

兰科植物欺骗性传粉

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摘要: 植物与传粉动物的互利关系在生态系统中非常普遍。然而, 有许多植物不为传粉者提供任何报酬, 而是利用各种欺骗方式诱骗昆虫拜访, 从而实现传粉, 即欺骗性传粉。兰科是被子植物大科之一, 其高度特化的繁殖器官和适应于昆虫传粉的精巧结构令人称奇。进化论创始人达尔文描述了许多兰花与昆虫精巧的传粉系统, 但他忽视了欺骗性传粉的存在。事实上, 近1/3的兰科植物都依赖于欺骗性传粉。欺骗性传粉可能是导致兰科植物多样性的原因之一。兰花利用或操作昆虫觅食、交配、产卵和栖息等行为, 演化出各种各样的欺骗性传粉机制, 常见的类型包括泛化的食源性欺骗、Batesian拟态、性欺骗、产卵地拟态和栖息地拟态。花的颜色、形态和气味在欺骗性传粉的成功实现中起到了重要作用。欺骗性兰花与传粉昆虫之间的演化可能是不同步的, 兰花追踪昆虫的行为信号而发生分化, 然而欺骗性传粉可能对昆虫造成一定的伤害, 从而对昆虫也施加选择压力。由于昆虫的学习行为, 欺骗性的兰花一般具有低的昆虫拜访率和结实率, 其繁殖成功率受各种因素的影响。欺骗性加剧了兰花对传粉昆虫的依赖, 使其具有更高的灭绝风险, 传粉生物学的研究能为兰科植物的有效保护提供指导。在欺骗性传粉系统中, 有报酬的伴生植物、拟态模型和其他拟态信号提供者对传粉成功有重要影响。因此, 研究欺骗性传粉兰花、传粉昆虫和相关的生物和生态因子的网状进化关系具有重要理论和实践意义。

关键词: 兰科, 欺骗性传粉, 食源性欺骗, 性欺骗, 产卵地拟态, 栖息地拟态, 演化, 保护

Deceptive pollination of orchids

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Abstract: Mutualism, or a mutually beneficial interaction between two organisms, are ubiquitous in ecological systems. However, some “empty flowers”, which offer pollinators no any kinds of rewards, design different strategies to attract pollinators without providing rewards to the pollinators. These pollination mechanisms are called deceptive pollination. The family Orchidaceae, representing one of the largest groups in angiosperms, is distinguished by high floral diversity and intricate adaptations to pollinators. Darwin described and identified most of the functional floral morphology and biomechanics in orchid pollination. However, he never recognized that many of the flowers that he examined lacked food rewards for pollinators. Floral evolution in the Orchidaceae appears to be dominated by modes of deceptive pollination, and more than one third of orchid species are thought to be pollinated by deceit. Deceptive pollination is thought to be one of key roles which has lead to relatively high species diversity within the Orchidaceae. Deceptive orchids frequently exploit the food foraging, sexual, oviposition and sleep/warmth behaviors of insects. The most common deception mechanisms include generalized food deception, Batesian floral mimicry, sexual deception, brood-site imitation and shelter imitation. Additionally, floral color, morphology and fragrance play key roles

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to cheat target pollinators. Relationships between deceptive orchids and their pollinators possibly involve asynchronous evolution; therefore orchids track the diversification of their pollinators. However, deception has negative impacts on the pollinators, which may exert selection on the pollinators. Because duped pollinators tend to avoid rewardless flowers, deceptive orchids suffer low visitation rates and fruit set, various environment factors can affect the reproductive success of these orchids. Deceptive orchids depend largely on insect pollinators for reproduction, and the proclivity of these species to use deceptive pollination strategies puts many of these species at a relatively higher rate of extinction. Therefore, pollination biology studies are needed to provide a scientific basis for proper conservation of orchids. At the community level, co-occurring mimic, non-mimic, and mimic signal providing plant species affect the reproductive fitness of orchids. Therefore, it is necessary to further study the co-evolution webs of deceptive orchids and pollinators along with other related biological and ecological factors.

Key words: Orchidaceae, deception pollination, food deception, sexual deception, brood-site imitation, shelter imitation, evolution, conservation

互利关系(mutualism)在生态系统中非常普遍,生命世界的任何一个有机体都参与到至少一对互利关系中。植物和传粉动物之间常常有着互利的对称关系,动物为植物传粉,植物为传粉者提供报酬(一般为花蜜或花粉)。但互利关系往往被欺骗者所利用(Bronstein, 2001),欺骗者(包括盗蜜者)在传粉媒介与花的互利关系中普遍存在(Bell, 1986)。花蜜是被子植物花提供给传粉者的最主要的报酬形式(Kevan & Baker, 1983),但相当多的物种存在无蜜的花,兰科植物尤为突出(Bell, 1986; Thakar *et al.*, 2003)。一些昆虫(至少是没有学习经验的昆虫)不能有效区别这些空花和有报酬的花朵,这些空花就在没有付出任何报酬的情况下获得了传粉成功(Thakar *et al.*, 2003),这种传粉方式就是欺骗性传粉(deceptive pollination)。最令生态学家和进化生物学家惊奇的是,将近有1/3的兰科植物通过欺骗昆虫达到传粉的目的(Cozzolino & Widmer, 2005; Jersáková *et al.*, 2006)。

兰科植物是被子植物的大科之一,约有800余属,至少25,000种,广泛分布于除两极和干旱沙漠地区以外的各种陆地生态系统中,特别是热带地区的兰科植物具有极高的多样性(Dressler, 1981, 1993),生活习性包括陆生、附生和腐生。兰科植物因其多样化的生活史、精巧的花结构以及与昆虫的协同作用而备受关注。从林奈或更早时期开始,兰花就是植物学家、园艺学家和生态学家心目中的明星植物类群。进化论创始人达尔文对兰花的传粉进行过详尽的观察,并于1862年出版了著名的专著——《兰花的传粉》,他对兰花传粉观察的目的就是希

望验证兰花与昆虫的关系是进化和自然选择的产物。但是达尔文并不相信兰花欺骗性传粉的存在,他认为兰花总是会为昆虫提供某种形式的报酬,例如他认为杓兰族唇瓣不具蜜腺,但唇瓣内表面被毛,其末端分泌一小滴稍有粘性的流质,可以作为传粉昆虫的报酬(Darwin, 1877)。尽管他观察到了杓兰族典型的锤状腺毛,但这些腺毛并不能为昆虫提供报酬。最早发现兰科植物欺骗性传粉可追溯到1793年, Sperengel在观察兰属(*Orchis*)植物传粉时发现一些兰花不给传粉昆虫提供报酬。Pouyanne (1917)和Coleman(1927)各自独立发现了一些产于地中海地区的眉兰属(*Ophrys*)和澳大利亚的*Cryptostylis*通过性欺骗来实现传粉,至此欺骗性传粉的面目逐渐被揭开。从达尔文至今,人们对兰科植物欺骗性传粉机制已有了较为详尽的认识,大量的欺骗性传粉现象被发现,一些重要的综述较为详细地介绍了兰科植物欺骗性传粉机制(Dafni, 1984; Ackerman, 1986; Nilsson, 1992; Roy & Widmer, 1999; Cozzolino & Widmer, 2005; Schiestl, 2005; Jersáková *et al.*, 2006)。

从进化和生态的角度解释兰科植物多样性,以及提示为什么会出现欺骗性传粉现象,是生物学家面临的难题(Mayer *et al.*, 2011)。现阶段,国际上对兰科植物传粉生物学研究的热点是探索兰科植物多样性和传粉式样演化之谜。有学者认为欺骗性传粉是导致兰科植物多样性的重要原因之一(Cozzolino & Widmer, 2005)。要解决这些难题,在全球兰科植物物种丰富的地区开展细致的传粉生物学研究是非常必要的。我国虽然不是兰科植物种类最丰

富的地区,但由于跨越热带、亚热带和温带3个气候带并拥有复杂的地理环境,而分布着各个气候带的兰科植物区系和生态类型,并且还保留着许多原始类群,特别是青藏高原等独特的地理区域,其相应的兰科植物多样性是世界上独一无二的(陈心启和吉占和, 1998)。中国西南山地是全球34个生物多样性中心之一(Mittermeier *et al.*, 2005),也是我国兰科植物最丰富的地区(陈心启和吉占和, 1998)。兰科植物传粉生物学是国际传粉生物学研究中最为活跃和成果颇丰的领域,我国该领域的研究起步较晚,但也已取得了一些重要进展(罗毅波等, 2003; Ren *et al.*, 2011)。本文对兰科植物欺骗性传粉进行了系统的介绍,希望能为从事兰科传粉生物学研究的人员提供参考。

1 兰科植物欺骗性传粉机制多样性

欺骗性兰花往往利用已存在的传粉关系或者昆虫的交配、产卵和筑巢等行为而达到欺骗昆虫的目的(Jersáková *et al.*, 2006)。根据兰科植物利用的信号种类,欺骗性机制主要分为食源性欺骗(food deception)和性欺骗(sex deception)两大类,前者大约包括了1/3的兰科种类,而性欺骗种类约有400种(Cozzolino & Widmer, 2005)。Jersáková等(2006)则将兰花的欺骗和拟态传粉方式分为泛化的食源性欺骗(generalized food deception)、Batesian拟态(Batesian floral mimicry)、性欺骗、产卵地拟态(brood-site imitation)和栖息地拟态(shelter imitation)等5种。

(1)食源性欺骗。指兰花利用昆虫的觅食行为,向目标昆虫提供假的食物信号,如没有蜜的花蜜距和假的花粉,诱骗昆虫到花上觅食,达到传粉的目的。绝大多数食源性欺骗的兰花都没有特定的拟态对象,即拟态模型,它们的诱骗目标是那些没有学习经验的“天真”的昆虫,这类拟态方式被称作泛化的食源性欺骗。杓兰属(*Cypripedium*)中由蜂类传粉的大部分种类属于这个类型(Bernhardt & Edens-Meier, 2010),其中离萼杓兰(*C. plectrochilum*)的访花昆虫多达14种,包括熊蜂、小型蜂、食蚜蝇、蚂蚁和蝴蝶等,但只有淡脉隧蜂(*LasioGLOSSUM* spp.)与兰花的功能结构相匹配,为有效传粉者(Li *et al.*, 2008)。Dafni和Ivri(1981)对广布于欧洲、中亚、北非至喜马拉雅地区的头蕊兰(*Cephalanthera longifolia*)中亚居群的研究表明,其唇瓣上的黄色乳突状

物质成功拟态了半日花科鼠尾草叶岩蔷薇(*Cistus salviifolius*)的花粉,从而吸引昆虫拜访,但没有鼠尾草叶岩蔷薇时昆虫也会拜访该兰花,这属于一种兼性花拟态现象(facultative floral mimicry)。分布在欧洲的另一种头蕊兰属植物*Cephalanthera rubra*则成功拟态了桔梗科的风铃草属植物*Campanula campanularum*,两者的花都为紫红色,且具有相同的反射光谱(Nilsson, 1983)。

(2)Batesian拟态。如果兰花拟态某一种特定的有报酬的植物,即有特定的拟态模型,这种欺骗方式就是Batesian拟态,已发现的例子不多。南非的无报酬兰花*Disa pulchra*拟态伴生的一种鸢尾科植物*Watsonia lepida*,两种植物分布重叠,都开粉红色的花,花形也相似(Johnson, 2000)。Sugiura等(2001, 2002)对日本分布的*Cypripedium macranthos* var. *rebunense*的研究第一次发现了杓兰属内有拟态对象的拟态现象,熊蜂传粉的*C. macranthos* var. *rebunense*通过拟态伴生植物马先蒿(*Pedicularis schistostegia*)来达到传粉成功。

(3)性欺骗。是兰花利用昆虫的交配行为,向目标雄性昆虫发出假的雌性昆虫性激素和形态信号,吸引雄性昆虫前来交配,从而达到传粉的目的。如欧洲分布的眉兰属种类唇瓣形态与雌性的泥蜂(*Campsoscolia*)相似,并具有长红毛,对雄性的泥蜂有强烈的性吸引,当雄蜂停落在唇瓣上会与唇瓣发生交尾行为,并使头部粘着花粉块(Schiessl *et al.*, 1999)。性欺骗在欧洲、澳大利亚、非洲、南美和中美洲的兰科植物中均有发现(Gaskell, 2010),但我尚未见相关报道。性欺骗除了最近在菊科植物*Goteria diffusa*中发现外(Ellis & Johnson, 2010),目前仅见于兰科植物。

(4)产卵地拟态。是指兰花利用昆虫的产卵行为,拟态昆虫的产卵地,吸引昆虫进入花内产卵,达到传粉的目的。产卵地拟态是一类较为复杂的欺骗方式,往往具有“陷阱”花,花色暗,具腐败气味。这类兰花通常拟态腐败的动物尸体、粪便和真菌的子实体(Urru *et al.*, 2011)。例如兜兰属(*Paphiopedilum*)的一些种类具有绿色的退化雄蕊,其唇瓣上有黑色突起物或者棍棒状腺毛以拟态蚜虫,吸引雌性噬蚜虫食蚜蝇来产卵,从而诱骗食蚜蝇掉入“陷阱式”囊中,达到为其传粉的目的(Atwood, 1985; Shi *et al.*, 2006, 2009)。火烧兰属(*Epipactis*)部分种类也有类似的产

卵地拟态现象(Stökl *et al.*, 2011)。

拟态真菌是否属于产卵地拟态一直没有得到很好的实验证据证实。分布于澳大利亚的*Corybas*生长于林下, 花黑色, 有报道认为菌蚊(*Gnoriste megarrhina*)为其传粉, 菌蚊在花内产卵, 因此推断*Corybas*拟态菌蚊的寄生真菌(Jones, 1970)。新热带分布的兰科植物*Dracula*的唇瓣与担子菌子实体的菌盖或菌褶非常相似, 并且发出真菌的气味, 因此被推测通过菌蚊或真菌上寄生的蝇类来传粉(Vogel, 1978a, b; Proctor *et al.*, 1996; Kaiser, 2006; Dentinger & Roy, 2010)。Kaiser(2006)对*D. chestertonii*的花气味成分进行了分析, 发现主要为典型的蘑菇气味的化合物。Endara等(2010)对厄瓜多尔分布的*D. lafleurii*和*D. felix*进行了传粉观察, 发现传粉昆虫为果蝇科以真菌为寄主的*Zygothrica*昆虫(在真菌上完成部分生活史), 这类果蝇在兰花的唇瓣上求偶和交配, 但没有发现产卵现象。他们认为兰花为果蝇提供庇护所和求偶的地点, 与真菌的作用相似。最新的研究发现, 果蝇在*Dracula*的唇瓣上有产卵前的寄主检查(palpation)行为(Raguso, 个人通讯)。Stoutamire (1967) 和 Vogel(1978a, b) 对栽培的*Cypripedium debile*观察发现, 其花下垂, 几乎贴地, 唇瓣上的条纹形似蘑菇的菌褶, 并有真菌气味, 推测它有菌蚊(或其他真菌上寄生的蝇类)传粉的综合征。Vogel的上述假说从1978年提出至今已有30余年, 但一直没有得到野外观察和实验的证实。

(5)栖息地拟态。是指兰花利用昆虫的栖息或者巢穴行为, 拟态其栖息地或者巢穴, 吸引昆虫进入花中栖息, 从而达到传粉的目的。*Serapias*是一个典型的例子, 其花冠成筒状, 为暗红色, 形似独居蜂*Ceratina*等巢穴的入口(Dafni *et al.*, 1981)。

(6)其他拟态方式。随着化学生态学的发展, 定量测定花气味和昆虫信息素技术日趋成熟, 特别是气相色谱与触角电位检测器联用技术(GC-EAD)的出现, 能有效检测化合物对昆虫触角的电位反应, 有力推动了花气味与昆虫行为相互关系的研究(Schiestl *et al.*, 2003; Johnson *et al.*, 2007)。近年来发现了许多新奇的主要与化学通讯相关的拟态机制, 如*Epipactis helleborine*和*E. purpurata*发出植物绿叶挥发物(green-leaf volatiles, GLV)吸引胡蜂(Brodmann *et al.*, 2008); *E. veratrifolia*则拟态蚜虫的报警信息素来吸引食蚜蝇(Stökl *et al.*, 2011); *Dendrobium*

*sinense*则拟态了蜜蜂的报警信息素来吸引胡蜂(Brodmann *et al.*, 2009)。

综上所述, 欺骗性传粉除了泛化的食源性欺骗没有特定的拟态模型外, 其他的欺骗方式都涉及到拟态生境中其他的生物或非生物对象, 其中, 雌性昆虫、产卵地、栖息地、真菌和信息素等都可以作为拟态对象(Jersáková *et al.*, 2006)。

2 欺骗性传粉如何实现?

在欺骗性传粉系统中, 一个重要的特点或成功的关键是被欺骗的昆虫不能有效地区分拟态者和模型(Vanewright, 1976)。欺骗性传粉得以成功实现, 花的颜色、形态和气味在其中起到了重要作用。一般认为, 花气味在远距离上起到吸引作用, 而形态特征在近距离上吸引昆虫访花。

通过性欺骗传粉的兰花一方面在形态上模仿雌性昆虫, 另一方面, 花中释放出吸引雄性昆虫的激素类挥发物质, 吸引进入繁殖期的雄性昆虫交尾, 从而达到传粉的目的(Schiestl *et al.*, 2003, Schiestl, 2005)。

食源性欺骗传粉是如何实现的呢?一种策略是兰花采取较鲜艳的花展示(Nilsson, 1980, 1983)。许多食源性欺骗的兰花都是早春开花, 并且有非常艳丽的花展示, 以吸引刚开始觅食的昆虫为其传粉。另外一种策略是兰花拟态有报酬的其他伴生物种。Batesian拟态就是其中一种类型, 在昆虫的视觉里, 拟态模型和兰花花色相同, 这可能是形成食源性拟态的最重要原因(Johnson, 1994, 2000, 2003a; Gumbert & Kunze, 2001; Anderson *et al.*, 2005)。早春开花的欺骗性兰花能有效避开来自有报酬植物的竞争; 晚些开花的兰花有较多的伴生植物, 往往会拟态有报酬种类而获得昆虫的拜访(Internicola *et al.*, 2008)。

泛化的食源性欺骗的兰花其花气味成分对昆虫也有明显的吸引作用。研究者通过对杓兰属植物花气味成分的分析找到了一些对传粉昆虫有吸引作用的活性成分(Nilsson, 1979; Bergstrom *et al.*, 1992; Barkman *et al.*, 1997; Li *et al.*, 2006)。但目前尚未发现Batesian拟态系统中同时存在化学拟态, 即花气味也相似的例子。花气味在拟态系统中起到非常重要的作用(Schiestl, 2005; Stökl *et al.*, 2010, 2011), 那是否存在单纯的化学欺骗或拟态呢?华

石斛(*Dendrobium sinense*)拟态了蜜蜂的报警信息素来吸引胡蜂(Brodmann *et al.*, 2009), 但单纯的化学拟态还需要进一步验证。Stökl 等(2010)报道了一种非兰科植物的化学拟态方式, 即天南星科植物海芋(*Alocasia macrorrhiza*)拟态酵母的气味来吸引传粉昆虫果蝇, 在这个拟态系统中, 花气味起到了关键的作用, 而没有形态上的相似性。

为了获得欺骗成功, 兰花可能会同时采取不止一种欺骗方式。例如, 西藏杓兰(*Cypripedium tibeticum*)的褐色花和暗红色花类型, 传粉昆虫为熊蜂, 其吸引机制是栖息地或巢穴拟态(nestsite mimic)和食物欺骗(Li *et al.*, 2006)。性欺骗的*Ophrys heldreichii*具有粉红色的侧瓣, 似乎对实现性欺骗并没有帮助, 但研究表明粉红色花能在近距离上增加雄性昆虫访问的准确性(Streinzer *et al.*, 2009)。*Epipactis veratrifolia*通过拟态蚜虫报警素和蚜虫形态来吸引食蚜蝇产卵, 但同时也分泌花蜜作为报酬(Stökl *et al.*, 2011)。*Serapias lingua*通过栖息地拟态来吸引蜂类(*Ceratina*), 进一步的研究发现, 其唇瓣基部的暗红色结构同样是一种性拟态, 花气味和传粉蜂性信息素成分分析验证这一点(Vereecken, 未发表资料)。食源性欺骗和性欺骗同时出现的现象也有报道(Gaskell, 2010)。

3 欺骗性兰花与昆虫的协同进化

一般认为, 互利关系的双方其演化是同步的, 即协同进化(coevolution), 然而, 最新的证据表明特化的植物与昆虫协同关系的进化可能是不同步或者依次序进化的。如收集花气味的蜂类(euglossine bees)与提供气味为报酬的兰花之间的演化就是不同的, 蜂类可能在兰花出现之前就开始收集从其他植物挥发的化合物, 而兰花在其传粉昆虫分化之后次序演化, 或追踪其传粉昆虫而演化(Ramírez *et al.*, 2011)。欺骗性传粉兰科植物通过模拟其他植物或动物的信号来操纵传粉者而取得传粉成功, 它们利用了环境中已存在的信号, 如原来已存在的昆虫采集花粉和花蜜的传粉关系、交配信号、产卵地和栖息地信号等。正因为如此, 一般认为欺骗性传粉兰科植物和传粉者之间是一种单方向的演化关系, 即传粉者是欺骗性兰科植物多样化的重要驱动力。有拟态现象的同一种植物在不同的居群可能会有不同的模型(Gumbert & Kunze, 2001)。头蕊兰分布

广泛, 在中亚发现其拟态半日花科植物, 但在我国西南地区并没有其拟态对象的分布, 笔者初步观察发现该兰花与石竹科和蔷薇科开白花的草本植物有一定的关联性, 有白色小花伴生的兰花花序结实率较高(任宗昕等, 未发表资料)。在食源性拟态普遍发生的南非, 存在大量的拟态模型物种在不同的地理环境下转变的现象, 同时模拟者(兰花)的性状也会追踪模型性状的演化而变化, 即性状追踪(trait tracking)(Johnson, 2010)。

然而, 在兰花的欺骗性传粉系统中, 传粉者本身以及其他被模拟的植物或动物并没有从欺骗性传粉系统中获得任何益处, 一般认为, 欺骗性兰科植物对传粉者的演化几乎没有影响(Jersáková *et al.*, 2006)。少数研究案例表明, 在性欺骗传粉兰科植物中, 植物对传粉者影响的方式和程度有所不同(Wong & Schiestl, 2002; Gaskell *et al.*, 2008)。从传粉者的个体水平来看, 可以分两种情况来考虑雄性传粉者的代价。一种情况是雄性传粉者与性欺骗传粉兰科植物假交配但没有射精。尽管没有直接浪费精子, 但雄性传粉者却浪费了时间和精力(Vereecken, 2009)。另一种情况是雄性传粉者直接将精液射在性欺骗传粉兰科植物上, 这种情况下雄性传粉者付出了代价(Gaskell *et al.*, 2008)。被欺骗的传粉昆虫为了避免无效或者受伤害的访花、产卵和射精等行为, 可能会与兰花形成拮抗协同进化关系(antagonistic coevolution)。

4 欺骗性传粉繁殖成功的影响因素

4.1 低拜访率和低结实率

一般来说, 无报酬兰花的传粉成功率和结实率都低于有报酬的物种(Nealand & Wilcock, 1998)。昆虫对首次见到的颜色和图案有明显的偏好, 且能学习避开那些没有报酬的刺激(Simonds & Plowright, 2004)。欺骗性空花的拜访经历会使昆虫避免拜访同一类型的花。因此, 欺骗性传粉兰花的昆虫拜访率往往较低, 从而结实率也较有报酬种类低。如已研究过的杓兰属植物在自然状态下结实率普遍偏低(Bernhardt & Edens-Meier, 2010)。

事实上, 一只昆虫必须在同种欺骗性的花上访问过两次, 才能有效地为植物传粉。昆虫第二次拜访的那朵花才是最终的“幸运儿”, 才能结实。一只携带欺骗性兰花花粉块的昆虫是否更倾向于访问

同一种兰花呢? Johnson等(2003b)的研究表明这个答案似乎是肯定的。而其他更多的研究则表明, 昆虫在受到欺骗后会迅速飞离, 因此花粉块的传播距离会远远大于有报酬的种类(Peakall & Beattie, 1996; Jersáková *et al.*, 2006)。正因为昆虫对无报酬兰花的逃避行为, 使得花粉块移出和结实率不符合通常的密度依赖(density dependent)和频度依赖(frequency dependent)规律, 而出现非密度和非频度依赖现象(Sabat & Ackerman, 1996)。

欺骗性传粉的兰花结实率受到很多因素的影响, 如花的开放时间、花序、生境、植株密度、种群大小和年际变化等(Tremblay *et al.*, 2005)。花朵的开放时间常常与昆虫的活动期相吻合, 居群内最先开放或最后开放的植株往往获得较高的结实率(Sabat & Ackerman, 1996)。花和花序特征影响传粉者的选择偏好, 花的高度和花展示大小受到的关注最多。一些食源性欺骗的植物花和花序的大小与花粉块移出和结实率成正相关(Murren & Ellison, 1996), 也有一些种类花展示大小对结实率没有影响(Sabat & Ackerman, 1996; Pellegrino *et al.*, 2005), 或昆虫更倾向于选择较小的花(O'Connell & Johnston, 1998)。*Cypripedium acaule*的繁殖成功率和花朵高度成明显的正相关(O'Connell & Johnston, 1998)。头蕊兰生长在开阔地的植株比林内的植株结实率高出40~50%(Dafni & Ivri, 1981)。*Calopogon tuberosus*中等大小的群体(直径1 m的范围内有2~8棵植株)比单花和植株数大于8的群体的结实率更高(Frimage & Cole, 1988)。*Cypripedium fasciculatum*, 有较高的结实率, 但年际间和不同地点间差异较大(Lipow *et al.*, 2002)。

但总的说来欺骗性传粉的种类结实率都很低, 既有传粉者限制和资源限制方面的原因(Primack & hall, 1990; Primack *et al.*, 1994; Kull, 1998; Neiland & Wilcock, 1998; Primack & Stacy, 1998; Tremblay *et al.*, 2005), 也有人为干扰方面的影响(Sugiura *et al.*, 2001)。近年来传粉者限制受到了更多关注(Tremblay *et al.*, 2005)。

4.2 伴生物种对欺骗性兰花繁殖成功的影响

动物与植物间的交互关系受到生境中非生物和生物因子的影响(Johnson & Bond, 1992; O'Connell & Johnston, 1998)。一般认为同期开花的伴生植物之间存在强烈的个体竞争, 以赢得更多的

昆虫拜访, 但越来越多的研究也发现同期开花物种间相互促进的事实(Feinsinger *et al.*, 1986; Feinsinger, 1987; Johnson *et al.*, 2003b)。其中一种方式就是“磁性物种效应”(magnet species effect), 即一种有报酬的物种能增加相邻的报酬较少的物种的传粉成功率(Thomson, 1978)。围绕欺骗性传粉的兰科植物也有同期开花的伴生物种竞争和促进之争, 一种观点认为兰花远离伴生物种能增加其传粉成功, 即“远离生境效应”(remote habitat effect), 并且得到实验证据支持(Lammi & Kuitunen, 1995)。而大量的实验也证明“磁性物种效应”的存在(Alexandersson & Ågren, 1996; Ferdy *et al.*, 1998; Johnson *et al.*, 2003b; Juillet *et al.*, 2007)。在群落水平上研究欺骗性的兰花与传粉昆虫、同期开花的伴生植物的网状进化关系有利于解释欺骗性的生态适应意义; 生境破碎化扰乱这些网状关系, 值得进一步关注, 从而促进对兰科植物的保育。

4.3 适合度的假说

无报酬植物种类相对于有报酬的种类, 由于昆虫的学习行为, 其拜访频率往往要低于后者, 因此欺骗性传粉的适合度问题一直是个谜和争论的焦点。学者们提出了各种不同的假说, 适合于所有无报酬植物的一般性假说包括资源限制假说和异交假说, 其中资源限制假说认为兰科植物的繁殖要付出很高的繁殖代价, 开花和结实都要消耗大量的能量, 花蜜的产生同样需要消耗大量的资源, 受到资源的限制, 这些种类的兰花不大量生产蜜来吸引昆虫(Calvo, 1993; Mattila & Kuitunen, 2000); 异交假说认为有蜜腺的兰花种类往往有较高的昆虫访问频率, 但相应增加了同株异花授粉的几率, 这种自交会导致植物后代适合度的降低, 而欺骗性传粉的种类虽然昆虫拜访频率低, 但同时也降低了自交的几率, 提高了植物后代的适合度(Johnson & Nilsson, 1999; Johnson *et al.*, 2004)。专门针对兰科植物的假说还有低密度假说、花粉块移出假说、传粉运输效率假说、花粉滞落限制假说等(Cozzolino & Widmer, 2005; Jersáková *et al.*, 2006; Scopece *et al.*, 2010)。

5 欺骗性兰花的保育

全球环境剧烈变化的今天, 互利关系对于全球生态系统的作用可能比以前所想象的更加复杂和

重要, 因为任何一对互利关系的破裂都可能导致一系列的物种灭绝事件(Kiers *et al.*, 2010)。对周围各种生物或非生物因子有强烈依赖的物种更容易灭绝, 因为当这些依赖关系中的任何一个因子的丧失都会导致物种受威胁或消失(Swartz & Dixon, 2009a, b; Phillips *et al.*, 2010)。兰科植物高度特化, 与真菌和传粉昆虫形成复杂的共生或依赖关系, 因而具有更高的灭绝风险。性欺骗传粉的兰花, 与昆虫往往是一对一的特化关系。如澳大利亚的 *Drakaea* 与传粉昆虫之间形成了高度特化关系, 很容易受到环境变化的影响(Hopper & Brown, 2007)。又如 *Rhizanthella gardneri*, 不仅有特化的菌根真菌和传粉昆虫, 还与周围的植物(*Melaleuca*)形成共同的内生真菌, 甚至有专一的哺乳动物为其散布种子, 因此其面临的灭绝风险更高(Warcup, 1985; Bougoure *et al.*, 2008, 2009; Swartz & Dixon, 2009b)。欺骗性的兰花与有报酬的兰花相比存在着更严重的花粉限制, 对受骗的传粉昆虫更加依赖(Neiland & Wilcock, 1998; Tremblay *et al.*, 2005)。

传粉生物学研究对兰科植物的保育具有重要意义, 因为大多数兰科植物与传粉昆虫在演化过程中形成了完美的协同进化关系, 有些甚至形成了一对一的专性传粉关系; 如果传粉者受到威胁, 就会直接影响到相应兰科植物的结实能力, 从而影响到该种兰科植物的生存。在对受威胁兰科物种制定恢复(recovery)方案时, 就必须以传粉生物学研究作为基础(罗毅波等, 2003)。无论是就地保护(*in situ*)还是迁地保护(*ex situ*), 对兰科植物传粉系统的认识都至关重要, 直接涉及到保育措施是否得当(Swartz & Dixon, 2009a, b)。

6 展望

目前, 兰科植物的传粉生物学研究在物种水平上继续沿着达尔文之路, 寻找花与传粉者之间“锁与钥匙”的关系, 随着花气味化学分析方法、GC-EAD 技术的应用, 以及光谱技术和昆虫行为学方法的革新使得兰科植物神秘的欺骗性传粉机制逐渐明晰; 在群落水平上围绕欺骗性传粉生态适应意义的解释, 兰花与伴生植物之间的交互关系得到越来越多的重视, 生境破碎化对欺骗性传粉关系网状结构的影响也开始引起人们的关注。但目前对热带亚洲的兰科植物的传粉生物学研究较少, 因此进

一步的研究将对揭示兰科欺骗性传粉的适应性进化和保育具有重要理论和实际意义。

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