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NOTES AND COMMENTS

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OPTIMALITY AND CONSTRAINT IN A SELF-FERTILIZED ALGA

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Darwin (1859) argued that animals and plants are not designed but contrived, and that they respond to selection by modifying preexisting structures rather than by inventing new ones. As a consequence, the products of evolution are often clumsy makeshifts, rather than precision engineering (Ghiselin, 1974). Darwin was concerned to make this point because, at the time, the theological argument from design was the chief rival to his theory of natural selection as an interpretation of the relationship between structure and function (Paley, 1845). This old controversy has recently been rekindled by the development of mathematical techniques for predicting such important characteristics of organisms as their diet or sex allocation (e.g., Pyke et al., 1977; Charnov, 1982), by defining their optimal states—the states, that is, which maximize reproductive success. Some biologists have objected to the widespread use of optimization theory because it ignores anatomical, physiological, or developmental constraints which may make it impossible for an organism to achieve the predicted optimum, at least in the short term (Lewontin, 1978; Gould and Lewontin, 1979; Maynard Smith, 1978; Oster and Wilson, 1978). It would clearly be valuable to analyze a system so simple that the twin threads of optimal design and developmental constraint can be unambiguously disentangled, and their separate contributions to the observed distribution of phenotypes identified. In this paper, we describe how the optimal sperm production of a simple self-fertilizing alga can be calculated. Having estimated the parameters of the optimization model, we compare the observed level of sperm production with the predicted optimal value. At the same time, we note that the small integer number of mitoses involved in spermatogenesis represents a developmental constraint. We then attempt to evaluate the contributions of constraint and optimal design to the observed phenotypic variance.

Eudorina elegans var *synoica* (Chlorophycophyta: Volvocales) is a green alga which forms motile colonies of 16 or 32 cells. Under appropriate conditions, some cells differentiate into sperm packets, each of which comprises 16 or 32 sperms. When the packets dissociate, these sperms fertilize the other cells of the colony, which then stops swimming and settles to the bottom as a clump of zygotes, in which meiosis occurs (Goldstein, 1964). In the strain we used, the sperm packets have never been seen to leave the colonial envelope (unlike other varieties

of the same species, which have dioecious colonies), despite long-continued observations under various conditions over a period of several years (M. E. Goldstein, pers. comm.; M. Praiss, unpubl.). The alga is therefore an exclusively self-fertilized haplont. The question we wish to answer is: how many sperms should be produced by a colony?

According to theories of optimal design, the answer to this question is: the number of sperm which maximizes the production of zygotes by the colony. This amounts to maximizing $w = E(1 - P_0)$, where E is the number of eggs in the colony (all those cells remaining after some have differentiated into sperm packets) and P_0 is the fraction of eggs which go unfertilized. Clearly, producing too many sperm will yield few zygotes because few cells remain to form eggs, while producing too few sperm will have a similar result because many eggs will go unfertilized. A precise quantitative argument defining the optimal intermediate level of sperm production requires a fertilization model (relating P_0 to sperm production) and an allocation model (relating E to sperm production), but nothing else; in particular, we do not need to take into account either zygote quality (since all zygotes are genetically identical) or the allocation made by other colonies in the same or in different clones (since there is no cross-fertilization). The simplest fertilization model states that sperm-egg encounters occur at random and have Poisson dynamics, so that $P_0 = \exp(-S/E)$, where S is the number of sperm produced. Since we do not know that all eggs are equally fertilizable, however, a more general model is $P_0 = A \exp(-kS/E)$, where A and k are constants to be determined by measurement. The simplest allocation model states that the total quantity of material available for gametogenesis G is fixed, so that $G = E\Delta + S\delta$, where Δ and δ are the masses of egg and sperm respectively. Since $dG/dS = 0$ by hypothesis, we have $dE/dS = -\delta/\Delta$. To find the optimal production of sperm, we observe that $dw/dS = (1 - P_0)(dE/dS) - E(dP_0/dS)$, where dE/dS and dP_0/dS are supplied by the allocation and fertilization models respectively. Substituting them into the expression for dw/dS and solving the resulting equation at zero yields $k(\Delta/\delta + S/E) - (1 - P_0)/P_0 = 0$, which must be solved numerically to get the sperm : egg ratio S/E which maximizes zygote production.

Our measurements of zygote production Z as a function of sperm : egg ratio are given in Table 1. Both sperm number and egg number contribute to

TABLE 1. The relationship between sperm production and zygote production in self-fertilized monoecious colonies of *Eudorina elegans*. Colonies were isolated by the method of Goldstein (1964) and maintained in soil-water medium in test tubes under a 16 hr photoperiod at $20 \pm 2^\circ\text{C}$. They were transferred weekly to tubes with fresh medium. Young asexual colonies were isolated into depression plates containing fresh soil-water and these were placed in an aqueous solution of sodium bicarbonate in covered petri dishes. When sexual colonies appeared, all sexual and asexual colonies were removed with the exception of a single sexual colony, for which the number of sperm packets and the number of sperm in each packet were recorded. After five or six days, the resulting zygotes were counted. The number of eggs is the number of cells in the colony less the number of sperm packets: $E = C - P$. The sixth column, $1 - Z/E$, is the fraction of eggs that go unfertilized.

C (cells per colony)	P (sperm packets)	S (total sperms)	Z (zygotes)		S/E (sperm : egg ratio)	1 - Z/E		N (sample size)
			Mean	SD		Mean	SE	
16	1	16	9.44	2.75	1.067	0.3704	0.0273	45
16	1	32	13.21	1.74	2.133	0.1191	0.0170	47
16	2	32	10.90	2.14	2.286	0.2214	0.0279	30
16	2	48	12.50	1.10	3.429	0.1071	0.0196	16
16	2	64	12.33	1.15	4.571	0.1190	0.0476	3
16	3	48	10.50	3.00	3.692	0.1923	0.1154	4
Pooled	1.39	29.9	11.39		2.071	0.2189		145
32	1	32	17.33	5.39	1.032	0.4409	0.0710	6
32	2	32	18.36	3.39	1.067	0.3881	0.0302	14
32	2	48	23.29	4.84	1.600	0.2238	0.0431	14
32	2	64	27.60	1.68	2.133	0.0667	0.0138	15
32	3	48	18.71	3.25	1.655	0.3547	0.0424	7
32	3	64	23	0	2.207	0.2069	0	2
32	3	80	25.33	2.52	3.759	0.1264	0.0501	3
Pooled	2.10	48.8	22.20		1.636	0.2539		61
All colonies pooled	1.60	35.5	14.59		1.941	0.2293		206

the proportion of eggs fertilized: the partial correlations with $\log(1 - Z/E)$ are -0.743 ($P = 0.01$) for sperm number and $+0.572$ ($P = 0.05$) for egg number. The fraction of eggs which go unfertilized is therefore negatively correlated with sperm production (for a given number of eggs) and positively correlated with egg number (for a given number of sperm). When stepwise multiple regression is used the ratio S/E is entered first, and neither S nor E separately causes a significant reduction in the residual variance. The sperm : egg ratio is therefore a good predictor of the fraction of eggs fertilized, with the absolute number of sperm or eggs being unimportant. From the linear regression of $\ln(1 - Z/E)$ on S/E , the parameters of the fertilization model were estimated to be: $\ln A = 0.6382 \pm \text{SE } 0.3286$ and $k = 0.5088 \pm \text{SE } 0.1568$; the regression has $r^2 = 0.49$ and $F = 10.5$ ($P = 0.008$), and there is no trend in the residuals. By measuring sperm and eggs in colonies bearing a single sperm packet and assuming eggs to be spheres and sperm prolate spheroids, we found Δ/δ to be 15.1 for packets bearing 16 sperm ($N = 27$ colonies each with a single packet of 16 sperm, one sperm and one egg measured from each colony) and 28.7 for packets bearing 32 sperm ($N = 28$); these are close to the values of 16 and 32 expected if cleavage occurred without loss of material.

Consider first the 16-cell colonies. When the estimates of parameters are substituted into the optimization argument, the optimal sperm : egg ratio is found to be 3.345 (if only 16-sperm packets occur; if only 32-sperm packets occur the very similar value of 3.280 is found); the observed mean value is 2.071 (Table 1). Since the standard error of the observed mean is only 0.071, there can be no doubt that it differs significantly from the predicted value, but this is not a satisfactory way of interpreting the result, because the hypothesis might be supported by imprecise observations with small sample size but falsified by a large and accurate data set whose mean value differed only slightly from prediction.

Any character has some range within which any conceivable value must fall. For the S/E ratio in 16-cell colonies of *E. elegans* this range extends from nearly zero (1 sperm and 15 eggs) to nearly 500 (480 sperm and 1 egg), given that at least one male and one female gamete must be produced for reproduction to occur at all. Within this range, possible character states are defined by developmental constraints. In this case, the relevant constraint is that sperm packets are formed by four or five mitoses, but never fewer or more; this is an invariable rule in *Eudorina*. The optimization hypothesis predicts that the observed states will in turn form a special set of the possible states, characterized by a

TABLE 2. Hierarchical analysis of the data for 16-cell colonies. The 1% point for D with $N = 145$ is 0.135, so the values reported here are beyond the range of tables. A value of D is given for the comparison between conceivable and possible phenotypes, but only for the sake of illustration; no statistical meaning can be attached to a comparison of two theoretical distributions. MSD_{opt} is the mean squared deviation of the distributions from the optimal value of 3.345.

Level	Test of significance: Kolmogorov-Smirnov D	Index of magnitude		
		MSD_{opt}	Reduction in MSD_{opt}	Proportion of MSD_{opt} removed
1. All conceivable phenotypes equally probable	$(D = 0.145)$	75,362.6	—	—
2. All possible phenotypes equally probable		20,898.3	54,464.4	0.723
3. Observed phenotype frequencies	$D = 0.938$ $P < 0.01$	2.35	20,896.0	0.999
4. Only best possible phenotype present	$D = 0.862$ $P < 0.01$	0.007	2.34	—
5. Only best conceivable phenotype present		0	0.007	—

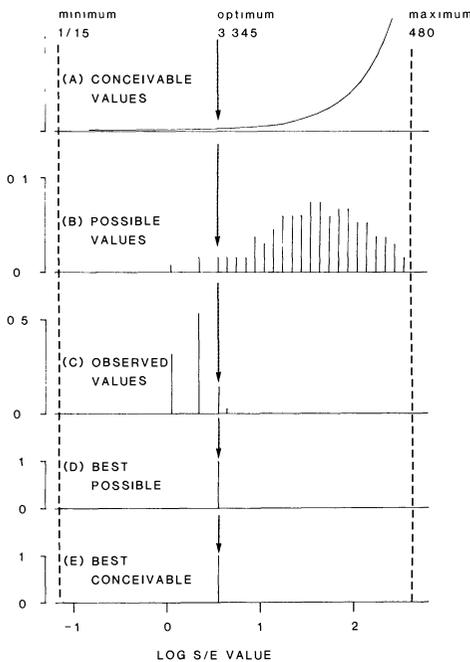


FIG. 1. Phenotype distributions relevant to the comparison of constraint and optimization hypotheses with observation. The y-axis is, in all cases, a frequency (see Table 2). A) The equiprobable distribution of conceivable S/E values. Note that since the x-axis is logarithmic the probability density increases by a constant factor from one interval to the next. The maximum value is set by the maximum (32) number of sperm per packet, and thus represents a weak developmental constraint, with-

high output of zygotes. The observed states should be clustered around a single phenotype associated with the greatest possible output of zygotes, within the constraint set of possible phenotypes. Finally, this phenotype should lie close to the ideal phenotype, which if it were attainable would maximize zygote production. There are, then, five relevant phenotype distributions: 1) the equiprobable distribution of all conceivable phenotypes; 2) the equiprobable distribution of all possible phenotypes; 3) the observed phenotype distribution; 4) the best possible phenotype; and 5) the best conceivable phenotype. These are illustrated in Figure 1.

To assess the roles of constraint and optimality in generating the observed distribution of phenotypes, two statistics are necessary. The first must have a known sampling distribution, in order to estimate the probability that the observations differ from some specified null hypothesis by chance; the second is needed to measure the magnitude of any significant difference. There is no standard procedure for assessing optimality hypotheses, but the techniques we have used are very broadly applicable. For a test of significance, we have used the cumulative frequency distribution of the absolute difference between character values and the predicted optimal value. The greatest difference between the distribution of observations and the distribution generated by a specified null hypothesis

out which conceivable values would extend to infinity. B) The equiprobable distribution of possible S/E values, assuming that sperm packets must contain either 16 or 32 sperm. C) The observed distribution. D) The best possible phenotype. E) The best conceivable phenotype.

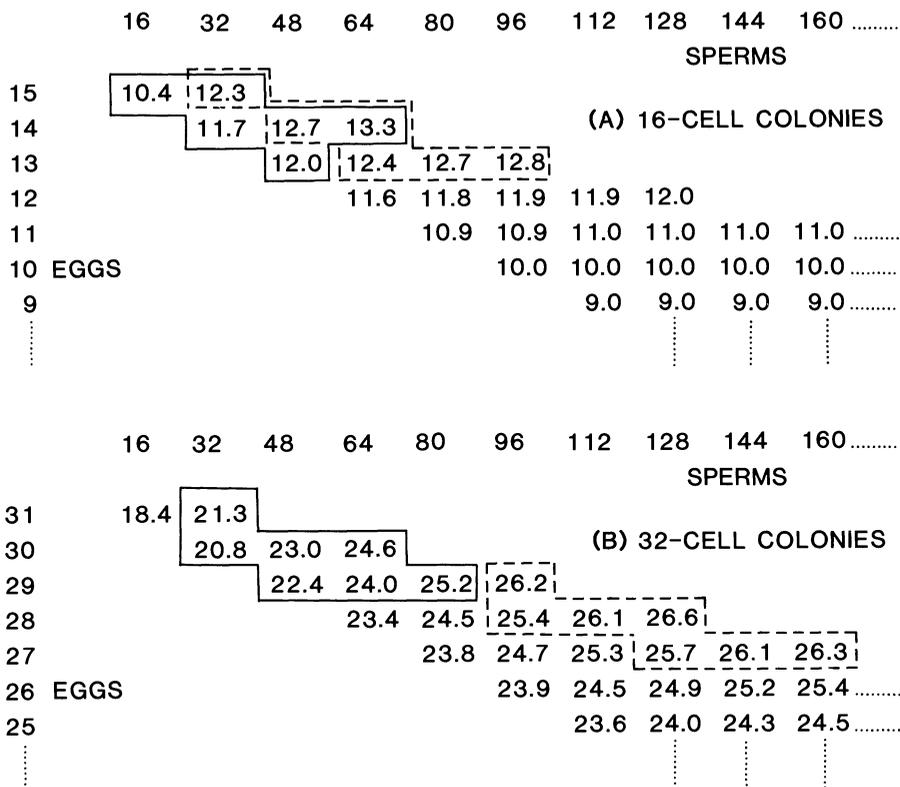


FIG. 2. Observed and optimal sets of phenotypes in self-fertilized monoecious colonies of *Eudorina elegans*. Possible values for the number of sperms are given along the top, and possible values for the number of eggs down the side. Entries in the body of the diagram are the expected number of zygotes produced by permitted combinations of sperm number and egg number. The observed set of phenotypes is surrounded by a solid line, the optimal set of equal size by a broken line, and the single best phenotype is indicated by an asterisk. The upper figure (A) refers to 16-cell colonies and the lower figure (B) to 32-cell colonies. In both cases, the possible phenotypes extend below and to the right of those indicated, but the phenotypes not shown are not included either in the observed or in the optimal sets.

is the Kolmogorov-Smirnov *D*-statistic (Siegal, 1956), which has a known sampling distribution and can be applied to any character measured on an ordinal scale or better. For an index of magnitude of effect, we have calculated the mean squared deviation from the optimal value (MSD_{opt}), which has properties similar to those of familiar variance measures, increasing from zero as the observations fall further away from the best conceivable phenotype identified by the optimization hypothesis. These statistics are given in Table 2. The constraint set includes a disproportionate number of low *S/E* ratios relative to the set of all conceivable phenotypes, but the observed distribution is still more strongly, and very significantly, biased towards low values. These low values represent an approach to the optimal value of 3.345, but the observations in turn differ from a unimodal population fixed for the best possible phenotype, which lies very close to the best conceivable phenotype. Developmental

constraint is by itself a major factor, accounting for 72.3% of the reduction in MSD_{opt} from that associated with the set of all conceivable phenotypes, and the optimization hypothesis accounts for 99.9% of the residual MSD_{opt} . There remains a small quantity of variation not accounted for either by constraint or by optimality.

The situation is illustrated in Figure 2, which compares the set of six observed phenotypes with the set of six phenotypes whose zygote production is maximal. These sets overlap, and there is no doubt that phenotypes producing large numbers of zygotes are disproportionately represented in the observations. However the observed set differs systematically from the optimal set, being shifted towards phenotypes with fewer sperm than predicted. We suggest that this discrepancy might be reduced by the inclusion of an effect of sperm size in the optimization model. It has been assumed that all sperm are equal, and our data show no effect of

sperm size on the proportion of eggs fertilized; however, the sperm are relatively large, and their substantial cytoplasmic contribution to the zygote may affect its viability. The greater viability of zygotes fertilized by larger sperm cannot be advanced post hoc as an explanation of our results, but the hypothesis can quite properly serve as the basis for a subsequent experiment. If it were found, it would reduce the mean squared deviation of the observations from a modified optimization hypothesis and account for the production of 16-sperm packets, which are always non-optimal under the present hypothesis. More profoundly, such an experiment could provide the materials for a model in which sperm size and sperm number were jointly optimized and in which the developmental constraint of the present model was itself explained as the outcome of optimal design.

In the 32-cell colonies, the discrepancy between observation and prediction is more marked. Against an observed mean S/E ratio of $1.636 \pm SE 0.082$, the predicted value is 4.409, and the optimal set of phenotypes does not overlap the predicted set (Fig. 1B). This is because the total number of cells is twice as great as in 16-cell colonies, while the number of sperms produced is about the same, except for the absence of colonies producing only 16 sperms. Since colonies with 32 cells are in a minority in our cultures, it is conceivable that selection acting on the more common form produces an inappropriate sex allocation phenotype in the less common form by a sort of evolutionary inertia—genes will be more effectively selected in the context in which they are most often expressed. However, this additional constraint does not appear to be testable by experiment.

In summary, we argue that developmental constraint alone biases S/E ratios towards the low values associated with high zygote production. However, the observed phenotypes are a highly nonrandom sample from the constraint set, characterized by high zygote production and clustered near the value predicted by the hypothesis of optimal design. A further improvement in predictive ability requires modifying the optimization hypothesis to accommodate such effects as that of sperm

size on zygote viability. If validated by experiment, such a model might account for the developmental constraint itself as a feature of optimal design and thus make it redundant as a level of explanation.

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