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生态学报

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封面图说: 云南松树冠——云南松为松科松属裸子植物,多生长在海拔 1000—3500m 的高山,喜光、耐干旱、耐瘠薄,适应酸性的红壤、黄壤,在其他树种不能生长的贫瘠石砾地或冲刷严重的荒山坡分布,易于天然更新。主要分布于四川西南部、云南、西藏东南部、贵州西部、广西西部,常形成大面积纯林,尤以云南分布最广,故有云南松之称。云南松树高可达 30m,胸径达 1m,树皮呈灰褐色,叶通常 3 针一束,鲜有两针,球果圆锥状卵圆形,种子近卵圆形或倒卵形。树干通直,木质轻软细密,是优质造纸、人造板原料,富含松脂是云南松的重要特点之一。

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樊晓丽, 林植华, 丁先龙, 朱吉峰. 鲶鱼和胡子鲶的两性异形与雌性个体生育力. 生态学报, 2014, 34(3): 555-563.

Fan X L, Lin Z H, Ding X L, Zhu J F. Sexual size dimorphism and female individual fecundity of *Silurus asotus* and *Clarias fuscus*. Acta Ecologica Sinica, 2014, 34(3): 555-563.

鲶鱼和胡子鲶的两性异形与雌性个体生育力

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摘要: 检测了鲶鱼(*Silurus asotus*)和胡子鲶(*Clarias fuscus*)繁殖期 18 个形态特征的两性异形以及雌性个体生育力。结果表明, 鲶鱼和胡子鲶雌雄性别比例均符合 1:1。One-way ANOVA 显示, 鲶鱼雌雄个体体长差异不显著, 胡子鲶雌性个体体长显著小于雄性个体($P<0.05$)。以体长为协变量的 One-way ANCOVA 显示, 特定体长的鲶鱼雌性个体的眼间距和体高显著大于雄性个体($P<0.05$), 两性间其它局部特征不存在显著的两性差异; 特定体长的胡子鲶雌性个体的体高、腹鳍基前距和腹鳍臀鳍间距显著大于雄性个体, 雌性个体的臀鳍基长、尾柄高和尾鳍长显著小于雄性个体($P<0.05$), 两性间其它局部特征不存在显著的两性差异。Two-way ANOVA 显示, 胡子鲶体长显著大于鲶鱼($P<0.05$), 性别及物种与性别两因素的相互作用对体长影响不显著。以体长为协变量的 Two-way ANCOVA 显示, 胡子鲶的头长、头宽、吻长、眼间距、尾柄高、尾鳍长、背鳍基前距、背鳍基长、腹鳍基前距、腹鳍臀鳍间距、体重和去内脏体重显著大于鲶鱼, 头高、体高、臀鳍基长显著小于鲶鱼($P<0.05$), 物种间的其他形态特征变量差异不显著; 雌性个体的体高、背鳍基前距、腹鳍基前距、腹鳍臀鳍间距显著大于雄性个体, 臀鳍基长、尾柄高、尾鳍长、背鳍基长显著小于雄性个体($P<0.05$), 两性间的其他形态特征变量差异不显著; 物种与性别两因素的相互作用对体高、臀鳍基长、尾柄高、尾鳍长、背鳍基长和腹鳍臀鳍间距影响显著, 对其余的形态特征变量影响不显著。15 个形态特征变量的主成分分析(Eigenvalue ≥ 1)发现, 前 2 个主成分共解释 68.4% 的变异。头宽、眼间距、尾柄高、尾鳍长、背鳍基前距、背鳍基长、腹鳍基前距和腹鳍臀鳍间距在第一主成分有较高的正负载系数, 臀鳍基长在第一主成分有较高的负负载系数(解释 51.2% 变异); 眼后头长在第二主成分有较高的负负载系数(解释 17.2% 变异)。胡子鲶在第一主成分和第二主成分的分值均显著大于鲶鱼, 雌雄两性的差异以及两因素的相互作用对分值的影响均不显著。实验检测的鲶鱼、胡子鲶的怀卵数量与体长和体重回归关系显著。One-way ANCOVA 及矫正平均值 Tukey's 检验显示, 特定体长的胡子鲶的产卵数量显著大于鲶鱼。性选择是胡子鲶大个体雄性形成的主要原因, 同时影响与运动相关的尾部特征。生育力选择更多的影响与雌性胡子鲶较大腹腔容积相关的形态特征变异。环境因子、食物可得性和营养状况同时影响了个体大小两性异形的形成。

关键词: 鲶鱼; 胡子鲶; 两性异形; 性选择; 生育力

Sexual size dimorphism and female individual fecundity of *Silurus asotus* and *Clarias fuscus*

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Abstract: We measured the sexual size dimorphism in eighteen morphological traits and female individual fecundity of *Silurus asotus* and *Clarias fuscus* collected from Lishui (Zhejiang, eastern China) in reproductive seasons. It had been found that their sex ratios were both 1:1. One-way ANOVA showed the adults of *S. asotus* were not sexually dimorphic in body length, while body length was significantly larger in adult males than in adult females of *C. fuscus* ($P<0.05$). One-way

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ANCOVA with body length as a covariate showed that the females of *S. asotus* with special body length were significantly larger than the males in interorbital width and body depth ($P < 0.05$), while other examined morphological traits did not differ between the sexes. Furthermore, the females of *C. fuscus* with special body length were significantly larger than the males in body depth, pelvic fin precoxal length, and length between pelvic fin and anal fin ($P < 0.05$), whereas their anal fin coxal length, caudal peduncle depth and caudal fin length were significantly shorter in females than in males, and there were no significant differences between the sexes in any other of the examined morphological traits. Two-way ANOVA showed that body length of *C. fuscus* was significantly larger than one of *S. asotus* ($P < 0.05$), both sex and the interaction of sex and species had no effects on the body length. Two-way ANCOVA with body length as a covariate showed that head length, head width, snout length, interorbital width, caudal peduncle depth, caudal fin length, dorsal fin precoxal length, dorsal fin coxal length, length between pelvic fin and anal fin, body mass and carcass mass of *C. fuscus* were significantly larger than them of *S. asotus*, while head depth, body depth and anal fin length of *C. fuscus* were significantly shorter than ones of *S. asotus* ($P < 0.05$). Meanwhile, there were no significant differences in other morphological traits between them. Body depth, dorsal fin precoxal length, pelvic fin precoxal length, length between pelvic fin and anal fin were significantly larger among females than among males, while anal fin coxal length, caudal peduncle depth, caudal fin length and dorsal fin coxal length were significantly shorter among females than among males ($P < 0.05$). There were no significant differences in other morphological traits between the sexes. The interaction of species and sex had significant effects on body depth, anal fin coxal length, caudal peduncle depth, caudal fin length, dorsal fin coxal, length between pelvic fin and anal fin, but it had no effect on the other morphological traits. A principal component analysis resolved two components (with eigenvalues ≥ 1) from fifteen size-free morphological variables, accounting for 68.4% of variation in the original data. The first component (51.2% variance explained) had high positive loading for size-free values of head width, interorbital width, caudal peduncle depth, caudal fin length, dorsal fin precoxal length, dorsal fin coxal length, dorsal fin coxal length, pelvic fin precoxal length, pelvic fin precoxal length, length between pelvic fin and anal fin, wherea the first component had high negative loading for size-free values of anal fin coxal length. The second component (17.2% variance explained) had high negative loading for size-free values of postorbital head length. *C. fuscus* had higher scores on the first and the second axes of a principal component analysis than did *S. asotu*, but both sex and the interaction of sex and species had no critical effect on the scores. The individual fecundity was significantly correlated with the body length and body mass in *C. fuscus* and *S. asotus* positively. One-way ANCOVA and Tukey's test showed that *C. fuscus* with special body length laid significantly more eggs than *S. asotus*. Sexual selection was the major evolutionary reasons for large males of *C. fuscus*, simultaneously had effects on tail traits correlated with locomotion. Fecundity selection affected the variations of morphological traits associated with abdominal cavity volume to a large extent. Environmental factors, food availability and nutritional status affected the evolution of sexual size dimorphism at the same time.

Key Words: *Silurus asotus*; *Clarias fuscus*; sexual dimorphism; sexual selection; fecundity

动物个体大小的两性异形(SSD)是一种非常普遍的现象,鸟类和哺乳类较多出现典型的雄性大于雌性的现象,但其余大部分动物类群会相对较多地倾向于大个体雌性的两性异形^[1-2],比如 66%蛇类^[3]、90%无尾类^[4]等。雌雄个体所经历的不同选择压力导致两性异形的不断进化^[5]。近年来,生物学家提出了个体大小两性异形进化的 3 种主要适应机制:性选择、生育力选择和生态位分化选择。生物

进化研究表明,不同物种间的两性异形程度与配偶竞争强度高度相关,动物的性选择主要通过直接获得雌性配偶的雄性间竞争、雌性喜好雄性的某一特定形态等途径来实现^[6-8],这种竞争通常是指雄性间竞争,尽管雌性间竞争也被人们逐渐认识^[9]。生育力选择学说认为,较大的雌性个体能通过储存和产出更多卵细胞来提高生育力^[10-11]。外部的生态压力(如食物可得性、捕食压力、生境选择等)也是作用于

生物个体大小进化的力量^[12-15]。例如,生活在坦噶尼喀湖的坦伯拉凤凰(*Telmatochromis temporalis*)雌雄个体都会利用空贝壳作为避难所和繁殖地,在不同生态压力(对雄鱼的捕食,对雌鱼所产卵的捕食)的限制下形成不同大小个体^[16]。生态位两性分化假说认为,两性异形能通过生物雌雄个体选择不同的生态位而不断进化,进而造成营养结构上的性二态^[17-18]。如果对一种性别的生态压力和对另一性别的其他生态压力之间的最适体型或强度不同,那么这可能会加速两性异形的进化^[16],而种间竞争强度的增加在一定程度上抑制了种群内两性异形的分化^[19]。

鲶鱼(*Silurus asotus*)和胡子鲶(*Clarias fuscus*)分属于鲶形目(Siluriformes)的鲶科(Siluridae)和胡子鲶科(Clariidae)^[20],均喜昼伏夜出营穴居生活,是以吃虾、鱼、水蚯蚓、福寿螺、水生昆虫为主的中下层潜伏性肉食性鱼类,普遍分布于浙江地区各水系^[20],其中,胡子鲶主要分布于我国南方水系,个体大、生长速度快^[21-22]。已有研究表明,鲶鱼的雌雄个体第二性征不显著,产粘性卵,幼鱼恋巢倾向明显,有阶段性的集群行为^[20];胡子鲶雌雄个体第二性征存在显著差异,雄性个体头部两侧和吻端之间有明显的白色珠星,生殖突长至肉质垂,而雌鱼无明显白色珠星,生殖乳突圆而短^[23];此外,胡子鲶的雄鱼和雌鱼分别有明显的营巢和护卵的抚育行为^[20, 24-25]。

目前鲶鱼和胡子鲶的生物学特征^[21, 24, 26]、胚胎发育^[23, 27]、人工繁育与养殖技术^[22, 28-29]等方面进行广泛研究,为这两种同在浙江水域分布鱼类的两性间形态差异的定量研究提供基础数据。本研究旨在通过比较鲶鱼和胡子鲶形态特征的两性异形程度及其雌性个体生育力的差异,探讨两性异形的原因及进化机制。

1 材料与方法

1.1 实验动物的形态测定

2010年5月13日,从浙江省丽水市府前菜场购买野生鲶鱼($N=60$)和胡子鲶($N=50$),带回丽水学院动物实验室,塑料袋密封包装后冰冻处死并保存,1周内解冻、测量和解剖。用数显游标卡尺测定样本的体长、头长、头宽、头高、吻长、眼后头长、眼径、眼间距、体高、臀鳍基长、尾柄高、尾鳍长、背鳍基前距、

背鳍基长、腹鳍基前距、腹鳍臀鳍间距等形态指标($\pm 0.01\text{mm}$),用Mettler电子天平称体重和去内脏体重($\pm 0.001\text{g}$)^[30-31]。

1.2 雌性个体生育力

用Nikon SMZ-1000解剖镜对卵巢进行观察和卵的计数。经检测,本实验涉及的鲶鱼和胡子鲶的最小个体分别为体长为211.00和251.01 mm的雌性性成熟个体(属Ⅲ期以上发育程度的卵巢^[20])。用雌体卵巢中开始出现卵黄沉积的卵数量表示个体生育力。雌体怀卵数量的测定:取出雌体卵巢称重(M),随机取一部分卵巢称重(m),计数此样品中开始出现卵黄沉积的卵数量(n),然后按公式计算雌体的怀卵数量:怀卵数量= $n \times M/m$ 。每个卵巢重复测定3次,取平均值作为雌体的怀卵数量^[30-31]。

1.3 数据处理

所有数据的统计分析用Statistica统计软件包完成。数据在作进一步统计分析前检验其正态性(Kolmogorov-Smirnov test)和方差同质性(F -max test)。经检验,部分形态学数据经 $\log_e$ 转换后符合参数统计条件。用线性回归、方差分析(One-way ANOVA和Two-way ANOVA)、协方差分析(One-way ANCOVA和Two-way ANCOVA)、Tukey's检验和主成分分析等处理和比较相应的数据,比较校正平均值前检验斜率的均一性。文中涉及的非参数统计为 G -检验。描述性统计值用平均值 $\pm$ 标准误(范围)表示,显著性水平设置为 $\alpha=0.05$ 。

2 结果

2.1 鲶鱼形态特征的两性异形

共检测鲶鱼个体60尾,雌性个体27尾,雄性个体33尾,其基本描述性统计见表1。实验涉及最小的雌性个体是体长为211.00 mm的怀卵个体,以此认定所检测的个体均为性成熟个体。雌雄性别比例符合1:1(G -检验, $G=0.60$, $df=1$, $P>0.25$)。

经检验,数据无需转换可直接进行参数统计。One-way ANOVA显示,鲶鱼雌雄两性个体体长差异不显著。以体长为协变量的One-way ANCOVA及后续的Tukey's检验显示,特定体长鲶鱼的雌性个体的眼间距和体高显著大于雄性个体($P<0.05$),两性间其它局部特征不存在显著的两性差异(表1)。

表 1 鲶鱼和胡子鲶形态特征的两性异形
Table 1 Sexual dimorphism of morphological traits in *S. asotus* and *C. fuscus*

形态变量 Morphological variables	鲶鱼 <i>S. asotus</i>			胡子鲶 <i>C. fuscus</i>		
	雌性 Females (<i>n</i> = 27)	雄性 Males (<i>n</i> = 33)	<i>F</i> 值和显著水平 <i>F</i> -values and significant levels	雌性 Females (<i>n</i> = 23)	雄性 Males (<i>n</i> = 27)	<i>F</i> 值和显著水平 <i>F</i> -values and significant levels
体长/mm	294.63 ±7.04	295.67 ±6.57	$F_{1, 58} = 0.01$	384.57 ±4.06	404.33 ±4.65	$F_{1, 48} = 9.89$
Body length	(211.00—347.00)	(219.00—347.00)	$P = 0.915$	(351.01—432.00)	(368.10—456.00)	$P < 0.003, F < M$
头长/mm	62.35 ±1.46	62.50 ±1.37	$F_{1, 57} = 0.01$	82.63 ±0.78	86.93 ±1.21	$F_{1, 47} = 0.47$
Head length	(44.71—73.89)	(46.93—74.26)	$P = 0.928$	(76.17—90.37)	(77.82—100.31)	$P = 0.497$
头宽/mm	40.34 ±0.89	40.53 ±0.93	$F_{1, 57} = 0.01$	66.28 ±0.52	68.27 ±0.83	$F_{1, 47} = 0.10$
Head width	(30.27—47.36)	(28.82—49.80)	$P = 0.909$	(61.81—70.51)	(61.75—77.35)	$P = 0.752$
头高/mm	20.49 ±0.48	20.29 ±0.54	$F_{1, 57} = 0.21$	20.99 ±0.30	21.57 ±0.40	$F_{1, 47} = 0.86$
Head depth	(14.97—24.86)	(14.96—27.05)	$P = 0.648$	(17.84—23.85)	(18.33—25.09)	$P = 0.358$
吻长/mm	21.32 ±0.54	21.20 ±0.56	$F_{1, 57} = 0.22$	29.49 ±0.36	30.73 ±0.43	$F_{1, 57} = 0.09$
Snout length	(15.51—25.57)	(14.10—28.18)	$P = 0.639$	(26.27—32.56)	(25.94—35.51)	$P = 0.763$
眼后头长/mm	37.49 ±0.88	38.34 ±0.82	$F_{1, 57} = 2.35$	47.63 ±0.59	49.66 ±0.68	$F_{1, 47} = 0.05$
Postorbital head length	(26.94—44.25)	(29.84—46.81)	$P = 0.130$	(41.01—52.69)	(42.29—55.71)	$P = 0.832$
眼径/mm	6.74 ±0.15	6.80 ±0.15	$F_{1, 57} = 0.09$	8.32 ±0.31	9.29 ±0.31	$F_{1, 47} = 0.46$
Eye diameter	(4.86—8.24)	(5.30—8.47)	$P = 0.763$	(6.28—11.73)	(7.30—13.74)	$P = 0.499$
眼间距/mm	26.99 ±0.55	26.26 ±0.53	$F_{1, 57} = 7.32$	41.94 ±0.39	43.60 ±0.51	$F_{1, 47} = 1.36$
Interorbital width	(20.80—30.44)	(20.91—32.65)	$P < 0.009, F > M$	(38.87—45.85)	(37.63—48.69)	$P = 0.250$
体高/mm	48.72 ±2.05	44.78 ±2.12	$F_{1, 57} = 4.51$	49.71 ±1.00	44.17 ±0.66	$F_{1, 47} = 31.76$
Body depth	(23.85—61.26)	(22.60—61.40)	$P < 0.038, F > M$	(41.47—57.70)	(38.33—50.43)	$P < 0.001, F > M$
臀鳍基长/mm	171.29 ±4.24	170.79 ±3.81	$F_{1, 57} = 0.36$	165.22 ±2.80	185.02 ±3.26	$F_{1, 47} = 10.04$
Anal fin coxal length	(118.85—202.16)	(122.52—205.38)	$P = 0.550$	(143.42—191.91)	(154.33—220.65)	$P < 0.003, F < M$
尾柄高/mm	13.66 ±0.34	14.32 ±0.42	$F_{1, 57} = 2.21$	26.43 ±0.40	29.46 ±0.45	$F_{1, 47} = 14.19$
Caudal peduncle depth	(10.20—16.83)	(9.03—18.50)	$P = 0.143$	(22.43—29.50)	(21.53—33.04)	$P < 0.001, F < M$
尾鳍长/mm	31.35 ±0.76	31.47 ±0.74	$F_{1, 57} = 0.01$	50.44 ±0.74	57.33 ±0.91	$F_{1, 47} = 19.06$
Caudal fin length	(23.49—37.67)	(22.10—37.88)	$P = 0.960$	(42.92—57.85)	(47.80—67.45)	$P < 0.001, F < M$
背鳍基前距/mm	88.05 ±2.12	87.50 ±2.09	$F_{1, 57} = 0.82$	130.12 ±1.33	132.92 ±1.70	$F_{1, 47} = 1.66$
Dorsal fin precoxal length	(65.36—108.80)	(64.80—105.81)	$P = 0.369$	(116.20—145.40)	(114.66—151.73)	$P = 0.203$
背鳍基长/mm	3.45 ±0.15	3.38 ±0.13	$F_{1, 57} = 0.21$	24.83 ±0.37	26.99 ±0.52	$F_{1, 47} = 0.77$
Dorsal fin coxal length	(2.06—5.43)	(1.97—5.35)	$P = 0.646$	(21.70—29.70)	(23.10—35.70)	$P = 0.385$
腹鳍基前距/mm	112.14 ±2.89	110.10 ±2.92	$F_{1, 57} = 2.54$	174.75 ±2.02	177.86 ±2.54	$F_{1, 47} = 4.27$
Pelvic fin precoxal length	(73.56—129.32)	(81.36—134.65)	$P = 0.116$	(152.31—187.66)	(159.67—202.60)	$P < 0.045, F > M$
腹鳍臀鳍间距/mm	7.97 ±0.31	7.74 ±0.23	$F_{1, 57} = 0.51$	35.41 ±0.85	33.39 ±0.69	$F_{1, 47} = 10.59$
Length between pelvic fin and anal fin	(4.75—12.16)	(5.38—10.18)	$P = 0.477$	(26.49—41.95)	(25.89—43.83)	$P < 0.003, F > M$
体重/g	260.46 ±16.40	247.50 ±17.69	$F_{1, 57} = 3.15$	558.66 ±16.16	592.44 ±22.27	$F_{1, 47} = 2.77$
Body mass	(99.20—394.70)	(88.40—399.90)	$P = 0.081$	(450.00—731.30)	(411.50—826.80)	$P = 0.103$
去内脏体重/g	212.69 ±13.45	212.23 ±14.41	$F_{1, 57} = 0.14$	464.75 ±17.25	545.34 ±21.48	$F_{1, 47} = 0.38$
Carcass mass	(72.60—317.80)	(78.90—359.10)	$P = 0.712$	(366.10—652.90)	(379.80—775.30)	$P = 0.541$

数据用平均值 ±标准误(范围)表示; 体长为 One-way ANOVA,其余均为以体长为协变量的 One-way ANCOVA; F:成年雌性; M:成年雄性

2.2 胡子鲶形态特征的两性异形

共检测胡子鲶个体 50 尾,雌性个体 23 尾,雄性个体 27 尾,其基本描述性统计见表 1。实验涉及最小的雌性个体是体长为 251.01 mm 的怀卵个体,以此认定所检测的个体均为性成熟个体。雌雄性别比例符合 1:1(*G*-检验, $G = 0.32, df = 1, P > 0.25$)。

One-way ANOVA 显示,胡子鲶雌性个体体长显著小于雄性个体。以体长为协变量的 One-way ANCOVA 及后续的 Tukey's 检验显示,特定体长的雌性个体的体高、腹鳍基前距和腹鳍臀鳍间距显著大

于雄性个体($P < 0.05$),雌性个体的臀鳍基长、尾柄高和尾鳍长显著小于雄性个体($P < 0.05$),两性间其它局部特征不存在显著的两性差异(表 1)。

2.3 鲶鱼和胡子鲶形态特征的比较

Two-way ANOVA 显示,胡子鲶体长显著大于鲶鱼,性别及物种与性别的相互作用对体长影响不显著(表 2)。以体长为协变量的 Two-way ANCOVA 显示,胡子鲶的头长、头宽、吻长、眼间距、尾柄高、尾鳍长、背鳍基前距、背鳍基长、腹鳍基前距、腹鳍臀鳍间距、体重和去内脏体重显著大于鲶鱼,头高、体高和

臀鳍基长显著小于鲶鱼 ($P<0.05$), 物种间的其他形态特征变量差异不显著; 雌性个体的体高、背鳍基前距、腹鳍基前距和腹鳍臀鳍间距显著大于雄性个体, 臀鳍基长、尾柄高、尾鳍长和背鳍基长显著小于雄性个体 ($P<0.05$), 两性间的其他形态特征变量差异不

显著; 物种与性别两因素的相互作用对体高、臀鳍基长、尾柄高、尾鳍长、背鳍基长和腹鳍臀鳍间距影响显著 ($P<0.05$), 对其余的形态特征变量影响不显著 (表 2)。

表 2 鲶鱼和胡子鲶形态特征的种间比较

Table 2 Inter-species comparison in morphological traits of *S. asotus* and *C. fuscus*

形态变量 Morphological variables	方差效应 ANOVA effect		
	物种 Species	性别 Sex	交互作用 Interaction
体长/mm	$F_{1, 106} = 272.08$	$F_{1, 106} = 2.99$	$F_{1, 106} = 2.42$
Body length	$P<0.0001$, fu>as	$P=0.087$	$P=0.123$
头长/mm	$F_{1, 105} = 8.79$	$F_{1, 105} = 0.14$	$F_{1, 105} = 0.22$
Head length	$P<0.004$, fu>as	$P=0.712$	$P=0.642$
头宽/mm	$F_{1, 105} = 299.57$	$F_{1, 105} = 0.11$	$F_{1, 105} = 0.23$
Head width	$P<0.0001$, fu>as	$P=0.739$	$P=0.632$
头高/mm	$F_{1, 105} = 40.60$	$F_{1, 105} = 0.94$	$F_{1, 105} = 0.07$
Head depth	$P<0.0001$, fu<as	$P=0.333$	$P=0.788$
吻长/mm	$F_{1, 105} = 16.69$	$F_{1, 105} = 0.09$	$F_{1, 105} = 0.06$
Snout length	$P<0.0001$, fu>as	$P=0.767$	$P=0.800$
眼后头长/mm	$F_{1, 105} = 0.11$	$F_{1, 105} = 0.47$	$F_{1, 105} = 1.10$
Postorbital head length	$P=0.739$	$P=0.493$	$P=0.296$
眼径/mm	$F_{1, 105} = 0.01$	$F_{1, 105} = 2.26$	$F_{1, 105} = 1.70$
Eye diameter	$P=0.970$	$P=0.136$	$P=0.195$
眼间距/mm	$F_{1, 105} = 240.61$	$F_{1, 105} = 0.50$	$F_{1, 105} = 3.00$
Interorbital width	$P<0.0001$, fu>as	$P=0.481$	$P=0.086$
体高/mm	$F_{1, 105} = 65.94$	$F_{1, 105} = 28.14$	$F_{1, 105} = 4.28$
Body depth	$P<0.0001$, fu<as	$P<0.0001$, F>M	$P<0.041$
臀鳍基长/mm	$F_{1, 105} = 368.39$	$F_{1, 105} = 6.60$	$F_{1, 105} = 11.02$
Anal fin coxal length	$P<0.0001$, fu<as	$P<0.012$, F<M	$P<0.002$
尾柄高/mm	$F_{1, 105} = 234.80$	$F_{1, 105} = 17.15$	$F_{1, 105} = 5.69$
Caudal peduncle depth	$P<0.0001$, fu>as	$P<0.0001$, F<M	$P<0.019$
尾鳍长/mm	$F_{1, 105} = 144.49$	$F_{1, 105} = 17.90$	$F_{1, 105} = 17.54$
Caudal fin length	$P<0.0001$, fu>as	$P<0.0001$, F<M	$P<0.0001$
背鳍基前距/mm	$F_{1, 105} = 84.98$	$F_{1, 105} = 4.27$	$F_{1, 105} = 1.26$
Dorsal fin precoxal length	$P<0.0001$, fu>as	$P<0.042$, F>M	$P=0.265$
背鳍基长/mm	$F_{1, 105} = 1445.91$	$F_{1, 105} = 7.30$	$F_{1, 105} = 9.50$
Dorsal fin coxal length	$P<0.0001$, fu>as	$P<0.008$, F<M	$P<0.003$
腹鳍基前距/mm	$F_{1, 105} = 107.90$	$F_{1, 105} = 7.75$	$F_{1, 105} = 0.82$
Pelvic fin precoxal length	$P<0.0001$, fu>as	$P<0.007$, F>M	$P=0.366$
腹鳍臀鳍间距 Length	$F_{1, 105} = 608.50$	$F_{1, 105} = 7.61$	$F_{1, 105} = 5.05$
between pelvic fin and anal fin	$P<0.007$, fu>as	$P<0.007$, F>M	$P<0.027$
体重/g	$F_{1, 105} = 10.51$	$F_{1, 105} = 2.73$	$F_{1, 105} = 0.01$
Body mass	$P<0.002$, fu>as	$P=0.102$	$P=0.909$
去内脏体重/g	$F_{1, 105} = 12.17$	$F_{1, 105} = 2.65$	$F_{1, 105} = 3.69$
Carcass mass	$P<0.001$, fu>as	$P=0.106$	$P=0.058$

体长为 Two-way ANOVA, 其余均为以体长为协变量的 Two-way ANCOVA; as: 鲶鱼; fu: 胡子鲶; F: 成年雌体; M: 成年雄体; Body length is compared with two-way ANOVA, the remaining variables are compared with two-way ANCOVA with body length as the covariate. as: *S. asotus*; fu: *C. fuscus*; F: adult females; M: adult males

15 个形态特征变量的主成分分析 (Eigenvalue ≥ 1) 发现, 前 2 个主成分共解释 68.4% 的变异 (表 3)。头宽、眼间距、尾柄高、尾鳍长、背鳍基前距、背鳍基长、腹鳍基前距和腹鳍臀鳍间距在第一主成分有较

高的正负载系数, 臀鳍基长在第一主成分有较高的负负载系数 (解释 51.2% 变异); 眼后头长在第二主成分有较高的负负载系数 (解释 17.2% 变异) (表 3)。物种间和雌雄两性间在第一和第二的分值差异

显著性见表 4。Two-way ANOVA 显示,胡子鲶在第一主成分和第二主成分的分值均显著大于鲶鱼($P <$

0.05, 图 1),雌雄两性的差异以及两因素的相互作用对分值的影响均不显著(图 1)。

表 3 15 个形态特征变量的主成分分析的负载系数

Table 3 Loading of the first two axes of a principal component analysis on fifteen morphological variables

形态变量 Morphological variables	负载系数 Factor loading	
	PC1	PC2
头长 Head length	0.595	-0.665
头宽 Head width	0.910	-0.061
头高 Head depth	-0.375	-0.649
吻长 Snout length	0.546	-0.346
眼后头长 Postorbital head length	0.260	-0.716
眼径 Eye diameter	0.150	-0.436
眼间距 Interorbital width	0.925	-0.007
体高 Body depth	-0.389	-0.658
臀鳍基长 Anal fin coxal length	-0.811	-0.333
尾柄高 Caudal peduncle depth	0.845	0.007
尾鳍长 Caudal fin length	0.801	-0.021
背鳍基前距 Dorsal fin precoxal length	0.843	-0.290
背鳍基长 Dorsal fin coxal length	0.883	0.338
腹鳍基前距 Pelvic fin precoxal length	0.817	-0.224
腹鳍臀鳍间距 Length between pelvic fin and anal fin	0.888	0.302
解释变异 Variance explained	51.2%	17.2%

用变量与体长的回归剩余值去除大小差异的影响,对每个主成分有主要贡献的变量用黑体注明,PC1:第一主成分,PC2:第二主成分; Size effects are removed in all cases by using residuals from the regressions on body length; Variables with the main contribution to each factor are in bold face; PC1: The first principal component, PC2: The second principal component

表 4 主成分分析各向量的 Two-way ANOVA 比较

Table 4 Two-way ANOVA results of the scores on the first and second axis of a principal component analysis

物种 Species	性别 Sex	交互作用 Interaction
PC1 $F_{1, 106} = 42.57, P < 0.0001, fu > as$	$F_{1, 106} = 1.80, P = 0.183$	$F_{1, 106} = 0.83, P = 0.364$
PC2 $F_{1, 106} = 4.47, P < 0.037, fu > as$	$F_{1, 106} = 0.17, P = 0.677$	$F_{1, 106} = 0.05, P = 0.832$

PC1:第一主成分 The first principal component, PC2:第二主成分 The second principal component

2.4 怀卵数量与形态特征的相关性分析

本实验检测的鲶鱼雌性个体 27 尾,其中 3 尾个体已产。怀卵数量在 5454 — 25428 粒之间,平均为 14449 粒。回归分析表明,鲶鱼的怀卵数量与体长 ($r^2 = 0.21, F_{1, 22} = 5.56, P < 0.028$) 和体重 ($r^2 = 0.20, F_{1, 22} = 5.54, P < 0.028$) 回归关系显著。

本实验检测的胡子鲶雌性个体 23 尾,怀卵数量在 33985 — 98955 粒之间,平均为 68627 粒。回归分析表明,胡子鲶的怀卵数量与体长 ($r^2 = 0.27, F_{1, 21} = 7.76, P < 0.012$) 和体重 ($r^2 = 0.18, F_{1, 21} = 4.60, P < 0.044$) 回归关系显著。

经 $\ln_e$ 转换后的 One-way ANCOVA 及后续的矫正平均值 Tukey's 检验显示,特定体长的胡子鲶的产

卵数量显著大于鲶鱼 ($F_{1, 44} = 74.20, P < 0.0001$, 图 2)。

3 讨论

3.1 雄性大个体的进化机制

Darwin 首次提出性选择是导致动物两性异形的主要机制,它通常针对于雄性个体,当性选择作用于雄性个体时将会对其局部雄性特征进行放大来提高交配的成功率^[6];当存在雄性格斗、精子竞争影响交配成功率时,就出现大个体雄性的进化,同时表现出雄性对后代的保护^[32-34]。例如,玫瑰软梳鲮 (*Malacoptenus macropus*)^[35]、蓝鳃太阳鱼 (*Lepomis macrochirus*)^[36]、三刺鱼 (*Gasterosteus aculeatus*)^[37]、沙

地 虾 虎 (*Pomatoschistus minutus*)^[38]、沙 塘 鳢 (*Odontobutis obscurus*)^[31]等都表现出大个体雄性,具有筑巢、防御领土、护卵等抚育行为。相对于鲶鱼而言,雄性胡子鲶有筑巢等行为^[20,23],有利于大个体雄性的进化,本实验数据验证了这一假设。另外,倾向于大个体雄性的两性异形常常实行一夫多妻的交配体制,雄性通过竞争占有重要资源(如食物、避难所、筑巢)来增加接近雌性的机会,提高繁殖成功率^[39]。例如,一条坦伯拉凤凰(*T. temporalis*)雄鱼领域内最多可达 6 条雌鱼^[16],一条凯利贝(*Lamprologus callipterus*)雄鱼领域内可多达 30 条只雌鱼^[40],它们均表现出雄性大于雌性的两性异形。鲶鱼常分散穴居生活^[28],而胡子鲶常数十只聚集在一起^[26],胡子鲶的群聚特点加剧了雄性竞争,从而形成大个体雄性的进化。

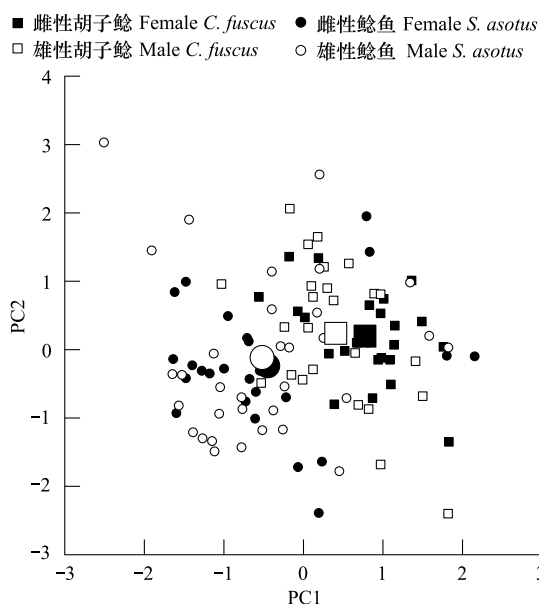


图 1 鲶鱼和胡子鲶的雌雄成体在由 15 个经矫正体长大小影响的形态特征变量区分出的第一 (PC1) 和第二 (PC2) 主成分轴上的空间位置

Fig.1 Spatial positions of both adult females and males of *S. asotus* and *C. fuscus* defined by the first and second axes of a principal component analysis based on fifteen size (body length) adjusted morphological variables

用变量与体长的回归剩余值去除大小差异的影响,放大符号代表前二个分轴上分类似繁殖习性的沙值的平均值

生态因子可能为动物的个体大小两性异形提供了其他选择压力^[41],鲶鱼和胡子鲶同属典型的底栖肉食性鱼类,但前者相对分布广、个体较小,后者主要分布于食物丰富的南方区域,个体较大,食性比鲶鱼广^[20],因此鲶鱼可能存在更为激烈的生态位竞

争,一定程度抑制了个体大小两性异形的分化^[17]。例如,Butler 等人发现蜥蜴的两性异形在物种稀少的环境下比物种丰富的栖息地中更为显著,其原因是种间竞争相对较弱^[19]。这种选择压力强调了身体大小上的两性异形更多地依赖于环境的多样性,从而使雌雄个体具有不同的生境偏好。

性选择压力和生态因子等在影响个体大小两性异形的时候,也影响动物个体的局部特征。鱼类躯干后部区域的形状差异主要存在于尾柄形状上,而尾柄被认为会影响鱼类的运动类型、运动表现以及捕食策略。较长的尾柄通常与持续性游泳有关,而较粗的尾柄则会产生强大的推动力,与疾速性游泳有关^[42]。胡子鲶雄性个体的尾柄高显著大于雌性,这可能有助于通过雄性个体通过爆发式游泳进行领域行为。与此同时,鱼类的背鳍和臀鳍不仅在平稳游泳和翻转时作为抑制翻滚运动的平衡器,而且同时协调尾鳍产生推动力^[43-45]。对于胡子鲶来说,雄性拥有较大的臀鳍基长和尾鳍长也有助于其产生更大的自身协调和运动能力,从而有利于筑巢、格斗行为的发生。具有类似繁殖习性的沙塘鳢 (*O. obscurus*) 雄性个体同样拥有较大的尾柄宽和背鳍基长^[31]。

3.2 雌性大个体的进化机制

食物可得性和营养状况可能对雌性个体生育力

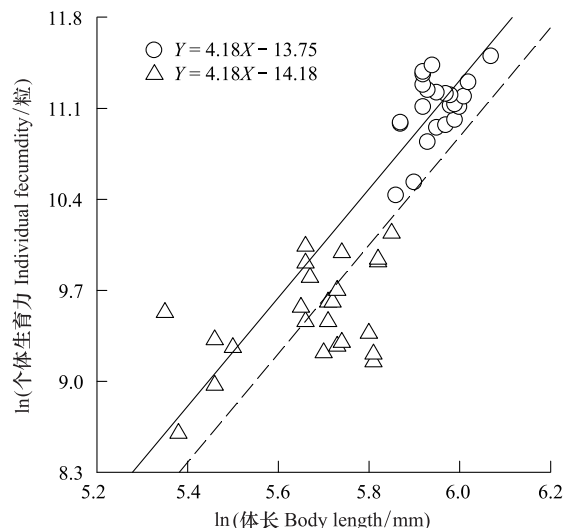


图 2 鲶鱼和胡子鲶的个体生育力与母体体长之间的回归关系

Fig.2 The linear regression of individual fecundity on body length of maternal *S. asotus* and *C. fuscus*

两个种回归线均用共同斜率(4.18)表示以利于比较; 鲶鱼: 三角形、虚线; 胡子鲶: 圆点、实线

具有重要的影响,生长和繁殖之间的能量分配在一定程度上会限制了大个体雌性的进化^[31]。雌性个体生育力数据表明,特定体长的胡子鲶生育力显著大于鲢鱼(图2),可能是由于食物可得性和营养状况的差异,例如特定体长的胡子鲶的体重和去内脏体重显著大于鲢鱼(表2);胡子鲶相对分布于我国南方^[20],良好的温度环境为胡子鲶提供更多的食物和发育等所需的环境温度。

回归分析表明,鲢鱼和胡子鲶雌性个体大小(体长和体重)与其个体生育力(怀卵数量)均呈显著的正相关,这表明生育力选择有利于鲢鱼和胡子鲶形成较大的雌鱼^[11, 46-47]。协方差分析表明,特定体长的胡子鲶的生育力显著高于鲢鱼(图2)。从局部特征考虑,鲢鱼有2项雌雄个体指标的差异,胡子鲶有7项雌雄个体指标的差异。主成分分析显示了种间的空间分布距离,同时显示了胡子鲶更为显著的种间差异(表4,图1)。胡子鲶雌性个体的体高、背鳍基前距、腹鳍基前距、腹鳍臀鳍间距显著大于雄性个体,表明了雌性个体通过局部特征的扩大来增加腹腔容量,以此提高个体生育力。

综上所述,相对于鲢鱼,胡子鲶具有更显著地个体大小和局部特征的两性异形。性选择是胡子鲶大个体雄性形成的主要原因,同时影响与运动相关的尾部特征。生育力选择更多的影响与雌性胡子鲶较大腹腔容积相关的形态特征变异。环境因子、食物可得性和营养状况同时影响了个体大小两性异形的形成。

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