Sex Ratio under Conditional Sex Expression

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We present a model to show that, when sex depends on environment rather than
genotype, the sex expressed under relatively unfavorable conditions will be more
abundant. This result refers to numbers of males and females in the population. By
contrast, no clear prediction can be made about the allocation of resources to the
two sexes. The model is constructed to highlight the logical relationship between
the distribution of resources to the two sexes and the relative numbers of males and
females. The predicted bias in numbers toward the sex developing under unfavor-
able conditions depends on the assumption that fitness either increases or decreases
steadily according to the quantitative variable on which sex expression depends.

In many organisms gender depends on environmental or nutritional conditions and
is independent of genotype. Typically, individuals that are small or in relatively
unfavorable circumstances will express themselves as a particular sex, whereas those
in favorable conditions will be of the opposite sex (Charnov, 1982). It is useful to
distinguish two broad categories.

First, sex expression may be responsive to environment before or during ontogeny
and then fixed after development. For example, sex in several reptile species depends
on temperature during development, a phenomenon known as Environmental Sex
Determination (ESD, see Bull, 1983 for many other cases and references). Parasitoid
wasps are another case. Several species lay a single egg on each host insect larva
encountered. The size of the host determines the quality of the environment for the
offspring during development. Since wasps are haplodiploid, sex is determined by
whether the mother fertilizes the egg to produce a diploid daughter or lays an
unfertilized egg to produce a haploid son. In this case sex expression is responsive
to the environment through the mother's ability to control fertilization.

Second, sex expression may be labile during the reproductive lifespan—sequential
hermaphroditism (Charnov, 1982). For example, in some species of plant an
individual may produce only pistillate (female) flowers under certain environmental
and nutritional conditions; by contrast, the same individual in a later year and under

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different conditions may produce only staminate (male) flowers. Individuals of certain fish species are mostly of a particular sex when young and small, and then as they grow older and larger some or all switch sex. In all cases mentioned here, sex expression depends conditionally on local environment, so we refer to these related phenomena as Conditional Sex Expression (CSE).

Can any general statement be made for these two categories about the relative *numbers* of males and females, that is, sex *ratio*? For ESD, Bull (1983, p. 131) has suggested verbally that the sex that develops under relatively unfavorable conditions is expected to be more abundant, and Bull (1981) has proved this result for some special cases. For sequential hermaphroditism, Charnov (1982, pp. 139–141) has provided a general proof, along with a statement of assumptions, that the sex expressed early in life, or when small and relatively limited in resources, is expected to be more frequent than the sex expressed under opposite conditions.

What about the relative investment of *resources* to males and females, that is, sex *allocation*? Bull (1981, 1983; Bull & Charnov, 1988) pointed out that under ESD one would not expect population-wide equal allocation of resources to males and females as predicted by Fisher (1930) because of a covariance between progeny sex ratio and fitness. Put another way, Fisher's argument requires that the relationship between allocation and fitness be the same for males and females from the point of view of whatever entity "controls" the allocation ratio (MacArthur, 1965). Frank (1987) has developed a general method for calculating the predicted sex ratio and sex allocation ratio given the relationships for males and females between fitness and allocation, and given the frequency distribution of resources among individuals.

We present a general model for sex ratio under CSE. We focus on conceptual issues; data concerning the theory discussed here are reviewed by Charnov (1982), Bull (1983), and Bull & Charnov (1988). Our model is similar to that given by Charnov (1982, pp. 139–141), but our derivation allows us to stress the relationship between sex ratio and sex allocation in a way that leads naturally to specific quantitative predictions (Frank, 1987). We prove the strong prediction that the sex ratio will be biased towards the sex developing under relatively unfavorable conditions—i.e., a bias towards the "cheaper" or "less costly" sex (Charnov, 1982; Bull, 1983). The predicted sex allocation ratio may, however, be biased towards either sex, and the direction and magnitude of bias is sensitive to particular assumptions.

The Model

Suppose that as conditions (size, resource quality, etc.) improve, fitness increases faster for one sex than the other. For illustration assume that males gain less than females under better conditions. Selection favors males to develop under relatively poor conditions and females to develop under good conditions; at some intermediate environment, Λ, an individual enjoys the same fitness whether it expresses itself as male or female (Charnov, 1979; Bull, 1981).

Let z be a number that summarizes the many dimensions of environmental and nutritional quality. For convenience standardize z so that it varies over the interval $(0, 1)$. The functions $\mu(z)$ and $\phi(z)$ are proportional to fitness for males and females,

respectively. The probability distribution $f(z)$ describes the frequency at which environmental states z occur in the population. Total male fitness is $\mu(z)$ weighted by the frequency of occurrence of conditions z under which individuals express themselves as males, $T(\mu) = \int_0^\Lambda \mu(z) f(z) \, dz$. Total female fitness is $T(\phi) = \int_\Lambda^1 \phi(z) f(z) \, dz$.

The major prediction is that males will be more abundant than females for any distribution $f(z)$ and for the general class of functions $\phi(z)$ and $\mu(z)$ such that ϕ and μ are monotonically nondecreasing in z, $\phi \neq \mu$, and ϕ/μ is monotonically nondecreasing in z. The sex ratio, or male frequency, is $S = \int_0^\Lambda f(z) \, dz$, the frequency of conditions under which individuals express themselves as males. The proof proceeds by first noting that at equilibrium standardized male and female fitness are equal at the transition point $\Lambda = \lambda$, in symbols $\mu(\lambda)/T(\mu) = \phi(\lambda)/T(\phi)$, or rearranging,

$$\phi(\lambda) \int_0^\lambda \mu(z) f(z) \, dz = \mu(\lambda) \int_\lambda^1 \phi(z) f(z) \, dz.$$

By the monotonicity assumption of this model male fitness is a maximum at λ, $\mu(\lambda) \geq \mu(z)$ on the interval $(0, \lambda)$, and female fitness is a minimum at λ, $\phi(z) \geq \phi(\lambda)$ on the interval $(\lambda, 1)$, therefore

$$\phi(\lambda)\mu(\lambda) \int_0^\lambda f(z) \, dz > \phi(\lambda)\mu(\lambda) \int_\lambda^1 f(z) \, dz.$$

Since the integral on the left side is the sex ratio, S, and the integral on the right side is $1 - S$, we have $S > 1/2$. If males develop under relatively poor conditions theory predicts that males will be more abundant. Likewise, if females develop under relatively poor conditions they are expected to be more abundant. Charnov (1982, pp. 139–141) has presented a useful way of predicting the magnitude of the sex ratio bias.

Conclusions

The model predicts the relative abundance of males and females without the need to specify which resources and conditions determine sex and fitness, since sex ratio $S > 1/2$ is true independently of any particular interpretation for environmental and resource variables z. By contrast, the model makes no statement about relative investment or allocation of resources into males and females at equilibrium.

How could one predict the relative allocation of resources into males and females? One obvious candidate is to define the proportion of total resources allocated to males as $\int_0^\lambda z f(z) \, dz / \int_0^1 z f(z) \, dz$, since z summarizes the resources and environmental variables on which both sex and fitness depend. The variables summarized by z are, however, often difficult to define and to measure, and may not be meaningful in some situations. For example, suppose that the major determinant of sex is temperature, as in many reptiles with ESD. Then any statement about allocation of resources to the two sexes would be mainly about allocation of temperature or developmental rate. On the other hand, if amount of food determines fitness and

the sex expressed, as in parasitoid wasps, then it may make sense to speak of total allocation of resources in males and females. For example, host weight is sometimes used as a surrogate measure for resource allocation.

If z is a measurable and meaningful resource, can any firm conclusion be drawn under CSE concerning the predicted population-wide allocation of resources in the two sexes? No, since the direction and magnitude of the allocation bias is sensitive to particular assumptions about the male and female fitness functions μ and ϕ within the general class of functions described above. The predicted allocation may range from very male biased to very female biased, whereas the predicted sex ratio is consistently biased towards the sex that is expressed under relatively poor conditions; details for calculating specific numerical predictions for both sex ratio and sex allocation ratio were presented elsewhere (Frank, 1987, section 3).

To summarize the theory, under CSE sex ratio bias is easy to predict and easy to measure, whereas sex allocation is difficult to predict and difficult to measure. Reliance on Fisher's equal allocation theory is at best conceptually misleading in this case, and, at times, a default prediction of equal allocation may yield a poor interpretation of observed patterns.

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