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金线侧褶蛙和泽陆蛙的两性异形与生育力

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摘要：比较金线侧褶蛙和泽陆蛙的两性异形和生育力，首次通过种间比较来验证生育力选择理论是否能解释两栖动物两性异形的进化。金线侧褶蛙和泽陆蛙均为雌体大于雄体的两性异形类型，其两性异形程度存在显著差异，金线侧褶蛙两性异形程度指数为 0.30，而泽陆蛙仅为 0.08。然而，两者的怀卵量无显著差异。因此，结果与生育力选择理论预测不一致。此种不一致性可能由下述原因导致：选择压力作用于雄体而非雌体、能量分配策略和死亡率的种间差异、以及系统发育历史的种间差异。金线侧褶蛙和泽陆蛙雄体的身体状态指数显著高于雌体。金线侧褶蛙的头，眼和四肢都显著大于泽陆蛙；两者雌体的前后肢长度显著大于雄体。两性金线侧褶蛙的前后肢随体长呈同速生长，而泽陆蛙的前后肢随体长呈异速生长。

关键词：金线侧褶蛙；泽陆蛙；两性异形；窝卵数；生育力选择

Sexual dimorphism and fecundity in the gold-stripe pond frog (*Pelophylax plancyi*) and the terrestrial frog (*Fejervarya limnocharis*)

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Abstract: "The fecundity selection" hypothesis has been used to explain why females grow larger than males in many animal species. To test whether this hypothesis is able to explain inter-specific differences in sexual dimorphism, we compared sexual dimorphism and female fecundity of two species of frogs, the gold-stripe pond frog (*Pelophylax plancyi*) and the terrestrial frog (*Fejervarya limnocharis*), in eastern China. In May 2002, 93 terrestrial frogs (51 males, 42 females) and 104 gold-stripe pond frogs (28 males, 76 females) were captured from Hangzhou, Zhejiang Province. The animals were weighed to the nearest mg and measured to the nearest mm for snout-urostyle length, head length and width, diameter of eye, and limb length. Clutch sizes were also determined by counting eggs inside the females. The snout-urostyle length of adult females was significantly larger than that of adult males in both species. Although the degree of sexual size dimorphism differed remarkably (0.30 in *P. plancyi* and 0.08 in *F. limnocharis*), clutch size was similar between the two species after the effects of female body size (snout-urostyle length) were statistically removed. Therefore, our results are not consistent with the fecundity selection hypothesis. This outcome may not necessarily mean that fecundity selection does not affect the evolution in sexual dimorphism in amphibian. Firstly, a comparison between two species is not enough to draw general conclusions. Secondly, other causes, which we were not able to test in the current study, could be responsible to failure of the fecundity selection hypothesis to predict the sexual dimorphism in these two species. These causes include selection pressures that affect males rather than females, interspecific differences in energy allocation or mortality rates, and the unknown phylogenetic history of the two species. Moreover, we found interspecific and between-sex differences in body condition and morphology in *P. plancyi* and *F. limnocharis*. In the reproductive season, females had lower body condition than males in both species. Gold-stripe pond

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frogs had larger heads, eyes and limbs than did terrestrial frogs when we statistically controlled for snout-urostyle length. In both species of frogs, limb length was larger in females than in males. Males and females showed different allometric growth patterns in limb length of *F. limnocharis*, as females grow faster than do males; this sex difference does not occur in *P. plancyi*.

Key words:*Pelophylax plancyi*; *Fejervarya limnocharis*; sexual dimorphism; clutch size; fecundity selection

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动物两性异形(sexual size dimorphism)进化主要基于性选择[1~5]。性选择理论认为两性异形进化是对各自角色的适应,以谋求各自最大的繁殖利益。雄性争斗导致雄体大于雌体两性异形的形成[2,6],而生育力选择(fecundity selection)被认为是雌体大于雄体两性异形的进化动力[7,8]。此外,自然选择压力也可促进两性异形的进化[9~13]。

两栖动物中,绝大多数种类雌体大于雄体[2],与其他类群一样,生育力选择理论也被用于解释此种两性异形的形成[7]。生育力选择假设认为,如果生育力(窝卵数)随雌体大小的增加而增加,雌体可通过增大个体提高繁殖输出。因此,大个体比小个体具有更多的后代,从而具有进化优势。然而,迄今为止,已有证据大多来自种内的个体大小与生育力关系分析[7,8,14],而种间比较证据匮乏[15,16]。

事实上,种间比较提供了崭新的视角,便于更深入洞悉两性异形的进化。由于种间个体大小存在显著的差异和特异性,因此,在种间比较中,关注的是两性个体大小差异程度的种间差异与生育力的关系。根据生育力选择理论,可以预期种间两性异形程度的差异也应与窝卵数成正相关,因为,相对于其他种类而言,雌体较大种类的进化动力应为相对较高的生育力。

本文报道金线侧褶蛙和泽陆蛙的两性异形和繁殖输出,首次通过两栖动物种间比较,验证生育力选择理论是否同样能解释两性异形的种间差异。

1　材料和方法

由于4～5月为金线侧褶蛙和泽陆蛙共同的繁殖盛期[17],所有动物于2002年5月采自浙江杭州郊区。冰冻处死实验动物,用数显游标卡尺测定动物的体长(吻端至泄殖腔的距离,Snout-urostyle length, SUL)、头长(吻端至下颌关节后缘的距离,Head length, HL)、头宽(头部最宽处,Head width, HW)、眼径(与体轴平行的眼睛直径,Diameter of eye, DE)、前肢长(肩关节至第3趾末端的长度,Forelimb length FLL)和后肢长(体后端正中部至第4趾末端的长度,Hindlimb length HLL)(±0.01 mm),用Mettler电子天平称体重(±0.001g),然后,解剖取出雌体卵巢称重(M),随即取一部分卵巢称重($M1$),计数其中卵数量($N1$),通过公式 $N = N1 \times M/M1$ 计算获得雌体的怀卵数量,每个卵巢重复测定3次,取平均值作为雌体的怀卵量。

两性异形程度的计算参照Gibbons and Lovich[18]。两性异形程度指数=1－体型较小性别的平均SUL/体型较大性别的平均SUL。

用Kolmogorov-Smirnov和Bartlett分别检验数据的正态性和方差同质性。经检验,数据符合参数统计条件。用t检验比较体长的两性差异,线性回归分析形态特征和体长的关系,以及怀卵量与雌体大小的关系。协方差分析用于比较与体长相关的形态和繁殖特征的种间和性别间差异。计算Log(体重)对Log(体长)的回归剩余值作为实验动物身体状态指标[19](为检测繁殖对身体状态的影响,该分析没有包括17只未怀卵泽陆蛙的数据),然后用双因子方差分析(two-way ANOVA)检测身体状态的种间和性别间差异。

2　结果

2.1　个体大小的两性差异及其两性异形程度

金线侧褶蛙雌体平均体长为58.58±0.61($N=76$),大于雄体的41.27±0.51($N = 28$)($t = 16.23$, $df = 102$, $p < 0.00001$)。泽陆蛙雌体平均体长(41.34 ± 0.70　0.61,$N = 42$)也大于雄体体长(37.98 ± 0.33,$N = 50$)($t = 4.56$, $df = 90$, $p < 0.0001$)。金线侧褶蛙和泽陆蛙体长的两性异形程度存在显著差异,金线侧褶蛙两性异形程度指数为0.30,而泽陆蛙两性异形程度指数仅为0.08(图1)。

2.2　身体状态

以种类和性别为双因子的方差分析显示,身体状态存在显著的种间差异($F_{1,175} = 23.82$, $p < 0.00001$)和两性差异($F_{1,175} = 8.68$, $p < 0.01$),种类和性别间无明显交互作用($F_{1,175} = 0.07$, $p = 0.80$)。金线侧褶蛙的身体状态指数高于泽陆蛙,雄体身体状态指数显著大于雌体(金线侧褶蛙雄体VS雌体:0.038 VS 0.009;泽陆蛙雄体VS雌体:－0.012 VS －0.047)。

2.3　形态特征

所测定的形态特征均与体长呈显著正相关(所有 $p < 0.01$)。以体长为协变量的协方差分析表明,形态特征存在显著的种间差异;当设置体长恒定时,金线侧褶蛙的头,眼径和四肢都显著大于泽陆蛙(表1)。然而,绝大多数形态特征均无两性差异,只

有雌性个体的前后肢长度显著大于雄体；同时在该变量上，性别和种类交互作用显著（表 1），表明前后肢长度两性异形具有种间变异。前后肢与体长的回归分析显示了该种间差异：两性金线侧褶蛙的前后肢长随体长呈同速生长（*FLL*，$F_{1,100}=0.48$，$p=0.48$；*HLL*，$F1,100=0.01$，$p=0.95$），而泽陆蛙的前后肢长随体长呈异速生长（*FLL*，$F1,89=57.43$ $p<0.0001$；*HLL*，$F1,89=87.90$，$p<0.0001$）（图 2）。

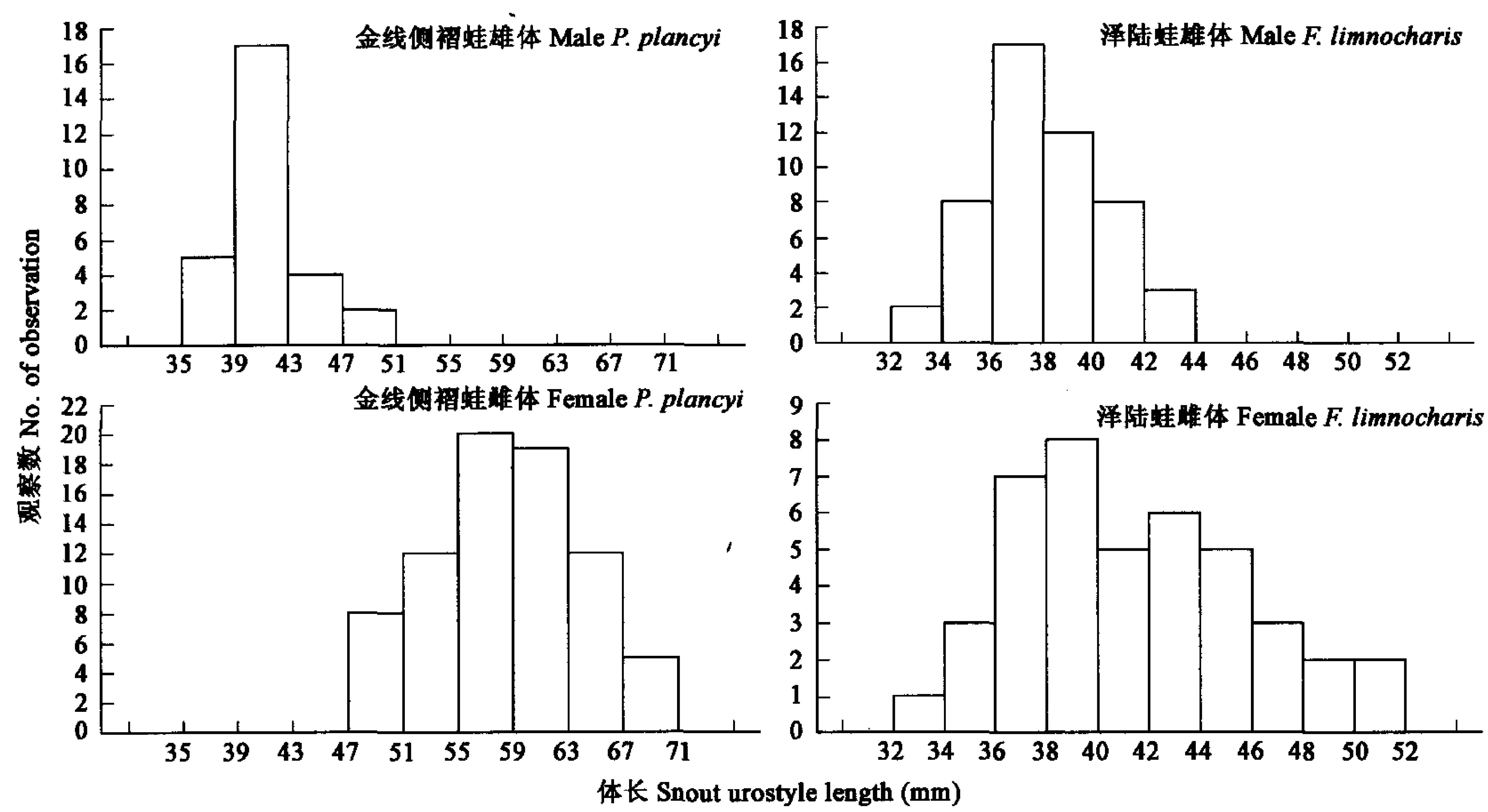

图 1 金线侧褶蛙和泽陆蛙两性个体体长的频率分布

Fig. 1 Histogram of snout urostyle length of males and females in the gold-stripe pond frog (*Pelophylax plancyi*) and the terrestrial frog (*Fejervarya limnocharis*)

表 1 金线侧褶蛙和泽陆蛙形态特征的种间和性别间差异

Table 1 Inter-specific and between-sex differences of morphological traits (M±1SE) for the gold-striped pond frog (*Pelophylax plancyi*) and the terrestrial frog (*Fejervarya limnocharis*)

种类 Species	性别 Sex	样本数 Sample size	头长(mm) Head length	头宽(mm) Head width	眼径(mm) Diameter of eye	前肢长(mm) Forelimb length	后肢长(mm) Hindlimb length
金线侧褶蛙 *P. plancyi*	♀	76	16.58±0.18	15.45±0.24	4.80±0.12	24.78±0.49	66.25±0.94
	♂	28	16.18±0.14	14.88±0.18	4.81±0.09	22.07±0.38	59.31±0.72
泽陆蛙 *F. limnocharis*	♀	42	14.07±0.12	13.51±0.15	4.47±0.07	19.29±0.31	56.94±0.60
	♂	50	14.18±0.13	13.43±0.17	4.46±0.08	18.85±0.35	53.90±0.66
种类 Species			$F_{1,191}=182.2^{***}$	$F_{1,191}=60.26^{***}$	$F_{1,191}=9.40^{**}$	$F_{1,191}=96.35^{***}$	$F_{1,191}=76.02^{***}$
性别 Sex			$F_{1,191}=0.76^{NS}$	$F_{1,191}=2.19^{NS}$	$F_{1,191}=0.001^{NS}$	$F_{1,191}=12.49^{***}$	$F_{1,191}=34.70^{***}$
交互作用 Interaction			$F_{1,191}=3.39^{NS}$	$F_{1,191}=1.79^{NS}$	$F_{1,191}=0.01^{NS}$	$F_{1,191}=9.43^{**}$	$F_{1,191}=7.66^{**}$

体长为协变量，设置为 44.79mm；*F* 值后的符号表示差异显著性水平；NS 差异不显著 Snout urostyle length was used as the covariate, which was set at 44.79 mm; Symbols immediately after *F* values represent significant level; NS nonsignificant; ** $p<0.01$, *** $p<0.0001$

2.4 生育力

金线侧褶蛙和泽陆蛙的怀卵量皆与体长正相关，以母体体长为协变量的协方差分析显示，金线侧褶蛙和泽陆蛙的怀卵量无显著差异（$F_{1,98}=2.83$ $p=0.10$）（图 3）。

3 讨论

研究结果表明，金线侧褶蛙的两性异形程度大于泽陆蛙，即金线侧褶蛙雌体的相对大小较泽陆蛙大，但两者的怀卵量无显著差异。该结果与生育力选择理论的预测不符。由于两性异形进化过程非常复杂，导致此种不一致性的可能原因有：

（1）进化选择压力作用于雄体而非雌体。泽陆蛙年产多次卵，且繁殖期（4～9 月份）远长于金线侧褶蛙（4～6 月份）[17]。因此，金线侧褶蛙雄体竞争配偶可能比泽陆蛙激烈。面对激烈的配偶竞争，雄体可能采取两种策略，一种策略是个体增大，在争斗中处于有利地位，从而获得较多的交配机会[2,20,21]，在雄体大于雌体的两性异形类型中，雄体常采取此种策略[2]。另一种策略是雄体以较小个体成熟，可提早获得交配机会，或因其较高的活动性而容易找到雌蛙，提高其繁殖成功率[22]。推测金线侧褶蛙采取后一种策略。当然，该推测尚需繁殖行为研究的证实。

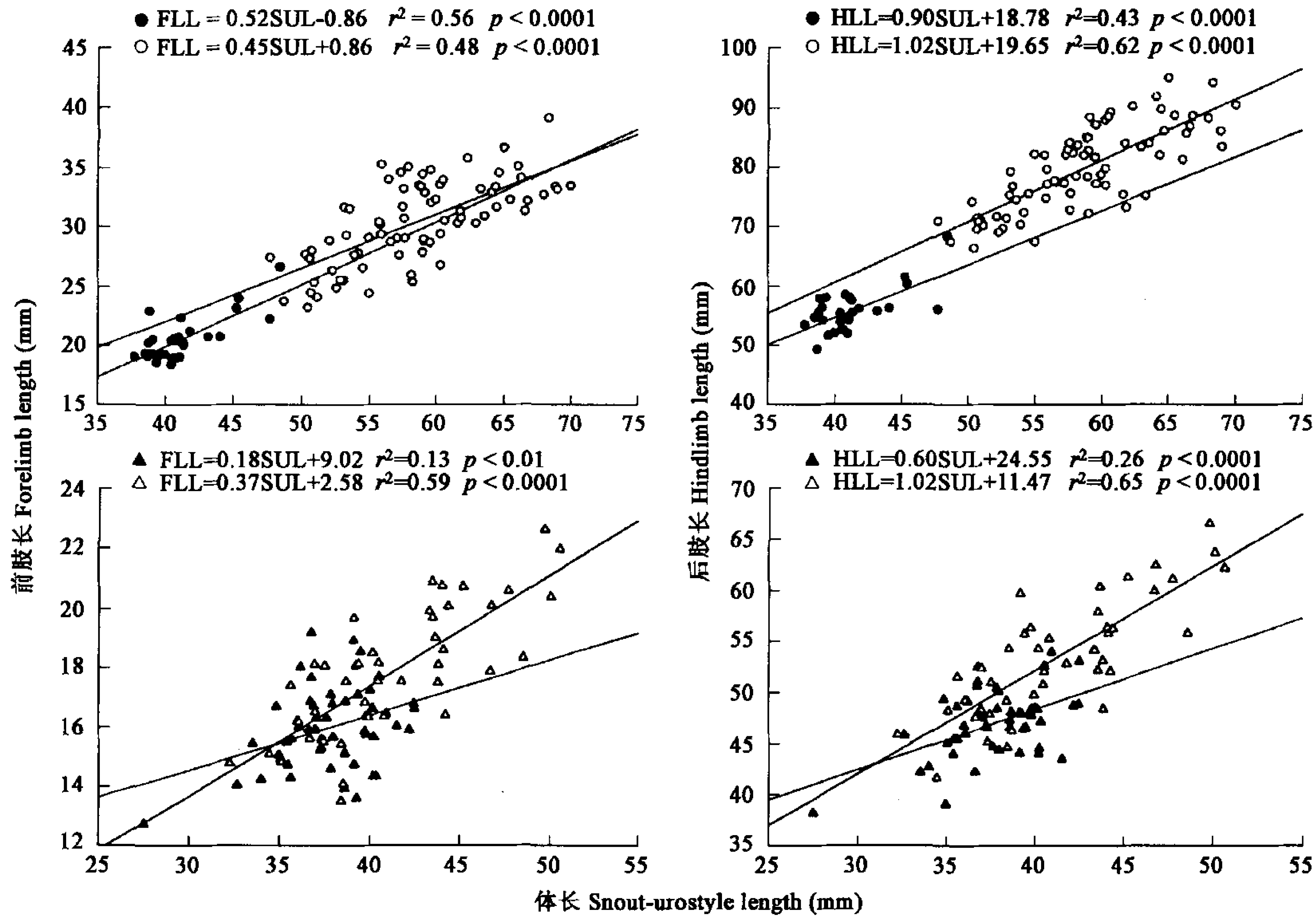

图 2　金线侧褶蛙和泽陆蛙前后肢长度与体长的关系

Fig. 2　The relationships between limb length and snout-urostyle length in the gold-striped pond frog (*Pelophylax plancyi*) and the terrestrial frog (*Fejervarya limnocharis*)

●金线侧褶蛙雄体 Male *P. plancyi*, ○金线侧褶蛙雌体 Female *P. plancyi*, ▲泽陆蛙雄体 Male *F. limnocharis*, △泽陆蛙雌体 Female *F. limnocharis*

(2) 雌体能量分配策略的种间差异。泽陆蛙繁殖期长,年繁殖多次,因此,尽管泽陆蛙和金线侧褶蛙的怀卵量相似,泽陆蛙年繁殖输出应该大于金线侧褶蛙。由此推测,在繁殖和生长间的能量分配中,与金线侧褶蛙相比,泽陆蛙雌体可能较多地照顾繁殖,从而导致个体较小。两性能量分配策略差异也被用于解释其它种类两性异形的进化[7,13]。

(3) 雌体的寿命或死亡率存在种间差异。与泽陆蛙相比,金线侧褶蛙雌体产后身体状态较好,而且繁殖期短[19],其自然死亡率低,寿命较长,因此,对终生生长的两栖类来说,个体生长时间较长意味着相对较大的个体。如果上述假设成立,那么检测到的个体大小种间差异可能由雌蛙年龄种间差异所致。雌雄个体寿命和死亡率的差异已被认为是导致两栖动物两性异形形成的重要原因[9,23]。

(4) 由于所比较的种类数量少,本文未能分析系统发育关系对蛙两性异形进化的作用。事实上,系统发育关系在进化特征的种间比较中有着重要的作用[24,25],因此,本文结果与生育力理论不符尚可能受种间系统发育关系的影响。进一步的工作可在获得更多种类的形态和繁殖数据的基础上,应用系统发育独立比较法(phylogenetically independent contrasts)分析两栖类两性异形与生育力选择的关系[25,26]。

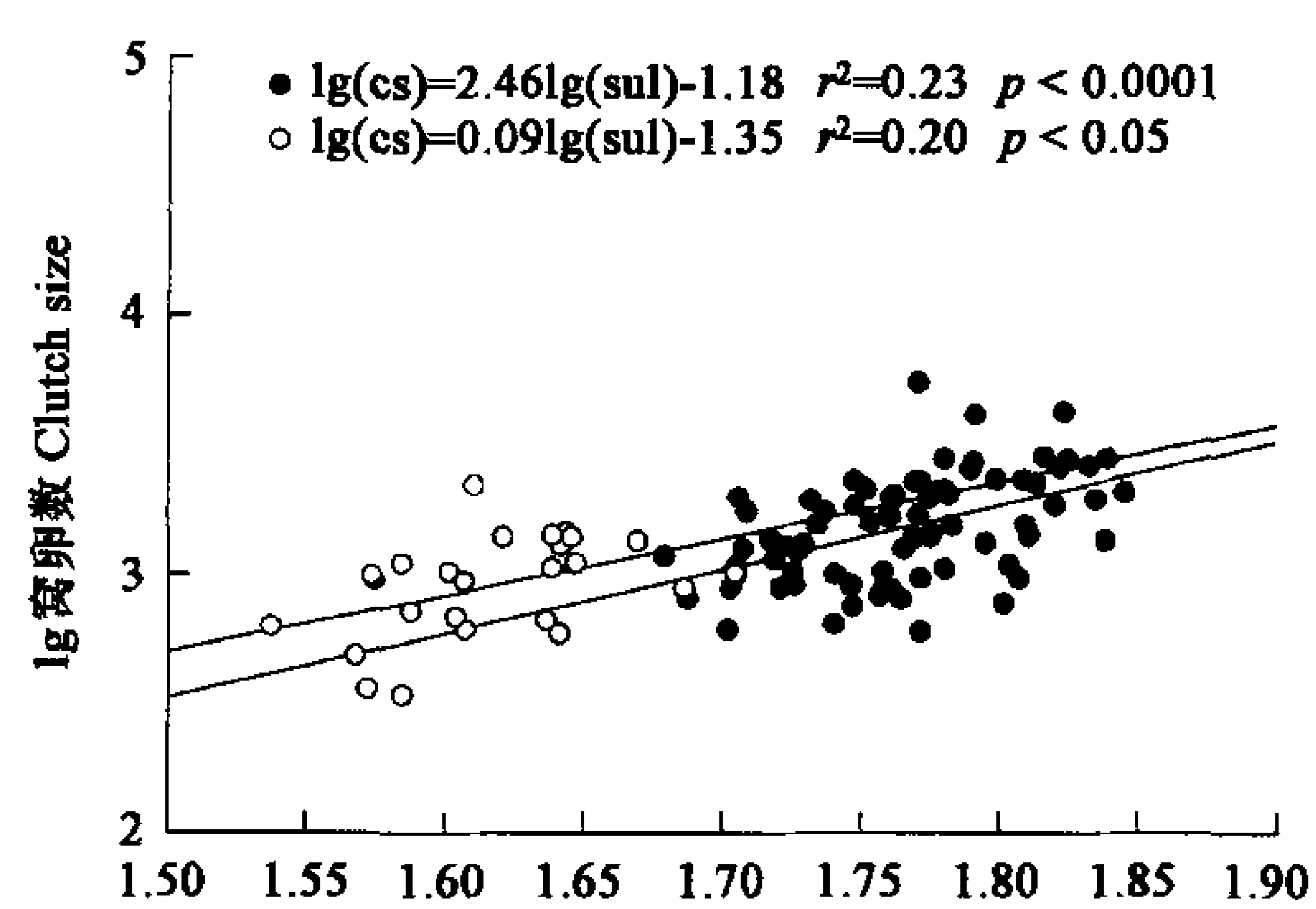

图 3　泽陆蛙和金线侧褶蛙的怀卵量与雌体体长的关系

Fig. 3　The relationships between clutch size and snout-urostyle length of females in the gold-striped pond frog (*Pelophylax plancyi*) and the terrestrial frog (*Fejervarya limnocharis*)

●金线侧褶蛙 *P. plancyi*, ○泽陆蛙 *F. limnocharis*

金线侧褶蛙和泽陆蛙身体状态均存在显著的性别差异,雌体的身体状态指数显著低于雄体。雌体较差身体状态与其较大的繁殖投入密切相关。当环境条件适宜时,雌蛙将大部分能量(包括体内储能和摄入能)分配用于繁殖,以产出大量卵[27,28]。较高

的繁殖输出可能导致产后雌体状态较差，具有较高的死亡率，因而其繁殖价也高[28,29]。而繁殖季节雄蛙的能量则主要消耗于持续鸣叫[30]。

金线侧褶蛙前后肢长度大于泽陆蛙(表 1)。与同属的黑斑侧褶蛙(*Pelophylax nigromaculata*)相同[14]，金线侧褶蛙两性个体的前后肢随体长呈同速生长，而泽陆蛙则表现为异速生长。同域分布的此两种蛙在生境选择上略有不同，金线侧褶蛙生活于水田、池塘、沟渠等静水域中，而泽陆蛙生活于静水域或附近的旱地草丛[19]。动物四肢主要与运动方式和能力有关，两者前后肢的上述差异是否为不同类群间的差异，还是对生存环境差异的适应，尚待进一步证明。此外，两种蛙前后肢均表现显著的两性差异，雌体前后肢长度大于雄体。此种两性差异具有重要的生态意义。雌蛙在怀卵期间具有较大的体重负担。相对较长的四肢可提高运动能力[31]，可弥补因生理负担导致的运动能力下降，从而能有效逃避被捕食，提高野外生存几率。

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