

# Effect of cassava exudate and prey densities on the survival and reproduction of *Typhlodromalus limonicus* (Garman & McGregor) *s.l.* (Acari: Phytoseiidae), a predator of the cassava green mite, *Mononychellus tanajoa* (Bondar) (Acari: Tetranychidae)

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(Accepted 11 April 1994)

## ABSTRACT

Toko, M., O'Neil, R.J. and Yaninek, J.S., 1994. Effect of cassava exudate and prey densities on survival and reproduction of *Typhlodromalus limonicus* (Garman & McGregor) (Acari: Phytoseiidae) *s.l.*, a predator of the cassava green mite, *Mononychellus tanajoa* (Bondar) (Acari: Tetranychidae). *Exp. Appl. Acarol.*, 18: 221–231.

**Key words:** Cassava, cassava green mite, predators, exudate, *Typhlodromalus limonicus*.

The effects of cassava exudate and prey densities on reproduction and survival of the predatory mite, *Typhlodromalus limonicus* (Garman & McGregor) (Acari: Phytoseiidae), were investigated in the laboratory. Females were provided either cassava exudate *ad lib.* daily, low or high numbers of the cassava green mite prey, *Mononychellus tanajoa* (Bondar) (Acari: Tetranychidae) daily, or exudate for 5 or 10 days before switching to a low or high prey diet. Females fed only exudate laid no eggs. Females fed exudate before prey experienced a significant decrease (30%) in the number of eggs laid compared to females fed high numbers of prey daily. The reduction in fecundity was the result of prolonged preoviposition periods (2.0 days on prey daily vs 4.0 days on exudate before prey) and reduced number of eggs laid per female per day (1.7 eggs per female per day on prey daily vs 0.4 eggs per female per day on exudate before prey). Females fed only exudate had a greater survival rate and longevity than females fed prey daily or females fed exudate before a diet of prey. These results suggest that *T. limonicus* can survive for a limited period on cassava exudate during periods of low prey availability, but requires prey to complete oögenesis and propagate the population.

## INTRODUCTION

Since its introduction from South America in the 1970s, the cassava green mite, *Mononychellus tanajoa* (Bondar) (Acarina: Tetranychidae), has been one of the

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most important pests of cassava, *Manihot esculenta* Crantz, in Africa (Nyiira, 1972; Lyon, 1973; Yaninek and Herren, 1988). In 1983, the International Institute of Tropical Agriculture (IITA) initiated a major work to search, introduce and establish exotic natural enemies against it (Herren and Bennett, 1984). Following several failures to establish phytoseiid mites from Colombia as predators of *M. tanajoa* (Rogg and Yaninek, 1990), explorations for other phytoseiids were focused on northeastern Brazil, a region climatically similar to areas within the African "cassava belt" (Yaninek and Bellotti, 1987). In 1989, *Typhlodromalus limonicus sensu lato* (Garman and McGregor) (Acari: Phytoseiidae), was identified as a candidate natural enemy of *M. tanajoa* and introduced to Africa (Yaninek *et al.*, 1993). Since its introduction, *T. limonicus* has shown promise of establishment in several localities and is currently a strong candidate for widespread release throughout Africa (Yaninek *et al.*, 1993).

High densities of *T. limonicus* have been observed in northeastern Brazil even in the near absence of *M. tanajoa* (Moraes, 1990). The persistence of *T. limonicus* at low prey densities suggests that it is able to use alternative food sources, including an exudate produced by cassava (Oduor, 1988; Bakker and Klein, 1992). Cassava exudate is composed of reducing sugars, fructofuranosides and some amino acids (Pereira and Splittstoesser, 1987). The exudate is produced at the petiole bases, the midribs of young leaves and occasionally on stems of cassava plants (Klein, 1990). The quantity and quality of the exudate vary with cultivar, plant vigor, plant age and time of day (Oduor, 1988; Klein, 1990). Oduor (1988) found that *T. limonicus* could survive, but not reproduce on a diet of cassava exudate.

That cassava exudate can sustain predators during periods of low prey availability may be critical to the successful introduction of exotic natural enemies like *T. limonicus* into Africa. Over much of the African "cassava belt", two distinct rainfall periods are typical (Yaninek *et al.*, 1989; Rogg and Yaninek, 1990), and *M. tanajoa* populations are typically significantly reduced in the wet season (May–October in Benin, West Africa) compared to the dry season (November–April) (Yaninek *et al.*, 1989). Thus, predators must be adapted to survive periods of low prey availability if they are to persist in the African cassava agroecosystem.

The objective of this study was to determine the effect of cassava exudate on *T. limonicus* survival and reproduction, particularly under conditions of low prey availability.

## MATERIALS AND METHODS

### *Field inventory of cassava exudate production*

The production of cassava exudate available as a food resource was evaluated in a cassava field planted at the IITA Benin Station, in May 1990. The field was divided using a split-split plot design where main plots consisted of three treatments: predator release, acaricide treatment, and control (no acaricide and no predator)

(Toko, 1993). Subplots consisted of two cropping systems: cassava monocrop and cassava intercropped with maize. In each subplot, the varieties "Agric" and TMS 30572 planted at a density of  $1 \text{ m}^{-2}$  constituted the sub-subplots which measured  $21 \times 11 \text{ m}$  each. All treatments were replicated 4 times. There were a total of 48 sub-subplots. In each sub-subplot, two cassava plants were randomly selected and tagged, making a total of 96 plants observed or 48 plants for each variety. The inventory was conducted from the third month after planting, when most plants had fully established, until the twelfth month when plant height limited observations. Plants were examined before 1200 hr. when detection was facilitated by minimal evaporation of the water in the exudate. The proportions of plants with exudate were calculated for each variety per sub-subplot and the values examined on a graph for seasonal trends. No corrections were made for exudate lost to other organisms such as ants which were frequently observed feeding on the exudate droplets. Rain-fall data were obtained from the IITA weather station located near the field trial. Means were compared using a paired *t*-test. Percentages were transformed using arcsin and the level of significance was set at  $\alpha = 0.05$  for all analyses.

*Effects of exudate and prey densities on survival and reproduction of T. limonicus*

*T. limonicus* were reared in the laboratory using the modified method of Mesa and Bellotti (1987), while *M. tanajoa* were reared on cassava plants in a greenhouse using the cassava-tree production system described by Haug and Mégevand (1989). To obtain cohorts of *T. limonicus*, about 500 mated females from the culture were confined in a rearing arena for 24–48 hours. The eggs laid provided a source of fresh adults. Newly-emerged females were transferred individually to leaf discs of 2.5 cm diameter fitted to the bottom of Petri dishes of the same size. For aeration, the sides of the dishes had two opposite holes (2 mm diameter) covered with fine nylon mesh. The leaf discs laid on wet cotton in the dishes were changed at weekly intervals. The discs were excised from leaves of six-month old cassava (variety: "Agric") grown in a nearby field. The leaves were previously washed in water to remove any arthropod present on them. For insemination, a single male was placed in each dish for 24 hr.

*T. limonicus* females were randomly selected and assigned to one of the following diets: (1) three adult *M. tanajoa* females daily (low prey input); (2) ten adult *M. tanajoa* females daily (high prey input); (3) exudate *ad lib.* daily; (4) exudate *ad lib.* for 5 days followed by 3 adult *M. tanajoa* females daily; (5) exudate *ad lib.* for 5 days followed by 10 adult *M. tanajoa* females daily; (6) exudate *ad lib.* for 10 days followed by 3 adult *M. tanajoa* females daily; and (7) exudate *ad lib.* for 10 days followed by 10 adult *M. tanajoa* females daily.

The low and high prey inputs required to establish minimum and maximum daily oviposition were determined in a preliminary experiment. Given 3 adult *M. tanajoa* females daily, *T. limonicus* initiated reproduction (at least one egg laid

per female per day) while given 10 *M. tanajoa* females daily, reproduction was maximized (4 to 5 eggs laid per female per day) *i.e.* no additional significant increase in reproduction was observed with higher numbers of prey.

There were 24 replicates of the exudate *ad lib.* daily treatment, 40 of the low and high prey treatment, 60 of each of the exudate *ad lib.* for 5 days followed by low or high prey densities, and 100 of each of the exudate *ad lib.* for 10 days followed by either low or high prey densities. Replicates were varied to compensate for mortality so that a reasonable number of females could be obtained to estimate reproductive parameters. The exudate used in the study was collected each morning from potted cassava plants grown in a greenhouse. Excess exudate was kept in a refrigerator for up to one week and used when necessary. Exudate was diluted with an equal volume of water to simulate the conditions observed in the field, and to facilitate the presentation as droplets on the midribs of the leaf discs.

Females were observed daily for oviposition and survival. For each treatment, longevity, preoviposition periods, oviposition periods, mean number of eggs laid per female per day, and total fecundity were recorded. In this study, the preoviposition period was defined as the time required to achieve oviposition once prey was included in the diet. Eggs laid were counted and removed. Only females that laid eggs were included in the statistical analyses of the reproductive parameters. To correct for differences in longevity, the number of eggs laid were divided by longevity in days to obtain eggs per female per day. Analysis of variance (ANOVA) was used to test for differences between treatments. Means were compared using Student Newman-Keuls (SNK) test at  $\alpha = 0.05$ .

## RESULTS

### *Cassava exudate production*

Exudate was produced throughout the growing season. However, production varied over time and appeared to be related to season (Fig. 1). The proportion of plants with exudate during the rainy season (August–November 1990) was higher on average compared to that observed during the dry season (November 1990–April 1991). Overall there was no significant difference in percentages of plants with exudate between TMS 30572 and “Agric” (ANOVA:  $F_{\alpha=0.05, d.f. = 1, 38} = 0.85$ ). However, in approximately one-half of the sample dates, higher percentages of plants with exudate were found for TMS 30572 than for “Agric” (Fig. 1). For the remainder of the sampling dates, no significant differences between varieties were found.

### *T. limonicus reproduction*

Preoviposition periods were significantly affected by the treatments (ANOVA:  $F_{\alpha=0.05, d.f. = 5, 106} = 23.2$ , Table 1). Females fed *M. tanajoa* daily started laying eggs significantly earlier (one or two days after adult emergence) than females fed exudate before *M. tanajoa* were supplied. The preoviposition period of females

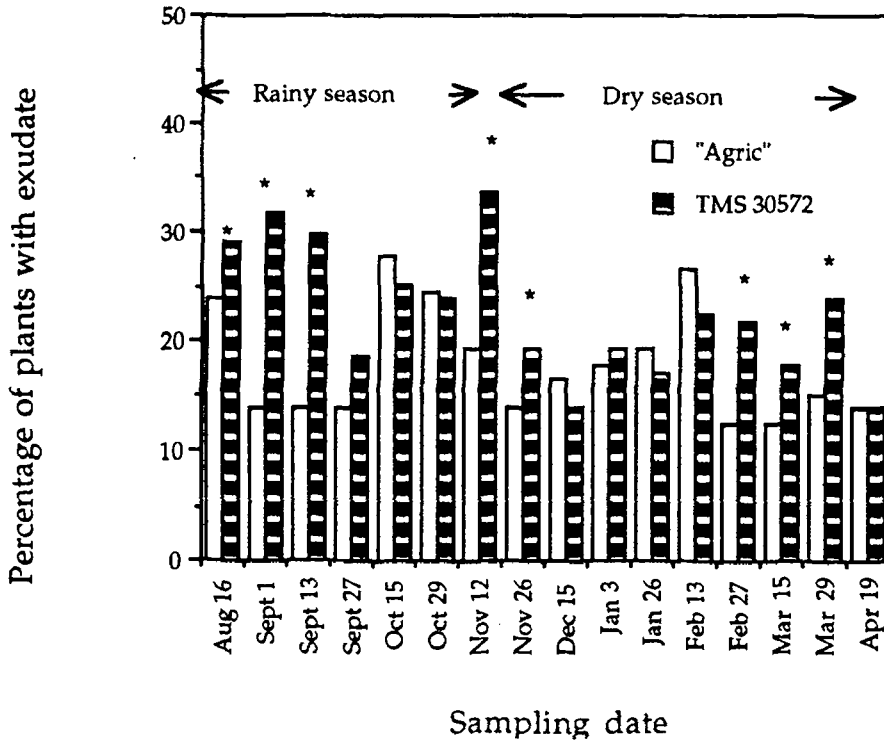


Fig. 1. Percentage of cassava plant varieties with exudate (TMS 30572 and "Agric") at IITA, Benin during the rainy and dry seasons of 1990–1991. Bars with asterisks indicate significant differences in percentages of plants with exudate for a given sampling date.

fed high numbers of *M. tanajoa* daily was significantly shorter than that of females fed low number of *M. tanajoa* daily. Similarly, preoviposition periods were significantly shorter for females fed the high prey diet after exudate compared to females fed the low prey diet after exudate whether exudate was provided for 5 or 10 days. Interestingly, the preoviposition period was significantly longer for females fed on exudate for 5 days before being provided prey compared to females fed on exudate for 10 days before being provided prey. Females fed only exudate did not lay eggs.

The oviposition periods were not affected by diet (ANOVA:  $F_{\alpha=0.05, d.f. = 5, 186} = 1.2$ , Table 1). *T. limonicus* fed exclusively *M. tanajoa* or exudate for 5 or 10 days followed by different prey densities oviposited during an average period of 7.2 days.

The mean number of eggs laid per female per day was significantly affected by the treatments (ANOVA:  $F_{\alpha=0.05, d.f. = 5, 175} = 54.4$ , Table 1). *T. limonicus* fed high numbers of *M. tanajoa* daily laid significantly more eggs (5 times) than females in all other treatments. *T. limonicus* fed low numbers of *M. tanajoa* daily produced 3-fold significantly more eggs (1.1) than all those fed exudate before *M. tanajoa*

TABLE 1

Mean values ( $\pm$  S.E.) for selected life history parameters on various dietary regimes<sup>1</sup>.

Means $\pm$ S.E. <sup>1</sup>					
Dietary <sup>2</sup> regime	Longevity (days)	Preoviposition period (days)	Oviposition periods (days)	Eggs/female/day	Overall fecundity
E <sup>3</sup>	11.3 $\pm$ 1.9 <sup>a</sup>	**	**	**	**
L	7.7 $\pm$ 1.1 <sup>b</sup>	1.80 $\pm$ 0.2 <sup>a</sup>	7.6 $\pm$ 1.1 <sup>a</sup>	1.1 $\pm$ 0.10 <sup>a</sup>	4.9 $\pm$ 0.8 <sup>a</sup>
H	8.9 $\pm$ 1.3 <sup>c</sup>	1.10 $\pm$ 0.1 <sup>b</sup>	9.0 $\pm$ 1.3 <sup>a</sup>	2.3 $\pm$ 0.20 <sup>b</sup>	13.6 $\pm$ 1.7 <sup>b</sup>
E5 L	6.8 $\pm$ 0.8 <sup>d</sup>	6.3 $\pm$ 1.3 <sup>c</sup>	5.1 $\pm$ 1.2 <sup>a</sup>	0.3 $\pm$ 0.04 <sup>c</sup>	0.25 $\pm$ .06 <sup>c</sup>
E5 H	8.7 $\pm$ 0.9 <sup>c</sup>	3.1 $\pm$ 0.5 <sup>d</sup>	6.5 $\pm$ 1.1 <sup>a</sup>	0.5 $\pm$ 0.2 <sup>c</sup>	0.87 $\pm$ 0.6 <sup>d</sup>
E10 L	5.9 $\pm$ 0.6 <sup>c</sup>	2.5 $\pm$ 1.5 <sup>ad</sup>	7.9 $\pm$ 1.2 <sup>a</sup>	0.3 $\pm$ 0.06 <sup>c</sup>	0.12 $\pm$ 0.04 <sup>ce</sup>
E10 H	6.8 $\pm$ 0.5 <sup>d</sup>	1.4 $\pm$ 0.2 <sup>ab</sup>	7.1 $\pm$ 0.9 <sup>a</sup>	0.4 $\pm$ 0.04 <sup>c</sup>	0.54 $\pm$ 0.2 <sup>d</sup>

<sup>1</sup> Means followed by the same letter in each column are not significantly different using Student Newman Kuuls test.

<sup>2</sup> E = exudate *ad lib.* daily, L = low prey (3 *M. tanajoa*) daily, H = high prey (10 *M. tanajoa*) daily, E5 L = exudate *ad lib.* for 5 days and then low prey daily, E5 H = exudate *ad lib.* for 5 days and then high prey daily, E10 L = exudate *ad lib.* for 10 days and then low prey daily, E10 H = exudate *ad lib.* for 10 days and then high prey daily.

<sup>3</sup> Females did not oviposit.

which produce an average of 0.4 eggs. There were no significant differences in the daily oviposition of *T. limonicus* fed exudate and then prey, regardless of the time spent on exudate or the numbers of prey provided.

*T. limonicus* fed low or high numbers of *M. tanajoa* daily accumulated the maximum number of eggs within the first 5 days of oviposition, after which the rate of egg production declined (Fig. 2). These females laid no more eggs towards the end of their lives. *T. limonicus* fed exudate before prey, accumulated lower numbers of eggs compared to *T. limonicus* fed prey daily. *T. limonicus* fed high numbers of prey following a diet of exudate accumulated slightly higher number of eggs than those fed low numbers of prey after a diet of exudate (Fig. 2).

Overall fecundity per female was affected by diet (ANOVA:  $F_{\alpha=0.05, d.f. = 5, 104} = 12.21$ , Table 1). The highest fecundity was observed in females fed high numbers of prey daily (15.1 eggs), followed by females fed low numbers of prey daily (6.3 eggs) and then by females fed exudate for 5 days before high numbers of prey were provided (5.1 eggs). All of these females produced significantly more eggs than females fed exudate for 5 days before low numbers of prey or exudate for 10 days before low or high numbers of prey were provided. The number of eggs laid by females in the latter treatment was not significantly different from that laid by females fed exudate for 5 days before high numbers of prey were provided.

#### *T. limonicus* survival

Few females died during the first 2–3 days of their life, irrespective of the dietary regime (Fig. 3). Survival decreased sharply by 75–80% in all treatments between

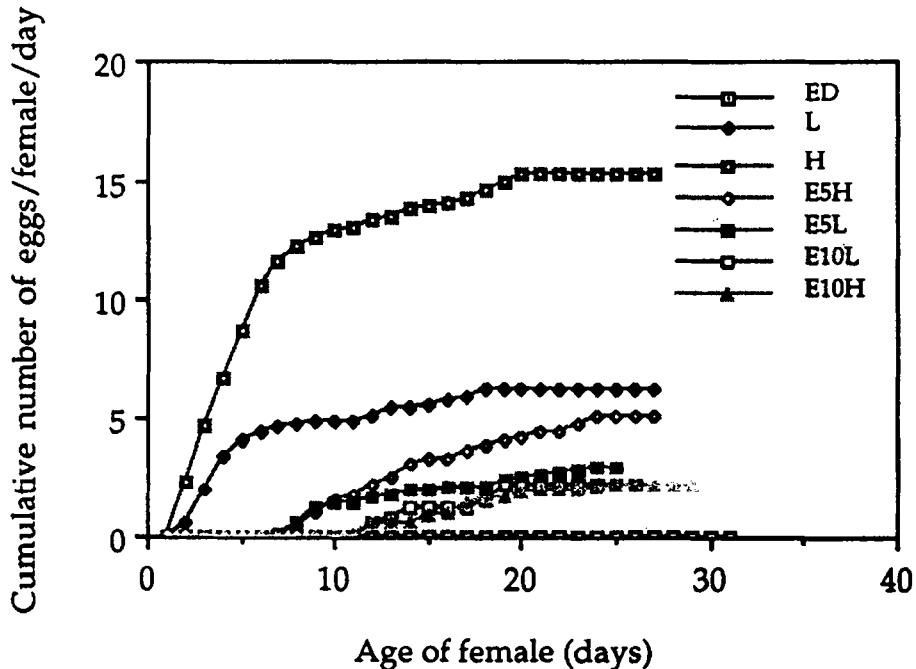


Fig. 2. Cumulative number of eggs laid per *T. limonicus* female fed under various dietary regimes. E = exudate *ad lib.* daily, L = low prey (3 *M. tanajoa*) daily, H = high prey (10 *M. tanajoa*) daily, E5 L = exudate *ad lib.* for 5 days and then low prey daily, E5 H = exudate *ad lib.* for 5 days and then high prey daily, E10 L = exudate *ad lib.* for 10 days and then low prey daily, E10 H = exudate *ad lib.* for 10 days and then high prey daily. Females fed exudate did not lay eggs.

the fourth and the tenth day. After 10 days, females fed only exudate had a higher survival rate than all other females. Survival of females fed prey daily was the next highest. Females fed exudate before feeding on *M. tanajoa* had similarly poor survival rates irrespective of the length of time exudate was provided.

Longevity of *T. limonicus* females was significantly affected by diet (ANOVA:  $F_{\alpha=0.05, d.f.=6, 366} = 3.29$ , Table 1). Overall, mean longevity was significantly higher for females fed exudate daily than for females in all other treatments. Mean longevity of females fed high numbers of prey daily (8.9 days) was not significantly different from the mean longevity of females fed exudate for 5 days followed by high numbers of prey daily (8.7 days). Mean longevity of these females was significantly higher than the mean longevity of females fed low numbers of prey daily (7.7 days) or any other combination of exudate and prey. Longevity of females fed low numbers of prey daily (7.7 days) was significantly longer than that of females fed exudate for 5 days before eating low numbers of prey (6.8 days) or females fed exudate for 10 days before eating low (5.9 days) or high numbers of

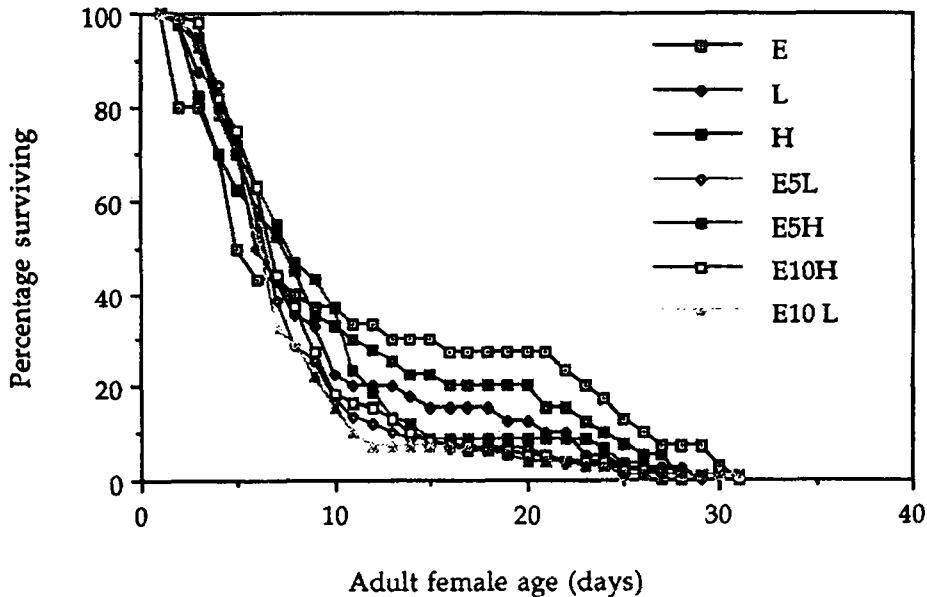


Fig. 3. Survivorship curves of *T. limonicus* under various dietary regimes. E = exudate *ad lib.* daily, L = low prey (3 *M. tanajoa*), H = high prey (10 *M. tanajoa*), E5 L = exudate *ad lib.* for 5 days and then low prey, E5 H = exudate *ad lib.* for 5 days and then high prey, E10 L = exudate *ad lib.* for 10 days and then low prey, E10 H = exudate *ad lib.* for 10 days and then high prey.

prey (6.8 days). The shortest longevity (5.9 days) was recorded for females fed exudate for 10 days then provided with low numbers of prey.

#### DISCUSSION

Although apparently affected by variety and season (Fig. 1), cassava exudate was present throughout the year. Seasonal differences may be related to intrinsic variability in plant productivity or extrinsic variability in ant foraging behavior, neither of which were measured directly in this study. Interestingly, the relative availability of exudate corresponded to low prey abundance as exudate was more abundant during the rainy season when prey are scarce (Yaninek *et al.*, 1989) than during the dry season when prey are abundant.

*T. limonicus* fed a high density of prey daily predictably laid more eggs than did those fed prey less frequently or at a lower prey density (Table 1, Fig. 2). This behavior suggests a numerical response to prey availability (Luck, 1984) that may prove important in the effective control of *M. tanajoa*. Predators fed a diet of exudate followed by prey experienced a delay in oviposition and a reduction in fecundity compared to females fed prey daily. This implies that exudate-fed predators are able to survive periods of low prey availability at the cost of their



fecundity. Females that have the option to feed on non-prey food sources during periods of low prey densities often survive to produce progeny, albeit at a reduced level.

*T. limonicus* fed cassava exudate only lived longer than predators fed prey only, suggesting a physiological adaptation to overcome periods of intermittent or low prey availability. *T. limonicus* do not reproduce on a diet of exudate alone (Table 1, Oduor, 1988). This suggests that prey-derived nutrients are essential for the completion of oögenesis in *T. limonicus*. Although predators were able to survive up to 30 days on exudate (Fig. 3), this is still far short of the four- to six-month rainy season during which *M. tanajoa* populations are greatly reduced (Yaninek *et al.*, 1989; Rogg and Yaninek, 1990). Thus, cassava exudate appears to provide a stopgap during the life time of an individual *T. limonicus* female, but can not sustain a population from one generation to the next.

The establishment of *T. limonicus* in Africa (Yaninek, J.S., unpublished data) suggests that it either survives periods of low prey availability on non-prey food sources such as cassava exudate or plant pollen. Although pollen was not in the dietary regime, *T. limonicus* s.s fed on castor bean pollen had a lower reproduction compared to a diet of *M. tanajoa* (Yaninek *et al.*, unpublished data). Until recently, *T. limonicus* was thought to be restricted to cassava and *M. tanajoa* (Bellotti *et al.*, 1987). However, recent works by Moraes *et al.*, (1993) in South America and Yaninek (unpublished data) in West Africa, record *T. limonicus* on several other host plants besides cassava. These plants may provide exudate, pollen or are refugias of alternate prey.

*T. limonicus* joins a growing list of predators whose life history characteristics have been studied under low prey inputs (Santos, 1982; Wiedenmann and O'Neil, 1990; Legaspi, 1991). Studying predator biology under low prey inputs exposes an entire suite of life history strategies, search behaviors and control potential not seen when predators are provided prey *ad lib.* (Wiedenmann and O'Neil, 1990; 1992). The ability of *T. limonicus* to survive periods of prey scarcity may be critical to its establishment in Africa. We suggest that further study of this and other candidate natural enemies should also consider the predator's ability to survive under conditions of low prey densities. In addition, the importance of plant-derived nutrition for predators may provide the key to understanding the difficulties in establishing exotic natural enemies, and warrants further investigation. The variability in exudate production between varieties and its importance to phytoseiid survival should also be further investigated.

#### ACKNOWLEDGEMENTS

This research was supported by a scholarship from the United Agency for International Development (USAID) to the Government of Zaire via the RAV Project (Project 091). The authors thank the Biological Control Center for Africa of the International Institute of Tropical Agriculture (IITA), at Cotonou, Benin for offer-

ing the facilities to conduct the research. They also thank Dossounon Honoré and Goulodji Jérémie for their technical assistance, and Gnanvossou Desiré for supplying *T. limonicus* females and Professor W. Modder and Dr. Frank Bakker for reading and commenting on the manuscript.

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