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# MEASURING THE COST OF REPRODUCTION. II. THE CORRELATION STRUCTURE OF THE LIFE TABLES OF FIVE FRESHWATER INVERTEBRATES

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The cost hypothesis states that any increment in present reproduction is associated with a decrement in the expectation of future reproduction. This follows from the limited quantity of resources available to organisms, so that increased allocation to present reproduction implies a withdrawal of resources from growth or maintenance and a consequent reduction of future fecundity or survival (Cody, 1966; Williams, 1966). This causal sequence is in turn held to imply a negative correlation between the present reproduction of individuals and their expected future reproduction when they experience the same conditions of life. In the first paper of this series (Bell, 1983) I have shown that these negative correlations do not exist in the life table of the rotifer Platvias patulus, when cultured under favorable conditions in the laboratory. Instead, the correlations between present fecundity and future survival or fecundity are generally zero or positive, whether we compare clonal mean values or the values for individuals within clones. The work that I shall describe here was undertaken to investigate the generality of the Platyias result, in order to eliminate the possibility that it arose from some special feature of the experimental organism. It will therefore lead to a general statement of the correlation structure of life histories observed under favorable conditions in the laboratory.

The basic experimental design follows Bell (1983), which is similar to that of Snell and King (1977). A number of asexual females are isolated in appropriate culture vessels and allowed to reproduce. Their offspring are removed as soon as possible after birth and in turn isolated. The founding female herself plays no further part in the experiment; the results of the experiment comprise observations of the reproduction of her progeny (and, if necessary, more distant descendants), cultured under conditions made as nearly uniform as possible, from birth until death. Small metazoans which can be maintained in small volumes of liquid medium are particularly convenient to culture, manipulate and score, and often have asexual life cycles of a few weeks. Five such organisms were chosen for detailed study.

A species of Aelosoma (Oligochaeta: Aelosomatidae), close to A. tenebrarum Vejdovsky, was isolated from tows through macrophytes in Lac Hertel, Mont St. Hilaire, southern Québec. It reproduces vegetatively by paratomy: a fission zone forms about two-thirds the way down the body, with the head of the new worm differentiating before detachment, so that the product of fission is an individual somewhat smaller than its parent but morphologically almost completely differentiated. Sexual structures were never observed in my material. In an early experiment the worms were cultured on tissue-culture plates (Linbro 76-033-05), using 3 ml of a stock suspension of the green alga Ankistrodesmus, which rapidly settles out and provides a green carpet on which the worms graze. This did not prove very satisfactory; many clones failed to reproduce, and it was often difficult to see the worms in the algal detritus. A single clone was allowed to proliferate and provided useful data. Most of the results described here, however, refer to a second experiment in which the worms were cultured in a soil-water me-

dium which after sterilization and refrigerator storage was allowed to stand uncovered at laboratory temperature for 48 h. Pristina (Oligochaeta: Naiadidae) is a second aquatic oligochaete which reproduces by paratomy. It is readily cultured and scored in Ankistrodesmus suspensions using 3 ml of medium in tissueculture plates. Our material was again isolated from macrophyte tows in Lac Hertel, and keys out close to P. aequiseta. Sexual structures were never observed. Philodina (Rotifera: Bdelloidea: Philodinidae) is a benthic rotifer from a class in which males or meiosis have never been reported. No specific identification was attempted; our material came from rock pools and moss washings sampled in a small rock outcrop in deciduous forest at Mont St. Hilaire. All samples were taken at least 2 m apart, and no more than one clone was developed from each sample. The animals were cultured in .1 ml of medium in tissue-culture microwells (Fisher 08-778). The culture medium was sterile soil-water to which bacteria isolated from rock-pool water taken at the sampling site were added and incubated at laboratory temperature for 48 h. Bdelloids produce a single asexual egg, huge relative to the size of the parent, every time they reproduce. *Cypridopsis* vidua (Ostracoda: Cypridae) is a very common ostracod which appears to be perennially asexual; no males appeared in our cultures. Our material was collected from natural populations (6 clones) and as contaminants of cladoceran cultures (18 clones). The animals were cultured in 3 ml of Ankistrodesmus suspension in tissue-culture plates. In the experiment reported here, they produced clutches of up to about 20 live young. Daphnia pulex (Cladocera: Daphniidae) is a common cladoceran of small ponds which is perennially asexual in Canada, though males can be induced in culture and sexual populations occur to the south. It produces either a clutch of up to 30 or so subitaneous eggs (which hatch and develop within the brood-pouch and are released as live young), or a clutch of two

dormant embryos enclosed within an ephippium. When cultured separately in 10 ml of Ankistrodesmus medium, frequently renewed, in small glass vials at laboratory temperature, the clutches are almost always subitaneous; those few individuals which produced ephippia have been excluded from the analyses reported here. Our material was collected from ponds in southern Ontario by Dr. P. Hebert, who has confirmed by electrophoresis that each clone is genetically distinct at a series of isozyme loci (Hebert and Crease, 1980; Loaring and Hebert, 1981). All five organisms were censused three times each week.

## RESULTS

Reproductive cost may manifest itself in two ways, which I have called the variable and acquired costs (Bell, 1983). The variable cost is the immediately causal relationship between increased present reproduction and subsequent reproduction or survival, and is detected by comparisons between individuals. The acquired cost is the relationship between increased present reproduction and subsequent reproduction or survival which has been created by long-continued selection in natural populations, but which is not necessarily expressed as a difference between individuals under the conditions of laboratory culture: it is detected by comparing the average values of groups of individuals. With the experimental design I have used, variable costs are detected by measuring the correlations between the reproductive characteristics of individuals within clones, and acquired costs by correlating the average values of different clones. An overall cost can be measured by using individuals from all clones in the analysis.

The variable survival cost was detected by calculating the linear regression of the output of reproductive propagules during some early period in the life history on the age at death, for individuals within a clone. An excess of negative regression coefficients (slopes) would support the cost hypothesis. With the ex-

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TABLE 1. Variable costs of reproduction. For each clone in each experiment the regressions of the age at death (survival cost) and fecundity later in life (fecundity cost) on the fecundity earlier in life of each individual were calculated. Entries in the body of the table are the number of cases in which the regression coefficient (slope) was positive or negative, both for all cases and for those in which the null hypothesis of zero slope was rejected at P < .05 with linear parametric regression.

				All r	esults	Resul P <	ts with	N
Mode of reproduction		Organism	Component	+	-	+	-	clones
		Aelosoma cf. tenebrarum	Survival	9	8	0	1	17
1.	Vegetative	(aelosomatid oligochaete)	Fecundity	10	7	2	0	17
	paratomy	Pristina cf. aequiseta	Survival	5	3	2	0	8
		(naiad oligochaete)	Fecundity	1	5	0	0	6
2.	Single large	Philodina sp.	Survival	1	17	0	6	18
	egg	(bdelloid rotifer)	Fecundity	7	11	0	0	18
		Cypridopsis vidua	Survival	15	9	1	1	24
3.	Many small	(cyprid ostracod)	Fecundity	15	9	2	0	24
	eggs	Daphnia pulex	Survival	9	7	0	0	16
		(daphniid cladoceran)	Fecundity	11	5	1	0	16

ception of *Philodina*, all the experiments gave an excess of positive coefficients, with overall 38 positive and only 27 negative results (Table 1). *Philodina* was very different: of the 18 clones studied, 17 showed the expected negative relationship between early reproduction and longevity (P < .001), and six of these results were in themselves formally significant at P = .05. This evidence strongly supports an association between increased early fecundity and decreased longevity in *Philodina* while the remaining four organisms give no support for the cost hypothesis. The variable fecundity cost was detected by calculating the linear regression of fecundity earlier in life on fecundity later in life, to obtain a positive or negative value for each clone, as before. No experiment showed a significant negative result, and overall there was a non-significant excess of positive coefficients, with 44 positive and 37 negative results from the 81 clones tested (Table 1).

The single clone of *Aelosoma* raised in green-water culture (N = 122 individuals) confirmed these results. Table 2 shows that the correlations between present and subsequent fecundity, or between present

TABLE 2. Attempt to demonstrate variable costs of reproduction within a single large clone of *Aelosoma*. *BX-Y* is the number of fissions between ages X and Y; w is the age of death (of individuals surviving to age Y at least). Entries in the body of the table are parametric correlation coefficients, with n.s. indicating P > .05.

	B0-9	B10–19	B20-29	B30–39	w
<u>B0-9</u>	*	188 n.s.	250 n.s.	+.267 n.s.	123 n.s.
B10–19		*	+.140 n.s.	007 n.s.	+.032 n.s.
B20–29			*	057 n.s.	282 n.s.
B30-39				*	+.370 P ~ .05
w					*

TABLE 3. Acquired costs of reproduction. For each clone in each experiment the mean age at death (survival cost) and the mean fecundity later in life (fecundity cost) were regressed on the mean fecundity earlier in life. Entries in the body of the table are the linear parametric regression coefficients (slopes), together with their standard errors and the associated probability of chance departure from zero slope. Calculating nonparametric correlation coefficients in no case produces a result significant at P < .05.

Mode of reproduction	Organism	Component	Slope ± 1 SE	Р	N clones
Vegetative paratomy	Aelosoma cf. tenebrarum (aelosomatid oligochaete) Pristina cf. aequiseta (naiad oligochaete)	Survival Fecundity Survival Fecundity	$\begin{array}{r} -3.166 \pm 7.334 \\184 \pm .358 \\ +18.45 \pm 19.39 \\305 \pm .196 \end{array}$	.67 .61 .38 .20	17 17 8 8
Single large egg	Philodina sp. (bdelloid rotifer)	Survival Fecundity	$-1.674 \pm 2.428 \\ +.487 \pm .368$	.50 .20	18 18
Many small eggs	Cypridopsis vidua (cyprid ostracod) Daphnia pulex (daphniid cladoceran)	Survival Fecundity Survival Fecundity	$\begin{array}{r}188 \pm .773 \\ +.727 \pm .890 \\085 \pm .234 \\ +.241 \pm .163 \end{array}$	.81 .42 .72 .16	24 24 16 16

fecundity and the age at death, are generally near zero, the only significant result being a positive correlation between fecundity rather late in life and the age at death.

An attempt to demonstrate acquired costs of reproduction is shown in Table 3. The average value of fecundity early in life is regressed on average fecundity later in life (the acquired fecundity cost) or on mean longevity (the acquired survival cost) for all clones in a given experiment, the test statistic being the linear regression coefficient. In no case was a significant negative relationship observed. Analysis of residuals and the calculation of nonparametric correlation coefficients failed to uncover any effect which might have been overlooked by the linear parametric analysis. It is particularly noteworthy that the very strong variable survival cost detected in *Philodina* does not imply the existence of an acquired survival cost.

Table 4 shows the overall costs as linear regressions of individual values. The strong within-clone effect exhibited by *Philodina* produces a highly significant negative slope when all individuals are plotted on the same graph, but otherwise

TABLE 4. Overall costs of reproduction. For each experiment the age at death (survival cost) and fecundity later in life (fecundity cost) were regressed on fecundity earlier in life, for all individuals. Entries in the body of the table are the linear parametric regression coefficients (slopes) of these graphs, together with their standard errors and the associated probability of chance departure from zero slope.

Mode of reproduction	Organism	Component	Slope ± 1 SE	Р	N indi- viduals
Vegetative paratomy	Aelosoma cf. tenebrarum (aelosomatid oligochaete) Pristina cf. aequiseta (naiad oligochaete)	Survival Fecundity Survival Fecundity	$+.205 \pm 1.906$ +.185 ± .107 +4.293 ± 3.775 414 ± .186	.91 .09 .26 .03	102 102 78 53
Single large egg	Philodina sp. (bdelloid rotifer)	Survival Fecundity	$-2.619 \pm .495$ $011 \pm .083$	.001 .90	138 126
Many small eggs	<pre>{ Cypridopsis vidua (cyprid ostracod) Daphnia pulex (daphniid cladoceran)</pre>	Survival Fecundity Survival Fecundity	$+.101 \pm .217$ +.435 ± .198 +.010 ± .082 +.020 ± .022	.64 .03 .91 .36	269 231 162 160



FIG. 1. Test for an acquired fecundity cost in *Cypridopsis*. The partial correlation coefficient was calculated for each of the 28 possible pairwise combinations of mean clonal fecundity during eight ageclasses spanning most of adult life. The three most extreme observations have .01 < P < .05. The cost hypothesis predicts a substantial excess of negative values.

there is little consistent pattern in the data. Both *Pristina* and *Cypridopsis* show a (barely) significant regression of early on late fecundity, but whereas the former is negative, the latter is positive.

The age-classes used in these analyses were chosen so as to maximize, as far as possible, the information that could be extracted from an experiment and summarized in a single statistic. Thus, when regressing early on late fecundity, the two age-classes were chosen to be of equal duration, with the later age-class not extending so far into old age that the number of surviving individuals would be insufficient for analysis. This choice is subjective, and might cause important effects to be overlooked, but more detailed analyses have revealed nothing of consequence which is not shown in the summary statistics of Tables 1, 3, and 4. An example is shown in Figure 1, which illustrates the apparent absence of any ac-

quired fecundity cost among the 24 clones of the ostracod Cypridopsis. Between the age at which reproduction has begun and that at which few individuals survive, the lifespan was divided into eight ageclasses, for each of which the mean fecundity of each clone was calculated. According to the cost hypothesis, the partial correlation between mean fecundity at any given age and that at any subsequent age should be negative. Figure 1 shows that the partial correlations of the 28 possible pairwise comparisions between the eight age-classes are not predominantly negative; instead, they are distributed roughly symmetrically about zero, with a slight excess (16 vs. 12) of positive results, the average of the coefficients being  $+.0758 \pm .0637.$ 

## DISCUSSION

The results of these experiments enable us to generalize the conclusion reached from work on the rotifer Platyias (Bell, 1983): the correlation between present reproduction and the expectation of future reproduction in asexual organisms maintained under favorable conditions in the laboratory is not negative, but is instead zero or positive. We are left with two questions. First, what is the meaning of the negative correlation between early fecundity and longevity observed in Philodina? And second, what relevance do these observations have to the general validity of the cost hypothesis?

Some small metazoans such as rotifers and gastrotrichs have determinate growth: embryogenesis proliferates a number of cells which subsequently differentiate but which do not increase in number throughout postembryonic life (Martini, 1907, 1912; Van Cleave, 1914; Shull, 1918; Pai, 1928; Birky and Field, 1966; review by Van Cleave, 1932). It is not yet clear, even in the intensively studied nematode *Caenorhabditis elegans* (Hirsh, 1979), to what extent this determinism applies to the germ line. However, reproduction often ceases completely when a certain number of eggs have been produced, though the individual may survive for a considerable period after the extrusion of the last egg, as in the rotifers Proales sordida (Jennings and Lynch, 1928), P. decipiens (Noyes, 1922), Platyias patulus (Bell, 1983) and Philodina (present work). In the gastrotrich Lepidodermella squammata surviving females produce four eggs (Sacks, 1964; occasionally five according to Brunson, 1949), while Chaetonotus tachyneusticus produces only two (Brunson, 1949), regardless of lifespan or ration. It is probable, therefore, that in many rotifers and gastrotrichs each individual can produce only a rather small and more or less fixed number of eggs. A life-history of this sort can generate very misleading correlations. Let the total number of eggs produced by an individual be B, with the first egg being produced at age a and death occurring at age w. The rate of egg production over the adult lifespan is then B/(w - a), and the cost hypothesis leads us to expect this rate to be negatively correlated with the rate of survival, which for any given individual, can be estimated only by w. If we plot B/(w - a)on w for the gastrotrich Lepidodermella squammata we obtain a very satisfactory negative regression (Fig. 2A). But almost all of the individuals in this figure produced exactly four eggs; moreover, while the postreproductive span is long and variable, the prereproductive period is much shorter and varies relatively little. The graph therefore amounts to little more than a plot of 1/w on w, and the pattern we observe is created by statis-

FIG. 2. Misleading relationships between reproductive rate and longevity in animals with determinate growth. A. Gastrotrich *Lepidodermella squammata* (Sacks, 1964 Table 1). Solid circles indicate individuals which produced four eggs, hollow circles those which produced three. B. Rotifer *Proales decipiens* (Noyes, 1922 Table 2). Two series, each of 50 individuals, are differentiated by solid and hollow symbols. C. Rotifer *Proales sordida* (Jennings and Lynch, 1928 Table 26), showing four different cultures. Individuals displayed on plots for each species are monoclonal.



TABLE 5. Misleading relationships between present and future fecundity in an animal with determinate
growth. Entries in the table are (upper) partial correlation coefficient between fecundity on day X, BX,
and fecundity on a subsequent day Y, BY, the linear effect of $BZ$ ( $Z \neq X, Y$ ) having been removed; and
(lower) associated probability of chance departure from zero correlation. For Proales decipiens, from
Table 2 (June series) of Noyes (1922).

	B1	B2	B3	B4	B5	B6
B1	_	211 .386	300 .212	349 .143	364 .126	160 .512
<i>B2</i>		_	145 .554	$378\\.111$	360 .130	400 .090
B3			_	402.088	724 .001	+.089 .718
B4				_	428 .067	+.213 .380
B5					_	+.046 .851
B6						_

tical autocorrelation rather than by reproductive cost. This argument applies to any organism with determinate reproduction, though it is not often that the results are as dramatic. Figures 2B and 2C display similar plots for the monogonont rotifers *Proales decipiens* and *P*. sordida. For the latter species there is some indication that B/w may increase with w when w is small, but this need imply nothing beyond the presence of sick or crippled individuals which are little able either to survive or to reproduce. Beyond a certain age all surviving individuals produce similar numbers of eggs, creating a negative relationship between B/w and w even in the absence of any direct effect of reproduction on survival.

Since *Philodina* has a highly determinate life history, with reproduction plunging steeply from about two eggs per 10 days during ages 20 through 80 days to nearly zero by day 100, the negative relationship between fecundity and longevity observed within clones of this organism is more economically explained as a statistical artefact arising from reproductive determinism than as an instance of reproductive cost. The same objection can be lodged against any similar study of organisms with determinate growth, including the widely-cited observations on the rotifer *Asplanchna* brightwelli made by Snell and King (1977). Moreover, it explains why, in *Philodina*, a variable cost but no acquired survival cost was found, since the clones used differed substantially in lifetime egg production.

But if this explanation is valid, we should expect also to observe a variable fecundity cost: those individuals which produce many eggs early in life will have few left to export later in life. Data for *Proales sordida* confirm this expectation: the partial correlation coefficients between present and future fecundity, for individuals within a clone, are negative in 12 of 15 possible pairwise comparisons, the largest nine coefficients all being negative (Table 5). In Philodina this effect was at first overlooked because the age-classes chosen for comparison, on the grounds of the availability of large sample sizes, were situated well within the fertile period of adult life (days 0-29 and 30-59). If we instead compare early fecundity with fecundity at the end of the period of egg production (days 80–109) then the expected negative relationship appears (Fig. 3). The many individuals close to the origin of this graph are those which concentrated their reproduction in the middle of the lifespan; the important



FIG. 3. Relationship between fecundity in widely-separated age-classes of *Philodina*. Numbers are number of individuals at given point; all individuals surviving to day 109 are plotted.

point is that when the total number of eggs is fixed and small, no individuals can produce many eggs both early and late in life.

No such negative relationships between early fecundity and survival or later fecundity were found in Platyias, despite its determinate growth. This appears to be because the total number of eggs produced per lifetime is more variable in *Platvias* than in comparable organisms. The coefficient of variation of total egg production is very low in Lepidodermella (CV = 19.0, Sacks, 1964 Table 1) and Proales decipiens (CV = 13.8, Noyes, 1922 Table 2, June series). It is rather greater in *Proales sordida* (CV = 34.2, Jennings and Lynch, 1928 Table 2) because the frequency distribution is negatively skewed, but much greater in *Platvias* (CV = 56.8), the frequency distribution being very broad. Thus we find a strong autocorrelated negative relationship between reproductive rate and longevity in Lepidodermella, a weaker but still negative relationship in Proales, and a very weak, or even positive, trend in Platvias.

In short, determinate growth necessarily generates correlations within the life table which mimic those which we expect

TABLE 6. Relationship between successive periods of egg production in *Lepidodermella squammata* (Sacks, 1964 Table 1). *T1* is the interval between hatching and production of the first egg; *T2* the interval between the first and second eggs; and so forth, with no individuals producing more than four eggs. Entries in the body of the table are partial correlation coefficients, the linear effect of the two intervals not directly involved in a given comparison having been removed, and associated probabilities; n.s. indicates P > .05.

the second se				
	TI	T2	T3	T4
<u>T1</u>	_	+.185 n.s.	+.481 P < .001	011 n.s.
Т2		_	+.256 $P \sim .05$	+.145 n.s.
Т3			_	016 n.s.
T4				_

to be produced by reproductive cost, and great caution is necessary when interpreting data of this sort. A possible approach is to look, not at the overall rate of egg production, but rather at the timing of successive eggs. The cost hypothesis leads us to expect a negative correlation between successive intervals of egg production, since if resources are quickly squandered to produce an egg it will take longer to assimilate sufficient resources to produce the next, while a careful husbanding of resources will enable two eggs to be produced in rapid succession. Such an hypothesis seems to involve no autocorrelation. However, when the data for *Lepidodermella* are analyzed, the partial correlations between successive intervals of egg production turn out to be predominantly positive (Table 6). We are back, then, to the zero or positive effects found in organisms with indeterminate fecundity, and the negative relationship between fecundity and survival observed in *Philodina* turns out to be a special case yielding little or no information about general principles.

The other four organisms involved in these experiments continue to reproduce throughout life, and though fecundity



FIG. 4. The relationship between longevity and the rate of reproduction in Cladocera. Plotted points represent, as nearly as possible, midpoints of the ranges of values given by an author or a number of authors. Species and authorities are as follows. 1: Sida crystallina (Zaffagnini, 1964; Green, 1966; Bottrell, 1975a, 1975b). 2: Latonopsis breviremis (Montu, 1973e). 3: Pseudosida bidentata (Montu, 1973e). 4: Diaphanosoma brachyurum (Weglenska, 1971; Montu, 1973a, Dumont et al., 1975). 5: Daphnia longispina (Banta, 1939; Green, 1956; Weglenska, 1971). 6: D. carinata (Navaneethakrishnan and George, 1971). 7: D. magna (Mac-Arthur and Baillie, 1929; Anderson, 1932; Anderson and Jenkins, 1942; Green, 1954, 1956; Zaffagnini, 1964). 8: D. pulex (Frank et al., 1957; Hrbackova-Esslova, 1962; Taub and Dollar, 1968; Arnold, 1971). 9: D. obtusa (Green, 1956; Hrbackova-Esslova, 1962; Elbourn, 1966; Kryutchkova and Sladacek, 1969). 10: D. galatea (Hall, 1964). 11: D. hyalina (Green, 1956; Korinek, 1970; Bottrell, 1975a, 1975b; Vijverberg, 1976). 12: D. schodleri (Lei and Clifford, 1974). 13: Simocephalus vertulus (Frank, 1952; Green 1956, 1966; Bottrell, 1975a, 1975b). 14: S. acutirostris (Murugan and Sivaramakrishnan, 1973). 15: Ceriodaphnia cornuta (Michael, 1962; Gras and Saint-Jean, 1969; Burgis, 1973; Montu, 1973d, Murugan, 1975). 16: Moina micrura (Gras and Saint-Jean, 1969; Burgis, 1973; Montu, 1973b). 17: M. reticulata (Montu, 1973c). 18. M. macrocopa (Terao and Tanaka, 1930; Ingle, 1933; Bellosillo, 1937). 19: Eurycercus lamellatus (Green, 1956; Bottrell, 1975a, 1975b). 20: Chydorus sphaericus (Keen, 1967; Weglenska, 1971; Bottrell, 1975a, 1975b). 21: Alona affinis (Green, 1956; Bottrell, 1975a, 1975b). 22: Acroperus harpae (Bottrell, 1975a, 1975b). 23: Graptoleberis testudinaria (Bottrell, 1975a, 1975b). 24: Pleuroxus uncinatus (Bottrell, 1975a, 1975b). 25: P. denticulatus (Keen, 1967). Cf. Lynch, 1980 Fig. 4. Reproductive rate is here plotted as B/(w - a + 1) divided by the cube of length, and therefore approximates the rate of egg production per day of adult life per unit adult volume. It should be noted that multiplying this quantity by egg volume (extensive data in Green,

may decline somewhat in old age, this does not involve the exhaustion of a fixed and finite number of potential propagules. None of them show any sign of the consistent negative correlation between present and future reproduction anticipated by the cost hypothesis. Indeed, one of the most interesting findings of these experiments was the way in which the correlations found between life-history characters when species are compared actually reverse sign when genotypes or individuals are compared.

Figure 4 shows the relationship between the rate of reproduction and longevity in a number of species of Cladocera. Graphs like this cannot be taken wholly at face value: the plotted points usually attempt to estimate the midpoints of very variable sets of data, and the axes are in any case autocorrelated. However, all I am concerned to demonstrate here is that such graphs can be constructed, and appear to make sound intuitive sense: early death is associated with a greater rate of reproduction during adult life. It is, I think, universally imagined that this relationship is at least indirectly causal, with early death following from the stress imposed by rapid reproduction, so that we are invited to infer a correlation between individuals from the observed correlation between species. But Figure 5 shows that when we culture one of the species from Figure 4, not only do we not obtain the expected negative relationship, we actually discover the opposite. These data are clonal means for *Daphnia pulex*; Figure 6 shows that the same positive correlation holds for individuals within a large clone of Aelosoma.

This result seems, from the experiments I have performed, to be very general: present and future reproduction are

 $\leftarrow$ 

<sup>1956),</sup> so that it becomes a rate of production of egg volume per unit adult volume, greatly increases the scatter of the points, since the longer-lived species tend to produce larger eggs.



FIG. 5. Relationship between the rate of reproduction and longevity in a single species of cladoceran, cultured under uniform conditions. Data for *Daphnia pulex*, from this study. Plotted points are clonal means. Correlation coefficient is r = +.537, P < .01.

not negatively correlated both within and between species, but are rather negatively correlated between species and positively correlated within species.

Reproductive cost has often been used merely as a concept (sensu Peters, 1980; see also Rigler, 1975; a non-testable device for ordering explanations) rather than as an hypothesis (i.e., an explicitly defined relationship between measurable quantities). As Sterns (1976) remarked some time ago, until we can measure reproductive cost "we will be left with unsatisfactory, post hoc explanations." The results I have described above falsify one particular cost hypothesis-that present and expected future fecundity are negatively correlated within or between clones raised under favorable conditions of culture-but my experimental design does not test other possible hypotheses. In particular, the lack of any controlled manipulation in the experiments raises two problems involving the interaction between genotype and environment. The first is that accident (injury at birth, for example) may create differences between individuals, even within a clone cultured under conditions made as nearly uniform



FIG. 6. Relationship between the rate of reproduction and longevity for individuals within a single clone of *Aelosoma*. Open circles represent individuals which did not reproduce. Variance of reproductive rate is large for individuals which died young, since they produce either a single offspring or none during their few days of life. Variance decreases with increasing longevity; the tendency for mean reproductive rate to increase with longevity is shown by the crosses, which indicate mean reproductive rate at 10-day intervals of longevity.

as possible. Individuals which by chance remain uninjured might be able to reproduce more and survive better at any age than injured individuals, giving rise to the positive correlations observed in my experiments. Ideally, this question should be settled by experiments in which present reproduction can be manipulated without directly affecting expected future fecundity. Experiments of this sort have generally yielded results which support the cost hypothesis (Askenmo, 1979; Dean, 1981; Partridge and Farquhar, 1981; Brown, 1982; Tallamy and Denno, 1982; Feifarek et al., 1983), though there are some exceptions (De Steven, 1980) and some results are difficult to interpret straightforwardly: Dean (1981), for ex-

ample, found that virgin female grasshoppers lived longer than mated females, despite producing eggs of similar size at the same rate. The second difficulty is that because these experiments expose organisms freshly collected from natural populations to novel conditions of culture, they may demonstrate only that fitness components are positively correlated in new environments, with some genotypes being preadapted for laboratory culture. The first possibility might explain positive correlation between present and expected future fecundity between individuals within clones (but not between clonal means), while the second could account for positive correlations between clones (but not between individuals within clones). A combination of both would explain the results that I have obtained, at the expense of invalidating the obvious procedure for measuring reproductive cost and requiring that a new cost hypothesis be constructed. The second point is crucial: if life-history theory is to be founded on reproductive cost, it must be founded on a particular cost hypothesis which specifies the protocol for its own possible falsification. Naturally, that hypothesis may be different for organisms which reproduce in different ways, with a general concept of cost being useful only in directing us towards promising hypotheses.

Finally, these experiments concern only the physiological cost of reproduction expressed by organisms reared under favorable conditions in isolation. It is possible that such costs are in themselves very small, but would greatly reduce potential reproduction in the presence of predators or competitors. An experiment designed to test this possibility will be described in a later paper in this series.

### SUMMARY

Previous work on the rotifer *Platyias* patulus showed that the correlations between present reproduction and future reproduction or survival were zero or positive. This paper shows that the same conclusion holds for five other asexual

freshwater invertebrates, reproducing in diverse ways: two oligochaetes which reproduce by paratomical fission, a bdelloid rotifer which produces a single large egg, and an ostracod and a cladoceran, which produce many small eggs. In almost all cases, individuals or clones with greater present reproduction have as great or greater an expectation of future reproduction. The bdelloid rotifer Philodina was an exception to this rule, these being a strong negative correlation between early fecundity and longevity for individuals within a clone. However, this is shown to be an outcome of determinate growth rather than an expression of reproductive cost. It is concluded that despite the negative correlation of present with future reproduction commonly observed when different species are compared correlations between individuals within species are generally positive.

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