Macrolophus caliginosus (Wagner) as an Intraguild Prey for the Zoophytophagous Dicyphus tamaninii Wagner (Heteroptera: Miridae)

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The zoophytophagous predator *Macrolophus caliginosus* (Wagner) (Heteroptera: Miridae) has previously been identified as a potential prey for the intraguild zoophytophagous predator *Dicyphus tamaninii* Wagner. Its value as an intraguild prey was tested for *D. tamaninii* nymphal development and adult survival. In the laboratory, plant (red tomato fruit, green tomato fruit, tomato leaf) and animal (aphids, whiteflies, pyralid eggs) resources were compared to frozen nymphs of *M. caliginosus* as an intraguild resource for *D. tamaninii*. *M. caliginosus* nymphs allowed complete and rapid development of *D. tamaninii* nymphs and generated low mortality of nymphal and adult stages. Performances were higher with the intraguild *M. caliginosus* resource than with plant resources. Tomato leaves did not allow the complete nymphal development of *D. tamaninii*. Tomato fruit generated lighter adults and doubled the nymphal developmental time compared with the *M. caliginosus* resource. In the animal resource group, there were no differences between the *M. caliginosus* and the other treatments (aphids, whiteflies, pyralid eggs) for nymphal mortality, average number of molts, nymphal developmental time, adult weight, and adult survival. *M. caliginosus* should be considered a high-quality resource for *D. tamaninii*. © 2001 Academic Press

***Key Words:* *Dicyphus tamaninii*; *Macrolophus caliginosus*; *Macrosiphum euphorbiae*; *Trialeurodes vaporariorum*; *Ephestia kuehniella*; *Solanum lycopersicum*; intraguild predation; prey quality; zoophytophagy; omnivory; Miridae; diet.**

INTRODUCTION

Zoophytophagous insects exploit both plant and animal food sources. These insects may be phytophagous but include carnivory in their feeding habit (Whitman *et al.,* 1994) or carnivorous but include some plant material in their diet (Jervis and Kidd, 1996; Fauvel, 1999). Several studies have shown that these feeding habits are relatively common among arthropods (Strawinski, 1964; Whitman *et al.,* 1994; Coll, 1998; Naranjo and Gibson, 1996; Fauvel, 1999).

The heteropteran family Miridae constitutes an example of the diversity of feeding habits which range from strictly phytophagous, phytozoophagous (species displaying facultative carnivory), zoophytophagous (species displaying facultative plant sap feeding), to strictly zoophagous (Strawinski, 1964; Fauvel, 1999). Among the mirids, *Macrolophus caliginosus* (Wagner) (or *M. melanotoma* (Costa) according to Carapezza, 1995) is currently commercialized in Europe for the control of whiteflies in tomato greenhouses. In the Mediterannean area, greenhouse colonization by *M. caliginosus* occurs naturally. This predator shares outside and greenhouse ecosystems with numerous other predators and belongs to several feeding guilds (aleurophagous, aphidophagous, acarophagous, etc.). In several crops, including field and greenhouse tomatoes, the other most abundant predator is the mirid *Dicyphus tamaninii* Wagner. The two mirids constitute, respectively, commercialized and potential agents for biological control in greenhouses (Gabarra *et al.,* 1988, 1995; Alomar and Albajes, 1996). Therefore, it is important to know their interactions and the consequences for biological control.

M. caliginosus and *D. tamaninii* usually reach high densities and have similar within-plant distribution on tomato plants (Alomar, 1994). Interactions occur and intraguild predation among almost all stages of the two species have been recorded (Lucas and Alomar, 2000). These two mirids are zoophytophagous predators, consumming both plant and animal food (Salamero *et al.,* 1987; Gabarra *et al.,* 1995; Castañe *et al.,* 1996; Albajes and Alomar, 1999; Sampson and Jacobson, 1999). Because intraguild predation could be motivated by the search for deficient nutrients (Polis *et al.,* 1989; Whitman *et al.,* 1994; Wissinger *et al.,* 1996), the nutritional value of the intraguild resource should be evaluated. Furthermore, it is crucial to know the feeding habits of zoophytophagous species and the associated benefits (Wiedenmann and Wilson, 1996).

This study aims to (1) evaluate the quality of *M. caliginosus* as a food source for *D. tamaninii* and (2) assess the zoophagous and phytophagous feeding habits of *D. tamaninii* by comparing its performances on different plant and animal food sources.

MATERIALS AND METHODS

Insect and Plant Sources

Mirids, *M. caliginosus* and *D. tamaninii,* were taken from permanent colonies on tobacco plants (*Nicotiana tabacum* L.), with eggs of *Ephestia kuehniella* Zeller (Lepidoptera: Pyralidae) and larvae of *Trialeurodes vaporariorum* Westwood (Homoptera: Aleyrodidae), and were maintained at 25° ± 2°C with a 16:8 h (L:D) photoperiod. Colonies originated from field-collected insects, and new material is taken from the field each year. Aphids, *Macrosiphum euphorbiae* Thomas (Homoptera: Aphididae), and whitefly (*T. vaporariorum*) came from colonies started at the beginning of the spring and maintained on potato (*Solanum tuberosum* L.) and tobacco, respectively. Tomato plants (*Solanum lycopersicum* L.) used in all tests were from the cultivar "Carmelo."

Experimental Setup

Tests were carried out in growth chambers held at 25° ± 2°C with a 16:8 h (L:D) photoperiod. The experimental setup consisted of a transparent plastic cage (75 mm diameter × 32 mm height) with a layer of agar (20 ml, 5%) at the bottom. The agar helped to keep humidity in the system and to prevent plant food desiccation. The lid had a meshed opening (muslin) to allow ventilation. Preliminary tests showed that agar is not a food source for either mirid. Water was provided in all arenas by a moistened cotton wick in an Eppendorf vial.

In the first experiment, 1-day-old nymphs of *D. tamaninii* were collected from the rearing units and put individually into each cage. Eight treatments were carried out: one without food but with water, three with plant resources, and four with animal resources. The classification was as follows: (1) no resource; (2) tomato leaf: a tomato leaf disk (34 mm diameter) was cut with a cork borer and put on agar (lower face visible); (3) green tomato fruit: an epidermal pericarp disk (34 mm diameter, 7–10 mm depth) was cut with the borer from green tomato fruit (unripe); to prevent agar degradation and development of fungi, the lower part of the disk was submerged in hot wax; once dried, the disk was put in the agar layer so that only the external surface of the tomato emerged; (4) red tomato fruit: same methodology as in the previous treatment, but with a red tomato disk (from ripe fruit); (5) whiteflies: 20 mg of frozen pupae (1 to 3 days old) of *T. vaporari-*

orum was put into the center of the cage in a circle of 34 mm diameter; (6) *Ephestia:* 20 mg of *E. kuehniella* eggs was put into the center of the cage in a circle of 34 mm diameter; (7) aphids: three *M. euphorbiae* adults were introduced into the cage 5 min before the predators; and (8) *Macrolophus:* four second to third instar *M. caliginosus* were frozen and put into the center of the cage.

Every 2 to 3 days, agar, water, and food sources were renewed. Nymphal mortality and nymph molts were recorded. The test finished when the nymph died or became adult. Adults were then weighed. Twelve replicates were carried out. The mortalities were compared using a likelihood ratio *G* test. The mean nymphal developmental time and the mean number of molts were compared using an ANOVA and subsequent post hoc Tukey tests. When comparing proportions, an arcsin transformation was applied to the data and when comparing the number of exuviae, a square root transformation was applied (SAS Institute, 1996; Sokal and Rohlf, 1981).

The second experiment was carried out to determine the effect of the diets on short-term adult survival. *D. tamaninii* adults came from the permanent colonies established in the laboratory. Using the same design, seven of the eight previous treatments were carried out: (1) no resource, (2) tomato leaf, (3) green tomato fruit, (4) red tomato fruit, (5) whiteflies, (6) *Ephestia,* and (7) *Macrolophus.* Three days later, agar, water, and food sources were renewed. At least 12 adults (between 7 and 14 days old) were used for each treatment. Adult mortality was recorded after 3 and 5 days and compared using a likelihood ratio *G* test.

RESULTS

Nymphal Mortality

The mortality of *D. tamaninii* nymphs differed according to the resource available ($G_7 = 36.10$; $P < 0.001$) (Fig. 1). *M. caliginosus* nymphs ("*Macrolophus*" treatment) generated a mortality of 50%, which was relatively similar to that obtained with other animal resources and with red and green tomato fruits. In contrast, the mortality of nymphs without resource or feeding on tomato leaves was significantly higher (100%).

Number of Exuviae

The "no resource" and the "tomato leaf" were the worst treatments for mirid development (less than one molt) ($F = 6.21$; $df = 7,88$; $P < 0.001$) (Fig. 2). Nymphs of the "*Macrolophus*" treatment achieved a mean of 3.5 molts, which was not significantly different from the other treatments.
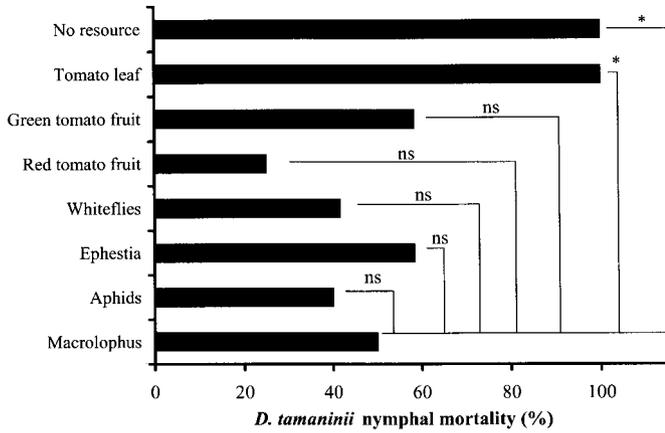
FIG. 1. Mortality of *D. tamaninii* nymphs during preimaginal development on different types of animal and plant resources. Asterisk means that the nymphal mortality is different between the treatments (*G* test, *P* < 0.05, *n* = 12).

FIG. 3. Nymphal developmental time of *D. tamaninii* reared on different types of animal and plant resources. Means followed by different letters are significantly different (ANOVA, *P* < 0.05, *n* = 12).

Nymphal Developmental Time

The type of resource affected the mean developmental time of the preimaginal stages (*F* = 40.51; *df* = 5,34; *P* < 0.001) (Fig. 3). No nymph reached the adult stage in the "no resource" or the "tomato leaf" treatments. All animal treatments, including the "*Macrolophus*," did not differ significantly and allowed a rapid nymphal development (18 to 22 days). In contrast, nymphal development required approximately twice as long on tomato fruit (42 to 46 days) as on animal resources.

Adult Weight

D. tamaninii adult weights were similar among animal treatments (1.3 to 1.5 mg) (*F* = 7.97; *df* = 5,31; *P* < 0.001) (Fig. 4). Adults from the plant treatments were significantly lighter (0.8 to 0.9 mg) than those of the animal treatments.

Adult Mortality

After 3 days, the mortality of *D. tamaninii* adults was lower than 13%. No significant differences were observed among treatments with males (*G*$_6$ = 4.35; *P* = 0.630) or females (*G*$_6$ = 6.33; *P* = 0.387). After 5 days (Fig. 5), the mortality in the "no resource" treatment (higher than 38%) was significantly higher than that in the "*Macrolophus*" treatment, both for males (*G*$_6$ = 28.66; *P* < 0.001) and for females (*G*$_6$ = 13.82; *P* = 0.032). The mortality in the other treatments was similar to that of the "*Macrolophus*" treatment both for males and for females (*P* > 0.05).

DISCUSSION

This study showed that *M. caliginosus* is a high-quality resource for the intraguild predator *D. tamani-*
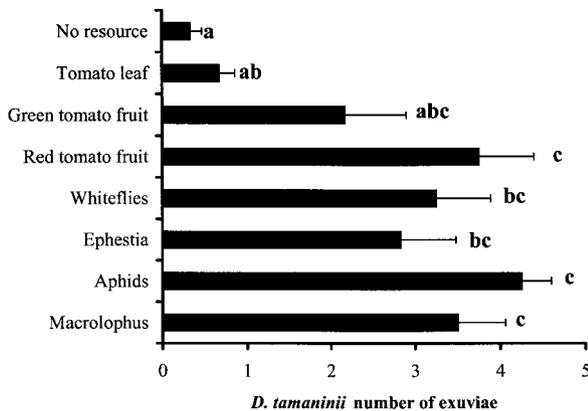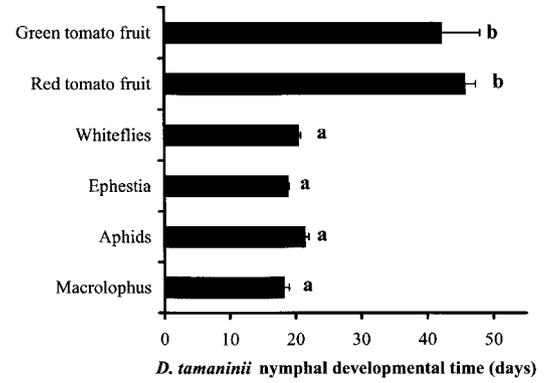

FIG. 2. Mean number of exuviae (per nymph) collected during the nymphal development of *D. tamaninii* reared on different types of animal and plant resources. Means followed by different letters are significantly different (ANOVA, *P* < 0.05, *n* = 12).
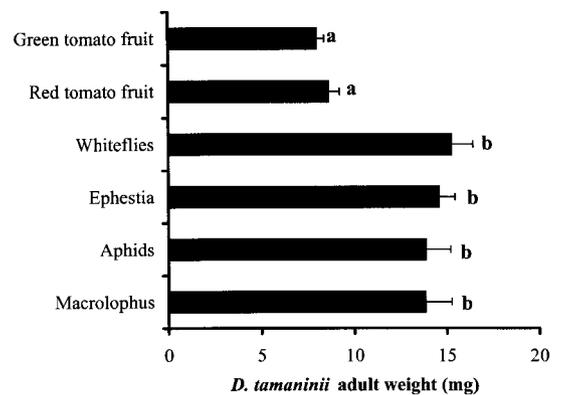

FIG. 4. *D. tamaninii* adult weights (sexes combined) when reared on different types of animal and plant resources. Means followed by different letters are significantly different (Wilcoxon, *P* < 0.05, *n* = 12).
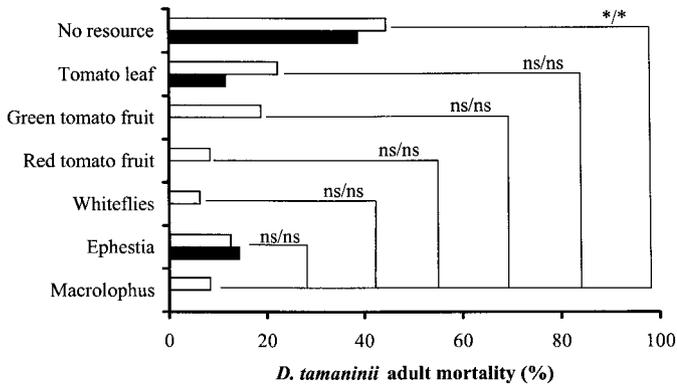
FIG. 5. Mortality of *D. tamaninii* males (open bars) and females (solid bars) reared on different types of animal and plant resources after 5 days. An asterisk indicates that the nymphal mortality is different between treatments, "ns" indicates no significant difference (*G* test, *P* < 0.05).

nii. Frozen *M. caliginosus* nymphs were eaten by *D. tamaninii* and allowed it to complete nymphal development. Nymphal developmental time was short (approx. 20 days) and the subsequent *D. tamaninii* adult weight did not differ from that on other animal diets. Adult mortality was also minimum with the *M. caliginosus* diet. All the parameters recorded were similar to the best identified diet, *E. kuehniella* eggs (Kaspar, 1982; Salamero *et al.*, 1987; Agustí, 1998).

The study also confirmed the zoophytophagous habits of *D. tamaninii*, because nymphs completed their development on both plant and animal food sources. The results confirm the zoophagous status of the genus (Strawinski, 1964). *D. tamaninii* also completes nymphal development on a plant diet. However, because phytophagy was also associated with detrimental effects on nymphal development, *D. tamaninii* may be more accurately considered a zoophytophague rather than a phytozoophague (Strawinski, 1964; Fauvel, 1999).

In the "no-resource" treatment, no *D. tamaninii* nymphs reached the adult stage and significant adult mortality ocurred after 5 days. Nevertheless, several nymphs were able to molt to second instar without any food source. It is therefore possible that first instar nymphs had some reserves or could survive on water only. In the Miridae, young nymphs may be more phytophagous than both older nymphs and adults (Kullenberg, 1944). Such a strategy may reduce risk of predation by other intraguild predators, as they do not have to search for prey. If this is the case, it may explain the very low predation rate by first and second nymphal stages recorded on the aphid *Myzus persicae* (Sulzer) (Perdikis *et al.,* 1999).

Tomato leaves were also a poor-quality diet for *D. tamaninii* because they did not allow complete nymphal development (100% mortality before 7 days). Herbivory in the genera *Dicyphus* and *Macrolophus*

(Miridae: Dicyphinae) has been studied and the plant was identified as a food/water source and as a substrate for laying eggs (Dolling, 1991; Riudavets and Castañe, 1998). Kaspar (1982) and Gillespie *et al.* (1999) showed that the mirids *M. caliginosus* and *Dicyphus hesperus* Knight die on tomato leaf without animal food. However, Perdikis and Lykouressis (2000) reported that *Macrolophus pygmaeus* Rambur survived on different plant leaves, such as tomato, in the absence of animal prey. Thus, it is difficult to generalize results on feeding habits and each predator species has to be evaluated separately for each plant–prey system.

Compared with the *M. caliginosus* diet, both green and red tomato fruits were low-quality resources for the predator. Tomato fruits allowed complete nymphal development, but the mean developmental time was much longer and the resulting adults were lighter than those with animal diets. *D. tamaninii* and *M. caliginosus* are known to feed on tomato (Salamero *et al.*, 1987; Albajes and Alomar, 1999; Alomar and Albajes, 1996; Sampson and Jacobson, 1999). Testing adults of *Dicyphus errans* Wolff, *M. caliginosus,* and *Cyrtopeltis tenuis* (Reuter), only adults of *D. errans* were able to survive on green tomato fruits without animal prey (Malausa, 1994). Survival on red tomato fruit without prey was good for both *D. errans* and *M. caliginosus.* The larger size of *D. errans* was proposed to explain its higher capacity to pierce fruit skin and therefore its higher survival. However, because we obtained good results with the smaller *D. tamaninii,* this should not be a key factor.

The higher quality of tomato fruit compared to leaves indicates that *D. tamaninii* nymphs will survive better in the crop during periods of prey scarcity (at least 40 days) when fruit is available. The concentration of allelochemicals in the plant may explain the differences among fruit and leaves. The tomatine (steroidal glycoalkaloid) contents in tomato leaves are higher than those in tomato fruit (Furui *et al.,* 1997), and the negative effects of tomatine have been demonstrated on several insects, including indirect effects on predators (Osier *et al.,* 1996; Stamp *et al.,* 1997; Weiser and Stamp, 1998). In another study with *D. hesperus,* tomato fruit were not attacked when leaves and fruit were present simultaneously (Gillespie *et al.,* 1999), which shows a high variability among closely related species. In the field, in the absence of prey, several behavioral adaptations (choosing rich plant tissues, eating a variety of plant tissues, increasing feeding rate, etc.) may also allow phytophagous species to compensate for the nutritional deficiencies in their plant food (Whitman *et al.,* 1994).

Animal diets (*M. caliginosus,* aphids, *E. kuehniella* eggs, and whiteflies) were high-quality food sources confirming previous studies on *Macrolophus* spp. and *Dicyphus* spp. (Kaspar, 1982; Salamero *et al.,* 1987;

Agustí, 1988; Perdikis and Lykouressis, 2000). All the results concerning nymphs (low mortality, short development time) and adults (low mortality, high weight) were homogeneous and demonstrated higher performances with animal than with plant resources. Our study confirms previous results showing that, among zoophytophagous Heteroptera, prey diets consistently allow faster development than plant diets, but that results on survivorship are variable (Naranjo and Gibson, 1996).

Intraguild predation and cannibalism have been identified as a search to improve diet quality (Polis, 1981; Polis *et al.,* 1989; Whitman *et al.,* 1994; Wissinger *et al.,* 1996). The gains may be particularly important for predators primarily feeding on plants (Polis *et al.,* 1989; Whitman *et al.,* 1994). Thus, according to the low or poor quality of plant diets and the high quality of the *M. caliginosus* diet, intraguild predation on *M. caliginosus* may be a highly adaptive strategy for *D. tamaninii* when alternative animal prey are scarce. Because both species use the same host plants, have similar within-plant distribution (Alomar, 1994), and can have relatively high densities (Alomar, 1994; Malézieux *et al.,* 1995; Malausa and Trottin-Caudal, 1996), intraguild predation may be a common interaction *in situ,* especially in the absence of alternative animal food. Moreover, intraguild predation provides advantages other than nutritional profits, such as the elimination of a competitor and a potential predator (Polis *et al.,* 1989; Polis and Holt, 1992). In our system, the interaction is symmetrical (E. Lucas and O. Alomar, unpublished data) and *M. caliginosus* is both a competitor and an intraguild predator of *D. tamaninii.* Therefore, for both mirid species, intraguild predation may be a very profitable strategy even in the presence of alternative prey.

As mirids appear to select slow-moving, easy, and safe prey when available (such as whitefly larvae or pupae) (Kullenberg, 1944; Kaspar, 1982), intraguild predation may be directed toward sessile stages such as eggs or molting stages. Such stages are highly susceptible to intraguild predation (Lucas *et al.,* 1998, 2000) and several zoophytophagous orthoptera also cannibalize weak, wounded, or molting conspecifics (Whitman *et al.,* 1994 and references therein).

From a biological control perspective, *M. caliginosus* survival or colonization may be adversely affected by *D. tamaninii,* especially during periods of prey scarcity. However, because both species prey on each other (E. Lucas and O. Alomar, unpublished data), the presence of *D. tamaninii* could constitute an animal food source for *M. caliginosus.* Furthermore, as *D. tamaninii* can damage tomato fruits at high densities (Alomar and Albajes, 1996), *M. caliginosus* could contribute to the reduction of *D. tamaninii* populations. Both species are the most common predators in tomato greenhouses in Catalonia (Spain). However, their respective abundances have changed in the past 10 years, with *M. caliginosus* becoming more numerous than *D. tamaninii* (Castañe *et al.,* 2000). Intraguild predation may have influenced these changes.

In summary, *M. caliginosus* was a high-quality diet for the zoophytophagous *D. tamaninii.* Intraguild predation directed toward *M. caliginosus* may be highly profitable and should be common in the field in the absence of alternative animal prey. Plant foods were identified as poor- or low-quality diets but could allow, in the case of tomato fruits, the survival of *D. tamaninii* during periods of prey scarcity.

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