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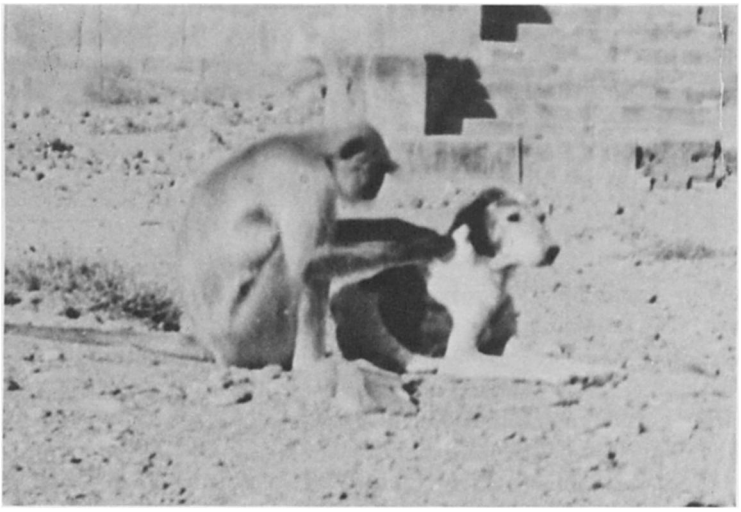

FIG. 1.—Old dog being groomed by langur

docile stray dogs—their natural enemies—at certain localities in the Jodhpur region. The likelihood of new behavioral relationships such as these has been implied by Klopfer (1964, pp. 3–5), Odum (1970, pp. 108–109), and Smith (1971).

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NATURAL SELECTION FOR VARIANCES IN OFFSPRING NUMBERS: A NEW EVOLUTIONARY PRINCIPLE

Natural selection is the "differential perpetuation of genotypes" (Mayr 1963, p. 107) due to fitness differences between the genotypes. What are these "fitnesses" and how are they conceptualized? A more fit individual is usually

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equated with a better adapted genotype and "the best adapted individuals of a species tend to leave more offspring *on the average* than do less well adapted genetic variants" (Emmel 1973, p. 5). A more fit genotype possesses a selective advantage and "whatever selective advantage a_2 possesses over a_1 is manifested in the kinds of phenotypes these alleles or genotypes, respectively, determine. If in a population the individuals carrying a_2 are, *on the average*, more viable, or longer lived, . . . the former will leave more offspring than the latter and the frequency of a_2 will consequently increase in the next generation" (Grant 1963, p. 193). These randomly chosen statements about evolution indicate a commonly held view that more fit individuals are those which have, *on the average*, more offspring. The need to mention the word average indicates the obvious presence in natural populations of stochastic environmental and developmental elements which cause different individuals of the same genotype to have differing numbers of offspring. When these stochastic elements are introduced into simple mathematical models of natural selection, a strange thing occurs: genotypes with higher average numbers of offspring do not necessarily increase in numbers over long periods of time. When the stochastic element is due to temporal fluctuations in the environment, for example, the best measure of fitness turns out to be the geometric mean of the offspring number, averaged over time, which is, approximately,

$$\mu - \tfrac{1}{2}\sigma^2 \tag{1}$$

where μ is the average number of offspring (a number close to one) and σ^2 is the variance in the number of offspring (Gillespie 1973). On the other hand, if the stochastic element is developmental, then the best measure of fitness is, approximately,

$$\mu - \frac{1}{N}\sigma^2 \tag{2}$$

where N is the population size (Gillespie 1974, 1975). Obviously these results indicate that the effects of variances in offspring number can be as important as mean effects and thus deserve a more prominent place in our general thinking about the evolutionary process. Perhaps the most intriguing aspect of these two measures of fitness is that both are decreasing functions of the variance in offspring number. Is this fortuitous or is there a very general principle which assures that adding a random element to the number of offspring a genotype has will cause a lowering of that genotype's fitness? I will argue that such a principle exists.

Consider, in a very general way, a species which has two alleles, A_1 and A_2, segregating at a particular locus in the tth generation. Let X be a random variable which represents the number of A_1 alleles in the $(t + 1)$st generation, and let Y, also a random variable, represent the number of A_2 alleles in the $(t + 1)$st generation. The specific nature of the various developmental and environmental factors which cause the randomness of X and Y need not concern us now. The

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frequency of the A_1 allele in the $(t + 1)$st generation will be

$$p = \frac{X}{X + Y}. \tag{3}$$

Let the means of X and Y be $\overline{X}$ and $\overline{Y}$. If the variances in these random variables are zero, then the mean of p in the $(t + 1)$st generation will be, trivially,

$$Ep = E\left(\frac{X}{X + Y}\right) = \frac{\overline{X}}{\overline{X} + \overline{Y}}. \tag{4}$$

But what if there is some variation in X and Y? Consider first the case where X has some random element but Y does not. In this case $p = X/(X + \overline{Y})$ is a *concave* function of X and, by Jensen's inequality (Breiman 1968, p. 80),

$$Ep \leq \frac{\overline{X}}{\overline{X} + \overline{Y}}. \tag{5}$$

Thus the addition of randomness to the number of offspring of A_1 results in the average *frequency* of A_1 being lowered in the next generation over what it would be were it to have a constant number of offspring with no variance. Conversely, suppose X is constant at $\overline{X}$ and Y is variable. In this case $p = \overline{X}/(\overline{X} + Y)$ is a *convex* function of Y so, again by Jensen's inequality,

$$Ep \geq \frac{\overline{X}}{\overline{X} + \overline{Y}}. \tag{6}$$

Thus, when the random element is added to the offspring number of A_2 it results in an increase in relative average frequency advantage for the A_1 allele. This demonstration indicates that the addition of a stochastic element to the offspring number of a genotype will effectively lower the fitness of that genotype as measured by its mean frequency in the next generation. The demonstration uses only two ideas: (1) in the evolutionary process we are concerned with *frequencies* of genotypes and the frequency of a genotype will always be a concave function of one of the variables and a convex function of the other, and, (2) Jensen's inequality, a very general inequality which gives the strongest possible relationship between the expectations of concave or convex function of random variable and the same function of the expectation of the random variable. These two fundamental ideas, one from biology, the other from mathematics, lead us to a very strong result on the action of selection on variances in offspring number.

There is another way to show the same relationship which uses more assumptions but provides more information. Write $X = 1 + \mu_x + \delta X$ and $Y = 1 + \mu_y + \delta Y$ (so $E\,\delta X = 0$, $EX = \overline{X} = 1 + \mu_x$, Var X = Var δX, etc.), and assume that μ_x, μ_y, Var X, Var Y, and Cov XY are all small and of the same order of magnitude and that the higher order moments of δX and δY (and, of course, the powers of μ_x and μ_y) are of a smaller order of magnitude. We can

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then write, using the geometric series expansion:

$$
\begin{aligned}
Ep &= E\left(\frac{\bar{X} + \delta X}{\bar{X} + \bar{Y} + \delta X + \delta Y}\right) \\
&= \frac{\bar{X}}{\bar{X} + \bar{Y}}\left[\left(1 + \frac{\delta X}{\bar{X}}\right)\Big/\left(1 + \frac{\delta X + \delta Y}{\bar{X} + \bar{Y}}\right)\right] \\
&= \frac{\bar{X}}{\bar{X} + \bar{Y}}\, E\left\{\left(1 + \frac{\delta X}{\bar{X}}\right)\left[1 - \frac{\delta X + \delta Y}{(\bar{X} + \bar{Y})} + \left(\frac{\delta X + \delta Y}{\bar{X} + \bar{Y}}\right)^2 - \cdots\right]\right\} \\
&\simeq \frac{\bar{X}}{\bar{X} + \bar{Y}} + \frac{-\bar{Y}\ \mathrm{Var}\ X + (\bar{X} - \bar{Y})\ \mathrm{Cov}\ XY + \bar{X}\ \mathrm{Var}\ Y}{(\bar{X} + \bar{Y})^3}.
\end{aligned}
\tag{7}
$$

Direct examination of this relationship shows that increasing the variance of X will lower the mean frequency of A_1, while increasing the variance in Y will increase the mean frequency of A_1. Under any reasonable biological model increases in the variance in offspring number of an individual of genotype A_1 and A_2 will result in an increasing of Var X and Var Y. This expression for Ep can be used with the proper expressions for Var X and Var Y, to arrive at the diffusion models leading to the measures of fitness (1) and (2).

We see from the above that natural selection can work on variances in offspring number and it works in such a way that increasing the variance in offspring number of a genotype will decrease its fitness. The strength of this selection varies from being equal to that on means in the case of environmental fluctuations to being proportional to the reciprocal of the population size in the case of developmental randomness. The demonstration of this requires very little in the way of assumptions, which gives confidence that these are not artifacts of the mathematics. With this understanding of the roles of variances in offspring number in evolution, certain problems in population biology may be attacked from a new direction. For example, variation between species in egg mass number and size in *Ambystomid* salamanders may be explained as a strategy to reduce the effects of predation by involving variance arguments (Wilbur 1976). Similarly, one possible explanation for the existence of genetic polymorphism in natural populations rests heavily on the action of selection in variable environments (Gillespie, 1976). It is possible that the adaptive significance of a number of life-history strategies can only be understood when proper attention is paid to the variance component in offspring number. For some indications of this see Slatkin (1974).

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EXPERIMENTAL MANIPULATION OF SOME SNAIL POPULATIONS SUBJECT TO CLIMATIC SELECTION

The land snail *Cepaea vindobonensis* is polymorphic for the intensity of its shell band pigment. In the limestone mountains of North Yugoslavia there is great microgeographical variation in morph frequency. Dark shells are found primarily in basins, and faint banded shells on the surrounding mountain slopes. This distribution appears to be affected by climatic selection, as the basins act as frost hollows and are therefore colder in the early morning than are the hillsides. Dark shells have a higher efficiency of absorption of solar energy than do faint. They can therefore attain a temperature suitable for activity earlier in the day than can faint banded individuals. Faint banded snails appear to be at a corresponding advantage in the warmer microclimate of the mountain sides (Jones 1973, 1974).

The importance of environmental selection in the control of genetic differentiation in natural populations has long been a source of argument (Lewontin 1974). *Cepaea vindobonensis* populations in North Yugoslavia appear to show an association of gene frequency with a selective agent whose mechanism of action is at least partly understood. We have attempted to measure the intensity of natural selection by transferring marked snails between basins and mountainsides and measuring survival.

Our experiments involved transferring marked snails from hillside colonies which contained both faint and dark individuals. In each of the experimental transfers, half the marked snails were removed to a basin and half to a foreign hillside as a control. In July and August 1971, 6,500 snails were transferred, and 1,000 of these were recaptured during repeated visits to the release sites in

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