THE EFFECTS OF POPULATION RECRUITMENT
ON SEX RATIO SELECTION

Fluctuation in population birthrate over time is the rule rather than the exception for most natural populations. Here we show that this variable recruitment selects for facultative sex ratio control by parents. This can occur in species which have two common characteristics: (1) multivoltine reproduction with overlapping generations, and (2) age-specific differences in survivorship and fecundity between males and females. These characteristics favor facultative sex ratios because the variable recruitment can affect differently the lifetime fecundity of the two sexes. In the discussion, we suggest that our model may also apply to alternative life history strategies within a single sex.

The model below will show how variable recruitment favors facultative sex ratios. Assume that normally a fixed number N of offspring are born in the population each generation. For simplicity, it is assumed that N is independent of the number of adult females in the population. This would occur in a species, for example, in which nest sites were limiting. Although N offspring are normally born, there are exceptional years in which $(1 + \alpha)N$ individuals are born. The question then is, Are parents favored to produce a sex ratio different from 50% sons in the generation of variable recruitment?

To answer the question, we will first fix attention on a certain sex under normal recruitment conditions and consider the gamete pool of that sex in a typical year. Let p_i be the proportion of gametes contributed by age class i. Each cohort has one chance at each age class, so the lifetime reproductive contribution of a cohort can be measured by $\Sigma p_i = 1$. Now suppose a certain cohort is exceptional and is $(1 + \alpha)$ times its normal size. If this is a rare event then when this cohort gets to age i, it will be the only exceptional cohort. Once that cohort achieves maturity, the size of the adult mating population will be altered because of the exceptional recruitment. If $\alpha > 0$, the adult mating population in that sex will increase in size; if $\alpha < 0$, the adult population will decrease. The effect is to alter the reproductive success of each adult because of the change in reproductive competition. We will assume for simplicity that a change in adult population alters the contribution of each breeding individual in that sex by the same factor. The contribution $\hat{p}_j$ of age class j (in the year when the exceptional cohort is age i) is

$$\hat{p}_j = p_j/(1 + \alpha p_i) \qquad j \neq i$$
$$\hat{p}_i = p_i (1 + \alpha)/(1 + \alpha p_i).$$

Now an individual born in that exceptional cohort will be a member of it every year so his expected lifetime reproductive success is the sum of the $\hat{p}_i$ divided by his relative cohort size. Thus the expected reproductive success of an individual

born in an exceptional cohort of size $(1 + \alpha)N$ is

$$W = \sum_i \{p_i/(1 + \alpha p_i)\}.$$

We have fixed attention on one sex. The other sex may have a different pattern of p_i and hence a different W. In an exceptional year selection should favor production of the sex with the higher value of W.

Thus it is important to understand the dependence of W on the $\{p_i\}$. The general result, loosely stated, is the following. For $\alpha > 0$, W is increased by making the p_i more nearly equal and decreased by spreading them out (increasing some at the expense of others). For $\alpha < 0$, the reverse is true: W is smaller the more nearly equal are the p_i. The underlying reason for this is that the function $\beta(p) = p/(1 + \alpha p)$ defined for $0 \leqq p \leqq 1$ is concave-down when $\alpha > 0$ and concave-up when $\alpha < 0$.

An illustration will make matters clear. When we speak of making the p_i more equal, recall that their sum must always equal unity. Let's fasten attention on two of the p_i, say p_1 and p_2, and see what happens when we move them but keep their sum constant. If their sum is k, then the point $k/2$ is halfway between them. If we move them closer together to p_1' and p_2' with the same sum, then $k/2$ will still be the midpoint. Now their contribution to W is $\beta(p_1) + \beta(p_2)$. In figure 1 the quantity $[\beta(p_1) + \beta(p_2)]/2$ is the height of the chord above $[p_1,p_2]$ on the β graph at the point $k/2$. Similarly $[\beta(p_1') + \beta(p_2')]/2$ is the height of the shorter chord at $k/2$. Since the graph is concave-down (for $\alpha > 0$) the shorter chord is higher. Hence W is increased by replacing p_1 and p_2 with the more nearly equal p_1' and p_2'. The same argument works for concave-up curves ($\alpha < 0$) with the opposite result.

Thus the important parameter determining whether a female or male bias is selectively favored in exceptional years is the actual distribution of reproductive success over the adult age classes. If the reproductive output of a sex is distributed evenly over many adult age classes (which gives nearly equal p_i), then the impact of a variable recruitment year upon the reproductive output of the cohort will be lessened because any one recruitment year has a relatively small impact upon the number of adults of that sex. In the sex with reproduction concentrated in relatively few adult age classes, the impact upon the cohort will be greater. Unequal age-specific distribution of reproductive output between the sexes occurs in many species and can be strongly influenced by sexual selection (e.g., selection for large individuals, different maturation rates between the sexes, etc.).

Our general result is that in generations of above average recruitment, a shift is favored toward the sex with the more even distribution of reproductive success over the age classes (p_i fairly equal), while a shift toward the sex with the greater concentration of reproductive success within particular age classes (p_i quite varied) is favored in generations of below average recruitment.

The equilibrium sex ratio can be determined for this model as follows. Assume that the population alters its sex ratio from 1/2 to proportion x of sons in the variable recruitment year. Given p_{mi} and p_{fi} for the normal contribution of the ith age class for males and females, respectively, then for the variable recruitment cohort

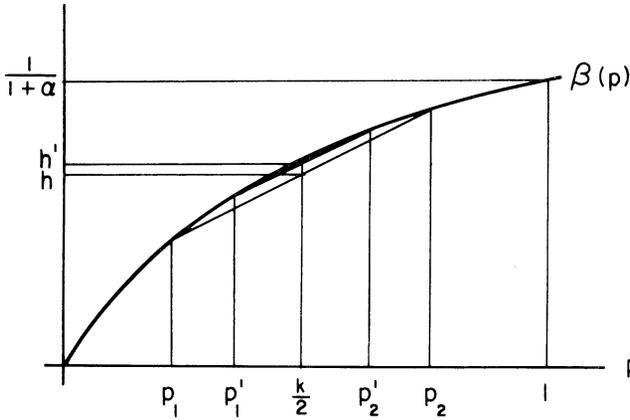$$W_\delta = \sum_i \frac{p_{mi}}{1 + p_{mi}[2x(\alpha + 1) - 1]}$$

FIG. 1.—A graph of $\beta(p) = p/(1 + \alpha p)$ for $\alpha > 0$. The points p_1 and p_2 have sum k and the more nearly equal points p_1' and p_2' also have sum k. The quantity $[\beta(p_1) + \beta(p_2)]/2$ is the height h of the chord on $[p_1,p_2]$ while $[\beta(p_1') + \beta(p_2')]/2$ is the height h' of the chord on $[p_1',p_2']$. Since β is concave-down for $\alpha > 0$, we have $h < h'$. Thus making the p_i more equal leads to a higher W value. If $\alpha < 0$, β is concave-up and the opposite is true.

$$W_\female = \sum_i \frac{p_{fi}}{1 + p_{fi}[2(1 - x)(\alpha + 1) - 1]}.$$

The quantities $2x(\alpha + 1)$ and $2(1 - x)(\alpha + 1)$ are the relative sizes of the exceptional male and female cohorts, respectively. The equilibrium sex ratio will be that which satisfies the condition $W_\male = W_\female$. We have calculated this for a four adult age-class model. The model assumes that from the first age of breeding forward, each sex has constant fecundity and constant annual mortality, which may be sex dependent. Low annual mortality results in an even distribution of reproductive success over ages, high mortality means reproductive success is concentrated in early ages. The equilibrium sex ratios for several combinations of male and female survivorship are shown in figure 2. As can be seen, fairly dramatic deviations from 50% sons can be expected in variable recruitment years. The largest sex ratio shifts are favored in low recruitment years (subtracting from the denominator has a greater effect than adding to the denominator.)

If α is small so that $p/(1 + p\alpha)$ can reasonably be approximated by $p(1 - p\alpha)$, then the equilibrium sex ratio equation $W_\male = W_\female$ can be approximately solved (ignoring α^2) to give a sex ratio deviation (from 1/2) of

$$x - 1/2 \cong \frac{\alpha}{2} \frac{\Sigma p_{fi}^2 - \Sigma p_{mi}^2}{\Sigma p_{fi}^2 + \Sigma p_{mi}^2}.$$

Thus in good years the sex ratio should shift toward the sex with the smaller value of Σp_i^2. In case of constant fecundity and annual mortality, μ, if we let $S = (1 - \mu)$ be annual survivorship, then $p_i = (1 - S)S^i$ (taking $i = 0$ to be the first age of breeding) and the equation becomes

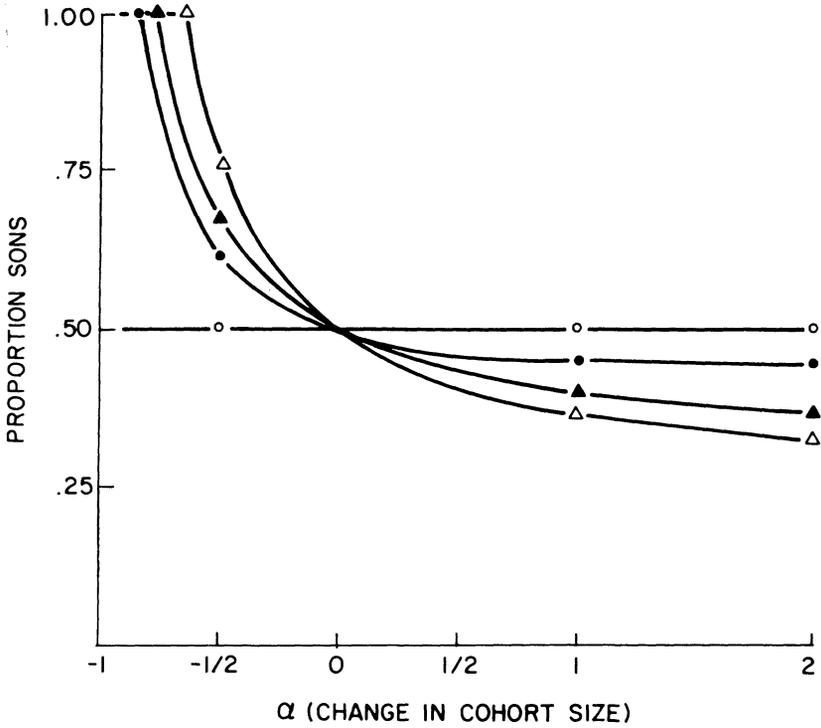$$x - 1/2 \cong \frac{\alpha}{2} \frac{S_m - S_f}{1 - S_m S_f}.$$

FIG. 2.—The equilibrium primary sex ratio for the variable recruitment cohort is shown for different adult annual mortalities. Given S_f = adult annual survival of females and S_m = adult annual survival of males, equilibrium sex ratio curves are shown for (a) $S_f = S_m$ (-O-); (b) $S_f = 1, S_m = .5$ (-●-); (c) $S_f = .5, S_m = .1$ (-▲-), and (d) $S_f = 1, S_m = .1$ (-△-). A sex ratio shift is favored toward the sex with more age-class concentrated reproduction when $\alpha < 0$ and toward the sex with more even reproduction when $\alpha > 0$.

In good years the sex ratio shifts toward the sex with the lowest mortality, as expected.

The simplified mathematical analysis presented here is dependent on the assumption that normal recruitment is constant. However, facultative sex ratios can still evolve when these assumptions are violated. In particular, a computer simulation confirms that facultative sex ratio alleles are also favored in response to variable recruitment when normal population recruitment is either (1) increasing or decreasing by a constant rate or (2) linearly dependent upon the number of adult females in the population.

Variations in recruitment are not the only demographic events that favor facultative sex ratio changes. For example, a year of exceptionally high or low adult mortality could favor a shift in the sex ratio produced the following year, for reasons much the same as those discussed above, even if this mortality had no effect on the overall adult sex ratio. The perturbation model of Werren and

Charnov (1978) considered the effects of exceptional adult mortality, but that model required the mortality to be sex specific. Seasonal life histories (Werren and Charnov 1978; Seger 1983) can also favor facultative sex ratios.

Because variations in recruitment and mortality are ubiquitous and often large, they may be important in favoring the evolution and maintenance of systems of sex discrimination that allow females to adjust the sex ratios of their progeny (e.g., Charnov 1982). Variable recruitment may be quite important in species with environmental sex determination (Bull 1980). When the primary sex ratio is fixed at 1:1, the sex ratio of investment can often be adjusted to some extent by differential care of offspring after birth (Maynard Smith 1980). Thus the selective mechanism described here may even apply to the sex ratio dynamics of mammals (Clutton-Brock and Albon 1982), birds, and other groups of animals with sex chromosomes. Naturally, if sex ratio adaptations to variable recruitment are to evolve, exceptional recruitment must either be detectable (e.g., through a change in population density) or associated with an environmental cue such as temperature, health, or resource quality.

Our general principle may well apply to other sets of alternative life histories which are facultatively determined at a certain stage in development. For example, Gross and Charnov (1980) discuss alternative male life histories in bluegill sunfish. They give evidence that sometime prior to age 2, the male becomes committed to one of two developmental patterns. *Parentals* spend the next five years growing and only then begin to breed as large territorial males and *sneakers* commence reproductive activity immediately without territories and may become satellite males later on. The data presented in Gross (1980) suggest the $\{p_i\}$ may in fact be different for the two patterns, though it is difficult to combine the sneaker and satellite graphs without some indication of the relative fecundity at these two stages (assuming these are consecutive stages of a single development alternative). Gross (1980) recognized that variable recruitment could have a differential impact on the two strategies, but he was not aware of the significance of relative age distribution in determining the outcome. If sneaking incurs high mortality (for two reasons: sneakers are smaller than territorials and the behavior itself may be risky), sneakers may have a more concentrated distribution of reproductive success and be favored in poor years. If the character is indeed facultative and not determined until age 2, there should be ample time for a fish to assess the relative size of his cohort.

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