

# Anisogamy, Expenditure of Reproductive Effort, and the Optimality of Having Two Sexes

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No good formal arguments exist for a central question in biology: Why, in species that have sexual reproduction, are there usually only “males” and “females”? We present a nonlinear optimization model that supports the conclusion that having only two sexes maximizes long-run viability.

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## 1. The General Question

The precise origins of sexual reproduction itself remain unclear (Bell 1982, Michod and Levin 1988), but the potential advantages of the genetic variation produced by sexual reproduction have been noted for almost half a century (Fisher 1958, Charnov 1982). Prime among these are the advantages to individuals, subject to changing environments, of being able to produce variable offspring through mechanisms such as recombination (e.g., Williams 1966; Ghiselin 1974, 1988) so that individuals can overcome the loss of genetic representation that accompanies sex. The mechanics of sexual reproduction can vary greatly across taxa. When only nuclear genetic information is exchanged, as in slime molds, for example, there can be more than two mating types (Hoekstra 1987, Hurst and Hamilton 1992); but when information is exchanged through the production of haploid gametes, the mating types reduce to two sexes. Furthermore, the gametes are typically (Parker et al. 1972, review by Low 2000, pp. 37–44) anisogamous (i.e., of unequal size). As we note in §2, anisogamy has implications for life history and behavioral ecology.

There are several main nonalternative current hypotheses for explaining the origins of anisogamy in gametic-sex species. Parker et al. (1972) (see also Charlesworth 1978; Maynard Smith 1978, 1982; Bell 1982; Charnov 1982) noted that two antithetical processes are required to create a successful zygote: traveling to “meet” another gamete, and saving energy to become large and therefore produce a well-invested zygote. These processes generate disruptive selection on the production of a successful zygote, favoring either very small or very large gametes at the expense of middle-sized gametes. Hurst and Hamilton (1992) and

Hurst (1995, 1996) noted that because genetic information is carried in the cytoplasm as well as in the nucleus, damaging conflicts of interest can exist, and one set of gametes might become small in response, divesting themselves of cytoplasm to avoid these conflicts.

Randerson and Hurst’s (2001) recent analysis, relating zygote and gamete sizes to fertilization probabilities and other fitness measures has re-ignited interest in the evolution of anisogamy in gametic-sex species. Bulmer and Parker (2002) have explored the implications of anisogamy versus isogamy in a game-theoretic context. In this paper, we present a mathematical model that relies on concepts in Maynard Smith (1978). Our model, although quite simple, takes advantage of heretofore unutilized tools of mathematical optimization to show how the existence and degree of anisogamy depends on (among other factors) the shape of the zygote fitness function.

## 2. Background

Parker et al. (1972) performed a critical thought experiment on the evolution of anisogamy. Using a simple model, they explained why having two sexes might be a good strategy: Imagine a population of individuals something like jellyfish, floating in the ocean. Each individual reproduces by releasing gametes into the sea. An individual’s gametes then recombine with those of other individuals to make zygotes—i.e., new individuals. Because the gametes of any individual, floating about in the ocean, can combine with any other gametes, we have nothing as specialized as male and female sexes at this point.

Now imagine that each jellyfish is capable of releasing gametes of various sizes, from tiny to extremely large. The

gametes have two basic tasks that must be accomplished to create a successful zygote: (1) encounter and join with another gamete; and (2) contribute to the makeup of a sturdy, well-endowed zygote.

The smaller the gamete, the cheaper it is to produce and the more likely it is to move far in the ocean currents, thus having a relatively high chance of bumping into other gametes. The larger the gamete, however, the more protoplasm mass it can contribute, resulting in a well-endowed zygote. Analyzing this process, Parker et al. (1972) argued that because the smallest and largest gametes are favored for these two distinct tasks, over time middle-sized gametes will eventually lose out to both large and small (disruptive selection). The system thus evolves, they speculated, into one in which an individual specializes in making either large or small gametes. The argument of Parker et al. has since been expanded and elaborated by Bell (1982), Charlesworth (1978), and Maynard Smith (1978). As noted above, conflicts of interest between information carried in maternal (egg) versus paternal (sperm) cytoplasm may exacerbate the process of anisogamy, because sperm reduce cytoplasm to reduce the conflicts (Hurst and Hamilton 1992; Hurst 1995, 1996).

Of course, any subsequent changes in gamete or gamete-producer that enhance size-related advantages will be favored by natural selection. For example, if a tiny gamete is produced that is also aerodynamically superior (e.g., ovoid and with a motile tail), it will be favored. Selection will also affect behavior of the whole population: Tiny-gamete-making individuals who can travel far, facilitating finding other gametes over a larger area, will be favored. Large-gamete makers who invest less and less in other functions, and more in future offspring, will also be favored. Thus behaviors, as well as the gamete build strategy, are affected. Perhaps the rarity of hermaphroditism in animals is related to this phenomenon (e.g., Charnov 1982), for it is difficult to maximize both search and endowment capacity simultaneously.

Once there are two sexes, then, they are likely to be very different. This anisogamous pattern is so ubiquitous that, without thinking about it, we tend to call small-gamete-makers “males” and large-gamete-makers “females.” We associate sets of behavioral characteristics with each of the sexes: The risk-taking travelers are assumed to be males; the nurturers, females. Indeed, “role reversal” involving larger or more colorful or more risk-taking females is rare (see Low 2000 for a review).

Behavioral specializations into mating (seeking) investors versus parental (nurturing) investors (Low 1978, 2000) have profound consequences for behavioral differences between the sexes. Mating effort, typical of males in most species, has a large “fixed cost”: Much must be invested to get any return whatsoever. A male must grow large (if physical combat is any part of competition), range far, and perhaps grow weapons or decorations, like a moose or a peacock; he might have to fight to maintain any gains,

as well. After this great initial investment the marginal cost of additional matings is small.

For parental investors, usually females, each offspring costs approximately as much parental effort as any other. What is invested in one offspring can seldom be recycled and re-invested in another. For example, although nests can represent generalizable parental effort (re-used for several clutches), feeding is offspring-specific—what one offspring eats, another cannot. Thus, the maximum possible number of offspring is likely to be lower for females than for males.

### 3. Modeling the Distribution of Gamete Build

The basic structure and assumptions we use to construct a very simple (perhaps even simplistic) mathematical model to explain the distributions of gamete sizes (hence the development of anisogamy) are based roughly on those proposed by Parker et al. (1972), Charnov (1982), and Frank (1987). Our model is somewhat simpler, ignoring, for example, the impact of gamete mobility on reproductive success. However, even our parsimonious model demonstrates the advantages of anisogamy—a pattern likely to be reinforced by other factors. We also make use of the possible shapes of zygote survival functions presented in Randerson and Hurst (2001, Figure 1). The major difference between our analysis and previous results is our use of mathematical optimization techniques to show those conditions for which anisogamy must occur. In particular, to date, all previous explanations of allocation of resources to various gamete sizes have been heuristic and in general have ignored gamete-build distributions other than “either male or female or a mixture of both.” As will be seen, we do not assume this polar situation to be true a priori.

#### 3.1. Basic Assumptions and Definitions

1. There is a large population of individuals of a single species. Each individual has a total amount of resources  $L$  available during each reproductive cycle dedicated to the endowment of protoplasmic material to gametes.

2. If an individual makes  $n$  ( $n = K, K + 1, \dots, N$ ) gametes (we say the individual has *productivity*  $n$ ), each gamete has a “size” equal to  $L/n$ . Note that the largest possible gamete has size  $L/K$  (the number of gametes made is  $K$ ), and the smallest viable gamete has size  $L/N$  (the number of gametes made is  $N$ ).

3. The productivity of each individual in the species is a random variable independent of the productivities (and other characteristics) of the rest of the population and is equal to  $n$  with probability  $p_n$ ,  $n = K, K + 1, \dots, N$ , where  $\sum_{n=K}^N p_n = 1$ .

4. The probability vector  $\mathbf{p} \equiv [p_K, p_{K+1}, \dots, p_{N-1}, p_N]$  is called the “gamete build strategy.”

5. A zygote is formed when any two gametes meet and successfully fuse.

6. A gamete remains viable for a limited period of time after its release, and is able to meet and fuse with another

gamete only if the latter has been released (by another individual) at approximately the same time as the former. Thus, the probability that any individual will “parent” a zygote (by having one of its gametes successfully meet and fuse with another gamete) is proportional to the number of gametes it produces (the probability of parenting more than one zygote in one reproductive cycle is considered to be negligibly small by comparison). This probability is assumed to be large enough so as to sustain a steady-state stable population.

7. The size of a zygote,  $S$ , is the sum of the sizes of its two “parent” gametes. That is, if  $n$  and  $m$  are the productivities of the respective parents, the zygote size is  $S(n, m) = (L/m + L/n)$ .

8. A zygote “fitness”  $\Phi$  is defined to be a scaling constant times the probability that it will survive to an age at which it can create its own gametes. We assume that the fitness is a function of  $S$  only, hence we write it as  $\Phi(S)$ .

9. The overall fitness is defined to be the expected number of zygotes in a generation that will survive to reproduce.

10. A population of individuals that has evolved a gamete build strategy  $\bar{\mathbf{p}}$  that maximizes overall fitness will be more likely to persist and grow.

Note that as a consequence of Assumption 2, all gametes produced by a particular individual have the same size. For convenience, in what follows we will refer to gametes of the largest possible size ( $L/K$ ) as “eggs,” individuals producing egg gametes as “females,” gametes of the smallest possible size ( $L/N$ ) as “sperm,” and individuals producing sperm gametes as “males.”

### 3.2. Optimizing Species Fitness

Consider two individuals that reproduce (i.e., release gametes) at approximately the same time. Using Assumptions 6 and 7, we can conclude that the probability that they will produce a zygote from gametes of size  $L/m$  and  $L/n$ , hence having size  $S = (L/m + L/n)$ , is proportional to  $(mp_m) \cdot (np_n)$ : Each of the two factors reflects the assumption that the probability of gametes meeting and fusing is proportional to the numbers of gametes produced. Using the product follows from the assumption that the component events are independent. The probability of having a successful mating followed by a surviving zygote is thus proportional to  $mnp_m p_n$  multiplied by  $\Phi(S) = \Phi(L/m + L/n)$  (again, assuming independence).

The probability that a zygote will be formed and survives is therefore proportional to

$$F(\mathbf{p}) \equiv \sum_{m=K}^N \sum_{n=K}^N \Phi\left(\frac{L}{m} + \frac{L}{n}\right) mnp_m p_n. \tag{1}$$

The expected number of surviving zygotes in the species, i.e., the overall fitness function (see also Charlesworth 1978, Equation (3b)), is proportional to  $F(\mathbf{p})$  (the coefficient of proportionality will depend on the number of individuals in the population and the frequency and number of reproductive cycles in an individual’s lifetime).

Assumption 10 thus suggests that the gamete build strategy that results in greater success of the species can be found as a solution to the following mathematical optimization problem:

$$\text{maximize } F(\mathbf{p}) \text{ with respect to } \mathbf{p}, \tag{2}$$

$$\text{subject to } \sum_{n=K}^N p_n = 1, \quad \mathbf{p} \geq 0. \tag{3}$$

Finding  $\bar{\mathbf{p}}$ , the solution to Equations (2) and (3) is, in general, a potentially computationally hard nonlinear (and possibly nonconcave) mathematical programming problem. However, as we demonstrate in §4 and Appendix A, there is a fairly general set of conditions on the form of the function  $\Phi(S)$  that leads to an interesting and provocative result: The optimal gamete build strategy  $\bar{\mathbf{p}}$  puts nonzero probability on *at most two* points—the extremes, representing a species that contains only two kinds of individuals, those that produce the smallest or largest possible sized gametes (sperm and eggs). Moreover, when the survival function has the form  $\Phi(S) = S^a$ , then for a wide range of values of  $a$ ,  $N$ , and  $K$ , the optimum gamete build policy is to produce sperm and eggs with roughly equal probabilities, as we show in §4.

## 4. Anisogamy as an Optimal Gamete Build

Applying first-order Karush-Kuhn-Tucker optimality conditions, we can characterize the local optimal solutions of problems (2)–(3) under various assumptions on the fitness function  $\Phi(S)$  (see Appendix A for details). For example, when  $\Phi(S)$  is a strictly convex twice differentiable function of  $S$ , we obtain Proposition 1.

PROPOSITION 1. *Suppose that  $\Phi(S)$  is twice differentiable and strictly convex. For any  $\bar{\mathbf{p}}$  that is a local maximizer of (2)–(3), only  $\bar{p}_K$  or  $\bar{p}_N$ , or both, can be positive.*

PROOF. See §§A.1 and A.2.  $\square$

Proposition 1 shows a remarkable result: When  $\Phi(S)$  is a strictly convex twice differentiable function of  $S$ , the components of any optimal solution  $\bar{\mathbf{p}}$  can have nonzero values only at the two “extreme” points  $\bar{p}_K$  and  $\bar{p}_N$ . In particular, every optimal solution has the form  $\bar{\mathbf{p}} = [\bar{p}_K, 0, \dots, 0, 1 - \bar{p}_K]$ , and using the conditions of the three candidate solutions discussed in §A.2 (and where, for convenience in notation and without loss of generality we rescale resource units such that  $L = 1$ ), we have

$$\bar{p}_K = \begin{cases} 1 & \text{if } K^2\Phi(2/K) \\ & \geq \max\{N^2\Phi(2/N), KN\Phi(1/K + 1/N)\}, \\ 0 & \text{if } N^2\Phi(2/N) \\ & \geq \max\{K^2\Phi(2/K), KN\Phi(1/K + 1/N)\}, \\ p_K^* & \text{otherwise,} \end{cases} \tag{4}$$

$$\bar{p}_N = 1 - \bar{p}_K,$$

where  $p_K^*$ , given by Equation (16), can be written in terms of the function  $\Phi(\cdot)$  as

$$p_K^* = \frac{KN\Phi(1/K + 1/N) - N^2\Phi(2/N)}{2KN\Phi(1/K + 1/N) - N^2\Phi(2/N) - K^2\Phi(2/K)}. \quad (5)$$

Note that when

$$K^2\Phi\left(\frac{2}{K}\right) = N^2\Phi\left(\frac{2}{N}\right) > KN\Phi\left(\frac{1}{K} + \frac{1}{N}\right),$$

both  $\bar{p}_K = 0$  (and hence  $\bar{p}_N = 1$ ) and  $\bar{p}_K = 1$  are global maximizers, and when

$$K^2\Phi\left(\frac{2}{K}\right) = N^2\Phi\left(\frac{2}{N}\right) = KN\Phi\left(\frac{1}{K} + \frac{1}{N}\right),$$

any vector  $\bar{\mathbf{p}} = [p_K, 0, \dots, 0, 1 - p_K]$  is a global maximizer.

To perform a more detailed analysis, consider the case when the zygote fitness function follows the power law

$$\Phi(S) = S^a. \quad (6)$$

Although we make no particular claims for this simple functional form, it is qualitatively similar to the first portion of the sigmoid shaped zygote fitness function  $s_2$  posited in Randerson and Hurst (2001), for example.

Define  $r \equiv N/K > 1$  to be the ratio of the maximum productivity to the minimum productivity (so that  $r$  is also the ratio of the minimum gamete size to the maximum gamete size). The following proposition shows that the solution  $\bar{\mathbf{p}}$  to problems (2)–(3) depends strongly on the relationship between  $a$  and  $r$  but always maintains the form  $\bar{\mathbf{p}} = [p_K, 0, \dots, 0, 1 - p_K]$ . Note that in this case, Equation (5) reduces to

$$p_K^* = \frac{(1+r)^a - 2^a r}{2(1+r)^a - 2^a r^{a-1} - 2^a r}. \quad (7)$$

PROPOSITION 2. Suppose that  $\Phi(S) = S^a$ ,  $a > 0$ , and let  $r = N/K$ . Then,

Case P1. If

$$0 < a \leq \frac{\ln r}{\ln((1+r)/2)},$$

then  $\bar{p}_N = 1$  is the unique optimal solution.

Case P2. If

$$\frac{\ln r}{\ln(2r/(1+r))} \leq a,$$

then  $\bar{p}_K = 1$  is the unique optimal solution.

Case P3. If

$$\frac{\ln r}{\ln((1+r)/2)} < a < \frac{\ln r}{\ln(2r/(1+r))},$$

then  $\bar{\mathbf{p}} = [p_K^*, 0, \dots, 0, 1 - p_K^*]$  is the unique optimal solution, with  $p_K^*$  given by (7).

PROOF. See §A.3. □

The results obtained in Proposition 2 are suggestive of the more general conclusions hinted at in Parker et al. (1972):

1. If

$$0 < a \leq \frac{\ln r}{\ln((1+r)/2)}$$

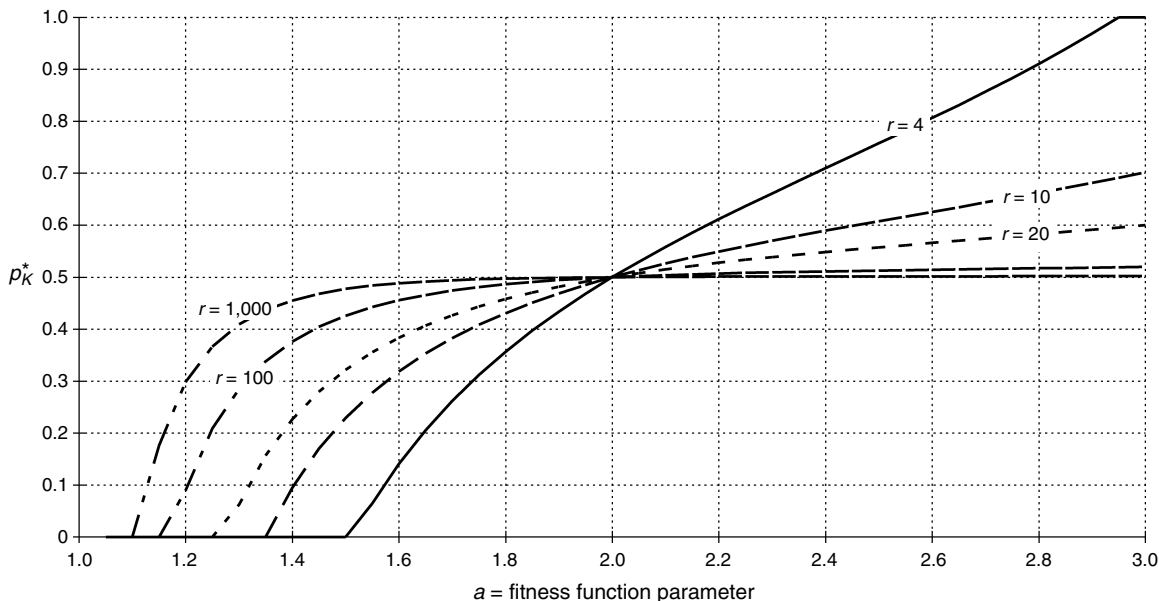
(Case P1), then  $\bar{p}_N = 1$ . Each individual produces essentially all sperm; thus having all males in the population is optimal. This has intuitive appeal because the decreasing returns to scale on gamete size has to be compensated for by an increased number of sperm.

2. If

$$\frac{\ln r}{\ln((1+r)/2)} < a \leq 2$$

(included in Case P3), then  $\bar{p}_K = p_K^* \leq 0.5$ . There are more sperm-producing individuals (males) than egg-producing individuals (females). When  $r$  is large, as shown in Figure 1,

Figure 1.  $p_K^*$  as a function of  $a$  for various values of  $r$ .



$\bar{p}_K = p_K^*$  is close to (but less than) 0.5, leading to roughly an equal number of males and females for a wide range of values of  $a \leq 2$ .

3. If

$$2 \leq a < \frac{\ln r}{\ln(2r/(1+r))}$$

(included in Case P3), then  $\bar{p}_K = p_K^* \geq 0.5$ . There are more females than males. As shown in Figure 1, when  $r$  is large,  $\bar{p}_K = p_K^*$  is close to (but greater than) 0.5, leading to roughly an equal number of males and females for a wide range of values of  $a \geq 2$ .

4. For

$$a \geq \frac{\ln r}{\ln(2r/(1+r))}$$

(Case P2),  $\bar{p}_K = 1$ . Having essentially all females is optimal.

### 5. Successful Egg-Sperm Matings

Along with the baseline ratios of the two sexes implied by the form of  $p_K^*$ , it is also of interest to find the fraction of successful matings that are “conventional,” i.e., due to egg-sperm interactions. This can be readily computed by noting that the  $(m = K, n = N)$  and  $(m = N, n = K)$  terms in the right-hand side of Equation (1) represent the proportional contribution of these matings to  $F$ . Thus, we can write

$$p_{es} \equiv \text{prob}\{\text{egg-sperm mating}\} = \frac{2p_K(1 - p_K)KN\Phi(1/K + 1/N)}{F(\mathbf{p})}, \tag{8}$$

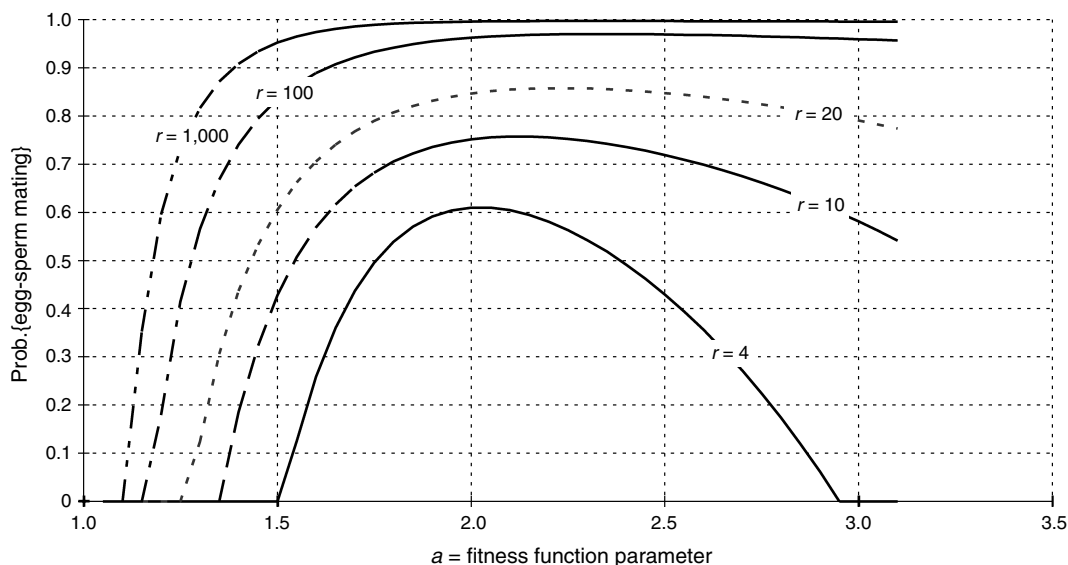
and evaluate this at  $p_K = \bar{p}_K$  and  $F = F(\bar{\mathbf{p}})$ . Figure 2 shows  $p_{es}$  as a function of  $a$  for various values of  $r$ , with  $K$  arbitrarily set equal to 1. We see that  $p_{es}$  is essentially unity when  $r$  is larger than 1,000 and  $a$  is larger than about 1.5. However, for smaller values of  $r$  there is a value of  $a$  such that  $p_{es}$  is maximized.

### 6. Discussion

In this paper, we provided a rigorous mathematical justification for the optimality of anisogamy in species with zygote survival functions that are convex, or follow a power law—a result that has been previously obtained heuristically or empirically. It is worth pointing out that certain assumptions we specify in §3 are somewhat different from those made in the analyses that motivated the present work. For example, our assumptions about gametes meeting and fusing differ from those of Parker et al. (1972) or Charlesworth (1978), which stipulate that meetings occur randomly in a pool of gametes released by individuals of the same generation. We also assumed that individuals select their productivities at random, rather than inherit them.

However, the results obtained in this paper are remarkably robust with respect to the reproductive model used. It is interesting to compare the optimal solution to the fitness maximization problem, given by (4) for the convex zygote fitness function, with results obtained by Charlesworth (1978) for the haploid model. Charlesworth considered the stability of gamete built strategies, under the assumption that an individual’s productivity is inherited from either of its parents, and characterized this stability by mathematical conditions. It can be shown that these conditions are, in fact, a relaxation of the Karush-Kuhn-Tucker (KKT) conditions in Appendix A. Following an argument quite similar to the proof of Proposition 1, we can demonstrate, for example, that if the zygote fitness function is convex, any stable gamete build strategy will have nonzero values corresponding to at most two different productivities. The fractions of individuals with each of the two productivities obtained by Charlesworth for the power function are similar to (7). Our results demonstrate that by picking a combination of the “most different” gametes, the species

**Figure 2.** Probability of egg-sperm mating as a function of parameter  $a$  and for various values of  $r$ .



not only exhibits a stable gamete build strategy but the one that maximizes the fitness as well.

Although any particular species might not in fact exhibit a convex zygote fitness function, the resulting optimal gamete build strategy given by Equation (4)—a mixture of only males and females—should be of more than passing interest to biologists. Moreover, for more general functional forms of  $\Phi(S)$ , the results of Appendix A show that a variety of optimal gamete build distributions can result. However, solving the associated nonconvex quadratic program presents such a potentially difficult computational challenge that it would be worthwhile to pursue only if a specific (perhaps empirical) form of  $\Phi(S)$  is available. We await the cooperation of our colleagues in the biological sciences to provide us with such information, and we look forward to perhaps verifying that multiple interior optima exist for some species.

## Appendix A. Analysis of Optimal Solutions of the Fitness Maximization Problem

### A.1. Necessary Conditions for Optimality

For convenience, we will represent the function  $F(\mathbf{p})$  of Equation (2) by

$$F(\mathbf{p}) = \sum_{m=K}^N \sum_{n=K}^N Q_{mn} p_m p_n, \quad (9)$$

where the matrix  $Q$  is defined to be

$$Q_{mn} = \Phi\left(\frac{1}{m} + \frac{1}{n}\right) mn,$$

for fitness function  $\{\Phi: [2/N, 2/K] \rightarrow \Re\}$ .

In (2)–(3) we are asked to maximize  $F(\mathbf{p})$  over a simplex. Provided that the function is differentiable, the following are necessary conditions for a vector  $\bar{\mathbf{p}}$  to be a local optimum (see, for example, Bertsekas 1999, Example 2.1.2):

$$\bar{p}_n > 0 \Rightarrow \left. \frac{\partial F(\mathbf{p})}{\partial p_n} \right|_{\mathbf{p}=\bar{\mathbf{p}}} \geq \left. \frac{\partial F(\mathbf{p})}{\partial p_m} \right|_{\mathbf{p}=\bar{\mathbf{p}}} \quad \forall m. \quad (10)$$

That is, for all components of  $\bar{\mathbf{p}}$  that are positive, the partial derivatives of the objective function with respect to these components are maximal and equal. (These conditions are equivalent to the usual first-order Karush-Kuhn-Tucker (KKT) necessary optimality conditions.) Exploiting the particular form of  $F(\cdot)$  given in Equation (9) gives

$$\left. \frac{\partial F(\mathbf{p})}{\partial p_n} \right|_{\mathbf{p}=\bar{\mathbf{p}}} = \sum_{i=K}^N Q_{in} \bar{p}_i = \sum_{i=K}^N in \Phi\left(\frac{1}{i} + \frac{1}{n}\right) \bar{p}_i, \quad (11)$$

so that Equation (10) can be rewritten as

$$\bar{p}_n > 0 \Rightarrow \sum_{i=K}^N Q_{in} \bar{p}_i \geq \sum_{i=K}^N Q_{im} \bar{p}_i \quad \forall m. \quad (12)$$

### A.2. Proof of Proposition 1 and Further Analysis for the Convex Zygote Fitness Function

We begin with the proof of Proposition 1 in §4.

PROOF OF PROPOSITION 1. Suppose that  $\Phi(S)$  is twice differentiable and strictly convex. Let  $\bar{\mathbf{p}}$  be a local maximizer of (2)–(3), so that it satisfies (12). Consider the collection of continuous functions

$$f_m(t) = \Phi\left(\frac{1}{t} + \frac{1}{m}\right) mt, \quad m=K, \dots, N, \quad t \in [K, N]. \quad (13)$$

Because

$$f_m''(t) = \frac{m}{t^3} \Phi''\left(\frac{1}{t} + \frac{1}{m}\right) > 0,$$

each of the  $N - K + 1$  functions in Equation (13) is strictly convex on its domain  $[K, N]$ . Now let

$$f(t) = \sum_{m=K}^N \bar{p}_m f_m(t), \quad t \in [K, N]. \quad (14)$$

Because  $f(t)$  is a convex combination of strictly convex functions, it itself is strictly convex, and therefore its maximum can occur only at one of the endpoints of its domain (or both endpoints, if  $f(K) = f(N)$ ).

Finally, consider the values of  $f(t)$  at integer values of  $t \in [K, N]$ . Combining Equations (9), (11), and (13) we have

$$f(n) = \left. \frac{\partial F(\mathbf{p})}{\partial p_n} \right|_{\mathbf{p}=\bar{\mathbf{p}}}.$$

Hence, the maximal partial derivative of the objective function (2) is with respect to either  $\bar{p}_K$  or  $\bar{p}_N$  (or both, if they happen to coincide). Applying the necessary conditions (10), the conclusion of the proposition follows.  $\square$

Using Proposition 1, we need only to consider at most three solutions to be candidates for local optimal solutions of (2)–(3) when  $\Phi(S)$  is strictly convex.

SOLUTION 1.  $\bar{p}_K = 1$  (so that  $\bar{p}_i = 0$ ,  $i \neq K$ ). By Equation (12), this is a candidate to be an optimum only if  $Q_{KK} \geq Q_{KN}$  or, equivalently,  $K\Phi(2/K) \geq N\Phi(1/K + 1/N)$ .

SOLUTION 2.  $\bar{p}_N = 1$  (so that  $\bar{p}_i = 0$ ,  $i \neq N$ ). By Equation (12), this is a candidate to be an optimum only if  $Q_{NN} \geq Q_{KN}$  or, equivalently,  $N\Phi(2/N) \geq K\Phi(1/K + 1/N)$ .

SOLUTION 3.  $\bar{p}_K > 0$ ,  $\bar{p}_N = 1 - \bar{p}_K > 0$  (and  $\bar{p}_i = 0$ ,  $i \neq K, N$ ). By Equation (12), this is a candidate to be an optimum only if a value of  $\bar{p}_K$  can be chosen so that

$$Q_{KK} \bar{p}_K + Q_{KN} (1 - \bar{p}_K) = Q_{KN} \bar{p}_K + Q_{NN} (1 - \bar{p}_K), \quad 0 < \bar{p}_K < 1. \quad (15)$$

Suppose that neither solution 1 nor 2 is a candidate for optimality because  $Q_{KN} > Q_{KK}$  and  $Q_{KN} > Q_{NN}$ . Then, the value of  $\bar{p}_K$  obtained by solving Equation (15) is

$$\bar{p}_K = p_K^* \equiv \frac{Q_{KN} - Q_{NN}}{2Q_{KN} - Q_{KK} - Q_{NN}} \in (0, 1), \quad (16)$$

and solution 3 is the unique local (hence unique global) solution.

**A.3. Proof of Proposition 2: Zygote Fitness Is a Power Function**

PROOF OF PROPOSITION 2. Suppose that fitness is represented by the power function  $\Phi(S) = S^a$ ,  $a > 0$ , and  $r = N/K > 1$ . We now show that the solution to problems (2)–(3) depends strongly on the relationship between  $a$  and  $r$ . In particular, we consider three cases.

Case P1.

$$0 < a \leq \frac{\ln r}{\ln((1+r)/2)}.$$

Because

$$1 < \frac{\ln r}{\ln((1+r)/2)},$$

the condition  $a \leq 1$  is included in this case. Therefore,  $\Phi(S)$  is not necessarily strictly convex, and Proposition 1 might not be applicable. However, if we can show that  $Q_{mn} \leq Q_{NN}$  for  $m$  and  $n$  such that  $m \leq n$  and  $m < N$ , then  $\bar{p}_N = 1$  is obviously an optimal solution (because by Equation (9) the value of  $F(\mathbf{p})$  is simply a convex combination of components of  $Q$ ). Indeed, for this case it is the unique optimal solution.

If the right-hand side of the case’s condition is strict, i.e.,

$$a < \frac{\ln r}{\ln((1+r)/2)},$$

then we show that  $Q_{mn} < Q_{NN}$  for  $m \leq n$  and  $m < N$  as follows. Let  $m < n \leq N$ , and define  $\rho = n/m$ . Because  $\rho \leq r$ , we have

$$a < \frac{\ln r}{\ln((1+r)/2)} \leq \frac{\ln \rho}{\ln((1+\rho)/2)}. \tag{17}$$

Using Inequality (17), along with the fact that  $Q_{mn} = mn \cdot (1/m + 1/n)^a$ , straightforward algebra verifies that  $Q_{mn} < Q_{nn}$ . Finally, for  $n < N$ ,  $Q_{nn} < Q_{NN}$  when  $n^{2-a} < N^{2-a}$ , which is true in this case because

$$a \leq \frac{\ln r}{\ln((1+r)/2)} < 2.$$

Thus,  $Q_{mn} < Q_{NN}$  for  $m \leq n$ ,  $m < N$ ; hence  $\bar{p}_N = 1$  is the unique optimum.

If

$$1 < a = \frac{\ln r}{\ln((1+r)/2)},$$

then  $\Phi(S)$  is strictly convex, and Proposition 1 applies. Note that in this case  $Q_{KK} < Q_{KN} = Q_{NN}$ , so that  $\bar{p}_N = 1$  is the unique optimum.

Case P2.

$$\frac{\ln r}{\ln(2r/(1+r))} \leq a.$$

In this case, because

$$1 < \frac{\ln r}{\ln(2r/(1+r))} \leq a,$$

$\Phi(S)$  is strictly convex, so Proposition 1 applies. Because  $Q_{NN} < Q_{KN} \leq Q_{KK}$ ,  $\bar{p}_K = 1$  is the unique optimum.

Case P3.

$$\frac{\ln r}{\ln((1+r)/2)} < a < \frac{\ln r}{\ln(2r/(1+r))}.$$

In this case, Proposition 1 applies. Moreover, straightforward algebra shows that  $Q_{KK} < Q_{KN}$  and  $Q_{NN} < Q_{KN}$ . Hence,

$$\bar{\mathbf{p}} = [p_K^*, 0, \dots, 0, 1 - p_K^*] \tag{18}$$

is the unique local and global optimal solution, where the value of  $p_K^*$  is given by Equation (16) and satisfies  $0 < p_K^* < 1$ .

**A.4. Additional Results: Zygote Fitness Function  $\Phi(S)$  Is Concave**

The function  $f(t)$  defined in Equation (14) is concave whenever  $\Phi(S)$  is concave. Hence, its maximum (without additional assumptions) typically occurs in the interior of its domain. This can potentially lead to many KKT points, each having positive “middle” component(s) of  $\bar{\mathbf{p}}$ .

However, we can find additional conditions that would be sufficient to ensure that  $\bar{p}_N = 1$  is a candidate to be a local optimum. For this to hold, it is necessary to have  $Q_{mN} \leq Q_{NN}$  for all  $m = K, \dots, N$  (see (12)). In other words,

$$\Phi\left(\frac{1}{m} + \frac{1}{N}\right) \leq \frac{N}{m} \Phi\left(\frac{2}{N}\right) \quad \forall m.$$

PROPOSITION 3. If  $\Phi(\cdot)$  is a differentiable concave function, and if

$$\Phi'\left(\frac{2}{N}\right) \leq N\Phi\left(\frac{2}{N}\right), \tag{19}$$

then (a)  $\bar{p}_N = 1$  is a KKT point; moreover, (b)  $\bar{p}_N = 1$  is the optimal solution of a restricted problem in which only  $\bar{p}_K$  and  $\bar{p}_N$  are allowed to be positive.

PROOF. The gradient inequality for a differentiable function  $\Phi(x)$  concave in  $x$  implies that

$$\Phi(x) \leq \Phi(y) + \Phi'(y)(x - y) \quad \forall x, y \in [2/N, 2/K]. \tag{20}$$

In particular, letting  $x = 1/m + 1/N$  and  $y = 2/N$ , and using Inequality (19), gives

$$\begin{aligned} \Phi\left(\frac{1}{m} + \frac{1}{N}\right) &\leq \Phi\left(\frac{2}{N}\right) + \Phi'\left(\frac{2}{N}\right)\left(\frac{1}{m} - \frac{1}{N}\right) \\ &\leq \Phi\left(\frac{2}{N}\right) + N\Phi\left(\frac{2}{N}\right)\left(\frac{1}{m} - \frac{1}{N}\right) = \frac{N}{m}\Phi\left(\frac{2}{N}\right), \end{aligned}$$

which establishes the first claim of Proposition 3—that  $\bar{p}_N = 1$  is a KKT point.

To prove the second claim of Proposition 3, letting  $x = 2/K$  and  $y = 2/N$  in Equation (20) and using Inequality (19), gives

$$\begin{aligned} \Phi\left(\frac{2}{K}\right) &\leq \Phi\left(\frac{2}{N}\right) + \Phi'\left(\frac{2}{N}\right)\left(\frac{2}{K} - \frac{2}{N}\right) \\ &\leq \Phi\left(\frac{2}{N}\right)\left(1 + N\left(\frac{2}{K} - \frac{2}{N}\right)\right) < \frac{N^2}{K^2}\Phi\left(\frac{2}{N}\right), \end{aligned}$$

so that  $Q_{KK} < Q_{NN}$ . Because it is readily shown that  $Q_{KN} \leq Q_{NN}$ ,  $\bar{p}_N = 1$  is the optimal solution of the “restricted” problem discussed in the proposition.  $\square$

Note that when  $Q_{mN} < Q_{NN}$  for all  $m < N$ , it can be shown that  $\bar{p}_N = 1$  is a strict local optimum. Strengthening the assumption of Proposition 3 to

$$\Phi'\left(\frac{2}{N}\right) < N\Phi\left(\frac{2}{N}\right)$$

is sufficient to ensure this. This is a direct consequence of Bazaraa et al. (1993, Theorem 4.4.2).

PROPOSITION 4. If  $\Phi(x)$  is a differentiable concave function, and if

$$\Phi'(x) \leq \frac{2}{x}\Phi(x), \quad x \in \left[\frac{2}{N}, \frac{2}{K}\right], \quad (21)$$

then  $\bar{p}_N = 1$  is a global optimum.

PROOF. It is sufficient to show that  $Q_{mn} \leq Q_{NN}$  for all  $m$  and  $n$ . Let  $m$  and  $n$  be arbitrary with  $m \leq n$ . Setting  $y = 2/n$  and  $x = 1/m + 1/n$  in Inequality (20), and  $x = 2/n$  in Inequality (21), gives

$$\begin{aligned} \Phi\left(\frac{1}{m} + \frac{1}{n}\right) &\leq \Phi\left(\frac{2}{n}\right) + \Phi'\left(\frac{2}{n}\right)\left(\frac{1}{m} - \frac{1}{n}\right) \\ &\leq \Phi\left(\frac{2}{n}\right) + n\Phi\left(\frac{2}{n}\right)\left(\frac{1}{m} - \frac{1}{n}\right) = \frac{n}{m}\Phi\left(\frac{2}{n}\right), \end{aligned}$$

hence  $Q_{mn} \leq Q_{nn}$ . Additionally, for arbitrary  $n$ , letting  $x = 2/n$  and  $y = 2/N$  in Equation (20), gives

$$\begin{aligned} \Phi\left(\frac{2}{n}\right) &\leq \Phi\left(\frac{2}{N}\right) + \Phi'\left(\frac{2}{N}\right)\left(\frac{2}{n} - \frac{2}{N}\right) \\ &\leq \Phi\left(\frac{2}{N}\right)\left(1 + N\left(\frac{2}{n} - \frac{2}{N}\right)\right) \leq \frac{N^2}{n^2}\Phi\left(\frac{2}{N}\right), \end{aligned}$$

hence  $Q_{nn} \leq Q_{NN}$ , and  $\bar{p}_N = 1$  is an optimal solution.  $\square$

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