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Frequency-dependent prey-selection of predacious water bugs on *Armigeres subalbatus* immatures

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Background & objectives: The predatory behaviour with reference to the frequency-dependent prey-selection of the water bugs *Sphaerodema annulatum* Fabricius and *S. rusticum* Fabricius was studied in the laboratory using the IV instar larvae and pupae of *Armigeres subalbatus* as prey to ascertain their efficacy as predator of mosquito immatures.

Methods: Field collected adult morphs of the water bugs were allowed to predate on larvae and pupae provided in different ratios and densities as per the model of Greenwood and Elton[1] for a fixed time period. The data obtained on their predation rate were analysed with respect to the model parameters, ln$V$—the frequency independent component and b— the frequency dependent component of selection.

Results: It was found that the prey-selection was dependent on the relative numbers of prey available, favouring apostatic selection. The b values and ln$V$ values for *S. annulatum* were 0.54 $\pm$ 0.01 and 0.92 $\pm$ 1.04 respectively whereas the corresponding values for S. rusticum were 0.71 $\pm$ 0.03 and 0.17 $\pm$ 1.57 respectively.

Interpretation & conclusion: The selection of preys by the water bugs was dependent on the relative number of the prey forms and thus they are expected to predate on the form more abundant in a heterogeneous prey population and adversely affect the adult emergence.

Key words *Armigeres subalbatus* – prey-selection – *Sphaerodema annulatum* – *S. rusticum* – water bugs

The water bugs *Sphaerodema annulatum* and *S. rusticum* (Heteroptera: Belostomatidae) are well known predators of aquatic snails and insects including different immature stages of mosquitoes[1-7]. On the basis of their predatory nature, many workers are of the view of using them in biological control of vector snails and mosquitoes. In the present study an attempt has been made to assess their frequency-dependent prey selection, following the Greenwood and Elton[8] model, in the laboratory using *Armigeres subalbatus* (Diptera: Culicidae) IV instar larvae and pupae as preys. Since prey numbers, particularly the form and size are the decisive factors in prey selection by a predator[9-12], it would help in evaluating the potential of a species as a bio-control agent in varied situations and in bringing variability and stability in the prey populations[13,14]. Thus the foraging strategy of the water bugs *S. annulatum* and *S. rusticum* was judged at varied relative abundance of the two immature stages of *Ar. subalbatus*.

Material & Methods

About 100 adult morphs of each of the water bugs *S. annulatum* and *S. rusticum* were collected from the Rabindra Sarovar Lake, Kolkata, India and were kept separately in two glass aquaria each of 26 x 26 x 26 cm^3 in volume containing pond water up to 23 cm height, in the laboratory for a period of seven days prior to the experimentation. To simulate natural conditions, some specimens of *Vallisneria* spp, were added to the glass aquaria. Mosquito larvae were provided *ad libitum* to the water bugs as food.

The IV instar larvae and pupae of *Ar. subalbatus* were collected from the sewage drains near Ballygunge Railway Station, Kolkata, time-to-time as per the requirement, and were kept in enamel trays 26 x 26 x 4 cm, containing sufficient amount of pond water. To augment pupation of IV instar larvae, some yeast capsules (Leviest®) were added to the trays (@ 1 capsule per 400 larvae; a Leviest® capsule contains about 2,50,000 yeast cells).

As mentioned in the model by Greenwood and Elton[1] the two preys, IV instar larvae and pupae were provided as food in five ratios in two densities—10 : 10, 15 :5 , 5 : 15, 32 : 8, and 8 : 32 (larvae : pupae) to the predators *S. annulatum* and *S. rusticum* separately in plastic containers of 16 cm radius and 8 cm depth containing three litres of pond water. Predation, in number was noted for a period of one hour. During this period, the prey ratio was kept constant by the addition of the particular prey type consumed. Ten trials were carried out for a particular prey ratio with respect to each predator species using an individual predator once only. Before considering a predator for a trial, it was fed to satiation followed by starvation for a period of 24 h.

According to the model[1], if a population consisting of two prey forms, A_1 and A_2 in numbers (relative or absolute) is available for a predator and the probabilities that a prey of either type is the first to be eaten by the predator, then,

$$P_1 = VA_1 / (VA_1 + A_2) \text{ and } P_2 = A_2 / (VA_1 + A_2)$$

Where, V is the coefficient measuring the selectivity for the first form compared to the second.

If the consumed preys are replaced, so that the numbers A_1 and A_2 are fixed at any point of time, the probabilities P_1 and P_2 will remain constant for the first and subsequent acts of predation. After a number of such acts, in which E_1 and E_2 are the numbers of two forms eaten, then V can be estimated by the cross product ratio A_2E_1/A_1E_2. A simple function satisfying this is:

$$E_1/E_2 = (VA_1/A_2)^b, \quad b > 1$$

Transforming the equation logarithmically—

$$\ln E = b \ln V + b \ln A$$

Where, $E = E_1/E_2$; $A = A_1/A_2$; and b determines the degree of frequency dependence and ln$V$ determines the degree of frequency independence.

The parameters b and V are merely fitted constants and are not independently measured parameters. The standard errors of b and ln$V$ can be estimated from:

$$S.E.\,(b) = s/\sqrt{?\,S_{xx}}$$

$$S.E.\,(\ln V) = (s/?)\sqrt{(1/n + \bar{y}^2/\,?^2 S_{xx})}$$

The slope of the regression— b is the frequency dependent component of selection, while the parameter V is a constant reflecting a frequency independent preference of one prey over the other. The null hypothesis, no frequency dependence, is when b is not significantly different from one, so that V = y, the mean of E_1/E_2, and a value of b significantly differing from one proves frequency dependency.

Statistical analysis of the data obtained was conducted following Zar[15].

Results

The regression statistic for ln ratio of IV instar larvae to pupae eaten by adult morphs of *S. annulatum* and *S. rusticum* is presented in Table 1. The values of b

Table 1. Regression statistics for In ratio of IV instar larvae to pupae of *Ar. subalbatus* consumed by *S. annulatum* and *S. rusticum*

Regression parameters	*S. annulatum*	*S. rusticum*
? x^2	62.58	62.58
? xy	33.65	44.09
SS groups (4) [among frequency]	18.37*	33.05*
? y^2 (1) [explained]	18.09*	31.07*
SS within (45)	0.28^{NS}	1.99^{NS}
$b_{y \cdot x}$ (regression coefficient)	54.71	28.99
F	0.54	0.71
y – intercept (a)	191.47*	46.84*
Y–bar	0.49	0.12
X–bar	0	0
r^2	0.99*	0.94*
Regression equation	lnE = 0.49 + 0.54 lnA	lnE = 0.12 + 0.71 lnA

*p < 0.001; only sum of squares (SS) values are given; degrees of freedom (df) in parentheses; N.S. = Not significant.

(index of frequency dependent selection) and ln$V$ (index of frequency independent selection) for *S. annulatum* and *S. rusticum* are presented in Tables 2a and 2b respectively. The b values are significantly different from unity, indicating frequency dependent selection by the water bugs. The ln$V$ values are not significantly different from zero. Comparisons of b values show significant difference (p < 0.001), suggesting

Table 2a. Estimates of *b* and ln*V* with S.E. for IV instar larvae and pupae selection by the water bugs

Predator species	No. of frequencies tested (trials/freq.)	b ± S.E.	ln$V$ ± S.E.
S. annulatum	5 (10)	0.54 ± 0.001*	0.92 ± 1.04^{NS}
S. rusticum	5 (10)	0.71 ± 0.03*	0.17 ± 1.57^{NS}

*p < 0.001; df = 48, t_{48} = 3.269.

Table 2b. Comparison of *b* values of *S. rusticum* and *S. annulatum*

(1) ANOVA

Source of variation	df	SS	MS	F
Among b's	1	0.87	0.87	43.5*
Weighted average of deviations from regression	96	2.27	0.02	

*p < 0.001, $F_{1,96}$ = 11.5; df — degrees of freedom; SS—Sum of squares; MS — Mean squares.

(2) t-test:

$$F_s = (b_1 - b_2)^2 / \left\{ (? X_1^2 + ? X_2^2)/(? X^2)^2 \right\}$$

$$T_s = \sqrt{F_s}$$

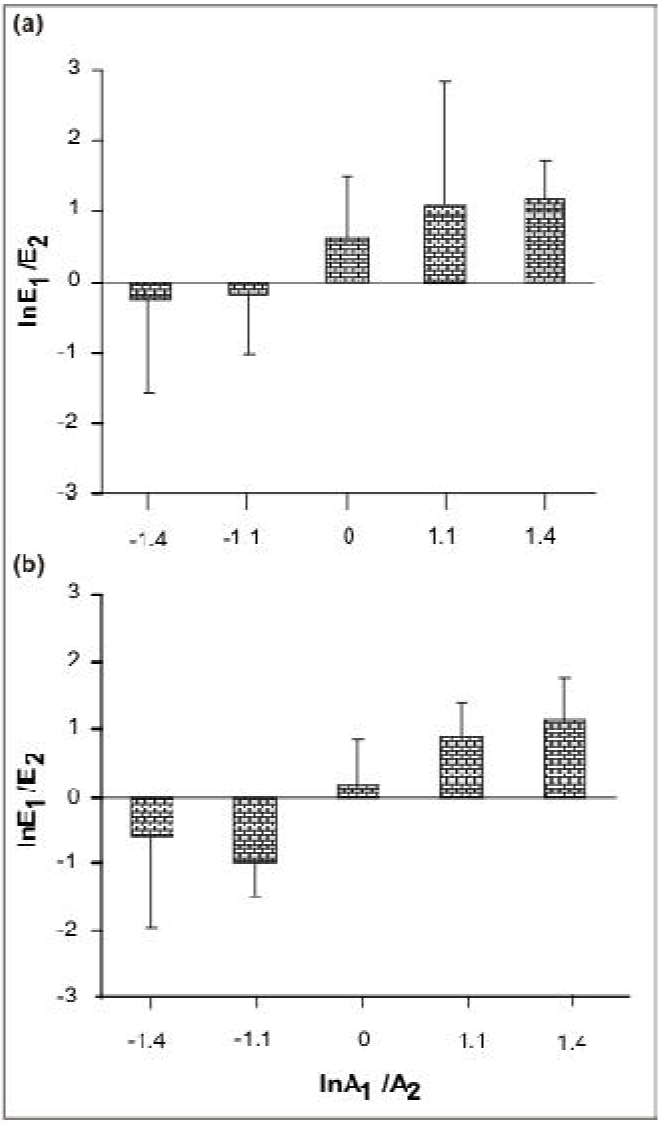

Fig. 1: The relative number (mean ± SE) of IV instar larvae to pupae of *Ar. subalbatus* consumed by the water bugs (a) *S. annulatum*; (b) *S. rusticum* (n = 10 trials)

a difference in predatory behaviour of the water bug species. The relationship of relative numbers of prey consumed and relative numbers of prey available to the water bugs are shown in Fig. 1.

Discussion

It is evident from the results that the water bugs, *S. annulatum* and *S. rusticum* selected both the prey forms depending on their relative numbers. Since, the reward factor, in terms of energy gain, was almost equal for both the prey forms (average weights of IV instar larvae and pupae of *Ar. subalbatus* are 10.1 and 9.8 mg respectively) the number of prey forms was the key factor in shifting of prey choice, though the role of experience on selection of prey could not be judged. Nevertheless, this frequency dependent prey selection by the water bugs is in favour of the view that in a population of heterogeneous prey forms, predation will be based on the relative abundance of the prey forms, and will help to stabilise the prey population. Several theories have been put forward in this regard, concerning prey-predator dynamics and foraging strategies of predators[13,14,16-18], especially for arthropod predators[11,19,20]. Detailed work on *Toxorhynchites splendens* Wiedemann (Diptera : Culicidae) larval instars by Amalraj and Das[21] are in the light of these theories. Our results too are in accordance with their findings. However, the prey-selection pattern by these water bugs with respect to immatures of other mosquito species needs to be evaluated both in the laboratory and field conditions. Also, in situations when two varied type of prey species are present, with unequal rewards, the foraging strategy may not be similar.

The difference in the *b* values of respective water bug species can be attributed to the predatory efficiency of the water bugs. *S. annulatum* can consume more preys compared to *S. rusticum*[5-8,22,23] due to larger body size at the adult stage. In case of the larval instars of *Tx. splendens* same kind of difference was noted[21].

However, irrespective of these, on the basis of the present findings, it can be said that the water bugs *S. annulatum* and *S. rusticum* can consume both IV instar larvae and pupae of *Ar. subalbatus*, in quite good numbers, depending on their relative abundance, unlike other arthropod predators of mosquito immatures that restrict their prey selection to the larval instars only[21, 24-27], and thus have an edge over other invertebrate predators. Predation of larval stages of mosquitoes, of course, reduces adult mosquito population, but killing larvae only leaves the pupae safe to succeed to adult morph. If the representations of the immature forms of mosquito—larvae and pupae are unequal in a heterogeneous population, then too, predators of larval stages only, will prove to be less efficient in reducing mosquito populations in conditions where pupal proportion is more, keeping apart the individual efficiency of the predators. In this context, the predation pattern of the water bugs *S. annulatum* and *S. rusticum*, similar to that of the fishes like *Poecilia reticulata* and *Gambusia affinis*[28], is expected to be more useful. To further strengthen this view, laboratory and field evaluations on the predation of mosquito immatures by *S. annulatum* and *S. rusticum* are required.

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