

## 亚洲叶猴社会行为学研究进展

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**摘要:** 叶猴以群居为主, 个体间具有丰富的社会行为, 包括相互理毛行为、等级关系、繁殖行为、杀婴行为和玩耍行为等。本文查阅了叶猴属 *Presbytis*、乌叶猴属 *Trachypithecus* 和长尾叶猴属 *Semnopithecus* 社会行为的相关文献, 综述社会行为所涉及的假说, 分析叶猴个体间和猴群间社会行为的作用和功能, 为今后国内叶猴或其他灵长类的研究提供参考和借鉴。

**关键词:** 亚洲叶猴; 叶猴属; 乌叶猴属; 长尾叶猴属; 社会行为

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### Process in the Study on Social Behavior of Asian Leaf Monkeys

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**Abstract:** Asian leaf monkeys, including genera *Presbytis*, *Trachypithecus* and *Semnopithecus*, are generally gregarious animals. Leaf monkeys have complex social behaviors, which have long been concerned. On the basis of previous relevant hypothesizes, this article summarized the process in the study on social behaviors of Asian leaf monkeys, including allogrooming, dominance, reproduction, infanticide and play. The current review provided primatologist with references for future study on social behaviors of leaf monkeys or other primates in China.

**Key words:** Asian leaf monkeys; *Presbytis*; *Trachypithecus*; *Semnopithecus*; social behavior

叶猴隶属于猴科 Cercopithecidae 疣猴亚科 Colobinae, 为亚洲特有, 包括叶猴属 *Presbytis*、乌叶猴属 *Trachypithecus* 和长尾叶猴属 *Semnopithecus*, 共 3 属 45 种 (Roos *et al.*, 2014)。叶猴以群居为主, 社群结构包括一雄多雌、多雄多雌和全雄群 3 种 (黄秉明等, 1996)。叶猴的社会行为可划分为 2 个层次, 即个体间社会行为和群体间社会行为。叶猴的社群结构和社会行为与其他非人灵长类相比有其特殊的一面。本文对涉及叶猴社会行为研究进展的相关假说进行了总结, 为今后同类物种的研究提供参考。

### 1 个体间相互行为

#### 1.1 相互理毛行为

叶猴的理毛行为 (grooming) 可分为相互理毛行为 (allogrooming) 和自我理毛行为 (autogrooming) (Hutchins & Barash, 1976; Dunbar, 1991)。自我理毛行为是个体对自己的毛发进行梳理, 有时从毛发中检出小颗粒放进嘴咀嚼或用嘴咬食; 相互理毛行为是个体间进行毛发梳理, 并不时地从分

开的毛发或露出的皮肤上检出小颗粒放到嘴中咀嚼或直接用嘴咬食 (Pérez & Veá, 1998)。目前关于叶猴相互理毛行为的功能有 3 种假说: 第一种假说是卫生功能假说 (hygienic functional hypothesis), 该假说认为相互理毛行为具有清洁毛发、除去皮肤寄生物和防止感染的功能 (Barton, 1985; Borries, 1992; Borries *et al.*, 1994)。许多研究表明相互理毛行为主要发生在个体无法或难以自我理毛的部位, 如尾基部、背部和头等部位, 对长尾叶猴 *S. entellus* (Borries, 1992; Borries *et al.*, 1994; Koenig & Borries, 2001)、黑叶猴 *T. francoisi* (胡艳玲, 2003; 周岐海等, 2006) 和戴帽叶猴 *T. pileatus* (Kumar & Solanki, 2014a) 等的研究有力地支持了卫生功能假说; 而 Borries (1992) 认为长尾叶猴的相互理毛行为是对无法自我理毛的一种补偿, 这实际上也是卫生功能假说的进一步深化。第二种假说是缓和功能假说 (distensive functional hypothesis), 该假说认为不同个体间的相互理毛行为被认为能减少潜在攻击或消除被理毛者的抵触情绪, 缓解个体间的紧张氛围, 使之趋向缓和 (Terry, 1970)。在对长尾叶猴和白头叶猴

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*T. leucocephalus*的研究中得到证据 (McKenna, 1978; 张颖溢等, 2001)。第三种假说是邓巴种群凝聚假说 (Dunbar's group-cohesion hypothesis), 该假说认为相互理毛行为的时间与种群大小呈正相关, 相互理毛行为不仅对社群成员间的凝聚力具有重要的作用, 而且影响种群扩散和社群性比 (Dunbar, 1991; Lehmann *et al.*, 2007)。对叶猴相互理毛的时间分析发现叶猴需要通过高比值的相互理毛行为时间来保持社群成员间的凝聚力, 相互理毛行为的时间比值是否影响社群大小和种群扩散模型仍需进一步的验证 (Matsuda *et al.*, 2015)。此外, 一些研究还发现相互理毛行为影响繁殖行为, 如长尾叶猴 (Nikolei & Borries, 1997) 和戴帽叶猴 (Islam & Husain, 1982; Kumar & Solanki, 2014a) 在交配前, 雌性常对雄性进行理毛, 而且戴帽叶猴的相互理毛行为中有 21% 回合发生在肛门-生殖区 (Kumar & Solanki, 2014a)。

### 1.2 等级关系

等级关系 (dominance) 普遍存在于群居的非人灵长类中 (Maslow, 1936; Rowell, 1974)。等级序位高的个体在享用资源和交配权中占有优势 (赵海涛等, 2011)。灵长类个体间的等级关系不仅有利于减少打斗和伤亡, 保持社群稳定, 而且能使弱者得到社群保护 (李宏群等, 2004)。在叶猴中, 等级主要通过 2 种方式来判别, 第一种方式是个体间的取代行为, 即原来占据优势资源的个体被赶走并被取代, 或是被其他个体趋近后短时间内主动让出原占有资源, 通过计算个体间的取代矩阵来判别等级 (张颖溢等, 2001; Lu *et al.*, 2013)。在长尾叶猴 (Koenig, 2000; Alam *et al.*, 2015) 和托马斯叶猴 *P. thomasi* (Sterck & Steenbeek, 1997) 中, 取代行为常发生在取食、占据食物斑块和空间位置等时; 一些取代行为则发生在相互理毛行为 (张颖溢等, 2001) 和性行为 (Borries *et al.*, 1991; 张颖溢等, 2001; Tiwary *et al.*, 2012; Alam *et al.*, 2015) 等社会行为中。第二种方式是个体间的攻击-屈服行为, 这是个体竞争资源能力最直接的体现, 通过计算个体间在资源竞争过程中攻击-屈服矩阵来判定 (Koenig *et al.*, 2004)。戴帽叶猴 (Stanford, 1991b)、黑叶猴 (胡艳玲, 2003) 和菲氏叶猴 *T. phayrei* (Koenig *et al.*, 2004) 个体间的攻击行为主要发生在食物出现时或饲喂时间段。虽然全雄群的社群成员组成较为松散, 个体间的等级关系不明显 (Mohnot, 1984), 但是首领猴通常领导猴群的活动, 特别在入侵两性群时, 首领猴会第一个移动 (Minhas *et al.*, 2010)。

### 1.3 繁殖行为

繁殖行为 (reproduction behavior) 是哺乳动物社会行为的重要组成部分, 在叶猴两性群中, 成年雌、雄个体会通过不同的行为来获得自身繁殖的成功。成年雄性会驱赶群内即将性成熟的亚成年雄性 (Rajpurohit *et al.*, 1995), 在雄性替换后, 新主雄也有类似的行为, 甚至会驱赶群内所有其他的雄性个体 (Rajpurohit & Sommer, 1993); 与怀孕的雌性相比, 雄性与未怀孕可生育的雌性交配比例更高 (Ostner *et al.*, 2006); 而一些研究则认为雄性在选择交配对象时偏好等级高个体

而不是未怀孕的个体 (Tiwary *et al.*, 2012); 成年雌性在发情期会对成年雄性进行邀配, 这可能与群内成年雄性数量少有关, 而邀配行为可提高雌性怀孕的概率, 在银色乌叶猴 *T. cristatus* (Bernstein, 1968)、紫面叶猴 *S. vetulus* (Rudran, 1973)、长尾叶猴 (Hrdy, 1980; Alam *et al.*, 2015)、黑叶猴 (梅渠年等, 1987) 和戴帽叶猴 (Solanki *et al.*, 2007) 中均得到证实。

雄性叶猴用更多的时间和精力与雌性交配, 抚育后代则主要由雌性完成 (Jay, 1963; Hrdy, 1980)。母猴对新生婴猴初期具有照顾、哺乳、携带和监督的作用 (Poirier, 1968; Hrdy, 1980; Dolhinow & DeMay, 1982; Rajpurohit, 1997; 黄乘明等, 1998; Zhao *et al.*, 2009; Kumar & Solanki, 2014b), 之后则是教授后代辨别食物、熟悉家域和训练技能等 (Fairbanks, 1990; Zhao *et al.*, 2009)。社群内非母亲成年或亚成年雌性参与抚育幼仔的行为称为阿姨行为或拟母亲行为 (allomothering) (Horwich & Manski, 1975; Fairbanks, 1990)。在叶猴中关于阿姨行为的社会功能有 3 种假说: 第一种是联盟形成假说 (the alliance formation hypothesis) (Hrdy, 1976), 该假说认为阿姨行为能促进其他雌性与幼仔母亲的社会联系, 有利于提高行为发起者的等级, 是雌性间的一种生殖合作 (Hrdy, 1976; Stanford, 1992; Kumar & Solanki, 2014b)。戴帽叶猴的阿姨行为使哺乳的雌性有更多的休息和取食时间 (Stanford, 1992), 也有利于刚生育的母猴恢复体力 (Kumar *et al.*, 2005); 雌性长尾叶猴间的婴猴转移行为可帮助母猴携带婴猴通过一些危险的地方 (Minhas *et al.*, 2010)。第二种假说是学习做母亲假说 (the learning-to-mother hypothesis) (Hrdy, 1980), 该假说认为雌性在参与抚育幼仔的过程中可增加育幼经验, 提高其将来成为母亲时育幼的成功率。在黑叶猴 (胡艳玲等, 2005) 和白头叶猴 (Jin *et al.*, 2015) 中无生育经验的雌性有更多的阿姨行为。第三种假说是婴猴受益假说 (the infant benefit hypothesis) (Chism, 2000), 该假说认为表面上看实施阿姨行为的个体是一种利他行为, 对实施阿姨行为的个体是纯损耗性的, 但对婴猴而言, 阿姨行为会增加对其的保护和照顾, 有利于提高其成活率 (Quiatt, 1979; Dolhinow & DeMay, 1982; Chism, 2000)。

### 1.4 杀婴行为

杀婴行为 (infanticide) 是导致同种类幼仔或胎儿在短时间内死亡的行为 (Hrdy & Hausfater, 1984)。关于叶猴的杀婴行为, 目前可归纳为 3 种假说: 一是雄性繁殖策略假说 (male reproductive hypothesis); 二是减少资源竞争假说 (reduce resource competition hypothesis); 三是病态行为假说 (pathological behavior hypothesis)。雄性繁殖策略假说认为雄性杀婴后, 失去幼崽的雌性会提前进入发情状态, 随之与其交配, 缩短雌性生殖间隔, 使雌性怀上其后代, 有利于自身繁殖的成功, 是目前灵长类杀婴行为的最重要解释 (Hrdy, 1974, 1979)。在长尾叶猴 (Maslow, 1936; Sugiyama, 1965; Sommer & Mohnot, 1985; Newton, 1986; Stanford, 1991a; Rajpurohit *et al.*, 2003; Sharma *et al.*, 2010)、紫面叶猴 (Rudran, 1973)、银色乌叶猴

(Wolf & Fleagle, 1977; Wolf, 1980)、白头叶猴 (Zhao *et al.*, 2011; Yin *et al.*, 2013)、黑叶猴 (Zhou *et al.*, 2013) 和约翰叶猴 *S. johnii* (Kavana *et al.*, 2014) 等叶猴中均得到证实, 杀婴是新主雄强烈的性冲动和迫切与雌性交配的结果 (Maslow, 1936), 在长尾叶猴中有 70% 的雌性在失去婴猴 8 个月之后会有新的婴猴出生, 刚好超过一个怀孕期 (6.5 个月) (Hrdy, 1974)。减少资源竞争假说认为杀婴会减少潜在的竞争者, 增加杀婴者和其后代对资源的获取, 杀婴是种群密度过高的结果 (Rudran, 1973)。如长尾叶猴新主雄会攻击年龄较大的幼猴 (Agoramoorthy, 1994; Sharma *et al.*, 2010)。但该假说不能解释一些新主雄只攻击婴猴而不攻击年长的幼猴或亚成年猴 (Rajpurohit *et al.*, 2003) 和发生在资源相对丰富地区的杀婴行为 (Sharma *et al.*, 2010)。病态行为假说认为杀婴是由于拥挤、人为干扰等因素引起雄性脾气暴躁、行为病态, 从而伤及婴猴 (Bogges, 1979; 张鹏, 2011)。相对雄性而言, 雌性对后代的生殖和抚养投入更多的时间和精力, 杀婴明显对雌性不利, 为了减少杀婴行为, 雌性采取的措施有: (1) 积极发情与新雄性交配 (Hrdy, 1979)。一些怀孕的雌性频繁与新主雄交配, 并出现提前流产的现象 (Agoramoorthy *et al.*, 1988); (2) 迁移。如雌性带着婴猴离开社群或在群外围活动 (Zhou *et al.*, 2013); 未怀孕的雌性迁移到雄性能力更强的两性群, 提高雄性对后代的保护能力 (Wich & Sterck, 2007); 雌性通过迁移使种群数量适中, 减少雄性的替换 (Steenbeek & van Schaik, 2001); (3) 混淆父子关系 (van Schaik *et al.*, 2004)。在多雄多雌群中杀婴的比率要低于一雄多雌群, 这可能和雌性与群内所有成年雄性交配有关 (Borries *et al.*, 1999); 通过对一群多雄多雌社群中长尾叶猴子代 DNA 分析发现, 有超过 21% 基因为非群内雄性的基因, 说明雌性还与群外雄性交配来混淆父子关系, 减少了雄性取代后的杀婴行为 (Launhardt *et al.*, 2001); (4) 加强对婴儿的保护。在栗红叶猴 *P. rubicunda* (Davies, 1987) 和托马斯叶猴 (Steenbeek, 1999) 中, 当两性群雄性替换之后, 带婴猴的雌性会提高对新主雄的警戒, 避免其伤害婴猴。

### 1.5 玩耍行为

玩耍行为 (play behavior) 是指由 2 个或多个个体共同参与的一种相互玩耍行为, 个体间的行为相互影响 (Jiang, 2004), 该行为在灵长类中表现尤为明显 (Baldwin & Baldwin, 1973)。玩耍行为常发生在婴猴和亚成年猴阶段, 一般形式是打斗、逃跑和追逐 (Pellis & Pellis, 1998)。目前解释叶猴玩耍行为的假说是运动-训练假说 (sports-training hypothesis), 该假说认为玩耍是一种肢体活动, 能提高个体身体协调性, 增强体能, 实践和提升运动、打斗和捕食等技巧 (Byers & Walker, 1995)。对长尾叶猴 (Minhas *et al.*, 2010)、金头叶猴 *T. poliocephalus* (Schneider *et al.*, 2010)、黑叶猴 (江峡, 2010; 黎大勇等, 2013) 和暗色叶猴 *T. obscurus* (Karimullah *et al.*, 2014) 的研究均符合该假说; 长尾叶猴 (Minhas *et al.*, 2010) 和黑叶猴 (黎大勇等, 2013) 中的雄性个体间有更多的打斗玩耍

行为。栖息地质量影响着婴猴的玩耍行为, 生活在高质量栖息地的雄性长尾叶猴与生活在贫瘠栖息地的相比, 前者的玩耍频次为后者的 6~7 倍, 内容更加丰富; 随着雨季来临, 食物种类的增加, 后者的玩耍频次也随之大幅增加 (Sommer & Mendoza-Granados, 1995); 在同一地域中, 栖息地为城市的长尾叶猴与栖息地为农村的相比, 前者的玩耍频次更高 (Alam *et al.*, 2015)。幼猴的玩耍行为受到母猴的限制, 如银色乌叶猴 (Amarasinghe *et al.*, 2009) 和长尾叶猴 (Minhas *et al.*, 2010)。

## 2 猴群间的社会行为

### 2.1 猴群间的冲突行为

叶猴的社群具有一定的家域性, 在重叠地区猴群可能会相遇, 在相遇初期常通过声音、视觉等信号进行警告 (Poirier, 1968), 而一些成年雄性则会大声吼叫, 如长尾叶猴和约翰叶猴 (Hohmann, 1989), 雄性的叫声有利于减少与临近社群雄性的冲突 (Wich *et al.*, 2002)。若相互警告无效后, 猴群间就会发生冲突。目前关于猴群间的冲突行为有几种假说, 第一种假说是保卫配偶假说 (mate resource defence hypothesis), 该假说认为两性群中的雄性为了保护占有群内的雌性, 会攻击尝试与群内雌性交配的入侵成年雄性 (David & Ehlers, 2014), 并控制群内雌性使其不迁移到其他猴群 (Stanford, 1991a)。而离开两性群的雄性为了提高入侵两性群的成功率, 会通过组群的方式组成全雄群 (Hrdy, 1980)。在全雄群入侵时, 不仅全雄群某个个体向两性群主雄发起进攻, 而且全雄群所有个体会集体入侵, 当雄性替换成功时, 新主雄由全雄群中等级最高的雄性担任 (Ostner *et al.*, 2006)。在戴帽叶猴 (Stanford, 1991b)、托马斯叶猴 (Steenbeek, 1999; Steenbeek *et al.*, 1999)、长尾叶猴 (Rajpurohit *et al.*, 2003)、菲氏叶猴 (Koenig & Borries, 2012) 和栗红叶猴 (David & Ehlers, 2014) 中均得到证实。一些学者通过雄性间的打斗是否发生在其家域的核域部分, 认为雄性对雌性的保护也是间接保卫食物 (David & Ehlers, 2014), 这实际上也是保卫配偶假说的进一步探讨。第二种假说是保卫食物资源假说 (food resource defence hypothesis), 该假说认为两性群主雄为了保卫现有食物资源攻击其他入侵其家域的雄性, 保护领域资源供群内雌性和后代使用 (Sterck & Steenbeek, 1997; David & Ehlers, 2014)。同时, 叶猴群间为了减少遭遇, 还有第三种假说, 即威胁-水平假说 (threat-level hypothesis)。该假说认为邻居或陌生者可能会与资源拥有者竞争, 对领地的拥有程度反应了其威胁水平, 更强的个体也意味着拥有更大的领地 (Temeles, 1994; Müller & Manser, 2007)。如菲氏叶猴雄性独猴减少在两性群家域边缘活动来避免与该群主雄发生冲突 (Gibson & Koenig, 2012)。

## 3 结论与展望

亚洲有 45 种叶猴, 在一些物种中开展了长达几十年的积累研究 (Borries *et al.*, 1991), 叶猴的社会行为研究取得了引人注目的成果, 在相互理毛行为 (Borries, 1992; Borries

*et al.*,1994)、等级关系(Borries *et al.*,1991)、杀婴行为(Hrdy,1974,1979)和猴群间关系(David & Ehlers,2014)等方面的研究已经成为灵长类社会行为研究的重要组成部分,并形成了有价值的假说;国内叶猴分布点的确定(江海声等,1991;王应祥等,1999;Li *et al.*,2007)、物种的有效保护(黄乘明等,1998)和一些科研基地的建设(张颖溢等,2001;Zhou *et al.*,2013)都为研究叶猴社会行为提供了坚实基础,我国在叶猴的社会行为研究也取得了重要的成果(张颖溢等,2001;胡艳玲,2003;Zhao *et al.*,2011;黎大勇等,2013;Yin *et al.*,2013;Zhou *et al.*,2013;Alam *et al.*,2015)。随着部分为解释叶猴社会行为而提出的假说在更多非人灵长类物种中得到验证,加强对叶猴社会行为的研究将有助于提高人们对非人灵长类社会行为的理解。

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