

# 四眼斑水龟个体大小和体形的两性异形

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**摘要:** 研究龟鳖的两性异形对理解形态适应具有重要意义。通过测量 41 只(21 ♀, 20 ♂)成体四眼斑水龟(*Sacalia quadriocellata*)的 20 个形态特征指标, 研究四眼斑水龟个体大小和体形的两性异形。结果表明: 除头长、头宽、尾长和尾长肛前段长外, 四眼斑水龟其他的形态特征均与背甲长呈正相关。雌性的背甲长、腹甲长、腹甲中线长、腹甲曲线长显著大于雄性; 雄性的头长、头宽、后肢长、尾长和尾长肛前段长显著大于雌性; 雌雄两性的体重、体周长、前肢长、腹甲宽、肛盾切口长、肛盾切口宽以及除背甲长外的所有背甲形态特征指标均无显著差异。研究结果表明, 四眼斑水龟存在个体大小和体形两性异形。

**关键词:** 四眼斑水龟; 两性异形; 性选择; 生育力选择

**中图分类号:** Q958 **文献标识码:** A **文章编号:** 0250-3263(2014)04-528-08

## Sexual Dimorphism in Body Size and Shape in the Four-eyed Spotted Turtle *Sacalia quadriocellata*

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**Abstract:** Study on sexual dimorphism can be crucial to understanding the morphological adaptation of turtles. In this study, 20 morphological traits were measured from 41 (21 ♀, 20 ♂) adult four-eyed spotted turtles (*Sacalia quadriocellata*) which collected from Qiongzong, Hainan for investigating sexual dimorphism in body size and shape. The results showed that the carapace length was larger in females ( $t = 2.26$ ,  $df = 39$ ,  $P = 0.029$ ), and the regression analysis indicated that all of the 20 morphological traits were positively related to carapace length, except for the head length, head width, tail length and preanal tail length. The result of ANCOVA analysis indicated that the plastron length was larger in females ( $F_{1,38} = 16.82$ ,  $P < 0.001$ ) whilst the hindlimb length was larger in males ( $F_{1,38} = 13.20$ ,  $P = 0.001$ ). In the contrary, the plastron width, forelimb length, body mass, total longitudinal circumference, analia to supracaudal junction and 5 carapace morphological traits did not differ between the sexes. The  $t$ -test of regression residual value showed that midline plastron length and curvilinear plastron length were larger in females ( $t = 3.85$ ,  $df = 39$ ,  $P < 0.001$  and  $t = 2.62$ ,  $df = 39$ ,  $P = 0.012$ , respectively), but the anal notch width did not differ between the sexes. The  $t$ -test indicated that head length ( $t = -4.34$ ,  $df = 28$ ,  $P < 0.001$ ), head width ( $t = -2.09$ ,  $df = 28$ ,  $P = 0.046$ ), tail length ( $t = -3.02$ ,  $df = 32$ ,  $P = 0.005$ ) and preanal tail length ( $t = -4.35$ ,  $df = 39$ ,  $P < 0.001$ ) were

**基金项目** 国家自然科学基金项目(No. 31372228);

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**收稿日期:** 2013-11-13, **修回日期:** 2014-03-14

larger in males. These results illustrated that sexual dimorphism in body size and shape did exist in *S. quadriocellata*.

**Key words:** *Sacalia quadriocellata*; Sexual dimorphism; Sexual selection; Fecundity selection

两性异形普遍存在于动物界,主要体现在个体大小、形态和体色上的两性差异(Shine 1979, Bonnet et al. 1998, 何南等 2011)。两性异形产生的机制主要有性选择压力、生育力选择压力和生态位分离假说(Shine 1989, Olsson et al. 2002, 廖灏泓等 2013)。性选择压力假说认为,较大的雄性个体在性内竞争或雌性选择中能够增加交配成功率,有利于进化出雄性偏大的两性异形模式(Shine 1979, Cox et al. 2003);而小个体雄性成熟早且活动灵活,可能具有较高的繁殖成功率而被进化所选择,从而导致雌性偏大的两性异形模式形成(St Clair 1998)。同时,雌性偏大的两性异形模式进化也可能是生育力选择的结果,因为雌性向较大个体发展有利于其增加生育力和繁殖输出(Olsson et al. 2002, Kupfer 2009, Luo et al. 2012)。与以上两个与繁殖相关的假说不同,生态位分离假说认为两性异形是两性个体通过形态上的差异适应不同的生态位所导致的(Slatkin 1984, Shine 1989)。两性异形的进化主要受性选择压力和非性选择压力中的某一因素影响,也可能受多种因素综合作用(张永普等 2004, Li et al. 2006, Du et al. 2011)。

爬行动物的两性异形研究主要涉及蜥蜴类(杜卫国等 2007, Qu et al. 2011, 罗来高等 2012)、蛇类(Ji et al. 1997, Tomović et al. 2002, Vincent et al. 2004)和龟鳖类(Iverson 1985, Willemsen et al. 2003, Lefebver et al. 2011)。龟鳖类无统一的两性异形模式,尽管陆龟科的多数物种雄性个体偏大,但有些物种则是雌性个体偏大,同时龟鳖类的两性异形差异程度普遍比蜥蜴类和蛇类大(Cox et al. 2007, Gosnell et al. 2009)。龟鳖类两性异形研究不仅范围广,涉及陆生、半水生和水生的多数种类(Berry et al. 1980),而且研究较为深入,从研究同一物种个体大小和体形的两性差

异(Gibbons et al. 1990, Bonnet et al. 2001),到比较不同物种间(Ben Kaddour et al. 2008, Barros et al. 2012)或同一物种不同地理种群间(Lovich et al. 2010, Djordjević et al. 2013)的变异,对龟鳖类两性异形产生和变异的原因进行了深入探讨。然而,目前国内龟鳖类的两性异形研究仅见个别报道(杜卫国等 2007)。

四眼斑水龟(*Sacalia quadriocellata*)隶属淡水龟科(Geoemydidae),在中国主要分布于广东、广西、江西、福建和海南省(张孟闻等 1998, 史海涛等 2011)。四眼斑水龟的体色存在明显的两性差异,雌性成体头背后侧 2 对眼斑为黄色,雄性为青色(史海涛等 2011),但目前尚无个体大小和体形的两性异形报道。本文比较了四眼斑水龟形态特征的两性差异,旨在揭示四眼斑水龟个体大小和体形的两性异形,为四眼斑水龟的形态适应研究提供依据。

## 1 材料与方法

研究用 41 只四眼斑水龟成体(21 ♀, 20 ♂)采自海南琼中湾岭,现饲养于海南师范大学动物行为实验室。2012 年 11 月,在实验室用电子天平(优越 DW,精确到 1 g)称体重(body mass, BM),用游标卡尺(TRICLE BRAND, 中国上海;精确到 0.02 mm)和软尺(精确到 1 mm)测量 20 个形态指标。背甲长(carapace length, CL)为颈盾前缘至臀盾后缘间距,背甲宽(carapace width, CW)为第 8 对缘盾处的背甲宽度,背甲中部宽(mid-body carapace width, MCW)为第 6 对缘盾处的背甲宽度,背甲高(carapace height, CH)为背腹甲之间的最大高度,背甲曲线长(curvilinear carapace length, CCL)为颈盾前缘至臀盾后缘之间的曲线长,背甲曲线宽(curvilinear carapace width, CCW)为第 6 对缘盾处背腹甲接缝之间的曲线长,腹甲长(plastron length,

PL)为喉盾前缘至肛盾后缘的间距,腹甲宽(plastron width, PW)为腹甲左右缘间的最大直线距离,腹甲中线长(midline plastron length, MPL)为喉盾切口沿腹甲中线至肛盾切口处的长度,腹甲曲线长(curvilinear plastron length, CPL)为喉盾切口沿腹甲中线至肛盾切口处的曲线长,体周长(total longitudinal circumference, TLC)为背腹甲纵向周长,肛盾切口长(analia to supracaudal junction, ASJ)为肛盾切口处至臀盾尖端间距,肛盾切口宽(anal notch width, ANW)为两肛盾尖端间距

(图 1, Bonnet et al. 2001, Djordjević et al. 2011),头长(head length, HL)为吻端至上下颌关节后缘间距,头宽(head width, HW)为左右颌关节间距,前肢长(forelimb length, FLL)为肘至掌间距,后肢长(hindlimb length, HLL)为胫部两端间距,尾长(tail length, TL)为尾基部(肛盾切口处)至末端间距,尾长肛前段长(preanal tail length, PTL)为尾基部(肛盾切口处)至泄殖腔前缘间距(图 1, Muñoz et al. 2006)。

所有数据的统计分析用 SPSS 16.0 软件包

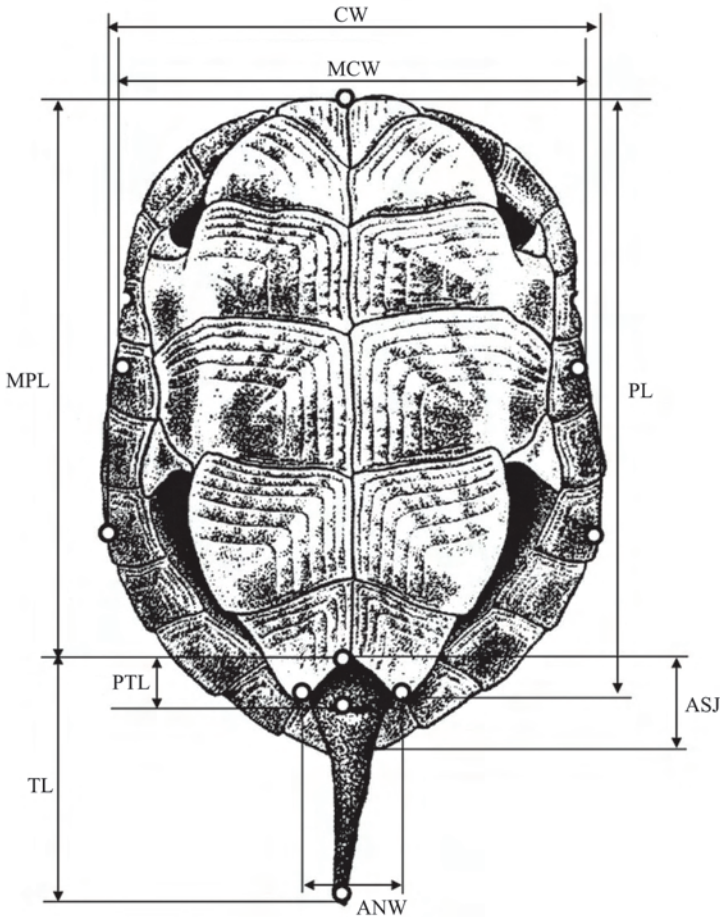


图 1 龟腹面观及部分测量值(改编自 Muñoz et al. 2006)

Fig. 1 Ventral view and measurements of turtle (modified from Muñoz et al. 2006)

CW. 背甲宽; MCW. 背甲中部宽; MPL. 腹甲中线长; PL. 腹甲长; ASJ. 肛盾切口长; ANW. 肛盾切口宽; TL. 尾长; PTL. 尾长肛前段长。

CW. Carapace width; MCW. Mid-body carapace width; MPL. Midline plastron length; PL. Plastron length; ASJ. Analia to supracaudal junction; ANW. Anal notch width; TL. Tail length; PTL. Preanal tail length.

完成。数据在作进一步统计检验前验证其正态性(Kolmogorov-Smirnov 检验)和方差同质性(Levene 检验)。用  $t$  检验检测雌雄背甲长的差异。用线性回归分析各形态特征与背甲长的关系,对与背甲长不相关的变量,用  $t$  检验比较雌雄的差异;对与背甲长相关的变量检验其斜率的同质性。对斜率同质的变量,以背甲长为协变量,应用协方差分析(ANCOVA)比较雌雄的差异;对斜率不同质的变量,计算各变量与背甲长的回归剩余值作为个体形态特征的矫正值,用  $t$  检验比较雌雄的差异。数据以平均值  $\pm$  标准误(Mean  $\pm$  SE)表示,显著性水平设置为  $\alpha = 0.05$ 。

## 2 结 果

四眼斑水龟雌性成体背甲长显著大于雄性成体(表1)。除头长、头宽、尾长和尾长肛前段长外,其他15个形态特征值均与背甲长呈显著的线性关系(背甲宽:  $r^2 = 0.64$ ,  $F_{1,39} = 70.11$ ; 背甲中部宽:  $r^2 = 0.63$ ,  $F_{1,39} = 67.62$ ; 背甲高:  $r^2 = 0.36$ ,  $F_{1,39} = 21.69$ ; 背甲曲线长:  $r^2 = 0.86$ ,  $F_{1,39} = 233.29$ ; 背甲曲线宽:  $r^2 = 0.59$ ,  $F_{1,39} = 56.18$ ; 腹甲长:  $r^2 = 0.85$ ,  $F_{1,39} = 221.57$ ; 腹甲中线长:  $r^2 = 0.80$ ,  $F_{1,39} = 158.19$ ; 腹甲宽:  $r^2 = 0.39$ ,  $F_{1,39} = 24.48$ ; 腹甲曲线长:  $r^2 = 0.81$ ,  $F_{1,39} = 171.24$ ; 体周长:  $r^2 = 0.90$ ,  $F_{1,39} = 365.57$ ; 肛盾切口长:  $r^2 = 0.21$ ,  $F_{1,39} = 10.21$ ,  $P < 0.003$ ; 肛盾切口宽:  $r^2 = 0.31$ ,  $F_{1,39} = 17.79$ ; 前肢长  $r^2 = 0.29$ ,  $F_{1,39} = 15.98$ ; 后肢长:  $r^2 = 0.14$ ,  $F_{1,39} = 6.09$ ,  $P < 0.018$ ; 体重:  $r^2 = 0.73$ ,  $F_{1,39} = 105.86$ 。除肛盾切口长和后肢长外,所有变量的  $P < 0.0001$ )。以背甲长为协变量的协方差分析结果表明,雌性腹甲长显著大于雄性,腹甲宽和肛盾切口长无两性差异;雄性的后肢长显著大于雌性,前肢长雌雄差异不显著;除背甲长外的所有背甲形态特征、体周长和体重均无两性差异(表1)。雌雄成体的腹甲中线长、腹甲曲线长和肛盾切口宽与背甲长的线性回归剩余值

进行  $t$  检验表明,雌性腹甲中线长、腹甲曲线长显著大于雄性,肛盾切口宽不存在两性差异(表1)。头长、头宽、尾长和尾长肛前段长的  $t$  检验结果表明,雄性头部显著大于雌性,雄性的尾长和尾长肛前段长显著大于雌性(表1)。

## 3 讨 论

**3.1 个体大小的两性异形** 本研究表明,四眼斑水龟的个体大小和体形均存在显著的两性异形。龟鳖类成体个体大小有3种类型:1)成体雄性大于成体雌性,如大多数陆生种类(Moskovits 1988)、半水生种类(Lovich et al. 1998)和水底活动的种类(Iverson 1985);2)成体雌性大于成体雄性,如中华花龟(*Mauremys sinensis*) (Chen et al. 1998)、乌龟(*Mauremys reevesii*) (杜卫国等 2007)和红耳龟(*Trachemys scripta*) (Gibbons et al. 1990)等水生种类;3)两性成体个体大小无显著差异,如巨头麝香龟(*Sternotherus minor*) (Tinkle 1961)、头盔泥龟(*Kinosternon subrubrum*) (Mahmoud 1967)和黄斑水龟(*Clemmys guttata*) (Litzgus et al. 1998)。四眼斑水龟个体大小的两性异形属于第2种类型。雌性偏大两性异形模式形成的原因可用生殖力选择压力(Cox et al. 2003)或小个体雄性优势假说(Blanckenhorn 2001, 2005)解释。Berry等(1980)在龟鳖类两性异形的研究中提出,由于小个体雄性具有较强的活动能力,在配偶搜索中会更具优势,获得更多的交配机会,因此性选择更青睐小个体雄性,使雄性向小体形的方向进化,从而产生雌性偏大的两性异形模式。四眼斑水龟年产单窝卵,且窝卵数仅为1~3枚(史海涛等 2002, 2011),生育力选择驱使雌性向较大个体进化的压力不大,其雌性偏大的两性异形可能是性选择驱使雄性向小个体的方向进化的结果。

**3.2 头部的两性异形** 成体雄性四眼斑水龟头部长显著大于雌性,这与头部在雄雄斗争和求偶炫耀中的作用有关。龟类在雄雄斗争中通常会有侧翻的危险,陆龟依靠背甲的几何形状作为支撑来翻身,而淡水龟主要依靠头部作为翻

表 1 四眼斑水龟成体形态特征的描述值和 t 检验及协方差分析结果  
Table 1 The morphological traits of adult *Sacalia quadriocellata* and results of t-test and one-way ANCOVA

形态特征 Morphological trait	雌性 Female		雄性 Male		结果 Result
	样本量 Sample size	平均值 ± 标准误 Mean ± SE	样本量 Sample size	平均值 ± 标准误 Mean ± SE	
背甲长 Carapace length (mm)	21	132.0±1.5	20	127.6±1.2	$t = 2.26^*$ ♀ > ♂
背甲宽 Carapace width (mm)	21	94.1±1.2	20	90.3±0.8	$F_{1,38} = 1.35^{ns}$
背甲中部宽(mm) Mid-body carapace width	21	91.4±1.1	20	88.9±0.8	$F_{1,38} = 0.05^{ns}$
背甲高 Carapace height (mm)	21	45.2±1.0	20	43.0±0.5	$F_{1,38} = 0.59^{ns}$
背甲曲线长(mm) Curvilinear carapace length	21	141.3±1.6	20	136.4±1.3	$F_{1,38} = 0.75^{ns}$
背甲曲线宽(mm) Curvilinear carapace width	21	99.7±1.5	20	96.6±1.1	$F_{1,38} = 0.01^{ns}$
腹甲长 Plastron length (mm)	21	119.0±1.4	20	112.7±0.9	$F_{1,38} = 16.82^{**}$ ♀ > ♂
腹甲中线长(mm) Midline plastron length	21	113.8±1.4	20	107.4±0.7	$t = 3.85^{**}$ ♀ > ♂
腹甲宽 Plastron width (mm)	21	80.5±1.1	20	78.8±1.2	$F_{1,38} = 0.13^{ns}$
腹甲曲线长(mm) Curvilinear plastron length	21	115.7±1.5	20	109.9±0.8	$t = 2.62^*$ ♀ > ♂
体周长(mm) Total longitudinal circumference	21	309.3±3.4	20	299.6±2.3	$F_{1,38} = 0.03^{ns}$
肛盾切口长(mm) Analia to supracaudal junction	21	22.4±0.6	20	22.5±0.5	$F_{1,38} = 0.71^{ns}$
肛盾切口宽(mm) Anal notch width	21	24.5±0.7	20	23.2±0.3	$t = 0.58^{ns}$
头长 Head length (mm)	15	27.7±0.5	15	30.7±0.4	$t = -4.34^{**}$ ♀ < ♂
头宽 Head width (mm)	15	18.9±0.2	15	19.5±0.2	$t = -2.09^*$ ♀ < ♂
前肢长 Forelimb length (mm)	21	22.3±0.4	20	22.5±0.4	$F_{1,38} = 3.69^{ns}$
后肢长 Hindlimb length (mm)	21	25.8±0.4	20	26.8±0.3	$F_{1,38} = 13.20^{**}$ ♀ < ♂
尾长 Tail length (mm)	17	45.7±0.8	17	49.1±0.8	$t = -3.02^{**}$ ♀ < ♂
尾长肛前段长(mm) Preanal tail length	21	13.0±0.6	20	16.8±0.6	$t = -4.35^{**}$ ♀ < ♂
体重 Body mass (g)	21	328.0±14.0	20	284.0±7.0	$F_{1,38} = 2.30^{ns}$

表中数据为原始数据统计描述值，肛盾切口宽、腹甲中线长和腹甲曲线长为以背甲长为自变量的回归剩余值作为矫正值进行比较，其余形态特征直接比较。t 或 F 值后的符号代表显著性水平，ns.  $P > 0.05$ ，\*  $P < 0.05$ ，\*\*  $P < 0.01$ 。

Descriptive statistics for the original measurements in the table, the anal notch width, midline plastron length and curvilinear plastron length are compared by calculating their regression residuals as adjusted values, while the other measurements are directly compared. The symbols after t and F values represent the significant level, ns  $P > 0.05$ ，\*  $P < 0.05$ ，\*\*  $P < 0.01$ 。

身的支点 (Delmas et al. 2007, Domokos et al. 2008)。野外和实验室观察到四眼斑水龟用头部作为支点翻身的行为, 头部较大的雄性可能在雄雄斗争中更有利。同时, 头部上下摆动是求偶炫耀的重要组成部分, 雄性四眼斑水龟在求偶时多次重复该动作 (Liu et al. 2008)。

**3.3 背腹甲的两性异形** 四眼斑水龟雌性成体腹甲长、腹甲中线长和腹部曲线长显著大于雄性成体, 这可能是生育选择压力使雌性成体的腹部倾向于增大。在食物资源充足的条件下, 雌性的腹腔会容纳更多的窝卵数和更大体积卵的方向进化 (Henen 1997, Zuffi et al. 2007), 因此许多龟鳖类的雌性腹腔容量较大, 主要体现在雌性具有较长的腹甲和相对宽而高的背甲 (Ben Kaddour et al. 2008, Djordjević et al. 2011)。但除背甲长外, 四眼斑水龟其他的背甲形态特征差异均不显著, 与地中海拟水龟 (*Mauremys leprosa*) 和窄胸长颈龟 (*Chelodina colliei*) 的研究结果不一致 (Bonnet et al. 2010)。这可能与四眼斑水龟年产单窝卵、且窝卵数少有关 (史海涛等 2002, 2011), 雌性成体能以较长而微凸 (腹甲曲线长) 的腹部容纳较少的窝卵数, 不需要背甲提供更多的空间。此外, 过高的背甲会影响水生龟类的游泳能力, 不利于捕食和躲避天敌 (Rivera et al. 2011)。这两方面的因素决定了雌雄之间除背甲长以外的其他背甲形态特征差异不显著。

腹甲相对于背甲的大小决定了龟鳖类头部和四肢的活动能力 (Bonnet et al. 2001), 四眼斑水龟雄性成体具有相对短的腹甲, 意味着头部和四肢具有更多的活动空间, 这有利于求偶炫耀和寻找配偶。肛盾切口大小也会影响龟鳖的交配和繁殖 (McRae et al. 1981, Djordjević et al. 2011, 2013)。四眼斑水龟的肛盾切口大小不存在显著的两性差异, 与地中海拟水龟相同 (Bonnet et al. 2010), 可能是较短的腹甲也为尾部提供了足够的活动空间, 有利于雄性交配。

**3.4 四肢的两性异形** 成体四眼斑水龟前肢

雌雄差异不显著, 但后肢存在显著的两性异形, 这可能与雄性的交配姿势有关。淡水龟类有两种交配姿势, 一种是雄性在雌性的背甲上用四肢抓住背甲进行交配; 另一种是雄性用后肢撑地支持身体, 用前肢抓住雌性背甲进行交配 (Liu et al. 2013)。四眼斑水龟属于后者 (Liu et al. 2008), 雄性较长的后肢有助于支撑身体进行交配。

**3.5 尾部的两性异形** 四眼斑水龟雄性成体的尾长和尾长肛前段长显著大于雌性, 与锦龟 (*Chrysemys picta*) (Rowe 1997)、黄斑水龟 (Litzgus et al. 1998)、地中海拟水龟 (Muñoz et al. 2006)、窄胸长颈龟 (Bonnet et al. 2010) 的研究结果相同。尾部是龟鳖类最普遍的两性异形特征, 较长的尾部可能是雄性具有较短腹甲 (相对于背甲长) 的结果 (Gibbons et al. 1990, Litzgus et al. 1998)。同时, 较大的尾长与雄性容纳阴茎有关, 而较长的尾长肛前段长使得雄性在交配时尾部的活动较自由, 泄殖腔的接触更有效 (Muñoz et al. 2006)。

**致谢** 海南师范大学生命科学学院杨灿朝副教授、洪美玲教授和王力军教授在数据处理及论文修改方面给予帮助, 陈懋同学协助绘图, 两名匿名审稿专家提出中肯的修改意见, 谨致诚挚谢意!

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