Prey Preference in *Stethorus punctum* (Coleoptera: Coccinellidae)

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ABSTRACT *Stethorus punctum* (LeConte) is an obligate predator of tetranychid mites. Laboratory studies were conducted to determine feeding preference of *S. punctum* at varying densities of *Panonychus ulmi* (Koch) and *Tetranychus urticae* Koch. Using the Strauss linear index of prey selection, *S. punctum* was found to have a weak but consistent preference (among individuals) for *T. urticae* following preconditioning to this species, but no preference was elicited when the beetle was conditioned to *P. ulmi*. Following conditioning of beetle larvae to *T. urticae*, newly eclosed (behaviorly naive) adult beetles showed a slight but nonsignificant preference for *T. urticae*.

KEY WORDS Biological control, Strauss linear index, *Panonychus ulmi*, prey preference, *Stethorus punctum*, *Tetranychus urticae*

THE COCCINELLID beetle *Stethorus punctum* (LeConte) is a key biological control component in the management of apple orchards in Pennsylvania (Asquith & Hull 1979), where during both larval and adult stages it is an obligate predator of the dominant phytophagous pests *Panonychus ulmi* (Koch) and *Tetranychus urticae* Koch (Acari: Tetranychidae). The two prey species are spatially and temporally patchy in orchards within a growing season (Hull et al. 1976) yet persistent across seasons. I examine here the strength and consistency of prey selection by adult female *S. punctum* as densities of the two prey vary under experimental conditions, the influence of conditioning on the strength and consistency of this preference, and the merits of the Strauss linear index (1979, 1982) for the general assessment of prey preference.

Materials and Methods

Culture Methods. Stocks of *P. ulmi* and *T. urticae* were collected from apple orchards in Centre and Adams counties, Pa., and were cultured on small apple trees (60–90 cm tall) in separate constant-temperature rooms at 22 ± 2°C. Light was provided by overhead fluorescent lights (photoperiod, 14:10 [L:D]). Humidity was between 70 and 80%. Trees were fertilized with 15-30-15 nutrient when introduced into the culture rooms, and watered regularly.

S. punctum was collected from the same geographical localities as were the mites and introduced onto mite-infested trees in the constant-temperature rooms, where they were permitted unrestricted movement. Laboratory orchards consisted of 20–30 trees and supported 40–100 adult beetles.

Adequate stocks of mites were necessary to maintain dependable resources of laboratory-grown beetles. Three kinds of mite cultures were maintained and rotated into use as needed: 1) monocultures on apple that contained expanding mite populations, without predation; 2) monocultures in the laboratory orchards, upon which beetles actively fed; and 3) emergency monoculture reserves. The reserves of *T. urticae* were grown on broad bean plants (*Vicia faba* L.) that were used as surrogates for apple trees to lower costs. However, to reduce undeterminable influences on mite palatability due to the chemical character of the plants themselves (Jesiotr & Suski 1976), mites were transferred to fresh apple trees 1 week before being used in predation experiments. Reserve stocks of *P. ulmi* could be successfully grown only on apple trees.

Experimental Design of Prey-preference Tests. Before testing, beetles fed freely in laboratory orchards on monocultures of one of the two prey species. The duration of conditioning before testing was a minimum of 2 weeks. Prey-preference tests were carried out on sections (3 × 5 cm) of apple leaf, with the midvein centrally located, floated abaxial-side down on water in a petri dish. Leaf surfaces were used because the behavior of arthropods can be influenced by artificial substrata (Rasmy & El-Benhawy 1974, Everson 1979, 1980).

Adult female mites were introduced onto the leaf-cut in predetermined numbers and allowed to move undisturbed for 15 min. An adult female beetle was then added to the leaf-cut and feeding events were recorded continuously for 3 h consecutively. Beetles were taken directly from the culture and were assumed to be in comparable states of repletion at the start of an observation period. Each such observation comprised a feeding trial.

Table 1. Factorial design of prey selection studies

p_T	N	T	$H_T:H_P$
0.02	8	24	1:40
0.05	8	24	1:20
0.09	8	24	1:10
0.11	8	24	5:40
0.17	8	24	1:5
0.20	16	48	10:40, 5:20
0.33	24	72	5:10, 10:20, 20:40
0.50	40	120	1:1, 5:5, 10:10, 20:20, 40:40
0.67	24	72	10:5, 20:10, 40:20
0.80	16	48	20:5, 40:10
0.83	8	24	5:1
0.89	8	24	40:5
0.91	8	24	10:1
0.95	8	24	20:1
0.98	8	24	40:1

N, total number of adult female beetles tested at a given proportion of mites; *T*, total number of observation hours contributing to given selection values.

Trials were replicated eight times, with eight different beetles, for any combination of absolute prey densities.

To ensure a stable mite density during feeding trials (with no prey depletion), each mite consumed was replaced with a live conspecific. Partially consumed mites were removed, as *S. punctum* occasionally can return to pierce a damaged mite a second time. Eggs or webbing produced by mites during testing were removed to reduce variability among replicates. Such manipulations were, however, only occasionally necessary during any 3-h test period.

A factorial design was used to establish combinations of mite densities tested. Proportions of the two mite species were tested at several absolute prey densities (designated H_T for *T. urticae* and H_P for *P. ulmi*). Preference was tested at all pairwise combinations of densities; H_T = 1, 5, 10, 20, and 40 mites per leaf-cut; H_P = 1, 5, 10, 20, and 40 mites per leaf-cut. Resulting relative densities of *T. urticae* (p_T) as proportions of total abundance resulting from these combinations are given in Table 1.

Transference of Preference Across Pupation. To determine the influence of larval conditioning upon adult prey selection, beetle larvae were conditioned from hatching to pupation to *T. urticae*. The pupae were then isolated and newly eclosed beetles were not exposed to any mites for 24 h. Then adult female beetles were placed on leaf-cuts with equal numbers of adult female *T. urticae* and *P. ulmi* (H_T and H_P = 5, 10, 20, and 40). Eight beetles were tested at each prey density and the feeding behavior of each beetle was observed for 3 h consecutively.

Measure of Prey Preference. The linear index of prey selection (L_i) (Strauss 1979, 1982) was applied to these data. It is defined as the unweighted difference in proportions:

$$L_i = r_i - p_i$$

where r_i is the proportion of prey *i* eaten by the predator and p_i is the proportion available.

The Strauss index has appealing statistical and experimental qualities (Pearre 1982) because it is

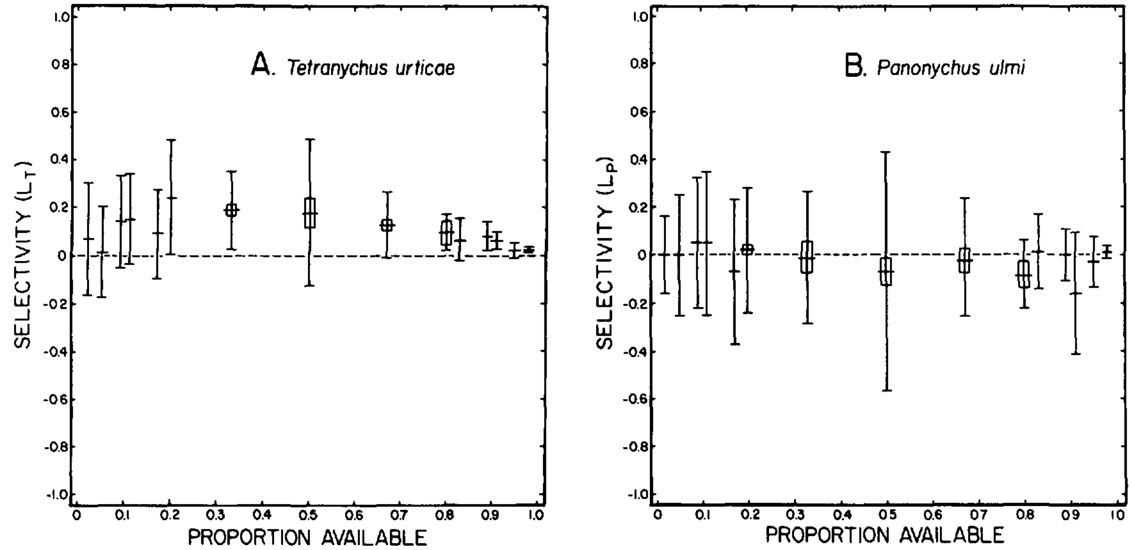

Fig. 1. Prey preference of *S. punctum* as measured by the Strauss linear index of prey selection. A selectivity (L_i) value of zero indicates random predation. Vertical bars represent the largest within-group standard deviations; boxes represent the standard errors of L_i. (A) Prey preference of *S. punctum* (conditioned to *T. urticae*) when presented varying proportions of both prey. L_T is the selection index for *T. urticae* expressed in relation to the proportion of *T. urticae* available. (B) Prey preference of *S. punctum* (conditioned to *P. ulmi*) when presented varying proportions of both prey. L_P is the selection index for *P. ulmi* expressed in relation to the proportion of *P. ulmi* available.

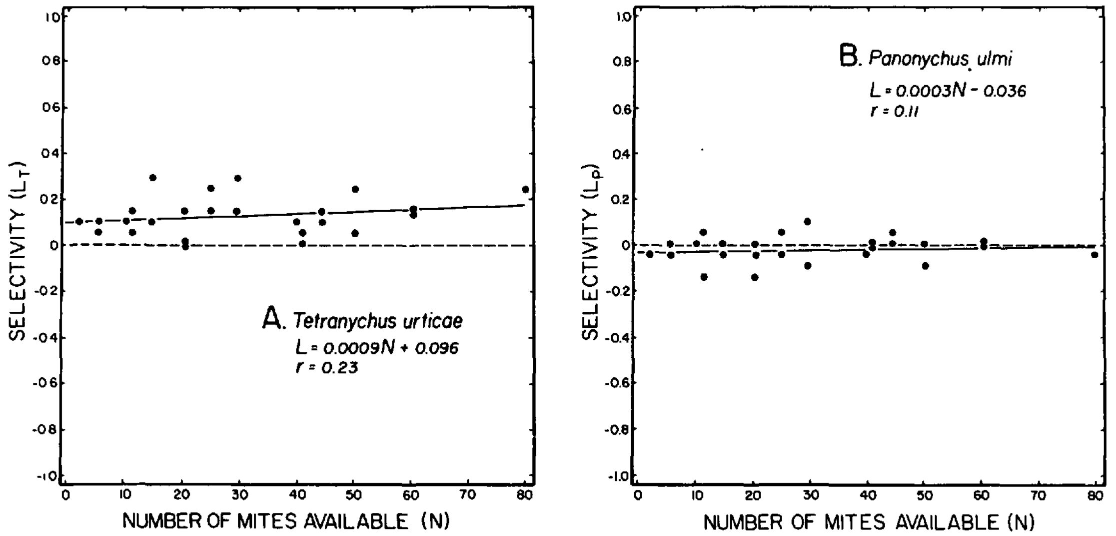

Fig. 2. Feeding selectivity (L_i) of *S. punctum* as related to the total absolute density of combined prey. (A) L_T is the index for selection of *T. urticae* following conditioning of *S. punctum* to *T. urticae*. (B) L_P is the index of selection of *P. ulmi* following conditioning of *S. punctum* to *P. ulmi*.

not complicated by the complex statistical and mathematical properties inherent in nonlinear ratio models. It varies symmetrically from -1.0 to $+1.0$; values across prey sum to zero. Positive values indicate positive prey preference and negative values indicate relative avoidance. Maximum prey preference occurs when $r_i = 1$ and $p_i = 0$, and maximum avoidance when $r_i = 0$ and $p_i = 1$ (see Lechowicz [1982] for graphical interpretation).

Because L_i is the difference between two binomially distributed parameters, it is itself approximately normally distributed (Strauss 1979). This allows the use of statistical tests based on assumptions of normality to evaluate L_i and statistical deviation from zero.

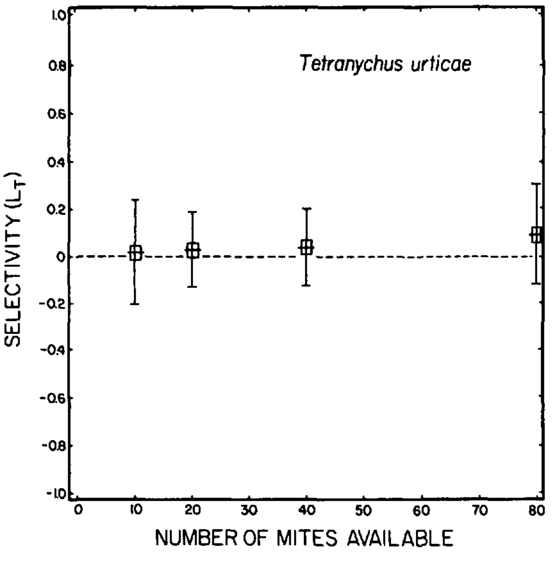

Fig. 3. Index of selection (L_T) of *T. urticae* consumed by adult female *S. punctum* previously conditioned as larvae to *T. urticae*. Equal numbers of *T. urticae* and *P. ulmi* (5, 10, 20, and 40 of each) were presented to *S. punctum* ($p_i = 0.05$). Prey selection is not significantly different from random.

Linear index values from sets of experiments were pooled to determine a mean index value (equivalent to averaging means weighted by sample size). Standard errors of L_i were estimated separately for each experiment; to be conservative, the largest standard error among a set of experiments was reported. Standard deviations for each set were calculated across trials.

Results and Discussion

Assessment of Preference. All mean values of L_T, the selection index for *T. urticae*, were greater than zero for *S. punctum* conditioned to *T. urticae* (Fig. 1A). This indicates that *S. punctum* had a significant preference for *T. urticae* following conditioning to that species. As the proportion of *T. urticae* available became low, selection became more variable. After conditioning to *P. ulmi* (Fig. 1B), however, the beetle showed no preference for either mite. All mean values clustered about zero, and standard deviations are broad at all but the highest prey proportions. Thus, *S. punctum* has a weak preference for *T. urticae* when conditioned to it ($0 < \bar{L}_T < +0.3$) and no preference when conditioned to *P. ulmi* ($-0.1 < \bar{L}_P < +0.1$). Variation in feeding behavior is generally greater when *P. ulmi* is the familiar prey than when *T. urticae* is familiar.

Consistency of preference among individual predators could be interpreted using the standard deviation of L_i for any p_i or the standard error of

L_i. The standard error of L_i has least distortion due to aberrant individuals and may be preferred as a measure of consistency. It does, however, require careful experimental design to accommodate a full range of absolute densities of prey. Applying the standard error of L_i as a measure of consistency, *S. punctum* could be said to have a consistent positive preference for *T. urticae* when it is familiar prey and a consistent nonselective response to *P. ulmi* when it is familiar.

Switching (Murdoch 1969) is a special case of nonrandom searching in which a predator exploits two prey but concentrates its feeding effort on whichever is more abundant. It is thought to be dependent upon the degree of preference a predator holds for the prey in question (Murdoch 1969, Cornell & Pimentel 1978). An operational measure to test switching requires 1) a quantitative statement of the strength of prey preference with a complementary null hypothesis, and 2) a quantitative statement of homogeneity among individuals to determine consistency of response at the population level. Switching can be interpreted here using values of L_i for strength of prey preference and standard errors of L_i as measures of consistency across relative densities. When *S. punctum* is conditioned to *T. urticae*, the strength of preference is weak but consistent; switching does not occur. When *S. punctum* is conditioned to *P. ulmi*, a slight indication of switching behavior is present but, due to the variance among predators and overlap of standard deviations, switching is considered as weak and ineffective (at the population level) in influencing community structure.

Although feeding selectivity of *S. punctum* was shown to vary with relative proportions of alternate prey, selectivity was not correlated with the absolute number of mites available (Fig. 2 A and B).

Transference During Pupation. Naive adults of *S. punctum* that had been conditioned as larvae to *T. urticae* exhibited a slight but nonsignificant preference for *T. urticae* (Fig. 3). This might result from transference of prior experience from the larval stage or might be innate.

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