

## Some Properties of Natural Selection with Single and Multiple Constraints

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Received April 19, 1991

The properties of selection restricted by single and multiple constraints are examined by using the Lagrange and Kuhn-Tucker conditions of calculus. We show for a general set of fitness equations containing any number of strategy components and subject to any single differentiable equality constraint that the marginal fitnesses of any two strategy components are equal at the evolutionarily stable strategy (ESS) when expenditures are measured in the same units, those of a binding constraint. Equal marginal advantages are a necessary, though not usually a sufficient, condition for an interior ESS. When selection is operating under more than one constraint, the marginal fitnesses of any two strategy components are equal at the ESS whenever both components are affected by only one, and the same, binding constraint. The equalization of marginal fitnesses allows the positions of constrained fitness maxima to be explored in theoretical models or empirical tests and is a convenient heuristic for understanding selection. © 1992

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### 1. INTRODUCTION

The natural selection of phenotypic traits is invariably restricted by one or more constraints. One class of constraint, a limit on a necessary resource such as energy, nitrogen, or time, is virtually ubiquitous. In addition, there are many other types of constraint that can affect the outcome of selection, including historical, mechanical, developmental, genetical, and ecological factors (Alexander, 1985; Maynard Smith *et al.*, 1985; Stearns, 1986; Loehle and Pechmann, 1988). A complete description of the process of selection on the phenotypic traits in any situation must take all appropriate

constraints into account. Here we examine some aspects of selection in the presence of single and multiple constraints, using the Lagrange and Kuhn–Tucker conditions of calculus.

A standard procedure for finding the outcome of selection on phenotypes is to locate an “evolutionarily stable strategy” (ESS) that cannot be invaded by any other strategy (Maynard Smith, 1982). In many theoretical models of selection on a single trait, such as a sex ratio or the size of offspring, the ESS is derived by considering the fitness,  $w_m$ , of a rare mutant with a phenotype  $x_m$  that is poised to invade a population that otherwise consists of individuals with a resident phenotype  $x_r$  with fitness  $w_r$ . In such single-species symmetric games, the ESS,  $\hat{x}$ , is found by locating the resident phenotype whose fitness cannot be exceeded by that of a slightly different, mutant phenotype. Thus, the fitness of a mutant with the ESS strategy will be greater than the fitness of a mutant having any other strategy in a resident population with the ESS strategy ( $w_m(\hat{x}_m, \hat{x}_r) > w_m(x'_m, \hat{x}_r)$ ). This is the same as the conditions for finding a Nash solution in classical game theory. Conceptually this is usually done by determining the fitness maximizing mutant strategy given an arbitrary constant “average” resident strategy. If the fitness maximizing mutant strategy is different from the resident strategy, it is assumed that selection will shift the resident strategy in the direction of the fitness maximizing mutant. Since fitness may be frequency dependent, the fitness maximizing mutant strategy may shift as the resident strategy shifts. This process should continue until the resident and the fitness maximizing mutant strategy coincide and there is no further selection for change. Computationally, the ESS is usually found by determining the formula for the fitness maximizing mutant strategy with an arbitrary constant resident strategy, then evaluating this formula with the resident strategy set equal to the fitness-maximizing mutant strategy, i.e., first calculating  $\delta w_m / \delta x_m = 0$  where  $\delta^2 w_m / \delta x_m^2 < 0$ , then setting  $x_m = x_r = \hat{x}$ , and finally solving for  $\hat{x}$  (and checking to be sure that  $\delta^2 w_m / \delta x_m^2 < 0$  still holds when  $x_m = x_r = \hat{x}$ ).

This relatively simple procedure of maximizing the fitness of a mutant with respect to a single trait is not possible when the set of phenotypes that selection operates on consists of two or more interrelated traits that are jointly constrained. When a number of traits affect fitness, selection will not necessarily maximize the fitness returns from any one of them, since the value of one trait may affect the value of others and traits may interact in their affects on fitness. In a previous paper, Lloyd (1988) showed that when strategy components are subject to a single resource constraint, selection equalizes the marginal fitnesses of components whose expenditures combine additively (allocations) or multiplicatively (size–number strategies) or by a mixture of both means.

In the present paper, working within the framework of static optimiza-

tion, we consider the effects of vector-valued equality and inequality constraints for single-species symmetric games. We point out that the equalization of marginal fitnesses is a general property of interior solutions for phenotypic selection problems when selection is subject to a single equality constraint (one that is active or "binding"). This property provides a principle for the allocation of limited resources that can be used to find ESS candidates in theoretical models or to empirically test properties of observed strategies. Several other properties of selection as a process of constrained maximization are also examined. Subsequently, the equalization of marginal fitnesses is considered under conditions where selection is subject to multiple constraints which may or may not be binding in any particular situation. It is shown that for interior solutions, two strategy components will have equal marginal fitnesses whenever they are each affected by only one, and the same, binding constraint. Situations where selection does, and does not, equalize marginal fitnesses are illustrated with three examples. The ability of selection to alleviate constraints and fitness limits is also discussed.

## 2. SELECTION WITH A SINGLE CONSTRAINT

Solving for the ESS using the Lagrange technique for constrained maximization shows that when fitness is subject to a single equality constraint, the marginal fitnesses are frequently equal. In most biological examples there are additional constraints requiring allocation, sizes, numbers, etc. to be non-negative. Explicit discussion of these non-negativity constraints, is deferred to the next section, but here we note that such constraints lead to the possibility that the equal-marginal-fitness ESS is biologically unattainable and that the biologically attainable ESS will be at a boundary (e.g., the production of none of a particular structure). At such boundaries, marginal fitness gains are not usually equalized. In the rest of this section we consider the situation where the ESS is an interior solution so that we can assume a single equality constraint.

Consider a rare mutant of phenotype M in a population that otherwise consists of a resident phenotype R. The mutant's fitness,  $w_m$ , is some function,  $f_m$ , of its own strategy (which can be described by a set of  $n$  variables under its control,  $x_{mi}$ , for  $i = 1, \dots, n$ ) and of the resident strategy (which can be described by a set of variables not under the mutant's control,  $x_{ri}$ , for  $i = 1, \dots, n$ ). The variables,  $x_{ri}$ , are treated as constants in the calculation of derivatives, which is the first step in determining the ESS.

In what follows we deal only with first-order necessary conditions, and assume that sufficiency conditions are met. Necessary conditions act as a screening device to eliminate unqualified ESS candidates, but they may

identify some spurious solutions, as we will see in the gynodioecy example below. Sufficiency conditions involve setting the resident strategy constant and equal to the ESS candidate and then showing that the mutant strategy is indeed at a local fitness maximum at the ESS. This can be done by showing that the determinant of the bordered Hessian is negative (see Intriligator, 1971, or Chaing, 1984).

The factors affecting selection are described in separate fitness and constraint functions and the problem can be stated as:

$$\text{Maximize } w_m = f_m(x_{m1}, \dots, x_{mn}; x_{r1}, \dots, x_{rn})$$

(where the  $x_{ri}$ 's, for  $i = 1, \dots, n$ , are treated initially as constants)

$$\text{subject to } g(x_{m1}, \dots, x_{mn}) = g(x_{r1}, \dots, x_{rn}) = 0 \text{ for } i = 1, \dots, n.$$

The Lagrange function is

$$L = f_m(x_{m1}, \dots, x_{mn}; [x_{r1}, \dots, x_{rn}]) - \lambda g(x_{m1}, \dots, x_{mn}), \quad (1)$$

where  $\lambda$  is the Lagrange multiplier for the equality constraint. The ESS satisfies the following simultaneous equations:

$$\frac{\delta L}{\delta x_{mi}} = \frac{\delta f_m(\cdot)}{\delta x_{mi}} - \lambda \left( \frac{\delta g(\cdot)}{\delta x_{mi}} \right) = 0, \quad \text{for all } i = 1, \dots, n \quad (2a)$$

$$\frac{\delta L}{\delta \lambda} = g(x_{m1}, \dots, x_{mn}) = 0. \quad (2b)$$

The final step in solving for an ESS is to set the  $x_{ri}$ 's equal to the  $x_{mi}$ 's and solve for the ESS values ( $\hat{x}_i$ 's). This procedure works for pure single-strategy ESS's. For polymorphic or mixed-strategy ESS's (involving more than one pure strategy) each supporting strategy must meet all of these conditions as well as the additional condition that the supporting strategies must have equal fitness (Lloyd, 1977; Maynard Smith, 1982). The latter condition may determine an equilibrium morph frequency for a polymorphic ESS.

The results, like all results based on phenotypic models of selection, are strictly valid only for asexual clones or for haploid or diploid sexually reproducing organisms provided the contrasted phenotypes have certain modes of inheritance. In particular, all genotypes with the same phenotype must have the same average fitness (Lloyd, 1977; Maynard Smith, 1981). This holds, for example, with phenotypes determined by fully dominant and recessive alleles. With all such modes of inheritance, fitter phenotypes always spread. In addition, Charnov (1989) has shown that the outcome of optimization models is generally the same as that obtained from the quantitative genetics approach of Lande (1982). See Mitchell and Valone (1990) for further discussion of the role of ESS models in evolutionary ecology.

The above equations have an intuitive biological meaning that is most readily understood in the context of concrete examples of biological constraints. The ubiquitous resource constraint is often expressed in one of the following forms: (1) as a proportional constraint where  $x_1 + x_2 + \dots + x_n = 1$  (re-expressed as  $g = x_1 + x_2 + \dots + x_n - 1 = 0$  for insertion into the Lagrange function), for which the  $x_i$  are the proportions of resources allocated to different structures; (2) as the absolute amounts of resources allocated to each type of structure,  $x_1, \dots, x_n$ , and the amount of resources available,  $R$ , for which the constraint then becomes  $g = x_1 + \dots + x_n - R = 0$ ; or (3) as a constraint on the size ( $x_1$ ) and number (quantities,  $x_2$ ) of one type of structure,  $g = x_1 x_2 - R = 0$ . Allocation and size-number strategies can be considered together as case (4)  $g = x_1 x_2 + \dots + x_m x_n - R = 0$ . In these four cases of resource constraint,  $\delta g / \delta x_{m_i}$  in (2a) is a scaling factor which converts units of structure into units of resource. For proportional or absolute allocations (cases 1 and 2) the allocations are already expressed on the same scale (in units of resource), so the scaling terms are all equal to one and drop out of (2a). At the ESS for these two cases, all marginal fitnesses equal  $\lambda$  and thus each other, giving the equal marginal fitness result for additive allocations (Lloyd, 1988)

$$\frac{\delta f_m(\cdot)}{\delta x_1} = \frac{\delta f_m(\cdot)}{\delta x_2} = \dots = \frac{\delta f_m(\cdot)}{\delta x_n}. \quad (3)$$

For size-number strategies (cases 3 and 4), the scaling terms for the numbers of different structures are their sizes which tell how much resource is necessary to produce a single structure. Conversely, the scaling terms for the sizes of different structures are their numbers. When the sizes and numbers (quantities) of structures of each type are written as  $s_1, q_1$ , etc., (2a) reduces to the result of Lloyd (1988)

$$\frac{\delta f_m(\cdot)}{\delta q_1} \cdot \frac{1}{s_1} = \frac{\delta f_m(\cdot)}{\delta s_1} \cdot \frac{1}{q_1} = \dots = \frac{\delta f_m(\cdot)}{\delta q_n} \cdot \frac{1}{s_n} = \frac{\delta f_m(\cdot)}{\delta s_n} \cdot \frac{1}{q_n}. \quad (4)$$

For the general problem, rearranging Eqs. (2a) and equating all the scaled marginal fitnesses with  $\lambda$  gives

$$\frac{\delta f_m(\cdot) / \delta x_{m_1}}{\delta g / \delta x_{m_1}} = \frac{\delta f_m(\cdot) / \delta x_{m_2}}{\delta g / \delta x_{m_2}} = \dots = \frac{\delta f_m(\cdot) / \delta x_{m_n}}{\delta g / \delta x_{m_n}} = \lambda. \quad (5)$$

In the general model the terms  $\delta g / \delta x_{m_i}$  are scaling factors which convert rates of change in fitness expressed in units of choice variables (the  $x_{m_i}$ 's) into rates expressed in units of constraint. The marginal fitnesses of different structures or functions are only equal after they have been rescaled

to common units. In microeconomics, the ratio of the scaling factors for two different choice variables is called the *marginal rate of substitution* of one variable for the other (e.g., the right hand side of (6) below is the ratio of scaling factors for structures 1 and 2 or the marginal rate of substitution of  $x_{m2}$  for  $x_{m1}$ ; cf. Caraco [1979] and Brown [1988] for ecological applications of the marginal rate of substitution concept). Thus the general form of the marginal fitness theorem states that *when changes are measured in the same units (i.e., are scaled by  $\delta g/\delta x_{mi}$ ), the marginal fitnesses of all strategy components are equal at the ESS*. For a resource constraint, this means that the marginal fitnesses of equal increments in the expenditure on any allocation or any component of any allocation are equal at the ESS.

The Lagrange multiplier has a biological interpretation in addition to being a helpful tool for obtaining constrained maxima. It equals the increase in fitness at the ESS that would result from a relaxation of the constraint. This interpretation of the Lagrange multiplier follows from a derivation based on the envelope theorem (see Intriligator, 1971, or Takayama, 1985). It is also evident in (5), where the incremental fitness of all strategy components associated with a unit change in resource is equal to the Lagrange multiplier. For resource constraints, the Lagrange multiplier equals the change in maximum fitness that results from a change in the amount of resources available, and therefore it scales resources to fitness at the ESS.

Equations (2a), when written as  $\delta f_m(\cdot)/\delta x_{mi} = \lambda(\delta g/\delta x_{mi})$ , can be interpreted as saying that, at the ESS, the marginal fitness benefit of an increase in structure  $x_i$  is equal to the fitness benefit that could have been attained by allocating the same amount of resources elsewhere (in economics, sometimes called the *missed opportunity cost* because it represents the marginal fitness cost of allocating resources to  $x_i$  rather than elsewhere). The term  $\delta g/\delta x_{mi}$  is the amount of resources consumed if one unit more of  $x_i$  is produced and  $\lambda$  equals the fitness gain at the ESS that would result from one more unit of resources. That marginal costs and benefits of allocation to  $x_i$  should be equal at the ESS is intuitively reasonable. If the marginal fitness of increasing  $x_i$  is greater than the marginal fitness obtainable by allocating the same resources elsewhere, the allocation to  $x_i$  should increase at the expense of other structures or functions. Likewise, if the marginal fitness of the allocation to  $x_i$  is less than that obtainable elsewhere, expenditure should be shifted toward these other structures or functions.

A useful geometric representation of the constrained optimization problem can be derived by rearranging the terms in (5). For the two-structure case, this gives

$$\frac{\delta f_m(\cdot)/\delta x_{m1}}{\delta f_m(\cdot)/\delta x_{m2}} = \frac{\delta g/\delta x_{m1}}{\delta g/\delta x_{m2}}. \quad (6)$$

By the implicit function theorem, the left side of the equality equals the negative of the slope of equal-fitness lines (lines in a plot of  $x_{m1}$  versus  $x_{m2}$  for which all points have equal fitness) and the right side equals the negative of the slope of the constraint line plotted on the same axes (situation 1 in Fig. 1c, where  $x_{m1} = a =$  paternal allocation, and  $x_{m2} = b =$  maternal allocation). Varian (1984) gives a derivation of the implicit function theorem in an analogous economics context. Thus at the ESS, the slope of the equal-fitness curve (called the *indifference curve* in economics) equals the slope of the constraint line (which is the marginal rate of substitution of maternal for paternal allocation [one for one in this case of proportional allocation]). This is a standard visualization of constrained maximization that is commonly used in economics, but has not been used very frequently in biology (e.g., Belovsky, 1984; Perrin *et al.*, 1987). This type of graphical analysis can be called "phenotype set analysis" since points in the graph represent phenotypes and the constraint lines delimit the set of feasible phenotypes (the stippled areas in Fig. 1c).

The same approach can also be used to provide an analytical framework for fitness set formulations. The equations and graphs can be re-expressed in terms of fitness components  $w_1$  and  $w_2$  derived from evolutionary variables 1 and 2 (i.e.,  $w_m = f_m(f_1, f_2)$ ), rather than in terms of phenotypes. Thus the family of equal fitness lines,  $f_m(f_1, f_2) = c$ , for different possible constant fitnesses,  $c$ , represents the adaptive function of Levins (1968) and a function describing the constraint on  $f_1$  and  $f_2$  becomes the boundary of a fitness set  $g(f_1, f_2) = 0$ . The problem is again to maximize  $w_m$  subject to  $g$ , and the analytical results above apply to this fitness set formulation (situation 1 in Fig. 1d). Graphically, the ESS is the point where the line of maximum fitness is tangent to the boundary of the fitness set (cf. Brown and Venable, 1986). It should be noted that the shape of the adaptive function is likely to shift with changes in the resident strategy in frequency-dependent problems, in contrast to the sorts of problems originally envisioned by Levins (1968).

### 3. SELECTION WITH MULTIPLE CONSTRAINTS

The theory developed above was based on having a single binding constraint, i.e., one that is expressed as an equality in the constraint equation. This corresponds to a single Lagrange multiplier. While the Lagrange technique is adequate for dealing with multiple equality constraints, it cannot handle nonbinding constraints (inequalities in the constraint equation). When there is more than one constraint, some may be nonbinding at the ESS. Also, we need to take into account non-negativity constraints, consideration of which was deferred to this section. Consider an example involving two essential resources: a plant that

produces two types of structure, each of which requires allocations of carbon and nitrogen. This problem involves two constraints which can be written as  $x_1 C_1 + x_2 C_2 \leq C^*$  and  $x_1 N_1 + x_2 N_2 \leq N^*$ , where  $x_1$  and  $x_2$  are the numbers (quantities) of the structures,  $C_1$ ,  $C_2$ ,  $N_1$ , and  $N_2$  are the amounts of carbon and nitrogen that are required to make one each of structures 1 or 2 and  $C^*$  and  $N^*$  are the amounts of carbon and nitrogen available. For each combination of expenditures, only one resource is being fully used, except for one combination of  $x_1$  and  $x_2$  (the intersection of the carbon and nitrogen constraint lines in Fig. 3). The binding constraint on a limiting resource is expressed as an equality, while a nonbinding constraint is represented as a strict inequality (the amount used being less than the total available). Similarly, whether foraging animals are time minimizers or nutrient maximizers depends on which constraint is binding.

The multiple constraint problem with  $n$  evolutionary variables,  $p$  inequality constraints, and  $n$  non-negativity constraints can be stated (following Intriligator (1971), but with our notation) as:

$$\begin{aligned} & \text{Maximize } w_m = f_m(x_{m1}, \dots, x_{mn}; [x_{r1}, \dots, x_{rn}]) \\ & \text{subject to } g_j(x_{m1}, \dots, x_{mn}) = g_j(x_{r1}, \dots, x_{rn}) \leq 0 \text{ and } x_{mi}, x_{ri} \geq 0 \\ & \text{for } i = 1, \dots, n; j = 1, \dots, p. \end{aligned}$$

At the ESS some constraints will be satisfied as equalities (e.g., the amount of nitrogen utilized equals the total available) and some may be satisfied as inequalities (e.g., the amount of carbon utilized may be less than the total available). Also, it is possible that the allocation for some structures will be zero (at a boundary) and for others it will be greater than zero (an interior solution). The Lagrange function for  $n$  structures and  $p$  constraints is

$$\begin{aligned} L = & f_m(x_{m1}, \dots, x_{mn}; [x_{r1}, \dots, x_{rn}]) \\ & - \lambda_1 g_1(x_{m1}, \dots, x_{mn}) - \dots - \lambda_p g_p(x_{m1}, \dots, x_{mn}). \end{aligned} \quad (7)$$

The Kuhn-Tucker conditions are a set of first-order conditions that must be satisfied at a local maximum with inequality and non-negativity constraints. We will use them to demonstrate certain properties of ESS's with multiple inequality constraints. The "complementary-slackness formulation" of the Kuhn-Tucker conditions states that

$$\left. \begin{aligned} \frac{\delta L}{\delta x_{mi}} = \frac{\delta f_m(\cdot)}{\delta x_{mi}} - \lambda_1 \left( \frac{\delta g_1}{\delta x_{mi}} \right) - \dots - \lambda_p \left( \frac{\delta g_p}{\delta x_{mi}} \right) \leq 0, \\ \text{but} = 0 \text{ if } \hat{x}_i > 0. \\ \hat{x}_i \geq 0, \text{ but} = 0 \text{ if} \end{aligned} \right\} \quad i = 1, \dots, n \quad (8a)$$

$$\left. \begin{aligned} \frac{\delta f_m(\cdot)}{\delta x_{mi}} - \lambda_1 \left( \frac{\delta g_1}{\delta x_{mi}} \right) - \dots - \lambda_p \left( \frac{\delta g_p}{\delta x_{mi}} \right) < 0 \end{aligned} \right\}$$

and

$$g_j(x_{m1}, \dots, x_{mn}) \leq 0, \text{ but } = 0 \text{ if } \hat{\lambda}_j > 0 \left. \vphantom{g_j} \right\} \quad j = 1, \dots, p. \quad (8b)$$

$$\hat{\lambda}_j \geq 0, \text{ but } = 0 \text{ if } g_j(\cdot) < 0$$

As usual, all derivatives in these equalities and inequalities are taken with respect to the mutant strategy,  $x_{mi}$ , for  $i = 1, \dots, n$ , and then the mutant and resident strategies are equated. Any ESS must satisfy the resulting equations and inequalities.

Expressions (8b) imply that, at the ESS, either each constraint is binding (satisfied as an equality), or the corresponding Lagrange multiplier equals zero, or both. It makes biological sense that the multipliers for nonbinding constraints equal zero. Remember that the multipliers are the marginal fitness gains from relaxing the constraints. If a constraint is not binding at the ESS (e.g., not all carbon is utilized), then relaxing it (e.g., adding more carbon) will not increase fitness at the ESS.

Expressions (8a) imply that a marginal fitness equation holds for each evolutionary variable, or the variable is at a boundary, or both. These marginal fitness equations can be written as

$$\frac{\delta f_m(\cdot)}{\delta x_{mi}} = \lambda_1 \left( \frac{\delta g_1}{\delta x_{mi}} \right) + \dots + \lambda_p \left( \frac{\delta g_p}{\delta x_{mi}} \right), \quad i = 1, \dots, n. \quad (9)$$

Equations (9) have a straightforward and intuitive interpretation in terms of the biological meaning of the Lagrange multiplier and the scaling factors. Stated in terms of the multiple resource example, the marginal fitness benefit to the mutant of making more of structure  $i$  equals the benefit that could have been obtained by reallocating those resources (now of more than one type, e.g., carbon and nitrogen) elsewhere. As for the single constraint case, the terms on the right can be thought of as a marginal cost of allocating the resources to  $x_{mi}$  rather than elsewhere (i.e., the *missed opportunity cost*). At the ESS, the marginal costs (missed opportunity costs) equal the marginal benefits for each trait (unless such equilibration occurs on the unattainable side of a zero boundary).

However, unlike the single constraint case, with multiple constraints the marginal fitnesses of different structures are not necessarily equal even for interior solutions since there are often several terms on the right side of Eqs. (9) and there may even be different numbers of terms (if, for example, a particular constraint is only applicable to some traits). To see when the marginal fitnesses are equal, solve each of the first  $n$  equations for the first nonzero Lagrange multiplier. Then

$$\lambda_1 = \frac{\delta f_m(\cdot)/\delta x_{mi} - \lambda_2(\delta g_2/\delta x_{mi}) - \dots - \lambda_p(\delta g_p/\delta x_{mi})}{\delta g_1/\delta x_{mi}} \quad (10)$$

for all  $i = 1, \dots, n$ ,  $j = 1, \dots, p$ . All these equations (one for each  $i$ ) are equal to one another, giving a multiple constraint analog to the equal marginal fitness theorem (such an equality could have been expressed in terms of any nonzero Lagrange multiplier). This equation may simplify considerably since a Lagrange multiplier equals zero if the constraint it corresponds to is not binding on a particular structure at the ESS. Specifically, (10) yields an equal marginal fitness equation similar to Eqs. (5) for the single constraint case if all except one of the Lagrange multipliers on the right side of Eqs. (9) equal zero at the ESS for any two of the strategy components (the  $x_{m,i}$ 's). If selection on some traits are constrained by zero boundaries, (9) will be an inequality and thus there will be no equation of form (9) or (10) for that trait. Thus, that trait in question will not appear in any equal marginal fitness expression. Thus in the multiple constraint problem, the *marginal fitnesses of any two strategy components, properly scaled, are equal at an interior ESS whenever both components are affected by only one, and the same, binding constraint*. Hence if all, or all except one, of the strategy components are limited by more than one binding constraint at the ESS, none of the components need have equal marginal fitnesses at the ESS. For example, in the two-structure nitrogen- and carbon-constraint problem already alluded to, if the ESS is at an interior point where the carbon constraint is binding but the nitrogen constraint is nonbinding, the marginal fitnesses will be equal, but only when scaled in terms of the carbon constraint. The reason some of the above statements are qualified by "usually" is because of the "or both" clauses in the Kuhn-Tucker conditions. That is, it is possible, even in the absence of a non-negativity constraint, that the ESS is exactly zero, so that  $\dot{x}_i = 0$  but (9) also holds as an equality. Similarly, it is possible that a resource constraint is satisfied as an equality and that the corresponding multiplier equals zero. This implies that all of the resource is utilized, but that having more would not increase fitness (the amount available is just enough).

#### 4. EXAMPLES

We now illustrate these principles with three examples which show the equivalence of different formulations of selection and illustrate situations where selection does, or does not, equalize the marginal fitnesses of strategy components.

##### 4.1. *A Separate Maximum Limit to the Expenditure on One or More, but Not All, Traits*

For various morphological or physiological reasons, the expenditure on specific traits is sometimes limited to a level below that imposed by the

total resources available. For example, there may be a restriction on the brood space available in invertebrates that care for their young in a brood pouch after fertilization. This limits maternal expenditure but does not affect paternal expenditure. Heath (1977, 1979) postulated that a limited brood space may explain the well-known correlation in invertebrates between hermaphroditism and brooding (Ghiselin, 1969). The ESS allocations were formally derived by Charnov (1982). Perrin *et al.* (1987) considered the effects of limited brood space on selection for iteroparity, using an analysis of the phenotype set.

The circumstances under which a constraint on brood space restricts maternal expenditure are illustrated in Fig. 1, where  $x_1 = a$  is the paternal expenditure and  $x_2 = b$  equals the maternal expenditure. One straightforward way to represent the operation of selection is through a display of the fitness curves relating the fitness obtained from paternal or maternal expenditure ( $f_a$  or  $f_b$ ) to the appropriate proportional expenditures,  $a$  or  $b$ , subject to the constraint  $a + b = 1$  (Fig. 1a). The total fitness of an individual is equal to the sum of its maternal and paternal fitness (i.e., where  $f_m = f_a + f_b$ ). The shape of each fitness curve is determined by the marginal fitness at different levels of expenditure (Fig. 1b). Assume that the fitness curves for both paternal and maternal expenditures are decelerating (have diminishing marginal fitnesses). When the brood space limit is greater than the one-constraint ESS ( $b_{\max(1)} > \hat{b}_{(1)}$ ; situation 1 in Fig. 1), the extra constraint will be nonbinding and does not affect the ESS. The marginal fitnesses of maternal and paternal increments are then equal at the ESS, which represents the maximum fitness. When the brood space limit occurs at a maternal expenditure that is less than  $\hat{b}_{(1)}$ , the ESS expenditure in the absence of the extra constraint, the constraint is binding at the ESS (situation 2 in Fig. 1). The maximum fitness possible when there is only one constraint cannot be reached. The ESS at the brood space limit,  $\hat{b}_{(2)}$ , equals  $b_{\max(2)}$  (Fig. 1a), where the marginal fitness of a maternal increment is still greater than that of an equal paternal increment (Fig. 1b). In terms of the theory presented above, the marginal fitnesses are unequal because one of the two strategy components is limited by more than one constraint so that Eqs. (10) do not simplify to an equal marginal advantage equation.

The selection of the morphs can also be portrayed in terms of either the phenotype set obtained by graphing the two expenditures against each other (Fig. 1c) or the fitness set obtained by graphing the resulting fitnesses against each other (Fig. 1d). The operation of selection is seen less directly in these representations, because the separate changes in the marginal fitnesses of male and female allocation, which control the process of selection, are not individually visible. The constraint line in Fig. 1c and the boundary of the fitness set in Fig. 1d do, however, illustrate the phenotypic or fitness

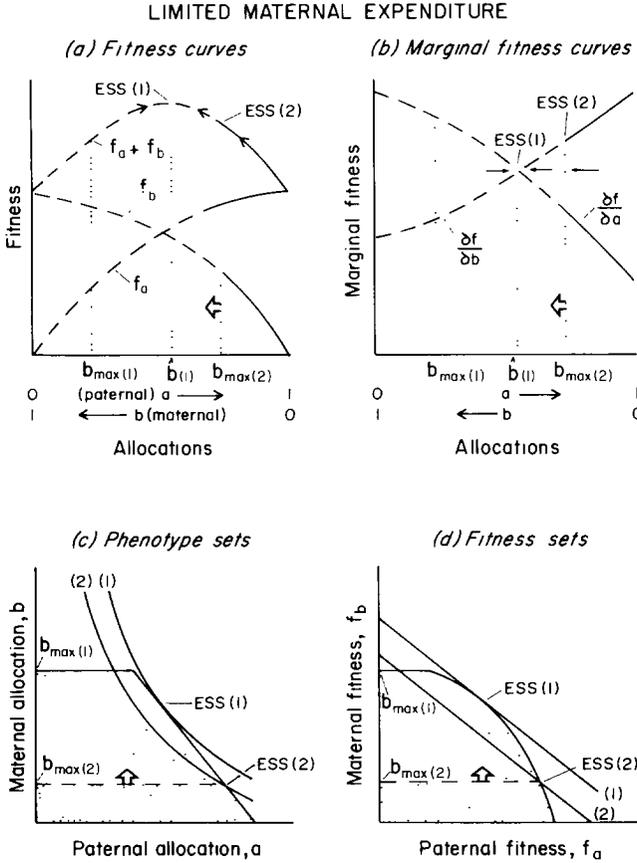


FIG. 1. Four representations of the process of selection when maternal expenditure is limited by brood space. (a) The paternal ( $f_a$  versus  $a$ ) and maternal ( $f_a$  versus  $b$ ) and total ( $f_a + f_b$  versus  $a$  or  $b$ ) fitness curves. (b) The marginal fitness curves for paternal and maternal allocations ( $\delta f_a / \delta a$  versus  $a$  and  $\delta f_b / \delta b$  versus  $b$  respectively). (c) The phenotype set (the set of all feasible phenotypes) is the stippled area bounded by the constraint lines,  $a + b = 1$  and  $b = b_{\max}$ . (d) The fitness set is the stippled area of feasible fitness combinations of  $f_a$  and  $f_b$ . The equal fitness curve (indifference curve) corresponding to the feasible phenotype with the highest fitness is plotted for each situation in (c) and (d). In situation 1, the limit to brood space occurs at a maternal allocation that is greater than the ESS in the absence of the brood space constraint ( $b_{\max(1)} > \bar{b}$ ). Then, at the selected allocation, fitness is maximized (in a), the marginal advantages are equal (in b), and the line of maximum fitness (the outer curve) touches the constraint line (in c) or the boundary of the fitness set (in d). In situation 2,  $b_{\max(2)} < \bar{b}$ . The single arrows (in a and b) indicate the directions of selection on allocations. The double arrows (in a, b, c, d) indicate the direction of long-term selection on the resource constraint in situation 2.

tradeoffs imposed by the constraint, and the equal fitness lines in Figs. 1c and 1d illustrate the tradeoffs that would be required to maintain constant fitness.

A maximum expenditure constraint might apply solely to the paternal function rather than the maternal function. In flowering plants, the entire paternal expenditure occurs prior to flowering, whereas maternal expenditure is concentrated after flowering in the production of fruit and seeds (Correns, 1928). The majority of plants occur in seasonal climates. In such plants, whether annuals or perennials, the resources available for reproduction increase during the growing season. Hence there are fewer resources available at the time of paternal expenditure than at the time of maternal expenditure. This constraint was emphasized by Charlesworth and Charlesworth (1987). They assumed separate resource pools for maternal and paternal reproduction, and performed a computer analysis of a model of the ESS allocations prior to flowering that a plant provides for male and female gametes and structures aiding the attraction of pollinators. The problem of allocation to maternal and paternal functions (or more generally, to pre- and post-flowering expenses) in the face of changing resources can also be modelled by assuming that only a fraction of the whole-season resource total is available for the earlier paternal function. This situation is exactly the converse of that already considered for the brood space constraint. Consequently, the constraint on male expenditure affects the selected sex allocations only if the ESS male expenditure in the absence of the extra constraint ( $\hat{a}$ ) is greater than the resource available at flowering ( $a_{\max}$ ) (cf. Fig. 1).

#### 4.2. *Gynodioecy, a Sex Dimorphism*

Gynodioecy is the condition of gender dimorphism in which members of one sex, the females, reproduce solely by female gametes while those of the other sex, males in the terminology of Lloyd (1975), reproduce predominantly by male gametes but obtain a minor part of their fitness through female gametes. The condition is well-known in flowering plants and grades into dioecy in which both sexes are functionally unisexual. Gynodioecy is of interest here because there is a mixed-strategy ESS (or, more specifically, a polymorphic ESS *sensu* Lloyd, 1984) consisting of an interior ESS (the male morph) at which the marginal fitnesses of maternal and paternal expenditures are equal, and a boundary ESS (the female morph) at which they are unequal. A third phenotype satisfies the equal marginal fitness condition but does not represent an ESS. The model assumes that the female condition (male sterility) is controlled by nuclear genes, so that the fitness of phenotypes can be used to describe selection.

When the paternal and maternal expenditures on pollen and seeds

respectively are written as proportional allocations, the resource constraint is  $a + b = 1$ . The paternal fitness curve is shown in Fig. 2a as decelerating. This reflects the likelihood that marginal gains diminish with increasing expenditure on pollen because the efficiency of pollen pickup decreases and there is increasing sib-competition between pollen grains from the same plant. The maternal fitness curve is more complex. Females can only persist in a gynodioecious population if they have greater seed fitness than males (Lewis, 1941). The increased seed fitness is likely to arise from increased outbreeding enforced by an absence of self-pollination (Lloyd, 1975; Charlesworth and Charlesworth, 1978). If a female produces even a tiny amount of pollen, this could readily result in a considerable degree of self-fertilization and reduce maternal fitness through inbreeding depression. Hence, at expenditures close to one, the maternal fitness curve is shown as accelerating through increased outbreeding. At lower maternal expenditures, the maternal curve is likely to decelerate as expenditures increase because of increasing sib-competition among offspring and other factors. The fitness curve for the maternal function is therefore concavo-convex (Fig. 2a), and the marginal fitness curve for female function is U-shaped (Fig. 2b).

The total fitness of an individual is the sum of its paternal and maternal fitness. As a result of the shapes of the component fitness curves, there are two ways of achieving a high total fitness: being a strict female or being a

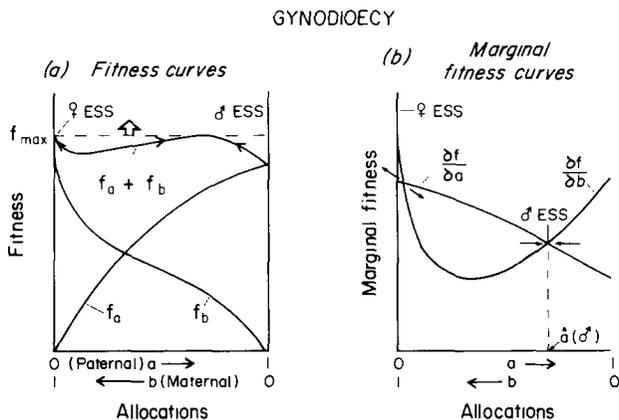


FIG. 2. The outcome of selection (a polymorphism consisting of male and female morphs) in a gynodioecious population. (a) The paternal ( $f_a$  versus  $a$ ), maternal ( $f_b$  versus  $b$ ), and total ( $f_a + f_b$  versus  $a$  or  $b$ ) fitness curves. (b) The marginal fitness curves for paternal and maternal allocations ( $\partial f_a / \partial a$  and  $\partial f_b / \partial b$ ). The single arrows indicate the directions of selection on the allocations. The double arrow indicates the direction of selection on the resource constraint.

male that obtains most of its fitness from pollen with a smaller contribution from seeds (Fig. 2a). The male ESS is an interior solution with positive expenditure on both pollen and seeds, at which the total fitness advantage is maximized because the marginal gains from increments of paternal and maternal expenditure are equal and each is decreasing (Fig. 2b). In contrast, the female ESS is a boundary point at which the marginal fitnesses are unequal. There is another point near strict femaleness (near  $b = 1$ ) where the marginal fitnesses are equal. At this point (a fitness minimum) the marginal gain from producing more pollen is decreasing but that of producing more seeds is increasing. Hence, there is no tradeoff and selection pushes seed production towards the allocations of the male or female morphs. Either the female or male morph can invade a resident population of the other, leading to a polymorphic ESS consisting of both morphs at an equilibrium sex ratio where they have equal fitnesses.

#### 4.3. *Multiple Resources*

Almost all strategy models to date, including most studies of life histories, sex allocations, and size-number compromises, have assumed that there is only one limiting resource (but see McGinley and Charnov, 1988, and, in a more ecological vein, cf. Tilman, 1988, and Abrams, 1987). In reality, there is often more than one potentially limiting resource, e.g., energy, nitrogen, phosphorus, etc., for morphological structures. Unlike the case of a specific maximum expenditure considered above, all traits are affected by each limiting resource. Whether or not a particular resource is actively limiting depends on the ability of an organism to acquire each resource, the relative resource requirements of the various traits, and the fitness curves for each trait. The ESS conditions can be obtained from the Kuhn–Tucker conditions as presented above and we will present a detailed analysis elsewhere. Here we present a simple graphical solution for one situation.

Suppose that two resources, say nitrogen and carbon, are available in quantities  $N^*$ ,  $C^*$ . Two types of structures, 1 and 2, are produced in numbers  $x_1$  and  $x_2$  and it requires  $N_1$  and  $N_2$  units of nitrogen and  $C_1$  and  $C_2$  units of carbon to produce one of each type of structure. Then when nitrogen is in limited supply,  $x_1 N_1 + x_2 N_2 = N^*$ , while when carbon is constraining expenditures,  $x_1 C_1 + x_2 C_2 = C^*$ . If the numbers of the two structures are graphed against each other, as in Fig. 3, the constraints are represented by a nitrogen constraint line,  $x_2 = N^*/N_2 - (N_1/N_2) x_1$  and a carbon constraint line,  $x_2 = C^*/C_2 - (C_1/C_2) x_1$ . Figure 3 shows a case where structures of type 1 use relatively more nitrogen and less carbon than structures of type 2. The feasible set of resource utilizations is the stippled quadrilateral. Suppose that points  $P$  and  $Q$  represent ESSs that might

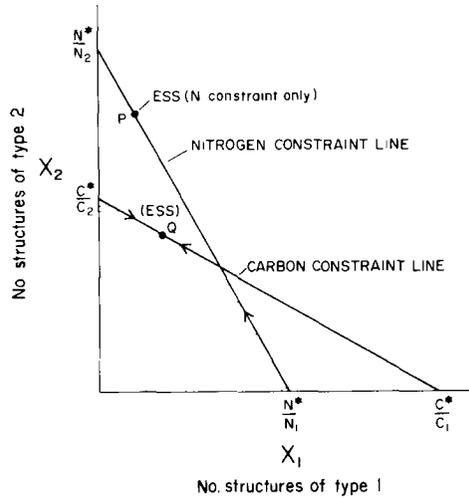


FIG. 3. Selection when there are two potentially limiting resources. The number (or quantity) of structures 1 and 2 are plotted on the axes and the two constraint lines show the quantities,  $x_1$  and  $x_2$ , that utilize all of the available "carbon" ( $C^*$ ) or "nitrogen" ( $N^*$ ). The stippled area indicates the values of  $(x_1, x_2)$  that satisfy both resource constraints (the feasible set). Points  $P$  and  $Q$  represent the ESS for an unspecified problem in which only nitrogen ( $P$ ) or carbon ( $Q$ ) is limiting. The single arrows show the direction of selection along the boundary of the phenotype set. Note that  $P$  is unattainable due to lack of carbon and that selection leads to  $Q$ . Adding carbon or nitrogen shifts the position of the constraint lines away from or toward the origin without affecting the slope. The "resource recipes" for making the structures determine the slope of the constraint lines.

apply in an (unspecified) single constraint problem ( $P$  if nitrogen were the single constraint,  $Q$  if carbon). As can be seen from an examination of the graph, changing the level of a resource moves its constraint line closer to, or farther from, the origin without changing the slope which is determined by the "resource recipe" for making a structure. With the resource levels as shown, selection will take allocations to the boundary of the phenotype set and thence towards whichever ESS is in the feasible set, as shown by the arrows ( $P$  is unattainable in the example due to an inadequate level of carbon). In the case illustrated in Fig. 3, selection will move the allocations to  $Q$ , at which point only the carbon constraint will be binding (since  $Q$  is inside the nitrogen constraint line, not all nitrogen is utilized at the ESS). As demonstrated generally in the Multiple Constraints section of this paper, the scaled marginal fitness advantages of increasing  $x_1$  or  $x_2$  will be equal at the ESS,  $Q$ , but only when measured in terms of carbon, the binding constraint.

The ESS for a particular problem can be obtained similarly for any other quantities of available nitrogen and carbon or ratios of resources required

to produce the different structures. If  $P$  and  $Q$  are both on the unattainable portions of their respective constraint lines, selection will move allocations to the intersection of the constraint lines and both resources will be limiting at the ESS. However, at this point, the marginal fitness advantages will not be equalized in terms of either resource. The conditions for any resource to be limiting and the ESS expenditures can be obtained for two or more resources and structures graphically, or more rigorously with the aid of the Kuhn–Tucker conditions (Pulliam [1974] provides an analogous example from foraging theory of a vector-valued strategy with two linear inequality constraints).

### 5. SELECTION ON CONSTRAINTS

In the section on single constraints, we pointed out that the Lagrange multiplier for a constraint represents the increase in fitness that would result from a relaxation of the constraint. Thus the Lagrange multiplier represents the force of selection on a constraint (both its direction and magnitude), evaluated at the ESS. Force of selection in this sense is similar to Lande's (1976, 1982) concept of selection gradients in that it is a partial derivative of a growth parameter ( $w_m$  in our case) with respect to a change in a trait (a resource constraint in this case). As with the case of selection gradients, evolution only occurs if appropriate genetic variances and covariances exist. The marginal fitnesses of the strategy components are also analogous to selection gradients, but for them heritable variation is assumed, subject to constraints (which may include negative genetic correlations). The main point here is that selection would remove a constraint if it could, and that the Lagrange multiplier indicates what the fitness consequences of relaxing the constraint would be. The double arrows in Figs. 1–2 illustrate the direction of the force of selection on the constraints in our different examples. By modelling constraints as givens, we have explicitly assumed that they cannot be relaxed. Nevertheless, it is an important biological question to ask which constraints are inaccessible to selection and which might more appropriately be brought into the problem as evolutionary variables themselves, with their own costs and benefits.

Unfortunately there is no general answer to this question. Each constraint involves a unique set of factors. Not only must each type of constraint be considered separately, but also the ability of selection to relax a particular constraint in the long term may vary from species to species. Consider the case described above where there is a limit on some, but not all, of a number of alternative expenditures. The correlation between brooding and hermaphroditism in invertebrates indicates that the brood

space constraint may often be operative (or else there is another explanation for the correlation). On the other hand, it seems unlikely that the resources available prior to flowering impose a binding constraint on paternal expenditure in many flowering plants. There are at least two ways in which that constraint can be removed. A brief postponement of flowering would allow more reserves to accrue, but this might cause a decrease in the supply of pollinators or reduce the time available for seed production. Many species in cool temperate and alpine conditions with a short growing season reduce the necessity to accumulate reproductive resources before flowering by initiating flowers during the season prior to the one in which they open (Mark, 1970; Endress, 1977). Resources for the earlier male expenditure, in particular, can then be drawn from the full budget for the previous year. Also, in some species, floral development and meiosis occur much earlier in male flowers than in females (Endress, 1977; McEwan, 1989).

## 6. DISCUSSION

The calculations provided above demonstrate an important principle of natural selection, that at an ESS the marginal fitnesses of increments of alternative expenditures are often equal when properly scaled. It is precisely the equalization of marginal fitnesses that confers maximum fitness on a strategy and makes it a candidate for an ESS. At a maximum, there can be no increase in fitness from an incremental change in any direction. Recognizing when marginal fitnesses are and are not equalized provides a powerful heuristic that can yield insights into specific problems of selection (e.g., Venable, 1992). It is curious that the principle of equalization of marginal gains, which has been a cornerstone of micro-economic theory for a century, has not received more attention in biology.

The examination of selection as a process of constrained maximization of the fitness of phenotypes requires the effects of relevant variables to be incorporated into a fitness equation and one or more constraint equations. It is frequently obvious whether a given factor is to be incorporated into the fitness or constraint equations, depending on whether it directly affects an item of expenditure or the fitness generated from that expenditure. Nevertheless, a particular selection problem can sometimes be formulated in various ways, and there may be a choice whether a factor affecting fitness is written into the fitness equation or a constraint equation (cf. Krebs and McCleery, 1984). The choice may be based on the ease of formulation or on which traits are to be explored. For example, the historically important studies of sex ratios have usually examined the relative numbers of male and female offspring by considering a single variable, frequently the

proportion of males,  $r$ . In this way, the constraint on the total offspring number or expenditure is incorporated into the fitness equation and the selection problem can be treated as one of unconstrained maximization (by setting  $\delta w_m / \delta r = 0$ ). The practice of reducing strategy questions to the examination of a single variable and subsuming the resource constraint in the fitness equation has probably been responsible for the delay in recognizing that the position of many ESSs is determined as the point where the marginal fitnesses of alternative expenditures are equal. Many strategy questions, however, cannot be reduced to consideration of a single variable. For example, the sex allocations of cosexual plants involve numerous structures besides pollen and seeds, such as petals and flower stems, and cannot be realistically treated as just two items, male and female allocations,  $a$  and  $1 - a$  (Lloyd, 1989).

The frequent occurrence of multiple constraints in selection problems may not allow all marginal fitnesses to be equalized on every occasion, but this does not render the equal marginal fitness principal useless for either theoretical modelling or empirical testing. Without doubt, theoretical models must include all important constraints in a system if they are to be fully satisfactory. Nevertheless there are many situations where valuable theoretical insights can be made by considering a single resource constraint, as the histories of studies of sex allocations, foraging, and size-number strategies attest. Moreover, in many situations extra constraints are nonbinding, or apply to only some structures or resources and thereby allow at least some marginal fitnesses to be equalized.

The numerous constraints on selection are of diverse kinds (Maynard Smith *et al.*, 1985; Stearns, 1986) and natural selection is never totally unconstrained. The presence of constraints limits the variety of phenotypes that can be tested by selection, but it does not eliminate the process altogether. As long as there is appropriate genetic variation in the traits under consideration, natural selection "chooses" the fittest genotypes and phenotypes available. Regardless of the number of constraints, selection causes the persistence of the phenotypes and genotypes with the highest fitness among those permitted by all constraints. The process of selection automatically takes structural restrictions into account, and it also operates within the limits imposed by all other constraints, such as those due to patterns of inheritance, resource limits, or the nature of an ecosystem (Loehle and Pechmann, 1988). Consequently, the structuralist program (Gould and Lewontin, 1979) is not an alternative to the adaptationist program, but a part of a more comprehensive approach that incorporates various constraints as well as natural selection. The examination of evolution by natural selection as a process of constrained maximization combines structural and fitness factors and other elements into a single biological program.

## ACKNOWLEDGMENTS

We are grateful to Peter Lloyd for assistance with the mathematics and parallels between biology and economics, and we thank him, Curt Lively, Joel S. Brown, and William A. Mitchell for critical comments on a draft of the manuscript. This work was supported in part by NSF grants BSR8516971 and BSR9107324.

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