

# Time and Resource Partitioning in *Stethorus punctum* (Coleoptera: Coccinellidae)

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**ABSTRACT** *Stethorus punctum* (LeConte) is an obligate predator of tetranychid mites. Laboratory studies examined the proportion of time beetles spent searching, feeding, and resting when adult females and third instars encountered an abundance of all instars of the tetranychid mite *Tetranychus urticae* Koch. Preference for various prey instars, relative handling times, and the influence of starvation on these behaviors were determined. Satiated female beetles spent 45.1% of their time searching, 14.4% feeding, and 40.5% resting. Female beetles that were starved spent a greater proportion of time feeding, with an increase in handling time per prey. The increase in handling time was due to a more complete extraction of body fluids from individual prey. Female beetles preferred mite eggs, and that preference was not significantly altered by starvation. Satiated larvae spent 78.4% of their time searching and 21.6% feeding; they did not spend any measurable amount of time resting. Starvation of larvae significantly increased the percentage of time spent feeding and the handling time per prey. Third instars preferred nymphal mite stages to other instars, and this preference was not significantly altered by starvation. The results are discussed in reference to predator-prey dynamics.

**KEY WORDS** Insecta, prey preferences, resource partitioning, *Stethorus punctum*

*STETHORUS PUNCTUM* (LeConte) is an obligate predator of tetranychid mites (Acari: Tetranychidae) (Putman 1955, McMurtry et al. 1970). In commercial apple orchards in Pennsylvania, it is the key predator in the biological control of the spider mites *Panonychus ulmi* (Koch) (European red mite) and *Tetranychus urticae* Koch (two-spotted spider mite) (Mowery et al. 1975, 1977; Hull et al. 1976, 1977; Asquith 1979). Statistical comparisons of predation curves (Houck & Strauss 1985) revealed that *S. punctum* expressed a weak but consistent preference for *T. urticae* (Houck 1986) and that prior conditioning significantly influenced the expression of prey preference (Houck 1980) in heterogeneous environments.

The laboratory studies reported here complement previous studies of the feeding behavior of *S. punctum* and specifically address (1) the proportion of time that adult female beetles and third instars allot to searching for prey, feeding, and resting; (2) the relative handling time per prey; (3) the mite stages preferred by adults and larvae; and (4) the influence of starvation on these feeding behaviors.

## Materials and Methods

*Stethorus punctum* were collected from apple orchards in Centre and Adams Counties, Pa. Beetles were cultured in the laboratory on apple seedlings heavily infested with the mite *T. urticae*, according to the methods of Houck (1980, 1986). Because previous studies indicated that prior ex-

perience influenced predation, beetles were conditioned for at least 2 wk on monocultures of the prey. Adult female beetles and third instars were randomly selected from laboratory stocks just before testing. Treatments were replicated 10 times in a constant-temperature chamber (24°C).

Each experiment lasted 1 h; each individual beetle was tested only once. The following behavioral categories were recorded: searching, feeding, and resting. In these experiments, the time spent in each behavior was recorded, as were the mite stages consumed by the beetle.

Searching in adult beetles was defined as any forward movement and was typically nonlinear and rapid. Beetle larvae frequently search for prey by attaching the pedal gland to the substrate and probing outward from the point of attachment. For this reason, searching in larvae was defined as any forward motion plus any probing flexion of the body.

Active feeding of both females and larvae included the time required to manipulate and consume a prey following a successful capture. Feeding was considered to be terminated when the beetle discarded the exoskeleton of the exsanguinous mite. Each feeding encounter was timed to determine the handling time per individual prey.

Resting was the residual time during which a beetle was not actively searching or feeding and included prey assimilation, preening, and other behaviors which could not otherwise be scored.

Replicate trials consisted of one beetle placed on an apple leaf (laboratory grown) heavily infested

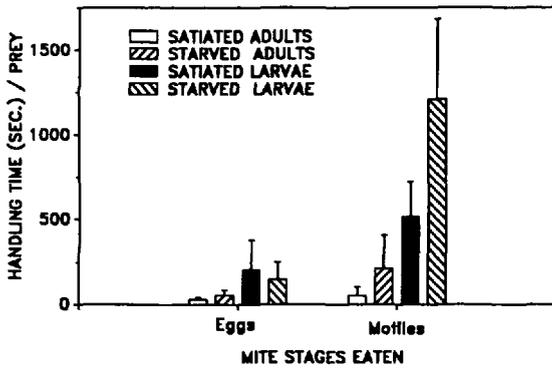


Fig. 1. Comparison of the handling time per prey (seconds) for *S. punctum* ( $n = 10$ ) feeding on *T. urticae*.

(>300 mites per leaf) with all mite stages. This prey-saturated environment provided an opportunity for maximum prey selection from among all developmental stages.

The effect of hunger on beetle behavior was also investigated. Satiation was defined as the condition of beetles upon removal from laboratory trees heavily infested with mites. Starvation was defined as the condition of beetles following a 24-h period of food deprivation. Death due to starvation in *S. punctum* occurs within 48–96 h. Twenty-four hours without food was considered to be sufficient to influence predation behavior but not severe enough to debilitate the predator.

A parametric analysis of variance (one-way ANOVA) using a general linear model, in conjunction with Tukey's Studentized range test, was used to determine significant differences of mean predation rates and handling times. A factorial analysis (two-way ANOVA) was applied to the data to determine factor interaction terms. Because of the stringent assumptions about within-group normality and homogeneity of variances, differences among means were also examined using Friedman's (nonparametric) two-way ANOVA of ranks (SAS Institute 1982).

## Results

**Time Budget of Adult Female Beetles.** Satiated females of *S. punctum* spent most of their time searching (45.1%) and resting (40.5%), with the remainder of the time (14.4%) spent in active feeding (Table 1). Starved females spent 24.4% of their time searching, 32.3% resting, and 43.3% in active feeding. The increased time devoted to feeding in starved females was due to an increase in handling time per prey (Fig. 1) rather than to a significant increase in the rate of predation (Table 2). Satiated adult females required  $29.7 \pm 10.9$  s ( $\bar{x} \pm SE$ ) to consume mite eggs ( $n = 149$ ), whereas starved females required  $54.4 \pm 30.7$  s ( $n = 179$ ) (Fig. 1). This difference was statistically significant in a one-way ANOVA ( $F = 20.87$ ;  $df = 1$ ;  $P \leq 0.0001$ ). Satiated adult females required  $51.0 \pm 54.9$  s/mo-

Table 1. Comparison of the percentage of time *S. punctum* spent in the three behavioral categories while feeding on *T. urticae*<sup>a</sup>

Parameter	Behavior		
	% Searching	% Feeding	% Resting
Satiated females			
$\bar{x}$	45.1%	14.4%	40.5%
SD	21.4%	7.5%	20.4%
Starved females			
$\bar{x}$	24.4%	43.3%	32.3%
SD	11.1%	24.2%	19.9%
Satiated larvae			
$\bar{x}$	78.4%	21.6%	0%
SD	19.3%	16.0%	0%
Starved larvae			
$\bar{x}$	47.1%	52.9%	0%
SD	26.6%	24.2%	0%

<sup>a</sup>  $n = 10$ .

tile mite ( $n = 18$ ) to handle such prey as opposed to  $216.4 \pm 191.6$  s/motile mite ( $n = 22$ ) for starved females. These differences were also statistically significant ( $F = 10.55$ ;  $df = 1$ ;  $P \leq 0.0026$ ).

When the interaction of the influences of hunger level and mite stage eaten on handling time were examined, the overall model for a parametric two-way ANOVA was significant ( $R^2 = 0.43$ ,  $n = 358$ ), as was the nonparametric Friedman's rank analysis ( $R^2 = 0.21$ ,  $n = 358$ ). Hunger significantly increased the handling time per prey in adult females (ANOVA:  $F = 84.5$ ,  $df = 1$ ,  $P \leq 0.0001$ ; rank:  $F = 24.4$ ,  $df = 1$ ,  $P \leq 0.0001$ ). The stage of mite consumed also significantly influenced the handling time per prey (ANOVA:  $F = 118.3$ ,  $df = 1$ ,  $P \leq 0.0001$ ; rank:  $F = 41.7$ ,  $df = 1$ ,  $P \leq 0.0001$ ). Handling time per motile prey was statistically higher than that for prey eggs. A significant interaction term for hunger level and mite stage eaten was reflected both in the two-way ANOVA analysis ( $F = 57.7$ ,  $df = 1$ ,  $P \leq 0.0001$ ) and the nonparametric rank analysis ( $F = 2.8$ ,  $df = 1$ ,  $P \leq 0.0001$ ).

**Time Budget of Third Instars.** Satiated larvae of *S. punctum* spent a mean of 78.4% of the time searching and 21.6% of the total time feeding (Table 1). Resting was not observed to occur in larvae during testing. When starved, larvae spent 47.1% of their time searching and 52.9% feeding. This 31.3 percentage-point increase in time allotted to feeding by starved larvae was the result of increased handling time per motile prey ( $F = 11.44$ ;  $df = 1$ ;  $P \leq 0.0028$ ) (Fig. 1) rather than to an increase in the handling time per egg ( $F = 0.70$ ,  $df = 1$ ,  $P \leq 0.419$ ) or to predation rate (Table 2).

The overall model for the parametric two-way ANOVA was significant ( $R^2 = 0.55$ ,  $n = 37$ ), as it was for the Friedman's rank test ( $R^2 = 0.79$ ,  $n = 37$ ). Hunger level influenced both the handling time of prey (ANOVA:  $F = 5.7$ ,  $df = 1$ ,  $P \leq 0.02$ ; rank:  $F = 3.6$ ,  $df = 1$ ,  $P \leq 0.07$ ) and the mite stages consumed (ANOVA:  $F = 17.4$ ,  $df = 1$ ,  $P \leq 0.0002$ ;

**Table 2.** Number and percentage of each stage of *T. urticae* consumed by adult females and larvae of *S. punctum*<sup>a</sup>

Parameter	No. adults	% adults	No. nymphs <sup>b</sup>	% Nymphs	No. larvae	% Larvae	No. eggs	% Eggs	Predation rate
Satiated ♀♀									
$\bar{x}$	0.50a	3.0	0.60a	3.6	0.10a	0.61	15.3a	92.7	16.5a
SD	0.53	5.1	1.20	5.4	0.30	1.50	7.2	11.4	—
Starved ♀♀									
$\bar{x}$	1.67a	7.5	0.80a	3.6	0.10a	0.45	19.8a	88.4	22.6a
SD	1.58	10.5	0.90	5.4	0.30	1.30	11.9	13.5	—
Satiated larvae									
$\bar{x}$	0a	0	1.20a	60.4	0	0	0.60a	39.5	1.88a
SD	0	0	1.20	45.4	0	0	0.70	45.3	—
Starved larvae									
$\bar{x}$	0.27a	13.7	0.90a	45.7	0	0	0.8a	40.6	1.97a
SD	0.47	40.0	0.70	43.5	0	0	1.2	34.4	—

Means followed by the same letter are not significantly different ( $P = 0.05$ , Tukey's Studentized range test).

<sup>a</sup>  $n = 10$ .

<sup>b</sup> Nymphs, protonymphs or deutonymphs.

rank:  $F = 81.4$ ,  $df = 1$ ,  $P \leq 0.0001$ ). Both the two-way ANOVA ( $F = 7.2$ ,  $df = 1$ ,  $P \leq 0.01$ ) and Friedman's rank analyses ( $F = 16.1$ ,  $df = 1$ ,  $P \leq 0.0003$ ) indicated a significant interaction between hunger level and the mite stages consumed by beetle larvae.

**Developmental Stages Eaten by Adult Female Beetles.** Satiated adult beetles preferred mite eggs; 92.7% of all prey consumed were eggs (Table 2). Starved females also preferred mite eggs (88.4%). Satiated females included a mean of 3.0% adult mites in their diet, whereas starved adult beetles included 7.5%. Nymphs made up 3.6% of the diet when females were satiated, and this proportion was not significantly altered by starvation. Larval mites composed an insignificant proportion of the diets of both satiated and starved adult beetles.

**Developmental Stages Eaten by Third Instars.** Satiated larvae of *S. punctum* did not consume adult mites during testing (Table 2). Predation was concentrated primarily on nymphal stages (60.4%) and secondarily on mite eggs (39.5%).

Starved larvae consumed 13.7% adult mites, 45.7% nymphal stages, and 40.6% eggs. If the percentage of all motile stages is considered as a single prey category (adults + nymphs) relative to egg consumption, the pooled percentages for satiated and starved larvae are not significantly different. No mite larvae were consumed by either satiated or starved beetle larvae during testing.

### Discussion

Although mite larvae did not make up a significant proportion of the diet of female beetles or larvae of *S. punctum*, there was no evidence that there was active avoidance of these prey. Mite larvae functionally represented an invulnerable age class in this study, but it is likely that small body size contributed to the reduced probability of predation. Mite larvae are similar to the eggs in size,

but unlike eggs, larvae have the ability to move about the habitat. This mobility, coupled with small size, further reduces the probability of random confrontation with the predator.

Female beetles expressed a strong preference for mite eggs over other developmental stages of *T. urticae*, and this preference was relatively unaltered by starvation. Consistent prey choice may be related to prey quality and the requirement of high energy resources for metabolism and reproduction by females. Mite eggs are high in lipids and proteins and may thus best satisfy nutritional needs.

The increased handling times of prey by females and larvae following starvation was due to a more complete removal of prey contents, as opposed to diminished feeding ability. When beetles fed on mite eggs, the contents were apparently fully consumed, but there was significant variation in the thoroughness of content removal for the mobile prey stages. Feeding could end before the prey contents were fully exhausted.

Feeding behavior consists of the piercing of the prey, siphoning of the prey juices, and the regurgitation of them back into the mite's carapace. When a meal ends, this behavior ceases and only a crenulated, crumpled exoskeleton remains. Frequently, satiated adult beetles were observed to pierce prey, initiate feeding, and subsequently abandon that prey. In some instances, prey were minimally damaged and able to flee. This behavior was not observed in starved beetles; starved beetles made a greater effort to extract potential material once feeding was initiated. Detailed energetic studies would be helpful in determining the relative energetic costs and benefits of predation on various developmental stages of prey. Similarly, an energy analysis of nutrient removal would be useful. Satiated animals may find the return for the effort of completely draining a mobile mite not worth the energetic cost.

From these data, hypotheses can be made about

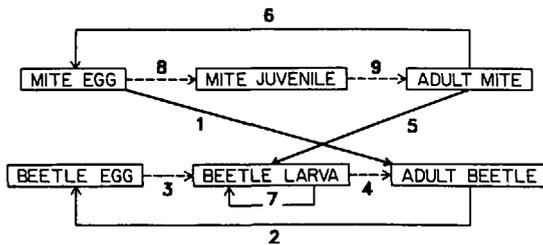


Fig. 2. Hypothesized pathways of mite-beetle interactions. An increased flow in pathway 1 results in an increase in pathway 2, resulting in an increase in pathway 3, causing an increase in pathway 5, causing a decrease in pathway 6, resulting in a decrease in pathway 1. See text for further explanation.

the potential role that instar preference plays in the observed stability in orchards (Fig. 2). For example, the number of adult beetles in the orchard at time  $T_1$  is directly proportional to the number of beetle larvae at time  $T_0$  (Fig. 2, paths 2-4). The number of adult mites at time  $T_1$  is proportional to the number of mite nymphs at time  $T_0$  (Fig. 2, paths 8-9). When the density of adult beetles increases in the population, the number of mite eggs is reduced because of selective predation (path 1), subsequently resulting in fewer adult mites available as prey for beetle larvae (paths 8, 9, and 5). Thus, fewer beetle larvae successfully reach maturity, and the adult beetle population at time  $T_2$  declines.

Intraspecific competition is reduced by the partitioning of preferred mite stages and may prevent severe oscillations in both the predator and the prey populations. A short circuit in the feedback system can occur if the larval cohort builds too rapidly in localized patches. *S. punctum* larvae become cannibalistic at high densities. The negative feedback due to cannibalism (path 7) is self-limiting and helps to restore any imbalance created on a local scale.

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