90	50.28 ± 0.61	28	45.95 ± 0.67	47.94 ± 0.74	$F_{1,65} = 5.372, p = 0.024*$
PL	CL	40	124.65 ± 1.81	120.61 ± 0.54	28	111.81 ± 1.49	117.58 ± 0.66	$F_{1,65} = 11.334, p = 0.001*$
MPL	CL	40	120.49 ± 1.73	116.67 ± 0.51	28	107.06 ± 1.36	112.51 ± 0.62	$F_{1,65} = 23.922, p < 0.001*$
MPL	PL	40	120.49 ± 1.73	115.5 ± 0.32	28	107.06 ± 1.36	113.62 ± 0.48	$F_{1,65} = 10.548, p = 0.002*$
PW	CL	40	80.56 ± 1.23	78.03 ± 0.52	28	73.19 ± 0.94	76.81 ± 0.64	$F_{1,65} = 1.996, p = 0.163$
BL	CL	40	45.18 ± 0.77	43.57 ± 0.29	28	38.80 ± 0.57	41.10 ± 0.36	$F_{1,65} = 25.703, p < 0.001*$
ASJ	CL	40	21.03 ± 0.57	20.16 ± 0.44	28	22.02 ± 0.55	23.27 ± 0.54	$F_{1,65} = 18.097, p < 0.001*$
ANW	CL	40	23.21 ± 0.52	−0.07 ± 0.26	28	21.09 ± 0.36	0.10 ± 0.31	$F_{1,65} = 0.185, p = 0.669$
TL	CL	36	50.35 ± 1.19	48.96 ± 1.01	28	51.66 ± 0.96	53.44 ± 1.16	$F_{1,61} = 7.529, p = 0.008*$
HL	CL	17	29.84 ± 0.55	29.00 ± 0.48	19	28.98 ± 0.49	29.73 ± 0.45	$F_{1,33} = 1.068, p = 0.309$
HW	CL	17	22.55 ± 0.34	21.94 ± 0.28	19	20.29 ± 0.32	20.83 ± 0.26	$F_{1,33} = 7.584, p = 0.010*$
HW	HL	17	22.55 ± 0.34	22.36 ± 0.26	19	20.29 ± 0.32	20.45 ± 0.25	$F_{1,33} = 27.291, p < 0.001*$

[a] CL = carapace length; PTL = preanal tail length; CCL = curved carapace length; CW = carapace width; CCW = curved carapace width; CH = carapace height; PL = plastron length; MPL = midline plastron length; PW = plastron width; BL = bridge length; ASJ = analia to supracaudal junction; ANW = anal notch width; TL = tail length; HL = head length; HW = head width; * = statistical significance (significance values correspond to adjusted means where applicable).

copulation success (Lande and Arnold 1985; Hedrick and Temeles 1989). Males are usually larger than females in species with male combat and/or forced insemination and are smaller than females when these behaviors are absent (Berry and Shine 1980; Mann et al. 2006). For species in the latter category, males often show elaborate precoital displays and highly developed nuptial structures (Stephens and Wiens 2009). In addition, SSD correlates with habitat types, which could affect male mating strategy. In truly aquatic species, males utilize elaborate precoital displays instead of combat or forcible insemination and are usually smaller than females (Berry and Shine 1980). Also in aquatic species, larger females could be more aggressive, making forced insemination an unreliable strategy (Plummer 1977; Berry and Shine 1980). The results of our morphological analysis are consistent with the hypothesis for truly aquatic species in that males of *S. bealei* are smaller than females. In addition, females are more aggressive during intrasexual or intersexual competition while males have much brighter coloration on their neck and limbs in order to attract females and utilize precoital displays during mating season (L. Lin, *pers. obs.*). Head width is greater in female than in male *S. bealei*. Greater head size in female turtles may function to increase the size range of food items, perhaps in response to calcium depletion after oviposition (Bonnet et al. 2001; Trembath and Freier 2004).

According to the hypothesis of natural selection for fecundity, larger females have increased reproductive potential, either through greater allocation to individual offspring (i.e., larger eggs), greater numbers of offspring

(i.e., more eggs), or the ability to reproduce more frequently (i.e., more clutches per year; Ernst et al. 1998; Zuffi et al. 1999; Djordjevic et al. 2011). Therefore, females in many turtle species have wider and higher shells than do males (Rowe 1997; Brophy 2006; Munoz and Nicolau 2006; Kaddour et al. 2008; Xiao et al. 2014). In *S. bealei*, females can reproduce only one time every year and lay 2.1 ± 0.8 eggs each time (*n* = 15; L. Lin, *pers. obs.*). Female *S. bealei*, compared with males, have higher shells and larger plastrons. Both of these characteristics could increase the intra-abdominal volume to hold larger or more eggs (egg length: 47.02 ± 3.96 mm, width: 23.09 ± 1.73 mm, *n* = 23; L. Lin, *pers. obs.*), which could increase the competitiveness and survival rate of offspring. Males are probably favored if they increase or maximize their searching efforts during courtship, copulation, and male–male combat (Travis 1994; Kaddour et al. 2008; Djordjevic et al. 2011). In the present study, the smaller plastron, shorter bridge, and longer ASJ of male *S. bealei* results in an increase in the size of openings in the shell. The size of the openings in the shell can limit the movements of the head, tail, and limbs (Bonnet et al. 2001); therefore, larger openings in the shells of males could thus enhance their mobility for moving and copulating with females (Kaddour et al. 2008). In turtles, the precloacal region of the tail accommodates the males' penis (Mosimann and Bider 1960); therefore, having a more posterior vent on the tail combined with greater space to move the tail could contribute to greater copulation success (Bonnet et al. 2001). Overall, the sexual shape dimorphism (SShD) of *S. bealei* could increase the fecundity of females and facilitate

the mobility of searching and copulation for males, respectively.

Sexual dimorphism in size and shape of *S. bealei* is less noticeable than that of its coloration, especially the ocelli on head. Various morphological measurements and statistical analyses should be conducted to verify the sexual dimorphism of turtles (Lovich and Gibbons 1992; Smith 1999). Furthermore, a dramatic decrease of wild populations makes sample collection difficult for most Chinese turtles. Only 2 other turtle species, the four-eyed spotted turtle *Sacalia quadriocellata* and the Chinese strip-necked turtle *Mauremys sinensis* have been studied for their sexual dimorphism in China (Chen and Lue 1998; Xiao et al. 2014). Decline in the wild is the likely reason SSD in *S. bealei* has not been described previously. Nevertheless, the knowledge of SSD and SShD is important for a better understanding of the adaptive evolution and mating strategy of this species.

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