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EVOLUTIONARY AND NONEVOLUTIONARY THEORIES
OF SENESCENCE

Theories of senescence fall into two categories. The first includes purely physiological hypotheses, which treat senescence either as the inevitable effect of unavoidable cellular wear and tear, or as the consequence of a gradual accumulation of toxins or radiological damage (see Weismann 1882; Metchnikoff 1907; Pearl 1928 for the early contributions to the present extensive literature reviewed by Comfort 1979). The second includes evolutionary hypotheses which interpret senescence as a characteristic which has evolved either because of the virtual absence of selection against degenerative changes in old age (Medawar 1952; Edney and Gill 1968), or because of positive selection for mutations which increase early reproductive success even when they drastically reduce the expectation of reproduction later in life (Williams 1957). These two categories have been developed quite separately, so that the most authoritative recent review of senescence (Comfort 1979) gives only a muddled account of modern evolutionary theories, while the most elegant recent attempt to discriminate between rival evolutionary theories (Rose and Charlesworth 1980) fails to mention nonevolutionary alternatives. The present paper describes an attempt to distinguish between evolutionary and nonevolutionary theories by experiment.

Evolutionary theories of senescence rely on age-specific differences in the contribution of reproduction to overall fitness, and senescence will evolve only if an increment in reproduction at some earlier age will yield a greater increase of fitness than an equal increment at subsequent ages. Clearly, this can be the case only when it is possible to distinguish unequivocally between parent and offspring, or, more precisely, between soma and germ line. Consider a protozoan reproducing by binary fission, in which the two fission products are equal in size and will both undergo a subsequent fission after the same lapse of time. We might regard this as a description of a parental cell which gives rise to an offspring whose prospects are the same as its own, or of a parental cell which dies in giving rise to two identical offspring. Since these descriptions are formally identical, there are no age-specific effects, and senescence will not evolve. The same argument applies, with only slightly lesser force, to a metazoan reproducing vegetatively by paratomical fission, in which the two fission products are similar in size and both require only a small amount of growth and differentiation to regain the actively reproducing adult state. It will apply with much less force to architomical fission, in which a large parental individual proliferates vegetatively a number of smaller progeny; and it will not apply at all to ovigerous reproduction, the case for which evolutionary theories of senescence are intended. By contrast, purely physiological theories of senescence make no necessary distinction between these different modes of reproduction: an inevitable process of cellular deterioration, or the poisoning of cells by accumulated metabolites, radiation, or oxidation will occur

whether the reproductive propagule is a single cell or a larger or smaller aggregate of cells.

The most important expression of senescence is a decrease in the rate of survival with age. Evolutionary theories suggest that the rate of survival should decrease with age in ovigerous organisms, but remain constant when reproduction is paratomical; nonevolutionary theories predict that no such differences should be observed. We can therefore distinguish between these two categories by measuring the age-specific rates of survival of organisms with diverse modes of reproduction in isolated laboratory culture.

I should emphasize that the arguments and experiments set out in this note apply only to the senescence of individuals, and not to that of lineages. The very large literature on temporal trends in the fission rate of protozoan clones maintained in isolate culture (reviewed by Jennings [1929]) is of no direct relevance to the problem examined here, and together with the limited data for metazoans will be reviewed elsewhere.

The distribution of senescence among major metazoan taxa has been reviewed recently by Comfort (1979). He documents strong evidence for senescence in virtually all members of ovigerous taxa (hydromedusae, nematodes, rotifers, crustaceans, insects, molluscs, and vertebrates) which have been maintained and observed throughout life. In architometal animals (sponges and nemertean) the evidence is inconclusive, and positive evidence against the occurrence of senescence is strongest in paratomical forms such as actinarians, *Hydra*, aelosomatid and naiad oligochaetes, and planarians. Some of this work (especially that involving *Hydra*) has been the subject of much controversy, however, and a direct experimental test of the prediction seemed desirable.

Six asexual freshwater invertebrates were chosen so as to make the suggested comparison as powerful as possible. *Aelosoma tenebrarum* and *Pristina aequisetata* are small oligochaetes which reproduce vegetatively by paratomy; *Philodina* sp. is a bdelloid rotifer which produces a single large egg; *Platyias patulus* is a monogonont rotifer; *Cypridopsis vidua*, a cyprid ostracod; and *Daphnia pulex*, a daphniid cladoceran, all of which produce several or many relatively small eggs. *Philodina* can be compared with *Platyias*, *Cypridopsis*, and *Daphnia* to exclude effects caused by propagule size alone; *Philodina* and *Platyias* can be compared with *Cypridopsis* and *Daphnia* to exclude any effect attributable to the highly determinate growth of the two former taxa. The crucial comparison then lies between the two vegetatively reproducing oligochaetes and the other four ovigerous animals.

A number of clones of each organism, freshly collected from natural populations, were grown in the laboratory, and the age at death of each isolated individual recorded. The data for *Aelosoma* and *Pristina* refer to anterior fragments. Details of culture conditions are given elsewhere (Bell 1983). The relationship of survival rate to age is given in table 1, which shows highly significant decreases in the survival rate of older individuals in each of the four ovigerous animals, but no change in survival rate with age for the two paratomical animals. To eliminate the possibility that heterogeneity in survival rates between clones might contribute to this result, large clones of *Aelosoma tenebrarum* ($N = 122$) and *D. pulex* ($N =$

TABLE 1
RELATIONSHIP BETWEEN SURVIVAL RATE AND AGE IN SIX FRESHWATER INVERTEBRATES WITH DIVERSE MODES OF REPRODUCTION

Mode of Reproduction	Species	<i>N</i>	Regression b_1	Regression b_2
Vegetative paratomy	<i>Aelosoma tenebrarum</i> (aelosomatid oligochaete)	211	+0.001020 ± 0.000389 <i>P</i> = .0142	+0.000035 ± 0.000008 <i>P</i> < .0001
	<i>Pristina aequisetum</i> (naiad oligochaete)	80	-0.002451 ± 0.002314 <i>P</i> = .310	+0.000279 ± 0.000107 <i>P</i> = .0242
Ovigerous (single large egg)	<i>Philodina</i> sp. (bdelloid rotifer)	142	-0.004467 ± 0.000475 <i>P</i> < .0001	-0.000011 ± 0.000015 <i>P</i> = .449
Ovigerous (many small eggs)	<i>Platyias patulus</i> (monogonont rotifer)	321	-0.011112 ± 0.001353 <i>P</i> < .0001	-0.000655 ± 0.000117 <i>P</i> < .0001
	<i>Cypridopsis vidua</i> (cyprid ostracod)	275	-0.003533 ± 0.000252 <i>P</i> < .0001	-0.000004 ± 0.000005 <i>P</i> = .370
	<i>Daphnia pulex</i> (daphniid cladoceran)	163	-0.009869 ± 0.001113 <i>P</i> < .0001	-0.000166 ± 0.000034 <i>P</i> = .0002

NOTE.—*N* is the number of individuals cultured. The regression coefficient b_1 is the slope of the parametric least-squares regression between the fraction of individuals surviving from the previous age-class (transformed as arcsin square-root into angles in radians) and age in days; the standard error and the associated probability of chance departure from $b_1 = 0$ are also given. Regressions are weighted by sample size. The regression coefficient b_2 is the second-order coefficient of the best-fitting quadratic regression. Note that: (1) b_1 is consistently negative for ovigerous but not for paratomical animals; (2) b_2 is either zero or negative for ovigerous animals, indicating that the rate of survival not only decreases with age but tends to decrease more quickly with advancing age. These cultures are polyclonal; results for monoclonal cultures of *Aelosoma* and *Daphnia* are given in the text.

199) were studied in a second series of experiments. For *D. pulex* the regression of survival rate on age, appropriately transformed (see legend to table 1), had a slope $b_1 = -0.01158 \pm 0.00128$ ($P < .0001$), while for *A. tenebrarum* the regression coefficient was -0.00410 ± 0.00278 ($P = .175$).

These experiments therefore clearly demonstrate a senescent decrease in the rate of survival among ovigerous organisms but not among those reproducing vegetatively by paratomy. They give powerful support to the idea that senescence evolves as a consequence of natural selection acting on age-specific rates of reproduction.

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