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Effect of stochasticity in the availability of pollinators on the resource allocation within a flower

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ABSTRACT

In this article, we develop a simple model to study the effect of stochasticity in pollination on evolutionarily stable (ES) resource allocation within a hermaphrodite flower of animal-pollinating plants. For simplicity, we consider trade-off in resource allocation between attractive structure (petals etc.) and female function (seeds and fruits) with neglecting the amount of resource allocated to male function (pollens and stamens). We show that ES resource allocation does not much depend on the detail of the probability distribution of the number of pollinator visit on a flower, but on the probability that a flower fails to be visited. We also find that: (1) When the flowers are self-incompatible, the ES allocation to the attractive structure monotonically increases as the availability of pollinators in the environment decreases. (2) When there is strong positive correlation among flowers in the number of pollinator visit, the ES allocation is larger than the case without the correlation. (3) When the flowers are self-compatible and engage prior selfing, the ES allocation monotonically increases as the availability of pollinators in the environment decreases to a threshold, under which it suddenly decreases to zero.

1. Introduction

For plants with animal-pollinating flowers, the availability of pollinators is a critical factor for their reproductive success. They must attract pollinators to receive the pollens of other conspecific plants for producing outcrossing seeds as well as to deposit their pollens for siring the seeds of other plants. Then the plants develop attractive structure (display) such as petal and sepals. The plants are expected to attract more pollinators in average as they develop larger and/or more displays (e.g. Bell, 1985; Conner and Rush, 1996; Ohashi and Yahara, 1998; Worley et al., 2000; Makino et al., 2007), while the excessive investment to the display can decrease their reproductive success through the trade-off among other reproductive efforts (production of pollens, ovules, seeds, fruits etc.). Then, a number of researchers have proposed resource allocation models for flowering plants among the display and other reproductive efforts (e.g. Charlesworth and Charlesworth, 1987; Haig and Westoby, 1988; Sakai, 1993, 2000; de Jong et al., 1999; Sato, 2002; Biernaskie and Elle, 2007; Burd, 2008).

In general, however, the pollinator visit on flowers is fundamentally uncertain events (e.g. Morgan and Wilson, 2005). It must be affected by a variety of external factors other than the display size or number, such as the density of flowering plants in the same site (Makino et al., 2007), local population size (Campbell and Husband, 2007) etc. A 'lucky' individual may be visited by more pollinators than the average of the population by chance even if it has the same size display with others. Such stochasticity may affect differently between the male and female fitness gains because of Bateman's principle (Bateman, 1948) that male fitness is mainly limited by mating opportunities while the female one by the amount of resources available for reproduction. However, most of the previous models on the resource allocation of flower assume deterministic visit of pollinators (e.g. Haig and Westoby, 1988; Sakai, 1993, 2000; Sato, 2002). Some studies suggest that stochasticity in pollinator visit may affect on the reproductive allocation strategy (Charlesworth and Charlesworth, 1987; Burd, 1994, 2008; Maurice and Fleming, 1995; Ashman et al., 2004; Hansen and Totland, 2006), while they are mainly concerned with the effect of pollen limitation (i.e. effect on female function) but rarely with the effect of pollen export (effect on male function).

In this article, we develop a simple model to study the effect of the stochasticity in pollinator visit on evolutionary stable strategy (ESS) for the resource allocation within an animal-pollinating flower. We assume that the stochasticity can affect on the ESS through both of the female and male fitness components. For simplicity, we consider trade-off in the resource allocation between the attractive structure (petals and sepals etc.) and the

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female function (seeds and fruits), with neglecting the amount of investment allocated to the male function (pollens and stamens). We also assume that each plant has one flower so that we can ignore the effect of geitonogamy.

We show that ESS does not depend on the detail of the probability distribution of the pollinator visit on a flower, but on the probability that the flower fails to be visited by pollinators. In addition, we find that: (1) When the flowers are self-incompatible, the evolutionarily stable (ES) resource allocation to the display monotonically decreases as the availability of pollinators in the environment decreases. (2) When there is a strong positive correlation among flowers in the number of pollinator visit, the ES allocation to the display becomes larger than the case without correlation. (3) When the flowers are self-compatible and engage prior selfing, the ES allocation to the display monotonically increases the availability of pollinators in the environment decreases to a threshold, under which it suddenly decreases to zero.

2. Mathematical models and analysis

2.1. Basic model

First, we assume a population of annual plant species with each individual bearing a single animal-pollinated hermaphrodite flower. The amount of resource for reproduction of each individual is assumed identical within the population, denoted by R, which is allocated into the attractive structure or display (petals) by x to attract pollinators, and into the pure female functions (ovules, seeds, fruits, etc.) by $R-x$. We consider the 'attractiveness' of the flower for pollinators r, which is an increasing function of the investment to the display ($r=r(x)$). Based on Bateman's principle (Bateman, 1948), we neglect the amount of resource allocated to pure male function, because it might cost much less resource relative to the display and the female function.

The fitness of the each individual plant ϕ consists of two components

$$\phi = \phi_F + \phi_M, \tag{1}$$

where the first term of the right hand side represents the fitness component via male function and the second via female function.

The flowers must attract pollinators to deposit their pollen and to receive pollen from other plants. First we assume that they are self-incompatible. For simplicity, a single visit of a pollinator is assumed enough to receive pollens for fertilizing all ovules (e.g. Bell, 1985), while some preceding models assume that the fraction of fertilized seeds is an increasing function of the number of pollinator visit (e.g. Haig and Westoby, 1988; Sakai, 1993, 2000; Sato, 2002; Burd, 2008). Then the expected fitness component of the focal individual through the female function is

$$\phi_F = (1-A)f, \tag{2}$$

where A is the probability that no pollinators visit the flower and f is the fitness gain through the female function when all ovules are fertilized. We assume that the flowers compete with each other then A depends not only on the attractiveness of the focal flower $r(x)$ but also on that of other flowers in the population. When y denote the strategy of the resident individuals, their attractiveness is equal to $r(y)$, then $A=A(r(x),r(y))$. The function $f(x)$ is a decreasing function of x, for it increases with the amount of the resource allocated to the female function $R-x$. Supposing the seed dispersal is efficient and the average density of the seeds over the habitat is low, we neglect density-dependent survivability among successfully fertilized seeds caused by local resource competition and species-specific predators or pathogens of the seeds or seedlings (Packer and Clay, 2000).

On the other hand, the reproductive success through the male function ϕ_M depends on the allocation to the female function of the flowers on which the pollens of the focal flower are delivered, as well as the amount of pollens competing to fertilize the ovules. We assume that the amount of pollens delivered from the focal flower to the others is proportional to the number of visit by pollinators, and each pollen delivered to a flower has equal chance to sire the seeds that the individual produce.

2.2. No correlation between flowers in the number of pollinator visit

First, we assume no correlation among the flowers in the number of pollinator visit. In this case, the expected fitness through the male function can be described as

$$\phi_M = \frac{r(x)}{r(y)}(1-A(r(y),r(y)))f(y). \tag{3}$$

This formula can be understood intuitively, as it shows that the mutant shares the paternity of sired seeds in proportion to the attractiveness relative to the wildtype, although we describe the detailed derivation in Appendix A.

From Eqs. (1)–(3), the whole reproductive success of the mutant individual is

$$\phi(x,y) = (1-A(r(x),r(y)))f(x) + \frac{r(x)}{r(y)}(1-A(r(y),r(y)))f(y). \tag{4}$$

Note that the fitness does not depend on the detail of probability distribution with respect to the number of pollinator visit but only on the probability of no visit A.

From the above equation, we derive a condition for ESS of the allocation to the display $\tilde{x}$

$$\left.\frac{\partial}{\partial x}\phi(x,y)\right|_{x=y=\tilde{x}} = -(1-A)f' - A'r'f + \frac{r'}{r}(1-A)f = 0, \tag{5}$$

where $f'=f'(x)$, $r'=r'(x)$, and $A'=\partial A(r(x),r(y))/\partial r(x)$. Eq. (5) can be rewritten as

$$(rf)' - \frac{A'}{1-A}rr'f = 0. \tag{6}$$

The condition of evolutionary stability is $\partial^2\phi/\partial x^2 < 0$ when $x=y=\tilde{x}$. From Eqs. (5) and (6)

$$2rr'(f')^2A' + f\{(-r'f''+f'r'')(-1+A+rA') + rf'(r')^2A''\} < 0, \tag{7}$$

where $f''=f''(x)$, $r''=r''(x)$ and $A''=\partial^2A(r(x),r(y))/\partial r(x)^2$.

When pollinators are so sufficient in the environment that the pollen limitation does not occur, A and the derivatives of A vanish. Then Eq. (6) becomes $(rf)'=0$. This condition is an analogue of the condition for classical sex allocation (Charnov, 1982), although in the present model r is not for the male function but for the attractiveness of a flower.

On the other hand, when the pollinator availability is not so abundant that A cannot be neglected, $(rf)'=A'/(1-A)rr'f$ must be negative, because A' is negative and $1-A$, r, r', and f are all positive. Assuming that $r(x)f(x)$ is a convex function of x ($(rf)''<0$) with a single peak, ESS with pollen limitation is always larger than the one without pollen limitation (Fig. 1).

We put $P_{r_1r_2}(i)$ as the probability that the number of pollinator visit on the flower by i times ($i=0,1,2,\ldots$) when its attractiveness is r_1 and the residents' one is r_2. From the definition $P_{r_1r_2}(0)=A(r_1,r_2)$. In addition, we assume $\sum iP_{r_1r_2}(i)=cr_1/r_2$, where c is a positive parameter indicating the availability of the pollinators in the environment. The flower with average attractiveness is expected to be visited $\sum iP_{r_2r_2}(i)=c$ times by pollinators.