

Teretrius nigrescens against larger grain borer *Prostephanus truncatus* in African maize stores: biological control at work?

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Summary

1. Following the accidental introduction of the bostrichid beetle *Prostephanus truncatus* into East and West Africa around 1980, a classical biological control campaign was launched in 1991; the histereid beetle *Teretrius nigrescens* was released as a biocontrol agent to prevent the destructive outbreak of the pest in small-farm maize stores. However, while the campaign has been ongoing, so has discussion in the scientific community about the merits of this campaign and its chances of success.

2. From published and unpublished data from experimental maize stores in Benin, West Africa, we derived statistical models describing the in-store insect population dynamics, and were thus able to point out significant biological interactions and to explain the observed lack of biological control.

3. We found that (i) *T. nigrescens* reduced significantly the population growth rate of both *P. truncatus* and the non-target pest, the weevil *Sitophilus zeamais*; (ii) *T. nigrescens* displayed a positive numerical response to both prey species, *P. truncatus* and *S. zeamais*; (iii) asymmetric competition existed between the two prey species, *S. zeamais* was negatively affected by *P. truncatus* but not vice versa; (iv) *T. nigrescens* and *S. zeamais* displayed negative intraspecific density-dependence whereas *P. truncatus* was resource-limited.

4. We conclude that classical biological control with *T. nigrescens* is not likely to become successful, mainly due to the predator's intraspecific density-dependence and its low population growth rate compared with its prey. We recommend that further research on *P. truncatus* integrated pest management takes into account the farmer as an active agent managing the store.

5. *Synthesis and applications.* When biocontrol does not result in satisfactory pest control, as in the case of *P. truncatus*, farmers should learn how to scout for the pest and take action when a need is detected. In areas where the pest is usually only a minor problem, the agricultural extension service should consider setting up a simple early warning system for their region. When attempts at classical biological control remain unsuccessful, as in the case of *P. truncatus* now for 10 years, policy-makers should prioritize training of extension service and farmers in integrated pest management techniques (e.g. need-based use of insecticides) as a necessary supplement to biocontrol.

Key-words: integrated pest management, predator, prey, population dynamics, *Sitophilus zeamais*.

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Introduction

The bostrichid beetle *Prostephanus truncatus* (Horn) was accidentally introduced from America into Africa around 1980, appearing first in East and then in West Africa (Dunstan & Magazini 1981; Harnisch & Krall

1984). It had by 2000 spread to 16 subSaharan countries (Farrell 2000) and has become the major pest of stored maize and cassava in the region. A campaign of classical biological control was launched, with the first releases of the histrid beetle *Teretrius* (earlier *Teretriosoma*; Mazur 1997) *nigrescens* (Lewis) in Kenya and Togo in 1991 (Giles *et al.* 1996; Richter *et al.* 1998), and has since been ongoing in Africa (Henning-Helbig 1995; Bell *et al.* 1999). Meanwhile the effectiveness of *T. nigrescens* has been disputed on theoretical grounds (Hodges 1994; Markham, Borgemeister & Meikle 1994a), and lack of control has been reported from Benin (Meikle *et al.* 2002) and Ghana (Birkinshaw & Hodges 2000). Successful control on a regional level was expected by Borgemeister *et al.* (1997) and Richter *et al.* (1997) but reports on such control are still outstanding on the continent.

Teretrius nigrescens larvae and adults are predators of *P. truncatus* eggs and larvae which, in confined food-choice experiments, are preferred over other stored-product pests (Rees 1987). Yet (i) the numerical response of the predator is enhanced when weevil larvae, *Sitophilus zeamais* Motschulsky, are offered in addition (Ayertey *et al.* 1999) and (ii) when offered *S. zeamais* alone, the predator develops nearly as fast as on its preferred prey (Oussou, Meikle & Markham 1998). Furthermore, the predator can reproduce when fed other bostrichid species (Rees 1991), although only in combination with plant substrate according to Pöschko (1992). Theoretically, this lack of specificity could either enhance (through food supplementation) or limit (through diversion of predation capacity) the effectiveness of the control agent. These theoretical speculations are further complicated by the search behaviour of *T. nigrescens*: in flight, the predator is attracted to the aggregation pheromone emitted by male *P. truncatus* (as are conspecifics) (Scholz, Borgemeister & Poehling 1998) but at short distances the predator seemingly avoids *P. truncatus* adults and larvae (Hodges & Dobson 1998). The final outcome of these mechanisms, in terms of the achieved field-level control of the target *P. truncatus* and non-target *S. zeamais*, the two major pests on stored maize in humid West Africa (Holst, Meikle & Markham 2000), must be studied under field conditions, which was the aim of the present study.

At a landscape level, the population dynamics of *P. truncatus* and *T. nigrescens* are played out in a mosaic formed by stocks of maize and cassava and natural, decaying wood (Markham, Borgemeister & Meikle 1994a; Borgemeister, Tchabi & Scholz 1998; Nansen, Meikle & Korie 2002) while *S. zeamais* is a widespread, granivorous insect (Longstaff 1981; Markham *et al.* 1994b). Both *P. truncatus* and *T. nigrescens* display periods of intense flight activity in response to weather conditions and other, unknown, factors (Borgemeister *et al.* 1997; Nansen *et al.* 2001). A readiness to migrate could be a strategy of these species to survive in a landscape of microhabitats that are scattered and

transient. *Prostephanus truncatus* and *S. zeamais* will infest maize both in-field and in-store, although the level of *P. truncatus* field infestation varies a great deal (see Borgemeister *et al.* 1994 and references cited therein). *Teretrius nigrescens* will follow *P. truncatus*, attracted to the male aggregation pheromone. In this system two alternative, but not mutually exclusive, hypotheses have been put forward by which biological control could be successful. (i) Regional control, in which control is achieved through the general depression of the pest population in the wild habitat where the pest, living on poor substrates, could more readily be overcome by the predator than in the rich substrate of stored produce (Markham, Wright & Rios 1991; Mutlu 1994). (ii) Local control, in which the predator seeks out and overcomes the pest inside the store before serious damage has accrued (Richter *et al.* 1997). In the present study we addressed the second of these hypotheses, identifying under which conditions local control could be possible and to what degree of success.

To model the dynamics of the populations inside the store, we must quantify the population growth rates and the intra- and interspecific relations among the populations. Thus questions arise. (i) Does *T. nigrescens* affect the population growth rate of *P. truncatus* and *S. zeamais*? (ii) What is the numerical response of *T. nigrescens* to *P. truncatus* and *S. zeamais*? (iii) Is there density-dependent regulation within the species and do *P. truncatus* and *S. zeamais* compete? From the answers to these questions, we can conclude whether biological control can be expected to work reliably and with which options this leaves farmers, extension agents and policy-makers.

We investigated these questions by applying regression analysis to previously published data sets from maize store experiments conducted in southern Benin (Meikle *et al.* 1998a,c), augmenting them with previously unpublished, concurrent data on *T. nigrescens* population dynamics.

Methods

INTRINSIC RATE OF INCREASE

To estimate the intrinsic (i.e. maximal) rate of increase of *T. nigrescens*, a simulation model based on laboratory life-table data was developed. The model was stage-structured and used the time-varying life-table approach (Gutierrez 1996) similar to the *P. truncatus* simulation model described by Meikle *et al.* (1998b). The duration of juvenile life stages was described by the day-degree (°D) approach, only extending the line with a dropping, parabolic curve at higher temperatures. Because data on the development rate of eggs were lacking, a simple experiment was set up in the laboratory: from females caught in Benin, 21 eggs were incubated at 15 °C and 26 eggs at 25 °C (70 ± 5% relative humidity) until eclosion. The maximum egg-laying rate observed in the laboratory is 0.8 day⁻¹ (Labite

1998) and we used this rate in the model. Estimates for the intrinsic rate of increase were obtained in the range 15–35 °C for *T. nigrescens* using this model, and for *P. truncatus* and *S. zeamais* using previously published simulation models with all density-dependent effects removed (Meikle *et al.* 1998b; Meikle, Holst & Markham 1999b).

FIELD DATA

Thirty-two time series of data were compiled from previous published studies carried out in southern Benin and conducted in the storage seasons 1994–95 (Meikle *et al.* 1998a) and 1995–96 (Meikle *et al.* 1998c). Data in both studies comprised adult density of *P. truncatus*, *S. zeamais* and *T. nigrescens* and grain weight loss from 16 experimental maize stores sampled monthly, eight times during the storage season. The stores were of traditional, local design. A full description of the experimental set-up is given by Meikle *et al.* (1998a,c). Density was calculated as beetles per kilogram of undamaged grain (i.e. original weight), which is an absolute measure of density that is always proportional to the total population inhabiting the store (Holst, Meikle & Markham 2000). In both storage seasons, insect populations reached considerable levels (*P. truncatus*, 1600 and 2800 kg⁻¹; *S. zeamais*, 1600 and 1400 kg⁻¹; *T. nigrescens*, 230 and 230 kg⁻¹). All stores were located in the humid tropics of West Africa, where temperature and grain moisture content are ideal for insect pests through most of the storage season. Grain moisture content is the more decisive factor, as it is usually too high for the insects in the first month after stocking (> 20%) and occasionally too dry during the dry season (< 9%) (range in experiments: 8–22%). Ambient temperature was measured by the weather station at the International Institute of Tropical Agriculture, Calavi, Benin, where the experiments were carried out.

STATISTICAL ANALYSIS

For all 32 time series we estimated for each pair of consecutive sampling dates the population growth rate as:

$$r_{sp}(i) = \frac{\ln \left(\frac{N_{sp}(i+1)}{N_{sp}(i)} \right)}{t(i+1) - t(i)}, \quad i = 1, 2, \dots, 7 \quad \text{eqn 1}$$

where the index *sp* denotes one of the three species, *t*(*i*) and *t*(*i* + 1) are the consecutive sampling dates (days after stocking), and *N*_{*sp*}(*i*) and *N*_{*sp*}(*i* + 1) the densities sampled (beetles per kilogram). The average density during the period was calculated as:

$$\bar{N}_{sp}(i) = \frac{1}{2}(N_{sp}(t_i) + N_{sp}(t_{i+1}))$$

When either density, *N*_{*sp*}(*i*) or *N*_{*sp*}(*i* + 1), was zero the growth rate calculation (equation 1) was prohibited. This caused a reduction in the number of observations,

from a potential 224 (32 time series, each with seven pairs of consecutive samples) to 170 for *r*_{*P*} and 106 for *r*_{*T*}; for *r*_{*S*} all 224 rates could be calculated.

The population growth rate (*r*) is composed of per capita rates of births (*b*), deaths (*d*), immigration (*i*) and emigration (*e*), *r* = *b* - *d* + *i* - *e*. However, in the present experiments the density of potential immigrants in the environment was not controlled for or assessed. Hence we limited the analysis to the post-colonization phase of store population dynamics, when effects of immigration are overshadowed by the other three processes considered to be governed by factors inside the store.

For *S. zeamais*, colonization was assumed to have taken place before stocking because it was present in all samples (minimum density 10.8 kg⁻¹). For the other two species, the heuristic rule for selecting post-colonization data was chosen to err more on the side of including too few rather than too many observations: (i) draw trend lines for *r*_{*P*} depending on the density of *P. truncatus* and *T. nigrescens* (Fig. 1); (ii) consider the maximum of the trend line in the two plots as demarcating the change from colonization to post-colonization; (iii) include in the regression analysis of *r*_{*P*} only those observations that fall into the post-colonization category in both plots; (iv) use the same procedure for *r*_{*T*} (Fig. 2). Trend lines were drawn applying the Loess procedure of TableCurve (SPSS, Chicago, IL).

The 224 observations of *r*_{*S*} were reduced to *n* = 162 for the statistical analysis by excluding those observations for which the density of either *P. truncatus* or *T. nigrescens* was zero (prohibiting log-transformation, see below). For the analysis of *r*_{*T*}, the heuristic selection procedure reduced the data set to *n* = 81 with no observations left from the early season, *r*_{*T*}(1) to *r*_{*T*}(3), i.e. for *i* = 1, 2, 3 (equation 1). For the analysis of *r*_{*P*} the procedure reduced the data set to *n* = 110 with no observations left of *r*_{*P*}(1). However, for *r*_{*P*}(2) only one observation remained; furthermore, the correlation between *r*_{*P*}(3) and *r*_{*P*}(4) observations was very high (*r* = -0.92). Therefore the data set was further reduced to include only observations *r*_{*P*}(4) to *r*_{*P*}(7) (*n* = 97). In a final selection of data, two unrealistic values of *r*_{*P*} (> 0.15 day⁻¹) were excluded, ending at *n* = 95.

A multiple regression analysis was carried out for each species using PROC MIXED of SAS (Littell *et al.* 1996), with population growth rate as the response variable and 12 regression terms (fixed factors), year (class variable designating 1994–95 or 1995–96), percentage weight loss, one linear (\bar{N}_{sp}) and one quadratic term (\bar{N}_{sp}^2) for each species, and the linear interaction terms between (\bar{N}_{sp}) of the dependent species and \bar{N}_{sp} of the other two species, year and weight loss. Prior to analysis, percentage weight loss was arcsine square-root transformed and insect densities log₁₀-transformed.

For each of the three regressions, the covariance matrix of *r*_{*sp*}(*i*) was inspected for obvious patterns and any structure detected was incorporated in the analysis as a random effect. For the analysis the covariance

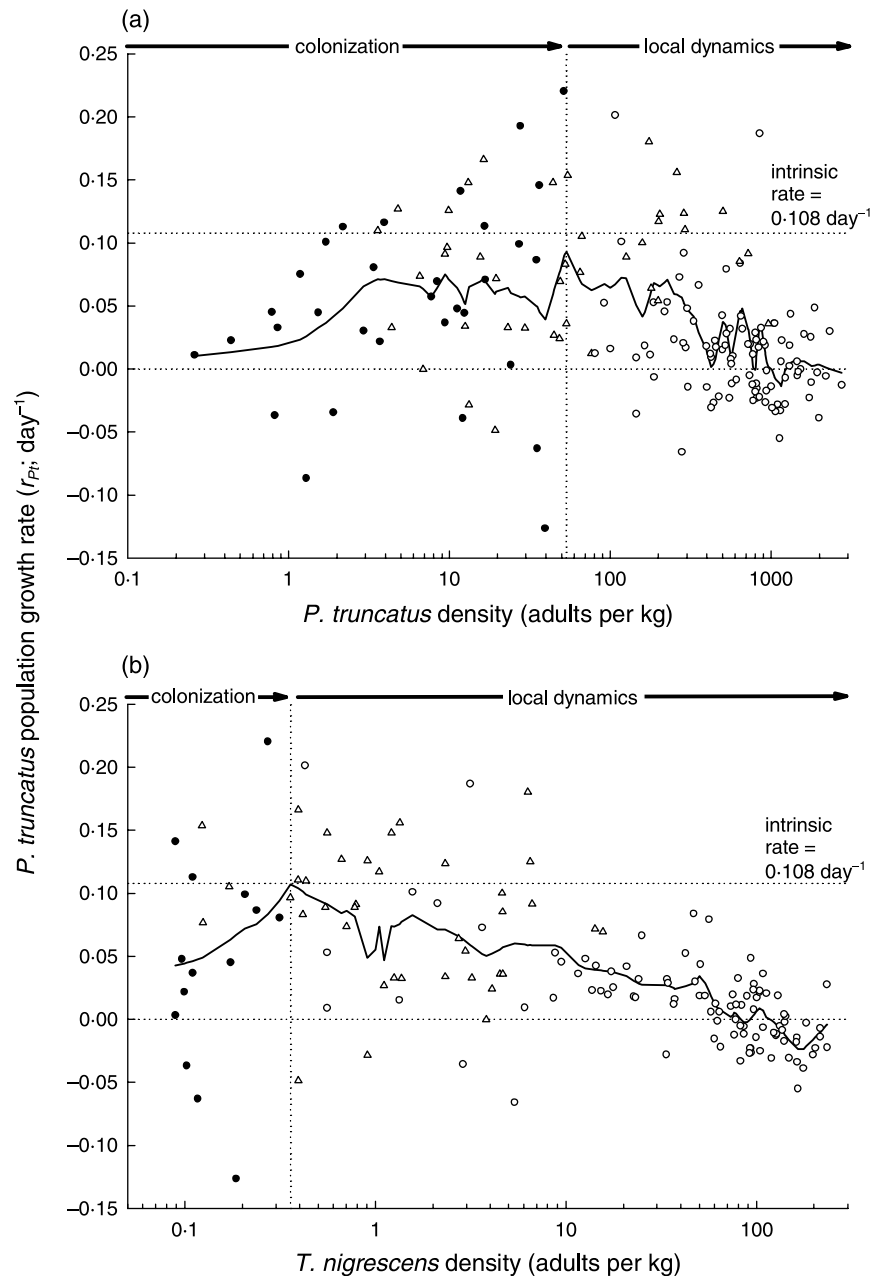


Fig. 1. Population growth rate (r_{Pt}) of *P. truncatus* depending on the density of conspecifics (a) and *T. nigrescens* (b), the curve showing the general trend. Data were classified according to trend maxima: data points to the left of the maximum in both a and b (solid circles), to the right of both maxima (open circles) or otherwise (triangles). The dynamics were divided into two phases, tentatively named 'colonization' and 'local dynamics'. Eighteen data points with zero *T. nigrescens* ($r_{Pt} = 0.0537 \pm 0.0679$ SD day⁻¹) are not shown in (b).

structure was specified by the SAS option TOEPH(m) (cf. SAS software help text), which allows for unequal variances in the diagonal (i.e. among sampling occasions) and for autocorrelation through time: none ($m = 1$), between $r_{sp}(i)$ and $r_{sp}(i + 1)$ ($m = 2$) and, in addition, between $r_{sp}(i)$ and $r_{sp}(i + 2)$ ($m = 3$). Starting with the full 12-term model, the model was reduced one term at a time, on each iteration excluding the term contributing least significantly ($\alpha = 0.05$). If several terms were highly non-significant, the more complex term would be excluded first (falling order of complexity: interaction, quadratic, linear). Residual plots were

assessed visually to check variance homogeneity. On some occasions pairs of terms could not be disentangled statistically: if both were included they were non-significant, while included separately they were each significant on their own. In such cases both terms were kept in the model.

Results

The development time of *T. nigrescens* eggs was 19.1 ± 1.40 SE days at 15 °C and 4.28 ± 0.689 SE days at 25 °C, and the available data on juvenile development

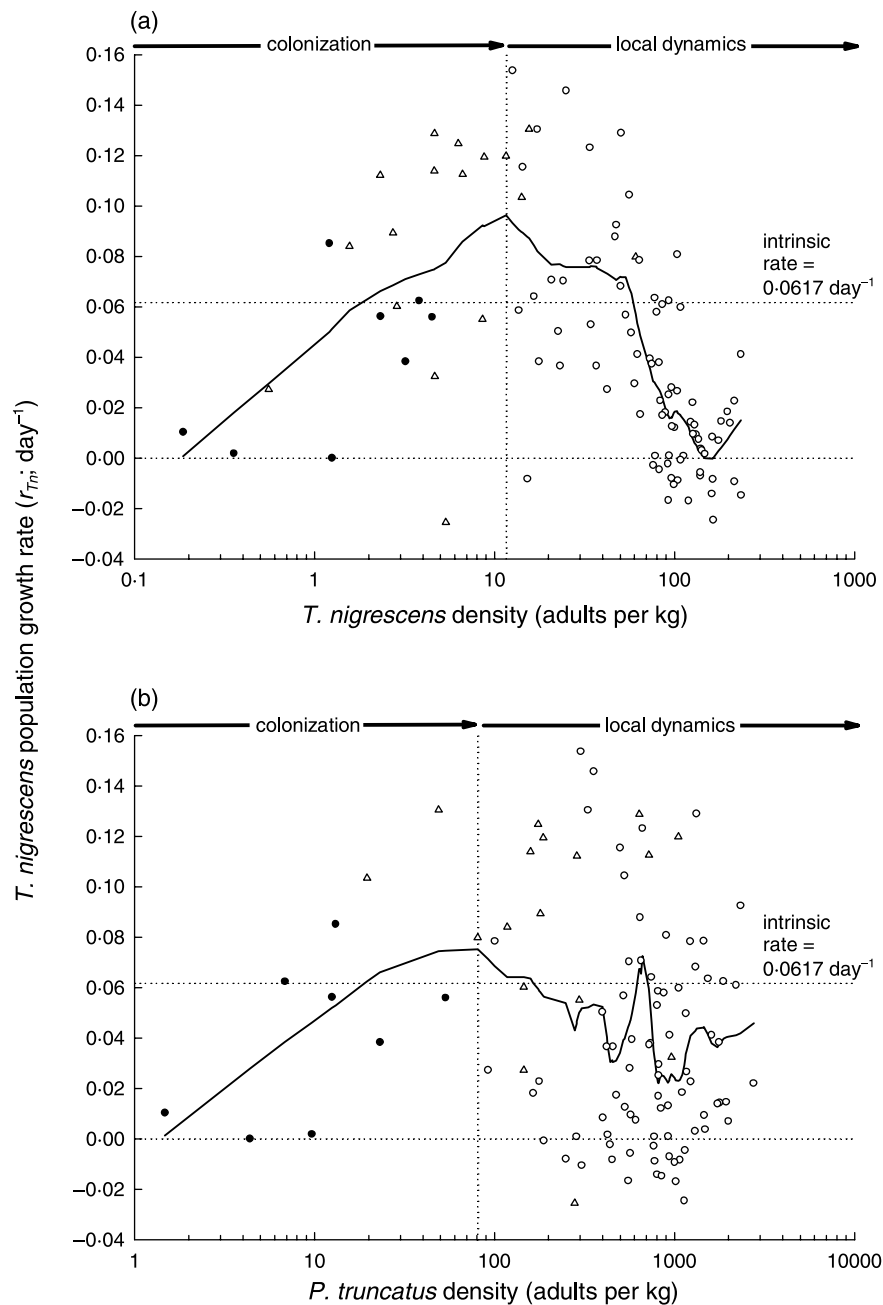


Fig. 2. Population growth rate (r_{Tn}) of *T. nigrescens* depending on the density of conspecifics (a) and *P. truncatus* (b), the curve showing the general trend. Data points were classified as in Fig. 1.

Table 1. Duration (L) of *T. nigrescens* life stages in day-degrees ($^{\circ}\text{D}$) according to lower threshold for development (T_0) and culmination of parabolic part of curve at (T_{opt} , r_{opt}) (Fig. 3)

Life stage	L ($^{\circ}\text{D}$)	T_0 ($^{\circ}\text{C}$)	T_{opt} ($^{\circ}\text{C}$)	r_{opt} (day ⁻¹)
Egg	55.4	12.1	32.0	0.330
First instar*	55.6	17.6	32.0	0.230
Second instar*	80.8	19.8	32.0	0.130
Pupa*	125	20.0	36.3	0.106
Adult†	630	20.0	32.0	0.0140

*After Noudahikpon (1995) and Oussou, Meikle & Markham (1998).

†Three months at 27 $^{\circ}\text{C}$ according to Rees (1985).

were adequately summarized on a day-degree scale, except at higher temperatures (Table 1 and Fig. 3). The intrinsic rate of increase was higher for the two pests than for the biocontrol agent, except above 31 $^{\circ}\text{C}$ when the growth rate of *T. nigrescens* would exceed that of *S. zeamais* (Fig. 4). Daily temperature during the experiments varied little, and the overall average of both seasons 1994–95 and 1995–96 was 27.3 ± 1.44 SD $^{\circ}\text{C}$. Store temperature tends to be stable due to the bulk of the stock and is generally 2 $^{\circ}\text{C}$ above ambient temperature (W. G. Meikle, unpublished data). Thus a temperature of 29.3 $^{\circ}\text{C}$ was used to calculate optimal rates of growth in-store during the experiments (Figs 1 and 2). Observations above the intrinsic rate of increase

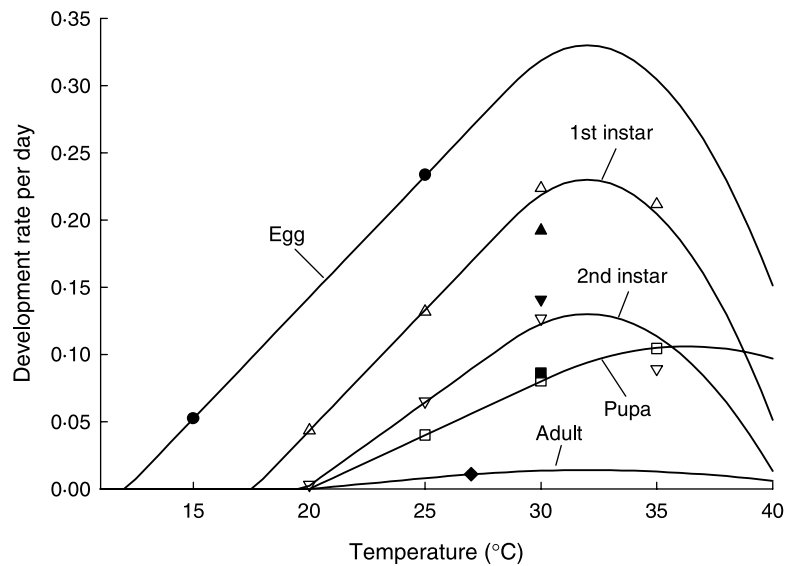


Fig. 3. Development rate of *T. nigrescens* life stages with parabolic part of curves fit by eye on the constraint that line and parabola have equal slope where they join. Data points: eggs (solid circles), first instar (triangles) and second instar (inverted triangles) larvae, pupae (squares), adults (diamonds). Sources: own data (solid circles); Noudahikpon (1995) (open symbols), pupae died at 20 °C; Oussou, Meikle & Markham (1998) (solid triangles, inverted triangles and squares); Rees (1985) (diamonds).

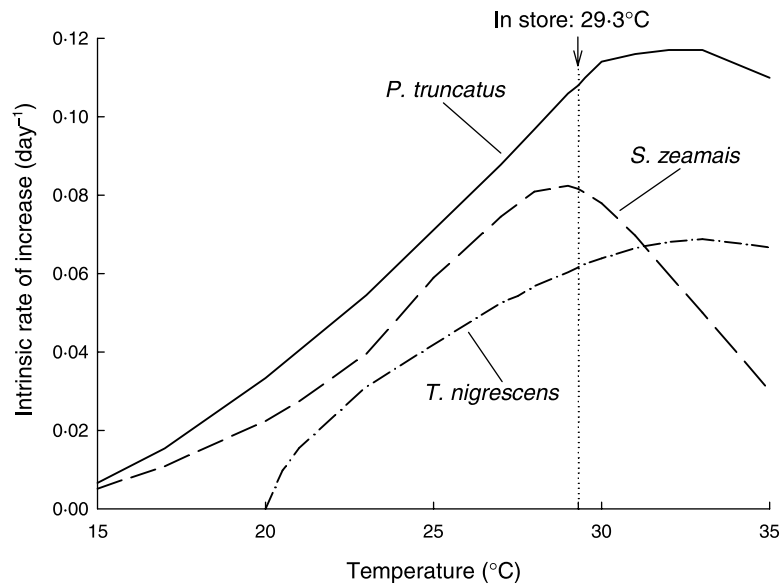


Fig. 4. Intrinsic rate of increase for the pests, *P. truncatus* and *S. zeamais*, and the beneficial *T. nigrescens* at different temperatures. The average store temperature estimated at 29.3 °C is indicated.

(*S. zeamais*, 4/224 = 2%; *P. truncatus*, 23/170 = 14%; *T. nigrescens*, 33/106 = 31%) could have purely statistical reasons (sampling error) as well as biological (immigration), both likely to be higher at lower in-store densities. However, the trend line of r_{Tn} clearly exceeds the intrinsic rate of increase (Fig. 2a), which is not the case for *P. truncatus* (Fig. 1a). Altogether, this suggests that the effect of immigration on in-store population dynamics was largest for *T. nigrescens*, less for *P. truncatus* and even less for *S. zeamais*.

For all three species the variance differed among sampling occasions (matrix diagonals in Tables 2–4). In addition, consecutive observations were correlated negatively for *P. truncatus* and *S. zeamais* [$r_{sp}(i)$ and $r_{sp}(i + 1)$ in Tables 2 and 3], and for *P. truncatus*

Table 2. Matrix of variances $\times 10^5$ (diagonal), covariances $\times 10^5$ (below diagonal) and correlations (above diagonal) of population growth rate, $r_{Pt}(i)$, estimated for *P. truncatus* at monthly intervals ($i = 4-7$)

	$r_{Pt}(4)$	$r_{Pt}(5)$	$r_{Pt}(6)$	$r_{Pt}(7)$
$r_{Pt}(4)$	46	-0.58	0.29	0.01
$r_{Pt}(5)$	-57	212	-0.64	0.47
$r_{Pt}(6)$	23	-106	128	-0.71
$r_{Pt}(7)$	1	57	-67	69

observations 2 months apart [$r_{Pt}(i)$ and $r_{Pt}(i + 2)$ in Table 2] were positively correlated. While the incorporation of these covariance structures was important for the proper application of the statistical procedure

Table 3. Matrix of variances $\times 10^5$ (diagonal), covariances $\times 10^5$ (below diagonal) and correlations (above diagonal) of population growth rate, $r_{S_z}(i)$, estimated for *S. zeamais* at monthly intervals ($i = 1-7$)

	$r_{S_z}(1)$	$r_{S_z}(2)$	$r_{S_z}(3)$	$r_{S_z}(4)$	$r_{S_z}(5)$	$r_{S_z}(6)$	$r_{S_z}(7)$
$r_{S_z}(1)$	57	-0.27	0.06	0.27	0.55	0.04	-0.55
$r_{S_z}(2)$	-9	20	0.06	-0.21	-0.58	0.57	-0.03
$r_{S_z}(3)$	2	1	15	-0.31	-0.04	0.01	0.05
$r_{S_z}(4)$	15	-7	-9	56	-0.35	-0.05	-0.09
$r_{S_z}(5)$	27	-17	-1	-17	42	-0.47	-0.19
$r_{S_z}(6)$	2	15	-0	-2	-18	35	-0.50
$r_{S_z}(7)$	-31	-1	1.5	-5	-9	-22	56

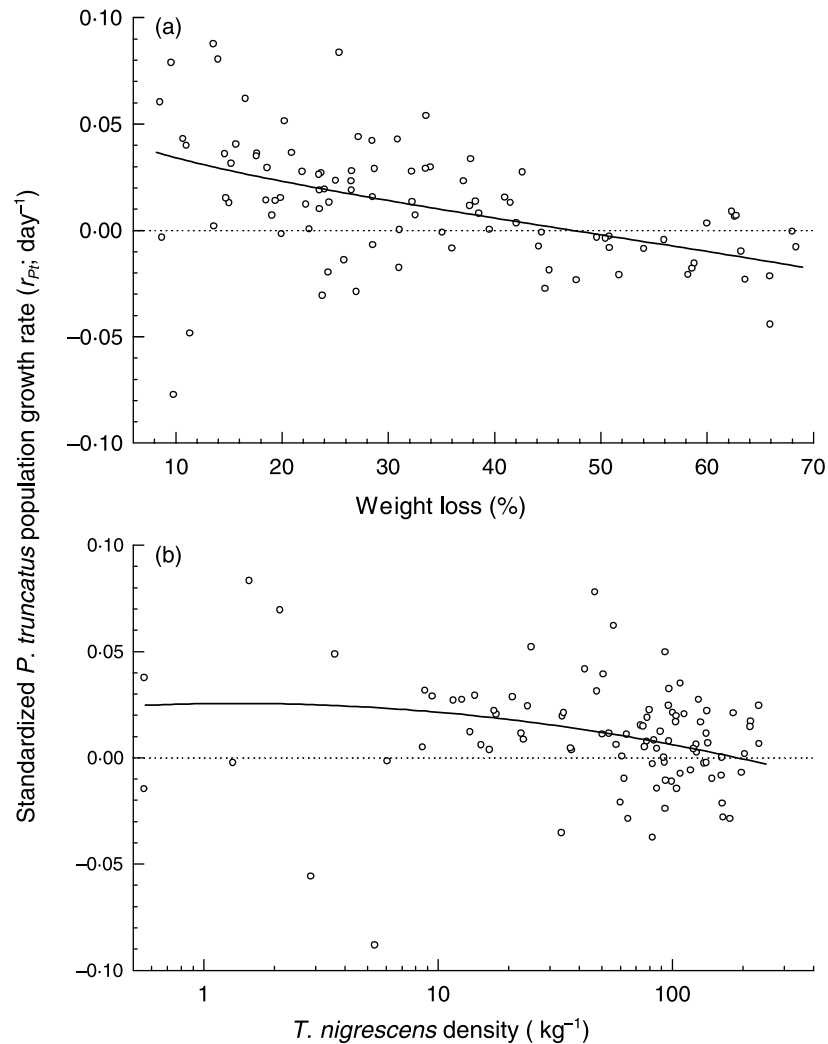
[m was set to 3, 2 and 1 for *P. truncatus*, *S. zeamais* and *T. nigrescens*, respectively, for the TOEPH(m) option], their biological interpretation is unclear. The negative correlation between consecutive observations can be explained as an artefact resulting from the computation of population growth rates: as $N_{sp}(i)$ occurs in denominator and numerator, respectively, when calculating $r_{sp}(i)$

Table 4. Matrix of variances $\times 10^5$ (diagonal), covariances $\times 10^5$ (below diagonal) and correlations (above diagonal) of population growth rate, $r_{T_n}(i)$, estimated for *T. nigrescens* at monthly intervals ($i = 4-7$)

	$r_{T_n}(4)$	$r_{T_n}(5)$	$r_{T_n}(6)$	$r_{T_n}(7)$
$r_{T_n}(4)$	280	-0.46	0.68	-0.30
$r_{T_n}(5)$	-73	90	0.00	0.10
$r_{T_n}(6)$	111	-0	95	0.01
$r_{T_n}(7)$	-34	6	1	46

and $r_{sp}(i+1)$ (equation 1), any sampling error on $N_{sp}(i)$ will draw consecutive values in opposite directions.

Limits to growth were set by intraspecific competition (*S. zeamais*, Fig. 6a; *T. nigrescens*, Fig. 7a), resource depletion (*P. truncatus*, Fig. 5a), asymmetric competition (*S. zeamais*, Fig. 6b) and predation (*P. truncatus*, Fig. 5b; *S. zeamais*, Fig. 6c). *Teretrius nigrescens* displayed a clear numerical response to both prey species (Fig. 7b,c). The positive interaction between the

**Fig. 5.** Multiple regression ($n = 95$) predicting the population growth rate of *P. truncatus* from grain weight loss (a) and *T. nigrescens* density (b). Regression curves and data points were standardized to the geometric average of *T. nigrescens* (48 kg⁻¹) (a) and average weight loss (32%) (b). Regression applied to data points right of both trend peaks in Fig. 3, except for 15 data points additionally excluded (see text).

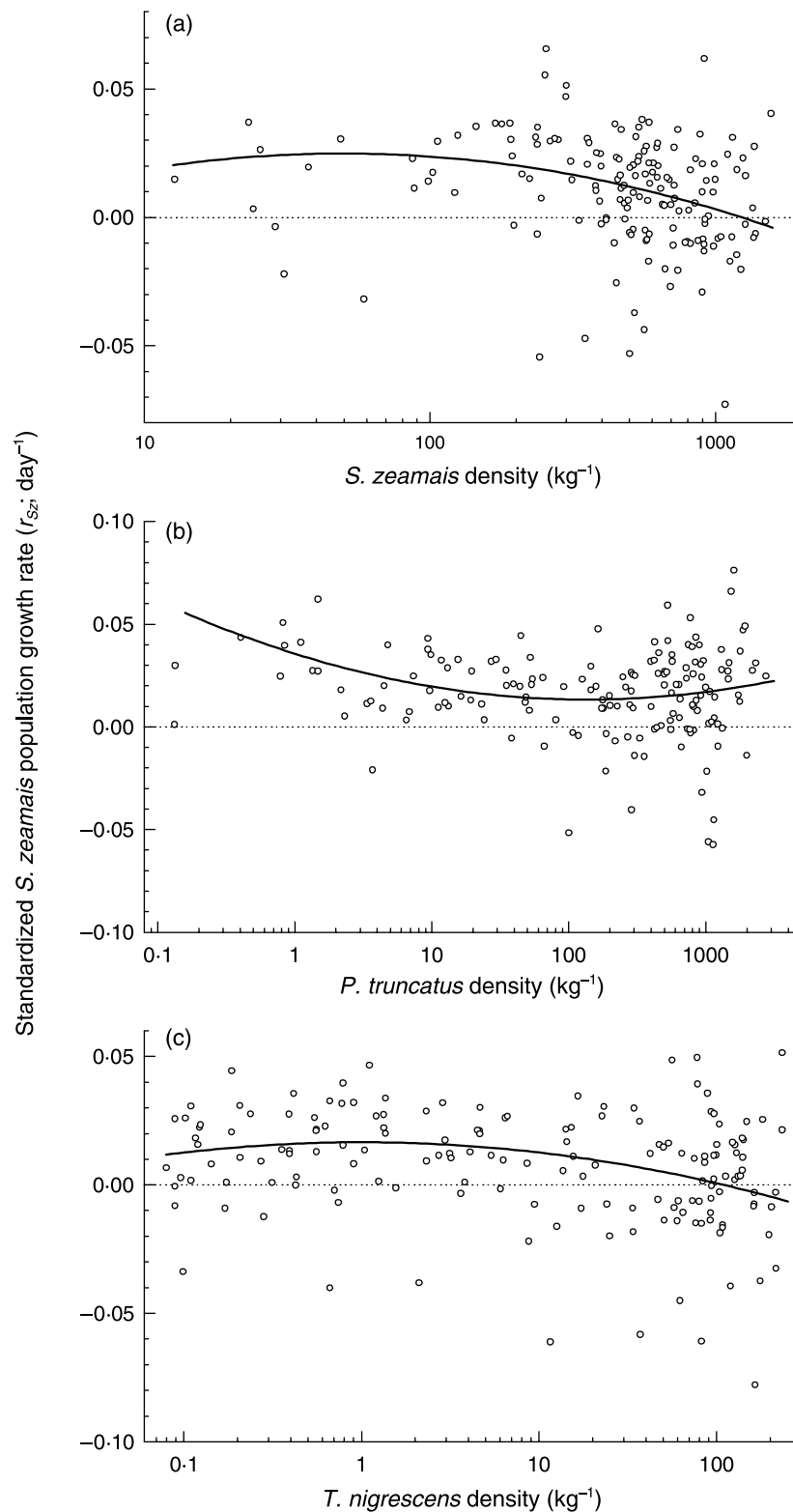


Fig. 6. Multiple regression ($n = 162$) predicting the population growth rate of *S. zeamais* from the density of conspecifics (a), *P. truncatus* (b) and *T. nigrescens* (c). Regression curves and data points were standardized to the geometric average of *S. zeamais* (443 kg^{-1}) (b and c), *P. truncatus* (147 kg^{-1}) (a and c) and *T. nigrescens* (8 kg^{-1}) (a and b).

density of *S. zeamais* and *T. nigrescens* on r_{Sz} (Table 5) causes the prey population growth rate to increase with increasing prey density, which indicates that the predation rate per predator declines (e.g. a type 2 functional response). Effective biocontrol was not observed in the

experimental stores, where both *P. truncatus* (Fig. 1a) and grain weight loss (Fig. 5a) reached high levels. Only at high density (above *c.* 60 per kg) was *T. nigrescens* observed to bring the population growth rate of *P. truncatus* down below zero, but not consistently (Fig. 5b).

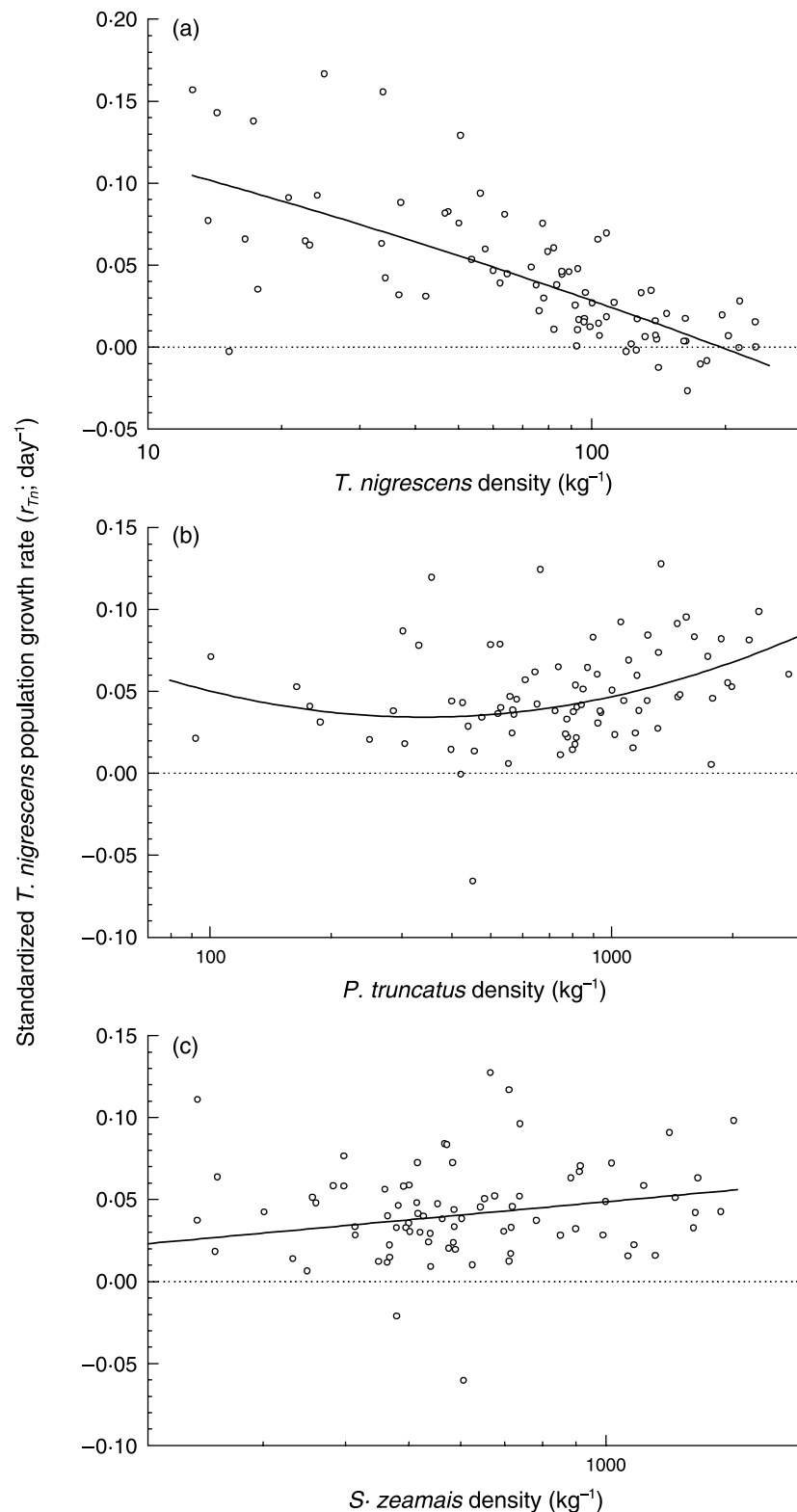


Fig. 7. Multiple regression ($n = 81$) predicting the population growth rate of *T. nigrescens* from the density of conspecifics (a), *P. truncatus* (b) and *S. zeamais* (c). Regression curves and data points were standardized to the 1994–95 season, and to the geometric average of *T. nigrescens* (74 kg^{-1}) (b and c), *P. truncatus* (735 kg^{-1}) (a and c) and *S. zeamais* (607 kg^{-1}) (a and b). Regression applied to data points right of both trend peaks in Fig. 4.

Discussion

When discussing the population dynamics of *T. nigrescens*, *P. truncatus* and *S. zeamais*, and the possibilities for successful control, it is important to distinguish between

the local scale (inside the store) and the regional scale (at landscape level). Our study was focused at the local scale, at which we found that satisfactory control will be an unlikely event. This explains the variability in the (often unsatisfactory) local control found in earlier maize store studies.

Table 5. Coefficients for the three regression equations describing the population growth rate of *S. zeamais* (r_{S_z}), *P. truncatus* (r_{P_t}) and *T. nigrescens* (r_{T_n}), depending on year, arcsine square-root transformed weight loss percentage, and \log_{10} -transformed population densities (\bar{N}_{sp}). Interaction terms not listed were all non-significant at $P = 0.05$

Regression term	<i>S. zeamais</i>		<i>P. truncatus</i>		<i>T. nigrescens</i>	
	r_{S_z} (day ⁻¹)	P	r_{P_t} (day ⁻¹)	P	r_{T_n} (day ⁻¹)	P
Intercept	0.0635	0.26	0.0725	< 0.0001	0.428	0.12
Year	–	NS	–	NS	–0.0159 ^{*c}	0.075 (0.0048)
Loss	–	NS	–0.0782	< 0.0001	–	NS
\bar{N}_{S_z}	0.0245 ^a	0.59 (< 0.0001)	–	NS	0.0366 ^c	0.057 (0.0025)
$\bar{N}_{S_z}^2$	–0.0128 ^a	0.17 (< 0.0001)	–	NS	–	NS
\bar{N}_{P_t}	–0.0209	< 0.0001	–	NS	–0.286 ^d	0.090 (0.022)
$\bar{N}_{P_t}^2$	0.00490	0.0003	–	NS	0.0565 ^d	0.061 (0.015)
\bar{N}_{T_n}	–0.0549	< 0.0001	0.00162 ^b	0.89 (0.036)	–0.0511 ^c	0.60 (< 0.0001)
$\bar{N}_{T_n}^2$	–0.00400	0.006	–0.00562 ^b	0.27 (0.0085)	–0.0108 ^c	0.69 (< 0.0001)
$\bar{N}_{S_z} \times \bar{N}_{T_n}$	0.0207	< 0.0001	–	NS	–	NS

NS, not significant at $P = 0.05$.

Terms paired by the same letter: when one term was left out the other turned significant (P -value shown in parentheses) and vice versa; hence, both terms were included.

*Offset for 1995–96 season.

Before and after the initial release of *T. nigrescens* in Togo in 1988–92, Richter *et al.* (1997) monitored maize stores at one locality. They found a steep decrease in the density of *P. truncatus* and a general reduction in final damage after 8 months from 60% to 20%. Similar results were obtained by Borgemeister *et al.* (1997) in a study at one locality in southern Benin, where final weight loss was reduced from 60% to 12% from before to after the appearance of *T. nigrescens*. A study from Togo in 1992, contrasting two villages with and two without *T. nigrescens*, was less conclusive (Mutlu 1994). Only in one season out of two was *P. truncatus* density in stores reduced by the presence of *T. nigrescens*. This was accompanied by a reduction in final loss but not in final damage. Finally, Richter *et al.* (1998) in 1990–92, again in Togo, made pair-wise comparisons of villages over three storage seasons with and without *T. nigrescens*. In all three cases, *P. truncatus* numbers were reduced by *T. nigrescens*, but final damage was reduced in only one of these (from 50% to 30%). Both Mutlu (1994) and Richter *et al.* (1997) looked for an effect on *S. zeamais* numbers but found none. Altogether, although these results were seen as ‘encouraging’ (Richter *et al.* 1998), they do support our conclusion that control of *P. truncatus* inside the store to a satisfactory level is, in general, not achievable with *T. nigrescens* alone.

In an impact assessment during the initial release of *T. nigrescens* in Kenya in 1991, Giles *et al.* (1996) found no biocontrol effect in maize stores. However, the two study locations were rather cool (average temperatures 17.7 °C and 22.2 °C), close to the lower threshold for development of *T. nigrescens* (Table 1).

Why does local biological control not work reliably, either in our study or according to previous studies (cited above)? After all *T. nigrescens* reduced the population growth rates of both pests, the target *P. truncatus*

(Fig. 5b) and the non-target *S. zeamais* (Fig. 6c). Furthermore, both pests put limits on themselves through dependency on either their resource (*P. truncatus*; Fig. 5a) or their own density (*S. zeamais*; Fig. 6a) and, in addition, *P. truncatus* interfered with *S. zeamais* (Fig. 6b). This interference has been found earlier, both in the laboratory (Böye 1988; cited by Mutlu 1994) and in the field in Togo (Mutlu 1994), although in loose maize *S. zeamais* may have the competitive advantage over *P. truncatus* (Giga & Canhao 1993). Our study points to the intraspecific density-dependence of the predator (Fig. 7a) as the main reason for the lack of local control. Of all the density-dependent relations identified, this was the steepest (Figs 5–7). Thus, although *T. nigrescens* has a positive numerical response to both prey species (Fig. 7b,c), this was far outweighed by the negative effect of its own density and only at a high density would *T. nigrescens* cause a decrease in *P. truncatus* density (Fig. 5b). Furthermore, on the rich substrate of maize, the intrinsic rate of increase is higher for *P. truncatus* than for *T. nigrescens* (Fig. 4).

The negative density-dependence of the predator may be due to several factors, three of which are: resource competition (causing reduced net reproduction and increased mortality), cannibalism and behavioural interference (reduced immigration, increased emigration and suppressed reproduction). Resource competition and cannibalism do not seem likely as prey populations remained plentiful during the experiments. Reduced immigration would be the result if arriving *T. nigrescens* take the presence of conspecifics as a ‘patch occupied’ signal and immediately leave, perhaps as an adaptation to natural microhabitats, which are less rich than stored produce. In confined choice experiments Hodges & Dobson (1998) found that at a short distance *T. nigrescens* adults will avoid male *P. truncatus* beetles. Thus a high in-store density of the

prey population might not only promote the population growth rate of the predator (Fig. 7b) but also add to its tendency to emigrate, although no such interaction was detected statistically (Table 5).

Other biocontrol agents have also been shown to behave counterproductively with respect to pest control. For example, the reproductive strategy of aphidophagous coccinellids and syrphids is to lay only relatively few eggs during the initial development of aphid colonies. This behaviour optimizes predator fitness, by making it more likely that the larvae have time to complete their development before prey becomes scarce, but also makes the predators ineffective as biocontrol agents (Hemptinne *et al.* 1993). In the case of *T. nigrescens*, it is important to consider the natural setting in which their behaviour has evolved. Like aphidophagous predators they have most probably evolved to exploit scattered and transient resources and could have become ineffective biocontrol agents due to this evolutionary background.

Reviewing the numerous laboratory studies that have demonstrated the non-specific food choice of *T. nigrescens* (confirmed by later studies; Oussou, Meikle & Markham 1998; Ayertey *et al.* 1999), Markham, Borgemeister & Meikle (1994a) proposes non-specificity as a possible benefit for biological control by enabling the predator to survive periods with scarce but diverse prey. The possibility of undesirable effects on non-target organisms, however, must be taken into account (Neuenschwander & Markham 2001). Our study showed that the indications from the laboratory do translate into the field, where non-specificity affected the population dynamics of both alternative prey (Fig. 6c) and the predator itself (Fig. 7c). Our interpretation is that *T. nigrescens* uses the aggregation pheromone of *P. truncatus* as a cue to find habitats well-supplied with a variety of food items, including its preferred prey. In that sense it is a specialist (cf. Henning-Helbig 1995).

Our analysis was based on store data from one locality in southern Benin through two storage seasons. We identified general relationships describing population growth rates depending on the density of populations and maize weight loss. However, the predictions are specific to maize stored on the cob in humid, tropical climates, where grain moisture content will only rarely drop as low as to limit pest population growth. *Teretrius nigrescens* seems unaffected by humidity, immature development being the same in the range 30–90% relative humidity (Oussou, Meikle & Markham 1998). Temperature is very stable in southern Benin (27.3 °C on average during the experiments) but cooler or hotter climates will affect the population growth rates (Fig. 4) and hence the population dynamics and damage process significantly. Differences in the occurrence of other pests must be taken into account when applying our analysis to other geographical regions.

As local control cannot completely solve the problem of a *P. truncatus*-infested store, the only other

possibility of obtaining a successful case of classical biological control is through regional control. However, reports so far are to the contrary. In Ghana, *P. truncatus* density varies much from year to year and still reaches outbreak levels, even though *T. nigrescens* has been present in the area since 1994 (Birkinshaw & Hodges 2000). Similarly in Benin, maize stores remain at high risk, which causes farmers to apply pesticides to stores, often inappropriately (Meikle *et al.* 1999a). The initial tendency of *P. truncatus* trap catches in southern Benin to drop, following the invasion of *T. nigrescens* from nearby Togo in 1992 (Borgemeister *et al.* 1997), has since been followed by a resurgence in trap catches (Nansen *et al.* 2001). Furthermore, judged from pheromone trap catches, *T. nigrescens* does not aggregate in areas where *P. truncatus* density is high (Nansen, Korie & Meikle 1999). Altogether, the rather positive assessments of the level of biological control obtainable in West Africa (Richter *et al.* 1997; Bell *et al.* 1999) do seem in need of qualification. Although our study does not dismiss the theoretical possibility of regional control, but only demonstrates that local control is unlikely, the empirical evidence so far shows that regional control is not happening.

Confronted with this evidence, alternative strategies are being developed. Birkinshaw *et al.* (2002) suggest a warning system for *P. truncatus* based on a network of pheromone traps; at unusually high catches a warning should be issued to farmers that stores are at high risk of infestation. A scouting plan, allowing for rapid detection of stores infested by *P. truncatus* before significant damage has occurred, was developed by Meikle *et al.* (2002) and could be applied by the farmer, either in isolation or in combination with the warning system suggested above. Both warning system and scouting plan were modelled by Holst, Meikle & Hodges (2002) and demonstrated in an Internet software application. Both systems would be sensitive to any effect of biological control at a regional level. In cases where *T. nigrescens* was actually exerting an effect, warnings would be issued and store infestations would be detected less often. This shift from the classical biological control strategy implies most importantly the inclusion of the farmer as an informed agent, actively taking management decisions.

To analyse the possible reasons for failure of biological control we calculated the population growth rates of pests and predator from replicated time series of population densities. The subsequent regression of these growth rates on possible determining factors was an effective method of detecting the population dynamic processes at work (density-dependence, competition, predation, numerical response) and should be of general utility (cf. Berryman 1991). Skovgård *et al.* (1993) used the same approach to analyse the population dynamics of cassava green mite *Mononychellus tanajoa*, although they did not correct for the autocorrelation of growth rate estimates, as we did, by specifying the covariance structure for a mixed-type of regression.

Ignoring autocorrelation will tend to overestimate the degrees of freedom (which could be much less than the sample size suggests because estimates are correlated) and hence lead to false significant results.

Which options does this leave to farmers, extension agents and policy-makers? Farmers should learn how to scout for *P. truncatus* in their stores and to apply insecticides appropriately when a need is thus detected; for maize stored on the cob this means checking 11 cobs per store every 3 months after stocking (Meikle *et al.* 2002). This method should be implemented as far as possible, no matter how well established *T. nigrescens* is in the area, as biocontrol does not effectively prevent losses to *P. truncatus*. In areas where maize or dried cassava is stored for periods longer than 3 months and where *P. truncatus* is usually a minor or non-existing problem, extension agents should consider running pheromone traps as an early warning system for their region or, alternatively, scout systematically for *P. truncatus* in farmer stores. If policy-makers, faced with the problem of how to control *P. truncatus*, must choose between (i) implementing biological control and (ii) educating extension service and farmers on the need-based use of insecticides, the latter strategy would be the best investment.

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