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Flexible antipredator behaviour in herbivorous mites through vertical migration in a plant

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Abstract When predation risk varies in space and time and with predator species, successful prey defence requires specific responses to each predator. In cassava fields in Africa, the herbivorous cassava green mite (*Mononychellus tanajoa*) is attacked by three predatory mite species that are segregated within the plant: the leaf-dwelling *Typhlodromalus manihoti* and *Euseius fustis* occur on the middle leaves, whereas the apex-inhabiting *T. aripo* migrates from the apex to the top leaves only during the night. We found that differential distributions of these predators allow prey to escape predation by vertical migration to other plant strata. We studied the role of odours in the underlying prey behaviour on predator-free plants placed downwind from plants with predators and prey or with prey only. Prey showed increased vertical migration in response to predator-related odours. Moreover, these responses were specific: when exposed to odours associated with *T. manihoti*, prey migrated upwards, irrespective of the plant stratum where they were placed. Odours associated with *T. aripo* triggered a flexible response: prey on the top leaves migrated downwards, whereas prey on the middle leaves migrated upwards. Odours associated with *E. fustis*, a low-risk predator, did not elicit vertical migration. Further experiments revealed that: (1) prey migrate up or down depending on the stratum where they are located, and (2) prey discrimination among predators is based upon the perception of predator species-specific body odours. Thus, at the scale of a single plant, odour-based enemy specification allows herbivorous mites to escape predation by vertical migration.

Keywords Predator avoidance · Predation risk · Multiple predators · Predator recognition

Introduction

Since predation is a key factor in determining herbivore survival (Hairston et al. 1960; Walker and Jones 2001), selection on prey will favour resistance to predators, for example by predator avoidance. Such behaviour is usually displayed at the cost of other fitness-related activities, such as foraging, mating, growing or producing offspring (Lima 1998; Martin and Lopez 1999; Gotthard 2000). Consequently, prey are expected to avoid their predators only when predation risk is sufficiently high (Charnov et al. 1976; Lima and Bednekoff 1999; Luttbeg and Schmitz 2000). Indeed, experimental studies show that prey tune avoidance to the risk imposed by predators (Snyder and Wise 2000; Venzon et al. 2000). Effects of such antipredator behaviour on population dynamics of prey can be as large as effects of predation (Schmitz et al. 1997).

The life of arthropod herbivores on a plant is even more risky than that of other prey because plants promote the effectiveness of predators by providing them with food, herbivore-induced signals and shelter (Price et al. 1980; Dicke and Sabelis 1988; O'Dowd and Wilson 1991; Sabelis et al. 1999a, 1999b, 1999c). Therefore, one may hypothesize that, unless herbivores create their own refuge (e.g. galls, silken webs, mines), they cannot hide from predators on a plant but will tend to avoid predation by moving to predator-free plants. However, when predation risk is heterogeneously distributed within a plant, herbivores could also reduce predation risk by moving to low-risk plant areas. Such small-scale within-plant avoidance in response to predation risk is the subject of this article.

We studied the predator-avoidance behaviour of the phytophagous cassava green mite (CGM; *Mononychellus tanajoa* Bondar) on cassava (*Manihot esculenta*, Crantz). Its main enemies, the predatory mites *Typhlodromalus*

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aripo (DeLeon) and *T. manihoti* (DeMoraes), live in the plant apex and on leaves in the middle of the plant, respectively. In the field, plants may be occupied by either of the two predators or even by both (Bakker 1993). Hence, depending on which of the two predators inhabits the plant, either apices or mid-stratum leaves are relatively safe for the prey. Field observations showed that the vertical distribution of CGM varied with the presence or absence of these predators, and even with the particular predator species present on the plant (Bakker 1993). Motivated by these observations, we investigate the possibility of herbivores finding a partial refuge from predation on an individual plant.

In this paper, we test whether prey distributions result from differential predation in particular strata, or from herbivorous mites escaping from predators by moving to predator-free strata. To separate the effects of migration from those of predation, we compare the vertical movement of prey on plants exposed to predator-derived odours to that of prey on plants exposed to odours of prey only. Specifically, we ask the following questions:

1. Do predator cues induce vertical migration of prey on a plant?
2. Does migration reduce predation?
3. Do ineffective predators elicit vertical migration on the prey?
4. Do CGM discriminate between different species of effective predators?

In addition, we discuss the possible source of the volatile cues that elicit vertical migration, how this behaviour could result in escape from predation and the effect of antipredator behaviour on distribution patterns and population dynamics in the field.

Materials and methods

The system

After its accidental transfer from South America to Africa in the 1970s (Yaninek et al. 1989), CGM developed into a pest. Africa-wide biological control was achieved by releasing two predatory mites species endemic to South-America: *Typhlodromalus manihoti* and *T. aripo* (Yaninek et al. 1998; Yaninek et al., in preparation). Predatory mites native to Africa, such as *Euseius fustis* (Pritchard and Baker), appear not to be effective in controlling CGM populations (Bruce-Oliver et al. 1996). *T. manihoti* and *E. fustis* occur on the middle leaves of the plant and rarely up in the apices (Bruce-Oliver et al. 1996; Bonato et al. 1999), whereas *T. aripo* is restricted to the apices during daytime and migrates to the leaves at night (Bakker 1993; A. Onzo et al., in preparation). CGM are mainly found in the upper plant strata in the absence of predators (Yaninek et al. 1991; Farias and Silva 1992). When *T. aripo* is the only predator present, CGM occur less often in the upper strata, but when only *T. manihoti* is present, CGM occur less often in the middle strata (Bakker 1993).

Cultures

Cassava (variety Agric) was grown in a greenhouse compartment at 20°C and 70–90% relative humidity (RH) at the International Institute for Tropical Agriculture (IITA), Cotonou, Benin. Stakes

(circa 20 cm) were planted in 2.5-l plastic pots, and watered every other day. In the experiments, we used 3-week-old plants with seven or eight leaves. CGM were reared on young potted plants in another greenhouse under identical abiotic conditions. Plants were infested by placing CGM-infested leaves at the base of one or more petioles. Cultures were refreshed every week by introducing CGM individuals collected from cassava fields. CGM may have experienced predators before collection, but not during rearing.

T. manihoti was reared in a climate room at 24±2°C, and 70–90% RH on black PVC arenas (30×30 cm) on top of a sponge surrounded by wet tissue and placed in a 40×30×10-cm plastic tray with water (Mégevand et al. 1993). Cultures were provided with two CGM-infested leaves 3 times a week. Every month, predator cultures were supplemented with individuals collected from cassava fields.

T. aripo and *E. fustis* were not cultured, but collected from nearby cassava fields. *E. fustis* was maintained for 1–3 days on maize pollen before being used in the experiments.

Experimental procedure

All experiments were performed between April and November 2000 in a greenhouse compartment at IITA, under the same conditions as our cassava culture.

We introduced predators and prey on a specific plant stratum (either a middle or a top leaf), and measured prey migration to other strata. To ensure that final prey distributions resulted from prey migration and not from differential predation in specific strata, we placed predators (with or without prey) on one plant and measured prey migration on another plant placed downwind. A wind source (a cylindrical plastic pipe, 40 cm in diameter, connected to a fan with air flow <2 km/h) caused air to move over one plant (3 m away) to the other, 1 m further down, thus causing odour transport from the upwind to the downwind plant. A mesh cage around the downwind plant prevented between-plant migration.

Except when stated otherwise, the experimental procedure was as follows: (1) A cassava leaflet with 150 adult CGM females was attached to a leaf of each of two upwind plants, the stratum of release varying with the test; (2) after allowing prey populations to settle for 5 h, 15 adult female predators (starved for 1 h) were introduced on the same leaf on one of the upwind plants, while the other (control) did not receive predators; (3) simultaneously, a leaflet with 150 adult CGM females was placed on a leaf of each of the two downwind plants, at the same stratum level as predators and/or prey on upwind plants; (4) 24 h later, leaves and apices of upwind and downwind plants were collected and labelled according to their position on the plant, and adult female CGM were counted using a stereoscope. Mites tested were not returned to the cultures to avoid pseudoreplication. After each trial, the door of the greenhouse was left open overnight to clean the air from volatiles. The sequence of odour sources was randomized to minimize the effects of temporal changes in biotic and abiotic conditions. Each treatment was replicated at least 6 times.

Migration in response to high-risk predators

To test whether CGM migrate vertically in response to high-risk predators, we exposed CGM on downwind plants to upwind plants with: (1) *T. manihoti* and CGM on the middle leaf, (2) *T. aripo* and CGM on the top leaf.

Predation risk

To test whether vertical migration of CGM reduces predation risk, we compared predation on upwind plants where CGM were free to migrate with predation on plants where CGM migration was prevented by a glue barrier around the leaf petiole. We introduced *T. aripo* on the top leaf and *T. manihoti* and *E. fustis* on the middle leaf, together with CGM.

Migration in response to a low-risk predator

The role of predation risk in inducing vertical migration was tested by exposing CGM to odours associated with *E. fustis*. This predator was introduced with CGM on the middle leaf and pollen was added as food for the predators.

Specificity of the response to the high-risk predators

To test the specificity of the response of CGM to the high-risk predators, we switched the position of *T. aripo* and *T. manihoti* on upwind plants: we put *T. manihoti* on the top leaf and *T. aripo* on the middle leaf. To retain predators on the introduction leaf, we placed a glue barrier around the leaf petiole. Glue on upwind plants does not affect CGM responses on downwind plants (S. Magalhães, personal observation).

Stratum-specific response

We tested whether varying the position of predators affects the response of prey by placing *T. aripo* and CGM on the top leaf of upwind plants, but CGM on the middle leaf of downwind plants. To ensure odour exposure, we elevated the downwind plants such that their middle leaf was at the same height as the top leaf of upwind plants.

Source of the predator-associated cue

To test whether predation was necessary to elicit a response, we introduced *T. manihoti* without CGM on the middle leaf of upwind plants.

Data analysis

In the figures, we present the fraction of CGM females recaptured on the strata above and below the introduction leaf (i.e. the fraction of CGM females that migrated up or down after 24 h). The effect of treatments was tested by multiple ANOVAs and least significant difference post-hoc tests for multiple comparisons. Data were arcsine-square-root transformed to meet the MANOVA assumptions. We used Mann-Whitney *U*-tests for assessing differences in predation rates.

Results

Migration of CGM from plants

On average 84.12 ± 2.35 (mean \pm SE) of the 150 CGM introduced were recovered, alive or dead, on upwind plants and 89.63 ± 2.14 on downwind plants. This difference is not significant (ANOVA, $F_1=0.238$, $P=0.627$). Among treatments with or without predators, numbers of dead plus live mites did not differ significantly (upwind plants ANOVA, $F_{10}=1.318$, $P=0.242$; downwind plants ANOVA, $F_8=0.935$, $P=0.494$). Thus, escape from plants was not enhanced by the presence of (upwind) predators during the experimental period. Losses ($\approx 40\%$) may be due to the introduction method and/or to CGM falling from plants.

Within-plant migration in the absence of predators

In predator-free trials, most of the CGM on downwind plants did not migrate: the fraction of CGM migrating up

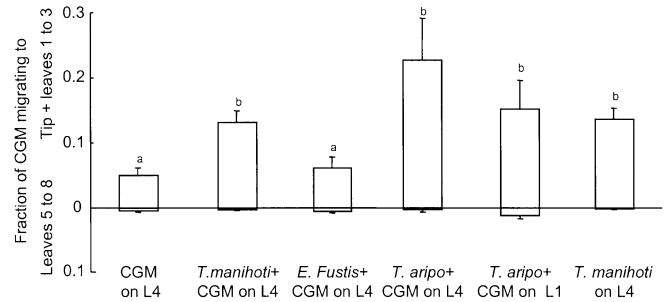


Fig. 1 Distribution of cassava green mite (CGM) on downwind plants 24 h after CGM introduction on the middle leaf (leaf 4, corresponding to the origin of the y-axis). Each bar corresponds to different species composition on upwind plants (indicated on the x-axis). No. of replicates: CGM, $n=14$; *Typhlodromalus manihoti*+CGM, $n=13$; *Euseius fustis*, $n=6$; *Typhlodromalus aripo*+CGM L4, $n=8$; *T. aripo*+CGM L1, $n=6$; *T. manihoti*, $n=7$. Vertical lines indicate 1 SEM. Different letters indicate significant differences in the migration fractions among treatments [least significant difference (LSD) post-hoc test, $P<0.05$]. L1 Species introduction on the top leaf, L4 species introduction on the middle leaf

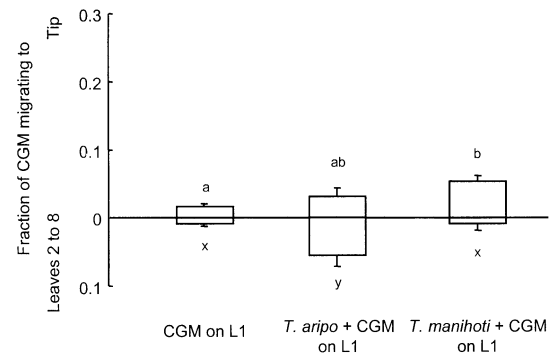


Fig. 2 Distribution of CGM on downwind plants 24 h after CGM introduction on the top leaf (leaf 1, corresponding to the origin of the y-axis). Each bar corresponds to different species composition on upwind plants (indicated on the x-axis). No. of replicates: CGM, $n=12$; *T. aripo*+CGM, $n=12$; *T. manihoti*+CGM, $n=6$. Vertical lines indicate 1 SEM. Different letters indicate significant differences in the migration fractions among treatments (LSD test, $P<0.05$). For abbreviations, see Fig. 1

and down did not exceed 5.5% of the total CGM remaining on plants (first bars of Figs. 1 and 2). Migration to the upper strata was significantly higher than to the lower strata, regardless of the leaf where CGM were introduced (ANOVA: $F_1=12.871$, $P<0.001$). Because total CGM (alive+dead) with and without predators on upwind plants did not differ, we calculated the fraction of CGM migrating in upwind plants relative to the total CGM (alive+dead). Since most predation occurred on the leaf of release, this procedure will, at most, underestimate the fraction migrating (individuals might be eaten before they move away).

CGM distribution on upwind and downwind plants did not differ significantly (top leaf MANOVA, $F_{2,15}=0.008$, $P=0.992$; middle leaf MANOVA, $F_{2,18}=1.639$, $P=0.222$). Thus, volatiles from plants with CGM only do not result in additional migration on downwind plants.

Migration in response to high-risk predators

On upwind plants, CGM migrated significantly more upwards from the middle leaf on plants with *T. manihoti* relative to control plants (MANOVA, $F_1=10.520$, $P=0.048$). On plants with *T. aripo*, CGM migrated significantly more downwards from the top leaf relative to control plants (MANOVA, $F_1=9.874$, $P=0.01$).

On plants downwind from plants with *T. manihoti* and CGM on the middle leaf, on average 13% of CGM migrated from the middle leaf upwards, whereas only 5% migrated upwards on plants receiving odours from CGM only (Fig. 1; LSD test following MANOVA, $F_{10,94}=4.32$, $P=0.001$). Thus, upward migration was enhanced by volatiles associated with *T. manihoti*. Migration to the lower strata (leaves 5–8) was negligible, both in the control and in replicates with predators (Fig. 1).

On plants downwind from plants with *T. aripo* and CGM on the top leaf, CGM migrated significantly more from the top leaf downwards than on plants downwind from plants with CGM only (Fig. 2; LSD test: $F_{4,52}=8.616$, $P<0.0001$). Few CGM migrated into the apices, but there was no difference in upward migration between control plants and plants exposed to predator odours. Hence, perception of predator-related odours increases vertical migration of CGM within the plant.

Predation risk

To study the function of vertical migration, we assessed predation rates on upwind plants where CGM could either migrate or not. Predation rates by *T. aripo* or by *T. manihoti* were significantly increased when CGM migration was prevented by a glue barrier around the petiole of the introduction leaf (Table 1; Mann-Whitney *U*-test, *T. aripo* and *T. manihoti*, $P=0.016$). Predation rates were similar between predators (*U*-test without glue $P=0.262$, with glue $P=0.337$). On plants without glue, predation occurred mainly on the introduction leaf. Thus, within-plant migration of CGM is an effective means to escape predation.

Migration in response to a low-risk predator

Few CGM died on upwind plants with *E. fustis* compared to the control (Table 1; Mann-Whitney *U*-test, $P=0.137$), confirming that *E. fustis* is a low-risk predator. On plants downwind from plants with *E. fustis* and CGM on the middle leaf, CGM did not migrate more than on control plants (third bar in Fig. 1; LSD test, $P=1$). Thus, CGM discriminate between *E. fustis* and the two high-risk predators.

Specificity of the response to the high-risk predators

CGM migrate in opposite directions depending on the predator species present (cf. second bars in Figs. 1 and 2),

Table 1 Predation rate^a (p) of *Typhlodromalus aripo*, *T. manihoti* and *Euseius fustis* on cassava green mite (CGM), and control (i.e. CGM mortality in the absence of predators) when CGM and predators may migrate within the plant and when they are confined to one leaf

	Predators and prey may migrate within the plant	Predators and prey are confined to one leaf
<i>T. aripo</i>	0.19±0.039	0.47±0.110
<i>T. manihoti</i>	0.27±0.045	0.75±0.119
<i>E. fustis</i>		0.05±0.008
No predators	0.02±0.006	0.04±0.008

^a p is calculated as: $p = -\ln(n/n_0) \times PR^{-1} \times t^{-1}$, where n_0 =no. of CGM at the beginning of the experiment, n =no. of CGM at the end of the experiment (24 h later), PR =no. of predators present at the end of the experiment, and t =time span (24 h). CGM mortality in the absence of predators is calculated using the same formula, but without PR . For each treatment, $n=6$

suggesting that the response is tuned to the predator species or their position on the plant. To test for enemy specificity, we switched the position of *T. aripo* and *T. manihoti* on upwind plants (and, as above, the position of CGM on downwind plants). With *T. aripo* on the middle leaf, CGM migrated up from the middle leaf (fourth bar in Fig. 1). The fraction migrating did not differ significantly from that in trials with *T. manihoti* on the middle leaf (LSD test, $P=0.405$). However, when predators were on the top leaf, the mean direction of migration differed according to the predator species present: more CGM migrated from the top leaf to the apices upon perception of *T. manihoti* compared to controls (last bar in Fig. 2; LSD test, $P=0.019$), whereas the fraction migrating down was not significantly different from that of controls (LSD test, $P=0.764$). This contrasts with the response to *T. aripo*, where the mean direction of migration was downwards (Fig. 2). Thus, the experiments with CGM starting on the top leaf show that they can respond specifically to odours of each predator species. Moreover, the response to *T. aripo* differs depending on the stratum where *T. aripo* and/or CGM are placed.

Stratum-specific response

To further test the effect of stratum on the direction of migration, we placed *T. aripo* with CGM on the top leaf of upwind plants and CGM on the middle leaf of downwind plants. CGM moved up; the fraction migrating did not differ from that with *T. aripo* on the middle leaf of upwind plants (fifth bar in Fig. 1, LSD test, $P=0.827$). Thus, the stratum on which *T. aripo* and CGM were placed on upwind plants did not influence the direction of CGM migration on downwind plants.

Nature of the predator-associated cue

CGM migration on upwind and downwind plants did not differ in trials with *T. aripo* (MANOVA, $F_{2,15}=0.370$,

$P=0.697$). However, in trials with *T. manihoti*, CGM migration on upwind plants was nearly twice that on downwind plants (24.5% versus 13%, respectively, MANOVA, $F_{2,16}=4.152$, $P=0.035$). Thus, contact with *T. aripo* does not enhance the response of CGM, whereas contact with *T. manihoti* does.

When CGM were exposed to odours from plants with only *T. manihoti* (i.e. without CGM), they migrated upwards more than in the controls (last bar in Fig. 1). This response did not differ significantly from the response to odours from upwind plants with both CGM and *T. manihoti* (LSD test, $P=1$), suggesting that CGM recognize predators by their body odour or any by-product of their physiological activities and that the occurrence of predation is not necessary to elicit a response.

Discussion

Our experiments show that prey can escape predation within a plant by migrating up or down to low-risk plant strata. Volatile cues associated with high-risk predators induce such vertical migration whereas cues from a low-risk predator do not. Whether prey move up or down depends on the stratum they occupy as well as on the high-risk predator species present. The direction of migration in response to these predators is flexible when CGM are exposed to the predator species that shows a diurnal distribution pattern (*T. aripo*), and fixed when CGM perceive odours of the stratum-specific predator, *T. manihoti*. To our knowledge, this is the first description of predator avoidance within an individual plant.

Why can prey escape from mobile predators within a plant?

Since the predators are more mobile than their prey, one may ask whether vertical migration is an effective means of escape in the long run. If all prey were mobile and moved up or down in response to predators, they would surely be quickly followed by the predators. Then, this escape would only be effective at a very short time scale. In an attempt to find the minimal conditions under which vertical migration as an escape response would work at a longer time scale, we hypothesize that predators remain behind because immobile prey stages, such as eggs, are left in the stratum with predators, thus temporarily arresting them. Since any prey that would escape without leaving eggs behind would have a selective advantage, prey will only evolve to lay eggs in predator-occupied strata if prey on a plant are related by descent (Williams 1996). Alternatively, the immigration of predators into prey patches may not be predictable enough to justify paying the costs of not laying eggs before predator arrival. In addition to predators arrested by leaves with immobile prey, there may be other reasons for predators staying in a specific stratum. *T. aripo* always occurs in apices during daytime, even when prey are only present

in lower strata. The reason for this restricted predator distribution is unknown, but it allows for a temporary refuge for CGM within a plant.

How are predators recognized?

Our experiments show that prey use volatiles to detect predators from a distance. Close-range cues may also be involved in the detection of predators because prey on plants with *T. manihoti* migrated twice as much as on plants downwind from these. CGM may use cues associated with the diet of predators to detect predation risk. It is known that prey can discriminate between predators that have been feeding on conspecific prey or on other food (Venzon et al. 2000; Perssons et al. 2001), and our high-risk predators were reared on CGM, while the low-risk predator, *E. fustis*, was fed maize pollen. However, diet-associated odours are not instrumental for the discrimination between the two high-risk predator species. Indeed, the specific response of CGM to these two predator species suggests that each predator has its own specific body odour, and that this odour, rather than general cues associated with predation, triggers the antipredator behaviour. The response of prey to odours of *T. manihoti* without prey is in agreement with this. This level of discrimination has probably evolved because the two high-risk predators and CGM share a long coevolutionary history. In line with this, it is possible that CGM do not recognize cues from *E. fustis* because they share a short coevolutionary history: this predator is endemic to Africa, while CGM was accidentally introduced to this continent around 30 years ago. The shorter coevolutionary history may thus be an alternative explanation for the lack of response of CGM to *E. fustis*, although some prey species respond to non-coevolved predators (Richardson 2001).

Migration as a way to escape predation

It is known that herbivorous arthropods avoid their predators by dispersing to predator-free plants (Roitberg et al. 1979; Bernstein 1984; Stamp and Bowers 1993). However, leaving a suitable host plant entails a high risk since the probability of finding another plant is very low, especially for passive dispersers such as spider mites, which are blown by the wind after take-off (Kennedy and Smitley 1985) and thus cannot control where they will land. Moreover, CGM are specific to cassava (De Moraes et al. 1995) and cassava fields are generally small and intercropped, which reduces the probability of landing on a suitable host. Thus, leaving a host plant to escape predation involves high costs. Costs may well be much lower if prey can escape predation by migrating within the plant in response to predators, as found in this study.

Our results show that prey tend to migrate more up than down when predator cues are present (cf. Figs. 1, 2).

Since *T. manihoti* is continuously present in the lower strata and *T. aripo* is only present in the apices during daytime, the apices are expected to be safer than the lower strata. However, prey tend to migrate upward even when predators are absent (first bars of Figs. 1 and 2 and Senkondo 1990), suggesting that there must be an extra advantage for moving upwards. Probably, the higher strata are more nutritive or nutrients are easier to retrieve. Moreover, migrating up allows for a better position for take-off, since mites usually disperse aerially from the upper strata (Kennedy and Smitley 1985).

How does predator-induced vertical migration affect population dynamics?

CGM migrate to predator-free strata in a plant in response to predators. Such a non-lethal effect of predation may promote the persistence of predator-prey systems in ways similar to that of prey refuges (Abrams 1993; Matsuda et al. 1993; Lima 1998; Van Baalen and Sabelis 1999; Luttbeg and Schmitz 2000). However, if the refuge in the plant is occupied by yet another predator species, CGM populations may become extinct sooner, as they are “between the devil and the deep-blue sea”. In cassava fields, CGM and the two predator species may occur together over a long time span, but species composition may still vary from plant to plant (A. Onzo et al., in preparation). The mechanisms underlying the persistence of such two-predator-one-prey systems are probably operating at the metapopulation level, but are yet to be elucidated. This will require not only insight into when and how CGM avoid predators within plants, but also when and how they move to other plants (e.g. Pallini et al. 1999).

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