Zeitschrift: Mitteilungen der Schweizerischen Entomologischen Gesellschaft = Bulletin de la Société Entomologique Suisse = Journal of the Swiss Entomological Society

Herausgeber: Schweizerische Entomologische Gesellschaft

Band: 70 (1997)

Heft: 1-2

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DOI: https://doi.org/10.5169/seals-402652

MITTEILUNGEN DER SCHWEIZERISCHEN ENTOMOLOGISCHEN GESELLSCHAFT
BULLETIN DE LA SOCIÉTÉ ENTOMOLOGIQUE SUISSE
70, 21 – 28, 1997

The functional responses of two *Hyperaspis notata* strains to their prey, the cassava mealybug *Phenacoccus manihoti*

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The number of prey individuals attacked by larvae and adults of the coccinellid *Hyperaspis notata* MULSANT (Col., Coccinellidae) as affected by the density of its prey, the cassava mealybug *Phenacoccus manihoti* MATILE-FERRERO (Hom., Pseudococcidae), was studied in the laboratory. The functional response parameters of two strains of *H. notata*, one originating from Southern Brazil and one from Colombia, were compared. In the case of larvae there were no differences between the Brazilian and the Colombian strain. Adult females of the Colombian strain showed, however, a higher searching rate but a lower prey demand rate than females of the Brazilian strain. Overall, Brazilian females attacked more than Colombian females. If food was abundant, 11 to 15 per cent of the prey individuals were injured by the predator without being consumed.

Key words: *Hyperaspis notata*, Coccinellidae, predator, cassava mealybug, functional response.

INTRODUCTION

In the early seventies the cassava mealybug, *Phenacoccus manihoti* MATILE-FERRERO (Homoptera: Pseudococcidae) was accidentally introduced into Africa where it caused substantial losses to cassava (NWANZE, 1982). In search of a sustainable solution, the International Institute of Tropical Agriculture (IITA) introduced the parasitic wasp, *Apoanagyrus (Epidinocarsis) lopezi* DE SANTIS (Hymenoptera: Encyrtidae) which was observed to control *P. manihoti* in a wide range of different ecosystems (HERREN & NEUENSCHWANDER, 1991). There are, however, zones in which *P. manihoti* could not be controlled satisfactorily (NEUENSCHWANDER *et al.*, 1990). To eliminate such 'hot spots' of infestation, we explored the potential of additional natural control agents to complement already existing biological control agents. The coccinellid *Hyperaspis notata* MULSANT (Coleoptera: Coccinellidae) was introduced and established in some East African countries (NEUENSCHWANDER & ZWEIGERT, 1994), while it could not be recovered in other areas of release. Originally, *H. notata* had been found in two ecologically and climatically different regions of South America, in southern Brazil/Paraguay and Colombia.

In this study the coccinellid strains from these two origins were studied in a series of laboratory experiments. Thereby, the number of prey individuals attacked by a single predator was evaluated in terms of a standard functional response. In general, to study the attack rate rather than the consumption rates is appropriate for prey death rate estimations, because prey may die after a predator attack without being consumed. The consumption rate, however, will permit the specification of the numerical response. The purpose of this work is to specify the standard functional response as a prerequisite to understand predator-prey population interactions in cassava fields. Moreover, experiments on attack and consumption rates are carried out in order to obtain information on both prey death rates and predator numerical response.

MATERIAL AND METHODS

To describe the number of prey individuals attacked, i.e. the functional response, the data were fitted to a model similar to the overall form of IVLEV's (1961) response function recently discussed by BUFFONI *et al.* (1994). The instantaneous per capita form has been presented by GUTIERREZ *et al.* (1981)

$$f(N) = b(1\text{-}\exp(-aN/b)) \qquad [1]$$

where a and b are parameters to be estimated and N is the number of prey offered. In the model of GUTIERREZ *et al.* (1981), *b* represents the predator's demand rate. According to GUTIERREZ *et al.* (1994), the parameter *a* represents the attack probability. In the case of predation ROYAMA (1971) obtained the overall per capita form of the function for the functional response by integrating the instantaneous form as follows:

$$F(N_0, t) = -(b/a)\ \ln[(1\text{-}\exp(-aN_0)/b)\ \exp(-abt) + \exp(-aN_0)/b] \qquad [2]$$

where N_0 is the number of prey initially offered, t stands for time (24 hours) and *a* and *b* are parameters to be estimated. Equation [2] accounts for the effect of the declining prey density during the experimental time. ROYAMA (1971) stated: "The essential difference between the overall and the instantaneous equation is that the former involves the effect of diminishing returns whereas the latter holds only at an instant and so does not involve this effect."

In the parameter estimation procedures the outliers specified in Fig. 1 were disregarded. An F-test, as proposed by HOUCK & STRAUSS (1985), was used to test the differences between the parameter estimates, at the P=0.05 significance level, for the two strains.

Assessment of the functional response of larvae

The test arena for the experiment with larvae of *H. notata* of both origins, southern Brazil (BB) and Colombia (CC), consisted of Petri dishes (14 cm in diameter and 1.5 cm in height). Cassava leaves were chosen so that they did not touch the walls of the Petri dish. The leaf-stalks were wrapped in wet cotton to prevent the leaf from wilting during the experiments. On day zero, the leaves were infested with 2, 4, 6, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21, 22, 24, 26, 32, 36, 40, 44, 48, 52, 56, 60, 64, 68, 72, 80, 88, 96, and 104 third instar larvae of the cassava mealybug. One third instar larva of *H. notata* of either BB or CC origin was added. Attacked prey was not replaced. Incubation was done at 25±1 °C. The experiment was replicated once, except the densities 44, 52, and 60 which were replicated twice. After twenty-four hours, the larvae of *H. notata* were removed and the living cassava mealybugs were counted.

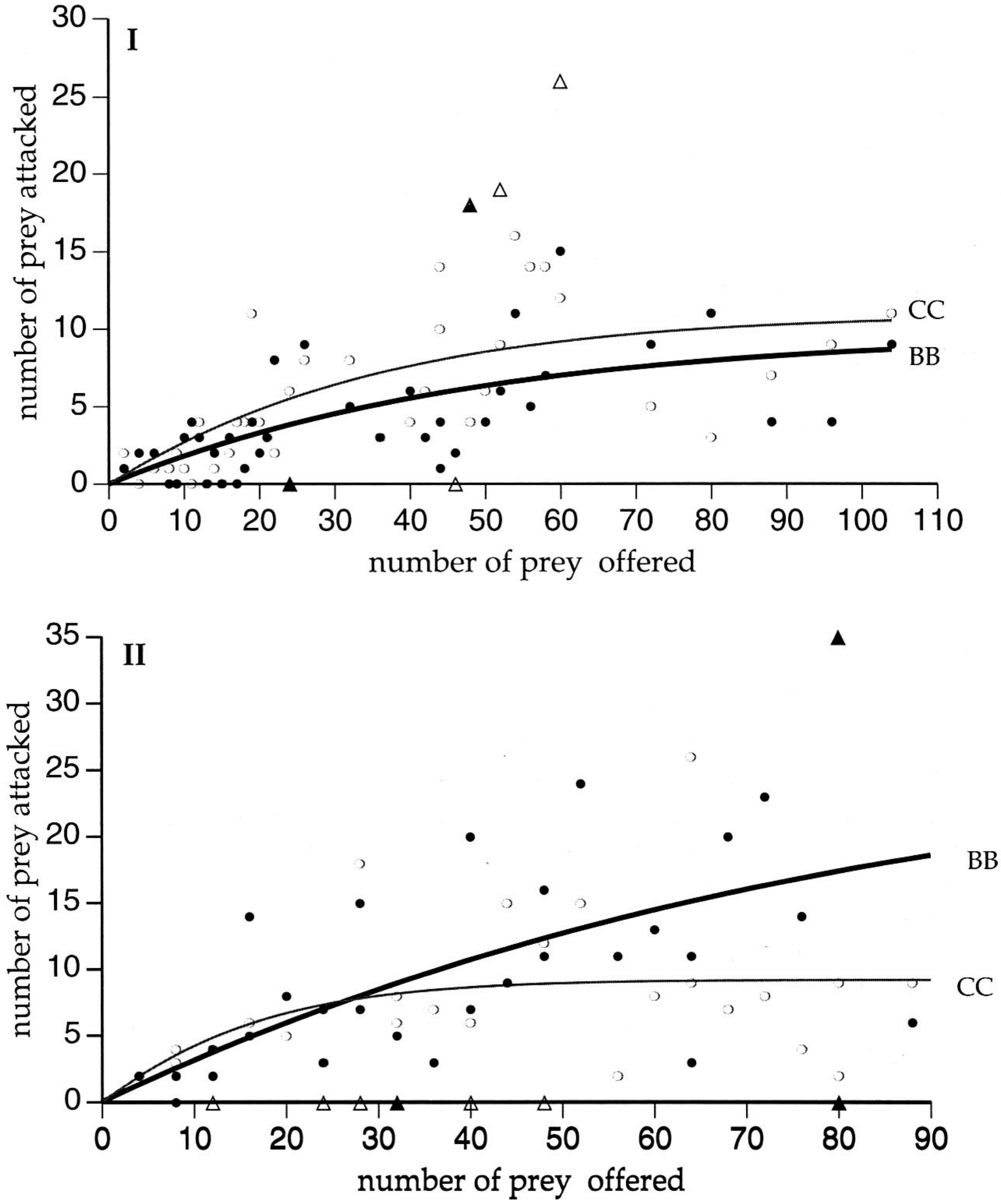

Fig. 1: Functional response of larvae (I) and adults (II) of *Hyperaspis notata* (● Brazilian origin BB; O Colombian origin CC). Curves were fitted to the equation [2] with outliers (▲ for BB, and △ for CC) disregarded.

Since the *H. notata* larvae are often inactive, a relatively long duration for the experiment, i.e. 24 hours was chosen. For technical reasons it was not possible to replace the attacked prey, and hence, the overall form of the functional response function was selected for the evaluation.

Assessment of the functional response reaction of adult females

Wooden cages (44 cm x 45 cm x 58 cm) with fine screen sides and glass tops were used as arenas. Potted cassava plants at 18 to 26 days after planting were infested with third instar larvae of the cassava mealybug the day before the experiment was started. The following prey numbers were offered (the numbers in brackets denote the number of replicates): 4, 8 (2), 12 (2), 16 (2), 20, 24 (2), 28 (2), 32 (2), 36, 40 (2), 44, 48 (2), 52, 56, 60, 64 (2), 68, 72, 76, 80 (2), and 88. Females of *H. notata* of either BB or CC origin were starved for 24 hours prior to the start of the study in order to assure a certain degree of homogeneity of the experimental insect population (HOUCK & STRAUSS, 1985). A single starved female was introduced into each cage. The experimental temperature was 27±2 °C. As in the former experiment the prey attacked was not replaced. After twenty-four hours, the females of *H. notata* were removed and the living cassava mealybugs were counted. As above, because of the relatively long duration of the experiment and because of the decrease in prey number the overall response equation [2] is used to analyze the data. The outliers specified in Fig. 1 were eliminated and the data were analyzed as described above: equation [2] was fitted to the data and a t-test was used to test for significant differences between the parameter estimates for the two strains.

Effect of mutilation on the prey death rate

Ten young non ovipositing females of *P. manihoti* were offered to single females of the two *H. notata* strains. The experiment was carried out in ten replicates. After 24 hours at 25±1 °C, the *H. notata* females were removed, and the prey was counted according to the following criteria: (1) intact; (2) injured; (3) consumed. A prey was judged to be injured if it was alive but exhibited bites; this phenomenon was visible because the wound made by the predator turned brownish. Consumed prey was almost completely eaten up, leaving behind a structureless remnant. Measurements were carried out for ten times using the same individuals.

The numbers recorded for each of the categories (i.e., intact, injured and consumed) were summed up for each female of *H. notata* BB and CC. From these sums the means for each origin were calculated. These means of the three categories for BB and CC were tested using a Chi-square test for differences, significant at P=0.05.

RESULTS AND DISCUSSION

Assessment of the functional response of larvae

The results obtained from the functional response experiment with third instar larvae of *H. notata* BB and CC are shown in Fig. 1. The shapes of the two curves were similar and the F-test indicated no differences in the parameters *a* and *b* between the two strains (Tab. 1). The maximum demand rate for the larvae of *H. notata* BB and CC were 15.2 and 16.2 larvae per day, respectively.

Although preliminary experiments had revealed that fourth-instar larvae of *H. notata* were more voracious than third-instar larvae, the functional response studies were done with the latter. The reason for this was that fourth-instar larvae of *H. notata* did not search for prey when offered few prey individuals but instead remained motionless. Interestingly, they were nevertheless able to pupate. But even third-instar larvae did not show striking responses to various prey densities, which is expressed in a small coefficient of determination, R^2 (see Tab. 1). This aspect is discussed below.

Tab. 1: Functional response of larvae and adults of *Hyperaspis notata* of Brazilian (BB) and Colombian (CC) origin at 25 °C. Values of parameters *a* and *b* (± SE) and coefficient of determination (R^2) according to equation [2] are given.

life stage	parameter a	parameter b	R^2
larvae			
BB	0.014 ± 0.006a[1)]	0.634 ± 0.103a	0.398
CC	0.022 ± 0.009a	0.676 ± 0.073a	0.456
adults			
BB	0.016 ± 0.012a	1.050 ± 0.407a	0.369
CC	0.049 ± 0.022b	0.617 ± 0.037b	0.276

[1)] parameters within the same predator stage followed by the same letter do not differ at P=0.05.

Assessment of the functional response of adult females

There was a high variability in the responses of adult *H. notata*, which did not show generally strong responses to the density of their prey (Fig. 1). For each curve, the coefficient of determination, R^2, was quite low (Tab. 1). The F-test indicated that *a* and *b* were statistically different between *H. notata* females BB and CC. For *H. notata* CC, the parameter *a*, representing the attack probability, is considerably higher than for *H. notata* BB (Tab. 1), indicating that CC displayed a stronger response to prey density than BB. Inversely, parameter *b*, which expresses the demand rate of the predator (GUTIERREZ & WANG, 1976), was found to be higher for BB than for CC. Accordingly, the BB females attacked more prey individuals at high density than their CC counterparts. This fact is also reflected in the maximal attack rate which was 25.2 mealybugs per day for the females of the Brazilian strain as compared to 14.8 for the Colombian strain. Note, however, that the estimation of the maximal attack rate for BB is not precise because the prey density range tested was not sufficiently large (Fig. 1).

Effect of mutilation on the prey death rate

After ten *H. notata* females were confronted each with ten young *P. manihoti* females within a Petri dish for 24 hours, 6.1 (for BB) and 4.9 (for CC) of the mealybugs remained intact, 2.7 (for BB) and 3.6 (for CC) were consumed, and 1.1 (for BB) and 1.5 (for CC) of the mealybugs were injured. These categories are expressed as percentages in Fig. 2. The Chi-square (X^2=6.255; DF=2) test showed that there were significant differences between BB and CC. Accordingly, the CC females killed more *P. manihoti* females by consuming and injuring them than the BB females. This observation indicates that the two coccinellid strains differ in feeding behaviour. Comparable phenomena were observed in other related predator-prey systems such as for coccinellids-aphid larvae (BANKS, 1956) and for *Hyperaspis marmottani* and *P. manihoti* (UMEH, 1982) but was not further quantified. The effect of mutilation of the prey and not only a functional response reaction should be considered in the evaluation of a biological control agent.

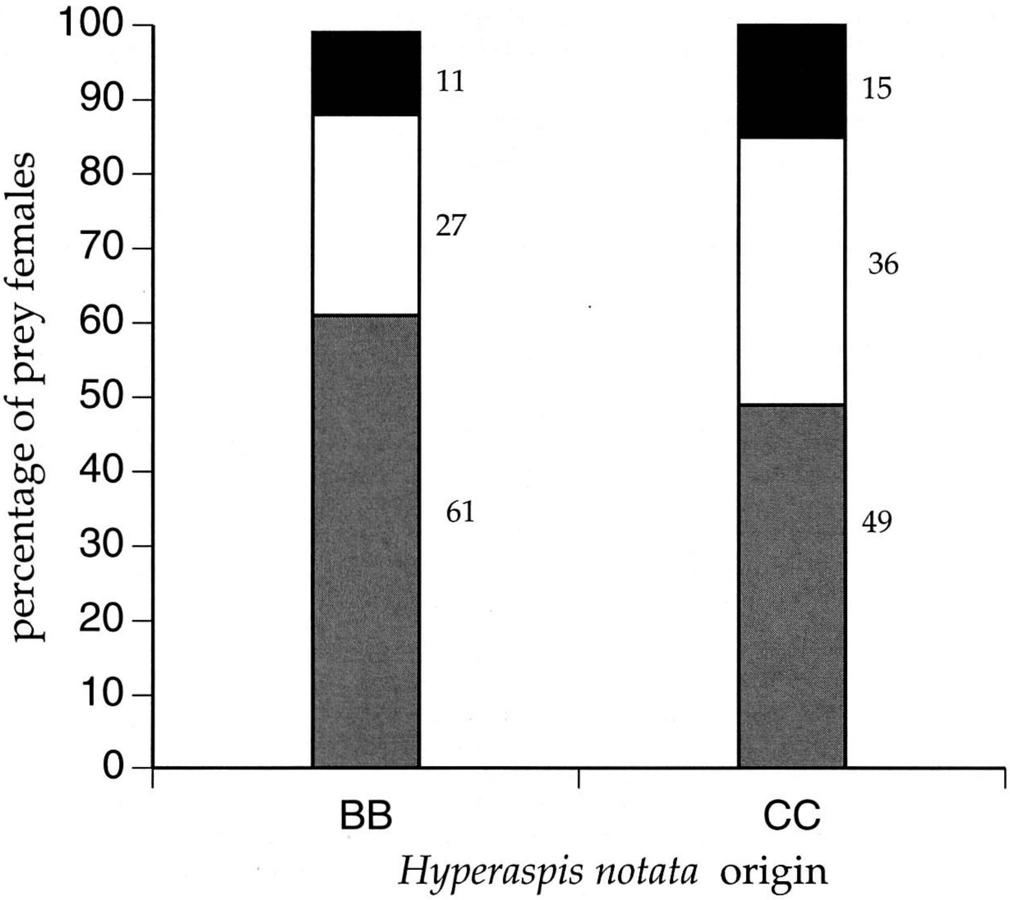

Fig. 2: Fate of non-ovipositing cassava mealybug females (■ intact, □ consumed, ■ injured) kept for 24 hours with a *Hyperaspis notata* female of Brazilian (BB) or Colombian (CC) origin. Ten cassava mealybug females and one *H. notata* female per arena.

Concluding remarks

In the laboratory, coccinellids have been observed to be quite active in finding prey, while in the field the same species spent about three quarters of their time motionless (FRAZER & GILBERT, 1976). In view of the possible use of *H. notata* as a biological control agent, the observed low aggressivity is not necessarily negative. Thus, while extremely voracious predators may disturb a system in an unpredictable manner, the comparatively low voracity of *H. notata* could meet the requirements for a complementary control agent to *A. lopezi*, and a sustainable solution for the *P. manihoti*.

To compare the voracity of larvae and adults of *H. notata* with published data on other coccinellid species is difficult because of different experimental conditions, because of the use of different data analysis procedures, and because the coccinellid instars used in published work differ from the ones studied here. Furthermore the present study focuses on the attack rate while other studies address the consumption rate. The latter is studied in STÄUBLI DREYER *et al.* (1997) who studied the consequences of prey consumption on survival, on development, and on reproduction.

The results obtained in this study are considered as a basis for the evaluation of *H. notata* and its two strains. Before *H. notata* can be qualified as a promising biological control agent which should be further studied and before an adequate strain for the different ecological zones in Africa can be identified, field experiments should be carried out and comprehensive models on predator-prey populations interactions should be constructed. For the cassava - *P. manihoti* - *H. notata* system the work by GUTIERREZ & WANG, (1976), GUTIERREZ *et al.* (1984, 1988) and BUFFONI *et al.* (1994) may serve as examples.

ACKNOWLEDGMENTS

The study was financed by the program 'Jeunes Chercheurs' of the Swiss Agency for Development and Cooperation (SDC). The authors wish to thank the colleagues at IITA for reviewing the manuscript.

ZUSAMMENFASSUNG

In Laborversuchen wurde die Anzahl Beutetiere, die von Larven und Adulten des Marienkäfers *Hyperaspis notata* MULSANT angegriffen wurden, in Abhängigkeit der Dichte der Beute, der Maniokschmierlaus *Phenacoccus manihoti* MATILE-FERRERO, untersucht. Die Parameter der funktionellen Reaktionsgleichung von zwei Stämmen wurden verglichen, wovon der eine aus Südbrasilien und der andere aus Kolumbien stammt. Bei den Larven konnten keine Unterschiede zwischen dem brasilianischen und dem kolumbianischen Stamm nachgewiesen werden. Die adulten Weibchen des kolumbianischen Stammes hingegen zeigten eine höhere Suchrate, aber eine niedrigere Beutenachfrage als der brasilianische Stamm. Die brasilianischen Weibchen verzehrten mehr Beutetiere als die kolumbianischen. Bei Beuteüberschuss wurden 11 bis 15 Prozent der Beuteindividuen verletzt, ohne dass sie gefressen wurden.

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(received March 19, 1996; accepted after minor revision August 3, 1996)