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Frequency-dependent prey selection by larvae of *Toxorhynchites splendens* (Diptera: Culicidae)

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Abstract

The foraging behaviour of frequency-dependent prey selection by larval instars of *Toxorhynchites splendens* (Wiedemann) was studied in the laboratory. Prey size selection (second vs fourth instars of *Aedes aegypti* Linnaeus or *Anopheles stephensi* Liston) by third and fourth instar predators was frequency-dependent. However, in the case of second instar predators, prey size selection was not frequency-dependent and the predator preferred second instar to fourth instar prey. When offered second instars of *Aedes aegypti* and *Anopheles stephensi* the preference for one species over the other was frequency-dependent in all the three predator instars. The role of frequency-dependent prey selection in the stability of prey–predator interaction at low equilibrium levels is discussed.

Introduction

Predation is widely acknowledged as one of the major factors regulating communities (Murdoch & Oaten, 1975; Martin, 1988). Several prey–predator models have shown that predators adopt different foraging strategies in response to energy values of the prey types and their relative frequencies. This was seen as an adaptation to maximize the long-term rate of energy gain (Schoener, 1971; Emlen & Emlen, 1975; Krebs *et al.*, 1977; Pyke *et al.*, 1977; Krebs, 1978). The functional basis of prey selection by predators has been reviewed (Greenwood, 1984). Preferences for the common type of prey (frequency-dependent) and rarer type of prey (frequency-independent) have been called 'apostatic' and 'anti-apostatic' selection, respectively (Clarke, 1962). While apostatic selection helps in maintaining the variability and stability of dynamics of prey–predator interactions (Clarke, 1962; Allen & Clarke, 1968), anti-apostatic selection results in the reduction of variability and stability (Allen, 1972).

Garcia (1982) and Holck (1988) in their review of the control of mosquitoes using predators indicated that aquatic stages of *Toxorhynchites* Theobald (Diptera: Culicidae), a genus of large non-biting mosquitoes have the greatest potential for controlling container-breeding mosquitoes. There have been few studies on the prey selection by aquatic stages of *Toxorhynchites* (Sempala, 1971; Padgett & Focks, 1981; Sherratt & Tikasingh, 1989). The purpose of the present study is to examine the prey selection by larval instars of *Toxorhynchites splendens* (Wiedemann) as a guide to understanding the foraging strategies of the predator. Such information would be of use in mass-rearing and inundative larval release programmes. We use a simple model to describe the prey selection in a series of trials relating the frequencies of the various prey types eaten to their relative frequencies. The preference indices of Greenwood & Elton (1979) made it possible to distinguish frequency-dependent and frequency-independent components of preference.

Materials and methods

The frequency-dependent prey selection by second, third and fourth instar *T. splendens* was examined in the laboratory. Standard laboratory cultures of *T. splendens, Aedes aegypti* Linnaeus and *Anopheles stephensi* Liston (Diptera: Culicidae) were used throughout these experiments. *Aedes aegypti* and *Anopheles stephensi* were selected as prey species on the basis of their different feeding behaviour, use of the foraging area and larval mobility (James & Liston, 1985). Larvae of *Aedes aegypti* are bottom feeders and they come to the water surface in order to breath through the caudal siphon; whereas larvae of *Anopheles stephensi* are surface feeders and their position in water is horizontal to the water surface. The two size classes

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of prey used are referred to as small (second instar) and large (fourth instar). The average wet weight of individuals of second/fourth instar *Aedes aegypti* and *Anopheles stephensi* have been estimated to be 1.18/10.1 mg and 0.56/10.79 mg respectively (Dominic Amalraj, 1993). The frequencies, used for examining prey size selection, were 10:10, 5:15, 15:5, 20:80 and 80:20 of second and fourth instars of either *Aedes aegypti* or *Anopheles stephensi*. The frequencies used for studying prey species selection were 10:10, 5:15, 15:5, 20:80 and 80:20 of second instar *Aedes aegypti* and *Anopheles stephensi*. Since the level of satiation can influence predation, all predators were fed to satiation and subsequently starved for 24 h prior to use. The required number of prey were placed in glass beakers containing 500 ml tap water with a single predator. Each test combination was replicated ten times ($n = 10$). The numbers of each respective prey type consumed were replaced as they were eaten during the 2 h observation period, so that at any given time the relative frequencies of the prey type remained constant. This was carried out in order to comply with one of the important assumptions of the Greenwood & Elton (1979) model employed in this study.

The model

In a population of prey where two forms are available for a predator and where their numbers (relative or absolute) are A_1 and A_2, the probabilities of an individual of either of these two being consumed first by the predator can be stimated by:

$$P_1 = VA_1/(VA_1 + A_2),\quad P_2 = A_2/(VA_1 + A_2)$$

The coefficient V measures the selectivity of the first form compared with the second. Suppose that consumed prey are replaced, so that the numbers are restored to A_1 and A_2, the probabilities of each of the two forms being eaten remain constant at P_1 and P_2 for the second and subsequent acts of predation. After a number of such acts, in which E_1 and E_2 of the two forms have been eaten, then V may be estimated by the cross-product ratio A_2E_1/A_1E_2. The model is derived from the function:

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

The logarithmic transformation of the equation is:

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

Where $E = E_1/E_2$ and $A = A_1/A_2$. E_1 and E_2 are the numbers of two prey types eaten from a population of A_1 and A_2. Thus normal linear regression methods using values of $y = \ln E$ and $x = \ln A$, derived from a set of n trials, give estimates of the regression parameters:

$$\alpha = b \ln V \text{ and } \beta = b$$

The parameter b, the slope of the regression, is defined as the frequency-dependent component of selection. The parameter V is a constant reflecting a frequency-independent preference for one prey over the other and that the 'null hypothesis', (i.e. no frequency-dependence), is when b is not significantly different from one, so that $V = Y$ the mean of E_1/E_2. In some situations, predation is disproportionately weighted towards the rarer forms even though there is frequency-dependency (Horsely *et al.*, 1979). In such cases the value of b is less than unity. The ratio $\hat{\alpha}/\beta$ estimates $\ln V$.

The estimates of these parameters and of the residual variance are:

$$\hat{\alpha} = \bar{y} - \hat{\beta}\bar{x}$$

$$\hat{\beta} = S_{xy}/S_{xx}$$

and

$$S^2 = (S_{yy} - S^2_{xy}/S_{xx})/(n - 2)$$

where S_{yy}, S_{xy} and S_{xx} are the usual corrected sums of squares and sum of products.

Here, b and V are merely fitted constants and are not independently measured parameters. Approximate standard errors for b and $\ln V$ may be obtained from

$$\text{S.E. } (\hat{b}) = S/\sqrt{S_{xx}}$$

$$\text{S.E. } (\ln \hat{V}) = (S/\hat{\beta})\sqrt{(1/n + y^{-2}/\hat{\beta}^2\, S_{xx})}$$

where $y = b \ln V + b \ln A$

The departure of the model parameters such as $\hat{b}$ and $\ln \hat{V}$ from unity and zero respectively were tested by an approximate t-test; where

$$t = (\hat{b} - 1)/\text{S.E.}(\hat{b}),\ \text{with } n - 2\ df$$

$$t = \hat{\alpha}/\text{S.E. } (\hat{\alpha})\ \text{with } n - 2\ df$$

Slopes of the regressions were tested for homogeneity before performing ANCOVA on the data following the method of Sokal & Rohlf (1981). Significant differences among the adjusted means were tested by computing lower and upper comparison intervals for the means by T-method (Gabriel, 1978).

Results

The influence of the size of prey on prey selection

The functional relationship between the ratios of small to large size prey consumed and the ratios of small to large prey offered was adequately described by the Greenwood & Elton model. The fit of the data to the model was good in all the cases (P 0.001 < 0.05); table 1; figs 1 and 2). In

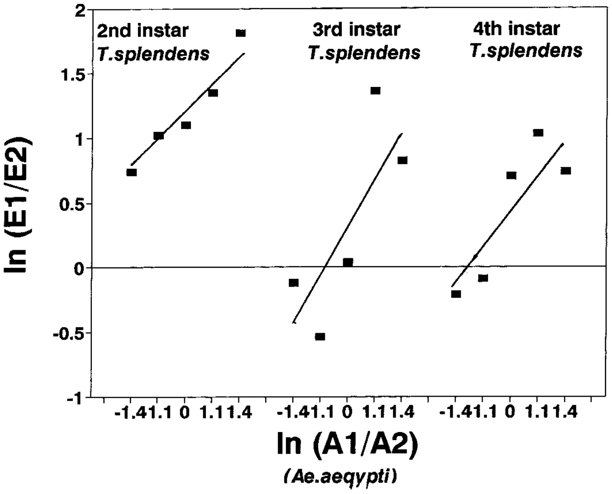

Fig. 1. Relationship of relative numbers of two forms eaten (E_1/E_2) to relative numbers available (A_1/A_2) for second, third and fourth instar *Toxorhynchites splendens* feeding on second and fourth instar *Aedes aegypti*.

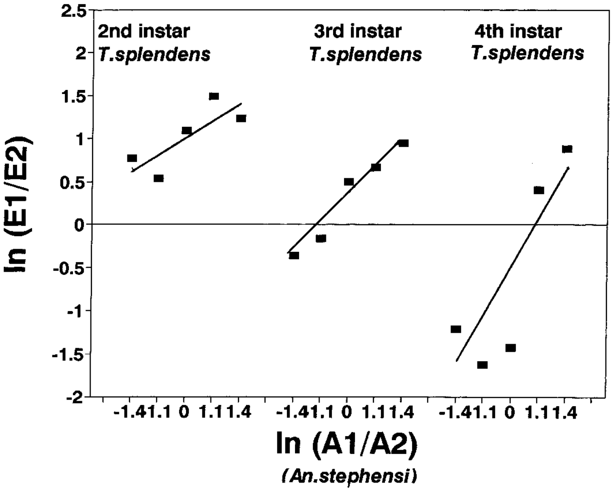

Fig. 2. Relationship of relative numbers of two forms eaten (E_1/E_2) to relative numbers available (A_1/A_2) for second, third and fourth instar *Toxorhynchites splendens* feeding on second and fourth instar *Anopheles stephensi*.

all the cases the slope of the regression ($b_{y.x}$) was found to be significantly different from zero (P 0.001 <0.05; table 1).

The estimates of parameters b (index of frequency-dependent predation) and ln V (index of frequency-independent selection) for the three predator instars feeding on the mixtures of second and fourth prey instars are given in table 2. In cases of third and fourth instar predators ln V was not significantly different from zero ($P > 0.05$) and b was significantly different from unity (P 0.001 <0.05). These provide the strong evidence for frequency-dependent (apostatic) prey-size selection. In the case of small predators (second instar), ln V was significantly different from zero indicating that the predation was not frequency-dependent. The value b was significantly less than unity which indicates that the predation was disproportionately directed towards second instar prey and thus in agreement with the findings of Horsley *et al.* (1979) who observed that in some situations, predation was disproportionately weighted towards the rarer forms. The value b was then less than unity. This could be explained by the fact that small predators fed on small prey as handling large prey might have been difficult.

Table 1. Regression statistics for ln ratio of small to large prey eaten by instars of *Toxorhynchites splendens*. Only *SS* are given; *df* in parenthesis.

	Instars of *T. splendens*		
	2	3	4
		Aedes aegypti	
Σx^2	62.58	62.58	62.58
Σxy	18.50	33.83	25.50
SS_{groups} (4) (among frequency)	6.49**	23.32***	12.08**
Σy^2 (explained) (1)	5.47***	18.29***	10.39***
$\Sigma d^2_{y.x}$ (unexplained) (3)	1.02 ns	5.03*	1.69 ns
SS_{within} (45)	16.97	15.49	29.95
$b_{x.y}$ (reg. coefficient)	0.30	0.54	0.41
F	16.06*	10.92*	18.48*
Y-intercept (a)	1.20	0.31	0.44
Y	1.20	0.31	0.44
X	0.00	0.00	0.00
r^2	0.84*	0.78*	0.86*
		Anopheles stephensi	
Σx^2	62.58	62.58	62.58
Σxy	16.78	27.04	51.09
SS_{groups} (4) (among frequency)	5.60***	12.26***	52.72***
Σy^2 (explained) (1)	4.50***	11.69***	41.71***
$\Sigma d^2_{y.x}$ (unexplained) (3)	1.10 ns	0.57 ns	11.01***
SS_{within} (45)	9.58	15.58	15.20
$b_{y.x}$ (reg. coefficient)	0.27	0.53	0.82
F	12.23*	61.56**	11.37*
Y-intercept (a)	1.02	0.32	−0.60
Y	1.02	0.32	−0.60
X	0.00	0.00	0.00
r^2	0.80*	0.95**	0.79*

*=P 0.01 <0.05; **=P 0.001 <0.01; ***=$P < 0.001$.
ns=not significant.

Since there was no significant ($P > 0.05$) heterogeneity among regression lines (table 3), ANCOVA was performed on the data, keeping the relative prey size frequency as co-variate. The results indicated significant variation in the frequency-dependent prey-size selection among predator instars ($P < 0.001$, table 4). The mean proportion of small size prey eaten by the second instar *T. splendens* was significantly higher than the mean proportion of small size prey eaten by third and fourth instars ($P < 0.001$; fig. 3).

Table 2. Estimates of b and ln V with S.E. for small vs large prey selection.

Prey species	Predator instar	No. of[1] frequencies tested	$b \pm$S.E.[2]	ln $V \pm$S.E.[3]
Aedes aegypti	2	5 (10)	0.30±0.02***	4.06±17.95***
	3	5 (10)	0.54±0.04***	0.57±2.51 ns
	4	5 (10)	0.41±0.03***	1.08±4.80 ns
Anopheles stephensi	2	5 (10)	0.27±0.02***	3.80±16.65***
	3	5 (10)	0.43±0.03***	0.74±3.37 ns
	4	5 (10)	0.82±0.06*	0.73±3.20 ns

[1] Number of trials/frequency is given in parenthesis.
[2] b is significantly different from unity (one) at $P < 0.001$ (***) and P 0.01 <0.05 (*).
[3] ln V is significantly different from zero at $P < 0.001$ (***).
ns=not significant.

Table 3. Test of equality of K (6) regression coefficients for frequency-dependent prey size selection by instars of *Toxorhynchites spendens*; *df* of the deviation in each group from its separate slope are $\Sigma(a{-}2k{=}(30{-}12){=}18$.

Source of variation	*df*	*SS*	*MS*	*F*
Among b's (variation among regression)	5	12.58	2.52	2.22 ns
Weighted average of deviation from regression	18	20.41	1.13	

ns=not significant.

The influence of the prey species on prey selection

The relationship of the relative numbers of the two forms eaten to the relative number available for second, third and fourth instar predators feeding on second instar *Aedes aegypti* and *Anopheles stephensi* is shown in fig. 4 and the regression statistics are given in table 5. In all the cases,

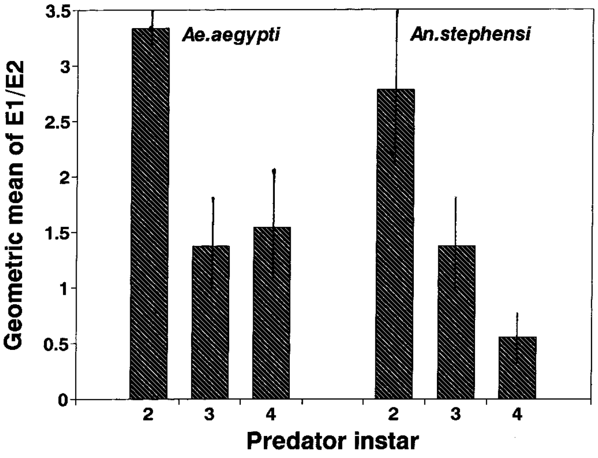

Fig. 3. 95% comparison limits by the T-method for the adjusted means of ln ratio of small to large prey eaten (E_1/E_2).

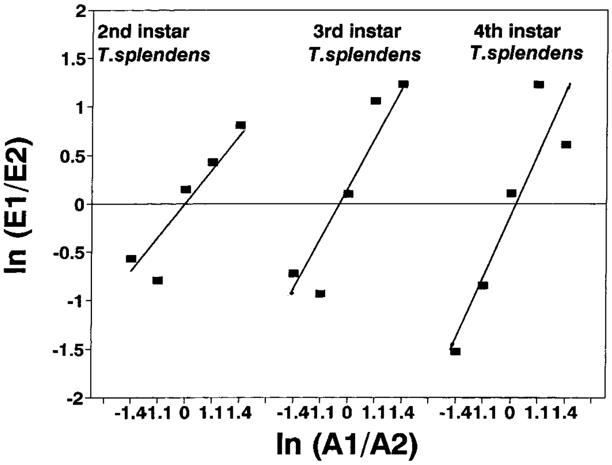

Fig. 4. Relationship of relative numbers of two forms eaten (E_1/E_2) to relative numbers available (A_1/A_2) for second, third and fourth instar *Toxorhynchites splendens* feeding on second instar *Aedes aegypti* and *Anopheles stephensi*.

Table 4. Analysis of covariance of the ln ratio of small to large prey eaten by instars of *Toxorhynchites splendens* shown in figs 1 and 2.

Source of variation	*df*	*SS*	*MS*	*F*
Regression	1	80.57	80.57	171.9***
Constant (adjusted means means among groups)	1	61.24	61.24	130.7***
Prey species	1	11.84	11.84	25.3***
Predator instars	2	73.11	36.55	78.0***
Species by instar	2	14.34	7.17	15.3***
Error (within cell)	293	137.34	0.47	

***=$P < 0.001$.

Table 5. Regression statistics for ln ratio of 2nd instar *Aedes aegypti* to 2nd instar *Anopheles stephensi* eaten by instars of *Toxorhynchites splendens*. Only *SS* are given; *df* in parenthesis.

	Instars of *T. splendens*		
	2	3	4
Σx^2	62.58	62.58	62.58
Σxy	32.48	48.87	52.68
SS_{groups} (4) (among frequency)	18.08***	39.17***	49.52***
Σy^2 (explained) (1)	16.86***	38.16***	44.35***
$\Sigma d^2_{y.x}$ (unexplained) (3)	1.22 ns	1.01 ns	5.17*
SS_{within} (45)	13.80	11.05	5.45
$b_{y.x}$ (reg. coefficient)	0.52	0.78	0.84
F	41.54**	113.70***	25.72*
Y-intercept (a)	0.008	0.15	0.09
Y	0.008	0.15	0.09
X	0.00	0.00	0.00
r^2	0.92**	0.85*	0.85*

*=P 0.01 <0.05; **=P 0.001 <0.01; ***=$P < 0.001$.
ns=not significant.

Table 6. Estimates of b and ln V with S.E. for prey species selection (*Aedes aegypti* vs *Anopheles stephensi*).

Predator instar	No. of[1] frequencies tested	$b\pm$S.E.[2]	ln $V\pm$S.E.
2	5 (10)	0.52±0.04***	0.02±0.26 ns
3	5 (10)	0.78±0.06*	0.19±0.91 ns
4	5 (10)	0.84±0.06 ns	0.11±0.54 ns

[1] Number of trials/frequency is given in parenthesis.

[2] b is significantly different from unity (one) at $P < 0.001$ (***) and P 0.01 <0.05 (*).

ns=not significant.

Table 7. Test of equality of K (3) regression coefficients for frequency-dependent prey species selection by instars of *Toxorhynchites splendens*; *df* of the deviation in each group from its separate slope are $\Sigma a{-}2k{=}(15{-}6){=}9$.

Source of variation	*df*	*SS*	*MS*	*F*
Among b's (variation among regression)	2	3.68	1.84	2.24 ns
Weighted average of deviation from regression	9	7.40	0.82	

ns=not significant.

Table 8. Analysis of covariance of the ln ratio of 2nd instar *Aedes aegypti* to 2nd instar *Anopheles stephensi* eaten by instars of *Toxorhynchites splendens* shown in fig. 4.

Source of variation	*df*	*SS*	*MS*	*F*
Regression	1	95.69	95.69	337.7***
Constant (adjusted means means among groups)	1	0.08	0.08	0.3 ns
Predator instars	2	1.36	0.68	2.4 ns
Error (within cell)	146	41.37	0.28	

***=$P < 0.001$.
ns=not significant.

the fit of the data to the regression was significant (P 0.001 < 0.05).

With all the three predator instars, ln V values were not significantly different from zero ($P > 0.05$; table 6) indicating frequency-dependent selection. Larval instars of *T. splendens* preferred larvae of *Aedes aegypti* or *Anopheles stephensi* depending on their frequencies.

Since there was no significant ($P > 0.05$) heterogeneity among regression lines (table 7) ANCOVA was performed on the data. The adjusted means did not vary significantly ($P > 0.05$; table 8). Hence, among the instars of *T. splendens* there was no significant ($P > 0.05$) difference in frequency-dependent preference for *Aedes aegypti* or *Anopheles stephensi*.

Discussion

The value of b, which is a measure of the degree of frequency-dependence of prey selection is known to vary from experiment to experiment and between different predators and different prey as well as with the number of prey consumed (Greenwood & Elton, 1979). When few prey are consumed, b values will be generally large whereas if more prey are consumed, b values tend to be small. In our experimental system, b values were consistently less than one because of the large number of prey eaten by the predator.

Our results indicate that prey-size selection by large size predators was frequency-dependent. This is in accordance with the finding of Corbet & Griffiths (1963) who found no size related prey preference when comparing 'small' vs 'large' *Aedes aegypti* fed to *Toxorhynchites brevipalpis* Theobald (Diptera: Culicidae). However, our results differed from observations made by other workers (Sempala, 1971; O'Flynn, 1975; Focks *et al.*, 1978; Lounibos, 1979; Padgett & Focks, 1981; Bradshaw & Holzapfel, 1983; Lounibos *et al.*, 1987; Sherratt & Tikasingh, 1989) who reported that fourth instar *Toxorhynchites* preferred fourth instar to second instar larvae of *Aedes* and *Culex* mosquitoes. In two field studies this conclusion was reached based on the observations that there was a shifting of size-class frequencies of larvae of *Aedes* and *Culex* towards younger instars in the presence of predominantly third and fourth instar *Toxorhynchites* in bracts of *Heliconia, Caribaea* and bamboo internodes (Lounibos, 1979; Lounibos *et al.*, 1987). The shifting of size-class frequencies towards younger instars might be due to the continuous recruitment of first instar prey in the breeding habitats. The number of younger larvae developing to older ones would be fewer due to predation. Therefore, the presence of more younger instar prey would have been misinterpreted as size-dependent predation by large predators.

In the present study, it was observed that second instar predators preferred second instar to fourth instar prey. This frequency-independent selection could be explained by the adaptive significance of the small predator 'keying in' on small size prey thereby offering the highest energy gain, i.e. ratio of energy spent to energy gain per capture (Pyke *et al.*, 1977; Padget & Focks, 1980, 1981; Stephens *et al.*, 1986). It has been reported that young larvae of *T. splendens* took a longer time to handle large prey because the more chitinized body of fourth instar of prey species made it more difficult for the predator to handle the prey and gave the prey a greater ability to evade attacks (Dominic Amalraj, 1993). Optimal foraging theory predicts that the predator will prefer those prey which provide the greatest return from the investment in handling the prey (Schoener, 1971; Charnov, 1976; Estabrook & Dunham, 1976; Sih, 1980; Ernsting & Mulder, 1981). It has also been reported that small size predators preferred small aquatic insects in the natural environment (Siegfried & Knight, 1976; Zaret, 1980; Menzie, 1981).

Our results indicate that the prey species selection by instars of *T. splendens* was frequency-dependent. This agrees with the conclusion that predators' diet in nature is largely determined by the frequency of concurrence with different prey species (Lounibos, 1979). This shows that there exists a switching behaviour among instars of *T. splendens*. Most studies of switching behaviour emphasize the importance of predator preference for the most abundant forms of its prey (Allen, 1972; Murdoch *et al.*, 1975). Our results agree with optimal diet theory (Pulliam, 1974), that changes in predator selectivity for a prey are driven by the goal of maximizing net rate of energy gain (Dukas & Ellner, 1993). Sherrat & Tikasingh (1989) reported that the energy content of prey types was not a suitable currency with which to measure fitness gain. A recent study has shown that instars of *Aedes aegypti* and *Anopheles stephensi* did not differ significantly in the amount of protein present per unit body weight (Dominic Amalraj, 1993). It has been reported that the prey species used in the present study differ in this use of space for foraging and in larval mobility (Kazana *et al.*, 1983; James & Liston, 1985; Lounibos *et al.*, 1987). In spite of these differences, it seems that the encounter rate between the predator and a prey is simply a function of frequency of that prey.

Frequency-dependent prey selection has been reported to provide stability in the dynamics of prey–predator interactions (Ginzburg & Resit Akcakaya, 1992) and results in the lowering of the equilibrium position of a pest population to below threshold level (Smith & Van den Bosch, 1967). From the control point of view, our results are encouraging because in a biocontrol programme involving inundative releases, frequency-dependent predation would be more cost-effective because the number of adult releases could be reduced and secondly control of both *Aedes aegypti* and *Anopheles stephensi* will be possible since both species share the breeding habitats of the predator especially in urban and semi-urban situations.

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