

# 爬行动物多父性生殖策略研究进展\*

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**摘要** 动物生殖策略是多种多样的。对一个种群交配体系的调查有助于了解生殖模式的进化情况, 并为一些濒危物种的保护计划提供理论依据, 同时也为经济养殖动物的人工繁育提供理论支持。多父性(multiple paternity)现象是一种重要的生殖策略, 在爬行类动物中普遍存在, 并且在主要类群中多父性的水平也比较高, 特别是多数有鳞类动物存在多父性现象的窝数可占到总检测窝数的 50% 以上, 这种现象强烈地支持雌性存在混交的进化过程。本文对多父性产生的组织结构、可能机制和多父性的检测手段等进行综述, 并对未来的研究方向提出了建议。

**关键词** 爬行动物; 多父性; 多重交配; 生殖策略; 微卫星

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**Reproductive strategy of multiple paternity in reptiles: A review.** BU Xing-jiang, NIE Liu-wang\*\* (*Key Laboratory for the Conservation and Utilization of Important Biological Resources, Anhui Province, College of Life Sciences, Anhui Normal University, Wuhu 241000, Anhui, China*). *Chinese Journal of Ecology*, 2011, **30**(12): 2888–2897.

**Abstract:** Animals have developed a variety of reproductive strategies. To better understand these strategies will not only provide insights into the evolution of animal reproductive mode, but also provide guidelines for more successful conservation managements and captive breeding programs for threatened or endangered species. Multiple paternity is an important reproductive strategy commonly occurred in reptiles, and at higher levels in major groups of reptiles. Especially for the majority of squamates, multiple paternity can be found in more than 50% of the clutches detected, which strongly suggests that there exists high level female promiscuity in the evolution of productive mode in these species. In this paper, the organizational structure, possible underlying mechanisms, and detection methods of multiple paternity were reviewed, and the prospects of related research were discussed.

**Key words:** reptiles; multiple paternity; multiple mating; reproductive strategy; microsatellite.

性别分化使有性生殖成为可能, 而有性生殖又为个体之间设置了一个冲突和竞争的环境, 因为雌雄个体都希望最大限度地把自己的基因传递给后代。性选择(sexual selection)理论认为, 性选择就是可以增加生殖成功性状的选择。对于雄性而言, 繁殖成功的最大障碍来自于配偶的获得, 因此雄性的策略就是要和尽可能多的雌性交配。相反, 雌性的繁殖成功更多地受自身卵子数量的限制, 而对配偶的数目没有要求。因此, 对于多重交配(multiple mating)的需求雄性比雌性强烈的多(Uller & Ols-

son, 2008)。而多重交配又为多父性(multiple paternity)现象的产生奠定了基础。多父性是指同一母本所产的同窝子代中存在多个父本的现象。多父性现象广泛存在于无脊椎动物和脊椎动物中。主要包括: 昆虫类(Song *et al.*, 2007; Hughes *et al.*, 2008)、甲壳类(Streiff *et al.*, 2004; Yue & Chang, 2010)、鱼类(Dierkes *et al.*, 2008; Sefc *et al.*, 2008)、两栖类(Myers & Zamudio, 2004; Adams *et al.*, 2005)、爬行类(McVay *et al.*, 2008; Ursenbacher *et al.*, 2009; Joseph & Shaw, 2010)、鸟类(Westneat & Stewart, 2003)和哺乳类(Kitchen *et al.*, 2006; Gottelli *et al.*, 2007)。但多重交配与多父性之间并非简单的一一对应关系(Griffith, 2007)。例如, 多重

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交配在隐性雌性选择和精子竞争等情况下就未必能产生多父性现象。同时窝卵数的多少也限制了多重交配和多父性这样的对应关系。可见,雌性交配体系的划分仅仅依赖单个亲权关系鉴定模式有时可能得到错误的结论(Uller & Olsson, 2008)。多父性的机理比较复杂,各种假说的争议也比较大。本文综述爬行动物的多父性模式、过程和未来可能的研究方向,以期为爬行动物多父性生殖策略及相关研究提供理论依据。

## 1 爬行动物生殖生物学

### 1.1 爬行动物储存精子的组织结构

爬行动物包括:喙头蜥类、鳄类、龟鳖类和有鳞类(包括:蜥蜴类和蛇类)(Townsend *et al.*, 2004)。对于爬行类动物而言,多父性现象的出现,不仅要有多重交配,更重要的是雌性应具备储存精子功能。部分雌性具有储精囊(sperm storage tubules),这是储存精子的结构,为后续雌性排卵受精做准备。据Davenport(1995)报道,在一条雌性的凯门鳄与雄性分离488 d后,产卵16枚,有1枚以上的卵发育成胚胎,由此推测雌性的凯门鳄生殖系统应该有储精功能。当然并不是所有的爬行动物都具有储精囊,但有趣的是,没有储精囊的爬行动物也有多父性现象。说明精子储存在雌性生殖系统的某处,如在密西西比鳄雌性生殖系统中未发现储精囊,但其仍然存在多父性现象;密西西比鳄的精子储存在两个地方:一是子宫和阴道的交界处,还有一个是漏斗口和输卵管峡部的交界处(Davis *et al.*, 2001; Gist *et al.*, 2008)。在脊椎动物中,爬行动物储存精子能力是最强的,精子储存时间最长的可达7年之久(Holt & Lloyd, 2010)。正是由于有了这些组织结构的存在,才使精子储存成为可能,也为多父性现象的发生提供了物质基础。

### 1.2 爬行动物的交配系统

爬行动物不仅形态千差万别,而且交配模式也多种多样。动物交配体系一般是指个体配偶数目,它是多种因素综合作用的选择结果。如配偶的选择、可供选择配偶的密度以及雌雄性成熟的同步性等,甚至全球变暖也会对交配体系产生影响(Olsson *et al.*, 2011)。在爬行动物中很少发现一雌一雄交配模式,而长期相互忠诚的伴侣更是少见(Bull, 2000)。在脊椎动物中,单配偶模式形成通常被认为是为了双亲抚育及配偶保护(Stamps, 1983)。在

爬行动物中,单配偶模式仅出现在某些高度社会性蜥蜴类,这主要为了间接抚育后代和家庭式生活能增加抗风险的能力(Chapple & Keogh, 2006)。此外,还存在季节性单配偶模式,这主要是强壮的雄性保卫领地内雌性的结果,如喙头蜥(Moore *et al.*, 2009)。某些爬行类物种雌雄相遇的机会少,从后代检测情况看,它表现出单配偶现象,可能实际情况并非如此,如棱皮龟(*Dermochelys coriacea*, 表1)。这些情况可能导致了多父性水平较低的现象。而大多数爬行动物都没有抚育后代的习性,它们属于混交模式,即一个雌性动物可以与多个雄性交配,同时一个雄性也可以与多个雌性交配。

### 1.3 储存精子的进化原因及作用

在爬行动物的各主要类群中精子储存是普遍存在的(Olsson & Madsen, 1998; Uller & Olsson, 2008)。然而,其进化原因存在争议。有些学者认为,在一些物种中,由于种群密度低,雌雄相遇机会小,因此,精子储存就可以避免没有精子给卵子受精的危险(Gist & Congdon 1998);但这种假设很难让人信服,因为,许多雌雄相遇几率很高的物种,它们也具有精子储存的能力,如在繁殖季节,蜥蜴和蛇类种群密度就非常高。对于高密度种群也存在精子储存的现象,有学者认为,隐性雌性选择可能是进化上导致精子储存产生的原因(Olsson & Madsen, 1998)。总之,精子储存使得交配与受精分离,不仅延长了雌性的繁殖周期,而且精子竞争和多重交配也有利于雌性选择更有活力的精子。精子储存减少了由于交配频率所引起的动物之间的捕食,降低了某些种群密度低或运动缓慢而带来的繁殖困难(Sarkar *et al.*, 2003; Adams *et al.*, 2005; Storrie *et al.*, 2008)。

## 2 多父性现象产生的可能机制

### 2.1 多父性产生的直接利益

一般来说,多重交配对于雌性的直接利益包括:雌性可以得到“婚礼”,多于一个雄性的帮助等。对于爬行类动物,这些直接利益并没有体现出来。原因有二,一方面,大多数爬行动物没有抚育后代的习性,因而雌性不需要雄性的帮助;另一方面,也没有证据表明雄性会送礼物给雌性。实际上,多数爬行动物趋向于自己储存繁殖所需的资源(Olsson & Madsen, 1998)。但对于雌性而言,直接利益就是多重交配能保证有足够的精子数量用于卵受精。因为

一些雄性不育或交配过程中出现精液转移不足,可能出现可供受精的精子数目不足的现象(Török *et al.*, 2003)。究竟多少次交配才能确保雌性爬行动物能成功受精还没有进行系统研究。在对普通蜥蜴(*Lacerta vivipara*)的研究中,蜥蜴多次交配最主要的原因可能是精子的限制或为了避免雄性不育情况的出现(Uller & Olsson, 2005)。此外,来自龟类的证据表明,当雌雄相遇机会低时,精子储存就成了连续产卵能够成功受精的保障了(Pearse & Avise, 2001)。可见,对于一些爬行动物野生种群来说,精子限制对于雌性可能是个真正的难题。为了避免这种情况的出现,雌性动物可能就会和所有遇到的雄性交配,这也降低了雌性在交配前对配偶的选择。

## 2.2 间接利益

对于爬行动物而言,多重交配的间接利益至少有4种可能机制来解释(Jennions & Petrie, 2000)。最容易理解的一个利益就是第二雄性配偶的受精优势,即雌性多配偶是为了“优中选优”(trading up),例如,当它们遇见一个比以前配偶更优秀的雄性(Jennions & Petrie, 2000; Pitcher *et al.*, 2003)。其他3个方面的利益与雌性同时储存有多个雄性精子有关,特别在受精过程开始之前或进行时。这样多重交配的第二个利益就是可以促进来自不同雄性间的精子竞争(sperm competition)(Parker, 1998)。这将确保卵子能与竞争中获胜的精子结合,假如这种优势能够遗传,那么它们子代的精液也将在精子竞争中处于优势地位。或者,精子竞争成功更有可能是与遗传质量有关系。例如,多重交配促进了精子竞争,这无疑增加了好的基因遗传给后代的机会(Jennions & Petrie, 2000)。第三个利益是隐性雌性选择(cryptic female choice),提高了后代遗传质量和成活数量(Tregenza & Wedell, 2000)。第四个利益就是遗传策略避险(bet-hedging),多重交配提高了后代遗传多样,这有利于抵御环境变化所带来的选择压力(Yasui, 2001)。

**2.2.1 “优中选优”** 该假说认为,如果一个雌性动物遇到第二个雄性(当然也可能是第三个,或更多)发现比以前的配偶更优秀,她很可能与这个雄性交配。虽然这个假说很有道理,也容易理解。但在爬行动物中还没有直接证据支持这一假说(Eizaguirre *et al.*, 2007; Zbinden *et al.*, 2007)。而且,也没有研究表明那些死的、流产的和无生存能力的后代就是某一特定父本所为。如果这个假说是事实的

话,那么这个父本应该是可以推知的。对于雌性动物是否会主动寻找配偶以及不同的雄性父本是否会引起同一窝后代产生不同的表型等,都需要提供有力的证据来说明(Stapley & Keogh, 2005)。此外,就目前实验研究所调查的雌性与交配地位和雄性质量相关的交配行为来看,没有发现雌性与更优秀雄性再交配概率的增加。更多的情况是雌性对雄性配偶是不加选择的(Olsson, 2001)。爬行动物中,交配前重视配偶选择少有证据,这也使得该假说很难对多数物种适用。这种情况的出现,也可能是这方面相关的研究开展较少,或者没有很好的设计能说明雌性选择配偶的实验(Olsson *et al.*, 2004; Jansson *et al.*, 2005)。交配行为研究结合分子亲权关系数据将可能给予解释。

**2.2.2 促进精子竞争** 该假说认为,多重交配促进精子竞争,从而有助于产生高质量的后代(Jennions & Petrie, 2000)。在爬行动物中该假说还没得到验证。证明受精成功是精子竞争的结果,需要有一个可遗传的性状标记或与遗传质量相关的标记。受精成功可遗传的性状标记在爬行动物中还没有研究。并且对于种内精子性状的变异以及它们可否遗传等相关证据很少(Schulte-Hostedde & Montgomerie, 2006)。然而,配偶的数目与后代的生存能力之间正相关性是与该理论一致的(Olsson *et al.*, 1994)。同时,两性之间的性别冲突可能导致不同的适合度反馈也是值得注意的,这种反馈主要体现在后代子女性别比例上,也直接关系到父本精子竞争能否成功(Arnqvist & Rowe, 2005),这也意味着这种遗传利益的获得必定包含了某种复杂精密的性别分配决策机制(Pischedda & Chippindale, 2006; Fawcett *et al.*, 2007)。它可能包括来自不同父本的精子匹配问题,即这种匹配要与调节同一窝子代性别比例相适应(Olsson *et al.*, 2005a)。与之相反的遗传质量理论认为,性比并不是均衡的,可能偏向某一性别。例如,当雌性沙蜥(*Lacerta agilis*)与高质量的雄性沙蜥交配后,所产生的子代性比偏向女儿(Olsson *et al.*, 2005a, 2005b)。而在果蝇(*Drosophila melanogaster*)的研究中则表明,雌果蝇与高质量的雄果蝇交配后,所产生的子代性比偏向儿子(Pischedda & Chippindale, 2006)。因此,既然父本的质量关系到生儿生女的适合度反馈,那么解决问题的关键应该是通过精心实验去求证,而不是简单依赖某个理论模型假设(Olsson *et al.*, 2005a, 2005b; Pischedda & Chipp-



indale, 2006)。

**2.2.3 隐性雌性选择** 隐性雌性选择指雌性操纵2个以上已经成功与之交配雄性的受精成功率的过程。多重交配增加了隐性雌性选择的可能性,这被认为是蜥蜴类动物在进化过程中出现雌性混交现象最可能的原因(Olsson & Madsen, 1998)。也支持早期实验室和野外对沙蜥的研究结果(Olsson & Madsen, 1996)。该理论与那些依赖“好基因”假设都表明亲权关系将强烈地偏向某个父本(Eberhard, 1996)。如果多重交配引起隐性雌性选择或者促进精子竞争以获得遗传利益这些情况存在,那么雌性实际交配的雄性数目应该远高于多父性数据所评估出的雄性数目。在蜥蜴和蛇类中,多父性现象是普遍的(表1),并已证明高于其他脊椎动物类群,经常每窝的后代出现多于2个父本的现象。

野生种群表现出高水平的多父性现象,给雌性控制受精的理论带来了挑战。隐性雌性选择有必要吗?即使多重交配后受精是随机的,雌性也是受益的,因为至少会有一部分后代是来自高质量的父本。很显然,在能准确阐明促进精子竞争和隐性雌性选择在雌性混交进化过程中所起的作用之前,需要实验检验交配顺序和个体基因型及表型与亲权关系模式之间的重要关系(Olsson *et al.*, 2004)。理想的情况下,这种检验应该与雌性对交配频率的适应性和多父性出现程度的测量相结合,同时对后代和胚胎的存活情况也应检测(Le Galliard *et al.*, 2005; Eizaguirre *et al.*, 2007)。在早期蛇类和蜥蜴类中开展的交配实验研究中,已经表明某些种的受精并不是随机的(Olsson *et al.*, 1996, 2004)。在对沙蜥长达十多年的跟踪研究中,发现如果与一个雌性所交配的雄性配偶“质量”差异比较大,那么该雌性所产每窝后代的多父性水平就会有所降低,表明有较强的隐性雌性选择存在,以免产生畸形后代(Olsson *et al.*, 2011)。

**2.2.4 避险策略** 遗传避险策略就是多重交配使同一窝后代能产生更多的遗传变异类型(Yasui, 2001)。由于环境条件经常变化,雌性在交配时很难预测哪种表型将来最能适应环境,这为避险策略的进化机制提供了可能,因为它能降低雌性繁殖成功的不确定性(Sarhan & Kokko, 2007)。虽然理论上有些道理,但有时也只能将它作为多父性现象高水平发生的一个可能解释(Calsbeek *et al.*, 2007),并且支持遗传避险策略的情况也是非常有限的

(Sarhan & Kokko, 2007)。此外,父本基因型的变异所引起的子代表型变异与环境波动选择之间有重要联系,在任何类群中都是很少有证据支持这一观点的。而要为避险策略找证据,必须要克服一个实验难题,就是这个实验需要比较来自多个父本的后代与来自单个父本的后代适合度的差异,这需要通过在可控环境下的繁殖实验来反映自然变异情况。到目前为止,避险策略对爬行类动物重要性的评估,还没有获得认可的证据。蝴蝶中可能有一个例子(Sarhan & Kokko, 2007)。

### 2.3 雌雄性别之间的冲突

即使对雌性来说没有直接和间接利益的时候,也能产生多父性现象(Lee & Hays, 2004; Arnqvist & Kirkpatrick, 2005)。多重交配和多父性现象无论何时在交配系统中出现,都可能更有利于雄性。假定雌性与多个雄性交配没有任何的直接或间接利益,且雄性交配不需任何成本,那么在一个群体内多重交配的水平将由配偶相遇频率和雌性交配所需成本确定。但即使存在雌性为交配需要付出成本,雄性也可能强行交配。例如,在束带蛇(*Thamnophis sirtalis*)中,雄蛇通过将雌蛇向地面挤压而迫使雌蛇泄殖腔张开,以便雄蛇交配器插入(Shine & Mason, 2005)。随后多父性表现程度可能受到精子竞争过程的影响,在没有雌性选择存在的情况下,这个过程就相似于一次“公平抽奖”活动了(Parker, 1998)。

在性别冲突这种假设条件下,野生种群多父性现象很大程度上反映了在每个繁殖周期中雌性与不同雄性相遇的概率。更重要的是,在非领域种群和高密度种群中,雌雄相遇的概率很可能是要高于平均水平的,而那些雌雄动物之间有稳定的配偶关系的种群可能要低于平均水平。在爬行动物中多父性的模式与这个假说是高度一致的。例如,在蜥蜴类群中,保持配偶关系的社会性小蜥蜴与相似生态环境中其他蜥蜴相比,显示较低的多父性水平。当然对于后者蜥蜴中具有领域保护的种其多父性水平也较低。此外,在龟类研究中,每窝多个父本的比例是与繁殖种群的大小呈正相关。例如,集体筑巢繁殖的太平洋丽龟(*Lepidochelys olivacea*)种群比单独筑巢繁殖的种群,每窝出现多个父本的概率要高的多(Jensen *et al.*, 2006)。

### 3 多父性的检测手段

要知道每窝卵是否存在多个父本,最直观的方法

表 1 爬行动物多父性相关研究总结  
Table 1 Summary of molecular genetic studies of multiple paternity in reptiles

物种名	多父性比例( 有多个父本的窝数/总检测窝数)	分子标记	文献来源
喙头蜥类			
楔齿蜥( <i>Sphenodon punctatus</i> )	18. 8% (3/16) 、8. 3% (1/12)	微卫星	Moore <i>et al.</i> ,2008,2009
鳄类			
美洲鳄( <i>Alligator mississippiensis</i> )	31. 8% (7/22) ,51% (47/92)	微卫星	Davis <i>et al.</i> ,2001; Lance <i>et al.</i> ,2009
佩滕鳄( <i>Crocodylus moreletii</i> )	50% (5/10)	微卫星	McVay <i>et al.</i> ,2008
龟鳖类			
蠵龟( <i>Caretta caretta</i> )	33. 3% ( 1/3 )、33% ( 1/3 )、31. 4% (22/70) ,95% (19/20)	微卫星、等位酶	Briscoe, 1988; Bollmer <i>et al.</i> , 1999; Harry & Moore & Ball,2002; Zbinden <i>et al.</i> ,2007
绿海龟( <i>Chelonia mydas</i> )	9. 1% ( 2/22 )、100% ( 3/3 )、100% ( 2/2 )、61% ( 11/18 )、50% (9/18)	微卫星	Peare & Parker, 1996; Fitzsimmons, 1998; Ireland <i>et al.</i> , 2003; Lee & Hays,2004; Lara-De la Cruz <i>et al.</i> , 2010
锦龟( <i>Chrysemys picta</i> )	4% ( 1/24 )、13. 2% ( 15/113 )、33% (71/215)	微卫星	McTaggart, 2000 *; Pearse <i>et al.</i> , 2001,2002
鳄龟( <i>Chelydra serpentina</i> )	66% (2/3)	DNA 指纹图谱	Galbraith <i>et al.</i> , 1993
木纹龟( <i>Clemmys insculpta</i> )	50% (5/10)	DNA 指纹图谱	Galbraith,1993
棱皮龟( <i>Dermochelys coriacea</i> )	10% (2/20) ,0 (0/17) ,0 (0/4)	微卫星	Rieder <i>et al.</i> , 1998 *; Dutton <i>et al.</i> , 2000 *; Crim <i>et al.</i> ,2002
太平洋丽龟( <i>Lepidochelys olivacea</i> )	20% ( 2/10 )、92% ( 12/13 )、30% (4/13)	微卫星	Hoekert <i>et al.</i> ,2002; Jensen <i>et al.</i> , 2006
肯普氏丽龟( <i>Lepidochelys kempi</i> )	57. 7% ( 15/26)	微卫星	Kichler <i>et al.</i> , 1999
侧颈龟( <i>Podocnemis expansa</i> )	100% ( 2/2)	微卫星	Valenzuela,2000
欧洲泽龟( <i>Emys orbicularis</i> )	10% (2/20)	微卫星	Roques <i>et al.</i> ,2006
玳瑁( <i>Eretmochelys imbricata</i> )	20% (2/10)	微卫星	Joseph & Shaw,2010
沙漠陆龟( <i>Gopherus agassizii</i> )	50% (6/12)	等位酶	Palmer <i>et al.</i> ,1998
佛州地鼠龟( <i>Gupterus polytemus</i> )	28. 6% (2/7)	微卫星	Moon <i>et al.</i> ,2006
欧洲陆龟( <i>Testudo graeca</i> )	20% (3/15)	微卫星	Roques <i>et al.</i> ,2004
四爪陆龟( <i>Testudo horsfieldii</i> )	27. 3% (3/11)	微卫星	Johnston <i>et al.</i> ,2006
蜥蜴类			
怀特石龙子( <i>Egernia whitii</i> )	11. 6% (6/50) ,34% (31/91)	微卫星	Chapple & Keogh,2005; While <i>et al.</i> , 2011
刺尾石龙子( <i>Egernia stokesii</i> )	25% (4/16)	微卫星	Gardner <i>et al.</i> ,2002
坎氏石龙子( <i>Egernia cunninghami</i> )	2. 6% (1/38)	微卫星	Stow & Sunnucks,2004
Southern water skink( <i>Eulamprus heatwolei</i> )	64. 7% ( 11/17)	微卫星	Morrison <i>et al.</i> ,2002
Southern snow skink( <i>Niveoscincus microlepidotus</i> )	75% (6/8)	AFLP	Olsson <i>et al.</i> ,2005c
Grand skink ( <i>Oligosoma grande</i> )	46. 7% (7/15)	微卫星	Berry,2006
Mt log skink ( <i>Pseudomoia eurecateuxi</i> )	53% (9/17) ,27% (3/11)	微卫星	Stapley <i>et al.</i> ,2003; Stapley & Keogh, 2006
松果蜥( <i>Tiliqua rugosa</i> )	19% (4/21)	微卫星	Bull <i>et al.</i> ,1998
胎生蜥蜴( <i>Lacerta vivipara</i> )	47. 0% ( 24/51 )、55. 3% ( 21/38 )、65. 4% ( 17/26 )、68. 2% ( 30/44 )、50. 0% ( 7/14 )、69. 2% (72/104)	微卫星	Laloi <i>et al.</i> ,2004; Fitze <i>et al.</i> ,2005; Hofmann & Henle,2006; Eizaguirre <i>et al.</i> ,2007
沙蜥( <i>Lacerta agilis</i> )	80% (4/5)	DNA 指纹图谱	Gullberg <i>et al.</i> ,1997
墙壁蜥蜴( <i>Podarcis muralis</i> )	87. 1% (27/31)	微卫星	Oppliger <i>et al.</i> ,2007
<i>Ameiva exsul</i>	9. 1% (1/11)	DNA 指纹图谱	Lewis <i>et al.</i> ,2000
华丽龙( <i>Ctenophorus ornatus</i> )	25% (5/20)	微卫星	Lebas,2001
高原条纹蜥( <i>Sceloporus virgatus</i> )	61. 5% (8/13)	DNA 指纹图谱	Abell,1997
侧斑蜥( <i>Uta stansburiana</i> )	72. 4% (89/123)	微卫星	Zamudio & Sinervo,2000
蛇类			
澳洲水蟒( <i>Liasis fuscus</i> )	85. 7% ( 12/14)	微卫星	Madsen <i>et al.</i> ,2005
北美水蛇( <i>Nerodia sipedon</i> )	85. 7% ( 12/14) ,58% (46/81)	等位酶、微卫星	Barry <i>et al.</i> ,1992; Prosser <i>et al.</i> ,2002
束带蛇( <i>Thamnophis sirtalis</i> )	37. 5% ( 6/16 )、50% ( 3/6 )、100% ( 4/4 )、75% ( 6/8 )、59. 1% (13/22)	微卫星、等位酶	Schwartz <i>et al.</i> ,1989; McCracken <i>et al.</i> ,1999; King <i>et al.</i> ,2001; Garner <i>et al.</i> ,2002; Garner & Larsen,2005
黑鼠蛇( <i>Elaphe obsolete</i> )	88% (30/34)	微卫星	Blouin-Demers <i>et al.</i> ,2005
蝰蛇( <i>Vipera berus</i> )	69% (9/13)	微卫星	Ursenbacher <i>et al.</i> ,2009

\* 引自 Pearse & Avise,2001。

法就是观察母本的交配行为,即是否存在多重交配情况。但在野外观察动物的交配情况,其难度可想而知。退一步说,就算能观察到一个雌性与多个雄性交配了,是否就能很肯定地说该雌性所产的统一窝子代一定存在多父性现象呢?由于存在精子竞争和隐性雌性选择的情况,因此,答案是否定的。可见,虽然观察交配行为是最直观的方法,但也是最难实现和最不确定的方法。随着分子遗传学技术的发展,正彻底地革新了交配系统的分析方法,随着分子标记技术的应用。对多父性现象的鉴定起到了至关重要的作用,如以前认为一些物种是单配制式,但通过分子标记分析确定雌性是混交模式(Wusterbarth *et al.*, 2010)。爬行类动物野生种群多父性鉴定的研究进展如表1。由表1可以看出,对多父性鉴定所用的分子标记有等位酶(allozyme)、DNA指纹图谱(DNA fingerprinting)、扩增片段长度多态性(AFLP)和微卫星(microsatellite)。从表1可以看出,目前,最常用的分子标记就是微卫星。这主要是因为微卫星具有位点丰富性、高度多态性、共显性、基因组DNA用量少,易检测和重复性好等特点,使其非常适合于多父性鉴定。

#### 4 结语与展望

对多父性产生的几种可能机制看,“优中选优”(配偶选择)和避险策略假说被认可的程度不高,在爬行动物中证据较少,还需要进一步的实验数据支持。尤其是配偶选择假说,即使在鸟类被高度认同的情况下,近来也还是有学者提出了质疑(Kotiaho & Puurtinen, 2007)。精子竞争和隐性雌性选择假说被认可的程度相对要高的多,支持的证据也多些。而性冲突假说可能在雄性体型比雌性大的情况下更为多见些。

对爬行动物多父性现象目前的研究主要集中在对野生种群多父性水平的估测,即对每个雌性所产的每窝卵进行多父性检测。而对于多父性产生的机制问题研究的较少,很多仍停留在假设阶段,需要更进一步的实验检测确认。本实验室目前也正在对中华鳖多父性的研究,以筛选到的多态微卫星为分子标记,检测中华鳖是否存在多父性现象,经过对遗传数据的初步分析发现中华鳖也存在多父性现象。笔者认为,对于多父性的研究,今后可从两方面进行深入研究,一方面,要将交配行为观察和分子遗传评估相结合,从而才可能更全面,更真实地了解爬行动

物的交配体系。如果仅依赖于一种手段,可能会得出错误的结论。例如,一些一雌多雄的爬行动物,仅依赖多父性检测的话,由于精子竞争和窝卵数的限制等原因,可能会发现每窝的子代均来自同一个父本,从而得出该物种是单配偶模式的结论。同样,如果仅依赖行为观察,可能就会失去一些存在多父性现象的例子(Moore *et al.*, 2009)。另一方面,对于很多关于多父性产生机理方面的假说,要进行去伪存真的实验鉴别。因为很多理论方面认为合理的假说,没有经过实验的检验,也没有多少证据来支持这些假说。最新研究表明,在一种社会性蜥蜴(*Egernia whitii*)种群中,原先认为单配偶模式的维持是由于性选择很弱,但现在的实验数据表明,即使在这样的单配偶模式下也有很强的性选择(While *et al.*, 2011)。今后在研究中周密可行的实验计划和检验是必需的。

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