

Can biological control resolve the larger grain borer crisis?

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Abstract

The accidental introduction of the larger grain borer, *Prostephanus truncatus*, in the early 1980s resulted in destructive pest outbreaks in small-farm maize stores in both East and West Africa. Studies comparing the situation in rural maize stores in Costa Rica (in the pest's neotropical area of origin) with that in Tanzania and Togo (the sites of the first outbreaks in Africa) provided circumstantial evidence that the pest might be under the control of natural enemies in Central America and that classical biological control of the pest in Africa might be feasible. The search for appropriate natural enemies is reviewed, with special attention to the predator *Teretriusoma nigrescens*, which posed special problems in view of its non-specific predation behaviour and ability to feed directly on stored products. This predator has now been released in three African countries, but no data are yet available on its impact. The benefits which may be expected from the release of *T. nigrescens*, and the difficulties involved in quantifying them, are discussed in terms of the principles of population dynamics and biological control. It is concluded that the predator is unlikely to achieve a homogeneous and acceptable level of control, and that supplementary, integrated control measures are likely to be needed, to moderate the damage suffered by individual farmers. The possible form of an integrated control strategy is indicated.

Introduction

The first outbreaks of the larger grain borer, *Prostephanus truncatus* Horn (Coleoptera, Bostrichidae) in Tanzania in the early 1980s (Dunstan and Magazini 1981) followed a pattern which has become all too familiar since the cottony cushion scale, *Icerya purchasi* Maskell (Homoptera, Margarodidae), introduced from Australia, devastated the fledgling California citrus industry in the late 1800s and initiated the modern era of classical biological control (Doutt 1964). The larger grain borer was highly destructive in traditional maize stores and caused widespread popular concern, as reflected by its 'official' common name 'dumuzi', the destroyer, in one of Tanzania's local languages (Hodges 1986). Early reports of damage were perhaps understandably exaggerated—by fear of the unfamiliar or by the need to attract foreign aid funds to cope with an additional crisis in a region already short of resources. Subsequent surveys, in the Tabora region, suggested that dry weight losses attributable to insects in traditional storage systems may have risen from an estimated 2–6%, based on previous surveys in eastern and southern Africa as a whole, to an average of almost 10% with the introduction of *P. truncatus* (Hodges et al. 1983). These losses seem quite modest, especially in the light of widely-quoted

figures that in developing countries over one-third of farm-stored commodities are lost postharvest. However, in these early Tanzanian surveys, it was immediately noted that the incidence of *P. truncatus* was particularly erratic, with individual farmers suffering losses in excess of 30% within a six-month storage season (Hodges et al. 1983). Losses between 30 and 40% were recorded by farmers growing 'improved' maize cultivars, susceptible to storage pests, in the Arusha region of Tanzania (Keil 1988). Meanwhile, surveys in Togo, which spanned the period of a second establishment of *P. truncatus*, directly documented a spectacular mean rise in losses from 7% to over 30% for a 6–9 month storage season (Pantenius 1987, 1988). Whatever the overall figures might be, it must be recognised that the outbreak of this pest caused real individual hardship: in attacking rural maize stores, *P. truncatus* threatens not only an important cash crop but the food security of vulnerable small-scale farmers, in some cases in regions where lack of infrastructure and other constraints severely limit the possibilities for substituting alternative crops.

The 'conventional' response to the larger grain borer outbreak, orchestrated by the Tanzanian Ministry of Agriculture and Livestock Development, the Food and Agriculture Organisation of the United Nations (FAO) and the Natural Resources Institute (NRI), followed a predictable cycle, beginning with attempted eradication, through containment, by statutory and other measures, to the testing of insecticide-based strategies for longer-term management of the pest (Golob 1988). In East Africa, considerable success was reported for a strategy based on a modification of traditional practices, involving shelling the grain, modifying storage structures and applying a binary insecticide combining a synthetic pyrethroid to control *P. truncatus* with an organophosphate to contain the more familiar storage pests (Golob 1988). In West Africa it has apparently proved more difficult to modify traditional storage practices. Although similar binary products are recommended, the humid conditions prevalent in much of the outbreak area limit the applicability of shelling and result in the rapid breakdown of pesticides applied to stored cobs. Our own recent surveys in Benin suggest that the recommended products are used by only some 20% of farmers and misuse of pesticides is widespread (A. Agbaka, IITA, Benin, unpublished data). Moreover, the tendency of synthetic pyrethroids to induce resistance, already documented in laboratory populations of *P. truncatus* (Golob et al. 1990; Haubruge et al. 1987), must provide grounds for concern regarding the sustainability of a strategy which depends heavily on the use of a single family of products.

Classical biological control was clearly an appealing alternative and a full-scale effort in this direction was launched in 1984 with the inception of the Biologisch-integrierte Bekämpfung des Grossen Kornbohrers project of the Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ) (Laborius 1990a; Laborius et al. 1989). This project started with an advantage over many other classical biological control initiatives in as much as *P. truncatus* was already somewhat familiar before its introduction to Africa, at least to the extent that the species had been described, its area of origin

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in Mexico and Central America was known (Wright 1984) and some work had been done on its basic biology and ecological tolerances (Shires 1977, 1979, 1980). However, this previous interest in the pest should itself have been some cause for concern from the biological control point of view. The work on the pest's biology had been stimulated by observations of severe damage to stored commodities in Nicaragua (Giles 1984; Giles and Leon 1974), ostensibly part of the pest's area of origin, where conventional wisdom suggested that a pest should be well controlled by its natural enemies. Nevertheless, the early GTZ studies, comparing the situation in outbreak areas of Tanzania and Togo with that in Costa Rica, part of the area of origin, provided grounds for optimism. Losses in Costa Rica were estimated at 5% after six months and 13% after eight months (Böye 1988), considerably less than those encountered by the parallel studies in Africa which, as noted earlier, had recorded losses in excess of 30% (Keil 1988; Laborius et al. 1989; Pantenius 1988).

Exploration for Natural Enemies

The GTZ studies in Tanzania and Costa Rica followed a similar pattern in which surveys of entomofauna and losses in local stores were combined with more detailed observations of pest population dynamics (Keil 1988; Böye 1988); the presence of insect natural enemies was recorded as part of the general observation of storage ecology. The study in Togo, launched under a separate GTZ project, concentrated almost entirely on losses. In addition, surveys were carried out with the specific aim of finding microbial control agents, and comparing the incidence of these organisms in Africa and Central America (Böye et al. 1988; Burde 1988).

The natural enemy complex on *P. truncatus*, as revealed by these studies, was not very diverse. In Costa Rica, four insect natural enemies were recorded: *Anisopteromalus calandrae* (Howard) and *Choetospila elegans* (Westwood) (both Hymenoptera, Pteromalidae), *Calliodis* sp. (Hemiptera, Anthocoridae) and *Teretriosoma nigrescens* Lewis (Coleoptera, Histeridae). Of these, the pteromalids were already well known as widespread generalist parasitoids, attacking a broad spectrum of stored-product pests, in Africa and elsewhere. *T. nigrescens* had previously been identified as a predator associated with *P. truncatus*, in samples sent from Mexico to NRI for identification (Haines 1981).

The results from the microbial surveys were more diverse but also somewhat equivocal, in that the pathogen complex associated with *P. truncatus* was broadly similar in Africa and Central America. Some 23 fungal isolates from Central America were tested, of which at least five were *Aspergillus* spp.; this was the only genus found in Mexico and Tanzania (Laborius 1990b). In addition, three species of protozoa were recorded from Central America (Burde 1988) and six from Africa (Laborius 1990b; Purrini and Keil 1989). One virus was also found in *P. truncatus* in Africa and 14 bacterial isolates were collected in Central America, but it is not clear whether these organisms were collected systematically, such that these figures would reflect relative diversity.

Screening of Natural Enemies

In preliminary cage tests in Costa Rica, the parasitoids *A. calandrae* and *C. elegans* together were shown to reduce *P. truncatus* populations (Böye 1988, 1990) and were passed on for further laboratory studies in Europe. They were subsequently rejected for use as classical biological control agents in Africa (Leliveldt 1990), though apparently on the basis of tests carried out on very small numbers of individuals. They

were also thought to be unpromising control agents on the grounds of their existing distribution in Africa (Laborius et al. 1989). This evaluation, however, ignored the possibility that these widespread parasitoids might exist in various host-adapted races; any that might be adapted to *P. truncatus*, and therefore potentially more effective as biological control agents, would be expected to occur in the host's area of origin. This possibility was taken up later in studies at the Colegio de Postgraduados in Mexico, in collaboration with the International Institute of Tropical Agriculture (IITA). The preliminary results of this study were encouraging in as much as a population of *A. calandrae* from the Mexican altiplano, where *P. truncatus* is abundant, seemed in laboratory tests to show a behavioural preference for this host over *S. zeamais* (C. Martínez, unpublished data). However, the reliability of the results was subsequently put in doubt when some colonies were found to be contaminated with other pteromalids and so this approach remains to be explored further. Meanwhile, a more optimistic evaluation of the potential of these parasitoids for the control of *P. truncatus* has been provided on the basis of laboratory studies on this host in the United States (Brower 1992) and of larger-scale trials of pteromalids for the control of *S. zeamais*.

Returning to the GTZ studies, *Calliodis* sp. was not subjected to intense screening, partly on the basis that it was a fragile insect, not well suited to the storage environment, and because it was observed to occur in the stores too late in the storage season, when damage was already severe (Böye 1988; Laborius 1990a).

Seven of the fungi isolated from *P. truncatus* proved to be somewhat pathogenic in laboratory tests. Five of these isolates, including the most pathogenic ones, proved to be *Aspergillus* spp., whose use was discounted on the grounds of potential mycotoxin risk (Laborius 1990b). Two isolates of the familiar control agents *Beauveria bassiana* and *Metarhizium anisopliae*, isolated from non-storage hosts were found to be more pathogenic to *P. truncatus*, but do not seem to have been further evaluated.

A species of neogregarine, *Mattesia* sp., was found in laboratory studies to kill 90% of first instar *P. truncatus* larvae and reduced the egg production of adult females (Leliveldt 1990; Laborius 1990b). This species and a *Nosema* sp. were applied to simulated rural grain stores in Togo, in a practical evaluation of their potential as biological control agents over two storage seasons; however, results were not promising, in terms of the pest mortality achieved and losses resulting (Henning 1993).

On the basis of both field observations and preliminary laboratory studies, *T. nigrescens* was felt to be the most promising biological control agent of the natural enemies encountered. Since this species is the main focus of current biological control efforts against *P. truncatus*, the evidence for its suitability as a control agent will be reviewed in more detail.

Evaluation of the Potential of *T. nigrescens*

The first evidence for the association of *T. nigrescens* with *P. truncatus* came, as mentioned above, from the occurrence of the species together in pest samples from stores sent for expert identification (Haines 1981). Their frequent co-occurrence was confirmed in a survey of stores in the Guanacaste region of Costa Rica, where both species occurred in 35% of 154 samples, *P. truncatus* alone in 23% and *T. nigrescens* alone in only one sample (Böye 1988; Leliveldt and Laborius 1990).

The isolation and synthesis of an aggregation pheromone of larger grain borer, originally intended for detection and monitoring of the pest in a chemical control campaign (Dendy et al.

1991), subsequently provided more evidence of the close adaptation of this predator to the target pest. In surveys based on pheromone-baited flight traps in Yucatan (Rees 1990), *P. truncatus* and *T. nigrescens* were both found in all the 'habitats', natural and agricultural, in which traps were exposed. Elsewhere in Mexico, the two species were caught together in 52 out of 176 traps laid out in transects along major roads (crossing maize production areas and natural woodland habitats of various kinds); *P. truncatus* was caught by itself in 100 traps but *T. nigrescens* was never caught alone (Ríos Ibarra 1991). Finally, it was shown in studies at NRI that the predator was not only attracted from a distance by the aggregation pheromone, it also responded to shorter range chemical stimuli left on the grain by the pest (Rees 1990).

T. nigrescens larvae proved in laboratory studies to be voracious predators of the larger grain borer, especially of its immature stages. The predator's consumption rate was estimated by NRI researchers at up to 3.5 prey larvae per day (Rees 1985) and in GTZ studies at 5.7 eggs or 4.9 larvae per day, when the predator foraged in continual darkness (Leliveldt and Laborius 1990). In the former study, predator larvae consumed about 60 prey individuals in the course of their development. On maize in jars in the laboratory, *T. nigrescens* was found to regulate *P. truncatus* populations at a predator:prey ratio of 1:10 but did not exterminate its prey (Leliveldt and Laborius 1990). A mean predator:prey ratio of 1:7.5 (range 2.8 to 10.7) was purportedly observed in rural stores in Costa Rica (Böye 1988; Leliveldt and Laborius 1990). The predator was readily maintained in the laboratory, where it proved hardy and long-lived. It was felt that voracious predation by both adults and larval *T. nigrescens* would outweigh any disadvantage from the predator's somewhat slow development time and low reproduction rate. Overall, the potential of *T. nigrescens* as a control agent looked sufficiently promising to justify field releases, which, in the end, provides the only sure means of proving the effectiveness of a biological control agent.

The main obstacle to field releases of *T. nigrescens* in Africa was concern regarding lack of specificity in its predation behaviour. Like most histerids, this species will attack a wide variety of appropriately-sized prey encountered in its foraging environment. Laboratory studies in Europe, carried out by both GTZ and NRI, showed that *T. nigrescens* was, to a greater or lesser extent, capable of feeding on, reproducing on and, in some cases, reducing the population of other stored-product Coleoptera (Rees 1987, 1991, 1992; Leliveldt 1990; Leliveldt and Laborius 1990). Some feeding on nontarget species has not previously been regarded as sufficient grounds for excluding histerids (or other predatory Coleoptera) from use as classical biological control agents, provided other characteristics were promising (Waage 1990), though current concern for nontarget organisms in the environment increasingly encourages caution in their use. In the present instance, some feeding on nontarget insects was felt to be potentially advantageous in helping to suppress populations of other storage pests and, more significantly, maintaining active populations of the predator during periods when *P. truncatus* might be rare or absent from stores (Leliveldt and Laborius 1990). Of more concern were persistent reports that *T. nigrescens* could not only survive for long periods on stored commodities in the absence of its prey, itself possibly a positive characteristic (Rees 1992), but that the predator could actually feed directly on the commodity. Natural enemies which feed on nectar, pollen or exudates of crop plants are often used in classical biological control programs, but there seems to be little or no precedent for the use of a control agent which feeds directly on the useful part of a crop or commodity.

With a view to addressing these concerns, developing a consensus on testing and introduction procedures and to coordinate the growing international research effort, a meeting was held in Cotonou, Republic of Benin, in 1989. Delegates suggested a number of tests that should be carried out to assess the extent to which the predator might be expected to feed on nontarget beneficial insects (silk worms, bees and representative natural enemies) and on commodities (Markham et al. 1990). It was recommended that releases should not be made until the evidence had been gathered and assessed. To this latter end, a similar group convened in Lomé, Togo, in November 1990 (Böye et al. 1992). In the meantime, trial releases were carried out in simulated local maize stores, confined in outdoor cages near Lomé, purportedly to evaluate the effectiveness of the predator under realistic conditions (Helbig et al. 1992).

Evidence presented to the Lomé meeting showed that *T. nigrescens* did not feed on silk worms (Laborius 1992; Murphy and Cross 1992). The predator could feed on, or at least damage, small numbers of honey bee eggs and other immatures in the comb (Laborius and Mautz 1992; Murphy and Cross 1992), as well as immatures of the parasitoid *A. calandreae* (Murphy and Cross 1992); however, it did not do so when larger grain borer immatures were also offered in a choice situation. When *T. nigrescens* adults were confined on 16 stored commodities, without living prey, they were able to survive on some for periods in excess of 24 months, as compared to mean survival of 38 to 67 days on various inert substrates (Pöschko et al. 1992). *T. nigrescens* could not reproduce on any of the plant products but were able to resume reproduction when offered larger grain borer once more, after periods of 9.5 and even 16 months. Weight losses in the commodities were assessed after six months, with most being undetectable or less than 1%. Only previously damaged groundnuts suffered slightly higher losses (1.48%) (Pöschko et al. 1992). It should be noted, however, that 'weight loss' in this case was assessed by weighing the 'flour' sieved off the grain sample at the end of the test period, divided by the initial weight of the sample. Since this method would not detect any material actually metabolised in the course of insect feeding, it may have underestimated the losses as compared with conventional measures of weight loss, based on the difference between initial and final weights of a particular sample.

In the open-air cage trials in Togo, pest populations were allowed to develop naturally in six granaries before the cages were closed and inoculations of 2000 predators per granary added to each of three of the 200 kg stores (Helbig et al. 1992a; Helbig 1993). Pest populations and losses were monitored for a further eight months. By this time, larger grain borer populations were 80% lower in the release stores and losses 42 to 47% lower (actual weight losses were approximately 19% in the release stores and 32% in the controls) (Helbig 1993).

On the basis of the various evidence presented to the Lomé meeting, it was concluded that *T. nigrescens* could not multiply on plants and plant products, posed no risk to beneficial insects and was 'ecologically specific'. It was therefore recommended that the predator should be released in Africa (Böye et al. 1992).

Releases and Monitoring of *T. nigrescens* in Africa

Releases of *T. nigrescens* began in Togo in early 1991, following a strategy described at the Lomé meeting (Biliwa et al. 1992). Initially two releases into the general environment were made: 300 individuals at the Cacavelli research station and a second of 9000 individuals at Lomé golf course, to test

the distance of attraction of the pheromone traps (Helbig et al. 1992b). A single release of 4000 individuals was then made into a store at Toagba, near Notsé, which had previously been allowed to become naturally infested. Dispersal from the release store was observed directly and using pheromone traps, whose distance from the release site was increased as *T. nigrescens* was recovered. In the following storage season, the release store was broken down and its infested maize distributed between several smaller stores at the same site. An additional 48 000 individuals were released at six localities near Vogon. In the third year of releases 1993, some 12 000 individuals were released at Moretan and several thousand more at various other localities (A. Biliwa and J. Richter, pers. comm.). The impact on pest populations was to have been monitored in detail, both by direct sampling of insects and estimation of losses (Mutlu 1992). Unfortunately, the monitoring program was severely disrupted by the turbulent political events in Togo which began at about the time of the releases and which continue up to the present. The results of the releases have therefore not been properly evaluated and published, so the effectiveness of *T. nigrescens* in this situation cannot yet be evaluated. However, verbal reports suggest that the preliminary results are equivocal, with damage in some release cribs numerically lower than in controls and higher in others (P. Mutlu, pers. comm.).

The 1992 and 1993 release sites in Togo included some within a few kilometres of the frontier with Benin. In addition, the national Plant Protection Service of Benin made a single release of about 750 *T. nigrescens* at Dadohoue in the southwestern part of Benin in November 1992. Monitoring carried out by the authors and collaborators, using pheromone-baited 'delta' flight traps (Trécé Pherocon II®) documented the rapid establishment and spread of the predator across a wide front in this part of the country. Traps were set up in zones, 5–8 km wide, parallel to the Benin/Togo border (which was assumed to be the main source of invasion of *T. nigrescens*), and reaching approximately 70 km inland from the coast. At the time of the first survey, December 1992, *T. nigrescens* was recovered only from traps in the zone nearest the frontier (Fig. 1a). In the second survey, in May 1993, the predator was found in all zones, though trap catches were apparently higher in the zone nearest the frontier (Fig. 1b). By October 1993 (Fig. 1c), the predator was well established in all zones and was as abundant in the zone 70 km from the border as it was in those 5 to 15 km from the border. The predator is also encountered frequently in our own experimental stores at Dadohoue, some 6 km from the Benin release site and 30 km from the Togo/Benin border. It is therefore concluded that *T. nigrescens* is firmly established and spreading rapidly in West Africa.

In East Africa, releases of *T. nigrescens* were made by NRI in experimental stores at two sites, Kiboko and Makueni, in the Eastern Province of Kenya, during May 1992. Reproduction of the predator has been observed in the release stores and adult predators have been recovered from control (nonrelease) stores and pheromone-baited traps, providing promising evidence for eventual establishment (Hill and Nang'ayo 1993).

Population Dynamics Revisited

Whilst awaiting the outcome of the predator releases in Africa, it is worth asking what may be expected of this intervention and what might be the criteria for success. In an idealised and conventional view of classical biological control, there may be an expectation that the pest population should fall, following the introduction of the natural enemy, from a high and destructive equilibrium level with wide oscillations, limited by relatively crude density-dependent mechanisms to

a new lower equilibrium, with narrower oscillations, moderated by the control agent's density-dependent intervention, which rarely if ever allows the pest population to exceed a damaging threshold (Stern et al. 1959). However, as May and Hassell (1988) point out, this situation has rarely been documented in actual control programs and may represent an idealisation, only encountered in highly simplified model systems. For instance, these authors describe regulation of *Callosobruchus chinensis* L. (Coleoptera, Bruchidae) by *A. calandreae* in a laboratory colony on cowpea which appears to follow this pattern (May and Hassell 1988).

Although a number of storage pests and their natural enemies have been used in this way, in the laboratory, as models for discussion of the basic principles of biological control, the control technique itself has, in practice, been exploited relatively little in stored-product protection. There are probably a number of factors involved, including the extremely low tolerances for insect infestation and damage in conventional large-scale food storage and the great efficiency of chemical pesticides, especially fumigants, in this setting. In the past there have also been formidable statutory obstacles, including the formal classification of natural enemies, along with various other materials, as 'filth', which could not be used to 'adulterate' food-stuffs; these restrictions have recently been eased, at least in the United States, opening the way for larger-scale and commercial trials of natural enemies. A number of other factors are now also favourable to the wider use of biological control in stored products (Arbogast 1984), including concerns about pesticide resistance in storage pests (Evans 1985; Zettler and Cuperus 1990), the safety of fumigants (White et al. 1983), the declining number of approved pesticides available (Brower 1991a) and widespread consumer concern regarding residues. As a result, a number of initiatives have been launched or renewed, including: the use of the predator *Xylocoris flavipes* (Reuter) (Hemiptera: Anthocoridae) (Brower and Mullen 1990) and the parasitoid *Bracon hebetor* Say (Hymenoptera: Braconidae) (Keever et al. 1985) for the control of pyralid moths on peanuts; the use of pathogens for the control of the same pests on dried fruits and nuts (Hunter et al. 1977; Kellen and Hoffman 1987); and the use various parasitoids to control Coleoptera in cereals (e.g. Brower 1991b; Smith 1992, 1993).

Despite the value of the commodities concerned and the well-developed theoretical base which is available, little progress has been made in applying population dynamics theory to underpin the practical application of biological control in stored-products protection. Most of the interventions mentioned above involve the 'inundative' use of natural enemies to achieve a required degree of pest suppression or to maintain damage below a low threshold. In this context, modelling should be of great value in developing and optimising release strategies: indeed, this is implied in some recent studies of parasitoid/pest systems on cereals which lay the groundwork for such an approach (Smith 1992, 1993; Smith and Press, 1992).

With on-farm stores of maize in the tropics, we are working with a rather different system, which is, in some ways, inherently more favourable for the application of biological control than the warehouses or silos of 'developed' agriculture. Cribs are open systems where a number of predators and parasitoids arrive, without intervention from the farmer, from outside populations. The relatively open structure of a maize crib allows parasitoids to penetrate readily to all parts of the store. And, very importantly, farmers have perforce become accustomed to accept a certain level of insect damage, perhaps as high as 5% weight loss over a storage season, while still regarding the level of pest control as satisfactory (McFarlane 1988). Nevertheless, for socioeconomic reasons which are

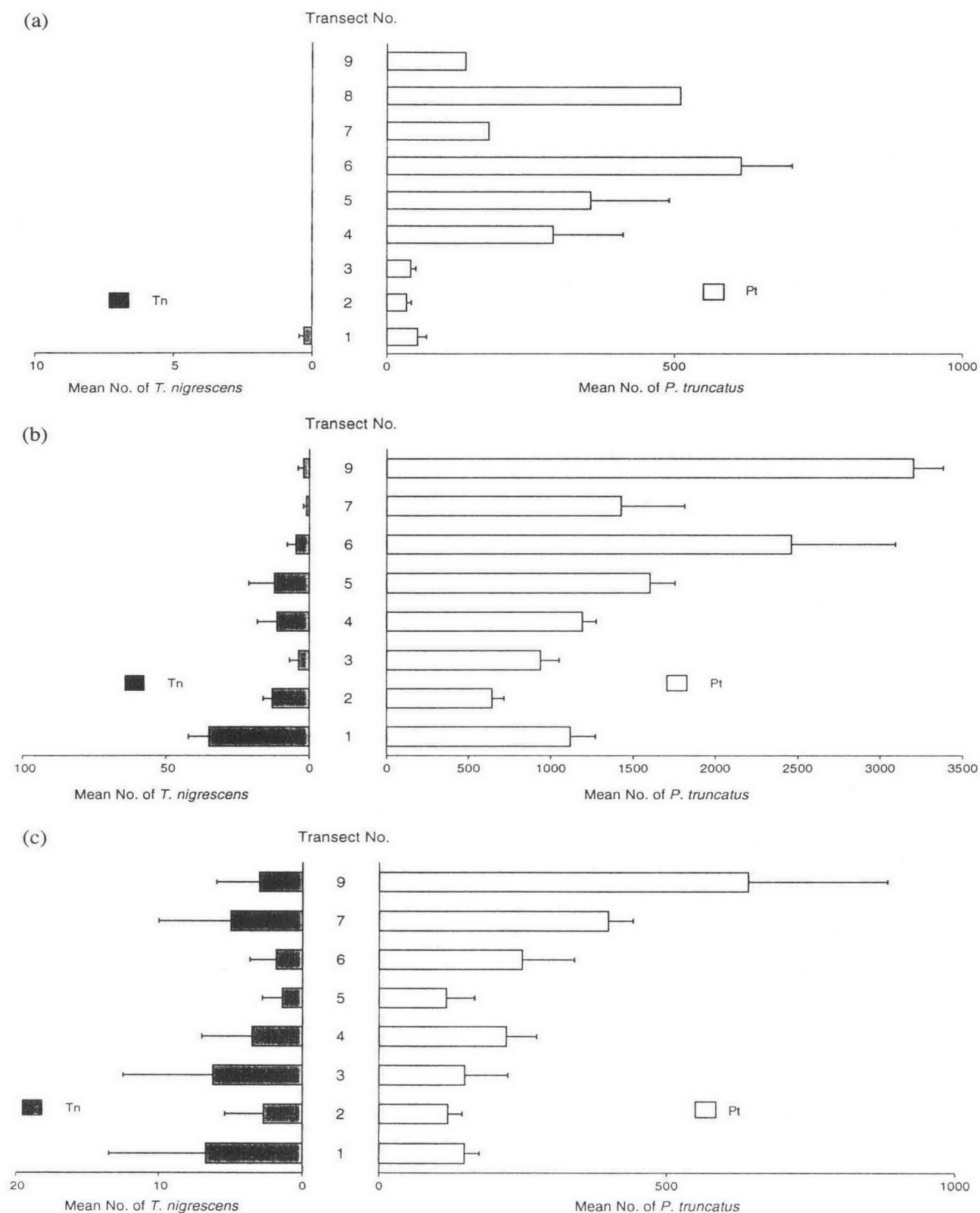


Fig. 1. Captures of *T. nigrescens* (Tn) and *P. truncatus* (Pt) in pheromone-baited flight traps in the Mono Department of Benin. Traps were arranged in zones (1–9), approximately 5–8 km wide, parallel to the Benin–Togo border. Data presented are mean no. insects/trap/week for different trapping periods (as below). Survey was repeated three times on the following dates, with different numbers of traps (t) and trapping locations (L) per transect (T):
 (a) October–December 1992 (9 weeks: T1 = 7t/7L, T2 = 6t/6L, T3 = 6t/6L, T4 = 6t/6L, T5 = 5t/5L, T6 = 3t/3L, T7 = 1t/1L and T9 = 1t/1L).
 (b) May 1993 (4 weeks: T1 = 36t/9L, T2 = 21t/6L, T3 = 8t/4L, T4 = 5t/4L, T5 = 11t/6L, T6 = 6t/3L, T7 = 4t/2L and T9 = 2t/1L).
 (c) October 1993 (4 weeks: T1 = 31t/14L, T2 = 21t/8L, T3 = 8t/4L, T4 = 6t/3L, T5 = 10t/5L, T6 = 6t/3L, T7 = 2t/1L and T9 = 2t/1L).

perhaps obvious, there has been little incentive to develop quantitative and dynamic models to guide the manipulation of such storage systems for the purposes of biological control.

This lack of a clear conceptual or quantitative model is especially obvious in the case of the release campaign of *T. nigrescens* against *P. truncatus*. Although at one level, this is clearly a classical biological control program, it has some elements reminiscent of an inundative program, which seem to have misled even some of those implementing the work. For instance, Leliveldt and Laborius (1990) note that, even with different initial densities, stock cultures tended to settle to a predator:prey ratio of about 1:10. This is not too unexpected in a laboratory system with replenished resources, based on the criteria mentioned by May and Hassell (1988) as above. However, the same authors go on to draw a parallel with observations from stores in Costa Rica where a slightly lower ratio was observed (which the authors suggest may be attributable to the predator's supplementary use of alternative prey sources). When field releases were made in Togo, it was also proposed that the size of the inoculation should be calculated to give the same 1:10 ratio in the stores (Biliwa et al. 1992), a strategy which seems to have been followed, at least approximately, in practice. The same conceptual confusion is apparent in relation to the field cage experiment in Togo where it is reported that *T. nigrescens* was released at a predator:prey ratio of 1:3.6 and that the ratio then 'surprisingly' narrowed (Helbig 1993).

Studies by our own research group in Mexico and Central America suggest a quite different situation in stores. At the experimental site at Chilcuautla in Mexico, *T. nigrescens* showed only a very weak numerical response to an exponentially increasing *P. truncatus* population (Fig. 2a) which eventually caused severe damage (Ríos Ibarra 1991; Ríos Ibarra et al. 1992), despite the early arrival of the predator in the stores. A series of 'peaks' in adult numbers early in the season also suggest that the predators were migrating into and out of the stores, presumably in response to imperatives other than prey availability (Ríos Ibarra et al. 1992). It may be argued in this case that conditions at this high altitude site (1880m) on the Mexican plateau were ecologically unfavourable to the predator. On the other hand, even more severe losses (Fig. 3) were recorded in two successive years of study of experimental stores in the Zamorano Valley of Honduras, at 800m with a warm, equable climate. At this site both *P. truncatus* and *T. nigrescens* increased exponentially, but at a predator:prey ratio of, very approximately, 1:100 (Fig. 2b). There is some evidence from this study that the rate of increase was slightly lower in the second year (when both pest and predator were apparently pre-established in the wooden frame of the stores); possibly, the predator may have contributed to this slower rate. However, the absolute levels of the pest population were higher in the second year, leading to even more severe losses in a shorter storage period.

In classical biological control, it is important to distinguish between strategies to optimise the chances of establishment at the release site and expectations about the eventual outcome of the release at the level of the store or region. Theoretically, it may be helpful to ensure that a predator:prey ratio is not too high at the time of release, so as to avoid the chances of a local extinction which could jeopardise establishment. However, this is highly unlikely in the present case, since the predator is extremely long-lived and highly dispersive. The size of the release population 'inoculated' into a particular store will also have no effect on the eventual level of control achieved (beyond the individual store) and, within the range of the scale of operation currently considered, it is unlikely even noticeably to affect the time taken to achieve the target level of control. It should be stressed that for control of *P. truncatus* in

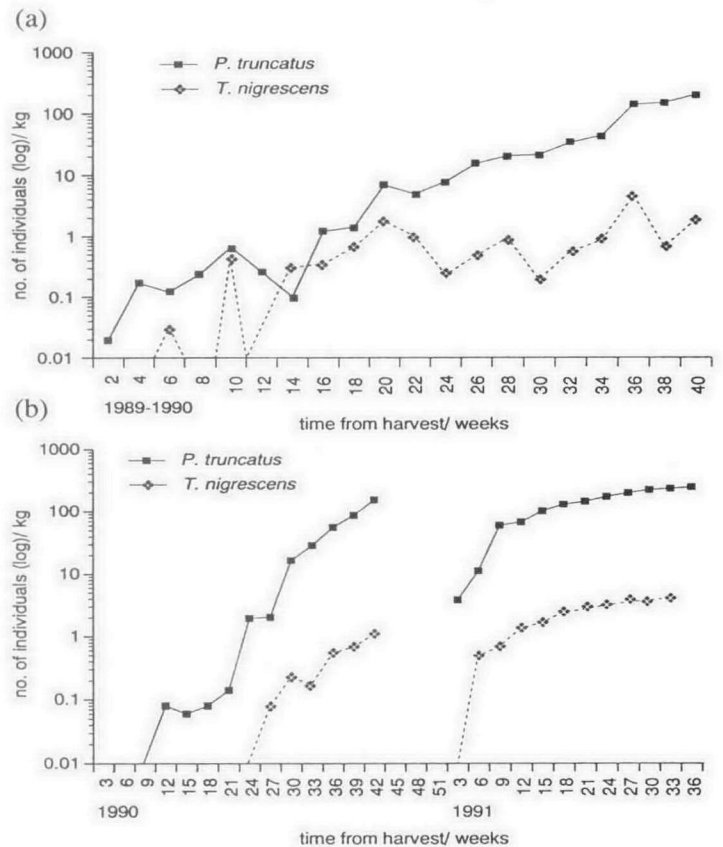


Fig. 2. Counts of numbers of adult *P. truncatus* and *T. nigrescens* per kg (dry weight) of grain in simulated traditional stores at study sites at a) Chilcuautla, Mexico and b) Zamorano, Honduras. Mexico data points are based on 9 samples of 20 cobs (taken from three levels of each of three experimental stores, in a stratified random manner) on each sampling occasion. Honduras data points are based on 9 samples of 10 cobs (taken from three levels of three separate bins in a single store) on each sampling occasion (ref. Ríos 1991; Novillo 1991).

Africa, socioeconomic constraints on rural storage effectively preclude any possibility of rearing and releasing *T. nigrescens* inundatively onto individual stores. Even in areas of Latin America where the economics might be more favourable, the long development time and slow reproductive rate of this species make this an extremely dubious proposition. Moreover, for similar reasons, it is unrealistic to expect a favourable equilibrium to be reached in individual release stores, even though this would be highly desirable from a public-relations point of view in promoting the value of biological control.

It is then reasonable to ask what can be expected of this predator-pest system. It seems evident that it is not realistic to expect *T. nigrescens* alone to control *P. truncatus* adequately within individual stores. The predator may nevertheless contribute to lower average pest population levels if a larger universe is considered. There is increasing evidence that *P. truncatus* is primarily a highly mobile forest pest, which comes only secondarily to maize stores, and that this behaviour pattern is preserved in the outbreak areas in Africa (Nang'ayo et al. 1993), despite the different host plant species available to the insect in natural vegetation there. The total population of larger grain borer will therefore consist of a mosaic of subpopulations or patches. Some of these will be on an artificial, but highly satisfactory substrate, maize, on which the insect rapidly reaches very high numbers and densities; others will be on wood, which appears to be the natural

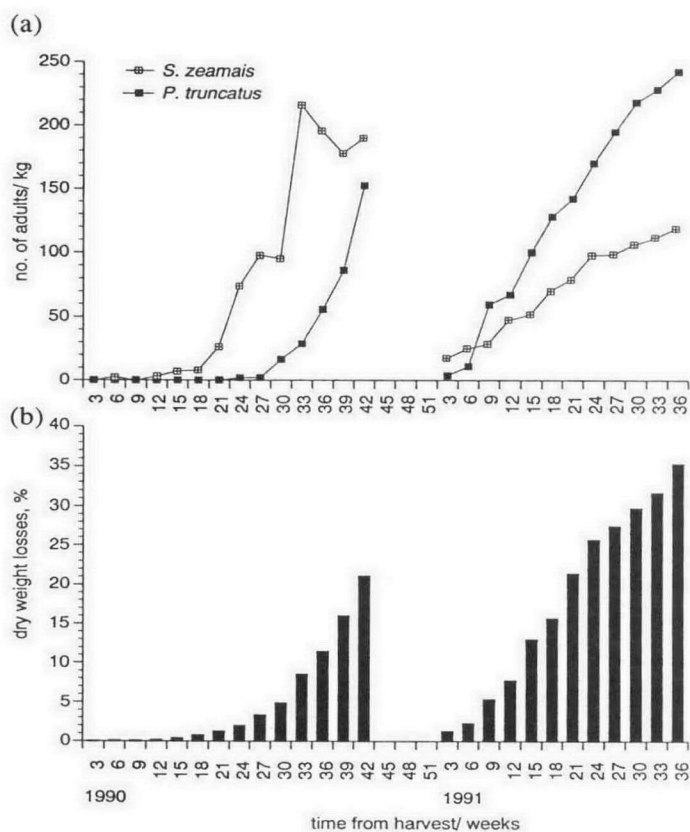


Fig. 3. Numbers of adult *P. truncatus* and *S. zeamais* per kg (dry weight) of grain (a) and percent weight loss (dry weight basis) (b) from experimental stores at Zamorano, Honduras. Insect data points are based on nine samples of 10 cobs (as per Fig. 2). Weight loss was estimated on the basis of 1000-grain samples drawn from the pooled grain of the same nine samples, using a count-and-weigh method (ref. Novillo 1991).

substrate, but on which development is somewhat slower (Nang'ayo et al. 1993). The population 'patches' in maize stores have only a finite life, being dispersed or terminated when the store is emptied (and before the substrate is exhausted); it seems possible that the 'patches' in wood may be of even shorter duration, if the supposition is correct that *P. truncatus* occupies a transient niche in the degradation of dead tree branches (Ramírez et al. 1989; Nang'ayo et al. 1993).

This postulated life-strategy of *P. truncatus* is consistent with the observed, highly-seasonal flight activity of the pest (Ríos Ibarra et al. 1992), the existence of an aggregation pheromone and the insect's strong, but variable, response to it. The behaviour of *T. nigrescens* is also consistent with this model, especially in its effective host-finding, based on the predator's response to its prey's aggregation pheromone, and the close coordination of the predator's flight activity cycle with that of its prey (Fig. 4). If accurate, this model has unfortunate implications for the biological control effort in Africa. Firstly, it will be particularly difficult to monitor pest populations and therefore the effectiveness of any control interventions. Stochastic effects will probably be very strong, with rapid pest build up in some 'patches' and extinctions in others, providing an example of a scenario described by Murdoch et al. (1985) in which overall control is the product of a mosaic of different local outcomes. Since the 'patches' we can measure most easily (and which are most important to us) are grain stores, we must expect extremely high variation between stores and therefore will require heavy replication to get an adequate estimate of overall mean population levels and losses. An alternative will be to use pheromone-baited

flight traps as an index of the general population, perhaps combined with some form of 'rapid assessment technique' for losses (J. Compton, pers. comm.). However, this approach is not without difficulties. Trap catches reflect flight activity and are highly variable with respect to site and season; they will therefore only reflect actual population levels in long-term trapping at consistent sites. A second implication is that, even with the predator firmly established and improved control achieved overall, high inter-patch variation will probably result in individual farmers continuing to suffer unacceptably high losses.

A Holistic Approach to Control of *P. truncatus*

From the foregoing, the prospects for classical biological control of *P. truncatus* may not appear very bright, but this is not necessarily an excuse for pessimism or inaction. Most obviously, any control of the pest achieved by natural enemies will probably have to be combined with other complementary control strategies in an integrated control approach. On the one hand, we are trying to better understand and measure the processes of biological control in maize cribs, so as to find measures that will quantitatively enhance their effectiveness. On the other, we are seeking qualitatively different strategies, which may work on different parts of the cycle of infestation.

Once we accept that *T. nigrescens* is not a control agent of the type whose basic dynamics ensure that the pest will fall below an acceptable equilibrium level and stay there, we become involved in the somewhat harder exercise of trying to measure the rates of processes (especially pest population increase and accompanying losses within limited time-frames) and examining their implications for store management. For instance, the relationship between predator and prey will likely be strongly affected by climatic effects (expressed as grain temperature and humidity) and the susceptibility of the maize substrate. It may also be affected by other biotic processes, especially competition with other pest species, parasitism and the pest's own density-dependent regulation processes (oviposition rate, emigration, mortality etc.). Through life table studies in maize cribs, we seek to assess the importance of natural enemy action in the context of other mortality factors. We want to analyse and examine the combined effects of these rate-dependent processes through dynamic modelling. The predictions of models, driven by climatic data, related to particular maize varieties, and realistically reflecting biological processes affecting pest population build-up, should generate predictions on the losses to be expected in particular situations. These projections can then be used to guide and optimise management decisions. In particular, these decisions would include when to harvest, whether to dehusk the maize and when to shell and/or sell the maize. This approach should also help to show whether, and under what circumstances, it is possible to avoid the use of insecticides during this initial drying-and-storage phase and so take advantage of conserving any natural enemy activity present.

Another, qualitatively different, approach which we are pursuing is to analyse the host-finding behaviour of *P. truncatus*, with a view to identifying factors which may affect its tendency to come to maize itself, or to the structure of stores. Host finding behaviour will also be considered in relation to seasonal flight activity cycles of the pest and how the timing or manner of harvest might be modified to minimise pre or postharvest migration of the pest to the maize. Survival between storage seasons and the possibility of pest build-up in nonmaize substrates also needs to be investigated in relation to different store types and sanitation practices, climatic regimes and natural environments. All these variables

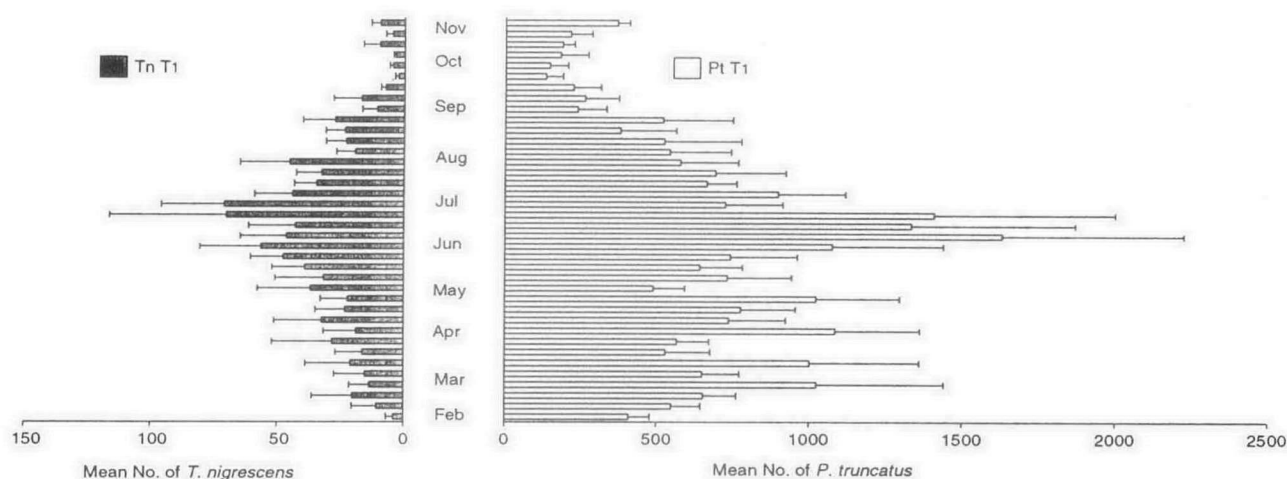


Fig. 4. Seasonal incidence of flight activity of *P. truncatus* (Pt) and *T. nigrescens* (Tn) as demonstrated by weekly trap catches in pheromone-baited flight traps in the Mono Department of Benin. Traps were arranged in a zone of approximately 10 km width, parallel to the Benin–Togo border. Traps were examined weekly between February and November 1993. Data presented are mean no. insects per 11 traps.

will have a bearing on the pest populations which initiate the in-store processes mentioned above.

In seeking alternative strategies we are not only working from basic biological principles, but also researching the experiences of traditional farmers, both in West Africa and Central America. We are using on-farm surveys and farmer interviews, followed by multivariate analysis, to try to identify circumstances and management practices which seem to be associated with particularly severe pest problems or with their absence. We are trying to test particular management strategies which seem to have an effect on pest populations in on-farm controlled trials. And we will try to introduce, from one region to another, any management practices which appear to be effective in mitigating pest problems and which seem to be compatible with local environmental and socio-economic constraints.

Within the discipline of biological control itself, we believe that possibilities for the use of pathogens should also be re-evaluated. Firstly, the experience of other biological control programs using pathogens suggests that a much larger collection of isolates may need to be screened to improve the chances of finding one or more with appropriate characteristics. New work on natural host plants of larger grain borer and the availability of flight traps which can be used in a wide variety of habitats, open possibilities for collecting fungal isolates from *P. truncatus* itself which were not open to previous researchers. In addition, isolates from existing collections, originating from other hosts, can also be more extensively screened. The availability of effective pheromone-baited live traps for *P. truncatus* opens up the possibility of developing a system in which migrating insects are trapped, inoculated with a pathogen, and released to disperse the infestation into new founder populations of the beetle.

Finally, it must be recognised that, however strong the evidence for or against the efficiency of a particular classical biological control agent prior to its release, its effectiveness can only be truly assessed by releases, accompanied by proper impact assessment. The considerations mentioned above should serve to indicate that the proper assessment of impact is by no means an easy procedure, conceptually or in practice. Indeed, the impact of the majority of classical biological control releases carried out to date has never been properly measured, let alone evaluated in economic terms. In light of the seriousness of the larger grain borer problem in Africa and

the continuing spread of this pest, it is very much to be hoped that proper impact evaluation will be done in the case of the introduction of *T. nigrescens*. This will then provide a rational basis for deciding how to proceed in extending control efforts against this pest. In particular, reliable information on the effectiveness of *T. nigrescens* will help to guide the relative emphasis to be placed on chemical, biological and integrated control approaches.

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