生物多样性 2008, **16** (1): 34–43 doi: 10.3724/SP.J.1003.2008.07231
Biodiversity Science http: //www.biodiversity-science.net

不同扰动生境中动物对酸苔菜种子的捕食和散布

赵 瑾[1,2] 陈 进[1*] 马绍宾[2]

1 (中国科学院西双版纳热带植物园, 云南勐腊 666303)
2 (云南大学生命科学学院, 昆明 650091)

摘要: 有效的种子散布是木本植物形成入侵种需要经历的过程之一, 但在预测入侵种时却常常被忽略。紫金牛科东方紫金牛(*Ardisia elliptica*)原产热带亚洲而在北美成为入侵植物, 分布在云南南部的其同属种酸苔菜(*A. solanacea*)与之具有相似的生物学特征。本文以酸苔菜为研究对象, 于2004年12月至次年2月分别在人为干扰轻的野象谷和人为干扰重的植物园进行酸苔菜的种子散布及捕食研究, 试图了解生境变化对其种子散布和种子捕食的影响。结果表明, 酸苔菜在两地的种子散布者均为白喉冠鹎(*Alophoixus pallidus*)、黑冠黄鹎(*Pycnonotus melanicterus*)和灰眼短脚鹎(*Iole propinqua*), 但3种食果实鸟类的组成比例、拜访行为、频率及种子捕食者的影响在两地均不相同。人为干扰轻的野象谷生境中白喉冠鹎、黑冠黄鹎与灰眼短脚鹎的拜访频率分别为25%、32%和26%, 取食后的第一次停栖地点有4%在10 m以外; 人为干扰重的植物园生境中3种鸟的拜访频率分别为67%、8%、5%, 取食后的第一次停栖地点有26%在10 m以外。人工摆放种子试验表明, 地面上种子捕食者主要是啮齿类；在两生境中种子捕食率均较低(2–6%), 但野象谷生境中种子捕食率仍显著高于植物园生境。野象谷生境中种子还受到象鼻虫幼虫的危害, 危害率为17.9±3.5%(n = 512); 而植物园生境中未发现种子被象鼻虫危害(n = 489)。干扰对生境中的动物组成及行为造成了明显影响, 并可能通过种子散布与捕食的改变而间接影响与其有密切关系植物的种群动态。

关键词: *Ardisia solanacea*, 人类扰动, 食果鸟, 种子散布, 种子捕食

Seed predation and dispersal of *Ardisia solanacea* in habitats with different degree of disturbance

Jin Zhao[1,2], Jin Chen[1*], Shaobin Ma[2]

1 *Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Mengla, Yunnan* 666303
2 *School of Life Sciences, Yunnan University, Kunming* 650091

Abstract: Effective dispersal is one essential course for invasive species on their process of invasion, while study on the effectiveness of seed dispersal was often neglected when predicting species' invasion. Native to Tropical Asia, *Ardisia elliptica* is an invasive species in North America. *A. solanacea* is a tree naturally distributed in southern Yunnan with biological characteristics similar to *A. elliptica*. In this study, we conducted observation on seed dispersal and seed predation of *A. solanacea* in two habitats with different degree of disturbance: the Wild Elephant Valley (WEV) with few disturbances and the Xishuangbanna Tropical Botanical Garden (XTBG) with high disturbances. The aim of the study was to understand how disturbances affect seed dispersal and seed predation of *A. solanacea.* In both habitats, three frugivorous birds were the main seed dispersers, i.e., *Alophoixus pallidus*, *Pycnonotus melanicterus* and *Iole propinqua*. However, the visiting frequency and feeding behaviour differed in the two habitats. In WEV, the visiting frequency of the three birds was 25%, 32% and 26%, respectively; while in XTBG, it was 67%, 8% and 5%, respectively. Only 4% of the birds got first stop far than 10 m away from the fruiting tree after feeding in WEV, but 26% in XTBG. Seed placement experiment indicated that rodents were the major predators to the seeds on ground. The predation rate in both habitats were rather low (2–6%) while seed predation rate in WEV was significantly higher than

收稿日期: 2007-08-29; 接受日期: 2008-01-02
基金项目: 中国科学院创新基金
* 通讯作者 Author for correspondence. E-mail: biotrans@bn.yn.cninfo.net

that in XTBG. In WEV, larvae of Curculionidae were another seed predator, which caused 17.9±3.5% (n = 512) of seeds parasitized. In contrast, no seeds was found to be parasitized by the larvae (n = 489) in XTBG. Disturbance significantly affect the composition and behaviour of animals inhabited. Consequently, those changes may influence seed dispersal and seed predation of related plants, and indirectly, affect the population recruitment of plants.

Key words: *Ardisia solanacea*, different disturbed habitats, frugivorous birds, seed dispersal, seed predation

散布(dispersal)是指植物以各种散布器官(散布体, diaspore)离开母体到达一个安全生境(适宜于萌发、生长和繁殖)的过程, 是联系母株和幼苗阶段的重要桥梁(Primack & Miao, 1992; Wunderle, 1997; Nathan & Muller-Landau, 2000; Foster & Tilman, 2003; Levin et *al.*, 2003)。在长期的自然进化过程中, 被子植物演化了多种多样的散布机制(Howe & Smallwood, 1982)。有些植物利用自身开裂、风力、水力、重力等非生物因素来传播其种子(Willson, 1993), 但大多数植物则依靠动物来传播种子(Howe & Smallwood, 1982)。据统计, 在热带雨林中, 平均约有75%的果实适于动物传播(Fleming, 1981)。传播种子的动物包括蚁类(Beattie & Hughes, 2002)、鱼类、哺乳类(Howe & Smallwood, 1982; Corlett, 1998; Herrera, 2002)、鸟类(Howe & Smallwood, 1982)、啮齿类(Forget & Milleron, 1991; Van der Wall, 1997)等。其中鸟类 (Yagihashi *et al.*, 1999)的种子传播作用尤为显著, 特别是对种子的长距离散布(Smith, 1975; Westcott & Graham, 2000; Hobson, 2005)。然而, 从种子到植株建成这一过程极为复杂, 人们往往难以预测种子散布后的命运及其对种群结构或群落动态所产生的影响(Cain *et al.*, 2000; Nathan & Muller-Landau, 2000)。

种子捕食对植物个体的繁殖、种群空间分布、植物群落的多样性(Janzen, 1970; Connell, 1971; Howe & Smallwood, 1982; Schupp, 1990; Willson & Whelan, 1990)等都有着极大的影响, 对种群动态(Manson & Stiles, 1998; Crawley, 2000; Cummings & Alexander, 2002)及物种多样性的保持起重要作用(Janzen, 1970; Connell, 1971)。同时, 种子捕食的程度在种子传播过程中非常重要, 它连接着种子的散布和幼苗建成(Herrera *et al.*, 1994; Schnurr *et al.*, 2004; Van der Wall *et al.*, 2005)。在热带雨林中, 种子在散布前的损失率为10%(Janzen, 1969), 而种子散布后的死亡率通常超过75%(Howe *et al.*, 1985; Crawley, 1997), 有些种类甚至达到100%(Chapman, 1989)。种子捕食者一般限于昆虫(Janzen, 1970; Toy & Toy, 1992; Lyal & Curran, 2000; Westerman *et al.*, 2003; Nakagawa *et al.*, 2005)、哺乳类(Curran & Leighton, 2000; Schnurr *et al.*, 2004; Wilson *et al.*, 2007)和鸟类(Janzen, 1971; Holmes & Froud-Williams, 2005)。Hulme(1993)认为影响种子捕食的因素很多, 包括生境类型、生境大小、种子大小、捕食者密度等。种子捕食的强度与捕食者密度的关系、不同捕食者对种子的选择以及捕食者时空变化对我们理解种子捕食者对植物种群或群落动态的影响起关键作用(Manson *et al.*, 1998; Crawley, 2000)。

生物入侵是目前生态学领域的热点问题(如Elton, 1958; Callaway & Aschehoug, 2000; Agrawal & Kotanen, 2003; Colautti *et al.*, 2004; Lambrinos, 2004; Stohlgren & Schnase, 2006; Herron *et al.*, 2007), 而木本植物形成入侵种需要经历引入(Mack, 1996)、繁殖(Rejmánek & Richardson, 1996)及有效的种子散布(Rejmánek, 1996; Seabloom *et al.*, 2003; Gosper *et al.*, 2005)等过程。其中有效的种子散布是理解区域性种群动态及入侵速率的基础(Ostfeld *et al.*, 1997; Neubert & Caswell, 2000), 但在预测入侵种时却常常被忽略(Richardson *et al.*, 2000; Křivánek & Pyšek, 2006)。尤其是当植物的散布动物在入侵地发生改变时, 种子传播机制的改变对其入侵或许有促进作用。如Renne等(2002)在研究乌桕树(*Sapium sebiferum*)时发现, 该物种在引入地的散布动物与原产地不同, 而正是散布动物的改变促进了它的入侵。除此以外, 许多研究者认为, 原产地及入侵地病虫害及其危害程度的差异也是造成植物入侵的重要原因之一(Siemann & Rogers, 2003; Colautti *et al.*, 2004; De Walt *et al.*, 2004; Hinz & Schwarzlaender, 2004; Torchin & Mitchell, 2004; Pratt e*t al.*, 2005; Newingham & Callaway, 2006), 如

入侵杂草生物控制的成功暗示了天敌在入侵种形成过程中的重要作用(Julien & Griffiths, 1998)。

紫金牛属东方紫金牛(*Ardisia elliptica*)于1900年作为观赏植物引入北美(Gordon & Thomas, 1997)后，迅速占领潮湿的次生生境并排挤本地种，目前被列为世界上危害最严重的100个入侵种之一(www.nbii.gov/index.html)。Koop(2003, 2004)在东方紫金牛入侵地研究了该物种与草食动物的关系、种群动态及其对当地鸟类组成的影响等方面，证明了当地食果实鸟类对东方紫金牛的入侵有促进作用，同时认为该物种较当地物种受到更少的捕食，两种因素造成了东方紫金牛的入侵现状。酸苔菜(*A. solanacea*)系东方紫金牛同属种，生物学特征与之相似，成株高6 m以上，一条主茎上生出短而相互垂直的小枝，花期2–3月，果期10月至次年1月，也有花开、果熟同时发生的情况。果实扁球形，直径7–9 mm，紫红色或带黑色，每果实含1粒种子，种子直径约5 mm。主要分布于东南亚和南亚地区，包括印度、尼泊尔、斯里兰卡、印度尼西亚、新几内亚以及我国广西西南、云南南部及东南部地区。

本文以不同生境中的酸苔菜为研究对象，对其种子散布者及种子捕食者进行调查，以期解释酸苔菜在不同生境中种子散布与捕食等方面的变化，试图回答以下几个问题: (1)不同干扰程度生境中酸苔菜种子散布者的种类及贡献; (2)不同干扰程度生境中的种子捕食情况; (3)探讨种子散布者、生境与种群动态之间可能的关系及其对入侵的启示。

1 研究方法

1.1 研究样地概况

研究地点分别位于云南省西双版纳勐腊县勐仑镇中国科学院西双版纳热带植物园(XTBG)罗梭江畔(21°41′N, 101°25′E)和勐养自然保护区的野象谷 (The Wild Elephant Valley, WEV)(21°57′N, 100°47′E)。中国科学院西双版纳热带植物园海拔570 m，年均温21.5℃，年平均降雨量为1,560 mm，人为干扰较严重，生境片断化，森林面积约20 hm^2。野象谷位于勐养自然保护区南缘，为低山浅丘宽谷地貌，海拔747–1,055 m，年均温18.1℃，年平均降雨量1,398 mm，人为干扰少，生境连续，保护区森林面积约1,000 km^2。

1.2 种子虫害调查

分别在两地随机选择成熟植株5株，每株在两个不同方向上选择结实数量相当的两枝，采集果实，统计果实数，并剖开果实检查是否有寄生昆虫，同时统计被寄生种子百分比。

1.3 动物对果实的收获

分别在两地选择5株结实植株，每株在不同方向上选择两个结实小枝并在果实上做标记(用针在果实上深刺3个小孔，并刺进种子，便于与未标记果实相区别)，每个小枝约标记50颗果实，在小枝的下方用1 m×1 m、高约1.5 m的网(网眼为1 mm)收集果实，收集到鸟类排泄的种子则检查种子表面是否具有标记。每天早晚各检查一次并记录果实掉落的情况，直到小枝上的果实完全丢失为止。

1.4 树上拜访动物种类及取食习性

在植物园和野象谷两地分别选择4和5株结实植株，于2004年果实成熟期的12月至次年1月进行观察。用望远镜在隐蔽处观察拜访动物，同时用照相机拍摄动物取食果实的照片。记录拜访动物种类、数量、具体时间、拜访时间长短、具体行为(啄、吞食整个果实、吞食果实并吐出种子、吞食并破坏种子)以及取食后第一次落点的大致距离(<5 m, 5–10 m, >10 m)。观察时间为07:00–08:00, 08:00–10:00, 10:00–12:00, 12:00–13:00, 13:00–16:00 和 16:00–18:00，每株连续观察3 d，总观察时间为297 h。

用网捕法捕捉鸟类，参照鲁长虎(2003)的方法。在2005年果实成熟盛期，选择5棵结实植株，共张开5个雾网(2.5 m×12 m)，每天张网时间为6:30–18:30，连续5 d。把捕到的鸟放入布袋中，带回实验室笼养3 d，喂食酸苔菜果实，观察鸟的取食情况，收集粪便中的酸苔菜种子，并记录种子通过鸟类消化道的时间，即体内滞留时间(retention time)。然后在显微镜下观察收集到的酸苔菜种子有无破损。

1.5 动物对地面种子的捕食

分别在植物园与野象谷两地选择投放点。采集酸苔菜果实，去果肉并将种子冲洗干净，在每个投放点间隔摆放4种处理的种子: 将种子放在倒置的培养皿盖(d = 12 cm)上，每种处理设两个密度，其中低密度2个种子，高密度10个。共8种处理，每个处理设置10个重复。每个密度中的4种处理间隔1 m作为一个相对独立的单位，独立单位间距大于5 m。

4种处理的方法: (1)开放: 将培养皿倒扣, 埋入土中, 底面与地面平齐; (2)排除蚂蚁: 将培养皿倒扣, 培养皿边缘涂上机械润滑黄油; (3)排除鸟类: 将培养皿倒扣, 埋入土中, 底面与地面平齐, 用一侧具有开口的铁丝网罩住培养皿; (4)排除啮齿类和鸟类: 将培养皿倒扣, 埋入土中, 底面与地面平齐, 并用铁丝网罩住培养皿。

从2005年1月14日至2月3日, 在每天早晨08:00–09:00记录剩余的种子数。每3 d在同一时间将所有剩余的种子取出, 然后重新摆放新鲜种子。在每个生境进行3次重复。

1.6　啮齿类和蚁类的调查

分别在两地用铗日法对啮齿类进行取样调查。每个微生境中将25个鼠铗排成一条直线为一行, 间距约5 m, 行距大于25 m, 共布铗100个。连布5个昼夜, 共计500个铗日。用花生米做诱饵, 每天早晚各检查一次。所捕获鼠类每种取一只做成标本以备鉴定, 其余的就地释放。

用陷阱法对蚁类进行取样调查。每个微生境样地中随机选择10个取样点, 每个取样点间隔大于5 m。将10个直径为7.5 cm的一次性塑料杯分别埋入各取样点, 杯口与地面平齐, 杯中装1/3的10%福尔马林溶液, 每3 d收集杯中的蚂蚁, 共收集3次, 分别装在10个不同的盛有75%乙醇溶液的小瓶中以备鉴定和数量统计。

1.7　数据分析

对动物在两地对果实拜访频率及取食后落点距离的差异使用软件SPSS 13.0 (SPSS, Chicago, IL, USA)进行卡平方检验, 方差分析处理酸苔菜种子捕食数据。

2　结果

2.1　昆虫对种子散布前的捕食

通过对酸苔菜果实观察(植物园489个, 野象谷512个)发现, 野象谷样地中酸苔菜种子常被象鼻虫(Curculionidae)寄生, 种子虫蛀率为17.9±3.5%。象鼻虫在果实未成熟期将卵刺入, 并在外果皮上留有一个直径约为1 mm的小孔, 孵化出的幼虫以胚乳为食, 虫蛀种子因而失去萌发力。植物园样地中未发现虫蛀现象。

2.2　动物对果实的收获

酸苔菜成熟果实大部分在自然落下前被树上动物取食。植物园和野象谷两个样地分别有94.6±0.5%和93.5±1.9%的果实被树上动物取食, 两地少有果实自然掉落, 每10 d仅分别掉落2±0.7个和3±0.6个。植物园白天和夜晚掉落的果实数相当, 分别为每10 d 2±1.2个和2±0.7个; 野象谷白天和夜晚的果实掉落情况与植物园相似, 分别为每10 d 4±0.9个和2±0.8个。

2.3　食果实鸟类的特征和捕食特点

在植物园样地中酸苔菜种群的拜访动物包括白喉冠鹎(*Alophoixus pallidus*)、黑冠黄鹎(*Pycnonotus melanicterus*)、灰眼短脚鹎(*Iole propinqua*)、紫颊太阳鸟(*Anthreptes singalensis*)和松鼠科(Sciuridae)动物; 在野象谷的拜访动物除以上4种鸟外, 还包括长尾缝叶莺(*Orthotomus sutorius*)、灰眶雀鹛(*Alcippe morrisonia*)、林鵙(*Tephrodornis virgatus*)、蓝翅叶鹎(*Chloropsis cochinchinensis*)、红额穗鹛(*Stachyris rufifrons*)、栗头雀鹛(*Alcippe castaneceps*)。两地的拜访鸟类共10种, 其中只有白喉冠鹎、黑冠黄鹎和灰眼短脚鹎为食果鸟, 其余7种主要取食树上的昆虫或花蜜。

3种鹎类的拜访时间相互交叉, 主要集中在上午10:00–12:00和下午12:00–17:00左右, 每天17:30以后基本不再出现; 平均拜访时间为1–6 min(且拜访后离开并不返回, 因此连续5 min内拜访的鹎类计为同一批拜访者)。白喉冠鹎常成群拜访, 黑冠黄鹎和灰眼短脚鹎多成对拜访结果的植株(图1)。3种鹎类拜访时行为相似, 红黑色成熟果实对它们的吸引力大, 取食时通常先尝试性地轻啄, 确定果实成熟可食时会将其整个吞食, 并在同一株母树上连续取食。

3种鹎类在两个样地的拜访百分比如表1所示。其中植物园样地中白喉冠鹎、黑冠黄鹎和灰眼短脚鹎的拜访百分比分别为67%、8%和5%, 野象谷则为25%、32%和26%(表1)。卡平方检验结果显示在两样地的拜访频率有显著差异(χ^2 = 39.039, df = 3, P = 0.029)。

各种鸟取食后的第一次落点距离母树多为5–10 m, 偶有5 m以内或10 m以上。3种鹎类在两地的第一次落点也有极显著差异(χ^2 = 38.012, df = 2, P<0.001), 在植物园样地的鹎类停落在10 m以外的几率高于野象谷, 两地分别为26%和4%(表2)。

显微镜下观察鸟粪中的酸苔菜种子并无破损,

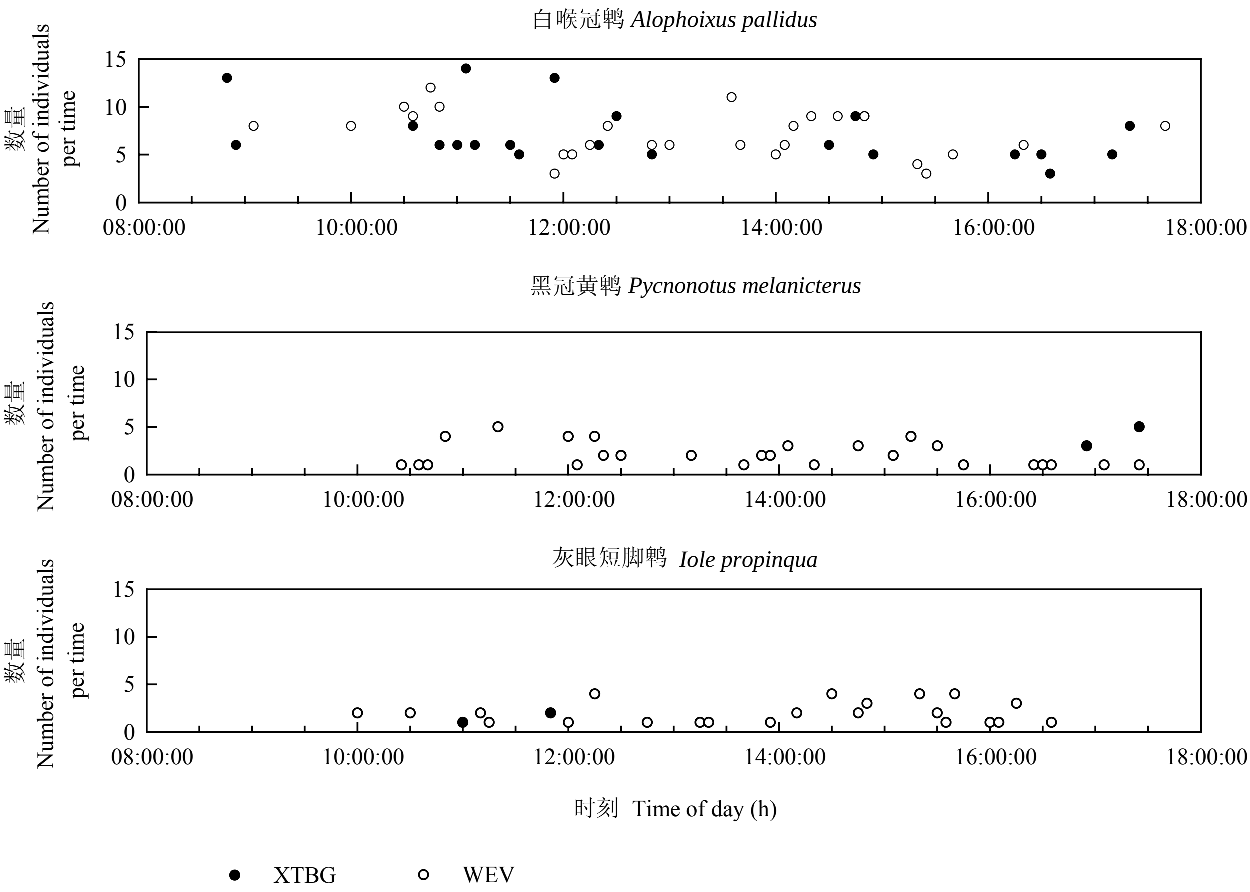

图1 西双版纳植物园(XTBG)和勐养自然保护区野象谷(WEV)生境中白喉冠鹎、黑冠黄鹎和灰眼短脚鹎3种食果鸟拜访酸苔菜结果植株的频率。数据为15 d的累计数; 连续5 min计为1次拜访。

Fig. 1 Comparison of visiting frequency of three frugivorous birds to the fruiting trees of *Ardisia solanacea* in Xishuangbanna Tropical Botanical Garden (XTBG) and Wild Elephant Valley (WEV). Data is an accumulation of 15-day observation. The time for continuous five minutes was recorded as one visit.

表1 酸苔菜的3种主要种子散布者在不同生境中的拜访频率(%)

Table 1 Visiting frequency (%) of the three major seed dispersers of *Ardisia solanacea* in two different habitats

种名 Species	生境 Habitats	
	植物园 XTBG	野象谷 WEV
白喉冠鹎 *Alophoixus pallidus*	67	25
黑冠黄鹎 *Pycnonotus melanicterus*	8	32
灰眼短脚鹎 *Iole propinqua*	5	26
其他 Others	20	17

说明3种鹎类对酸苔菜的种子均有传播作用。种子在白喉冠鹎、黑冠黄鹎和灰眼短脚鹎消化道的滞留时间相似(表3)。

2.4 地面动物对种子的捕食

种子在地面的捕食实验显示, 4种处理下的种子捕食强度均不高(图2A)。开放条件下的种子捕食强度最高, 接近8%; 排除蚂蚁和排除鸟类处理下的种子捕食强度相当; 而排除啮齿类和排除鸟类处理下基本没有种子丢失, 只有少数种子由于网的倾斜而掉落。在野象谷样地的捕食强度极显著高于在植物园的捕食强度(图2B)。无论在植物园还是野象谷, 高密度下的种子捕食强度均极显著高于低密度种

表2　植物园和野象谷两生境中拜访酸苔菜的食果鸟离开母树后的第一次落点位置的差异(以次数表示, 括号内为百分比)
Table 2　Distance between the fruiting tree and the first stop of visitors (indicated by times and percentage)

种名 Species	植物园 XTBG				野象谷 WEV			
	<5 m	5–10 m	>10 m	合计 Total	<5 m	5–10 m	>10 m	合计 Total
白喉冠鹎 *Alophoixus pallidus*	7 (11)	35 (58)	19 (31)	61	2 (6)	30 (91)	1 (3)	33
黑冠黄鹎 *Pycnonotus melanicterus*	0 (0)	8 (100)	0 (0)	8	10 (24)	31 (73)	1 (3)	42
灰眼短脚鹎 *Iole propinqua*	0 (0)	3 (100)	0 (0)	3	8 (24)	24 (70)	2 (6)	34
合计 Total	7 (10)	46 (64)	19 (26)	72	20 (18)	85 (78)	4 (4)	109

表3　酸苔菜种子在3种食果实鸟消化道内的滞留时间
Table 3　Retention time of *Ardisia solanacea* seeds in the digestive systems of the three frugivorous birds

种名 Species	滞留时间 Retention time		
	均值 ± 1标准误 Mean± 1SE	样本数 n	变幅 Range
白喉冠鹎 *Alophoixus pallidus*	23.6 ± 0.51	5	22.9–23.9
黑冠黄鹎 *Pycnonotus melanicterus*	22.7 ± 0.53	5	21.7–23.6
灰眼短脚鹎 *Iole propinqua*	22.4 ± 0.37	5	21.7–23.0

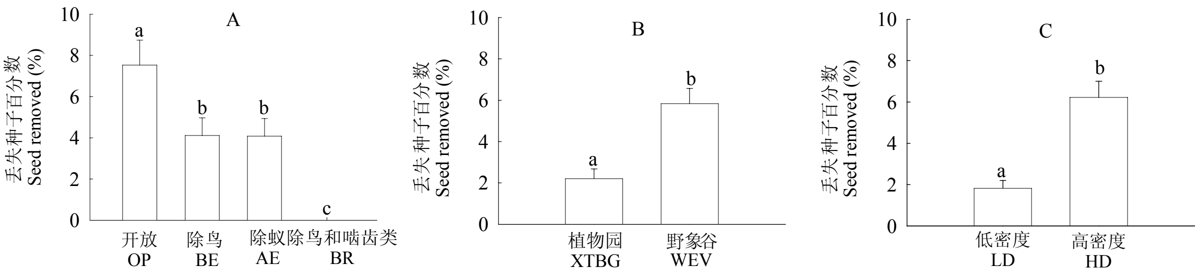

图2　不同处理、不同生境和不同种子摆放密度对种子捕食强度的影响(以丢失种子百分数表示, 平均值±1标准误)。A: 不同处理(N=360)。开放: 种子直接摆放地面上; 除鸟: 排除鸟的拜访; 除蚁: 去除蚂蚁拜访; 除鸟和啮齿类: 排除鸟和啮齿类的拜访。B: 不同生境(N=720)。C: 不同密度(N=720)。不同字母表示差异显著(P<0.05)。
Fig. 2　Degree of seed predation influenced by different treatments, habitats and seed density (Seed predation is indicated by percentage of seed removed. Data are means±1SE. A, Treatments (N = 360): OP, seeds were directly placed on the ground; BE, birds' visit was excluded, AE, ants' visit was excluded; BR, both birds and rodents were excluded. B, Different habitats. C, Different seed density: LD, 2 seeds; HD, 10 seeds. Different letters indicate that the mean values are significantly different (P<0.05).

子(图2C), 但两者均不高, 最高仅为6%。

啮齿类与蚁类调查中, 在野象谷样地共捕捉到7只刺毛鼠(*Niviventer fulvescens*), 植物园样地没有捕捉到啮齿类动物。且两地均无蚁类出现。

3　讨论

本研究中两个不同生境中酸苔菜植株成熟果实中的绝大多数(>93%)都被3种食果鹎类取食, 似乎不存在种子散布者限制的现象。然而, 不同生境中食果鸟的拜访频率不同: 在人为干扰轻的野象谷生境中白喉冠鹎、黑冠黄鹎与灰眼短脚鹎的拜访频率分别为25%、32%和26%; 在人为干扰重的植物园生境中白喉冠鹎拜访频率达67%, 而黑冠黄鹎和灰眼短脚鹎仅占8%和5%。不同食果鸟的拜访行为也不同: 白喉冠鹎通常成群拜访结果的植株并一起飞离, 每群数量多达7.4±0.4 只, 而黑冠黄鹎与灰眼短脚鹎通常成对拜访结果的植株, 暗示白喉冠鹎每次拜访时较黑冠黄鹎与灰眼短脚鹎携带更多种子离开。与此同时, 同一种鸟在不同生境中的行为也有差异, 3种鸟在植物园样地第一次停栖的地点总体上较野象谷更远(表2)。种子在食果实鸟类消化道的滞留时间意味着潜在的传播距离和能否到达适宜的萌发地(Murray, 1988)。野外观察难以确定酸苔菜种子被散布的实际距离, 但笼养实验表明, 种子在消化道的滞留时间为20 min 左右, 在此时间段内飞行的鸟可以将种子传播到较远的区域。而3种

鹎在取食酸苔菜果实后的第一次落点均在取食点5 m以外，且离开后未观测到返回，这就意味着酸苔菜种子至少被传播到5 m以外。暗示白喉冠鹎不仅能够更高效地散布种子，且散布距离远，在酸苔菜种子散布过程中起到较黑冠黄鹎与灰眼短脚鹎更重要的作用。同时食果鸟拜访频率及行为的差异也将带来散布种子空间结构的差异。

影响食果鸟拜访的因素很多，其中生境的破坏及片断化直接影响食果鸟的种类、数量及组成比例(Restrepo *et al*., 1999; Moran *et al*., 2004; Newmark, 2006)，并进一步影响种子的散布(Galetti *et al*., 2003; Forget & Cuijpers, 2007)。Bleher和Böhning-Gaese(2001)分别在南非与马达加斯加两地研究了橄榄科没药属(*Commiphora*)植物的种子散布与当地食果鸟的关系。结果显示，由于生境片断化马达加斯加的食果鸟多样性明显低于南非，造成种子在马达加斯加仅有7.9%被散布，而南非却有高达70.9%的种子被散布。Santos 和 Tellería(1994)在研究生境片断化对西班牙刺柏(*Juniperus thurifera*)的影响时也发现，由于片断化森林中食果鸟种类及数量的改变，刺柏种子的散布比例明显下降。本研究中酸苔菜的种子散布者种类在不同生境中没有改变，但其组成比例有所不同。白喉冠鹎由于成群拜访，拜访时的散布效率显著高于其他两种鹎类；人为干扰严重生境中的白喉冠鹎比例增加，有利于酸苔菜种子的散布，增加酸苔菜在当地的组成比重。这种人为干扰生境中种子散布比例的下降仅是针对本地种而言，而对于入侵种，生境片断化造成的食果鸟种类及数量改变反而促进了入侵种的种子散布(Buckley *et al*., 2006)，如乌桕(Renne *et al*., 2002)、马缨丹(Gosper & Simth, 2006)等。

同时啮齿类、鸟类及蚂蚁在植物园和野象谷样地均没有对人工摆放的酸苔菜种子形成强烈捕食，种子捕食率 ＜6%。但在野象谷有17.9%的种子被象鼻虫寄生而失去萌发能力，而在植物园却未发现该种象鼻虫。形成这种差异的原因有待进一步研究。一种可能的原因是酸苔菜引入植物园样地时间较短(最大植株大约18年)，通常是寄主密度依赖型的象鼻虫尚未对酸苔菜形成危害。而有关入侵种的逃避天敌假说认为，外来种在入侵地居留并迅速繁殖的原因是由于它逃离了天敌的攻击，它在入侵地没有或者只有很少天敌，不足以对它的生长造成影响，最终使它成为入侵种(Keane & Crawley, 2002; Torchin *et al*., 2002, 2003; Mitchell & Power, 2003)。而植物入侵则是由于逃离了草食动物及病原体微生物等其他天敌的控制(Packer & Clay, 2000; Agrawal & Kotanen, 2003; Mitchell & Power, 2003; Knevel *et al*., 2004)。本研究中酸苔菜在人为干扰重的植物园中未发现象鼻虫，暗示象鼻虫的消失或许对酸苔菜在人为干扰生境中扩张种群有利。结合其同属种东方紫金牛入侵特性与环境的关系，推测酸苔菜也具有入侵的潜质。

综上所述，酸苔菜在人为干扰轻的野象谷中其种子散布者种类与人为干扰重的植物园中种类相同，但由于人为干扰程度的不同，种子散布者的行为(如取食后的落点距离)发生改变进而影响酸苔菜的繁殖更新；而两地的种子捕食者种类不同，野象谷中种子遭到捕食的几率较植物园高，而在植物园中的酸苔菜几乎没有捕食者。这对该物种的繁殖极为有利，但易造成当地植被的单一化，降低生物多样性，并对生态环境造成影响(Santos & Tellería, 1994; Bleher & Böhning-Gaese, 2001)。因此，有关人类活动对植物种子散布及捕食的影响需加强研究，为理解人为干扰严重地区的生物多样性单一化及其与植物入侵的关系提供基础性资料。

参考文献

Agrawal AA, Kotanen PM (2003) Herbivores and the success of exotic plants: a phylogenetically controlled experiment. *Ecology Letters*, **6**, 712–715.

Beattie AJ, Hughes L (2002) Ant–plant interactions. In: *Plant–Animal Interactions: An Evolutionary Approach* (eds Herrera CM, Pellmyr O), pp. 211–235. Blackwell Science, Oxford.

Bleher B, Böhning-Gaese K (2001) Consequences of frugivore diversity for seed dispersal, seedling establishment and the spatial pattern of seedlings and trees. *Oecologia*, **129**, 385–394.

Buckley YM, Anderson S, Catterall CP, Corlett RT, Engel T, Gosper CR, Nathan R, Richardson DM, Setter M, Spiegel O, Smith GV, Voigt FA, Weir JES, Westcott DA (2006) Management of plant invasions mediated by frugivore interactions. *Journal of Applied Ecology*, **43**, 848–857.

Cain ML, Milligan BG, Strand AE (2000) Long-distance seed dispersal in plant populations. *American Journal of Botany*, **87**, 1217–1227.

Callaway RM, Aschehoug ET (2000) Invasive plants versus their new and old neighbors: a mechanism for exotic invasion. *Science*, **290**, 521–523.

Chapman CS (1989) Primate seed dispersal: the fate of dispersed seeds. *Biotropica*, **21**, 148–154.

Colautti RI, Ricciardi A, Grigorovich IA, MacIsaac HJ (2004) Is invasion success explained by the enemy release hypothesis? *Ecology Letters*, **7**, 721–733.

Connell JH (1971) On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. In: *Dynamics of Populations: Proceedings of the Advanced Study Institute on Dynamics of Numbers of Populations* (eds Den Boer PJ, Gradwell GR), pp. 298–310. Center for Agricultural Publishing and Documentation, Wageningen.

Corlett RT (1998) Frugivory and seed dispersal by vertebrates in the Oriental (Indomalayan) region. *Biology Review*, **73**, 413–448.

Crawley MJ (1997) Plant–herbivore dynamics. In: *Plant Ecology* (ed. Crawley MJ), pp. 401–474. Blackwell Science, Oxford.

Crawley MJ (2000) Seed predators and plant population dynamics. In: *Seeds: The Ecology of Regeneration in Plant Communities* (ed. Fenner M), pp. 167–182. CAB International, Wallingford.

Cummings CL, Alexander HM (2002) Population ecology of wild sunflowers: effects of seed density and post-dispersal vertebrate seed predators. *Oecologia*, **130**, 274–280.

Curran LM, Leighton M (2000) Vertebrate responses to spatiotemporal variation in seed production of mast-fruiting Dipterocarpaceae. *Ecological Monographs*, **70**, 101–128.

De Walt SJ, Denslow JS, Ickes K (2004) Natural enemy release facilitates habitat expansion of the invasive tropical shrub *Clidemia hirta*. *Ecology*, **85**, 471–483.

Elton CS (1958) *The Ecology of Invasion by Animals and Plants*. Methuen, London.

Fleming TH (1981) Fecundity, fruiting pattern, and seed dispersal in *Piper amalgo* (Piperaceae), a bat-dispersed tropical shrub. *Oecologia*, **51**, 42–46.

Forget PM, Milleron (1991) Evidence for secondary seed dispersal by rodents in Panama. *Oecologia*, **87**, 596–599.

Forget PM, Cuijpers L (2007) Survival and scatterhoarding of frugivores-dispersed seeds as a function of forest disturbance. *Biotropica*, doi: 10.1111/j.1744-7429.2007.00358.x (OnlineEarly Article)

Foster BL, Tilman D (2003) Seed limitation and the regulation of community structure in oak savanna grassland. *Journal of Ecology*, **91**, 999–1007.

Galetti M, Alves-Costa CP, Cazetta E (2003) Effects of forest fragmentation, anthropogenic edges and fruit colour on the consumption of ornithocoric fruits. *Biological Conservation*, **111**, 269–273.

Gordon DR, Thomas KP (1997) Florida's invasion by nonindigenous plants: history, screening, and regulation. In: *Strangers in Paradise* (eds Simberloff D, Schmitz DC, Brown TC), pp. 21–37. Island Press, Washington, DC.

Gosper CR, Stansbury CD, Vivian-Smith G (2005) Seed dispersal of fleshy-fruited invasive plants by birds: contributing factors and management options. *Diversity and Distribution*, **11**, 549–558.

Gosper CR, Smith GV (2006) Selecting replacements for invasive plants to support frugivores in highly modified sites: a case study focusing on *Lantana camara*. *Ecological Management and Restoration*, **7**, 197–203.

Herrera CM (2002) Seed dispersal by vertebrates. *Plant–Animal Interactions: An Evolutionary Approach* (eds Herrera CM, Pellmyr O), pp. 185–208. Blackwell Science, Oxford.

Herrera CM, Jordano P, Lopez-Soria L, Amat JA (1994) Recruitment of a mast-fruiting, bird-dispersed tree: bridging frugivore activity and seedling establishment. *Ecological Monographs*, **64**, 315–344.

Herron PM, Martine CT, Latimer AM, Leicht-Young SA (2007) Invasive plants and their ecological strategies: prediction and explanation of woody plant invasion in New England. *Diversity and Distributions*, **13**, 633–644.

Hinz HL, Schwarzlaender M (2004) Comparing invasive plants from their native and exotic range: What can we learn for biological control? *Weed Technology*, **18**, 1533–1541.

Hobson KA (2005) Using stable isotopes to trace long-distance dispersal in birds and other taxa. *Diversity and Distributions*, **11**, 157–164.

Holmes RJ, Froud-Williams RJ (2005) Post-dispersal weed seed predation by avian and non-avian predators. *Agriculture, Ecosystems and Environment*, **105**, 23–27.

Howe HF, Smallwood J (1982) Ecology of seed dispersal. *Annual Review of Ecology and Systematics*, **13**, 201–228.

Howe HF, Schupp EW, Westley LC (1985) Early consequences of seed dispersal for a neotropical tree (*Virola surinamensis*). *Ecology*, **66**, 781–791.

Hulme PE (1993) Post-dispersal seed predation by small mammals. *Symposia of the Zoological Society of London*, **65**, 269–287.

Janzen DH (1969) Seed eaters versus seed size, number, toxicity and dispersal. *Evolution*, **23**, 1–27.

Janzen DH (1970) Herbivores and the number of tree species in tropical forests. *The American Naturalist*, **104**, 501–528.

Janzen DH (1971) Seed predation by animals. *Annual Review of Ecology and Systematics*, **2**, 465–492.

Julien MH, Griffiths MW (1998) *Biological Control of Weeds: A World Catalogue Agents and Their Target Weeds*, 4th edn. CABI Publishing, Wallingford, UK.

Keane RM, Crawley MJ (2002) Exotic plant invasions and the enemy release hypothesis. *Trends in Ecology and Evolution*, **17**, 164–170.

Knevel IC, Lans T, Menting FBJ, Hertling UM, van der Putten W (2004) Release from native root herbivores and biotic resistance by soil pathogens in a new habitat both affect the alien *Ammophila arenaria* in South Africa. *Oecologia*, **141**, 502–510.

Koop AL (2003) Population dynamics and invasion rate of an invasive, tropical understory shrub, *Ardisia elliptica*. PhD dissertation, University of Miami, Florida.

Koop AL (2004) Differential seed mortality among habitats limits the distribution of the invasive non-native shrub *Ardisia elliptica*. *Plant Ecology*, **172**, 237–249.

Křivánek M, Pyšek P (2006) Predicting invasion by woody species in a temperate zone: a test of three risk assessment schemes in the Czech Republic (Central Europe). *Diversity and Distributions*, **12**, 319–327.

Lambrinos JG (2004) How interactions between ecology and evolution influence contemporary invasion dynamics. *Ecology*, **85**, 2061–2070.

Levin SA, Muller-Landau HC, Nathan R, Chave J (2003) The ecology and evolution of seed dispersal: a theoretical perspective. *Annual Review of Ecology, Evolution and Systematics*, **34**, 575–604.

Lu CH (鲁长虎) (2003) Biology of mistletoe (*Viscum coloratum*) and its seed dispersal by frugivorous birds. *Acta Ecologica Sinica* (生态学报), **23**, 834–839. (in Chinese with English abstract)

Lyal CHC, Curran LM (2000) Seed-feeding beetles of the weevil tribe Mecysolobini (Insecta: Coleoptera: Curculionidae) developing in seeds of trees in the Dipterocarpaceae. *Journal of Natural History*, **34**, 1743–1847.

Mack RN (1996) Predicting the identity and fate of plant invaders: emergent and emerging approaches. *Biological Conservation*, **78**, 107–121.

Manson RH, Ostfeld RS, Canham CD (1998) The effects of tree seed and seedling density on predation rates by rodents in old fields. *Ecoscience*, **5**, 183–190.

Manson RH, Stiles EW (1998) Links between microhabitat preferences and seed predation by small mammals in old fields. *Oikos*, **82**, 37–50.

Mitchell CE, Power AG (2003) Release of invasive plants from fungal and viral pathogens. *Nature*, **421**, 625–627.

Moran C, Catterall CP, Green RJ, Olsen MF (2004) Fate of feathered fruit-eaters in fragmented forests. In: *Conservation of Australia's Forest Fauna*, 2nd edn (ed. Lunney D), pp. 699–712. Royal Zoological Society of New South Wales, Sydney.

Murray KG (1988) Avian seed dispersal of three neotropical gap-dependent plants. *Eco1ogical Monographs*, **58**, 271–298.

Nakagawa M, Takeuchi Y, Kenta T, Nakashizuka T (2005) Predispersal seed predation by insect vs. vertebrate in six dipterocarp species in Sarawak, Malaysia. *Biotropica*, **37**, 389–396.

Nathan R, Muller-Landau HC (2000) Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends in Ecology and Evolution*, **15**, 278–285.

Neubert MG, Caswell H (2000) Demography and dispersal: calculation and sensitivity analysis of invasion speed for structured populations. *Ecology*, **81**, 1613–1628.

Newingham BA, Callaway RM (2006) Shoot herbivory on the invasive plant, *Centaurea maculosa*, does not reduce its competitive effects on conspecifics and natives. *Oikos*, **114**, 397–406.

Newmark WD (2006) A 16-year study of forest disturbance and understory bird community structure and composition in Tanzania. *Conservation Biology*, **20**, 122–134.

Ostfeld RS, Manson RH, Canham CD (1997) Effects of rodents on tree invasion of old fields. *Ecology*, **78**, 1531–1542.

Packer A, Clay K (2000) Soil pathogens and spatial pattern of seedling mortality in a temperate tree. *Nature*, **404**, 278–281.

Pratt PD, Rayamajhi MB, Van TK, Center TD, Tipping PW (2005) Herbivory alters resource allocation and compensation in the invasive tree *Melaleuca quinquenervia*. *Ecological Entomology*, **30**, 316–326.

Primack RG, Miao SL (1992) Dispersal can limit local plant distribution. *Conservation Biology*, **6**, 513–519

Rejmánek M (1996) A theory of seed plant invasiveness: the first sketch. *Biological Conservation,* **78**, 171–181.

Rejmánek M, Richardson DM (1996) What attributes make some plant species more invasive? *Ecology*, **77**, 1655–1661.

Renne IJ, Barrow WC, Randall LAJ, Bridges WC (2002) Generalized avian dispersal syndrome contributes to Chinese tallow tree (*Sapium sebiferum*, Euphorbiaceae) invasiveness. *Diversity and Distributions*, **8**, 285–295.

Restrepo C, Gomez N, Heredia S (1999) Anthropogenic edges, tree fall gaps, and fruit–frugivore interactions in a neotropical montane forest. *Ecology*, **80**, 668–685.

Richardson DM, Allsopp N, D'Antonio CM, Milton SJ, Rejmánek M (2000) Plant invasions—the role of mutualisms. *Biological Review*, **75**, 65–93.

Santos T, Tellería JL (1994) Influence of forest fragmentation on seed consumption and dispersal of Spanish juniper *Juniperus thurifera*. *Biological Conservation*, **70**, 129–134.

Schnurr JL, Canham CD, Ostfeld RS, Inouye RS (2004) Neighborhood analyses of small-mammal dynamics: impacts on seed predation and seedling establishment. *Ecology*, **85**, 741–755.

Schupp EW (1990) Annual variation in seedfall, post-dispersal predation, and recruitment of a neotropical tree. *Ecology*, **71**, 504–515.

Seabloom EW, Harpole WS, Reichman OJ, Tilman D (2003) Invasion, competitive dominance, and resource use by exotic and native California grassland species. *Proceedings of the National Academy of Sciences, USA*, **100**, 13384–13389.

Siemann E, Rogers WE (2003) Herbivory, disease, recruitment limitation and success of alien and native tree species. *Ecology*, **84,** 1489–1505.

Smith AJ (1975) Invasion and ecesis of bird-disseminated woody plants in a temperate forest sere. *Ecology*, **56**, 19–34.

Stohlgren TJ, Schnase JL (2006) Risk analysis for biological hazards: what we need to know about invasive species. *Risk Analysis*, **26**, 163–173.

Torchin ME, Lafferty KD, Kuris AM (2002) Parasites and marine invasions. *Parasitology*, **124**, S137–S151.

Torchin ME, Lafferty KD, Dobson AP, McKenzie VJ, Kuris AM (2003) Introduced species and their missing parasites. *Nature*, **421**, 628–630.

Torchin ME, Mitchell CE (2004) Parasites, pathogens and invasions by plants and animals. *Frontiers in Ecology and the Environment*, **2**, 183–190.

Toy RJ, Toy SJ (1992) Oviposition preferences and egg survival in *Nanophyes shoreae* (Coleoptera, Apionidae), a weevil fruit-predator in South-east Asian rain forest. *Journal of Tropical Ecology*, **8**, 195–203.

Van der Wall SB (1997) Dispersal of singleleaf pion pine (*Pinus monophylla*) by seed-caching rodents. *Journal of Mammalogy*, **78**, 181–191.

Van der Wall SB, Kuhn KM, Beck MJ (2005) Seed removal, seed predation, and secondary dispersal. *Ecology*, **86**, 801–806.

Westcott DA, Graham DL (2000) Patterns of movement and seed dispersal of tropical frugivore. *Oecologia*, **122**, 249–257.

Westerman PR, Hofman A, Vet LEM, van der Werf W (2003) Relative importance of vertebrates and invertebrates in epigaeic weed seed predation in organic cereal fields. *Agriculture, Ecosystems and Environment*, **95**, 417–425.

Wilson DJ, Wright EF, Canham CD, Ruscoe WA (2007) Neighbourhood analyses of tree seed predation by introduced rodents in a New Zealand temperate rainforest. *Ecography*, **30**, 105–119.

Willson MF, Whelan CJ (1990) Variation in postdispersal survival of vertebrate-dispersed seeds: effects of density, habitat, location, season and species. *Oikos*, **57**, 191–198.

Willson MF (1993) Dispersal mode, seed shadows, and colonization patterns. *Vegetatio*, **108**, 261–280.

Wunderle JM (1997) The role of animal seed dispersal in accelerating native forest regeneration on degraded tropical lands. *Forest Ecology and Management*, **99**, 223–235.

Yagihashi T, Hayashida M, Miyamoto T (1999) Effects of bird ingestion on seed germination of two *Prunus* species with different fruit-ripening seasons. *Ecological Research*, **14**, 71–76.

(责任编委: 高贤明　责任编辑: 周玉荣)