Field observations of the effects of fenitrothion and *Metarhizium anisopliae* var. *acridum* on non-target ground dwelling arthropods in the Sahel

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Received 30 May 2002; accepted 22 October 2002

Abstract

The effect of the chemical insecticide, fenitrothion, and a mycoinsecticide based on *Metarhizium anisopliae* var. *acridum* on the activity of non-target epigeal arthropod scavengers was investigated in areas of open savannah in southeast Niger Republic, West Africa. Both insecticides were applied as full cover sprays to unreplicated 800 ha plots to assess their season-long control of Sahelian grasshoppers. Compared with control plots, fenitrothion caused an immediate but temporary reduction in grasshopper numbers, whereas *M. anisopliae* var. *acridum* provided delayed but prolonged control. Scavenging rates of pyrethroid-killed grasshoppers placed along transects in unsprayed plots and those treated with fenitrothion and *M. anisopliae* var. *acridum* at various intervals after spraying were assessed. In the fenitrothion plot, an immediate reduction in scavenging activity occurred that was still apparent after 40 days at the plot center, although recovery at the plot edges was more rapid. By contrast scavenging rates remained high over equivalent areas in the *M. anisopliae* var. *acridum* and two untreated plots. Concurrent to the scavenging study, counts of grasshopper cadavers resulting from the spray treatments were conducted. These counts revealed that the density of grasshopper cadavers remained low throughout the *M. anisopliae* var. *acridum* plot and explained <1% of the reduction in live grasshoppers resulting from treatment, compared with >20% in the fenitrothion plot. This shortfall in grasshopper cadavers resulting from the spray treatment in the *M. anisopliae* var. *acridum* plot was unexpected because in a monitoring study, fungus-killed (unlike pyrethroid-killed) grasshoppers were unattractive to scavengers and readily persisted in this plot, and thus should have become apparent. Given we did not observe significant grasshopper dispersal, the scarcity of cadavers generated in the *M. anisopliae* var. *acridum* plot, together with unquantified visual observations, suggests that predation of infected but living grasshoppers was high. Our data provide circumstantial evidence that the different effects of chemical and biological grasshopper control on grasshopper natural enemies may influence the efficacy of large-scale treatments.

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Keywords: Entomopathogenic fungus; *Metarhizium anisopliae*; Sahelian grasshoppers; Mycoinsecticide; Fenitrothion; Intraguild predation

1. Introduction

Concerns over the environmental and human health impacts of chemical control of locusts and grasshoppers (Orthoptera: Acrididae) have led to considerable interest in the development of alternative control methods using mycoinsecticides based on entomopathogenic fungi in the genera *Metarhizium* and *Beauveria* (Deuteromycotina: Hyphomycetes) (Bateman, 1997; Jaronski and Goettel, 1997; Milner, 1997). One such product comprising an oil formulation of conidia of *Metarhizium anisopliae* (Metschnikoff) Soruskin var. *acridum*, a naturally occurring fungal pathogen of locust and grasshoppers, has provided effective control of a range of economically important acridid species throughout Africa (Lomer et al., 2001). A similar isolate of *M. anisopliae* var. *acridum* has also proved successful in tests...
against a number of important locust and grasshopper pests in Australia, including largely successful trials up to 30,000 ha (Milner, 2000).

Although the products mentioned above can provide effective control, a number of ecological studies conducted with *M. anisopliae var. acridum* have indicated that both biotic and abiotic factors influence the overall efficacy of spray applications across time and/or space. For example, the speed of kill can be highly variable and depend strongly on environmental temperatures and host thermal biology (Blanford and Thomas, 1999a,b, 2000). In addition, *M. anisopliae var. acridum* may alter host feeding, fecundity, and mobility (Arthurs and Thomas, 2000; Seyoum et al., 1994; Thomas et al., 1997). There is also potential for recycling of the fungus to new generations of acridids through horizontal transmission (Thomas et al., 1995).

Recently, there has been a growing recognition of the importance of higher-level interactions between competing natural enemies. Such interest has been stimulated by a number of well-documented cases of intraguild predation (i.e., when different groups of natural enemies that compete for the same host/prey are themselves engaged in predator–prey type interactions) amongst natural and introduced biological control agents. Both theoretical and empirical evidence suggests that this type of competitive interference can have important but variable consequences for the population dynamics of biological control agents and target pests, and hence food webs and community structure (Polis and Holt, 1992; Rosenheim et al., 1995). However, most studies of the interactions between arthropod control agents are laboratory based, while examples from the field tend to be manipulative and rarely focus on a population level.

In this study we examine the effects of an operational scale application of *M. anisopliae var. acridum* on non-target natural enemies in the sub-Saharan Sahel, exploring both direct effects (i.e., direct impact on grasshopper natural enemies) and indirect effects (i.e., the effect on the grasshopper–natural enemy interaction) compared with a conventional insecticide treatment. Grasshoppers in this region of the Sahel frequently cause significant damage during the short rainy season by migrating into seasonally cultivated crops [mainly rain-fed pearl millet, *Pennisetum glaucum* (L.)] and require frequent control measures from the national crop protection services (Stonehouse et al., 1998). Full details of the large-scale spray trial alongside which the studies presented here were conducted are given in Langewald et al. (1999), although to provide the necessary background, information particular to the current study and the basic results obtained in the spray trial are included in the methods. Because of the scale and cost involved, the spray trial was not replicated and hence rigorous statistical testing of our data is impossible. Nevertheless differences among treatments were dramatic and consistent over a wide area and thus, interpreted sensibly, we believe still yield valuable insights into the different effects of the chemical and biological treatments.

2. Materials and methods

2.1. Spray trial

Aerial spray treatments were applied towards the beginning of the rainy season in August 1997 to two 800 ha plots near the Maine Soroa district in southeast Niger Republic, West Africa, using a single Cessna Ag. Truck 188 employing 4 Micronair AU5000 atomizer nozzles attached to the trailing wings. Full details can be found in Langewald et al. (1999). One plot was treated with an oil miscible flowable formulation of *M. anisopliae var. acridum* (strain IMI 330189) at 0.5 L/ha, delivering $2.5 \times 10^{12}$ conidia/ha. Conidia were produced in vitro at a pilot production plant in Benin, West Africa (Cherry et al., 1999). An equivalent plot was treated with technical fenitrothion, an organophosphate widely used for acridid control (FAO, 1998), at 0.225 L/ha. Two similar untreated areas served as a control for each of the treated plots with all plots separated by at least 5 km.

Assessments of live grasshopper densities within treated and control plots were made every 3 days from 10 days pre-treatment until 22 days post-treatment (Fig. 1 shows efficacy data from Langewald et al., 1999). Grasshopper density within untreated plots remained high (>10 m$^{-2}$) throughout the assessment period. Treatment with fenitrothion caused a dramatic fall in density within 24 h of spraying. However, in this plot recolonization was relatively swift, and from day 7 after spraying onwards, there was no significant difference in

![Fig. 1. Mean counts (±SE) of grasshoppers per m$^2$ in 800 ha plots treated with an oil-based formulation of *Metarhizium anisopliae var. acridum* and fenitrothion in the Sahel. Taken from Langewald et al. (1999).](image-url)
grasshopper density between fenitrothion-treated and control plots. In contrast, a slower but more prolonged reduction in live grasshoppers was observed within the *M. anisopliae* var. *acridum* plot. In this plot, grasshopper densities differed significantly from control plots by day 16, and populations remained low (~90%) with no recolonization observed within the assessment period. Generally, similar patterns were observed in replicated 50 ha plots in 1996 (Langewald et al., 1999).

### 2.2. Field site

The studies described below were conducted throughout the 1997 rainy season (August–October). The study areas comprised lightly wooded open savannah within widely spaced mobile and fixed dunes. Vegetation was principally annual, ranging from 2 to 20cm in height. There was a gradient of species diversity throughout the 1997 rainy season (August–October). Generally, similar patterns were observed in the fenitrothion plot, transects ran along a perpendicular northeast to southwest line, whereas in the fenitrothion plot, transects originated from an equivalent northeasterly point until the central area but continued in southeasterly direction until the plot boundary. The different arrangement in the latter case was to prevent disturbance to a grasshopper sampling area. Transect locations were within the accuracy given by using hand-held GPS equipment.

For sampling, all transects were baited with intact cadavers (equal ratios of three grasshopper species) that were placed in a slight depression (~5 mm) on an area of bare ground and marked with a small flag to enable relocation. Each cadaver was revisited in the same sequence 48 h later and assessed for presence/absence. Because not all scavenged cadavers were completely removed, partial scavenging was included, whereby cadaver remains were initially ranked as either ‘3,’ intact excluding appendages; ‘2,’ damage to one body section; ‘1,’ damage >1 body section/hollow or ‘0,’ removal. A scavenging rate was obtained for each sampling location by calculating as the overall proportion of whole/partial cadavers (combined) remaining at the location after 48 h.

Preliminary assessments from three untreated areas showed that consistently high rates of scavenging (>95% removal) could be expected using this baiting technique. The cadaver baiting method was repeated at exactly the same locations on six occasions between days 2 and 42 and eight occasions between days 3 and 40 after spraying within the *M. anisopliae* var. *acridum* and fenitrothion plots, respectively. On each occasion, cadavers were baited at equivalent co-ordinates within control plots. Due to the time taken to visit all locations, each treated plot together with its associated control location were baited/assessed on consecutive days. Differences in scavenging rates between and within treated and control plots were determined by one- and two-way ANOVA on the average scavenging data (normalized via arcsines-transformation) for each sampling location. This approach seems valid due to the arrangement of cadavers (spaced widely over a 150 m transect) and mobility of scavengers (i.e., we were effectively subsampling within a bigger pool of scavengers on each occasion). Lines of least variance were fitted to the overall data for central and border locations within each treated plot (SPSS, 1997).
2.4. Estimating grasshopper mortality through cadaver counts

The densities of grasshopper cadavers resulting from treatment were periodically assessed and their decomposition/scavenging rates measured. It was anticipated that this approach would help identify the proximate causes of grasshopper mortality in treated plots. To estimate cadaver density, dead grasshoppers were scouted for at different locations on seven occasions between days 7 and 42 and on three occasions between days 6 and 36 after spraying within the fenitrothion and \( M. \) \( \text{anisopliae var. acridum} \) plots, respectively. On each sampling occasion, counts were made at four locations that appeared representative of the area, two at central locations and two at outer locations of treated plots; >1.2 km and within 300 m of the treatment border, respectively. A thrown stick was used to randomly select a position and all visible cadavers (regardless of minor damage) within a 1-m\(^2\) quadrat were counted. Cadavers were not apparently aggregated. Thirty quadrats were counted at each of the four sampling locations and the same process repeated at equivalent locations in control plots. Due to the low numbers in most cases (mode = 0), the means from each sampling location (\( n = 30 \)) were transformed via a Poisson distribution with a log-link function and change in deviance attributable to a factor tested against values of \( \chi^2 \) using GLIM 3.77 (Crawley, 1993).

2.5. Persistence of grasshopper cadavers

To estimate decomposition/scavenging rates of grasshopper cadavers, the persistence of fungus-killed and insecticide-killed grasshoppers was assessed. Fungus-killed insects were infected adult \( A. \) \( \text{blondeli} \) and \( P. \) \( \text{cognata} \) that were collected alive within the \( M. \) \( \text{anisopliae var. acridum} \) plot and allowed to die from fungal mycosis within laboratory cages. Both freshly killed cadavers with non-sporulating fungus and those that had sporulating fungus were used. ‘Non-sporulating cadavers’ exhibited characteristic red (mycotoxin) coloration but were not allowed to develop saprophytically, whilst ‘sporulating cadavers’ were incubated on damp filter paper in Petri dishes for 72 h and exhibited both internal and external fungal growth. Insecticide-killed grasshoppers originated from equivalent insects collected from an untreated site and killed with a non-residual pyrethroid within 24 h of use.

The procedure for estimating decomposition/scavenging rates of fungus and insecticide-killed grasshoppers in epigeal locations follows that of Arthur et al. (2001), except that measurements were made within a \( M. \) \( \text{anisopliae} \)-treated area, as opposed to an unsprayed site, and thus scavenging rates would reflect any effect of the \( M. \) \( \text{anisopliae} \) treatment. For the first study (effect of fungal mycosis), 108 fungus- and insecticide-killed grasshoppers in equal proportions were placed individually on bare ground in a random stratified sequence at 4-m intervals within a 50 × 50 m area. In addition, to estimate whether strictly epigeal arthropods were the main cause of scavenging as opposed to non-epigeal arthropods and vertebrates (birds, lizards, etc.), we compared the scavenging rate on the ground with an adjacent paired sample maintained ~10 cm above the ground. For this second study (effect of microsite), 72 insecticide-killed grasshoppers were either placed individually on bare ground or were loosely tied to an adjacent stick placed upright in the ground (paired sample), using a similar layout to the previous study. In both studies, small flags were used to mark the position of each cadaver, which was revisited daily for 30 days to check for presence/absence. The cumulative rate of cadaver disappearance over this period was assessed using Kaplan–Meier survival analysis (SPSS, 1997). Differences in the mean persistence among categories of cadavers were tested using a log rank test with significance levels of multiple comparisons adjusted using a Bonferroni correction.

3. Results

3.1. Effects of treatments on non-target epigeal arthropods

Beetles and ants were by far the most abundant ground-dwelling arthropods observed and evident scavengers in all plots. The tenebrionids (notably Zo- phosis posticalis (Deyrolle) and Ephydridae spp., and Erodius laevigatus), and ants (predominantly Monomorium spp. but also Messor galla (Mayr), Pheidole spp., and Cataglyphis spp.) were the most common species recovered from grasshopper cadavers during the day and carabid beetles (Anthia sexmaculata (F.) and an unidentified Scarites sp.) were also observed scavenging at dusk. All these non-target ground-dwelling species were abundant in the same region in August 1996, when together the four insect families, Carabidae, Tenebrionidae, Formicidae, and Ephydridae made up about 75% of the total pitfall catch (Peveling et al., 1999).

Scavenging rates in the fenitrothion plot were initially significantly depressed but recovered to levels found in the control and \( M. \) \( \text{anisopliae var. acridum} \) plots, which remained high (>95%) throughout the assessment period. A one-way ANOVA repeated across equivalent sampling periods showed that overall, scavenging rates within the fenitrothion-sprayed plot remained significantly depressed (\( df = 1, 22; P < 0.05 \)) compared with control plots until 44 days post-spraying, after which time no differences were observed. No difference (\( P > 0.05 \)) was detected for any equivalent sampling
periods between the *M. anisopliae* var. *acridum* and untreated plots.

The results from the fenitrothion plot suggest there were spatial differences in the recovery of scavenger activity. Fig. 2 compares within plot scavenging rates between the four transects nearest the spray border with the four in the most central locations in both treated plots. In the *M. anisopliae* var. *acridum* plot fitted lines describing these data are linear and show no difference between central and border locations. By contrast, central transects within the fenitrothion plot recorded lower removal rates compared with border transects at each equivalent sampling period. One-way ANOVA showed that the decrease in scavenging rate at central areas was significant on day 7 ($F_{1.6} = 7.15; P < 0.05$) and the final three sampling periods after spraying (day 28 onwards) ($F_{1.6} = 13.35; P < 0.01; F_{1.6} = 10.07; P = 0.05; F_{1.6} = 12.97; P < 0.01$). Scavenging rates from border transects in the fenitrothion plot were no longer significantly different (df = 1, 6; $P < 0.001$) to equivalent locations in *M. anisopliae* var. *acridum* and untreated plots after 35 days while those from central transects remained significantly lower on all equivalent dates until the end of the assessment period.

### 3.2. Estimating grasshopper mortality through cadaver counts

There were differences in densities of grasshopper cadavers between treatments. In the *M. anisopliae* var. *acridum* and control plots, the overall mean density of cadavers remained low ($<0.25\text{m}^2$) throughout the assessment period. Statistical analysis revealed no significant difference in cadaver density between the *M. anisopliae* var. *acridum* and either control plots at any equivalent sampling period. In contrast, cadaver density in the fenitrothion plot was significantly higher ($\sim2\text{m}^2$) compared with both *M. anisopliae* var. *acridum* ($\chi^2 = 9.2; P < 0.01$) and control plots ($\chi^2 = 8.7; P < 0.01$) at the equivalent first sampling period 6–7 days after spraying, although fell to a similar low level by the end of the assessment period. We suspect cadaver density was highest shortly after the fenitrothion application, although counts were not made before day 7. Fig. 3 compares cadaver density between the two sampling locations nearest the spray boundary with the two in central locations in both treated plots. Within plot comparisons revealed no differences between border and central sampling locations at equivalent periods in either treated plot, although comparisons were restricted by the small number of sampling locations. However, differences are apparent between border and central locations across plots. Here, the difference in the density of grasshopper cadavers observed between the *M. anisopliae* var. *acridum* and fenitrothion plots at 6–7 days post-spraying was significant between central locations ($\chi^2 = 6.01; P < 0.025$) but not for border locations ($\chi^2 = 3.3; P > 0.05$).

### 3.3. Persistence of grasshopper cadavers

In the cadaver persistence study, the numbers of cadavers used were relatively small, but the results were

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**Fig. 2.** Comparison of cadaver scavenging rates from 4 central¹ (●) and border¹ (▲) locations within plots sprayed with a mycoinsecticide (grey) and fenitrothion (black). [¹ Equivalent to (>900 m; >1.2 km) and (<300 m) from plot edges, respectively]. Mean removal rates (±SE) are shown with time post-spraying and least variance models fitted. Mycopesticide plot border and central locations are described linearly (broken line) by $y = -0.22x + 101.57$ ($R^2 = 0.71$) and $y = -0.22x + 101.69$ ($R^2 = 0.86$), respectively. Fenitrothion plot border and central locations are described logarithmically (solid line) by $y = 12.78\ln(x) + 50$ ($R^2 = 0.63$) and $y = 15.91\ln(x) + 20.58$ ($R^2 = 0.54$), respectively. Data from equivalent untreated plots are not shown but did not differ from the mycopesticide plot (see Section 3).

**Fig. 3.** Comparison of cadaver density from 2 central¹ (●) and border¹ (▲) locations within plots sprayed with a mycoinsecticide (grey) and fenitrothion (black). [¹ Equivalent to (>1.2 km and <300 m) from plot edges, respectively.] Mean densities (±SE) are shown with time post-spraying and least variance models fitted; mycopesticide plot border and central locations are described linearly (broken line) by $y = 0.007x + 0.007$ ($R^2 = 0.55$) and $y = 0.006x - 0.018$ ($R^2 = 0.99$), respectively. Fenitrothion plot border and central locations are described (solid line) by $y = 1.593e^{-0.064x}$ ($R^2 = 0.78$) and $y = -1.084\ln(x) + 4.102$ ($R^2 = 0.93$), respectively. Equivalent assessments from control plots (not shown) recorded low densities ($<0.2/m^2$).
striking (Table 1). As in the last study, pyrethroid-killed grasshoppers placed on the ground were rapidly scavenged (within 48 h) by ground-dwelling beetles and ants. By contrast, these insects did not actively scavenge equivalently placed *Metarhizium*-killed grasshoppers, which on average, persisted in the field for several weeks. The persistence of cadavers that harbored *Metarhizium* appeared to be related to a gradual weathering. Cadavers had sporulating fungus tended to fragment and disintegrate during rainfall. Insecticide-killed grasshoppers were far less likely to be scavenged when held just above the ground, out of the reach of epigeal arthropods.

4. Discussion

A potential criticism of these data concerns the pseudo-replicated design imposed by the original spray trial. The decision to treat a single large area at the expense of true replication followed the spraying of smaller (50 ha) replicated plots with *M. anisopliae* var. *acridum* and fenitrothion in the previous year (1996) and was taken to allow the season-long population dynamics of grasshoppers to be observed following an operational scale campaign (Langwald et al., 1999). Similarly, a large treated area may better reflect changes in the activity of many mobile non-target epigeal arthropods compared with smaller replicated plots which tend to suffer from problems of dispersal from treated areas within a few days or weeks. Although the effect of non-independent sampling bias must be considered for the present data, it cannot reasonably explain the extent to which patterns of scavenging and apparent grasshopper mortality differed between treated plots in the weeks following spraying. The chemical and biological treatments appeared to affect non-target epigeal arthropods differently. Moreover, as discussed below, such differences (in selectivity) may arguably influence the efficacy of such large-scale treatments.

In direct exposure assays, *M. anisopliae* var. *acridum* has low toxicity to the Hymenoptera, Coleoptera, and Homoptera (Ball et al., 1994; Peveling and Demba, 1997; Prior, 1997). The present field assessment also detected no reduction in scavenging activity of non-target epigeal arthropods in the *M. anisopliae* var. *acridum* plot compared with untreated locations. This complements previous assessments in the same region in 1996, which showed that the median effect of *M. anisopliae* var. *acridum* on the abundance of the same non-target groups within replicated 50 ha plots (via pitfall traps) was <25% and the product was classified as ‘low risk’ (Peveling et al., 1999). In the present study fenitrothion caused an immediate and dramatic reduction in the scavenging activity of these non-targets, which appeared to last 40 days at the plot center, although as might be expected recovery at the plot edges was more rapid. This ‘functional’ measurement builds on the studies of Peveling et al. (1999), who measured a similar reduction in the abundance of non-target groups within replicated 50 ha plots treated with fenitrothion in 1996, although in the latter case most of the non-target fauna had fully recovered after 31 days. Cadavers of all non-target species mentioned in Section 2 were evident throughout the fenitrothion plot in the days following spraying, although only live specimens were observed elsewhere.

Regrettably predation of grasshoppers per se was not quantified at sampling locations. However, the cadaver density assessments coupled with the estimated persistence of insecticide- and fungus-killed grasshoppers provides indirect evidence that grasshopper natural enemies played a role in the ultimate fate of grasshoppers within the *M. anisopliae* var. *acridum* plot. In this plot, although the population of live grasshoppers was reduced by 92% after 22 days (Fig. 1), few signs of disease could be observed; indeed >1% of the population reduction could be explained by the density of *Metarhizium*-killed grasshoppers accumulating throughout this plot (Fig. 3). This shortfall was despite the fact that *Metarhizium*-killed grasshoppers placed in the field in the presence of scavengers persisted for several weeks within the *M. anisopliae* var. *acridum* plot (Table 1), and thus should have become apparent had grasshoppers

### Table 1

<table>
<thead>
<tr>
<th>Control (epigeal)</th>
<th>Control (pyrethroid-killed)</th>
<th>Metarhizium-killed, initially showing</th>
<th>Metarhizium-killed, initially showing</th>
</tr>
</thead>
<tbody>
<tr>
<td>No sporulation</td>
<td>Above ground</td>
<td>External sporulation</td>
<td>External sporulation</td>
</tr>
<tr>
<td>1.3 ± 0.1 a (0)a</td>
<td>1.5 ± 0.7 a (0)</td>
<td>24.3 ± 1.6 b (63.9)</td>
<td>6.4 ± 2.3 b (0)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>15.8 ± 1.3 c (19.4)</td>
<td></td>
</tr>
</tbody>
</table>

* Different lower case letters represent differences between cadavers at the 1% level (log rank test).

b The percentage of cadavers censored (not disappeared) after 30 days if not zero.
been killed directly by the fungus. The scavengers, *Z. posticalis*, *E. laevigatus*, and *Monomorium* spp., as well as active predators included mantids (Mantodea: Mantidae), robber flies (Diptera: Asilidae), and sphecid wasps (Hymenoptera: Sphecidae), were observed preying upon live but often apparently sluggish grasshoppers in the *M. anisopliae* var. *acridum* plot. Interestingly, both *Monomorium* spp. and tenebrionids are generally considered more as scavengers than predators (Peveling et al., 1999). Given we did not observe significant grasshopper dispersal in the first weeks after spraying, the shortfall in grasshopper cadavers in the *M. anisopliae* var. *acridum* plot, together with unquantified visual observations, suggests that predation of diseased but still living grasshoppers was high. This shortfall of grasshopper cadavers was far less apparent in the fenitrothion plot, where grasshopper natural enemies presumably suffered a similar fate as their prey.

The circumstantial evidence for enhanced susceptibility of live but *Metarhizium*-infected grasshoppers to field predation is supported by small-scale studies in other environments. Both the rice grasshopper *Hieroglyphus daganensis* (Krauss) in northern Benin and the brown locust *Locustana pardalina* (Walker) in the South African Karoo that were infected with *M. anisopliae* var. *acridum* and tethered in the field, suffered higher rates of predation during the disease incubation period compared with controls (Arthurs and Thomas, 1999; Thomas et al., 1998). During field trials with the same fungal isolate in the Mauritania desert, signs of fungal infection could not be observed on *Schistocerca gregaria* (Forskål) hopper bands treated in the field because of severe cannibalism and heavy predation by birds, which resulted in three out of four treated bands being completely eliminated within 4–5 days despite apparently little mortality of locusts within untreated bands (Kooymen and Godonou, 1997). During similar trials in the Buzi floodplain in Mozambique, the cohesive break down and disappearance of bands of red locust, *Nomadacris septemfasciata* (Serville), was attributed to the fungus, although few cadavers were found (Price et al., 1997).

The present studies and those of Peveling et al. (1999) provided no evidence that *M. anisopliae* var. *acridum* directly infected and killed (i.e., acted as an intraguild predator) indigenous non-target arthropods under field conditions. Rather, by selectively consuming live but infected prey, natural enemies of grasshoppers may have functioned proximally as intraguild predators of the fungus, although this did not appear to be the case postmortem once the fungus had started saprophytic development (Table 1). The type of interspecific interactions described above may influence the efficacy of a spray campaign. Given the slow action of entomopathogenic fungi has been identified as a potential constraint to uptake of the technology (Bateman, 1997; Bateman and Thomas, 1996), enhanced predation of infected hosts could be beneficial by enhancing the effective mortality rate. Moreover, it seems likely that the conservation of and synergistic interactions with other natural enemies might also enhance the persistence of a large-scale mycopesticide treatment by enabling natural control to act as a buffer against the recolonization of treated areas once pest populations have been reduced. This is in contrast to current chemical pesticides, such as fenitrothion, which may cause grasshopper resurgence (Lockwood et al., 1988). However, because *Hyphomycete* fungi can only initiate new infections following the death of the host (Hajek and St. Leger, 1994), predation of live infected hosts may reduce or eliminate the potential for further cycles of the disease and so reduce the impact of spray applications in the long-term. Certainly this latter point would help explain why horizontal transmission following spray applications is generally far less apparent than predicted by theoretical models (Thomas et al., 1995). It is clear that such intraguild interactions may be complex and warrant local level investigation.

In conclusion, biopesticides offer an environmentally safe alternative for locust and grasshopper control. Although selectivity of biopesticides is normally considered from the perspective of environmental safety, the implications for efficacy are poorly understood. These data support growing evidence that the effect of grasshopper and locust control measures (both chemical and biological) on indigenous natural enemies should be viewed more holistically and not considered simply in terms of direct short-term mortality rate, especially where treatments are conducted over a large area. The testing of microbial control products should be encouraged at the appropriate scales across time and space to infer useful generalities associated with operational use.

**Acknowledgments**

The authors are grateful to members of the LUBILOSA team from IITA (Cotonou) and DFPV (Niamey) for field assistance. LUBILOSA is funded by the development agencies of Canada (CIDA), Netherlands (DGIS), Switzerland (SDC), and UK (DFID). Comments from John Lawton, Carlos Bogram and two anonymous reviewers improved the manuscript.

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