

Sex ratio, sex change, and natural selection

(population genetics/sequential hermaphrodites/gonochores)

EGBERT G. LEIGH, JR.*, ERIC L. CHARNOV†, AND ROBERT R. WARNER*‡

*Smithsonian Tropical Research Institute, Box 2072, Balboa, Canal Zone; and †Department of Biology, University of Utah, Salt Lake City, Utah 84112

Communicated by James F. Crow, July 29, 1976

ABSTRACT We describe the analogy between the theory of natural selection on sex ratio in newborn gonochores (which will not change sex), and on the age of sex change in sequential hermaphrodites (which are all born into one sex and change to the other later on). We also discuss the conditions under which natural selection favors sequential hermaphrodites over gonochores and vice versa. We show that, in a nearly stable population of nearly constant age composition, selection favors a rare mutant if it increases the prospective reproduction of its newborn bearers that are (or while they are) members of one sex by a percentage exceeding the percentage loss to the other sex.

Ghiselin (1) suggested that when fertility increases more rapidly with age in one sex than in the other, then individuals should be born into the sex where the penalty of youth is less, where fertility increases less rapidly with age, and change later to the sex where age is more advantageous. Simulations (2) and elementary theory (3) suggested plausible conditions where natural selection would favor a sex-changing or "sequentially hermaphroditic" genotype over a gonochore genotype whose bearers stay the same sex all their lives. The bluehead wrasses of Caribbean reefs satisfy these conditions for sex change, and they are normally born female, turning male when they are becoming large enough to hold reproductive territories and attract females in their own right (3). Here, we will try to establish more generally when selection favors sexchangers over gonochores and vice versa.

That enquiry led us to a very striking analogy that we shall also report, between the theory of the proper age for a sequential hermaphrodite to change its sex and the proper ratio of male to female births in a gonochore population, an analogy which made sex ratio theory much clearer to us.

Our theory presupposes nearly static populations of nearly stable age composition, but permits fertility and death rate to vary arbitrarily with age and sex. In this way, the theory generalizes our earlier efforts (3).

A bestiary of methods: Sex ratio theory revisited

To illustrate the methods of this paper, we review the proof that if a male birth costs its parents the same as a female's, selection favors an allele whose carriers bear equal numbers of each sex. We will show in detail how to decide which of two alternative alleles is favored over the other, and how to find the optimum sex ratio. This calculation serves as prototype for all our others.

Consider a locus with two alleles, *A* and *B*, in a population of sexual haploids. Let $N_{Am}(t)$, $N_{Af}(t)$, $N_{Bm}(t)$, and $N_{Bf}(t)$ be the numbers, respectively, of *A* males, *A* females, *B* males, and *B* females at time *t*. Let the offspring of matings between *A* and *A* be all *A*-bearers, born in the ratio of $1 + k$ females to $1 - k$ males; let half the offspring of matings between *A* and *B* be *A*-bearers, born in the ratio of $1 + k$ females to $1 - k$ males, and

half be *B*-bearers, born in the ratio of $1 + k + \Delta k$ females to $1 - k - \Delta k$ males; and let the offspring of matings between *B* and *B* be all *B*-bearers, born in the ratio of $1 + k + \Delta k$ females to $1 - k - \Delta k$ males. In the language of Spieth (4), ours is a constant total expenditure model. Notice that we have assumed sex ratio among newborns is governed by the genes of those newborns: most models assume, as Fisher (5) implied, that the genes of the parents govern the sex ratio of the offspring. Suppose also that the death rate per head of males and females of age *x* is $d_m(x)$ and $d_f(x)$, respectively, regardless of genotype, while the fertility of males and females aged *x* are proportional, respectively, to $b_m(x)$ and $b_f(x)$. b_m and b_f are defined only up to a constant factor: strictly speaking, the ratio of the fertility of *x*- to *y*-year-old males is $b_m(x)/b_m(y)$, and similarly for females.

We shall assume that the population consists almost entirely of *A*-bearers, whose age composition is static and whose numbers do not change with time, while the *B*-bearers are rare enough to have a constant logarithmic growth rate yet common enough to have attained a stable age distribution. Then the logarithmic growth rate *s* of the number of *B*-bearers represents the selective advantage of *B* over *A*.

Since *A*-bearers are so common that they mate essentially only with each other, we may write

$$0 = dN_{Am}/dt = -d_{Am}N_{Am} + \frac{1}{2}B_A(1 - k), \quad [1]$$

where d_{Am} is the average per capita death rate among *A* males (because the age composition of the population is constant, this and other such averages are constant too) and B_A is the total number of *A* organisms born per unit time, of which a fraction $\frac{1}{2}(1 - k)$ are male. The number of *A* males aged *x* in the population is the number of *A* males born *x* years ago times the proportion $L_m(x)$ of males surviving to age *x*; since the total birth rate $\frac{1}{2}B_A(1 - k)$ is constant from year to year, the number of *A* males aged *x* is proportional to $L_m(x)$. thus, we may set

$$d_{Am} = \int_0^\infty d_m(x)L_m(x)dx / \int_0^\infty L_m(x)dx. \quad [2]$$

We may express the number of *A* organisms born per unit time as $rV_{Am}N_{Am}V_{Af}N_{Af}$, where

$$V_{Am} = \int_0^\infty b_m(x)L_m(x)dx / \int_0^\infty L_m(x)dx \quad [3]$$

and V_{Af} , defined similarly, measure the average fertility of *A* males and *A* females, $L_f(x)$ is the proportion of females surviving to age *x*, and *r* is a scaling factor which makes $rV_{Am}N_{Am}V_{Af}N_{Af} = B_A$. *r* is necessary because the *b*'s, and hence the *V*'s, are defined in a purely relative manner: only the ratios V_{Am}/V_{Bm} and V_{Af}/V_{Bf} have empirical meaning. We may accordingly write, for the *A*-bearers,

$$0 = dN_{Am}/dt = -d_{Am}N_{Am} + \frac{1}{2}r(1 - k)V_{Am}N_{Am}V_{Af}N_{Af}, \quad [4]$$

‡ Present address: Department of Biological Sciences, University of California, Santa Barbara, Calif. 93106.

$$0 = dN_{Af}/dt = -d_{Af}N_{Af} + \frac{1}{2}r(1+k)V_{Am}N_{Am}V_{Af}N_{Af}. \quad [5]$$

Since B is so rare, matings between B and B contribute negligibly to B 's numbers. Nearly all B are born from matings between A and B , half the offspring of which are B . Since B is in logarithmic phase,

$$dN_{Bm}/dt = sN_{Bm} = -d_{Bm}N_{Bm} + \frac{1}{4}r(1-k) - \Delta k)(V_{Am}N_{Am}V_{Bf}N_{Bf} + V_{Bm}N_{Bm}V_{Af}N_{Af}), \quad [6]$$

$$dN_{Bf}/dt = sN_{Bf} = -d_{Bf}N_{Bf} + \frac{1}{4}r(1+k) + \Delta k)(V_{Am}N_{Am}V_{Bf}N_{Bf} + V_{Bm}N_{Bm}V_{Af}N_{Af}). \quad [7]$$

Since the chances of death are the same for all males the same age, whatever their genotype, d_{Bm} differs from d_{Am} only through differences in the age composition of A and B males. These age compositions are different: only e^{-sx} times as many B were born x years ago as now, so the relative number of B males aged x is $e^{-sx}L_m(x)$. Thus,

$$d_{Bm} = \int_0^\infty d_m(x)e^{-sx}L_m(x)dx / \int_0^\infty e^{-sx}L_m(x)dx, \quad [8]$$

$$V_{Bm} = \int_0^\infty b_m(x)e^{-sx}L_m(x)dx / \int_0^\infty e^{-sx}L_m(x)dx. \quad [9]$$

Notice that Eqs. 4 and 5 imply $V_{Am}V_{Af}N_{Af} = 2d_{Am}/r(1-k)$ and $V_{Af}V_{Am}N_{Am} = 2d_{Af}/r(1+k)$, respectively, and that 6 and 7 imply

$$\begin{aligned} N_{Bm}(d_{Bm} + s)/(1-k-\Delta k) \\ = N_{Bf}(d_{Bf} + s)/(1+k+\Delta k) \\ = \frac{1}{4}r(V_{Am}N_{Am}V_{Bf}N_{Bf} + V_{Af}N_{Af}V_{Bm}N_{Bm}), \quad [10] \end{aligned}$$

$$N_{Bf} = (d_{Bm} + s)(1+k+\Delta k)/(d_{Bf} + s)(1-k-\Delta k). \quad [11]$$

Using Eqs. 4 and 5 to clear N_{Af} and N_{Am} from 6, expressing N_{Bf} in terms of N_{Bm} , and dividing through by N_{Bm} , we find

$$\begin{aligned} d \log N_{Bm}/dt = s = \\ -d_{Bm} + (1/2) \left\{ \left[\frac{1+k+\Delta k}{1+k} \right] \left[\frac{d_{Af}(d_{Bm} + s)V_{Bf}}{(d_{Bf} + s)V_{Af}} \right] \right. \\ \left. + d_{Am} \left[\frac{(1-k-\Delta k)V_{Bm}}{(1-k)V_{Am}} \right] \right\}. \quad [12] \end{aligned}$$

Eq. 12 can in theory be solved for s by successive approximations. Find a first approximation to s by evaluating the right-hand side of 12 for $s = 0$ (which makes $d_{Am} = d_{Bm}$, $d_{Af} = d_{Bf}$, $V_{Am} = V_{Bm}$, etc.). Then plug this first approximation to s into the right-hand side of 12 to get a second approximation, and continue in this wise until successive approximations differ insensibly. Notice that the first approximation to s predicts the direction of selection: that is to say, if $d \log N_{Bm}/dt > 0$ when we set $s = 0$ on the right-hand of 12, then B is favored over A .

In this instance, B is favored if

$$\begin{aligned} (d_{Bm}/2) \left\{ \left[\frac{1+k+\Delta k}{1+k} - 1 \right] \right. \\ \left. + \left[\frac{1-k-\Delta k}{1-k} - 1 \right] \right\} > 0. \quad [13] \end{aligned}$$

In words, B is favored if the percentage gain it confers on its bearers' female offspring exceeds the percentage loss to its males. Notice that if Δk is small,

$$\begin{aligned} \frac{1+k+\Delta k}{1+k} - 1 &\approx \Delta k \frac{d}{dk} \log(1+k), \\ \frac{1-k-\Delta k}{1-k} - 1 &\approx \Delta k \frac{d}{dk} \log(1-k). \quad [14] \end{aligned}$$

Since $d_{Bm} > 0$ and $\log(1+k) + \log(1-k) = \log(1-k^2)$, B is favored over A if $\Delta k(d \log(1-k^2)/dk) > 0$, that is to say, if $\log[1 - (k + \Delta k)^2]$ exceeds $\log(1-k^2)$.

The optimum sex ratio for newborns is that for which $\log(1-k^2)$ is maximum, which occurs when males and females are born in equal numbers. In other words, selection favors a mutant allele if the product of the numbers of males and females born per capita is always higher for the mutants than for their wild-type contemporaries (for any one moment in time this product increases with $1-k^2$). However, this substitution need not permanently increase the product of the numbers of males and females born per unit time, just as the selective substitution of one allele for another need not permanently increase population size or growth rate.

Assuming haploidy makes no difference: the results apply also to diploids, so long as the sex ratio in heterozygotes lies between those of the two homozygotes. If we let A represent the common homozygote AA , and B represent the mutant heterozygote AB , then the conditions for AB 's increase when rare are the same as those for B 's increase in the haploid theory. This is because $AB \times AA$ matings produce half AB offspring, just as $A \times B$ matings produce half B offspring. It is only these matings which we need to consider when the mutant is rare (i.e., for the equilibrium).

The proper age to change one's sex

Consider a single locus with two alleles, A and B , in a population of sequentially hermaphrodite sexual haploids. Suppose all individuals are born female, and that A -bearers turn male at age T while B -bearers turn male at age $T + \Delta T$. In some populations, of course, individuals are born male and turn female, in which case one exchanges the subscripts m and f in the mathematics. When is B favored over A ?

Assume that the population is composed almost entirely of A -bearers, whose numbers are static: A 's arise, then, almost exclusively from matings of A with A . The number of A born (which are all female) just balances the number of A females dying plus the number of A females turning male. In symbols,

$$0 = dN_{Af}/dt = -d_{Af}N_{Af} + B_A(t) - L_f(T)B_A(t-T), \quad [15]$$

where d_{Af} is the average death rate per head of A females, $B_A(t)$ is the total number of A born per unit time at time t , and $L_f(T)B_A(t-T)$ is the total number of A females turning male at time t , which is the number $B_A(t-T)$ born T time units earlier times the proportion $L_f(T)$ surviving to the age T of sex change.

As the number of A 's is unchanging, B_A is independent of time, and the relative number of A females aged x is accordingly measured by the proportion $L_f(x)$ that survive to age x . Thus,

$$d_{Af} = \int_0^T d_f(x)L_f(x)dx / \int_0^T L_f(x)dx. \quad [16]$$

B_A may be expressed as $rV_{Am}N_{Am}V_{Af}N_{Af}$, where V_{Am} and V_{Af} are the average fertilities per head of A males and females, as before. In particular,

$$V_{Af} = \int_0^T b_f(x)L_f(x)dx / \int_0^T L_f(x)dx. \quad [17]$$

If the proportion of a putative cohort of individuals born male that would survive to age x is $L_m(x)$, and if the death rate for males aged x is independent of how long ago they changed sex, then the proportion of A newborns surviving to the age $x > T$

is $L_m(x)L_f(T)/L_m(T)$. $L_m(x)$ is the relative number of males aged x , so

$$V_{Am} = \int_T^\infty b_m(x)L_m(x)dx / \int_T^\infty L_m(x)dx. \quad [18]$$

In summary, the number of A females obeys the equation

$$0 = dN_{Af}/dt = -d_{Af}N_{Af} + r[1 - L_f(T)]V_{Am}N_{Am}V_{Af}N_{Af}. \quad [19]$$

Since A males can only be "born" by transforming from A females,

$$0 = dN_{Am}/dt = -d_{Am}N_{Am} + rL_f(t)V_{Am}N_{Am}V_{Af}N_{Af}. \quad [20]$$

Now assume that B is so rare that its bearers are still in "logarithmic phase," yet common enough to have attained a stable age distribution. Then matings between B and B will be too infrequent to matter; B can only be born from matings between A and B. Remembering that only half the offspring of these matings are B, we write

$$dN_{Bf}/dt = sN_{Bf} = -d_{Bf}N_{Bf} + \frac{1}{2}r[V_{Am}N_{Am}V_{Bf}N_{Bf}(t) + V_{Af}N_{Af}V_{Bm}N_{Bm}(t)] - \frac{1}{2}rL_f(T + \Delta T)[V_{Am}N_{Am}V_{Bf}N_{Bf}(t - T - \Delta T) + V_{Af}N_{Af}V_{Bm}N_{Bm}(t - T - \Delta T)], \quad [21]$$

where s is again the selective advantage of B over A;

$$d_{Bf} = \int_0^{T+\Delta T} d_f(x)L_f(x)e^{-sx}dx / \int_0^{T+\Delta T} L_f(x)e^{-sx}dx; \quad [22]$$

and d_{Bm} , V_{Bm} , and V_{Bf} are defined similarly (see 8 and 9). The population of B's is not static, so we have denoted the time dependence. $N_{Bm}(t - T - \Delta T) = e^{-s(T+\Delta T)}N_{Bm}(t) \approx e^{-sT}N_{Bm}(t)$ —we assume s and ΔT so small that their product is negligible—and $N_{Bf}(t - T - \Delta T) \approx e^{-sT}N_{Bf}(t)$. We may accordingly write

$$dN_{Bf}/dt = sN_{Bf} = -d_{Bf}N_{Bf} + \frac{1}{2}r[1 - L_f(T + \Delta T)]e^{-sT}[V_{Am}N_{Am}V_{Bf}N_{Bf} + V_{Af}N_{Af}V_{Bm}N_{Bm}], \quad [23]$$

$$dN_{Bm}/dt = sN_{Bm} = -d_{Bm}N_{Bm} + \frac{1}{2}rL_f(T + \Delta T)e^{-sT} \times [V_{Am}N_{Am}V_{Bf}N_{Bf} + V_{Af}N_{Af}V_{Bm}N_{Bm}]. \quad [24]$$

Eqs. 19 and 20 imply $rV_{Am}N_{Am} = d_{Af}/V_{Af}[1 - L_f(T)]$ and $rV_{Af}N_{Af} = d_{Am}/V_{Am}L_f(T)$, while Eqs. 23 and 24 imply

$$(d_{Bf} + s)N_{Bf}/[1 - L_f(T + \Delta T)]e^{-sT} = (d_{Bm} + s)N_{Bm}/L_f(T + \Delta T)e^{-sT}, \quad [25]$$

$$N_{Bf} = (d_{Bm} + s)[1 - L_f(T + \Delta T)]e^{-sT} \times N_{Bm}/(d_{Bf} + s)L_f(T + \Delta T)e^{-sT}. \quad [26]$$

To find whether B is favored over A, substitute for $rV_{Am}N_{Am}$, $rV_{Af}N_{Af}$, and N_{Bf} in Eq. 24 and set $s = 0$ on the right. Call d_{Am} , $d_m(T)$; d_{Af} , $d_f(T)$; and set

$$\int_{T+\Delta T}^\infty d_m(x)L_m(x)dx / \int_{T+\Delta T}^\infty L_m(x)dx = d_m(T + \Delta T), \quad [27]$$

$$\int_0^{T+\Delta T} d_f(x)L_f(x)dx / \int_0^{T+\Delta T} L_f(x)dx = d_f(T + \Delta T), \quad [28]$$

for the values of these averages are set by the age of sex change. With this relabeling and some rearrangement, we find B is favored if

$$2 < \frac{V_f(T + \Delta T)[1 - L_f(T + \Delta T)]d_f(T)}{V_f(T)[1 - L_f(T)]d_f(T + \Delta T)} + \frac{V_m(T + \Delta T)L_f(T + \Delta T)d_m(T)}{V_m(T)L_f(T)d_m(T + \Delta T)}. \quad [29]$$

To simplify, notice that

$$L_f(T) = \exp - \int_0^T d_f(x)dx; \quad d \log L_f/dx = -1/L_f; \quad [30]$$

$$\int_0^T d_f(x)L_f(x)dx = - \int_0^T (dL_f/dx)dx = 1 - L_f(T); \quad [31]$$

$$V_f(T)[1 - L_f(T)]/d_f(T) = [1 - L_f(T)] \int_0^T b_f(x)L_f(x)dx \times \int_0^T d_f(x)L_f(x)dx = \int_0^T b_f(x)L_f(x)dx, \quad [32]$$

which last we call $R_f(T)$, the reproductive value (5) of a newborn programmed to turn male at age T , during the female part of its life cycle. Likewise,

$$V_m(T)L_f(T)/d_f(T) = [L_f(T)/L_m(T)] \int_T^\infty b_m(x)L_m(x)dx = R_m(T). \quad [33]$$

Since $L_f(T)L_m(x)/L_m(T)$ is the chance of a newborn female living to age x if it turns male at an age $T < x$, $R_m(T)$ is the prospective reproductive value of that newborn during the male part of its life. Substituting Eqs. 32, 33, and their analogues into Eq. 29, we find B is favored if

$$2 < R_f(T + \Delta T)/R_f(T) + R_m(T + \Delta T)/R_m(T). \quad [34]$$

Proceeding as in Eqs. 13 and 14, we find B is favored if

$$0 < \left[\frac{R_f(T + \Delta T)}{R_f(T)} - 1 \right] + \left[\frac{R_m(T + \Delta T)}{R_m(T)} - 1 \right], \quad [35]$$

$$0 < \Delta T \{ \log [R_f(T + \Delta T)/R_f(T)] + \log [R_m(T + \Delta T)/R_m(T)] \}. \quad [36]$$

B is favored if it increases a newborn's reproductive value during the female part of its life by a percentage exceeding the percentage loss as a male. When phrased thus, the conclusion applies whatever the mortality that might be associated with sex change, and whatever the lull in reproduction changing sex might impose.

Substituting back from the R 's of Eq. 36, we find that if sex change is instantaneous and costs nothing, it is best to change sex at that age T when

$$\frac{d}{dT} \log \left\{ \int_0^T b_f(x)L_f(x)dx \right\} + \frac{d}{dT} \log [L_f(T)/L_m(T)] \int_T^\infty b_m(x)L_m(x)dx = 0, \quad [37]$$

that is to say, when

$$\frac{d}{dT} \log \int_0^T b_f(x)L_f(x)dx + d \log L_f/dT - d \log L_m/dT + \frac{d}{dT} \log \int_T^\infty b_m(x)L_m(x)dx = 0, \quad [38]$$

$$\frac{b_f(T)L_f(T)}{\int_0^T b_f(x)L_f(x)dx} - d_f(T) = \frac{b_m(T)L_m(T)}{\int_T^\infty b_m(x)L_m(x)dx} - d_f(T). \quad [39]$$

Suppose first that males and females have the same fertility and death rates, so $L_m(x) = L_f(x)$, $d_m(x) = d_f(x)$, and $b_m(x) = b_f(x)$. Then females should change sex at the age T' when

$$b_f(T')L_f(T') \int_0^{T'} b_f(x)L_f(x)dx = b_f(T')L_f(T') \int_{T'}^\infty b_f(x)L_f(x)dx, \quad [40]$$

$$\int_0^{T'} b_f(x)L_f(x)dx = \int_{T'}^{\infty} b_f(x)L_f(x)dx. \quad [41]$$

In words, females should change sex at the age T' when a cohort of females born all at once would have exhausted half the reproductive value they would have were they to stay female all their lives.

Now suppose that males gain fertility more rapidly with age than females, so that if $x > y$, $b_m(x)/b_m(y) > b_f(x)/b_f(y)$. Assume, to be specific, that $b_m(x) = g(x)b_f(x)$, where $g(x) > 0$ and $g(x) > g(y)$ if $x > y$. Then

$$b_m(x)/b_m(y) = [g(x)/g(y)]b_f(x)/b_f(y) > b_f(x)/b_f(y). \quad [42]$$

Suppose, moreover, that males and females of the same age have the same death rate, so that $d_m(x) = d_f(x)$, $L_m(x) = L_f(x)$. Then the optimum age T'' to change sex is that for which

$$\frac{b_f(T'')L_f(T'')}{\int_0^{T''} b_f(x)L_f(x)dx} = \frac{g(T'')b_f(T'')L_f(T'')}{\int_{T''}^{\infty} g(x)b_f(x)L_f(x)dx}, \quad [43]$$

$$\int_0^{T''} b_f(x)L_f(x)dx = \int_{T''}^{\infty} [g(x)/g(T'')]b_f(x)L_f(x)dx. \quad [44]$$

Since $g(x) > g(T'')$ for $x > T''$, we may set $g(x)/g(T'') = 1 + h(T'', x)$, where $h > 0$ for $x > T''$. Out of pure whimsy we may rewrite 44 as

$$\int_0^{T''} b_f(x)L_f(x)dx + \int_{T''}^{\infty} b_f(x)L_f(x)dx = \int_{T''}^{\infty} b_f(x)L_f(x)dx - \int_{T''}^{\infty} b_f(x)L_f(x)dx + \int_{T''}^{\infty} h(T'', x)b_f(x)L_f(x)dx. \quad [45]$$

If T' is the best age to change sex when $g(x) = 1$ for all x , so that $\int_0^{T'} b_f(x)L_f(x)dx = \int_{T'}^{\infty} b_f(x)L_f(x)dx$, we find that when $dg/dx > 0$ the best age to change sex is that age T'' when

$$2 \int_0^{T''} b_f(x)L_f(x)dx = \int_{T''}^{\infty} h(T'', x)b_f(x)L_f(x)dx. \quad [46]$$

As h , b_f , and L_f are all positive, Eq. 46 implies $T'' > T$. This is as we would expect: the more fertile older males are relative to younger, the greater the proportion of matings garnered by the older males, and the older a newcomer must be to compete profitably for mates.

Selection between gonochores and sexchangers

When would a sequentially hermaphrodite genotype replace gonochores? Consider a dimorphic locus with alleles A and B in our customary population of sexual haploids: let the A -bearers be gonochores, a proportion $\frac{1}{2}(1 - k)$ of which are born male, and let the B -bearers be hermaphrodites changing sex at age T . Suppose first that the population consists almost entirely of A -bearers whose numbers are in balance, while the B -bearers are rare enough to be in logarithmic phase yet numerous enough to have attained a stable age distribution. Then

$$0 = dN_{A_f}/dt = -d_{A_f}N_{A_f} + \frac{1}{2}r(1 + k)V_{A_m}N_{A_m}V_{A_f}N_{A_f}, \quad [47]$$

$$0 = dN_{A_m}/dt = -d_{A_m}N_{A_m} + \frac{1}{2}r(1 - k)V_{A_m}N_{A_m}V_{A_f}N_{A_f}, \quad [48]$$

$$sN_{B_f} = dN_{B_f}/dt = -d_{B_f}N_{B_f} + \frac{1}{2}r[1 - L_f(T)e^{-sT}] \times [V_{A_m}N_{A_m}V_{B_f}N_{B_f} + V_{A_f}N_{A_f}V_{B_m}N_{B_m}], \quad [49]$$

$$sN_{B_m} = dN_{B_m}/dt = -d_{B_m}N_{B_m} + \frac{1}{2}rL_f(T)e^{-sT} \times [V_{A_m}N_{A_m}V_{B_f}N_{B_f} + V_{A_f}N_{A_f}V_{B_m}N_{B_m}]. \quad [50]$$

Using Eqs. 47 and 48 to eliminate N_{A_m} and N_{A_f} from 50, expressing N_{B_f} in terms of N_{B_m} as in 26, setting $s = 0$ on the right, and dividing through by d_{B_m} , we find B is favored if

$$1 < \left[\frac{1 + L_f(T)}{1 + k} \right] \frac{V_f(T)d_{A_f}}{V_{A_f}d_f(T)} + \left[\frac{L_f(T)}{1 - k} \right] \frac{V_m(T)d_{A_m}}{V_{A_m}d_m(T)}. \quad [51]$$

If, as in Eqs. 30–33, we express the V/d terms as reproductive values, we find B is favored if

$$1 < \frac{\int_0^T b_f(x)L_f(x)dx}{(1 + k) \int_0^{\infty} b_f(x)L_f(x)dx} + \frac{[L_f(T)/L_m(T)] \int_T^{\infty} b_m(x)L_m(x)dx}{(1 - k) \int_0^{\infty} b_m(x)L_m(x)dx}. \quad [52]$$

Let the male reproductive value per newborn gonochore individual be defined as $R_m(k)$ or $\frac{1}{2}(1 - k) \int_0^{\infty} b_m(x)L_m(x)dx$, and similarly for females. Then B is favored if

$$2 < R_m(T)/R_m(k) + R_f(T)/R_f(k). \quad [53]$$

Here again, a rare mutant allele will spread if it confers a percentage gain in reproductive value on one sex that exceeds the percentage loss to the other.

Suppose first that males and females have identical death and fertility rates (modulo the scaling factor for sex ratio), so $d_m(x) = d_f(x)$. Suppose, moreover, that

$$\int_0^T b_f(x)L_f(x)dx = \frac{1}{2}(1 + u) \int_0^{\infty} b_f(x)L_f(x)dx. \quad [54]$$

Then B is favored over A if

$$1 < \frac{1(1 + u)}{2(1 + k)} + \frac{1(1 - u)}{2(1 - k)}, \quad [55]$$

or if $1 - k^2 < 1 - ku$. If u is smaller in absolute value than k , or of the opposite sign, the hermaphrodites are favored when rare, just as if they were gonochores bearing male and female offspring in the ratio $1 - u$ to $1 + u$. Notice that hermaphrodites cannot even hold their own against gonochores bearing equal numbers of male and female offspring unless $u = 0$, unless the prospective reproductive value of newborn hermaphrodites is divided precisely equally between the male and female phases of their lives. Death rates vary from generation to generation, so the age of sex change appropriate for one generation is wrong for the next. Thus a gonochore allele producing half males and half females will in practice outcompete any sequentially hermaphrodite allele: sex change entails a purely "genetical" penalty in addition to its physiological cost.

Sex change, however, is favored if one sex gains fertility much more rapidly with age than the other, as in the bluehead wrasse (3), where females will wait their turn to mate with a larger male even if smaller ones are free, thus conferring disproportionate fertility on the largest males.

Suppose now that $b_m(x) = g(x)b_f(x)$, where $g(x) > g(y)$ if $x > y$; that $L_m(x) = L_f(x)$; and that

$$\int_0^{\infty} g(x)b_f(x)L_f(x)dx = \int_0^{\infty} b_f(x)L_f(x)dx. \quad [56]$$

Defining u as in Eq. 54, we find that the hermaphrodite allele B is favored when rare if

$$2 < \frac{1 + u}{1 + k} + \int_T^{\infty} g(x)b_f(x)L_f(x)dx / (1 - k) \int_0^{\infty} b_f(x)L_f(x)dx. \quad [57]$$

Since g is an increasing function of x , Eq. 56 implies

$$\int_T^\infty g(x)b_f(x)L_f(x)dx = U \int_T^\infty b_f(x)L_f(x)dx, \quad [58]$$

where $U > 1$. We may therefore rewrite Eq. 57 as

$$2 < (1 + u)/(1 + k) + U(1 - u)/(1 - k). \quad [59]$$

If $k = 0$, 59 becomes $2 < 2 + (U - 1)(1 - u)$, which is always true if $u < 1$. If gonochores are at their optimum sex ratio and if males gain fertility more rapidly with age than females, selection will favor a rare hermaphrodite allele, as Warner's simulations (2) suggested.

Now consider a rare gonochore allele in a stable population of sequential hermaphrodites which change sex at the optimum age, and let the assumptions leading to 57 apply. Will selection exclude all gonochore mutants? An argument corresponding to Eqs. 47-52 shows that selection favors a rare gonochore allele if

$$1 < \frac{(1 + k) \int_0^\infty b_f(x)L_f(x)dx}{4 \int_0^T b_f(x)L_f(x)dx} + \frac{(1 - k) \int_0^\infty b_m(x)L_f(x)dx}{4 \int_T^\infty b_m(x)L_f(x)dx}. \quad [60]$$

Eq. 60 implies that if the hermaphrodites exclude gonochores bearing only females and gonochores bearing only males, they will also exclude gonochores bearing young in any intermediate sex ratio. Gonochores bearing only females ($k = 1$) are excluded if

$$2 \int_0^T b_f(x)L_f(x)dx > \int_0^\infty b_f(x)L_f(x)dx. \quad [61]$$

Eq. 61 holds if the hermaphrodites change sex at the optimum age. Likewise, if the gonochores bear only males ($k = -1$), they are excluded if

$$2 \int_T^\infty b_m(x)L_f(x)dx > \int_0^\infty b_m(x)L_f(x)dx. \quad [62]$$

If we set $b_f(x) = p(x)b_m(x)$, where $p(x) < p(y)$ if $x > y$, an argument parallel to Eqs. 42-46 shows that 62 holds when the hermaphrodites change sex at the optimum age.

The above calculations suggest that if one sex gains fertility even slightly faster with age than the other, then selection will favor sex change. This is true only if changing sex costs nothing; in fact, the fertility differential must be sufficient to outweigh the cost of changing sex, and in higher vertebrates the cost of changing sex is apparently impossibly high.

We are most grateful to an anonymous referee who pointed out, among other things, how our result applied to diploids. E. L. is greatly indebted to William Schaffer and the University of Utah for a stimulating visit there, which provided opportunity to cross the Rockies and follow the Colorado through many a familiar canyon, and which permitted him to discuss sex change with Eric Charnov.

1. Ghiselin, M. T. (1969) "The evolution of hermaphroditism among animals," *Q. Rev. Biol.* 44, 189-208.
2. Warner, R. R. (1975) "The adaptive significance of sequential hermaphroditism in animals," *Am. Nat.* 109, 61-82.
3. Warner, R. R., Robertson, D. R. & Leigh, E. G., Jr. (1975) "Sex change and sexual selection," *Science* 190, 633-638.
4. Spieth, P. T. (1974) "Theoretical considerations of unequal sex ratios," *Am. Nat.* 108, 837-849.
5. Fisher, R. A. (1930) *The Genetical Theory of Natural Selection* (Clarendon Press, Oxford).