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Reproductive Value and the Cost of Reproduction in *Daphnia carinata* and *Echinisca triserialis* (Crustacea: Cladocera) Exposed to Food and Cadmium Stress

T. Chandini

Ecology Laboratory, Department of Zoology, University of Delhi, Delhi-110007, India

Organisms vary in terms of stopping growth and starting to breed. This is an important criterion for fitness (Calow 1979). In the struggle for existence, advantage rests with those organisms which are most efficient in utilizing available energy for reproduction. Fisher (1958) introduced the concept of Reproductive Value (RV). RV of any organism can be partitioned into reproduction occuring at the present age (m_x) and that occurring in all subsequent classes which is the Residual Reproductive Value (RRV). Under optimal conditions, the reproductive value will be maximized and any deviations from normal reproductive patterns, such as predation (Koufoponou and Bell 1984), vertical migration (Stich and Lampert 1984) result in energy expenditure by the organisms, reducing their RV. The present study is a laboratory investigation on the effects of food and cadmium stress on the RV and the RRV of the two cladocerans Echinisca triserialis and Daphnia carinata. The present study also attempts to test the "cost of reproduction hypothesis" on whether the energy invested by organisms at a particular time in reproduction could affect their future survival and reproduction.

MATERIALS AND METHODS

A laboratory culture of both the species were raised from populations appearing in blooms during September-February in freshwater ponds and pools of Delhi. Preliminary experiments were run to determine the optimal range of pH, temperature and food suitable for their growth and production. Based on these stock cultures were maintained at a temperature of 24±1°c, pH of 7.0 ± 0.2 and food concentration of $1\text{-}2\times10^6$ Chlorella cells/mL for three months before initiation of toxicity studies.

Send reprint requests to T. Chandini, Division of Control of Pollution, Min. of Env. & Forests, GOI, C.G.O. Complex, New Delhi 110 003, INDIA.

Based on the preliminary studies, concentrations of 0.5, 1.5, and 4.5 X 10^6 Chlorella cells/mL were set as low, medium and high levels of food respectively, for the test populations. The range of 0, 2.5, 5, 10 and 20 ug/L was selected as the range for chronic toxicity studies from a series of acute toxicity studies (Chandini 1988). The concentrations were prepared by serial dilution from a stock of 100 mg/L $CdCl_2 . 2\frac{1}{2}H_2O$ (Analytical Grade). A cohort of five neonates (<24H) of Daphnia carinata and 10 neonates of Echinisca triserialis were introduced into three replicates of 100 mL beakers filled to 80 mL of the medium of the appropriate food and cadmium levels. Everv 24h, the dead adults and neonates were counted and discarded and the survivors transferred to a fresh medium of the same food-cadmium levels. The test was terminated when the last individual of the test population died.

Survivorship (l_x) and fertility (m_x) were computed for all the cladoceran cohorts using standard life table methods (Poole 1974; Krebs 1978). RV (v_x) and RRV (v_x^*) were calculated using the following formulae (Pianka 1978):

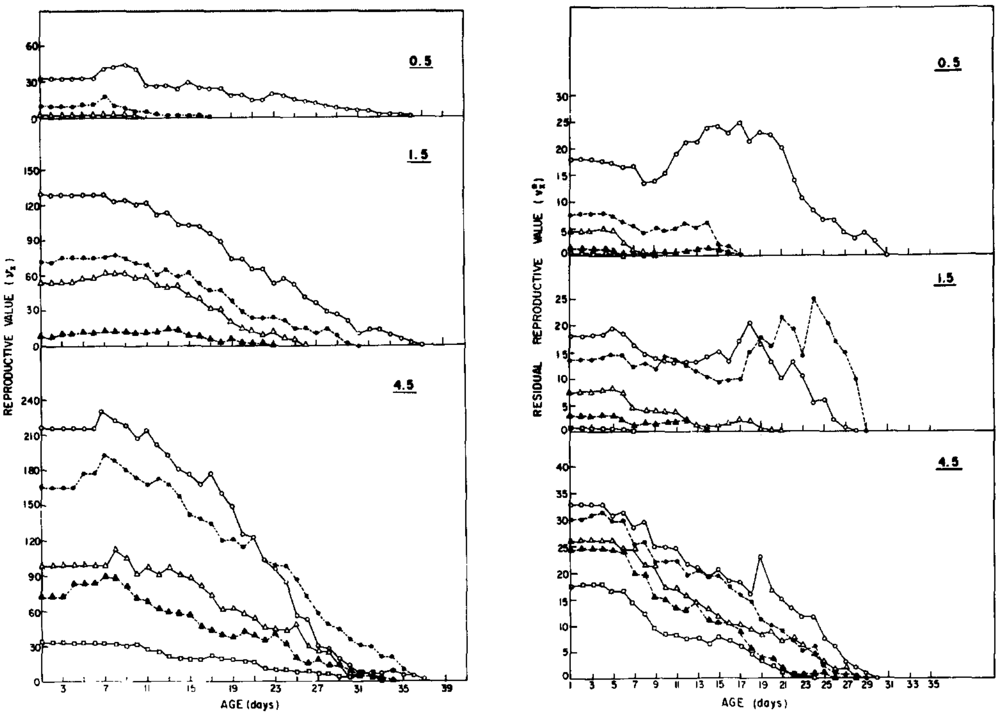
$$v_x = \sum_{t=x}^{\infty} \frac{l_t m_x}{l_x}$$

$$v_x^* = \frac{l_{x+1}}{l_x} v_{x+1}$$

Statistical tests included Student-Newman-Keul's (SNK) test, two-factorial Analysis of Variance (ANOVA) and correlation tests.

RESULTS AND DISCUSSION

The trends in RV values for Daphnia carinata and Echinisca triserialis were widely different. In E. triserialis the v_x value was related to both the factors, food and Cd toxicity [Fig. 1(A)]. Control population at high food level showed peak v_x values at birth (v_o) which gradually declined with age and with increasing cadmium concentration. At medium and low food level, the peak shifted to the right indicating that the highest reproductive value was at the age of 15-21 days. The reproductive value at birth (v_o) for E. triserialis was however, not affected significantly by either cadmium or food stress ($p<0.05$, ANOVA). The Residual Reproductive Value (v_x^*) also showed nearly identical trends in relation to food and cadmium stress [Fig. 1 (B)]. The v_x trends for D. carinata were different in that no such peaks were observed except for a small peak in v_x around

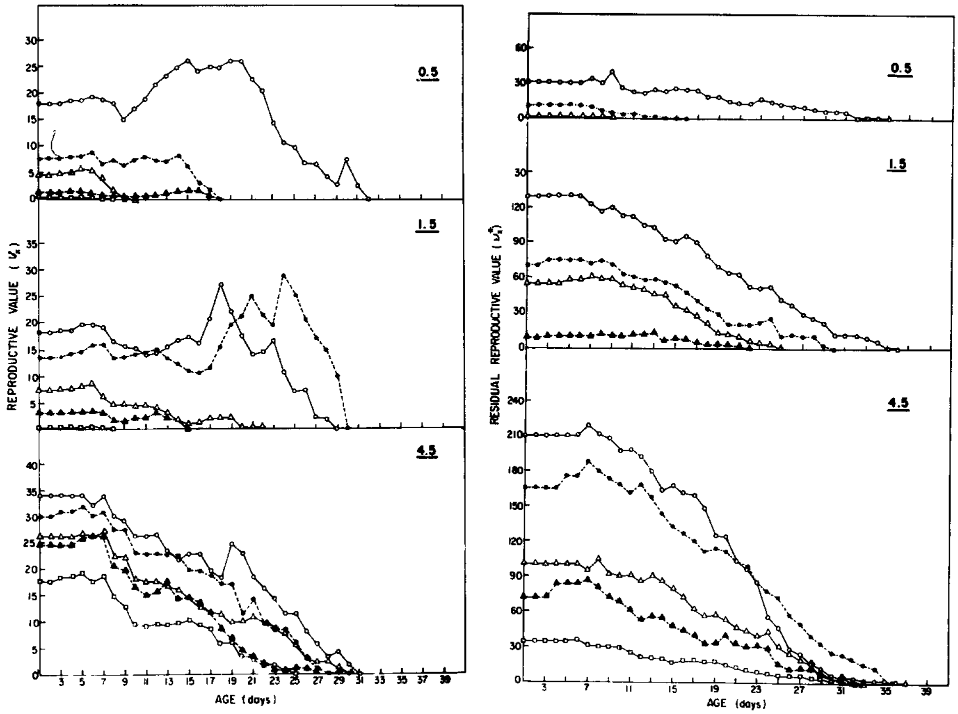


(A) (B)

Figure 1. Reproductive Value (v_x) (A) and Residual Reproducctive Value (v_x^*) (B) in relation to age (x) of Echinisca triserialis exposed to different cadmium concentrations of O(o), 2.5(●), 5.0(Δ), 10(▲), and 20(□) ug/L at three food levels of 0.5, 1.5 and 4.5 X 10^6 cells Chlorella/mL.

the seventh day for controls at low and high food levels [Fig. 2(A)]. The residual reproductive values (v_x^*) in relation to age showed similar trend [Fig. 2(B)]. For populations exposed to cadmium levels of 150 ug/L and above at low food level and to 200 ug/L at medium food level, v_o was not estimated as no reproduction occurred at these levels. Populations at 200 ug/L Cd level at high food regime showed a higher v_o than that shown by control population of low food levels indicating a positive effect of food in mitigating cadmium stress. Populations at almost all cadmium-food levels showed a lower v_x in relation to age compared to that of control population Both cadmium and food stress and their synergistic interaction reduced the v_o of D. carinata significantly ($p<0.001$, SNK test).

The reproductive value determined for E. triserialis and D. carinata can be separated into two components, current reproduction (m_x) and the residual reproduc-



(A) (B)

Figure 2. Reproductive Value (v_x) (A) and Residual Reproductive Value (v_x^*) (B) in relation to age (x) of <u>Daphnia carinata</u> exposed to different cadmium concentrations of 0(o), 50(●), 100(△), 150(▲) and 200(□) ug/L at three food levels of 0.5, 1.5 and 4.5 X 10^6 cells <u>Chlorella</u>/mL.

tive value (v_x^*). The concept of cost of reproduction hypothesis suggests that natural selection could optimize age-specific reproduction if an increment in present production leads to a decrement in future survival (survival cost) or in future fecundity (fecundity cost) (Bell 1984a). Thus, according to "cost hypothesis, an increment in m_x should lead to a decrease in v_x^*. Since residual reproductive value itself is a product of future survival and future reproduction, separate correlation analysis for examining the survival cost [m_x vs l_{x+1}] or [$l_{(x+2)}$] and also the fecundity test [m_x vs $m_{(x+1)}$ or $m_{(x+2)}$] were conducted. From the correlation coefficients (Tables 1&2), some negative and some positive, some statistically significant and others not, it is evident that the cost hypothesis fails to get a strong support in the present study.

The possible existence and role of age-specific reproductive strategies among population in response to changing environment has in the past decades received consi-

Table 1. The relation between present fecundity (m_x) and future survival [$l_{(x+1)}$ and $l_{(x+2)}$] in *E.triserialis* and *D.carinata* exposed to different cadmium concentrations at three food levels. Values given below are the correlation coefficients (r) and their levels of significance.

Cadmium concentration (ug/L)	Food level: x 10^6 cells of *Chlorella*/mL					
	0.5		1.5		4.5	
	$l_{(x+1)}$	$l_{(x+2)}$	$l_{(x+1)}$	$l_{(x+2)}$	$l_{(x+1)}$	$l_{(x+2)}$
E. triserialis						
0 (Control)	-0.13	-0.14	0.64*	-0.57*	-0.16	-0.14
2.5	-0.17	-0.35	-0.56*	-0.53	0.03	0.04
5	0.6	0.42	0.36	0.33	0.23	0.27
10	0.3	0.17	0.42	0.28	0.44	0.5
20	0.91	0.7	1.0	1.0	0.34	0.34
D. carinata						
0 (Control)	0.41*	0.43	0.22	0.28	0.4*	0.4*
50	0.36	0.46	0.14	0.09	-0.06	-0.06
100	-0.14	0.51	-0.01	0.01	0.12	0.12
150	-	-	-0.18	-0.14	0.31	0.28
200	-	-	-	-	0.01	0.2

* Populations whose future survival has been significantly affected by present fecundity. ($p<0.05$)

Table 2. The relation between present fecundity (m_x) and future fecundity [$m_{(x+1)}$ and $m_{(x+2)}$] in *E. triserialis* and *D. carinata* exposed to different cadmium concentrations at three food levels. Values given below are the correlation coefficients (r) and their level of significance.

Cadmium concentration (ug/L)	Food level: x 10^6 cells of *Chlorella*/mL					
	0.5		1.5		4.5	
	$m_{(x+1)}$	$m_{(x+2)}$	$m_{(x+1)}$	$m_{(x+2)}$	$m_{(x+1)}$	$m_{(x+2)}$
E. triserialis						
0 (Control)	0.088	0.158	0.06	0.12	0.33	0.27
2.5	-0.308	0.174	0.27	-0.04	-0.18	0.486*
5	0.33	-0.06	0.096	-0.2	-0.2	0.31
10	0.39	0.236	-0.106	-0.12	0.14	0.53*
20	0.4	0.67	1.0	-	-0.03	0.43*
D. carinata						
0 (Control)	0.40*	0.41*	0.03	0.12	0.11	0.53*
50	-0.02	0.08	0.31	0.17	0.15	0.015
100	-0.6	1.0	0.35	0.12	-0.016	0.07
150	-	-	-0.13	-0.28	-0.106	0.001
200	-	-	-	-	-0.12	-0.14

* Populations whose future fecundity has been affected by present fecundity. ($p<0.05$)

derable attention from population ecologists (Pianka and Parker 1975; Stearns 1976 1977; Snell and King 1977; Calow 1979; Bell 1984 a, b). Snell and King (1977) demonstrated a significant negative relation between age-specific fecundity and future reproduction and survival of the rotifer, Asplanchna brightwelli lending support to the "cost of reproduction hypothesis". Many later studies, particularly on rotifers (Bell 1984 a, Rao and Sarma 1986) and on other asexually reproducing invertebrates (Bell 1984 b), found either no negative correlation or in many instances a positive correlation, thereby questioning the validity of the cost hypothesis. Faifarek et.al (1983) have stated that the cost of reproduction hypothesis should be applied with caution to a population of females in which clutch size varies as was the case for both the cladocerans used in the present study.

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