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Packaging and provisioning in plant reproduction

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SUMMARY

Plant reproductive ecologists investigate many aspects of reproductive design not covered by simple offspring size/number models or simple sex allocation models, such as inflorescence design, pollen packaging or fruit design. General models for hierarchical packaging of reproductive allocation which cover these and other cases are developed here. These demonstrate that selection will tend to equalize fitness elasticities of reproductive components when these are properly scaled to take account of reproductive costs. Elasticities are defined as the proportional change in a fitness component with a proportional change in the trait contributing to that component (e.g. the proportional change in the fitness per seed with a proportional change in seed size). For the simplest reproductive design models, selection will favour the equalization of the elasticities of all female hierarchical provisioning and packaging fitness components or all male packaging components, both in single sex models or cosexual models. For simple cosexual models, selection favours allocation to each sex in proportion to the gender-specific fitness elasticities. More generally, selection tends to equalize all component elasticities when these are properly scaled to account for the total resource costs of changes in each component. The models are extended to cover more complex biology, including links between female and male packaging components, packaging components that contribute to the fitness of both genders, accessory costs that may or may not contribute to both genders, and allometric costs and trade-offs. As assumptions about fitness interactions and life history trade-offs become less restrictive, the models more closely approach a general equal-marginal-advantage model. The models provide tools for understanding how and when different components of the reproductive design constrain and selectively impact each other. The utility of the model for aiding in the design and analysis of specific research problems is discussed with reference to some empirical examples.

1. INTRODUCTION

For the last several decades, simple theoretical models explaining the partitioning of reproductive allocation in plants have existed. These include offspring size and number models (Smith & Fretwell 1974; Lloyd 1987; Venable 1992) and models of sex allocation (Charnov 1979; Charlesworth & Charlesworth 1981; Lloyd 1984). The empirical literature shows that botanical interests have grown beyond the scope of these simple frameworks. Plant ecologists recognize that, due to the modular construction of plants, seed number is a vector of hierarchical packaging decisions: the number of seeds per fruit, the number of fruits per infructescence and the number of infructescences per plant. Each of these hierarchical components of seed number has its own evolutionary ecology and many are active areas of empirical pursuit. For example, seed number per fruit has important consequences for seed predation (Bradford & Smith 1977; Herrera 1984), seed dispersal (Augspurger 1986) and sib competition (Casper 1990; Casper *et al.* 1992). Likewise, the number of fruits per inflorescence may impact frugivore behaviour by affecting either attractiveness or handling time involved in feeding (Schupp 1993).

When seed number is considered as a hierarchical packaging strategy, some of its components are intimately related to floral traits and it becomes more difficult to justify ignoring male function in cosexual plants. The number of fruits per inflorescence is influenced by the number of flowers per inflorescence, if only in that it must be less than or equal to it (unless one considers fruits that separate into separate units which take on the ecological functions normally pertaining to the whole fruit, e.g. *Crossosoma*). Similarly, the number of infructescences and inflorescences per plant are intimately biologically related. Thus, seed provisioning and packaging decisions impact flower size and number decisions through the rich frequency-dependent interplay of female and male function.

Male function is also a set of hierarchical provisioning and packaging strategies. How large should pollen grains be? There are interesting relationships between pollen size and style length (e.g. Williams & Rouse 1990; Kirk 1992) and pollen size and selfing (Barrett *et al.* this issue). Pollen grain number can be divided into the number of pollen grains per anther (or even per dosage in species with carefully controlled within-anther dispensing strategies; e.g. Buchmann *et al.* 1977), the number of anthers per flower, the number of flowers per inflorescence and the number of inflorescences per plant. Each of these levels has its complex ecology related to pollinator behaviours such as transport and consumption of pollen, or visitation frequencies and durations (Harder & Thomson 1989). For example, having more flowers per inflorescence sometimes leads to greater attractiveness and more visits per flower (Rodriguez Robles *et al.* 1992), but also more geitonogamy, the impact of which varies with the breeding system (Harder & Barrett 1995). More pollen grains per anther may make a flower more attractive to pollen collecting insects and result in more or longer visits, but a declining fraction of the grains may be successfully transported to appropriate stigmas (Harder & Thomson 1989).

Selection operates simultaneously on the hierarchical components of reproductive design. In this paper I develop theoretical tools for considering all of the components together. The model can be used to address the following questions: How does selection on different components of female and male fitness interact? Are there simple rules that explain such interactions? When is it safe to consider the evolutionary ecology of subcomponents of the reproductive design in isolation? What is being left out when we do?

2. MODELS

First I will consider seed size and number models from a hierarchical-packaging point of view. Then I will progressively add the complications of cosexuality, cost allometry, and interacting male and female reproductive components.

(*a*) *Seed size and number with hierarchical packaging*

The standard Smith–Fretwell model is a convenient starting point because it is familiarity (figure 1). An often sigmoidal curve gives the set of feasible seed sizes and corresponding seed fitnesses for a plant species in a particular environment.

Algebraically, fitness for this model is described as $W(s,n) = nf(s)$ where $ns = R$. W equals maternal fitness (here a function of seed size and number), s equals seed size, $f(s)$ is the seed size fitness function for a plant species in a particular environment, graphed above as a sigmoidal curve, n equals seed number and R equals the resources available for making seeds. The first equation states that maternal fitness equals the number of seeds times the fitness per seed (which depends on seed size). The second equation explains how seed number is constrained by seed size and resources.

This model can be converted into a hierarchical provisioning and packaging model if we redefine seed number to be the product of n (= number of seeds per fruit), N (= number of fruits per inflorescence) and J (= number of inflorescences per plant). The complex ecology of each hierarchical number component can be considered by expressing the fitness of each by a potentially nonlinear general function: $W(s,n,N,J) = f_J(J)f_N(N)f_n(n)f_s(s)$ subject to $JNns = R$. The evolutionary problem, as in the simple Smith–Fretwell model, is to find the provisioning-packaging strategy that maximizes maternal fitness.

This can be done by maximizing $W(s,n,N,J)$, subject to the resource constraint, using the technique of Lagrange multipliers (see Chaing 1984; Lloyd & Venable 1992; Venable 1992). This technique brings the resource constraint into the function being maximized, in such a way as to insure that the constraint is satisfied at the fitness maximum. The Lagrange function for the above problem is:

$$L = f_J(J)f_N(N)f_n(n)f_s(s) - \lambda(JNns - R).$$

Notice that when the resource constraint is satisfied, the term to the right of the first minus sign drops out and the Lagrange function is the same as the fitness function. The technique involves finding the partial derivative of L with respect to each packaging component, also treating λ as a variable, setting each derivative equal to zero, finding the simultaneous solution and checking for sufficiency conditions.

The partial derivative with respect to each variable has a similar structure which can be illustrated with the partial derivative of J:

$$\begin{aligned}\frac{\partial L}{\partial J} &= \frac{\partial f_J(J)}{\partial J} f_N(N)f_n(n)f_s(s) - \lambda Nns \\ &= \frac{\partial f_J(J)}{\partial J}\frac{J}{f_J(J)}\frac{W(J,N,n,s)}{J} - \lambda Nns \\ &= \frac{\partial \ln f_J(J)}{\partial \ln J}\frac{W(J,N,n,s)}{J} - \lambda Nns.\end{aligned}$$

Likewise for the other variables,

$$\frac{\partial L}{\partial N} = \frac{\partial \ln f_N(N)}{\partial \ln N}\frac{W(J,N,n,s)}{N} - \lambda Jns$$

$$\frac{\partial L}{\partial n} = \frac{\partial \ln f_n(n)}{\partial \ln n}\frac{W(J,N,n,s)}{n} - \lambda JNs$$

$$\frac{\partial L}{\partial s} = \frac{\partial \ln f_s(s)}{\partial \ln s}\frac{W(J,N,n,s)}{s} - \lambda JNn$$

$$\frac{\partial L}{\partial \lambda} = JNns - R.$$

After setting each partial derivative equal to zero, the simultaneous solution is found by solving the first four equations for λ and setting them equal to each other:

$$\frac{\partial \ln f_J(J)}{\partial \ln J} = \frac{\partial \ln f_N(N)}{\partial \ln N} = \frac{\partial \ln f_n(n)}{\partial \ln n} = \frac{\partial \ln f_s(s)}{\partial \ln s} \qquad (1)$$

$$JNns = R.$$

Thus the fitness-maximizing values of seed size, seed number per fruit, fruit number per inflorescence and inflorescence number per plant are found by equalizing the slopes of the component fitness functions with fitness functions and size and numbers expressed on log axes (cf. Venable 1992). This equality must further satisfy the condition that the product of the numbers and size equals the resources available for making seeds as reflected in the last equation. The appropriate sufficiency condition to insure a fitness maximum

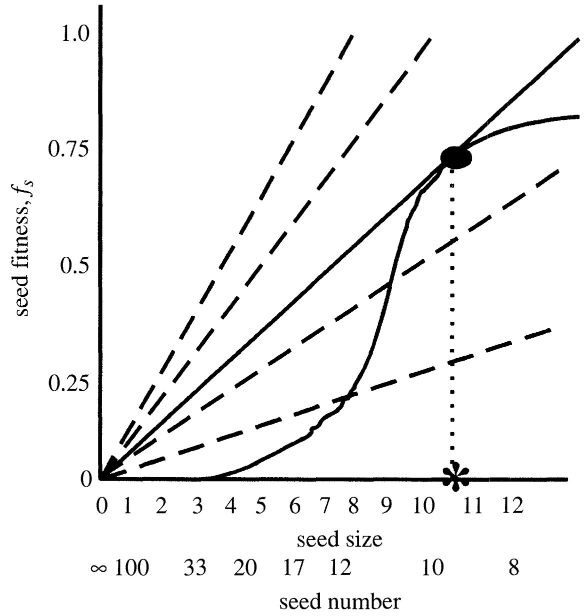

Figure 1. Graphical representation of the Smith–Fretwell model. The sigmoidal curve gives the set of feasible seed sizes and corresponding seed fitnesses for a plant species in a particular environment. For a given amount of resources, the seed-size axis implies a seed-number axis. Straight lines intersecting the origin represent lines of equal maternal fitness. For example, the second steepest dashed line passes through points with 10 seeds with fitness 1.0, 20 seeds with fitness 0.5, and 100 seeds with fitness 0.1. The steeper the straight line passing through the origin, the greater the maternal fitness. Thus the seed-size-number combination that maximizes maternal fitness in this particular environment is given by the point where an equal-maternal-fitness line is tangent to the curve of feasible seed sizes and fitnesses (all other points on the curve of seed-size fitness have maternal-fitness lines with a shallower slope).

rather than a minimum or saddle point is that the Hessian matrix is negative definite (Chaing 1984).

These partial derivatives on logarithmic scales are called 'elasticities' in economics and demography and they have intuitive conceptual meanings. Log changes can be thought of as proportional or percent changes. Thus $\partial \ln f_s(s)/\partial \ln s$ can be thought of as a proportional or percent change in per-seed fitness with a proportional or percent change in seed size. In economics, elasticities tell such things as how demand for a commodity will change with a change in price (both calculated as percent changes). In demography, elasticities represent the proportional change in the population growth rate with a proportional change in a life-table parameter. As proportional changes, elasticities are independent of the scale on which a particular parameter is measured and also of the current values of the parameter.

Equation (1) tells us that selection operating on components of offspring size and number favours the equalization of the elasticities of the component fitness functions. There is no selection for change when the proportional increase in the fitness return from a size or number component due to a proportional increase in the magnitude of that component is equal for all size and number components. The logarithmic scale is natural due to the multiplicative nature of the allocation constraint and of the fitness components.

The equal-elasticities solution reduces to the Smith–Fretwell model if fitness is a linear function of seed number and seed number is a single variable, i.e. if $W(s) = nf(s)$ where $ns = R$:

$$\frac{\partial \ln f_n(n)}{\partial \ln n} = \frac{\partial \ln f_s(s)}{\partial \ln s} \Rightarrow 1 = \frac{\partial \ln f_s(s)}{\partial \ln s} \Rightarrow 1 = \frac{\partial f_s(s)}{\partial s}\,\frac{s}{f_s(s)}$$

$$\Rightarrow \frac{\partial f_s(s)}{\partial s} = \frac{f_s(s)}{s}$$

$$ns = R.$$

The equation on the second line can be stated geometrically as, fitness is maximized where the slope for the seed-size-fitness function (the sigmoidal curve in figure 1) equals the slope of a straight line passing through the origin, which is given by the value of the ordinate, $f_s(s)$, over the abscissa, s, for any point on the line (the dashed lines in figure 1).

The operation of selection on hierarchical-provisioning and packaging decisions can be visualized graphically with figure 2. Selection will favour reapportionment of the available resources among the seed-size and number components until the slopes of the curves in figure 2 are equal. For simplicity and clarity of presentation, in the rest of this paper I will assume that fitness components have graphs with the general shapes given in figure 2. This is done to insure the sufficiency conditions for a fitness maximum. If a function curved upwards, equalizing its slope with that of other functions might result in minimizing fitness with respect to that fitness component. In such cases selection favours equalizing slopes at some other position on the graph where the slope curves downward or allocating at one of the boundaries of the x axis (e.g. the largest or smallest possible seed sizes – coconuts and orchids?). The formal mathematical treatment of such cases is given in Lloyd & Venable (1992).

The most important implication of this model is that factors that determine or alter the shape of the three seed-number functions will alter the way selection operates on seeds size and vice versa. Only if all three functions were linear, would several of the implications of the Smith–Fretwell model hold. These are that (1) the hierarchical partitioning of seed number will not affect fitness (alternative fruit designs and displays are selectively neutral) and (2) the seed-size-fitness function alone will determine the fitness-maximizing seed size (when resource availability varies, it is absorbed in seed number, not size).

(*b*) *Seed packaging and sex allocation*

The number of fruits per infructescence and number of infructescences per plant will also be affected by factors impinging of floral ecology, as these are linked to floral traits through the level of fruit set. To explore these interactions for hermaphroditic plants requires explicit consideration of male function which may compete with female function for resources. Selection is

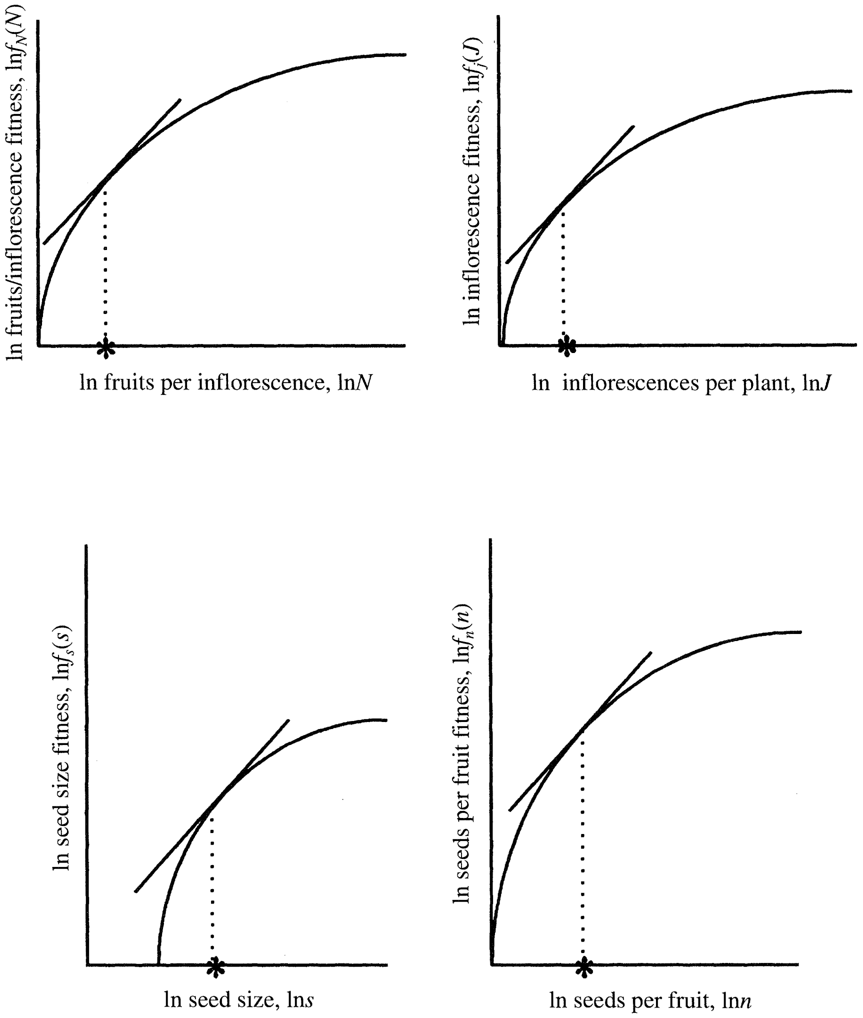

Figure 2. Graphical representation of the operation of selection on hierarchical provisioning and packaging strategies. Selection will favour reapportionment of the available resources among the seed size and number components until the slopes of the curves of log fitness components against log trait values are equal for all size and number traits (see equation (1)).

frequency dependent because fitness through each sexual function depends not only on what an individual does, but upon the sexual strategies of its potential mates and sexual competitors.

Simple sex allocation models can be solved in terms of the elasticities of male and female fitness, which will be useful for integrating sex into hierarchical size-number problems. Let m equal allocation to male function, f equal allocation to female function, R equal total allocation, $f_{♂}(m)$ equal male fitness before the operation of frequency-dependent interactions with the rest of the population (e.g. successful pollen production or removal), $f_{♀}(f)$ equal female fitness (e.g. seed production or successful seed dispersal). While female fitness of an individual can be considered to equal $f_{♀}(f')$ where the prime indicates the allocation decision of an individual in question, an individual's male fitness equals the total female fitness of the population times the proportion of these seeds sired by the individual in question. This equals $P f_{♀}(f) f_{♂}(m')/P f_{♂}(m)$ where P equals the population size of the mating group and the allocations without primes refer to those of the rest of the population (the individual in question is assumed to be a small fraction of the total population such that its strategy has an insignificant impact on the total female fitness and total male fitness in this expression). With the latter assumption (large population size), the Ps cancel so that the fitness of an individual with sexual allocations m' and f' in a population with sexual strategies m and f is given by

$$W(m', f', m, f) = f_{♀}(f') + \frac{f_{♀}(f) f_{♂}(m')}{f_{♂}(m)}, \qquad (2)$$

subject to the resource constraint $f' + m' = R$.

The Lagrange function is

$$L(m', f', m, f) = f_{♀}(f') + \frac{f_{♀}(f) f_{♂}(m')}{f_{♂}(m)} - \lambda(m' + f' - R).$$

The first step in finding the ESS allocation to female and male function is to take the derivatives of the Lagrange function with respect to the individual's sexual strategy and the Lagrange multiplier (λ) and set the resulting expressions equal to zero:

$$\frac{\partial L}{\partial f'} = \frac{\partial f_{♀}(f')}{\partial f'} - \lambda = 0$$

$$\frac{\partial L}{\partial m'} = \frac{f_{\text{♀}}(f)}{f_{\text{♂}}(m)}\frac{\partial f_{\text{♂}}(m')}{\partial m'} - \lambda = 0$$

$$\frac{\partial L}{\partial \lambda} = f + m - R = 0.$$

The ESS is found by solving these simultaneous equations and setting the individual sex allocation equal to the population sex allocation ($f' = f = \hat{f}$, $m' = m = \hat{m}$):

$$\frac{f_{\text{♀}}(\hat{f})}{\partial \hat{f}} = \frac{f_{\text{♀}}(\hat{f})}{f_{\text{♂}}(\hat{m})}\frac{\partial f_{\text{♂}}(\hat{m})}{\partial \hat{m}} \Rightarrow \frac{\partial f_{\text{♀}}(\hat{f})}{\partial \hat{f}}\frac{\hat{f}\hat{m}}{f_{\text{♀}}(\hat{f})} = \frac{\partial f_{\text{♂}}(\hat{m})}{\partial \hat{m}}\frac{\hat{m}\hat{f}}{f_{\text{♂}}(\hat{m})}$$

$$\Rightarrow \frac{\partial \ln f_{\text{♀}}(\hat{f})}{\partial \ln \hat{f}}\hat{m} = \frac{\partial \ln f_{\text{♂}}(\hat{m})}{\partial \ln \hat{m}}\hat{f}$$

$$\Rightarrow \frac{\dfrac{\partial \ln f_{\text{♀}}(\hat{f})}{\partial \ln \hat{f}}}{\hat{f}} = \frac{\dfrac{\partial \ln f_{\text{♂}}(\hat{m})}{\partial \ln \hat{m}}}{\hat{m}}$$

$$\hat{f} + \hat{m} = R.$$

At the ESS, female and male allocations are adjusted so that the fitness elasticity of female function divided by the female allocation equals the fitness elasticity of male function divided by male allocation and so that the resource constraint is satisfied. Rather than equalizing elasticities as in the hierarchical-packaging and provisioning problem above, selection favours allocating to male and female functions in proportion to the fitness elasticities:

$$\frac{\hat{m}}{\hat{f}} = \frac{\dfrac{\partial \ln f_{\text{♂}}(\hat{m})}{\partial \ln \hat{m}}}{\dfrac{\partial \ln f_{\text{♀}}(\hat{f})}{\partial \ln \hat{f}}}.$$

Sex allocation models often use power functions to describe male and female fitness components, e.g. $f_{\text{♀}}(f) = af^{\alpha}; f_{\text{♂}}(m) = bm^{\beta}$ (Lloyd 1984). The elasticities of power functions are the exponents. Thus, the ESS allocation ratio using these functions is $\beta{:}\alpha$ which can be interpreted in terms of the curvature of the male and female fitness functions (often called 'gain curves').

To convert such a model into a hierarchical provisioning and packaging model, we subdivide male and female allocation into hierarchical size and number components. Once again let seed size be s and seed number be the product of n (= number of seeds per fruit), N (= number of fruits per infructescence) and J (= number of infructescences per plant). The corresponding component fitness functions are still $f_s(s), f_n(n), f_N(N)$ and $f_J(J)$. The product of these will describe female fitness in an expanded equation (2). A variety of male packaging and provisioning fitness components can also be included in the model by letting p equal pollen grain size, w equal the number of pollen grains per stamen, x equal the number of stamens per flower, z equal the number of flowers per inflorescence and I equal the number of inflorescences per plant. In this initial model we will assume that selection operates separately on fruit and flower numbers per inflorescence or infructescence (subject to $N \leqslant z$), such that fruit set is simply the consequence of these separate selective outcomes. Likewise, we will initially assume that selection operates separately on infructescence and inflorescence numbers per plant (subject to $J \leqslant I$). The potentially nonlinear male fitness components are given by $f_p(p), f_w(w), f_x(x), f_z(z)$ and $f_I(I)$. The resource constraint for this problem is $snNJ + pwxzI = R$ where the first product is total female allocation and the second is total male allocation. The equation for individual fitness is given by:

$$W(s', \ldots, J', p', \ldots, I', s, \ldots, J, p, \ldots, I)$$
$$= f_s(s')f_n(n')f_N(N')f_J(J')$$
$$+ \frac{f_s(s)f_n(n)f_N(N)f_J(J)f_p(p')f_w(w')f_x(x')f_z(z')f_J(I')}{f_p(p)f_w(w)f_x(x)f_z(z)f_I(I)}.$$

The Lagrange function is

$$L(s', \ldots, J', p', \ldots, I', s, \ldots, J, p, \ldots, I)$$
$$= f_s(s')f_n(n')f_N(N')f_J(J')$$
$$+ \frac{f_s(s)f_n(n)f_N(N)f_J(J)f_p(p')f_w(w')f_x(x')f_z(z')f_I(I')}{f_p(p)f_w(w)f_x(x)f_z(z)f_I(I)}.$$
$$-\lambda(s'n'N'J' + p'w'x'z'I' - R).$$

The ESS is found by finding the individual's hierarchical sex-allocation strategy that maximizes L for a given set of population parameters, then setting the individual's values of the reproductive-packaging components equal the population's values. The partial derivatives with respect to each component of an individual's reproductive strategy have similar structures which can be illustrated with the partial with respect to s':

$$\frac{\partial L}{\partial s'} = \frac{\partial f_s(s')}{\partial s'}f_n(n')f_N(N')f_J(J') - \lambda n'N'J$$

$$= \frac{\partial f_s(s')}{\partial s'}\frac{s'\text{♀}tot'}{f_s(s')} - \lambda s'n'N'J'$$

$$= \frac{\partial \ln f_s(s')}{\partial \ln s'}\frac{\text{♀}tot'}{s'} - \lambda n'N'J'.$$

where $\text{♀}tot'$ equals total female fitness of the individual in question $(= f_s(s')f_n(n')f_N(N')f_J(J'))$.

Similarly for the other variables

$$\frac{\partial L}{\partial n'} = \frac{\partial \ln f_n(n')}{\partial \ln n'}\frac{\text{♀}tot'}{n'} - \lambda s'N'J'$$

$$\frac{\partial L}{\partial N'} = \frac{\partial \ln f_N(N')}{\partial \ln N'}\frac{\text{♀}tot'}{N'} - \lambda s'n'J'$$

$$\frac{\partial L}{\partial J'} = \frac{\partial \ln f_J(J')}{\partial \ln J'}\frac{\text{♀}tot'}{J'} - \lambda s'n'N'$$

$$\frac{\partial L}{\partial p'} = \frac{\partial \ln f_p(p')}{\partial \ln p'}\frac{\text{♂}tot'}{p'} - \lambda w'x'z'I'$$

$$\frac{\partial L}{\partial w'} = \frac{\partial \ln f_w(w')}{\partial \ln w'}\frac{\text{♂}tot'}{w'} - \lambda p'x'z'I'$$

$$\frac{\partial L}{\partial x'} = \frac{\partial \ln f_x(x')}{\partial \ln x'}\frac{\text{♂}tot'}{x'} - \lambda p'w'z'I'$$

$$\frac{\partial L}{\partial z'} = \frac{\partial \ln f_z(z')}{\partial \ln z'}\frac{\text{♂}tot'}{z'} - \lambda p'w'x'I'$$

$$\frac{\partial L}{\partial I'} = \frac{\partial \ln f_I(I')}{\partial \ln I'}\frac{\text{♂}tot'}{I'} - \lambda xp'w'x'z'$$

$$\frac{\partial L}{\partial \lambda} = snNJ + pwxzI - R.$$

Setting all of these equations equal to zero, setting the individual packaging and provisioning strategy equal to the population strategy, recognizing that at the ESS, $\text{♀}tot = \text{♂}tot$ and obtaining the simultaneous solution (by solving all but the last equation for λ), yields the following ESS condition:

$$\frac{\frac{\partial \ln f_s(\hat{s})}{\partial \ln \hat{s}}}{\hat{s}\hat{n}\hat{N}\hat{J}} = \frac{\frac{\partial \ln f_n(\hat{n})}{\partial \ln \hat{n}}}{\hat{s}\hat{n}\hat{N}\hat{J}} = \frac{\frac{\partial \ln f_N(\hat{N})}{\partial \ln \hat{N}}}{\hat{s}\hat{n}\hat{N}\hat{J}} = \frac{\frac{\partial \ln f_J(\hat{J})}{\partial \ln \hat{J}}}{\hat{s}\hat{n}\hat{N}\hat{J}}$$

$$= \frac{\frac{\partial \ln f_p(\hat{p})}{\partial \ln \hat{p}}}{\hat{p}\hat{w}\hat{x}\hat{z}\hat{I}} = \frac{\frac{\partial \ln f_w(\hat{w})}{\partial \ln \hat{w}}}{\hat{p}\hat{w}\hat{x}\hat{z}\hat{I}} = \frac{\frac{\partial \ln f_x(\hat{x})}{\partial \ln \hat{x}}}{\hat{p}\hat{w}\hat{x}\hat{z}\hat{I}} = \frac{\frac{\partial \ln f_z(\hat{z})}{\partial \ln \hat{z}}}{\hat{p}\hat{w}\hat{x}\hat{z}\hat{I}}$$

$$= \frac{\frac{\partial \ln f_I(\hat{I})}{\partial \ln \hat{I}}}{\hat{p}\hat{w}\hat{x}\hat{z}\hat{I}}$$

$$\hat{s}\hat{n}\hat{N}\hat{J} + \hat{p}\hat{w}\hat{x}\hat{z}\hat{I} = R.$$

For this initial case, none of the female packaging/provisioning components are also male packaging/provisioning components (or functions thereof) and vice versa. Under these conditions, the fitness elasticities for the female packaging/provisioning components will be equal to each other at the ESS just as in the hierarchical packaging model without sex. Likewise, male packaging/provisioning components will have equal elasticities at the ESS. The relationship between male and female elasticities satisfies $\text{♀}\hat{e}/\hat{f} = \text{♂}\hat{e}/\hat{m}$ subject to the resource constraint $\hat{f} + \hat{m} = R$, where $\text{♀}\hat{e}$ and $\text{♂}\hat{e}$ stand for female and male elasticities at the ESS and $\hat{f} = \hat{s}\hat{n}\hat{N}\hat{J}$ and $\hat{m} = \hat{p}\hat{w}\hat{x}\hat{z}\hat{I}$ are total female and total male allocations at the ESS (note that we need not specify which male and female elasticities, because they are all equal at the ESS). Thus under the conditions of this model the results of the separate hierarchical seed-size-and-number model and sex-allocation model are maintained: selection favours equilibration of size-number elasticities and favours allocation to male and female function in proportion to the male and female elasticities.

The interactions between male and female packaging strategies may be more complicated. For example, the values of female provisioning and packaging components may constrain the values of male packaging components or vice versa. For example, fruit set could have some evolutionarily fixed value so that fruit number per infructescence and flower number per inflorescence constrain each other's evolution. Another issue that complicates the analysis is explicit consideration of accessory floral or fruit structures which represent indirect fitness components and may or may not impact both female and male reproductive success. Such factors include the production of nectar, petals and fruit dispersal structures.

The effects of such factors can be seen in the following model. Begin with the assumptions of the previous model, except let infructescence number per plant be constrained to equal inflorescence number ($J = I$). Let fruit number per inflorescence be $N = kz$, where fruit set, k, is a constant fraction of the number of flowers per inflorescence, z. Also let l be accessory floral costs (e.g. petals or nectar) that contribute to both male and female function and let d be fruit dispersal costs that contribute only to female fitness. The constraint on resource allocation is $snkzI + pwxzI + dkzI + lzI = R$, where the terms, from left to right, represent allocation to female size-and-number components, allocation to male size-and-number components, allocation to fruit dispersal and allocation to petals and nectar. The fitness function is:

$$W(s', \ldots, I', s, I) = f_s(s')f_n(n')f_{\text{♀}l}(l')f_d(d')f_{\text{♀}z}(z')f_{\text{♀}I}(I') + \frac{f_s(s)f_n(n)f_{\text{♀}l}(l)f_d(d)f_{\text{♀}z}(z)f_{\text{♀}I}(I)f_p(p')f_w(w')f_x(x')f_{\text{♂}l}(l')f_{\text{♂}z}(z')f_{\text{♂}I}(I')}{f_p(p)f_w(w)f_x(x)f_{\text{♂}l}(l)f_{\text{♂}z}(z)f_{\text{♂}I}(I)},$$

where $f_{\text{♀}l}(l)$ and $f_{\text{♂}l}(l)$ represents the female and male fitness consequences of the level of allocation to petals or nectar and $f_d(d)$ represents the fitness consequences of the level of allocation to fruit dispersal structures. The same calculation procedures as for the previous model yield the following ESS conditions:

$$\frac{\frac{\partial \ln f_s(\hat{s})}{\partial \ln \hat{s}}}{\hat{s}\hat{n}k\hat{z}\hat{I}} = \frac{\frac{\partial \ln f_n(\hat{n})}{\partial \ln \hat{n}}}{\hat{s}\hat{n}k\hat{z}\hat{I}} = \frac{\frac{\partial \ln f_d(\hat{d})}{\partial \ln \hat{d}}}{\hat{d}k\hat{z}\hat{I}} = \frac{\frac{\partial \ln f_{\text{♀}l}(\hat{l})}{\partial \ln \hat{l}} + \frac{\partial \ln f_{\text{♂}l}(\hat{l})}{\partial \ln \hat{l}}}{\hat{l}\hat{z}\hat{I}}$$

$$= \frac{\frac{\partial \ln f_{\text{♀}z}(z)}{\partial \ln \hat{z}} + \frac{\partial \ln f_{\text{♂}z}(\hat{z})}{\partial \ln \hat{z}}}{(k(\hat{s}\hat{n} + d\hat{d}) + \hat{p}\hat{w}\hat{x} + \hat{l}) \times \hat{z}\hat{I}} = \frac{\frac{\partial \ln f_{\text{♀}I}(\hat{I})}{\partial \ln \hat{I}} + \frac{\partial \ln f_{\text{♂}I}(\hat{I})}{\partial \ln \hat{I}}}{(k(\hat{s}\hat{n} + d) + \hat{p}\hat{w}\hat{x} + \hat{l})\,\hat{z}\hat{I}}$$

$$= \frac{\frac{\partial \ln f_p(\hat{p})}{\partial \ln \hat{p}}}{\hat{p}\hat{w}\hat{x}\hat{z}\hat{I}} = \frac{\frac{\partial \ln f_w(\hat{w})}{\partial \ln \hat{w}}}{\hat{p}\hat{w}\hat{x}\hat{z}\hat{I}} = \frac{\frac{\partial \ln f_x(\hat{x})}{\partial \ln \hat{x}}}{\hat{p}\hat{w}\hat{x}\hat{z}\hat{J}}$$

$$(\hat{s}\hat{n}k + \hat{d}k + \hat{p}\hat{w}\hat{x} + \hat{l})\hat{z}\hat{I} = R.$$

Under the current assumptions, the fitness elasticities for the female packaging/provisioning components are no longer all equal to each other at the ESS. Likewise, male packaging/provisioning components do not all have equal elasticities at the ESS. Size-number components that impact only one gender function still have equal fitness elasticities at the ESS. Specifically, seed size and number per fruit have equal elasticities as do pollen grain size, pollen number per stamen and stamen number per flower. Also, size-number components that impact fitness of both genders have equal elasticities at the ESS, but it is the sum of their female and male elasticities that is equalized by selection. Thus, the sum of the female and male elasticities of the inflorescence number fitness component equals the sum of the fruits per inflorescence and flowers per inflorescence elasticities.

In the previous model, the denominators of the equal elasticity equation could be simply interpreted as total female or male allocation and the similarity to the simple nonhierarchical sex-allocation model was clear. More generally, the denominator in these expressions represents a scaling factor which converts a proportional change in a reproductive attribute into its total allocational cost. To calculate the total allocational cost associated with a shift in seed size, a given proportional change in seed size (e.g. 1 per cent) is multiplied by the current seed size to give the cost per seed of this change. It is then further multiplied by the number of seeds per fruit, the number of fruits per inflorescence and the number of inflorescences per plant to get the full reproductive cost of a 1 per cent change in seed size. Thus the ESS equality can be thought of as stating that the fitness elasticity of each fitness component will be equalized, when properly scaled to take into account the reproductive cost of a proportional change in each hierarchical size or number attribute. Because a 1 per cent change in seed number per fruit has the same total reproductive cost as a 1 per cent change in seed size, these costs cancel and the unscaled elasticities of seed size and seed number per fruit are equalized.

Some size-and-number attributes contribute to fitness through both male and female functions. The proportional fitness increase due to a proportional change in these attributes equals the sum of their female and male component elasticities (cf. terms for z and I in this model).

There are two fitness components in the model that do not represent male and female gamete packaging strategies, but rather accessory structure allocations. Since accessory structures do not have the same proportional costs as anything else, their denominators will not cancel.

The conclusion of this model is that equilibration of unscaled elasticities only occurs for proportional allocations that have the same proportional costs (e.g. the simple or hierarchical versions of the Smith–Fretwell model or the same-sex packaging components in the sexual model with no intersexual dependencies or accessory costs). Equilibration of elasticities for allocations with different reproductive costs requires scaling by the total reproductive cost of a proportional change in the component allocation.

It may frequently be the case that fitness components interact in ways that are not adequately accounted for by separate multiplicative fitness components. For example, the shape of the seed-size fitness function might change for different numbers of seeds per fruit. As the model is extended to allow for such interactions, the ESS conditions more closely approach a general equal-marginal-advantage equation (Lloyd & Venable 1992). Such ESS conditions state that, when changes in traits are scaled to represent common units of resource, the marginal fitness of all traits are equal at the ESS.

3. THE ALLOMETRY OF LIFE HISTORY TRADE-OFFS

The constraint equations for the previous models (e.g. $sn = R$) are intuitive, but a plant functional morphologist would tell us that they are not likely to be empirically realistic. A ten-seeded fruit may cost more or less than ten times the production cost of a one-seeded fruit due to various fixed costs (economies of scale) or accelerating costs. Such cost non-linearities are frequently accounted for with allometric power equations, such that the resource cost of seed number per fruit, for example, might equal bn^{β}. Fixed costs imply $\beta < 1$ (a ten-seeded fruit costs less than ten times a one-seeded fruit) and accelerating costs are given by $\beta > 1$ (a ten-seeded fruit costs more than ten times a one-seeded fruit). Thus a more realistic constraint equation allowing cost non-linearities for size-number components and accessory structures for the previous model is given by $(as^{\alpha}\, bn^{\beta}\, k + cd^{\gamma}\, k + ep^{\epsilon}\, ow^{\theta}\, mx^{\mu} + ql^{\pi})\, rz^{\rho}\, tI^{\tau} = R$, where the Greek letter exponents are allometric constants translating reproductive attributes into their resource costs. For generality, I use general functions to translate reproductive attributes into their resource costs:

$$(g_s(s)g_n(n)k + g_d(d)k + g_p(p)g_w(w)g_x(x) + g_l(l))\, g_z(z)\, g_I(I) = R.$$

When this constraint equation is used with the previous model, the ESS is found to be given by the following conditions:

$$\frac{\dfrac{\partial \ln f_s(\hat{s})}{\partial \ln \hat{s}}}{\dfrac{\partial \ln g_s(\hat{s})}{\partial \ln \hat{s}}\, g_s(\hat{s})\, g_n(\hat{n})\, k g_z(\hat{z})\, g_I(\hat{I})} = \frac{\dfrac{\partial \ln f_n(\hat{n})}{\partial \ln \hat{n}}}{\dfrac{\partial \ln g_n(\hat{n})}{\partial \ln \hat{n}}\, g_s(\hat{s})\, g_n(\hat{n})\, k g_z(\hat{z})\, g_I(\hat{I})}$$

$$
\begin{aligned}
&= \frac{\dfrac{\partial \ln f_d(\hat{d})}{\partial \ln \hat{d}}}{\dfrac{\partial \ln g_d(\hat{d})}{\partial \ln \hat{d}}\, g_d(\hat{d})\, k g_z(\hat{z})\, g_I(\hat{I})} = \frac{\dfrac{\partial \ln f_{\text{♀}l}(\hat{l})}{\partial \ln \hat{l}} + \dfrac{\partial \ln f_{\text{♂}l}(\hat{l})}{\partial \ln \hat{l}}}{\dfrac{\partial \ln g_l(\hat{l})}{\partial \ln \hat{l}}\, g_l(\hat{l})\, g_z(\hat{z})\, g_I(\hat{I})} \\
&= \frac{\dfrac{\partial \ln f_{\text{♀}z}(\hat{z})}{\partial \ln \hat{z}} + \dfrac{\partial \ln f_{\text{♂}z}(\hat{z})}{\partial \ln \hat{z}}}{\dfrac{\partial \ln g_z(\hat{z})}{\partial \ln \hat{z}}\, (k(g_s(\hat{s}) g_n(\hat{n}) + g_d(\hat{d})) + g_p(\hat{p}) g_w(\hat{w}) g_x(\hat{x}) + g_l(\hat{l}))\, g_z(\hat{z})\, g_I(\hat{I})} \\
&= \frac{\dfrac{\partial \ln f_{\text{♀}I}(\hat{I})}{\partial \ln \hat{I}} + \dfrac{\partial \ln f_{\text{♂}I}(\hat{I})}{\partial \ln \hat{I}}}{\dfrac{\partial \ln g_I(\hat{I})}{\partial \ln \hat{I}}\, (k(g_s(\hat{s}) g_n(\hat{n}) + g_d(\hat{d})) + g_p(\hat{p}) g_w(\hat{w}) g_x(\hat{x}) + g_l(\hat{l}))\, g_z(\hat{z})\, g_I(\hat{I})} \qquad (3) \\
&= \frac{\dfrac{\partial \ln f_p(\hat{p})}{\partial \ln \hat{p}}}{\dfrac{\partial \ln g_p(\hat{p})}{\partial \ln \hat{p}}\, g_p(\hat{p}) g_w(\hat{w}) g_x(\hat{x})\, g_z(\hat{z})\, g_I(\hat{I})} \\
&= \frac{\dfrac{\partial \ln f_w(\hat{w})}{\partial \ln \hat{w}}}{\dfrac{\partial \ln g_w(\hat{w})}{\partial \ln \hat{w}}\, g_p(\hat{p}) g_w(\hat{w}) g_x(\hat{x})\, g_z(\hat{z})\, g_I(\hat{I})} \\
&= \frac{\dfrac{\partial \ln f_x(\hat{x})}{\partial \ln \hat{x}}}{\dfrac{\partial \ln g_x(\hat{x})}{\partial \ln \hat{x}}\, g_p(\hat{p}) g_w(\hat{w}) g_x(\hat{x})\, g_z(\hat{z})\, g_I(\hat{I})} \\
&\qquad (g_s(\hat{s})\, g_n(\hat{n}) k + g_d(\hat{d}) k + g_p(\hat{p})\, g_w(\hat{w})\, g_x(\hat{x}) + g_l(\hat{l}))\, g_z(\hat{z})\, g_I(\hat{I}) = R.
\end{aligned}
$$

These ESS conditions are very similar to the previous ones: the elasticities of all male and female fitness components will be equilibrated at the ESS when properly scaled to take into account the reproductive cost of a proportional change in each hierarchical size or number attribute. The resource cost scaling factor still takes into account the total reproductive cost of a proportional change in each hierarchical size or number attribute. But because costs are non-linear, the cost elasticity appears in the scaling factor. The resource-cost elasticity of a reproductive trait such as seed size is the proportional change in seed-size cost with a proportional change in seed size. This equalled one with the previous linear cost constraint. Thus, it dropped out of all previous ESS conditions. Now, a given proportional change in seed size (e.g. 1 per cent) is multiplied by seed-size cost elasticity to get the proportional change in resource cost corresponding to the 1 per cent change in seed size. This proportional change in resource costs is then multiplied by the current cost of a seed (given by the potentially non-linear allometric cost function $g_s(s)$) to give the cost per seed of a proportional change for a seed of that size. The result is further multiplied by the costs associated with the number of seeds per fruit, the number of fruits per inflorescence and the number of inflorescences per plant to get the full reproductive cost of the 1 per cent change in seed size.

One consequence of allometric constraints is that none of the reproductive traits will have equal unscaled fitness elasticities at the ESS unless their resource-constraint elasticities happen to be equal. More specifically, if the resource-cost elasticities are equal for the sets of traits that had equal unscaled elasticities in the previous model, selection will still favour equalizing their unscaled elasticities in the present model. All cost elasticities in the previous model equalled one, which satisfies this rule. For allometric resource constraints described by power functions, the elasticities are the exponents of the power functions. Thus the conclusions of the previous model would still hold in the present model if all reproductive traits had non-linear resource costs with the same allometric constant.

The impact of these allometric considerations is seen in the following example. In the previous non-allometric model seed size and seed number per fruit were predicted to have equal unscaled elasticities at the ESS. Assume that seed-size and number-per-fruit cost allometries are described by power functions so that their cost elasticities equal α and β respectively. Assume that the seed size and number per fruit fitness components have the same general shape as in figure 2. Also, assume that both seed-size and number-per-fruit involve fixed costs so that α and $\beta < 1$ and a seed that is twice as big costs less than twice as much to produce (and a ten-seeded fruit costs less than ten one-seeded fruits). If α equals β, selection will favour equalizing the unscaled fitness elasticities of seed size and number per fruit (see equation (3)). If α does not equal β, selection will favour an allocation pattern that results in the ratio of seed-size to seed-number fitness elasticities equalling α/β (this is derived from the equality of the first two terms in equation (3)). Thus if the fixed costs of seed size were greater than those for seed number ($\alpha < \beta$), at the ESS, the fitness elasticity of seed number per fruit will be larger than that of seed size. With reference to figure 2, this implies larger seeds in fewer-seeded fruits than for the case of equal allometric constants. Thus in the presence of greater fixed costs for seed size than for seed number, selection favours greater allocation to the trait with greater fixed costs than would be predicted by equalizing fitness elasticities. When a cost is an accelerating function of allocation to a trait (i.e. when the cost elasticity is greater than one), selection will favour less allocation to it than would otherwise be the case.

Cost non-linearities can be described in a variety of ways besides power functions. But the general result holds that greater fixed costs for a reproductive trait results in selection for more allocation to that trait than would otherwise be favoured.

4. DISCUSSION

The models developed here help to integrate our ideas of how the evolutionary ecologies of different reproductive components impact each other and provide general conceptual tools for specifying these interactions. For example, some types of inflorescences, such as spadices and capitulae, tend to have sessile fruits with little change in the configuration of the infructescence from that of the inflorescence (with a few obvious exceptions such as Mimosoideae). In such inflorescences, fruits and flowers tend to respond closely to each other's evolution (Ramirez & Berry 1995) and separate models of their floral or fruit biology would be incomplete. While the importance of selective interactions and constraints among different reproductive characters has been widely recognized (e.g. Primack 1987), there have not been effective conceptual tools for dealing with them simultaneously in the frequency-dependent setting of sexuality.

There are many specific applications of this model that, while not necessarily dealing with the integration of the whole reproductive deployment, can help with the design and interpretation of specific experimental or comparative studies of subsets of traits not treated by conventional models. Such specific applications usually require further development or reduction of the models.

As an example, consider the evolution of inflorescence size in *Asclepias*. The early studies of *Asclepias* inflorescence design were very influential in proposing the 'male function hypothesis' for the evolution of floral attraction (Willson & Rathcke 1974; Queller 1983). Subsequently a fairly large and somewhat confusing literature has developed regarding *Asclepias* inflorescence size and inflorescence size in general (references in Willson 1994; Wyatt & Broyles 1994). Some confusion exists about how to integrate selection operating on inflorescence size and number, taking into account potentially synergetic or competing gender functions that operate in the frequency-dependent population context of sexuality. Authors variously discuss female versus male fitness on a per-plant, per-inflorescence, or per-flower basis. Also, the nature of resource constraints is sometimes unclear with occasional discussions of the advantages for both gender functions of the production of more and larger inflorescences.

The issues can be clarified by applying the general framework presented here to the problem of the number of flowers per inflorescence, z, and the number of inflorescences per plant, I. Focusing on the female and male fitness consequences of these hierarchical packaging components from equation (3), we have:

$$\frac{\dfrac{\partial \ln f_{\female z}(\hat{z})}{\partial \ln \hat{z}} + \dfrac{\partial \ln f_{\male z}(\hat{z})}{\partial \ln \hat{z}}}{\dfrac{\partial \ln g_z(\hat{z})}{\partial \ln \hat{z}}} = \frac{\dfrac{\partial \ln f_{\female I}(\hat{I})}{\partial \ln \hat{I}} + \dfrac{\partial \ln f_{\male I}(\hat{I})}{\partial \ln \hat{I}}}{\dfrac{\partial \ln g_I(\hat{I})}{\partial \ln \hat{I}}}$$

$$g_z(\hat{z})\, g_I(\hat{I}) = R.$$

This ESS condition states that, but for potential differences in allometry, selection favours equalizing the sum of male and female elasticities of inflorescence size and number, subject to the constraint on resources. Assuming the same allometric constant for inflorescence size and number, i.e., $rz^{\rho}tI^{\rho} = R$ (or ignoring allometry, i.e. $zI = Q$), this reduces to

$$\frac{\partial \ln f_{\female z}(\hat{z})}{\partial \ln \hat{z}} + \frac{\partial \ln f_{\male z}(\hat{z})}{\partial \ln \hat{z}} = \frac{\partial \ln f_{\female I}(\hat{I})}{\partial \ln \hat{I}} + \frac{\partial \ln f_{\male I}(\hat{I})}{\partial \ln \hat{I}},$$

subject to $zI = R^{1/\rho}/rt$ or $zI = Q$, where $R^{1/\rho}/rt$ or Q is total number of flowers per plant. If fitness can be assumed to be a linear function of inflorescence number such that the main nonlinearities occur with respect to inflorescence design, the ESS condition further reduces to

$$-\frac{\partial \ln h_{\female z}(\hat{z})}{\partial \hat{z}} = \frac{\partial \ln h_{\male z}(\hat{z})}{\partial \hat{z}}, \tag{4}$$

where $h_{\female z}(z)$ and $h_{\male z}(z)$ are per flower female and male inflorescence size fitness components. This simple ESS condition can be stated verbally as follows: selection favours a shift in the number of flowers per inflorescence until the percent increase in male fitness per flower is cancelled by an equal but opposite percent decrease in female fitness per flower. This simple expression combines, under one specific set of assumptions, the operation of selection on inflorescence size and number, taking into account both gender functions operating in the frequency-dependent population context of sexuality. It emphasizes per-flower fitness components and a balance between competing female and male function. If both female and male per-flower fitness components increased or decreased with inflorescence size (i.e. did not compete), this equality could not be met. Thus, the ESS would be to produce either one large inflorescence (with increasing per flower fitness components) or many single-flowered inflorescences (if both female and male per flower fitness components decreased with inflorescence size). Also, if $\ln h_{\female z}(z)$ declines and $\ln h_{\male z}(z)$ increases with the number of flowers per inflorescence, but both functions curve upward, the equality given by equation (4)

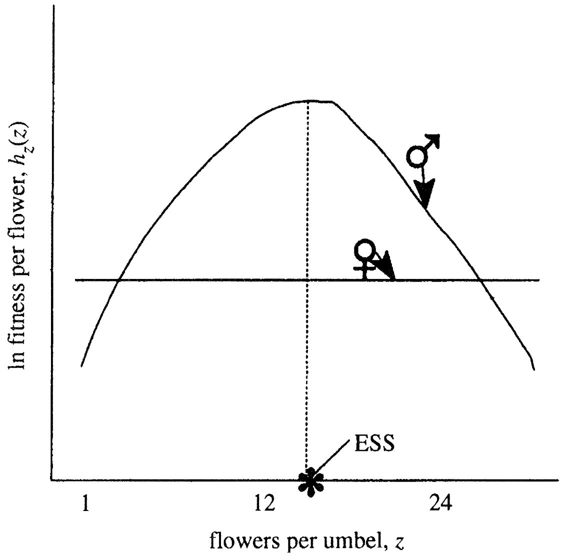

Figure 3. Graph of the general shapes of female and male per-flower fitness functions, obtained by measuring pollinia removal and deposition rates and fruit initiation rates in experiments which manipulated umbel size and number in natural field populations of *Asclepias tuberosa* (Fishbein & Venable 1996). Applying equation (4) to these data predicts that the ESS should be at roughly 12 flowers per umbel which is very close to the population and species mean for *Asclepias tuberosa*.

would be a fitness minimum and the ESS will be to produce either one large or many single-flowered inflorescences (whichever has the higher fitness). These caveats about the shapes of the fitness curve represent an informal treatment of the sufficiency conditions for the ESS equality.

Fishbein & Venable (1996) use equation (4) to evaluate the fitness curves obtained by measuring pollinia removal and deposition rates and fruit-initiation rates in experiments which manipulated umbel size and number in natural field populations of *Asclepias tuberosa*. The female and male per-flower fitness functions, $h_{♀z}(z)$ and $h_{♂z}(z)$, have the general shapes illustrated in figure 3. Equation (4) predicts that the ESS should be at roughly 12 flowers per umbel, which is very close to the population and species mean for *Asclepias tuberosa*. Thus the general model reduces to a form that permits rigorous thinking about inflorescence design and aids the interpretation of experimental data.

Other potential applications of the framework outlined here are not difficult to find. Harder & Thomson (1989) provided empirically-derived pollen-packaging fitness curves and evaluated the male-fitness consequences of changes in pollen packaging under a variety of ecological scenarios. In their discussion they recognize that packaging allometry and female function may modify the way selection operates on pollen packaging. Vonhof & Harder (1995) provide an analysis of within- and between-species allometry of pollen size and number for 21 species of legumes. These allometric relationships are directly interpretable as the allometric constraint functions in the present paper. The models presented above provide a framework for combining information such as that of Harder & Thomson (1989) with that of Vonhof & Harder (1995) to see how the pollen packaging predictions might change. The models also provide a general framework for the ideas developed by Schoen & Dubuc (1990) regarding allometric constraints on inflorescence construction and the implications of inflorescence size for geitonogamy in self-compatible and incompatible species. For example, they could be used to interpret the empirical results on the female and male fitness consequences of geitonogamy in Barrett *et al.* (1994) and Harder & Barrett (1995) under specific assumptions about the strength of inbreeding depression in *Eichornia paniculata*. Perhaps the greatest utility of the model will be in such applications.

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