Parallels between sexual strategies and other allocation strategies

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Summary. Allocation strategies in which a limited resource is apportioned among alternative activities are applicable to diverse structural, genetical and behavioral topics, including male versus female investments. In a model of sex allocation strategies, the absolute fitnesses of individuals are calculated by summing the production of male and female gametes or offspring, each weighted by its reproductive value. The ESS is obtained by examining the fitness advantage of one phenotype over another. An analogous method is used to obtain a general model of allocation strategies that incorporates some widespread features. Allocation strategies are affected by the sizes and shapes of the reward curves, stochastic factors, and constraints on the allocations permitted. A number of parallels among diverse types of allocation strategies, including the occurrence of fixed, conditional and mixed strategies, and matching rules, are discussed.

Key words. Sexual strategies; allocation models; matching rules; fixed strategies; mixed strategies.

Introduction

Biological strategies concerned with deploying the various adaptive mechanisms operating in a population are usually considered according to the nature of the strategy. Hence we examine strategies dealing with life histories, sex ratios, foraging behavior, flowering periods, seed dormancy, sperm size, etc. But if we wish to explore the shared features of diverse strategies and the common principles underlying them, we need to consider these strategies according to the kinds of decisions being made. Several major classes can then be distinguished, including phenology strategies, size-number compromises and packaging strategies (e.g. putting seeds into a particular number of fruit). The most diverse and widespread class of strategies is the class of allocation strategies, in which an individual apportions a limited resource, such as energy or time, among two or more competing activities. Much of the pioneering work on allocation strategies has dealt with sex allocations. These take two forms[11]. In dioecious (gonochoristic) populations, the allocations involve the proportions of male and female offspring. Explanations of sex ratios began with the well-known (but, it will be argued below, still under-appreciated) argument of Fisher[19], who concluded that parents optimally invest equal resources in sons and daughters. The second major class of sex allocation concerns investment in paternal and maternal reproduction by cosexes (equivalent to hermaphrodites in the animal kingdom, but encompassing a variety of genetically monomorphic sex conditions in plants, only one of which is hermaphroditism). Various allocation ratios may be selected[10–12, 34].

In addition to sex allocation strategies affecting male versus female offspring or gametes, a wide range of allocation strategies involve morphological, genetical or behavioral alternatives. These include:

1) In repeated behavioral sequences, animals may perform different behaviors randomly with fixed probabilities (a mixed *s.s.* or stochastic strategy) or confine themselves to one behavior (a fixed strategy) or choose either behavior according to the circumstances (a conditional strategy)[40, 42].

2) The open developmental system of plants allows them to produce their organs repeatedly. Plants frequently produce at one time two kinds of structures that perform the same function – a multiple strategy. Examples include simultaneous heterophylly, heteromorphic seeds or fruits, sexual and asexual embryos, etc.[35].

3) When alleles of autosomal loci undergo unequal segregation, modifying genes that alter the segregation ratio may be selected[17, 36, 45]. That is, resources put into gametes and offspring are allocated among alleles.

4) Foraging strategies are concerned primarily with the proportions of different food items or time spent in different patches in natural environments (cf. 9)[28, 38, 47].

5) An animal testing different types of food may have a learning strategy by which it samples alternatives (allocates food-seeking efforts) according to past rewards[24, 43].

6) An altruist may dispense its favors in varying proportions to different classes of relatives with which it shares its genes with different probabilities[1, 55].

7) Colonies of social insects produce varying frequencies of distinct sterile castes[44, 68].

8) In a spatially heterogeneous environment, individuals can occupy different patch types with varying frequencies, e.g. ideal-free distributions[20].

9) In psychology, animals in operant conditioning experiments choose between alternative reinforcements available in a limited period of time (cf. 4)[26, 57, 58].

10) Individual humans buying goods from a market are engaged in choosing the proportions of various products within a limited budget[27, 48].

This list of alternative allocations is by no means exhaustive. Moreover, other biological allocation strategies of a somewhat different nature are concerned with the amounts of investment in one kind of reward at different times (e.g. strategies for reproductive effort or germination time), or with allocations to two (or more) activities which are both required before one function succeeds (e.g. diaspores require allocations for dispersal *and* for subsequent growth). We are concerned here only with allocations between alternatives which provide separate rewards.

With few exceptions, studies of the various allocation topics have developed independently of each other. In recent years, some psychologically oriented behaviorists and zoologically oriented behaviorists and other biologists have actively forged connections between their previously separated approaches[28, 46, 57, 58]. Both groups have also developed connections with economics, particularly in methodology (compare for instance, the formulation of fitness sets, feedback functions and budget lines[27,32,48]. Parallels between the empirical results of economics and biology are limited, however, because economists are largely concerned with the effects of varying the prices of competing goods, whereas biologists rarely concentrate on variation in unit costs.

The theme of the present paper is that the similarities between allocation strategies dealing with different topics of plant and animal behavior are so fundamental and extensive that these diverse allocation topics should be brought into a single framework. Shared phenomena call for a common explanation. Towards this end, the primary elements of sex allocation theory are first presented, and then an analogous model which utilizes parallel features of other allocation topics is developed. The selection models are deterministic phenotypic models that assume selection operates on individuals in populations with discrete generations. Some of the principles and patterns that are shared by diverse allocation topics are subsequently discussed.

A model of sexual strategies

Various methods of analysing the theory of sex ratios and cosexual allocations have been developed[12], including fitness set analysis, the Shaw-Mohler equation, and maximization of the product of male and female fitnesses. Here I examine the basic features of sex ratio strategies using the simplest and most general method available. This entails summing contributions from male and female offspring weighted by their reproductive values, and comparing the absolute fitnesses of phenotypes that differ in the sex ratio of their progeny.

Since the sexual functions of males and females are complementary, the contributions that sons and daughters make to the fitness of their parents are non-substitutable alternatives that can be added together. The fitnesses of the sons and daughters of a parent may be unequal, however, so the numbers of the two sexes cannot be simply added to provide a measure of parental fitness. To make male and female progeny commensurate, the numbers of each sex are weighted by their reproductive values, which measure the expected contributions to the 'ancestry of future generations'[19]. If parent i produces s_i sons and d_i daughters (counted at fertilization or later) with reproductive values v_{si} and v_{di}, the parent's fitness,

$$w_i = d_i v_{di} + s_i v_{si}. \qquad (1)$$

The exploration of sex ratio strategies then centers on specifying the effects of various factors on the reproductive values of sons and daughters, which can be split into as many components as necessary. One convenient factor is the individual 'fitnesses' of sons and daughters, w_{si} and w_{di}, including appropriate viability and fertility factors, but not their mating success.

Using Bateman's Principle[3] that the fitness of females is usually limited by their resources, whereas that of males is characteristically limited by their ability to fertilize eggs, we define the reproductive value of *mature* daughters as one and express the reproductive value of mature sons in female units as the number of females they fertilize, weighted by the proportion of each female's eggs that they fertilize. If a son of parent i has an expected 'competitive share', c_{ij}, of mate j's eggs, then

$$w_i = d_i w_{di} + s_i w_{si} \sum_j c_{ij}. \qquad (2)$$

When all males have the same fitness and all females are equally fit, the reproductive value of a mature male is simply the ratio of females to males in the population (i.e. $\sum_j c_{ij} = F/M$).

To determine the outcome of selection of the sex ratio, an ESS is found by examining the fitness advantage that a rare mutant in a population has over the prevalent phenotype that has a slightly different sex ratio. The ESS occurs where neither phenotype has a fitness advantage. Consider the situation in which sons and daughters are equally expensive to produce and survive at equal rates during the period of parental expenditure, but have different post-independence 'success' rates, p_d and p_s, which may reflect differential survival or fertility. If sons and daughters compete with the progeny of numerous parents, an individual's own sex ratio has a negligible effect on the sex ratio experienced by its progeny. When individuals of the prevalent phenotype, 1, in a population produce n offspring, in any proportions r_1 and $1 - r_1$ of sons and daughters at independence, and a rare mutant of phenotype 2 produces the sexes in proportions r_2 and $1 - r_2$, the fitnesses of the competing phenotypes, using (2), are

$$w_1 = n\left[(1 - r_1)p_d + r_1 p_s \cdot \frac{(1 - r_1)p_d}{r_1 p_s}\right],$$

and

$$w_2 = n\left[(1 - r_2)p_d + \frac{r_2(1 - r_1)p_d}{r_1}\right].$$

The fitness advantage,

$$w_2 - w_1 = np_d\left[(1 - r_2) + \frac{r_2(1 - r_1)}{r_1} - 2(1 - r_1)\right],$$

and

$$\frac{\partial(w_2 - w_1)}{\partial r_2} = np_d\left[-1 + \frac{1 - r_1}{r_1}\right].$$

Neither phenotype has a fitness advantage when $\partial(w_2 - w_1)/\partial r_2 = 0$, i.e. when

$$\frac{r_1}{1 - r_1} = 1. \qquad (3)$$

The second derivative is zero, indicating that there is an equilibrium at which r_2 may have any value when the population as a whole produces equal numbers of males and females[19,56]. The model shows that when the number of offspring produced by parents varies independently of the sex ratio, the sex ratio that is selected is not affected by the total number of offspring or their individual size or cost or proficiency. In these circumstances, sex ratio strategies can be decoupled from reproductive effort and other life history strategies.

The costs of raising sons and daughters to maturity may differ. If parents spend R resources on their families and each son and daughter costs E_s and E_d respectively, the number of offspring that can be produced, $n = R \div [r_i E_s + (1 - r_i) E_d]$. Substituting for n in the above derivation gives at equilibirum,

$$\frac{r_1}{1 - r_1} = \frac{E_d}{E_s}, \quad \text{or} \quad r_1 E_s = (1 - r_1) E_d. \tag{4a}$$

The rates of survival of sons and daughters during the period of parental investment may also differ. Suppose that fractions s_s and s_d of the sons and daughters respectively survive, and that average fractions f_s and f_d of the full investments in offspring are spent before the proportions $(1 - s_s)$ and $(1 - s_d)$ of sons and daughters die. Then $n = R \div \{r_i [s_s + (1 - s_s) f_s] + (1 - r_i)[s_d + (1 - s_d) f_d]\}$. Substituting for n in the above derivation gives at equilibrium, when

$$\frac{r_1}{1 - r_1} = \frac{s_d + (1 - s_d) f_d}{s_s + (1 - s_s) f_s}$$

or

$$r_1 [s_s + (1 - s_s) f_s] = (1 - r_1)[s_d + (1 - s_d) f_d]. \tag{4b}$$

Examination of (3) and (4a, b) shows that in all cases parental investments in the two sexes are equal, whether their costs are equal or unequal. The numerical ratio of sons and daughters invested in is affected by sex-differential expenditure or survival during the period of parental investment but not by differential survival after parental investment has ended, as Fisher argued verbally in 1930[19].

These derivations of Fisher's results differ from most sex ratio models in two respects.

First, the use of absolute fitnesses weighted by reproductive values permits a very simple and versatile formulation of selection, obviating the need for more complex procedures such as the Shaw-Mohler equation or fitness set analysis. Parental fitness can be expressed in terms of the expected contributions of the immediate progeny, rather than in terms of the number of grandchildren, as is usually done. (The number of post-investment grandchildren is not a valid measure of fitness when the costs of male and female progeny are unequal.) Taylor[60] has also pointed out that the coefficients $1/f$ and $1/m$ in the Shaw-Mohler equation should be regarded as measuring the relative value of placing a gene in a female or male offspring.

Although Fisher used the concept of reproductive value in several contexts, including sex ratios and comparisons of the products of self- and cross-fertilization[19], his example has rarely been followed (e.g. Uyenoyama[65]). The concept of reproductive value has been used primarily for comparisons of different age classes, and is often defined as the age-specific expectation of future offspring. The concept of reproductive value raises difficulties when used as an index of the intensity of selection in age-structured population[9], but these difficulties do not apply to the situations considered here.

Second, the procedure of examining the fitness advantage of a rare mutant is a variation of the popular method of finding an ESS by examining the fitness of a mutant. The use of a fitness advantage, which seems to have been introduced by Hamilton[23], is superior in several respects. It portrays selection realistically as a process of competition[44] rather than optimization and thus emphasizes that the primary outcome of selection is the persistence of certain types based on their sustained competitiveness, not the attainment of optimality on any absolute scale. Hence the principal merit of the ESS concept, the notion that selection produces strategies that persist, is incorporated explicitly into the derivation of an ESS. In addition, fitness advantage formulations are able to predict the full course of selection, not just the ability of a rare mutant to spread, and are therefore able to predict equilibrium frequencies in a polymorphism[33,60].

The gender allocation strategies of cosexes can be studied by an analogous method. If a cosexual individual, i, allocates resources to paternal and maternal reproduction so that it produces m_i female units and l_i male units with reproductive values v_{mi} and v_{li} respectively, then

$$w_i = m_i v_{mi} + l_i v_{li}. \tag{5}$$

If the female units (eggs, zygotes, or seeds, etc.) are given reproductive value of one, the reproductive value of male units (sperm, pollen grains, etc.) can be expressed as the number of eggs they are able to fertilize, weighted if necessary by their subsequent behaviors. If the maternal fitness of mate j of individual i is m_j, and i fertilizes a competitive share, c_{ij}, of that fraction of j's eggs that it is eligible to fertilize, e_{ij}, then

$$w_i = m_i + \sum_j m_j e_{ij} c_{ij}. \tag{6}$$

Equation (6) can be used to derive gender allocations[33,34], just as (2) was used above for sex ratios.

Factors affecting sex allocations

Theoretical studies have shown that a considerable number of factors can affect the selection of sex ratios or gender allocations. These are listed in the table. All deterministic factors (all those except sex ratio homeostasis) can be analyzed using the method outlined above. The factors may be grouped into five classes according to how they affect the male or female fitness curves which describe how the fitness obtained from male or female investment increases as the allocation increases. *'Intrinsic'* factors that affect the number, or cost or efficiency of all male or female units do not affect the sex ratio selected (above) or the selected allocations in cosexes[34].

Size factors determine the maximum fitness that can be obtained from male or female investment if all reproductive resources were committed to one function (fig.). The unique and omnipresent feature of sex in anisogamous species is the obligatory interdependence of male and female functions that arises from fusion of their gametes or nuclei. In the absence of complicating factors, this complementarity causes equal investments in male and female functions and serves as a baseline to compare other factors against. Although male and female gametes contribute autosomal genes equally in the population as a whole, varying circumstances may cause particular parents to have unequal opportunities for fitness through their male and female gametes or offspring[5, 37, 64]. In cosexual plants for instance, when pollen and seeds are dispersed equal distances the selected ratio of allocations is equal to the ratio of the viabilities of an individual's progeny from pollen and seeds[37] i.e.

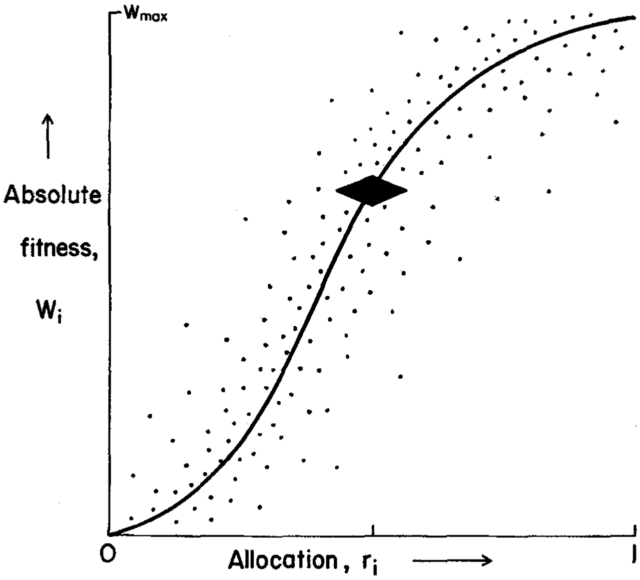
$$\frac{a}{1-a} = \frac{v_p}{v_s}. \qquad (7)$$

Shape factors modify the shape of a fitness curve (fig.). If the paternal and maternal fitnesses of a cosex are proportional to their respective allocations raised to the powers y and z respectively, then[10-12, 34]

$$\frac{a}{1-a} = \frac{y}{z}. \qquad (8)$$

If the allocation curves decelerate ($y < 1, z < 1$), the equilibrium at (8) is fully stable. The best-known shape factors are local mate competition[12, 23] and local resource competition[14], in which the male or female fitness returns respectively are limited by competition among the products of a restricted number of parents. Unilateral local competitions occur sporadically among animals, but are virtually ubiquitous among seed plants because of the limited distances that seeds and pollen travel[6, 34]. Most of the other shape factors affect the selection of gender allocations but not that of sex ratios. Nevertheless they can favor, and help to stabilize, either combined or separate sex conditions (table).

The only *stochastic* factor that has been examined to date is the chance fluctuations in the sex ratio that occur when mating groups are small. The offspring sex that happens to be in the minority in a group will have a higher reproductive value than the other sex. Verner[67] and Taylor and Sauer[63] have shown that selection for sex ratio homeostasis leads to a fully stable sex ratio at equality.



Four kinds of factors affecting a reward curve that describes how the rewards from investment in an activity increase as the proportional allocation increases. The shape of the curve illustrating a deterministic factor (solid line) is one that accelerates at first, then decelerates as it approaches the maximum reward when the allocation is 100% (the potential 'size' of the rewards). The scattered points represent stochastic variation in the reward. The diamond figure in the center represents the limited deviation in sex ratios and other segregation ratios that is imposed by a 'segregation constraint' (see text for further explanation).

A number of *constraints* may restrict the ability of size and shape factors to modify sex ratios or gender allocations. The chromosome machinery imposes a severe 'segregation constraint' on deviations in the ratios of genetically determined sexes whenever deviations are caused by eliminating a fraction of one sex[41]. The eliminations impose a cost on deviation that is permissible only if the forfeited investment is a small fraction of the total investment required per offspring. Another constraint, an 'assessability constraint', arises from the inability of parents to judge whether male or female offspring, or those from maternal or paternal investment, are likely to be fitter. This is particularly important in plants, which have only limited means of sensing their environment, and restricts the number of plants that choose their sex according to the conditions[37].

More factors affect the gender allocations of cosexes than affect the sex ratios of dioecious organisms (table). Together with the segregation constraint that severely restricts deviations in sex ratios, this means that the gender allocations of cosexes offer much more scope for analyzing a variety of sex allocation strategies. Nevertheless, most sex allocation studies to date have examined the less pliable sex ratios of dioecious populations.

A general model of allocations

A number of features that occur repeatedly in various allocation decisions can be explained by a general theory. Every allocation topic has unique aspects, and some subjects already have more complex theories than that provided below. The present aim is not to cover every eventuality in specific topics, but to demonstrate the generality of certain features that are shared by seemingly unrelated subjects.

Suppose there are two activities, A and B, that make separate contributions to the total reward which an individual receives. The alternative activities may be morphological structures, the segregation of genes or gene combinations, or be biochemical, physiological or behavioral acts. The individual allocates proportions a and $1 - a$ of a single limited resource (energy, a nutrient, time, etc.) to A and B respectively. The contributions from A and B, c_a and c_b, are functions of the allocations to the activities.

The contributions from A and B are measured on a single scale of rewards (reproductive fitness, rate of food intake, reinforcement rate, utility etc.) by assigning reward values, v_a or v_b, to units of the two activities. Then the total reward for individual i,

$$R_i = c_a + c_b = f(a)\,v_a + f(1-a)\,v_b.$$

To find the stable strategy, the relative allocations that do not have a competitive disadvantage over any other, we examine the situation where a single individual of type 2, with allocations to A and B of a_2 and $1 - a_2$, competes

Factors affecting sex allocations

Factor	Direction of deviation, effect on stability		References
	Dioecism sex ratio	Cosexuality gender allocation	
A) Size factors			
1) Sex complementarity	♂ = ♀	♂ = ♀	19, 39, 56
2) Variable parental status or progeny success	> ♂ or ♀	> ♂ or ♀	5, 37, 63
3) Self-fertilization	–[a]	> '♀'	10
B) Shape factors			
1) Finite population	No deviation (S)[a]	No deviation (S)	33, 62
2) Local mate competition	> ♀ (S)	> ♀ (S)	23, 62
3) Local resource competition	> ♂ (S)	> ♂ (S)	14
4) Unilateral fixed cost	No deviation (S)	> ♂ or ♀ [c](D)	11, 34
5) Unilateral fitness limit	No deviation (D)	> ♂ or ♀ (S)	12, 34, 59
6) Interference between sex functions	– (S)	> ♂ or ♀ (D)	34
7) Facilitation between sex functions	– (D)	> ♂ or ♀ (S)	34
C) Uncertainty of fitness returns			
1) Sex ratio homeostasis	No deviation (S)	No deviation (S)	63, 67
D) Constraints on allocation			
1) Segregation constraint	Limits deviation	–	41
2) Assessability constraint	Limits variation	Limits variation	5, 37
E) Allocation-independent intrinsic factors[b]			
1) Sex-differential costs	No effect	No effect	8, 19
2) Sex-differential proficiency or survival of gametes or progeny	No effect	No effect	19, see text
3) Reproductive effort	No effect	No effect	See text

[a] – = not relevant. (S) = stabilizes sex ratio or gender allocation. (D) = destabilizes sex ratio or gender allocation. [b] Sex differential costs or success affect the numbers of the two sexes or gametes, but not the allocations. [c] Unilateral fixed costs affect gender allocations if they are included in the allocations (Lloyd, unpubl.).

with all other individuals of type 1 with allocations a_1 and $1 - a_1$. Then the reward for the prevailing type,

$$R_1 = f(a_1)\, v_a + f(1 - a_1)\, v_b.$$

The reward for the single individual of type 2,

$$R_2 = f(a_2)\, v_a + f(1 - a_2)\, v_b.$$

The advantage of type 2 changes with its allocation according to

$$\frac{\partial(R_2 - R_1)}{\partial a_2} = f'(a_2)\, v_a + f'(1 - a_2)\, v_b.$$

Neither type has an advantage when $\partial(R_2 - R_1)/\partial a_2 = 0$, i.e.

$$f'(a_2)\, v_a + f'(1 - a_2)\, v_b = 0. \qquad (9)$$

The stationary point represents a stable equilibrium if the second derivative is negative,
i.e.

$$f''(a_2)\, v_a + f''(1 - a_2)\, v_b < 0,$$

which includes the situation when both reward curves are decelerating.

Equation (9) is a marginal value theorem that applies to allocations between any alternatives that provide additive rewards. At the ESS allocation, the absolute values of the marginal gains for the two activities, weighted by their reward values, are equal.

The Shaw-Mohler equation[12] for sex allocations is a special case of (9). In considering allocations to male and female gametes, or to sons and daughters, pollen grains and seeds, etc., the total fitnesses of males and females in a population are equal i.e. $v_♂\bar{m} = v_♀\bar{f}$. Substituting into (9) and rearranging gives the Shaw-Mohler equation,

$$\frac{dm}{\bar{m}} + \frac{df}{\bar{f}} = 0.$$

Equation (9) shows that the ESS for alternative allocations depends on the shapes of the reward curves and on size factors represented by the reward values. The effects of size and shape factors can be seen more clearly when they are represented by specific functions. Suppose that when all resources go to A (or to B), the individual produces n_a (or n_b) units. If both activities are conducted, a linear combination of numbers is produced. The units of each activity experience allocation-independent success rates s_a or s_b, associated with their post-investment survival rate, efficiency at locating appropriate environments, etc. Hence the effective numbers of A and B activities are $n_a a s_a$ and $n_b(1 - a)s_b$. The contributions that the two activities make to the rewards are proportional to the numbers raised to a power, y for A or z for B, which express the shapes of the reward curves.
Then

$$f(a) = (n_a a s_a)^y \quad \text{and} \quad f(1 - a) = [n_b(1 - a)s_b]^z,$$

so

$$f'(a) = y\,(n_a s_a)^y a^{y-1}$$

and

$$f'(1 - a) = -z\,(n_b s_b)^z (1 - a)^{z-1}.$$

The reward values can be specified in a competition model that assumes that there are restricted numbers of opportunities, O_a or O_b per parent, for the activities to contribute to the rewards, because of limits in the available space to grow or numbers of food items, time requirements, etc. The reward values of A and B units are then the number of available opportunities divided by the number of competing units. The competition pools for O_a and O_b are considered here to be completely separate; that is,

$$v_a = \frac{O_a}{[n_a a s_a]^y} \quad \text{and} \quad v_b = \frac{O_b}{[n_b(1-a)s_b]^z}.$$

Substituting for v_a, v_b, $f'(a)$ and $f'(1-a)$ in (9) gives

$$\frac{a}{1-a} = \left(\frac{y}{z}\right)\left(\frac{O_a}{O_b}\right). \tag{10}$$

Also,

$$\left.\frac{\partial^2(R_2 - R_1)}{\partial a_2^2}\right|_{a_1 = a_2 = a} = y(y-1)a^{-2}O_a + z(z-1)(1-a)^{-2}O_b.$$

A number of conclusions from the model are parallel to those presented above for sex allocations. First, both mixed s.l. strategies (do two things in combination) and pure strategies (do only one thing in any given circumstance) are possible. The strategy that is most competitive depends on the shapes of the reward curves. When the curves decelerate ($y < 1$, $z < 1$), the second derivative is negative and there is a mixed strategy at a stable equilibrium specified by (10). When the curves are linear ($y = 1$, $z = 1$), an equilibrium is obtained in which any combination of activities is equivalent when the average ratio of investment in the population is equal to the ratio of opportunities, O_a:O_b (cf. (3, 4)). If the curves accelerate, a mixed strategy is unstable and restriction to one or other activity provides the most competitive reward.

Second, the shapes also affect the exact allocation in mixed strategies. The activity for which the rewards decelerate most quickly is allocated less (cf. (8)).

Third, the differences in the costs of single A or B activities (incorporated into n_a, n_b) and the success rates of A and B (s_a, s_b) do not affect the most competitive allocation ratio (cf. (3, 4)).

Fourth, the allocation ratio of a mixed strategy depends on the size factors, O_a and O_b. The property of the model that A and B activities offer rewards that are separately limited introduces a frequency-dependent element into their rewards (compare the effects of O_a and O_b in (10) with the ratio $(1 - r_1)/r_1$ in the derivation of (3)).

Fifth, if the shapes of the allocation curves are identical ($y = z$), the ratio of allocations is equal to the ratio of opportunities (cf. (3, 7)). This is not so when the shapes are not identical.

Sixth, the separate size and shape factors have multiplicative effects on the equilibrium allocation ratio. It has similarly been shown that a number of combinations of factors have multiplicative effects on gender allocation ratios[37] or on other mixed strategies for plants[35], provided the factors vary independently of each other.

This general model is analogous to that presented above for sex allocations, but it differs in allowing the total opportunities for the two activities to vary independently of each other. The general model could be extended by the inclusion of numerous specific factors, as has happened in models of sex allocation. It would be relatively easy to add some factors to the model, e.g. local competitions, fixed costs, upper limits to one or other reward, or certain types of constraint. Other potential additions to the model, e.g. three or more alternative activities, the simultaneous operation of different limiting resources such as energy and time, partially substitutable activities, or randomly varying rewards for a given allocation, may require more complex mathematical procedures such as linear or dynamic programming. The inclusion of any of these additional factors would increase the ability of the general theory of allocations to provide a unified explanation of the diverse types of allocation decisions.

Observed patterns of allocation strategies

The following brief survey notes some of the features common to sexual strategies and a variety of other allocation strategies for which the competing alternatives provide separate rewards.

A) Classes of strategies

There are several principal classes of allocation strategies[35, 40, 42]:

1) *Fixed* strategies: individuals choose the same option under all permissive conditions. The complementarity of male and female gametes precludes parents from following a fixed sex allocation strategy; they produce either two types of gametes or two sexes of progeny. For many biological functions, fixed strategies are the norm.

2) *Conditional* strategies: individuals choose different options according to the circumstances. Conditional strategies include sex-choosing, which is more common among animals[5, 12] than among plants[37], and occur sporadically for other subjects, such as choices between open and cleistogamous flowers or sexual and asexual embryos in plants[35], and some alternative mating strategies and other environmentally determined 'polymorphisms' such as winged versus non-winged or horned versus non-horned individuals[2, 18, 25].

3. *Mixed* strategies: individuals carry out two or more activities with non-zero probabilities. Mixed strategies occur in some instances in each of the ten topics listed in the introduction. The subclass of multiple strategies occurs when individuals carry out both activities at the same time, as in simultaneous hermaphroditism, seed heteromorphism, etc.[35, 54, 66]. The subclass of stochastic strategies occur when alternative behaviors are performed in succession with constant probabilities, as in some foraging and learning strategies[42, 43].

B) Mixed strategies are associated with separately limited rewards

In the case of sex allocation strategies, male and female gametes have complementary roles that cannot be substituted for each other as long as sexual reproduction is retained. The ways in which the alternative activities of other mixed strategies provide separately limited opportunities are being investigated in many fields e.g. flowers with adaptations for self- or cross-fertilization, seed heteromorphisms, seed and vegetative reproduction[35, 65]. The separate advantages of distinct sterile castes in social insects are being explored[44, 68]. In foraging strategies, the concept of resource depression describes situations where predators acquire separately diminishing gains from patch types because prey are depleted or take evasive action[13, 30]. Operant behaviorists have recognized that their experiments frequently contain separate time limitations on alternative reinforcements[57]. Conversely, some fixed strategies are associated with a lack of separate limitations on the rewards from different activities e.g. learning experiments with constant reward rates[43, 57], single syndromes for externally mediated pollination or dispersal[35].

C) Matching rules

In operant conditioning experiments, particularly those with variable-interval schedules, a 'simple matching law' (or rule) has been repeatedly observed[26, 58]. The rule is that the ratio (or proportions) of responses (investments) to two signals is equal to the ratio (or proportions) of positive reinforcements (rewards) obtained from the two signals. The matching rule of psychologists may be generalized to cover situations in any topic of allocation strategies in which the relative rates of investment in alternative activities, a_1 and a_2, match the relative rewards from the activities, R_1 and R_2,

i.e.

$$\frac{a_1}{a_2} = \frac{R_1}{R_2}, \quad \text{or} \quad \frac{a_1}{a_1 + a_2} = \frac{R_1}{R_1 + R_2}. \tag{11a}$$

The matching rule may also be expressed as a statement that the total benefit to cost ratios of two activities are equal. By transposition from (11a),

$$\frac{R_1}{a_1} = \frac{R_2}{a_2}. \tag{11b}$$

Matching rules occur in diverse allocation strategies. The classical conclusion of Fisher in 1930[19] that parents in a dioecious population are selected to invest equally in sons and daughters follows the generalized matching rule, since males and females contribute (autosomal) genes equally in the population as a whole, as Fisher noted. A comparable matching rule applies to the maternal and paternal allocations of cosexes[39]. Moreover, when there is variation within a cosexual population in the ability of parents to produce offspring via male and female gametes, or in the relative opportunities for the two classes of offspring, the selected ratio of investments is equal to the ratio of parental or offspring opportunities (cf. (7) above), provided the allocation curves have the same shape[37]. The males of gynodioecious plant populations also produce some seed, and the relative investments in pollen and seed match their fitness returns (Lloyd, unpubl.). It can also be shown that the increase in seed investment by a cosexual plant as the frequency of self-fertilization increases[10] exactly matches the proportionate increase in the fitness the parent obtains from expenditure on seeds rather than pollen (Lloyd, unpubl.). Matching rules are also observed in 'ideal free distributions' of animals settling in a patchy environment[20], and are predicted by theory as a learning rule for animals sampling rewards from different behaviors[24] and for genes modifying the segregation ratio of certain autosomal loci[36]. Similarly, in one of two digger wasp colonies observed[4], females dug new burrows or used old ones in frequencies such that the average fitnesses derived from the two behaviors were equal.

Some observations do not conform to the matching rule. In a second digger wasp colony, the two nesting strategies did not provide equal fitnesses[4]. In operant conditioning experiments, variable-ratio schedules do not generally follow the rule[26, 57]. Some outcrossing plants do not spend equal resources on pollen and seeds[34].

The models presented above for sexual and other types of allocations predict that the matching rule will be followed in some situations but not in others. With only two alternatives, the marginal rewards from the two activities are necessarily equal at equilibrium. This follows because the total reward is the sum of rewards from the two activities, so when there is no net change a small change in one must be opposed by an equal and opposite change in the other. This is 'molecular' or 'local' matching in the terminology of psychologists. But there is no necessity for the total or overall benefits from two activities to match – for 'molar' or 'global' matching. The models show that this occurs only when the shapes of the two allocation curves are identical. If they are not, as in the presence of unilateral fixed costs or local competitions or any other unilateral shape factors, the ratios of rewards to costs for different activities are expected to be unequal at equilibrium. Peter Taylor has discovered a general form of the Shaw-Mohler equation that is valid for local mate competition and can be regarded as a generalized matching rule[61] (pers. comm.).

D) Constraints on allocations

Although each type of allocation is likely to have its own combination of constraints limiting the allocation strategies that can be achieved, a number of constraints have parallel effects on different subjects. Three examples will suffice. First, a segregation constraint severely restricts the ability of 'outlaw' genes to segregate preferentially[36], just as a segregation constraint on sex ratios is a major barrier to the selection of deviant ratios[41]. Second, the generally poor ability of plants to assess the prospects of alternative activities is a major constraint on both sex-choosing strategies and conditional strategies involving a variety of vegetative and reproductive functions[35, 37]. Similarly, great tits do not restrict their foraging to the most rewarding prey but show a 'partial preference' for lower-ranking prey (i.e. a mixed strategy) in part because they cannot discriminate accurately between the various types of prey[51]. Third, in some plant species, limited resources associated with smaller size or poorer conditions affect the ability of a plant to function as a maternal parent[37] or to produce chasmogamous (open) flowers[54], and thus impose a cost constraint.

E) Risk sensitivity

The benefits obtained from any given allocation are likely to fluctuate. If variation in potential rewards cannot be predicted before an investment is made, a response to the particular conditions experienced by an individual is precluded, and the variation is perceived as effectively random. Stochastic models suggest that organisms that take account of random variability by risk-sensitivity strategies improve their fitness[7, 21, 49, 50, 52]. Jensen's inequality, a theorem of statistical decision theory, compares the expected utility from a constant benefit with randomly varying benefits that have a mean value equal to the certain returns. It shows that when reward curves decelerate, individuals do better by engaging in diversified activities – a risk-averting mixed strategy. When reward curves accelerate, individuals do better by concentrating on the potentially more rewarding activity – a risk-prone fixed strategy[7, 29, 52]. Hence the stochastic effect of the shapes of reward curves operates in the same general direction as the deterministic effect of shape factors discussed above.

When the local breeding populations are small and subject to random variation in the ratio of males to females, selection for risk-aversion leads to sex ratio homeostasis[63]. Comparable risk-sensitive strategies have been discussed for a considerable variety of allocation subjects, including reproductive effort[15, 22, 31, 53], dormancy[16, 66], foraging[7] and others.

Conclusion

Although each type of allocation has its own characteristics, both the theoretical models and empirical results demonstrate that diverse allocation topics share an impressive number of features. In particular, several features of sex allocations that have been discovered over the past 50 years have direct parallels in other fields. These shared features warrant common explanations. There are considerable heuristic advantages to be gained from uniting these hitherto largely unconnected topics. Efforts to develop widely applicable principles should reduce the duplication of labor involved in rediscovering the same concept independently in different fields, as has happened repeatedly in the past. Broadening the applications of general principles will increase the explanatory power of the theories that have been applied to particular types of allocation. The total range of phenomena will be explained more economically by general theories than by a series of parallel but unconnected theories for each specific subject.

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Sex determining mechanisms: An evolutionary perspective

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Summary. Theories on the evolution of sex determining mechanisms are reviewed for male and female heterogamety, environmental sex determination, and briefly, haplo-diploidy and hermaphroditism. Because of their discrete and well-defined nature, sex determining mechanisms lend themselves to three types of evolutionary questions: *what* variety occurs and might be expected but does not occur, *how* do changes occur from one mechanism to another, and *why* do certain changes occur? All three approaches were illustrated for these different sex determining mechanisms. A generality emerging from these studies is that, at the level of selection on the sex ratio, there are no intrinsic problems in evolving from one sex determining mechanism to another: straightforward transitions between different mechanisms exist under various conditions.

Key words. Sex; sex determination; sex ratio; evolution; animals; genetics.

1) Introduction

The beginning of this century marked the onset of studies on the inherited and environmental basis of sex, and a variety of sex determining mechanisms are now known in plants and animals*. The two major categories of sex determining mechanisms are dioecy (separate sexes) and hermaphroditism (both sexes within the same individual), but there is further variety within both of these classes. Considering dioecious species, the most widespread mechanism is *heterogamety,* in which one sex is labeled XX and the other XY. Systems slightly more complicated that this, involving three or more factors, are also known. In addition, some species are haplo-diploid, with females arising from fertilized eggs, males from unfertilized eggs. In contrast to these systems, some dioecious species have environmental sex determination, whereby sex is determined in response to environmental effects experienced early in life. With hermaphroditic species, the distinction between male and female is not inherited as such, because both sex types occur in each individual (whether sequentially or simultaneously). However, the extent of male/female expression may be subject to genetic and environmental influences[20].

The diversity of sex determining mechanisms poses an interesting set of questions to study from an evolutionary