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How larvae of *Thrips tabaci* reduce the attack success of phytoseiid predators

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Abstract

Neoseiulus barkeri (= *Amblyseius mckenziei*) and *Amblyseius cucumeris* (Acari:Phytoseiidae) are used as control agents of *Thrips tabaci* (Insecta:Thripidae) in greenhouse crops. Their success in capturing prey larval stages is related to both the feeding state of the predators and to the size of the larvae. When starved, predators are more successful in seizing larvae. Upon contact with a starved predator second stage prey larvae incur a lower death risk than first stage larvae. The larvae of *T. tabaci* reduce the attack success of their predators by jerking the abdomen and by producing a drop of rectal fluid. When this defensive behaviour is prevented by anaesthetising the larvae with CO₂, predator attack success increases. Anaesthesia does not, however, level out the difference in death risk of the two larval stages. Conceivable causes for this discrepancy are discussed.

Availability of suitable prey is dependent on the dynamics of the age structure of the prey population and, hence, may be lower than total thrips density suggests. If so, alternative food sources may be important to maintain the predator population.

Introduction

Thrips tabaci Lindeman is a pest of many greenhouse crops in Europe and North America. Mainly due to Ramakers' work two species of phytoseiid predators, *Neoseiulus barkeri* Hughes (= *Amblyseius mckenziei* Schuster & Pritchard) and *Amblyseius cucumeris* Oudemans have been used successfully in biological control of this pest (Ramakers, 1978, 1980; Ramakers & Van Lieburg, 1982). Although other successes have also been reported (Hansen, 1988; De Klerk & Ramakers, 1986; Bakker, in press), there is still little quantitative understanding of the impact that predatory mites

can have on the population dynamics of *T. tabaci*. This paper deals with an important component of predator capacity to control the pest population: the capture success ratio (CSR).

CSR is defined as the fraction of predator-prey encounters that results in food intake by the predator and death of the prey. An encounter occurs when the tarsi of legs I or the pedipalps of the predator come into contact with a prey. Observations of Fransz (1974) and Sabelis (1981, 1986), showed that the CSR of phytoseiid mites is related to 1) the satiation level of the predator, and 2) properties of the prey related to the developmental stage. As a general rule starved predators are more likely to attack and

seize a prey than well-fed ones, and they are less successful in capturing prey stages that are in a more advanced stage of development. Given the same prey type interspecific differences have also been recorded (Sabelis, 1981).

Preliminary observations indicated that the capacity of thrips larvae to counter an attacking predator is probably related to the stage of development (De Klerk, 1984; F. M. Bakker unpubl.). Because the other stages either inhabit the soil (pupae) or easily escape from attack by phytoseiids (eggs, adults), we compared the defensive capacity of young and old thrips larvae at various levels of food deprivation of the predator for *N. barkeri* and *A. cucumeris*.

Methods and materials

Because of their high rate of food turnover only gravid females were used in the experiments (Sabelis, 1981, 1986). After consumption of a prey larva the females were deprived of food and water in small plastic vials for a predetermined period at 20 °C. This vial was subsequently placed on a floating leaf disc of cucumber (5 cm²) with 20 larvae of *T. tabaci*. The leaf disc had been infested 24 h earlier either with small-sized, and therefore young, first stage larvae or with big second stage larvae. The two classes of larvae were discriminated by visual means and the weight of the larvae was determined afterwards for the purpose of standardization. From the moment the predator walked out of the vial onto the leaf she was observed continuously until successful capture of a prey larva when no larva was captured the experiment was terminated after 3 h. During the observations all contacts between predator and prey were recorded. After the experiment the records were classified according to the period of food and water deprivation at the moment of contact (hereafter referred to as *t*). Because the decrease in gut content (satiation level) of phytoseiids is best described exponentially (Sabelis, 1981, 1986; F. M. Bakker, unpubl.), *t* was classified on a logarithmic scale. The CSR (fraction of 'successful' encounters) was calculated for each *t*-class.

To investigate to what extent prey behavioural defence determines the CSR, the experiments with

N. barkeri were repeated with immobilised larvae. Immobilisation was achieved by anaesthetising the larvae with CO₂ prior to the experiment. As soon as movements were observed the experiment was stopped. Only fit larvae were put back in the vial with CO₂ for further use in the experiments.

Results and conclusions

Influence of predator satiation level on CSR. Regarding first stage larvae the relationship between the CSR and the time of food and water deprivation (*t*) is sigmoid for both predator species. There are, however, conspicuous differences. For *N. barkeri* the CSR remains low until *t*=8, whereas the CSR of *A. cucumeris* starts increasing at *t*=2 (Fig. 1). Moreover, the CSR of *A. cucumeris* is always higher than the CSR of *N. barkeri*. For 2 < *t* < 12 the CSRs of the two species differ significantly (*P* < 0.001) in all *t*-classes. For *t* > 12 (data pooled) the *P*-value is 0.0324 (Binomial test for differences of proportions). For 0 < *t* < 2 the CSR values do not differ significantly (*P* = 0.0892).

In contrast to their success in capturing first stage larvae, both phytoseiids appear to be unsuccessful in seizing second stage larvae when starved. The CSR of *A. cucumeris* significantly increased from 0.01 to 0.16 (*P* < 0.001) only at *t* = 25.5.

Influence of prey defensive behaviour on CSR. Behavioural observations showed that when touched by a predator all stages of *T. tabaci* react by 'jerking' their abdomen. Crespi (1986) coined the term 'wagging' for this behaviour in *Hoplothrips pedicularius* (Haliday), where it is a component of male fighting behaviour, and involved in the competition for mates. Apart from this behaviour another response was observed that is related to defence: the production of a drop of rectal fluid. This phenomenon is described also for other thysanopterans (Lewis, 1973). We observed that *T. tabaci* often uses both mechanisms simultaneously. After contact with the apparently sticky fecal droplet individuals of both predator species withdrew and started cleaning themselves. If, however, the predators first contacted

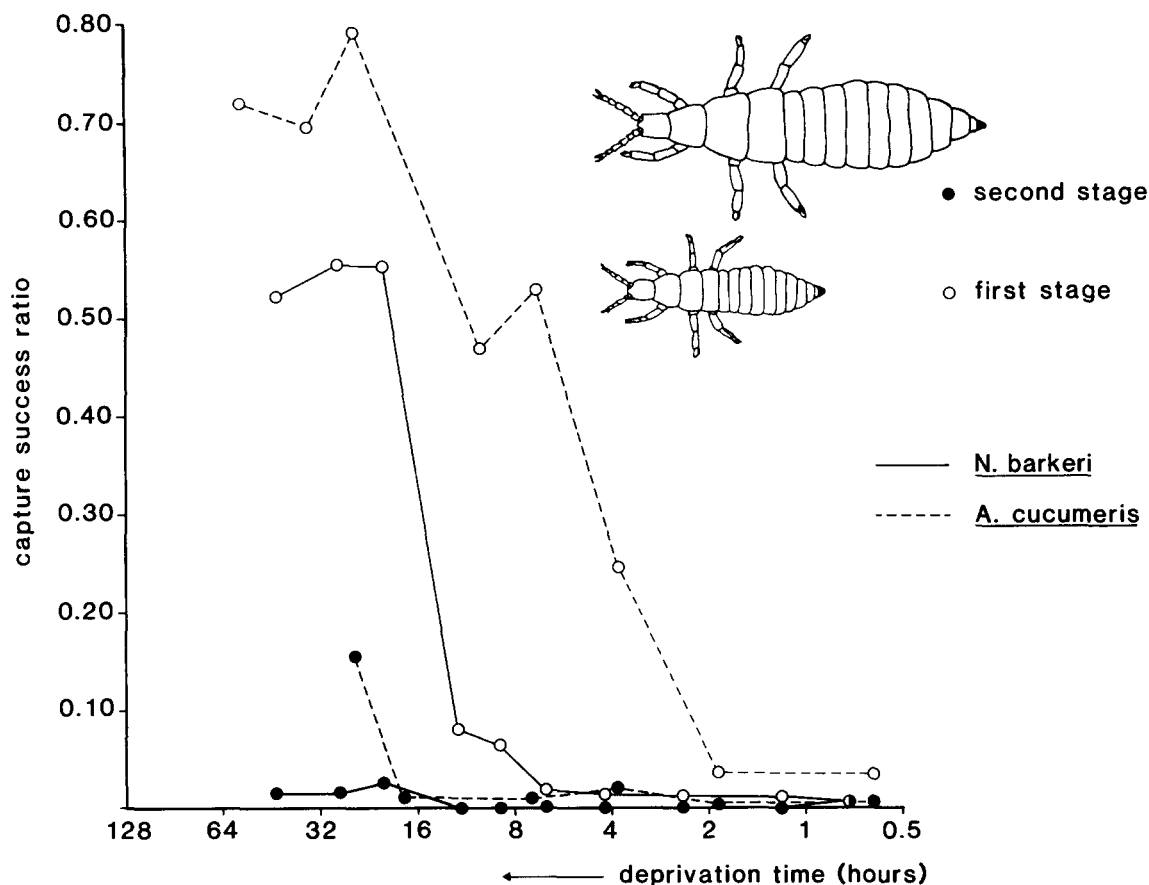


Fig. 1. The capture success ratio (CSR) of *N. barkeri* and *A. cucumeris* in relation to the time of food and water deprivation (t) and the size of the larvae of *T. tabaci*. Temperature: 20°C.

the prey in the thorax region both the jerk and the droplet were ineffective. If second stage larvae were captured they were usually attacked in this vulnerable region.

The second stage larvae used in this experiment weighed ca. 4 times as much as the first stage larvae ($16.3 \pm 2.5 \mu\text{s}$ vs. $4.5 \pm 1.8 \mu\text{g}$; $n=30$ for both stages). Our hypothesis was that a difference in physical strength caused the observed difference in the CSR with respect to both prey types. To test this hypothesis we repeated the first series of experiments for *N. barkeri* with anaesthetised prey larvae. The results are summarised in Table 1.

The CSR of *N. barkeri* (for $t > 16$ h) encountering CO₂-treated second stage larvae is almost twelve times the value of CSR observed with untreated lar-

vae as prey. This shows that the defence of second stage prey larvae reduces the attack success of starved predators by a factor of 12. First stage larvae reduce the CSR of predators in this t -class with a factor of 1.4. Hence, when $t > 16$, the defence of second stage larvae is more than 8 times as effective in countering attacks of *N. barkeri* than the defence of first stage larvae.

There is, however, a more pronounced effect of the defence of first stage larvae on the CSR of *N. barkeri*. With untreated first stage larvae as prey the CSR-curve increases steeply at $t = 11$. This point will be referred to as the CSR-switchpoint. When the larvae are anaesthetised, the plateau part of the curve is reached at $t \pm 3$. This shift of the CSR-switchpoint results in a large reduction of the CSR

for $3 < t < 11$. If the data in this class are pooled the reduction factor is 35, but, as shown in Table 1, it can be as high as 52.7 ($4 < t < 8$).

Discussion

The differential effect of predator satiation level and prey defence in determining the CSR is best illustrated by the experiments with *N. barkeri*.

The data on first stage larvae in Table 1, show that for $0 < t < 2$ the CSRs in the experiments with and without CO₂-treatment do not differ significantly. Here the only determinant of the CSR is predator satiation level. For $3 < t < 11$ it was found that first stage larva behavioural defence reduces the CSR by a factor of 35. In this range of t the CSR is largely determined by prey defence. Above $t = 16$ first stage larvae are able to reduce the CSR only slightly (factor of 1.4). Here again the CSR is determined by the predators' satiation level. Second stage prey larvae, on the other hand, show a more pertinent and severe wagging behaviour. Due to this mode of defence the CSR of starved predators ($t > 16$) is reduced by a factor of 11.5.

However, blocking the defence mechanism of second stage larvae did not result in a CSR equal to that of first stage larvae, whether these are treated or not (Table 1). Therefore, in addition to wagging behaviour other factors must be involved as well. Possible hypotheses are: (1) The cuticle of most second stage larvae is too tough for penetration by predator mouthparts, (2) the food quality of these larvae is such that they are avoided, and (3) the effective

defence of second stage larvae imposes such a high risk (e.g. physical damage, time spent cleaning) that the predators avoid the larvae, whether these are anaesthetised or not.

The experiments revealed a phenomenon of possible practical significance for biological control of *T. tabaci*. Both commercially distributed predatory mites rely predominantly on first stage larvae of *T. tabaci* as prey. Therefore when this prey stage is scarce and no other foods are available, the predator population can only be sustained by alternative food sources. Such scarcity of suitable prey may arise either because of inherent fluctuations in the age distribution of the pest (e.g. due to the synchrony in emergence from winter diapause) or because of pest suppression by the predators and/or other agents.

Zusammenfassung

Wie Thrips tabaci Larven den Angriffserfolg von Raubmilben mindern

Neoseiulus barkeri (= *Amblyseius mckenziei*) und *Amblyseius cucumeris* (Acari: Phytoseiidae) werden zur Bekämpfung von *Thrips tabaci* (Insecta: Thripidae) in Gewächshauskulturen eingesetzt. Sowohl der Ernährungszustand der räuberischen Milben als auch die Grösse der Thripslarven haben Einfluss auf das Ausmass der Beutenahme. Die Prädatoren sind erfolgreicher, wenn sie eine Zeitlang ohne Nahrung gehalten wurden. Beim Zusammentreffen mit einer ausgehungerten Raubmilbe besteht für Thripslarven des zweiten Stadiums ein geringeres Risiko erbeutet

Table 1. Effect of anaesthesia of thrips larvae on the capture success ratio (CSR) of *N. barkeri*. n = number of encounters.

larval stage	t-class	Untreated		Treated		Reduction factor	Level of significance
		n	CSR	n	CSR		
first	0 – 2	105	1.0	68	4.4	–	P = 0.0588 (n.s.)
	2 – 4	185	2.2	69	11.6	5.3	
	4 – 8	188	1.1	69	58.0	52.7	P < 0.0002
	8 – 16	59	6.8	–	–	–	–
	> 16	68	54.4	83	76.0	1.4	P = 0.005
second	> 16	897	1.7	240	19.6	11.5	P < 0.002

und gefressen zu werden als für Larven des ersten Stadiums. *T. tabaci* Larven mindern den Angriffserfolg der Prädatoren durch kräftiges Hin- und Herschlagen des Abdomens und durch Abgabe eines Tropfens Rektalflüssigkeit. Wird dieses Abwehrverhalten der Larven durch Anaästhesie mit CO₂ verhindert, erhöht sich der Angriffserfolg der Prädatoren. Anästhesie nivelliert jedoch nicht das für beide Larvenstadien unterschiedlich hohe Risiko erbeutet zu werden. Mögliche Ursachen für diesen Unterschied werden diskutiert.

Die Verfügbarkeit geeigneter Beutetiere hängt ab von der zeitlichen Entwicklung der Altersstruktur ihrer Population. Das Angebot an wirklich geeigneten Beutetieren kann also unter Umständen geringer sein, als dies die Gesamthripsdichte zunächst vermuten lässt. Ist das der Fall, dürften alternative Nahrungsquellen für die Ernährung der Prädatorenpopulation wichtig sein.

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