

BRC 99140/12413

Functional responses of feral and colonized strains of *Neoseiulus idaeus* Denmark & Muma feeding on the cassava green mite *Mononychellus tanajoa* (Bondar) (Acari: Phytoseiidae, Tetranychidae)

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(Received September 28, 1999)

ABSTRACT: The effect of long term laboratory breeding on the functional response of the Neotropical predatory mite *Neoseiulus idaeus* Denmark and Muma (Acari: Phytoseiidae) was studied under laboratory conditions. Cassava green mites *Mononychellus tanajoa* (Bondar) (CGM) eggs are used as prey at densities of 1, 3, 5, 10, 20, 30, 40, 50 and 60, foraging in a 3.14 cm² leaf disc of "Odongbo", a local CGM-susceptible cassava variety. All functional responses observed were of the Holling type II curve with plateaux determined by predator's strain and density. Mean highest number of 16.5 CGM eggs/5hrs consumed by feral *N. idaeus* was significantly different from the 14.7 CGM eggs/5hrs by colonized *N. idaeus* for females foraging singly ($P < 0.05$). Mutual interference among predators in the same arena was significantly greater ($P < 0.05$) for the feral strain and increased at higher predator density. The quest constant, search rate and killing power of the feral strain was superior to those of the colonized strain. There was significant negative correlation between predator's search rate and prey density in all treatments. Laboratory selection of individuals with low predatory attributes and therefore inferior biological control agents when given CGM prey is suggested.

Key Words: Predatory mites; Cassava green mite; *Neoseiulus idaeus*; *Mononychellus tanajoa*.

Introduction

The accidental introduction and spread of the neotropical pest, the cassava green mite *Mononychellus tanajoa* Bondar (Acari: Tetranychidae) in the early seventies was rapid, causing severe damage to the crop and reducing tubal yields far below economic injury levels (1, 2, 3). The use of introduced natural enemies to control exotic pests below their economic injury levels termed classical biological control (4) was recommended. This was to be achieved by importing several predatory mites from the neotropics (1, 5, 6, and 7).

Based on the above recommendation, *Neoseiulus idaeus* (first imported into Africa in May 1983) and six other phytoseiid mites selected for the classical biological control were kept in culture at the International Institute of Tropical Agriculture (IITA) biological control facilities located in Cotonou, Republic of Benin.

In the process of establishing laboratory population of *N. idaeus* for Africa-wide releases, it was believed that genetic changes occurred in the population. This however was from a lower genetic pool present in the now closed founder's sample. The force of natural selection is known to affect the distribution of gene frequencies in a newly established laboratory population. Laboratory rearing conditions differ undoubtedly from those encountered in the field, certain individuals not favoured in the natural conditions may become more fit in the laboratory, thereby increasing the frequency of the other (8 and 9). This selection had in several cases affected the biological characteristics, induced genetic recombination and mutation of the colonized population.

One of the characteristics depicting the predatory ability of *N. idaeus* is the functional response (10, 11, and 12). The functional response of a predator is its ability to attack and consume prey, its life history in relation to that of the prey and tolerance to environment stresses (13). The functional response curve describes the relationship between the number of prey consumed by an individual per unit of time and prey density (14). This typical nature expressed as type II curve was affected when *Amblyseius potentillae* (German) feeding on *Panonychus ulmi* (Koch) larvae was reared on a laboratory diet over a long period of time (12). In addition, predation rate, diapause induction, response to volatile chemicals and maximum starvation period of the predator were adversely affected. The Colombian biotype of *N. idaeus* has been in colonization for over six years at the beginning of the study and its subsequent release has been largely unsuccessful against CGM in Africa (15, 16, and 17). No establishment of this biotype has been recorded to date.

This study was undertaken therefore to determine the effect of prolonged laboratory colonization on the functional response and associated behavioural characteristics of the colonised strain by comparing it with the feral (field collected population) of the same biotype.

Materials and Methods

All experiments were conducted in an air-conditioned laboratory maintained at 60-75% RH and 23-25°C. Experimental arena and infestation of adult females were according to Akpokodje *et al.* (4). To obtain eggs of CGM for the experiment, a number of ovipositing females were introduced onto the experimental arenas 18 hours before commencement of the experiment. From eggs laid by these females, the desired CGM eggs densities were obtained and the excess eggs were removed.

Cohorts of predators used for the experiment were continuously obtained by rearing 100 eggs of each strain laid within a maximum period of 8 hours each week on McMurtry-Scriven arenas (18, 4). Adult females that moulted within a period of two to four hours and mated immediately were used. Introducing twice the number of males into each arena ensured mated females. Predators were starved as shown in Table 1 to obtain a homogeneous hunger state according to the prey density treatment. This is to assure that satiation and hunger-state were correctly balanced for each density offered. Hence a predator has the same probability of finding prey at a low prey density and a higher state of hunger as at a higher prey density and a lower state of hunger.

Densities of 1, 2, 3 and 4 adult females of each strain of *N. idaeus* were transferred using a slightly moistened No. 000 camel hair brush onto the experimental arenas containing cohorts of 12 to 18 hour -old CGM eggs. Prey egg densities of 1, 3, 5, 10, 15, 20, 30, 40, 50 and 60 per disc in each arena, replicated 50 times in a completely randomized fashion. The number of prey consumed at each density was recorded under a binocular microscope at a magnification of 16x every half-hour. After each observation the number of prey consumed at each density were replaced to maintain constant prey density throughout the duration of the experiment. The total number of prey consumed during a five-hour period was recorded.

Table 1: Period (in hours) during which *N. idaeus* females were starved and the prey density they were exposed to after starvation.

Prey density to which predators were exposed after starvation	Length of period predators were starved
1 and 3	24 hours
5	12 hours
10	6 hours
15	4 hours
20	2 hours
30 and 40	1 hour
50 and 60	no starvation

The data were subjected to a one-way analysis of variance (ANOVA) to test for significance between means and the Duncan's New Multiple Range Test to compare means (19).

The search rate of a single predator at each predator density was calculated using the formula of Hassell (20). Graphs of the search rates were plotted against prey density for all treatments. This line was fitted with a second power polynomial function to determine the maximum search rate (i.e. the y-axis intercept). The "mutual interference constant" (m) and the "quest constant" (Q) were calculated empirically from the regression of log search rate against log predator density using the Hassell and Varley (21) formula.

The handling time (Th) and the attack coefficient (a) were calculated from the regression line of the Rogers (22) random predator model. The slope of the regression and the y - axis intercept represent Th and a respectively.

The carrying capacities were calculated from the k-value (killing power of the predator) (23).

Results

Functional responses of feral and colonized strains of *N. idaeus* depicted a monotonic rise to a plateau between prey densities of 30 and 40 eggs. Observed responses depended on the predator's strain and density (Fig. 1). All functional responses were of the Holling type II curves. The highest prey consumption for predator density of 1, 2 and 3 were 13.1, 11.8 and 10.1 respectively for the feral strain. These values were significantly higher ($P < 0.05$) than the corresponding values of 10.7, 10.2 and 9.6 respectively for the colonized strain. There was no significant difference in consumption between the two predator strains at the highest predator density (Table 2). Fig. 2 shows the differences between the number of CGM eggs killed by the feral and colonised strains of *N. idaeus* [Na (feral) minus Na (colonised)] at each predator-prey density depicting that the feral strain, most of the time, fed on high number of CGM eggs. These differences were highest at predator density of one, and decreased with increase in predator density. At predator density of four, the colonized strain consumed more CGM eggs at prey densities of 3, 5, 10, 15 and 20 resulting in negative differences. In addition, negative values were also recorded for predator densities of two and three foraging at prey density of three.

There was a high negative correlation between k-values and log initial prey density for both predator strains (Fig. 3). The correlation coefficients of both strains are highly significant ($P < 0.05$) and ranged between -0.939 and -0.986 . The intercepts are higher for the feral strain than for the colonized strain. At predator density of four however, the colonized strain had a slightly higher intercept of 0.69 than that of the feral strain (0.64). The search rate (as a measure of Nicholson area of discovery) at all predator densities showed a decaying curve within the range of prey densities tested (Fig. 4). There was a significant non-

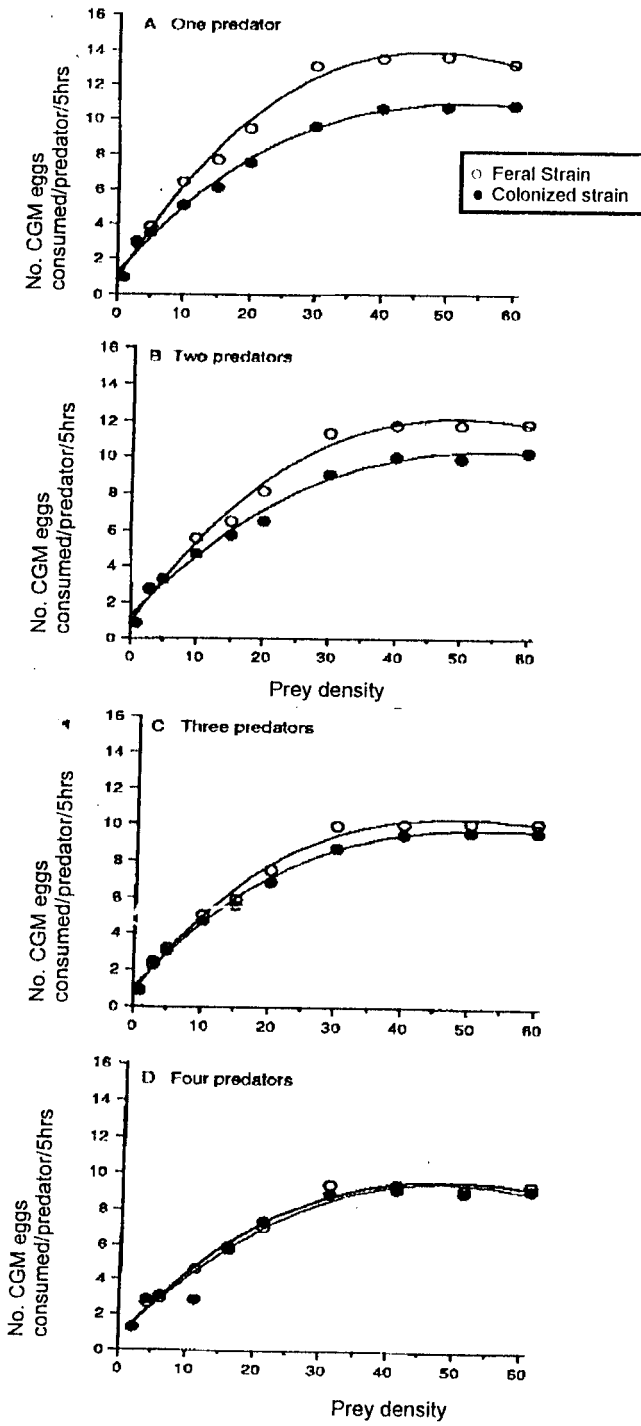


Fig 1 Functional response of different densities of feral and colonized strains of *N. idaeus* to increasing density of CGM eggs.

linear negative correlation ($P < 0.05$) (r ranging from -0.930 to 0.993) between search rate and prey density for both strains of *N. idaeus*.

Table 2: Mean maximum number of CGM eggs eaten by *N. idaeus* (feral or colonized strain) at four predator densities during a five-hour period.

Predator density	Mean max. number CGM eggs eaten (% decrease)	
	Feral	Colonized
1	13.50(0)*a \pm 0.32	10.76(0)b \pm 0.26
2	11.82(10.05)* \pm 0.15	10.21(5.11)b \pm 0.24
3	10.11(23.06)a \pm 0.11	9.63(10.50)b \pm 0.20
4	9.11(30.67)a \pm 0.08	8.85(17.75)a \pm 0.14

Means (\pm S.E.) followed by the same letter in a row are significantly different ($P < 0.05$).

* % decrease based on the maximum number of CGM eggs eaten at the predator density of 1.

The intercept depicts the maximum search rate, i.e. when a predator is actively searching in an area with zero prey. This parameter was higher for the feral strain than the colonized strain at predator density one, two and three (Table 3). At predator density of four however, maximum search rate of the colonized strain was higher. The graph of log search rate and log predator density describes the relationship between the quest constant (Q) and the mutual interference constant (m). The line of best fit describes the equation: $y = a + bx$, where a , the y-intercept and b , the slope of the curve represent the quest constant (Q) and the mutual interference constant (m) respectively. (Table 4). The quest constant, which decreases with increase in prey density, was significantly higher for the feral strain than for the colonized strain at high prey densities ($P < 0.05$). The mutual interference constant at high prey densities (10 and above) was significantly higher for the feral strain ($P < 0.05$). The handling time of the feral strain was shorter than that of the colonized strain and increased with increase in predator density for both strains (Fig. 5). The feral strain showed a corresponding decrease in the attack coefficient while this relationship was not clear-cut for the colonized strain.

Table 3: Maximum search rates ("a") of four densities of feral and colonized *N. idaeus* preying on eggs of CGM.

Predator density	Maximum search rates	
	Feral	Colonized
1	2.83	2.65
2	1.70	1.49
3	1.02	0.70
4	0.60	0.70

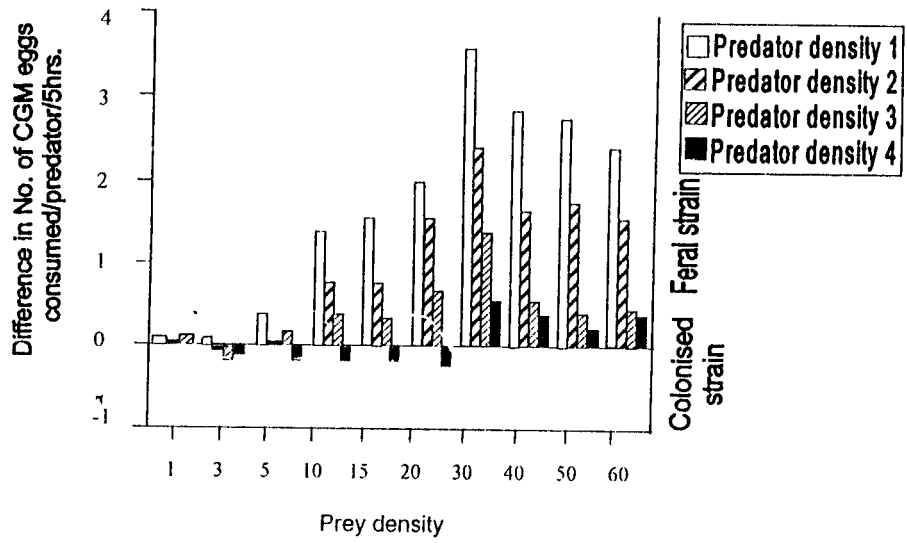


Fig. 2. The difference in the number of CGM eggs killed (i.e. $N_a(\text{feral})$ Minus $N_a(\text{colonised})$) at four densities of feral and colonised *N. idaeus* at different prey densities.

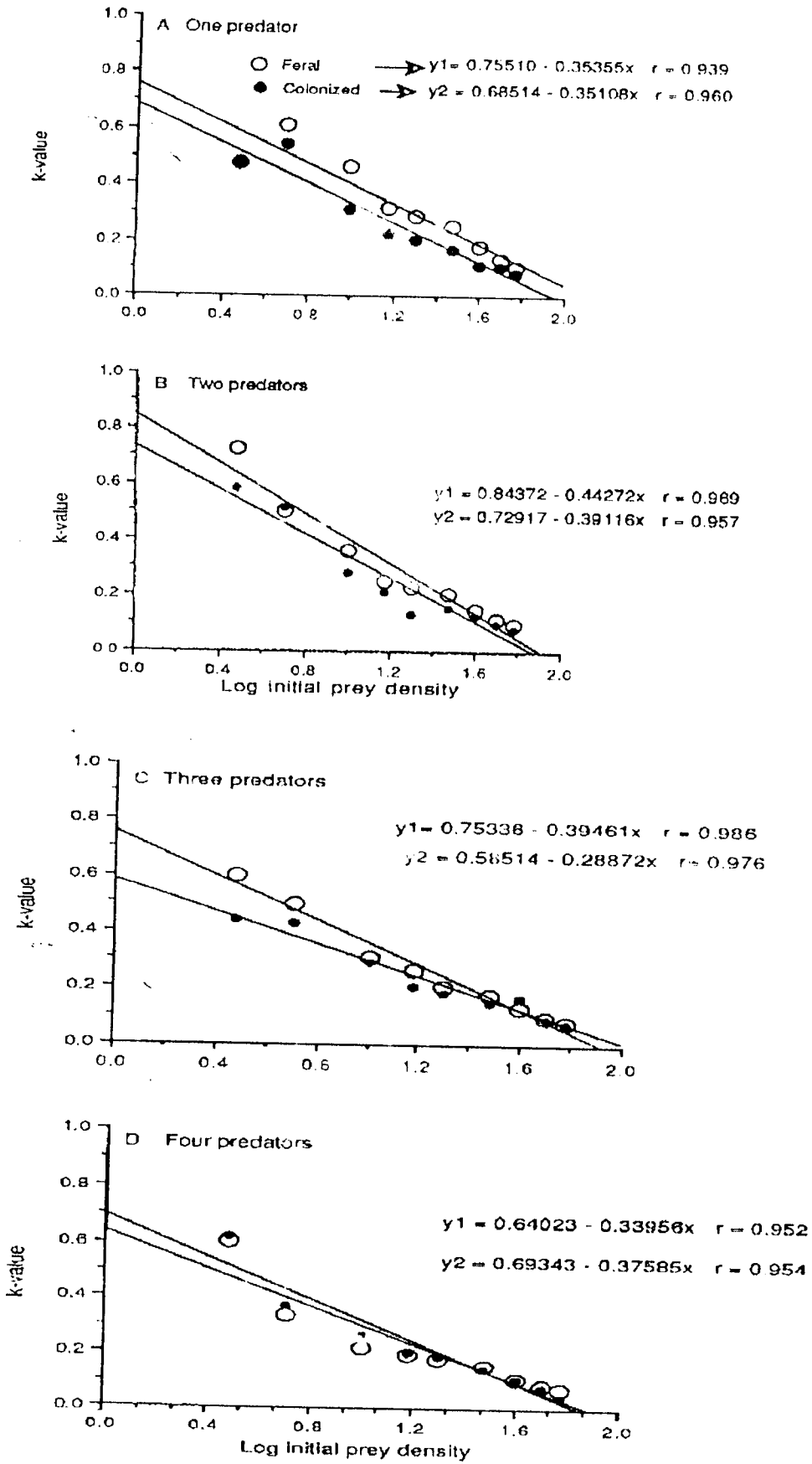


Fig. 3 Test for density relationship: regression of k-values on log initial density at the four densities of feral and colonized *N. idaeus*.

Table 4: The quest ("Q") and mutual interference ("m") constants of *N. idaeus* preying on CGM eggs.

Prey density	Feral		Colonized	
	"Q"	"m"	"Q"	"m"
1	0.359	0.085	0.392	0.290
3	1.218	0.907	1.108	0.947
5	0.851	0.941	1.175	1.262
10	1.041	1.415	0.683	1.100
15	0.707	1.334	0.503	1.070
20	0.654	1.333	0.440	1.060
30	0.581	1.339	0.376	1.092
40	0.415	1.331	0.303	1.109
50	0.319	1.332	0.239	1.144
60	0.240	1.347	0.198	1.127
Mean ± S.E.	0.64 ± 0.30	1.14 ± 0.4	0.54 ± 0.35	1.02 ± 0.27

Discussion

Feral and colonized strains of *N. idaeus* showed functional response curves that were basically of Type II. This result was similar to those observed in *P. persimilis* to the glasshouse red spider mite (24) and *T. occidentalis* to densities of the spotted spider mite eggs (25). Similarly Friese and Gilstrap (26) reported Type II functional response curve for *P. persimilis*, *Amblyseius californicus* (McGregor) and *Metaseiulus cinnabarinus* (Boisduval). Badii and McMurtry (27) works on *Phytoseiulus longipes* fed on different developmental stages of its prey. *Tetranychus pacificus* also recorded Type II curves. *Iphiseius degenerans* and *N. idaeus* females supplied different developmental stages of CGM also produced Type II curves (4).

Higher curve plateaux depicted by the feral strain imply that this strain responded better than the colonized strain to increasing prey density. However, the varying plateaux associated with different predator densities may be due to a number of factors among which are developmental stage, age at adulthood, sex, temperature and feeding history of the predator. Klay (28) mentioned the importance of the effect of space (to be measured as predator density) as a factor limiting population increase in rearing cultures. The rate of population increase during laboratory rearing is directly proportional to the functional response of the reared predator to the density of its prey. The results obtained in this study showed that increasing predator density had an inverse effect on the level of the plateau of the response curve, search rate and the maximum predation rate (Fig. 1, 4 and Table 3). For instance, a 4-fold increase in predator density reduced individual *N. idaeus* predation rate by 18-31% (Table 2). This could be associated with increased number of encounters among predators (mutual interference), decreased relative searching area available to individual predators and intraspecific competition among predators as their density increased. These effects, being more pronounced in the feral strain, might be attributable to the feeding history of both strains. The functional responses of *I. degenerans* and *P. persimilis* were influenced by the nutritional history before the start of the study (29). Fransz (25) also argued that the differences in the functional response plateaux exhibited by adult females of *T. occidentalis* were due to their feeding history. Feeding history as used in the present study was defined as the prey species on which both strains of *N. idaeus* fed previous to the start of the experiment. Whereas the feral strain was feeding on CGM before and during the experiment, the colonized strain was feeding on TSM eggs continuously for approximately six years before this work.

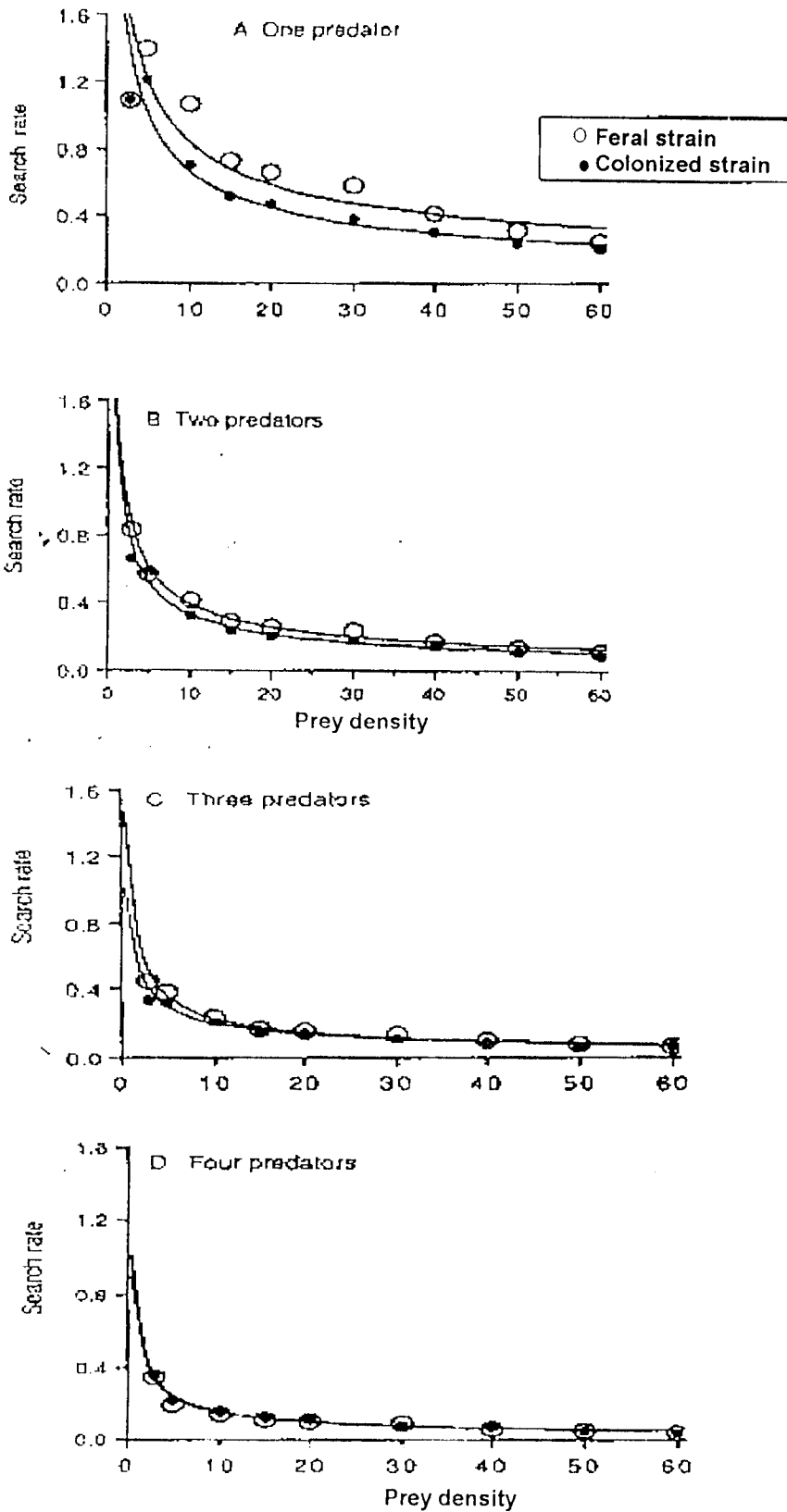


Fig 4 Relationship between search rate (=Nicholas's area of discovery) of four densities of the feral and colonized strains of *N. idaeus* and different initial densities of CGM eggs.

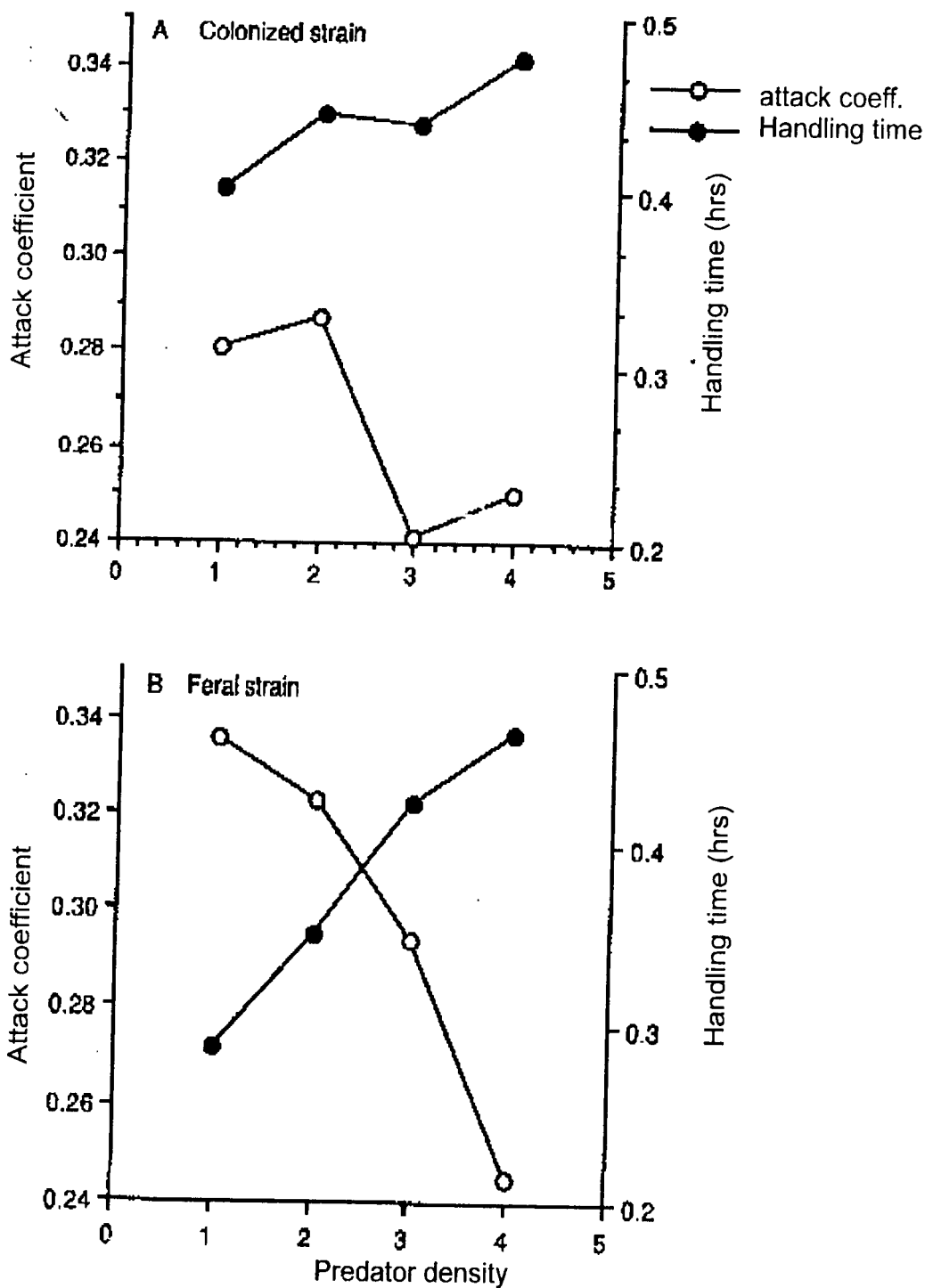


Fig. 5. Relationship between attack coefficient and handling time with four densities of the feral and colonized strains of *N. idaeus* attacking CGM eggs.

The k-values of both strains of *N. idaeus* are inverse density dependent since inverse density dependent factor is that factor the effect of which decreases as a percentage of the population density (30). Reduction in inverse density dependent nature of *N. idaeus* k-values could be attributed to the reduced power of the individual to cause population change (23). This reduction was more pronounced in the colonized strain implying that constant provision of adequate food could diminish the aggressiveness (predatory ability) of a predator.

The greater quest and mutual interference constants of the feral strain was probably due to its observed higher density-dependence, a characteristic that apparently diminished in the colonized strain (Fig. 3). The greater the mutual interference constant, the greater the tendency for predator-prey interactions to stabilise (21). The releases of the feral strain for biological control of CGM is, therefore, expected to have a greater impact than that of the colonized strain.

The feral strain of *N. idaeus* spent less time in handling its prey than the colonized strain at each predator density. The attack coefficient of the feral strain decreased with increase in predator density while that of the colonized strain had no straightforward trend. The attack coefficient (a') is the proportion of the total area searched by a predator per unit of searching time. It determines how rapidly the functional response curve approached the upper plateau. It is a function of the maximum distance at which the predator can perceive a prey, speed of movement of prey and proportion of attacks that are successful (31 and 32). Closely associated with this, is the ratio of the total time (T_t) (the total amount of time both prey and predators are exposed to each other) and the handling time (T_h) which determines the maximum number of prey that can be eaten. However, handling times and attack rates in this and similar studies were used mainly for comparative purposes (27).

In this study, predators searching singly apparently found it easier to find/catch and kill/eat prey than predators searching together on a leaf disc. The relationship between the attack coefficient and handling time for the feral strain (Fig. 5) is similar to that of Badii and McMurtry (27) who reported that handling time of *P. longipes* increased and attack coefficient decreased as prey got larger. Thus, it appears that an increasing predator density produced the same effect as increasing prey size on the attack coefficient and handling time. Similarly, Mogi (23) found that handling time decreased with successive increases in the size of a spider feeding on *Drosophila* of same size. Thompson (34) reported that damsel fly larvae feeding on water fleas had decreased attack rate and increased handling time as prey got larger or predator got smaller.

For the colonized strain, the relationship (especially in the case of the attack coefficient) is not clear probably because the colonized strain seemed to handle CGM eggs in approximately equal periods irrespective of predator density. Hence the irregularity could be attributed to density-independence (30). The consistently higher handling times recorded for the colonized strain at the four densities tested could be related to its lower inverse density dependent behaviour.

In conclusion, the functional response of *N. idaeus* has been affected to some degree by continuous laboratory rearing on the alternate prey *T. urticae*. This is likely to affect its ability to control CGM in most African cassava agroecosystems where *T. urticae* is present.

ACKNOWLEDGEMENT: Funds for this work was provided by The International Institute of Tropical Agriculture (IITA), Ibadan, Nigeria at its biological control facilities located in Cotonou, Republic of Benin.

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