

Optimization of the Sex Ratio when Family Size
and Sex Ratio Can Vary

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INTRODUCTION

In his review of optimization methods in ecology Maynard Smith (1978) used sex ratio as an example of a characteristic whose optimal value depends on the ecological conditions which are assumed to hold. Thus, Fisher, (1958) in the original treatment, assuming that the total reproductive effort is fixed and that the cost of males is a constant times the cost of females, concluded that the reproductive effort devoted to each sex should be equal. Crow and Kimura (1970), assuming that the total number of offspring is fixed regardless of sex, concluded that a 1:1 sex ratio is best. MacArthur (1965), assuming that sex ratio and clutch size might vary simultaneously, asserted that natural selection will produce that clutch size and that sex ratio which will maximize the product of the number of males M times the number of females F raised to reproductive age.

MacArthur's result was intended to be a generalization of Fisher's, but, insofar as it is correct, it represents a strengthening, rather than a weakening, of the assumptions made by Fisher. The explicit assumptions made by MacArthur are not sufficient to assure his conclusion. An examination of the conditions under which MacArthur's result fails reveals some biologically important possibilities. For example, if, within a population, certain types are better at producing males and other types are better at producing females, then it is not necessary that natural

selection will favor a single sex ratio that maximizes MF. In this case the different types should have different sex ratios. This possibility has been suggested by Trivers and Willard (1973).

Similarly, if the relative quality of the environment for producing males and females varies from place to place and the animals can adjust the sex ratio of their offspring according to habitat, they should do so and should not produce the same sex ratio everywhere.

Charnov (1979) has considered the case of parasites laying their eggs in hosts of different relative quality for male and female offspring. The optimal strategy found by Charnov satisfies MacArthur's product rule. The animals considered by Charnov do not have to search for hosts and it is not necessary in the model to distinguish between relative and absolute abundance of different quality hosts.

If the parasites must search for hosts and assess the quality of each host found, then the optimal strategy (and consequently the optimal sex ratio) will depend on the relative abundance of hosts. This result differs from the corresponding result from optimal foraging theory (Pyke, Pulliam and Charnov 1977).

SOME BASIC RESULTS

The Results of Kolman, Verner and MacArthur

Fisher (1958) argued that if the costs of producing males and females are constant and the total reproductive effort for an animal is fixed, then equal effort should be made to produce offspring of each sex. The idea is that if all individuals have both fathers and mothers, then if more effort were being devoted to producing offspring of one sex,

then effort to produce offspring of the other sex would be better rewarded and selection would favor a change that increased effort toward producing offspring of that sex which was receiving less effort.

Kolman (1960), using a method introduced by Shaw and Mohler (1953), constructed a mathematical model that confirmed Fisher's conclusion. Kolman pointed out that it is the total reproductive effort for the whole population that should be evenly divided between the sexes. If within a population there exist types that devote more effort toward producing young of one sex than the other selection will not act against those types as long as the overall effort is divided equally between the sexes. This is an important point. Selection favors changes that move the population sex ratio toward 50% males, but does not necessarily favor changes of individual sex ratios toward 50% males. Such changes may be impossible, as Kolman assumed.

In making his argument Kolman assumed the existence of two types, with M individuals of one type devoting $.5 + m$ of their reproductive effort toward producing males and N individuals of another type devoting $.5 - n$ of their reproductive effort toward producing males. Kolman assumed that the proportion of reproductive effort devoted to males for each type was fixed and that selection could only operate on the frequency of the types in the population. For Kolman's model a stable equilibrium for the relative frequencies of the two types would exist, with $M/N = n/m$. Kolman concluded that while selection tends to make the average proportion of reproductive effort devoted to the production of each sex the same it does not affect the variance of that proportion.

Verner (1965) disputed this last conclusion of Kolman by considering a model with several types that could devote various proportions of their reproductive effort to the production of each sex. Verner found that an equilibrium could be achieved with several different types but he pointed out that the equilibrium would be unstable in the sense that selection would favor a change in any type toward equality of reproductive effort devoted to the two sexes. Verner concluded that selection not only favors devoting equal reproductive effort to each sex but that it also tends to reduce the variance between individuals in the proportion of their reproductive effort devoted to each sex. Verner's model differed from Kolman's in that he considered more than two types, and he assumed that the sex ratio produced by a type could change.

Both Kolman (1960) and Verner (1965) assumed, as did Fisher (1958), that costs of males and females were fixed and that the total expenditure (reproductive effort) was fixed. MacArthur (1965) referred to this as assuming that clutch size and sex ratio vary independently and he tried to relax this assumption. MacArthur considered the possible set of values for the numbers of males, M , and females, F , that could be produced, and he represented these possibilities in two-dimensional space. He assumed that the possible set of points (M,F) could be thought of as the area below a curve (call it L) as shown below:

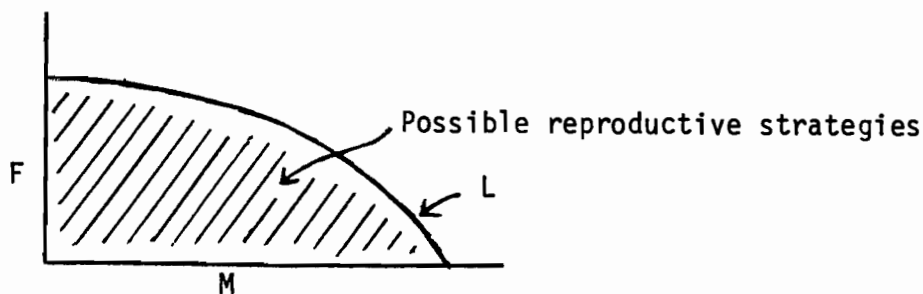


Figure 1: Set of possible reproductive strategies (values of (M,F)).

MacArthur, using the same argument as Shaw and Mohler (1953), Kolman (1960) and Verner (1965), considered an individual carrying a gene \underline{a} which influences sex ratio and/or family size and he looked at C_a , the proportion of the second generation of descendants that would have the gene:

$$C_a = \frac{1}{2} \frac{M_a}{M_a + M_r} + \frac{1}{2} \frac{F_a}{F_a + F_r} ,$$

where M_a is the number of males raised to reproductive age by the individual and having gene \underline{a} and M_r is the number of males raised by everyone else. F_a and F_r are the corresponding numbers of females.

MacArthur asserted that selection maximizes C_a . Since the best strategy must lie on line L MacArthur looked at the derivative of C_a as a point moves along curve L and concluded that C_a is maximized for that point on L for which MF is largest. Thus, MacArthur concluded that selection favors that strategy which maximizes the product of the number of males times the number of females raised to reproductive age. If the curve L is a straight line we have the classic case of Fisher and MF is maximized when the representative effort is the same for both sexes.

Unfortunately there are two difficulties with MacArthur's argument. First, using his method he found a strategy such that if everyone followed that strategy selection would not permit some types of change to a slightly different strategy. The strategy he found using this method is not necessarily unique, however. If the curve L happens to be tangent to the curve $MF = c$ for some constant c and convex (upward) in some neighborhood of the point of tangency (M_1, F_1) , then that point will provide an equilibrium sex ratio stable against small changes. Such a point (M_1, F_1) would

be locally stable and would provide a locally maximum product $M_1 F_1$, but this local maximum would not have to equal the global maximum.

The second difficulty with MacArthur's approach is his assumption that selection should favor everyone having the same sex ratio. Even if there is only one possible local maximum of MF (which would be the case if L were convex in $\log M$ - $\log F$ space) the best strategy could be mixed.

For example, consider a case where MF is maximized on curve L at $(5,5)$ but where the point $(10,2)$ also lies on L . Consider only two types, one producing 5 males and 5 females, another producing 10 males and 2 females. Eventually the population will consist of proportion .625 of the $(5,5)$ -types (with .3125 males and .3125 females) and proportion .375 of the $(10,2)$ -types (with .3125 males and .0625 females). Thus the population will have an excess of males. Since random mating is assumed the $(5,5)$ -types will be responsible for proportion .667 of the mating and the $(10,2)$ -types will be responsible for proportion .333 of the mating (although they will produce proportion .375 of the offspring since they have 12 offspring as opposed to 10 offspring for the $(5,5)$ -types). In this case it is interesting to notice that the point $(6.67,4)$, which represents the weighted average of the points $(5,5)$ and $(10,2)$ determined by the mating frequencies of the two types, is also the point on the line connecting the points $(5,5)$ and $(10,2)$ that maximizes the product of its components.

This example may be thought of as a version of Kolman's result with the cost of males lower than the cost of females.

A New Interpretation of MacArthur's Result

The example given above shows that MacArthur's assertion that selection favors the reproductive strategy that maximizes MF , the product of the number of male times the number of female offspring, is not true without assumptions on the set of possible strategies.

MacArthur's conclusion will hold if the curve L bounding the set of possible strategies is strictly convex or if the maximum of MF is achieved at a point (M_0, F_0) such that all possible strategies except (M_0, F_0) lie below the line $F = -(F_0/M_0)M + 2F_0$, which is tangent to curve L at point (M_0, F_0) . MacArthur did not explicitly assume that the set of possible strategies was convex, but his Figure 1 (p. 390) (which, however, shows a set convex in $\log M - \log F$ space, not $M - F$ space) suggests that he had this in mind.

If the set of possible strategies is convex (with L strictly convex) or if (more generally) all possible strategies other than the (M_0, F_0) that maximizes the product MF lie below the line $F = -(F_0/M_0)M + 2F_0$, then MacArthur's result may be interpreted in terms of Fisher's classic result that selection favors that sex ratio which equalizes the total effort devoted to producing males and females. If, instead of having the set of possible strategies bounded by the curve L we consider the set to be expanded to include all strategies bounded by the tangent line $F = -(F_0/M_0)M + 2F_0$, then the "best" strategy within this augmented set of strategies would be (M_0, F_0) . That is, the point (M_0, F_0) represents the strategy which equalizes reproductive effort devoted to the two sexes if we consider the augmented set of strategies and interpret the M and F

intercepts of the line $F = -(F_0/M_0)M + F_0$, namely, $2M_0$ and $2F_0$, as the number of males and females, respectively, that could be produced with maximum reproductive effort. If maximum effort devoted to one sex could produce $2M_0$ males and $2F_0$ females, then the strategy (M_0, F_0) could be thought of as devoting equal reproductive effort to each sex. Not all strategies in the augmented set of strategies would actually be possible, but Fisher's "best" strategy, namely, (M_0, F_0) , would be possible. Other strategies along the line $F = -(F_0/M_0)M + 2F_0$ could exist in (neutral) equilibrium with (M_0, F_0) , as Kolman (1960) showed, but such coexistence is impossible if the actual curve L bounding the set of possible strategies is strictly convex, or simply if it lies below line $F = -(F_0/M_0)M + 2F_0$ everywhere except at (M_0, F_0) . In this case the point (M_0, F_0) , which maximizes the product MF , represents the best strategy and is favored by selection over any other strategy or set of strategies.

This discussion is illustrated in Figure 2:

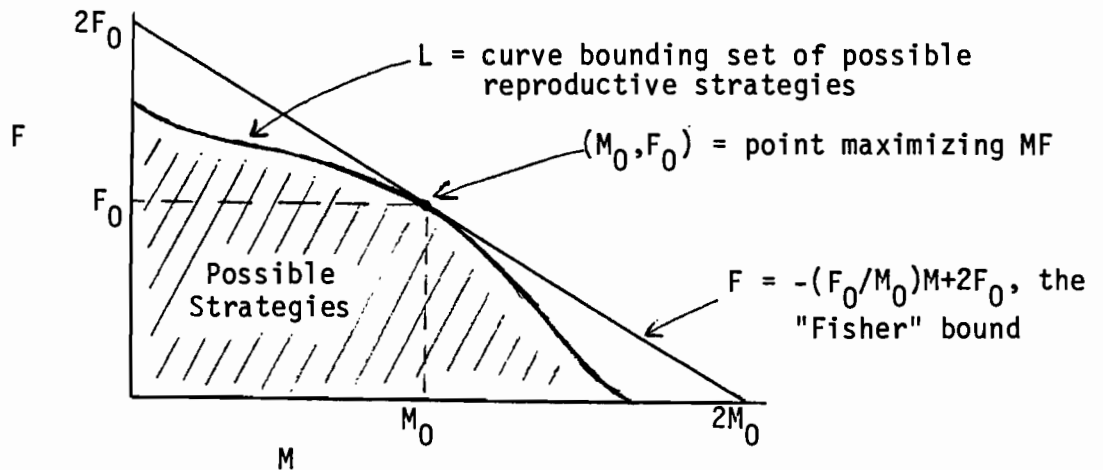


Figure 2: Possible strategies (cross hatched area) and line F tangent at point (M_0, F_0) that maximizes MF .

Thus if the set of possible strategies is assumed to be convex (or some similar assumption is made) MacArthur's conclusion that selection favors the strategy that maximizes the product MF will be correct. The

effect of the convexity assumption is to restrict the set of strategies more than Fisher (1958) (or Kolman (1960) or Verner (1965)) would have done. The "same" best strategy is available in the restricted set of strategies. Requiring L to be strictly convex eliminates the issue raised by Kolman and Verner about whether variance in sex ratios is neutral or is selected against. That issue only arises when the set of possible strategies is bounded by a straight line (or a line straight in some interval around the point (M_0, F_0) that maximizes the product of MF within the set of possible strategies).

A Concave Boundary on the Possible Strategies: Variability
in Sex Ratio is Favored

The case illustrated in Figure 2 shows a curve L bounding the possible reproductive strategies that lies below the tangent line $F = -(F_0/M_0)M + 2F_0$ everywhere except at the point of tangency (M_0, F_0) which maximizes the product MF for possible strategies. Selection will favor the strategy (M_0, F_0) .

The alternative case, in which there are strategies (points (M, F)) that lie above the line $F = -(F_0/M_0)M + 2F_0$, where (M_0, F_0) is a point where MF is maximum for possible strategies, is theoretically important. In such a case a mixture of strategies would be favored over any fixed strategy. The example given on p. 6 illustrates this point. In that example it may be seen that selection favors that mixture of strategies such that the average numbers of males, M_1 , and females, F_1 , produced by breeding adults maximizes the product MF for all possible mixtures. The product $M_1 F_1$ will exceed the product MF for any other possible strategy (M, F) .

We might then extend MacArthur's (1965) result to the general case where the curve L bounding the set of possible reproductive strategies has arbitrary shape. If L is not convex we may consider augmenting the set of possible strategies by including all possible mixtures of strategies. These mixtures correspond to points in strategy space lying between points in the space of possible strategies. The augmented set of strategies is the convex hull of the set of possible strategies. Now the best strategy (or best mixture of strategies) will be represented by that point (M_1, F_1) in the augmented set of strategies that maximizes MF . If (M_1, F_1) lies in the set of possible strategies then selection will favor the single strategy represented by (M_1, F_1) . However, if (M_1, F_1) lies in the area added to the set of possible strategies by including mixtures, then selection will favor a mixture of strategies where reproducing individuals will produce an average of M_1 males and F_1 females.

This discussion is illustrated in Figure 3:

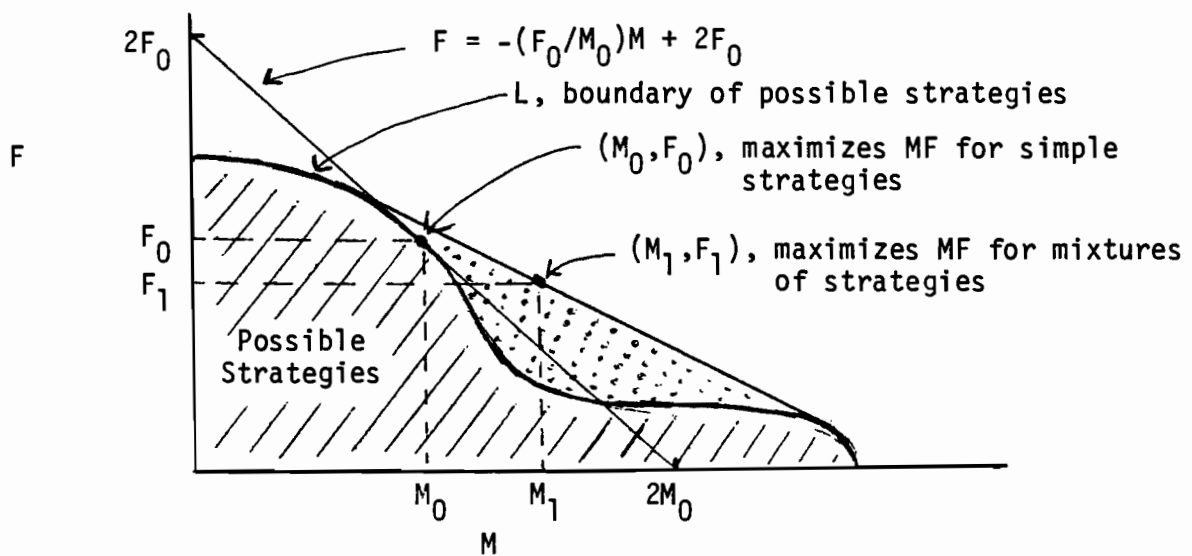


Figure 3: Possible strategies (crosshatched area) and mixtures of possible strategies (stippled area).

This case, where the boundary on the possible strategies is necessarily concave (to some extent, at least), is theoretically important because it shows that selection may favor mixtures which possess stable equilibria and not just neutral equilibria as in the cases considered by Kolman (1960) and Verner (1965). Such a case could arise if some types are better at producing males while others are better at producing females, or if it is easier to produce clutches with only one sex.

Charnov, Maynard Smith and Bull (1976) have considered this case in which the set of possible strategies is concave in part. They suggested that this could result in a mixture of females and hermaphrodites. Their concern, however, was with the distribution of sexual function (whether male, female, or hermaphrodite) rather than the sex distribution of offspring produced.

NONGENETIC VARIATION IN THE SET OF POSSIBLE REPRODUCTIVE STRATEGIES

It is difficult to imagine situations in which individuals of one genotype would be better at producing males while those of a different genotype would be better at producing females. There are, however, two conditions which are likely to arise that could result in variability in the set of possible reproductive strategies. One involves variability in the quality of parents while the other involves variability in the quality of the environment.

Variation in the Quality of Parents

The first of these conditions, suggested by Trivers and Willard (1973), is that the quality of parents may vary. In animals with extended

parental care of young, as, for example, mammals, healthier mothers might produce healthier young which, in turn, might have better reproductive success than offspring of less healthy mothers. If the variability of reproductive success is greater for one sex than another then the healthier mothers should produce more of that sex whose reproductive success is more variable, since the advantage of being healthier would be greater for that sex. Thus, Trivers and Willard suggest that in mammals, where paternal care is much less than maternal care and male reproductive success is more variable than that of females, healthier females might be expected to produce relatively more males than less healthy mothers would. Trivers and Willard claim there is empirical evidence to support their idea. Myers (1978) has disputed the evidence offered by Trivers and Willard.

Williams (1979) has discussed Trivers and Willard's idea of adaptive variation in sex ratio and has compared it with the opposite idea, which he attributes to Verner (1965), that sex ratio should show less than random variation. Williams says that: "Evidence from vertebrates is unfavorable to either theory and supports, instead, a non-adaptive model, the purely random (Mendelian) determination of sex." (p. 567). Especially impressive is the data from humans. Greenberg and White (1967) looked at the sex of successive children in 116,458 Mormon families and failed to reject the independent-event hypothesis.

Greenberg and White, however, considered the primary sex ratio. Trivers and Willard (1973) would probably not dispute these results; following Leigh (1970) they point out that differential mortality between the sexes can produce the differences which their theory predicts.

Trivers and Willard assume that the quality of the animals varies but they do not consider changes in environmental quality. Charnov et al. (1978) consider the example of protandrous hermaphrodites (which start life as males and later become females). The assumption is that larger animals make better females but size is not important to males. Charnov has shown that the correct time to change sex depends on environmental conditions, on how many large and small individuals there are. If there are few females then the optimal size at which to change sex is smaller than if there are many females. In this example sex is not determined for young but for adults.

Variation in patch quality

The second condition that could produce variability in the set of possible reproductive strategies is that the environment might vary. While for many vertebrates parental quality probably influences offspring quality, in most lower animals parental quality probably only affects offspring number. If young result from unprovisioned and unattended eggs, then the condition of the young will depend on the quality of the environment in which they develop. For example, if a parasitic insect lays eggs on hosts which vary in size, then a large host might be considered a good environment and a small host a bad environment. In this case host size plays a role similar to parental quality in the case of mammals considered by Trivers and Willard. One difference is that one insect parasite will probably encounter hosts of different sizes while an unhealthy mammal is not so likely to become a healthy one. For mammals parental quality will vary between individuals while for insect parasites host quality will vary for each individual from host to host.

In the theory of Fisher (1958), Kolman (1960), MacArthur (1965), and Verner (1965) the reproductive strategies considered consist of producing certain numbers of males and females. All the individuals of a sex are assumed to be equally good. If, in fact, individuals vary in quality, then one good male might be equivalent to two poor males (in terms of the number of matings likely to be achieved), or one good female equivalent to one and a half poor females (in terms of the number of young born or eggs laid).

These differences in quality could be converted to differences in number of equivalent young by saying that a good male counted double and a good female counted one and a half times a standard. If the cost of producing good offspring is the same as the cost of producing poor offspring (but only good quality parents (or hosts) could produce good offspring) then the reproductive strategies available would differ with quality of parents (or hosts). In theory, then, we might expect to see different strategies (and different sex ratios) for different quality mammalian mothers and for insects parasitizing different sized hosts.

Trivers and Willard (1973) said that healthier mothers should have more sons because male reproductive success varies more than that of females. However, it is not only the variability in reproductive success that matters but also the ability of the parent or the environment to affect the offspring's reproductive success. It is possible, for example, that the quality of males may vary little in terms of size, activity or longevity, and be little influenced by the environment, even though their reproductive success may vary greatly, while the quality of females may be greatly influenced by the environment even if their reproductive success

varies less than that of males. That is, it is not only the amount of variation in reproductive success within a sex that is important, but also the ability of the quality of parents or the environment to influence reproductive success.

Certain conditions are relatively better for the production of one sex than the other. We might therefore expect the sex ratio to vary under different conditions. Williams (1979) claims that the evidence for such adaptive variation in sex ratios is poor for outcrossed vertebrates. This may be true because in such animals the mechanisms for varying sex ratio, such as differential mortality between the sexes, are inefficient. However, in animals with an efficient mechanism for determining the sex of their offspring one might expect such adaptive variation in sex ratio.

Arrhenotoky, in which unfertilized eggs become males and fertilized eggs become females, seems to provide such an efficient mechanism for sex determination. Parasitic Hymenoptera, which possess this mechanism, do seem to show adaptive variation in sex ratio. Sandlan (1979) has presented evidence that the ichneumonid parasite Coccygomimus turionella L. lays relatively more fertilized (female) eggs on larger hosts. Sandlan showed that females from larger hosts were larger, lived longer and produced more eggs over their lifetime than females from smaller hosts.

It is not clear what effect host size has on male offspring. If male reproductive success is little influenced by host size then theory would predict that relatively more females should be produced from larger hosts. It will be assumed here that female quality is affected by host size more than is male quality.

The situation described here has been modelled by Charnov (1979), who considered a genetic model for sex ratio in an arrhenotokous animal laying eggs in hosts of two qualities. Charnov assumed that the proportion of eggs deposited in each quality host was fixed. This assumption reflects the experimental setup (van den Assem, 1971) which motivated Charnov's model. In this setup the animal is sequentially presented at a fixed rate with hosts of known sizes. The animal chooses the sex of eggs deposited in different sized hosts, but it does not have to search for hosts. Charnov's model can, however, be extended to the case where the animal must search for hosts. Charnov's results need not hold in such a case.

Charnov's Model

In Charnov's (1979) model parasites may lay their eggs on hosts of two sizes. Proportion P of the hosts are small and proportion $1 - P$ are large. Fitness of males and females on small hosts are assumed to be equal to 1 while on large hosts males are assumed to have fitness $W_1 > 1$ and females have fitness $W_2 > W_1$. A parasite will use a strategy: produce proportion r_1 males in small hosts and produce proportion r_2 males in large hosts.

Charnov solved for the optimal r_1 and r_2 by considering an explicitly genetic model and solving for that strategy which could not be successfully invaded by mutants using any other strategy. This strategy which cannot be successfully invaded by any other strategy is called the "evolutionarily stable strategy" or ESS. Since Hartl and Brown (1970) have shown with a genetic model that Fisher's principle applies to arrhenotokous animals it is easy to find the best strategy in Charnov's model by finding the values

of r_1 and r_2 that maximize the product of the number of males times the number of females produced. This done here.

The set of possible strategies may be illustrated graphically. There are three possible cases, determined by the relative frequency of large and small hosts. The cases are (in order of relative frequency of small hosts-- Case 1 has the lowest proportion of small hosts):

Case 1: $P/(1-P) < W_1$.

Case 2: $W_1 \leq P/(1-P) \leq W_2$.

Case 3: $P/(1-P) > W_2$.

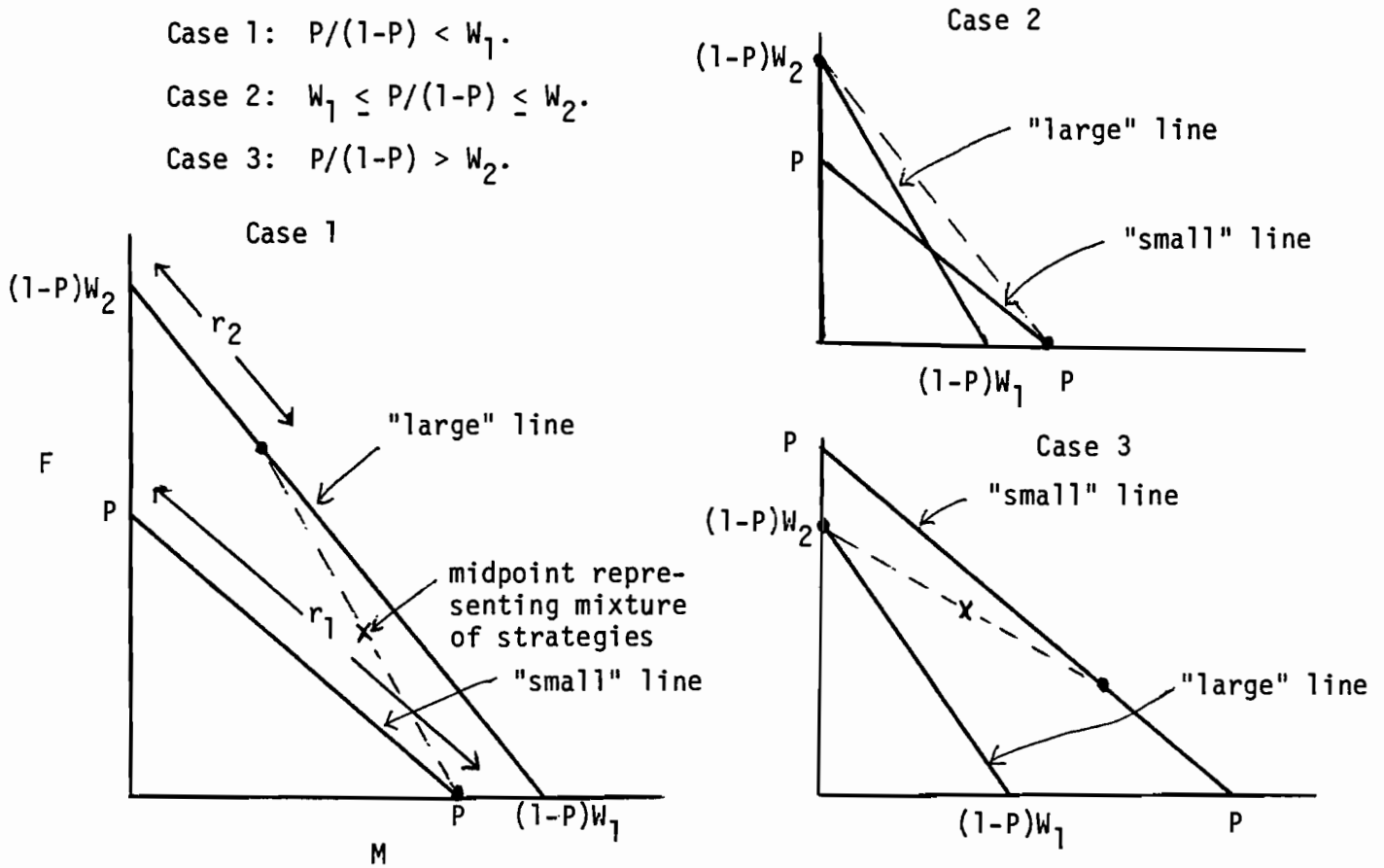


Figure 4: Set of possible reproductive strategies, characterized by r_1 and r_2 the proportion of reproductive effort devoted to producing r_1 and r_2 the proportion of reproductive effort devoted to producing males in small and large hosts, respectively. Heavy dots represent optimal strategies.

A strategy will be represented by a pair of points, one on the "small" line (representing the number of offspring possible from small hosts) and one on the "large" line. The proportion of males produced in small and large hosts, respectively, will be r_1 and r_2 .

For a given strategy, the midpoint of the line segment connecting the points represents $MF/4$. The problem is to find the points on the lines (or, equivalently, the values of r_1 and r_2) that maximize MF .

It is clear geometrically that in Case 2 the product MF is maximized for $r_1 = 1$, $r_2 = 0$. Similarly, in Case 1 we have $r_1 = 1$ and in case 3 we have $r_2 = 0$.

In general, we have

$$F = (1-r_1)P + (1-r_2)(1-P)W_2 \text{ and}$$

$$M = r_1P + r_2(1-P)W_1 .$$

For Case 1 we want to maximize

$$MF = (P + r_2(1-P)W_1)((1-r_2)(1-P)W_2).$$

Differentiate with respect to r_2 , set the derivative = 0 and find:

$$r_2 = \frac{(1-P)W_1 - P}{2(1-P)W_1} .$$

Similarly, for Case 3 we want to maximize

$$MF = (Pr_1)((1-P)W_2 + (1-r_1)P)$$

and we find

$$r_1 = \frac{(1-P)W_2 + P}{2P} .$$

These are the results obtained by Charnov (1979).

The results show, roughly, that when small hosts are rare they should all be used for males and a majority, but not all, of the large hosts should be used for females. When large hosts are rare they should all

be used for females and a majority, but not all, of the small hosts should be used for males. For some intermediate host size frequencies, all the large hosts should be used for females and all the small hosts used for males.

In fact, evidence does show that parasites can alter the sex ratio of their offspring according to the size of the hosts used. This was demonstrated by van den Assem (1971) with Lariophagus distinguendus, a wasp parasitic on granary weevils.

Charnov et al. (1980) have recently relaxed the assumption of just two host sizes and have pointed out that if host sizes vary continuously and the ratio of female to male relative fitness increases monotonely with host size, then the best strategy is to produce male offspring in hosts below a certain size and to produce only females in larger hosts.

While there is evidence that female fitness is influenced by host size, it is more difficult to determine whether male fitness is less influenced by host size than is female fitness. This differential effect of host size on the two sexes is an essential assumption of the theory. The experimental evidence is good that parasites do, in fact, produce a different sex ratio under different conditions.

A FORAGING MODEL FOR SEX RATIOS

In Charnov's (1979) model the parasite is assumed simply to choose the sex of its offspring. When hosts are offered to the parasite one at a time, as was done in the experiments described by Charnov et al. (1980), this assumption may well be justified. However, a naturally foraging parasite may encounter unsuitable hosts.

In the following model it is assumed that the parasite has three alternative choices when it encounters a potential host. The parasite may lay a fertilized (female) egg, an unfertilized (male) egg, or no egg at all.

In my model I assume:

1. It takes time t_1 to assess the size of a potential host and this time does not depend on the host's size.

2. It takes time t_2 to lay an egg and resume searching. This "down time" does not depend on whether or not the egg laid is fertilized. The parasite may actually be able to lay a series of eggs in rapid succession and then take time to prepare a new batch of eggs. In this case the "down time" may be thought of as the time it takes to prepare each egg of the next batch.

3. Host size is uniformly distributed between 0 and 1. This assumption, which is made for mathematical convenience, can be made without loss of generality. I assume that hosts are found randomly with respect to size and that one host, on average, is found in each unit of time. Density of hosts may be varied in the model by varying t_1 and t_2 . If those values are large, it is equivalent to having a dense host population.

4. Relative fitness for each sex will be a monotone non-decreasing function of host size, x . Male fitness will be written: $W_m(x)$, and female fitness: $W_f(x)$. Fitnesses are measured relative to an individual offspring in the largest host, which will have size 1. Thus, $W_m(1) = W_f(1) = 1$. The ratio $W_f(x)/W_m(x)$ is a monotone non-decreasing function of x . It is this last assumption that permits the simple solution of the optimization problem given by Charnov et al. (1980), namely, lay male eggs on small hosts and female eggs on large hosts.

If adult mortality is independent of the foraging strategy used, depending only on the time spent foraging for hosts, then, using the product rule, we can find the best foraging strategy by maximizing the product of the rates of producing males and females.

Because male fitness is assumed to be a monotone function of host size and the ratio of female to male fitness is a monotone function of host size it can be seen that the best strategy must be of a simple form similar to that found by Charnov et al. (1980). No eggs are laid in the smallest hosts, unfertilized (male) eggs are laid in intermediate sized hosts, and fertilized (female) eggs are laid in the largest hosts. The best strategy will be characterized by two values of host size, x_1 and x_2 . No eggs are laid in hosts smaller than size x_1 , unfertilized eggs are laid in hosts of size between x_1 and x_2 , and fertilized eggs are laid in hosts larger than size x_2 .

The resulting product of rates will then be

$$(1) \quad MF = \int_{x_1}^{x_2} W_m(x) dx \int_{x_2}^1 W_f(x) dx / (1 + t_1 + t_2(1 - x_1))^2,$$

where $\int_{x_1}^{x_2} W_m(x) dx$ is the average fitness value of males produced in each visit to a host (a male may or may not result from each visit--the fitness is averaged over all host sizes),

$$\int_{x_2}^1 W_f(x) dx \text{ is the average fitness value of females}$$

produced in each host visit, and

$$(1 + t_1 + t_2(1 - x_1)) \text{ is the average time spent}$$

on each host visit. The 1 represents the average time to find a host, t_1

represents the time to assess the host's quality, and t_2 represents the "down time" if an egg is laid. An egg is laid on any host of size greater than x_1 and host sizes are assumed to be uniformly distributed between 0 and 1. Therefore, proportion $1 - x_1$ of the hosts visited will have eggs laid on them and the average "down time" per host visited will be $t_2(1 - x_1)$.

A Simple Example

In order to illustrate the model and show how the best strategy depends on the parameters of the model, I consider the simplest case, in which all hosts that are suitable for a particular sex are equally suitable. Hosts of size less than \underline{a} are unsuitable for either sex, hosts larger than \underline{a} are suitable for males and hosts larger than \underline{b} (which, in turn, is larger than \underline{a}) are suitable for females.

(I assume that $\underline{b} - \underline{a} > 1 - \underline{b}$ (that is, the proportion of hosts suitable for males alone is greater than the proportion suitable for both males and females) since otherwise the best strategy (characterized by the host sizes $x_1 = \underline{a}$, $x_2 = (1 + \underline{a})/2$) will be to produce half males and half females.)

In this example, $x_2 = \underline{b}$ and the problem is to find the value of x_1 that maximizes

$$MF = (b - x_1)(1 - b)/(1 + t_1 + t_2(1 - x_1))^2 .$$

We differentiate MF with respect to x_1 and set the derivative equal to zero and obtain

$$(2) \quad x_1 = (2b - 1) - (1 + t_1)/t_2 .$$

The value of x_1 given by (2) will represent (along with $x_2 = b$) the best strategy if it is greater than or equal to \underline{a} . If not, $x_1 = \underline{a}$ will be the best value.

The sex ratio determined by (1) will be

$$\frac{x_2 - x_1}{1 - x_1} = \frac{1 - b + \frac{1 + t_1}{t_2}}{2(1 - b) + \frac{1 + t_1}{t_2}}$$

Notice that for t_2 large the sex ratio will be close to .5. This is equivalent to saying that when the "down time" is large, or, equivalently, the density of hosts is high, the parasite should be selective and produce roughly equal numbers of males and females.

On the other hand, if t_2 is small, which is equivalent to saying that hosts are sparse, the parasite should lay an egg on almost any host it finds, and in my example, in which more hosts are suitable for males alone than are suitable for males or females, the sex ratio should favor males.

In general, when foraging is taken into account, the optimal sex ratio may depend on the absolute density of hosts as well as the relative abundance of hosts suitable for producing offspring of each sex.

The General Case

If the expression (1) given for MF achieves a maximum for values x_1 and x_2 such that $0 < x_1 < x_2 < 1$ and if MF possesses negative second partial derivatives with respect to x_1 and x_2 , then the best strategy may be found by taking the partial derivatives of (1) with respect to x_1 and x_2 and setting them equal to zero. The resulting equations correspond to theoretical biological principles.

1. The equation $d(MF)/dx_2 = 0$ is equivalent to

$$(3) \quad \frac{W_m(x_2)}{\int_{x_1}^{x_2} W_m(x) dx} = \frac{W_f(x_2)}{\int_{x_2}^1 W_f(x) dx}$$

which says that the relative change in total male and female fitness with a given small change in x_2 should be the same. This is just the condition MacArthur found in obtaining his product rule for sex ratios.

2. The equation $d(MF)/dx_1 = 0$ is equivalent to

$$\frac{2t_2}{1 + t_1 + t_2(1 - x_1)} = \frac{W_m(x_1)}{\int_{x_1}^{x_2} W_m(x) dx} ,$$

which may be rewritten as

$$(4) \quad \frac{W_m(x_1)}{t_2} = \frac{2 \int_{x_1}^{x_2} W_m(x) dx}{1 + t_1 + t_2(1 - x_1)} .$$

The expression on the right side of (4) is twice the rate of producing males (weighted by male fitness). The expression on the left side of (4) represents the marginal rate of gain in male production (weighted by male fitness) if the critical value for accepting hosts to produce male offspring is lowered by a small amount. Expression (4) is analogous to Charnov's (1976) "marginal value theorem," which says that an optimal forager, which searches in patches it depletes of prey, will leave a patch at the time when its rate of finding prey there just equals the highest long term rate attainable.

The Analogous Optimal foraging Model

A predator that forages for randomly distributed individual prey items of differing quality would be analogous to a parasite searching for hosts. Assume, as in the sex ratio model, that the size of prey is uniformly distributed on the interval (0,1), that each potential prey item encountered takes time t_1 to assess, that the predator has "down time" (digestion time) t_2 after each prey is eaten, and that the nutritional gain from each prey item is $W(x)$, a monotone non-decreasing function of prey size. Then the best strategy will be to eat prey larger than some size x_1 and bypass smaller prey. The long term rate of nutritional gain using this strategy will be

$$(5) \quad G(x_1) = \frac{\int_{x_1}^1 W(x) dx}{1 + t_1 + t_2(1 - x_1)} .$$

The value of x_1 which maximizes (5) may be found under suitable regularity conditions by differentiating $G(x_1)$ with respect to x_1 and setting the derivative equal to zero. The resulting equation will be

$$\frac{t_2}{1 + t_1 + t_2(1 - x_1)} = \frac{W(x_1)}{\int_{x_1}^1 W(x) dx} ,$$

which may be rewritten

$$(6) \quad \frac{W(x_1)}{t_2} = \frac{\int_{x_1}^1 W(x) dx}{1 + t_1 + t_2(1 - x_1)} .$$

The right side of (6) is simply the long term rate of nutritional gain and the left side is the marginal rate of nutritional gain if the critical value of acceptable prey size is lowered by a small amount. This is a

version of the "marginal value theorem" (Charnov 1976).

If in a foraging sex ratio model it is assumed that hosts of a given size are equally good for males and females, then the numerator of the right side of (4) might be interpreted as the sum of the fitnesses for both sexes. This is analogous to the total nutritional gain for a predator and expression (6) is almost identical to (4).

Under suitable regularity conditions the optimal solution to the foraging sex ratio problem satisfies (3) and (4). Expression (3) may be thought of as a version of the Charnov et al. (1980) extension of MacArthur's (1965) product rule. Expression (4) is analogous to Charnov's (1976) marginal value theorem.

SUMMARY

Fisher (1958) argued on intuitive grounds that in animals with two sexes selection should favor devoting equal effort toward producing offspring of each sex. A genetic model confirming Fisher's principle was proposed by Shaw and Mohler (1953). This model was used by Kolman (1960), who pointed out that it is the effort of the entire population and not each individual that should be divided equally between the production of male and female offspring. Verner (1965) showed that if different types within a population produce different sex ratios selection will favor a change toward .5 in the proportion of effort devoted by any type of producing males.

Fisher, Kolman and Verner all assumed a fixed cost for offspring of each sex and a fixed total effort possible for each parent. MacArthur (1965) relaxed this assumption by assuming that sex ratio and total number

of offspring could vary independently. MacArthur argued that selection would favor that strategy which maximizes the product of the number of male and the number of female offspring produced. MacArthur's argument is not correct in general, but it is correct if the set of possible reproductive strategies is strictly convex. A diagram given by MacArthur suggests that he had convexity in mind. In this case the possibility of a stable mixture of strategies suggested by Kolman and disputed by Verner does not arise.

The case in which the set of possible reproductive strategies is concave, at least in part, is important theoretically. In such a case a stable mixture of reproductive strategies might occur, with different types within a population having different sex ratios. Charnov et al. (1976) considered this case and pointed out that an example known as gynodioecy, in which a population consists of a mixture of females and hermaphrodites, does occur.

A possible source of variation in sex ratio within a population has received considerable attention recently. The idea, suggested by Trivers and Willard (1973), is that parents in different conditions should produce offspring with different sex ratios. The suggestion is that females in better condition should produce relatively more males. The basis of the difference in parental condition need not be genetic. Trivers and Willard cited evidence for their idea, but their evidence has been disputed by Myers (1978). Williams (1979) reviewed the evidence for adaptive variation in sex ratio in outcrossed vertebrates and found no strong evidence for either greater than random variation in sex ratios (suggested by Trivers and Willard), or less than random variation (an idea attributed

to Verner). Williams, however, considered the primary sex ratio and discounted differential mortality as an important mechanism in varying the sex ratio. Trivers and Willard suggested differential mortality as a possible mechanism for varying the sex ratio. Myers (1978) produced an unconvincing model to dispute Trivers and Willard's idea. However, differential mortality is an inefficient mechanism for varying sex ratio. If there is no more efficient mechanism available for most vertebrates then one should not expect to see much variation in vertebrate sex ratios.

Arrhenotoky, in which unfertilized eggs become males and fertilized eggs become females, is a system of sex determination which provides an efficient mechanism for varying the sex ratio. Arrhenotoky is found in several groups of invertebrates, including hymenoptera. For invertebrates, differences in parental quality are more likely to be reflected in offspring number than in offspring quality. However, in parasitic wasps, offspring quality may be affected by host quality, which may be determined by host size. Thus, for parasitic wasps, variation in host quality corresponds to variation in parental quality for vertebrates in Trivers and Willard's theory.

Experimental evidence (van den Assem 1971, Sandlan 1979) shows that parasites produce different sex ratios on different sized hosts. Charnov (1979) has shown theoretically that such results should occur if offspring quality improves with host size and that increasing host size benefits female offspring more than male. Sandlan (1979) has shown that female fitness increases with host size, but there is no evidence yet (Charnov et al. 1980) that male fitness increases less with host size than does female fitness.

Charnov (1979) constructed a genetic model for the simple case in which parasites lay eggs on fixed proportions of hosts of two different sizes. Charnov et al. (1980) have generalized this result to the case in which host sizes have a continuous distribution. The best strategy, which maximizes the product of the total fitnesses of males and females produced, is to produce males in hosts below a certain size and females in hosts above that size, if the ratio of female fitness to male fitness is a monotone increasing function of host size.

Charnov (1979) and Charnov et al. (1980) have treated the host size distribution as fixed and have assumed that the only choice a parasite has is whether to lay a fertilized or an unfertilized egg on each host. This assumption reflects the laboratory experiments that inspired the theory, but in the field parasites must search for hosts and may find some hosts that are unsuitable.

It is possible to construct a foraging model that retains the assumptions of Charnov et al. but which incorporates foraging for hosts. In such a model the best strategy will be lay fertilized eggs on the largest (best) hosts, to lay unfertilized eggs on intermediate sized hosts, and to leave the smallest potential hosts without laying any eggs on them.

For a given critical host size above which the hosts will receive eggs, the best strategy, which may be characterized by the host size that separates male and female offspring, will be that found by Charnov et al. (1980) which maximizes the product of total fitness of males and females produced. The critical host size, however, depends on the time to assess host size, the "down time" after laying an egg and, implicitly, the absolute density of hosts.

When hosts must be sought, as they must be in nature, the sex ratio that results from the optimal strategy does not simply depend on the distribution of host size, but also on host density, assessment time, and the time it takes for a parasite to prepare a new batch of eggs. The rules that determine the best strategy are similar to MacArthur's (1965) product rule for sex ratios and Charnov's (1976) "marginal value theorem" for optimal foraging.

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the case in which parasites must search for hosts, will be useful to people interested in sex ratio theory.

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