The Cost of Reproduction in a Freshwater Copepod

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Summary. An experimental study of the copepod *Mesocyclops edax* documented that females which reproduced throughout their lifetime survived at a lower rate than unmated females which did not reproduce. This cost of reproduction was most apparent in animals receiving periodic, non-lethal temperature stress. However, among reproductive females, no significant correlations were detected between reproductive output and survival, suggesting caution concerning the application of cost of reproduction arguments to a population of females in which clutch size is seen to vary.

Introduction

The idea that current reproduction compromises future survival illustrates the assumption of trade-offs, fundamental to theoretical analyses of life history variation (Stearns 1976). This "cost of reproduction" argument underlies the semelparity-iteroparity question because without some cost, iteroparity will always be superior (Bell 1980). Most examples of trade-offs come from comparisons across taxa. It is preferable to compare populations of the same species, as Bell (1980) did using data collected by Leggett and Carscadden (1978 and cited in Bell) for the shad *Alosa sapidissima*. Populations which evidenced the greatest fecundity were least likely to show repeat spawning. However, such comparisons do not answer the question of whether two individuals of the same population, which allocate different amounts of energy to reproduction, will differ in their survival probabilities.

Several recent attempts to investigate experimentally the cost of reproduction have not always produced supporting evidence. Snell and King (1977) compared clones of the rotifer *Asplanchna brightwelli* cultured in the laboratory. Clones which showed high, early fecundity had reduced survival probabilities compared to other clones which produced fewer eggs over a longer time. Tallamy and Denno (1982) and Browne (1982) also found evidence of a negative correlation between reproductive output and longevity in a hemipteran and a brine shrimp, respectively. However, Dean (1981) found no cost of reproduction in a grasshopper, while Giesel and Zettler (1980) obtained positive correlations among several fitness measures in drosophila.

In this study we ask whether female copepods not allowed to mate and produce eggs show higher survivorship than reproducing individuals. The freshwater cyclopoid copepod *Mesocyclops edax* (Forbes) does not reproduce unless mated, and one mating is sufficient for lifetime reproduction. Adults do not grow, so the trade-off is limited to survival vs. reproduction. Preliminary experiments indicated that virgin females survived longer than reproductive females, as was observed for the hemipteran *Dysdercus fasciatus* (Clarke and Sardesai 1959) and the carabid *Agonum fulginosum* (Murdoch 1966). However, implicit in cost of reproduction arguments is the idea of surviving through occasional periods of food scarcity, escaping damage from predators, etc., which call on energy reserves that may or may not have been expended in previous reproduction. In a benign laboratory setting such energy demands are minimal or absent. We used a sub-lethal temperature shock to simulate this stress. The shock was of short duration (1 h every 4 days) so that the effect would not be increased metabolic rate, but rather weak-bond structural alterations of protein structure and nucleic acid protein interactions (Hochachka and Somero 1973). We presume that repair of these effects requires energy expenditure by the organism.

In addition, we examined the relationship between reproductive output and longevity for mated females. In this experiment no temperature shock was utilized; instead we ask whether individuals which produce the most eggs do so at some cost in their length of life.

Methods

Immature females (CIV or CV) collected from Lake Thonotosassa, Hillsborough County, Florida were placed individually or with a mature male in 50 mm petri dishes containing 10 ml of defined medium (D'Agostino and Provasoli 1970) supplemented with Huttner's trace elements (Murphy 1970). Copepods were maintained on a 14:10 LD cycle at 30°C (25°C in one additional life table) and fed newly hatched *Artemia salina* nauplii and the algae *Cryptomonas erosa var. reflexa* Marsson ad lib. The medium was changed every other day.

To determine the maximum sub-lethal thermal stress, groups of ten virgin females, each in 10 ml of medium in a separate test tube, were placed in water baths at 30°, 34°, 36°, 38.5° and 41° C for 1 h. Survival then was observed at 24 h intervals. As survival was 100% up to 36°, and
Comparison of Mated VS Unmated Females

For mated females, but not for unmated females, survivorship was significantly reduced by periodic exposure to 36°C (P<0.05, Kolmogorov-Smirnov test for goodness of fit, Sokal and Rohlf 1969). Mated females survived at a lower rate than unmated females for both stressed and unstressed comparisons (P<0.05). The reduction in survivorship in mated compared to unmated females was greater for stressed females (Fig. 1).

The average clutch size of reproductive females was 27.5 eggs, the average number of clutches 5.0, and the average between clutch interval was 2.5 days. Clutch size for M. edax in the laboratory was lower than observed in nature (50's-70's during maximal period, Wyngaard, unpubl.), perhaps due to a more restricted diet, but well within the normal range. The presence of oil globules, especially in unmated females, was indicative of adequate nutrition. Unstressed females showed a shorter, but not significant (0.05<P<0.10), interval from reaching CVI to producing the first clutch: 4.5 as compared to 5.4 days for stressed females. This delay in reproduction for the stressed group was not associated with any change in fecundity, as the two groups did not differ over their lifetime in cumulative egg production.

Longevity VS Reproductive Output

We examined the relationship between average number of eggs per clutch and age at death in mated females, and found a non-significant positive correlation, contrary to expectations. An additional life table conducted at 25°C (Wyngaard, unpubl.) was used to compare survival of females of differing reproductive output, because it offered a larger sample size. Age at death did not correlate significantly with number of eggs per lifetime (r=0.17, 27 df), nor with number of eggs in the first two clutches (r = -0.26, 25 df) (Fig. 2).

Discussion

An absence of a cost of reproduction, or in some instances a positive correlation among fitness traits expected to show trade-offs, has been reported by several workers (Giesel and Zettler 1980; Smith 1981; Dean 1981; and references therein). One reason for an absence of any negative correlation may be that laboratory conditions are sufficiently favorable that physiological trade-offs are not incurred. Browne (1982) found that unmated brine shrimp lived significantly longer than mated females under low food, but no differences were observed under higher food conditions. This is consistent with our observation that periodic heat stress increased the difference in survival between mated and unmated females, relative to unstressed individuals. Positive correlations among fitness measures may be generated by subtle differences among environments (e.g. in food availability) experienced by each individual (Smith 1981). This result also may be due to innate differences among individuals in their ability to meet the adaptational challenge of laboratory cultivation. Finally, the sign of the cor-