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The sugarcane borer *Diatraea saccharalis* (Fabr.) (Lep., Crambidae) and its parasitoids: a synchrony approach to spatial and temporal dynamics

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Abstract: A data set on *Diatraea saccharalis* and its parasitoids, *Cotesia flavipes* and tachinid flies, was analysed at five spatial scales – sugarcane mill, region, intermediary, farm and zone – to determine the role of spatial scale in synchrony patterns, and on temporal population variability. To analyse synchrony patterns, only the three highest spatial scales were considered, but for temporal population variability, all spatial scales were adopted. The synchrony–distance relationship revealed complex spatial structures depending on both species and spatial scale. Temporal population variability [SD $\log(x + 1)$] levels were highest at the smallest spatial scales although, in the majority of the cases, temporal variability was inversely dependent on sample size. All the species studied, with a few exceptions, presented spatial synchrony independent of spatial scale. The tachinid flies exhibited stronger synchrony dynamics than *D. saccharalis* and *C. flavipes* in all spatial scales with the latter displaying the weakest synchrony levels, except when mill spatial scales were compared. In some cases spatial synchrony may at first decay and then increase with distance, but the presence of such patterns can change depending on the spatial scale adopted.

Key words: *Cotesia flavipes*, *Diatraea saccharalis*, spatial synchrony, tachinid flies, temporal variability

1 Introduction

Ecologists have always been interested in population fluctuations, focusing primarily on population cycles (Elton and Nicholson, 1942; Korpimäki and Krebs, 1996; Kendall et al., 1998, 1999). There has been growing interest in understanding the mechanisms responsible for these cycles. Early researchers assumed that population cycles would be responsible for synchrony (Royama, 1992). However, Moran (1953) dismissed the need for a single causal hypothesis and pointed out that, if two populations had the same density-dependent structure, then correlated density-independent factors would bring population fluctuations into synchrony. This is known as the 'Moran effect' (Royama, 1992).

Spatial population synchrony, or spatial covariation, has received particular attention and it has shown that synchrony in animal and vegetal populations is a frequent phenomenon in a wide range of taxa in nature (Lindén, 1988; Pollard, 1991; Thomas, 1991; Hanski and Woiwod, 1993; Ranta et al., 1995, 1997a; Sutcliffe et al., 1996). Curiously, it is not the fact that there is synchrony in nature that has interested ecologists, but its pattern. A number of explanations have been put forward to explain such widely variable patterns. These include processes such as dispersion (and migration), regionally correlated climatic variables and mobile natural enemies (Ruxton and Doebeli, 1996; Ranta et al., 1998; Lloyd and May, 1999). Research on population synchrony has reached an interesting point, where both theory and statistical methods have guided new empirical directions to assess causal processes (Bjørnstad et al., 1999; Ripa, 2000). Some of these causal processes have been attributed to dispersion and migration. These conclusions come from new theoretical and empirical studies based on the fact that the degree of synchrony decreases with distance (Ranta et al., 1998; Koenig, 1999). If synchrony is not correlated with dispersal distance, it suggests that environmental factors can have an important influence on population synchrony (Paradis et al., 1999). Kendall et al. (2000) developed a spatially structured population model showing that dispersal and environmental correlation need to be considered together as explanations for observed population synchrony patterns.

Empirical studies may fail to detect synchrony dynamics, if the spatial scale used is inappropriate. Several theoretical and empirical studies have attempted to address these questions (Sutcliffe et al., 1996; Heino et al., 1997; Paradis et al., 1999).

Another interesting question is the effect of spatial covariance on extinction risks for local and global

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populations (metapopulation approach). Some theoretical studies have argued that asynchronous local populations have smaller global extinction risks than the synchronous local ones, and hence are of particular concern in conservation (Hanski, 1999; Hudson and Cattadori, 1999). The same features that cause concern to conservationists are an aid for those attempting to control pest outbreaks. The spatio-temporal effects of control intervention in these cases can lead to desynchronizing effects in local populations. For example, recent work on measles has shown that, although vaccination reduces the size of epidemics, it desynchronizes populations, promoting global persistence (Earn et al., 1998). In whooping cough the pattern is reversed, even considering pre- and post-vaccination effects (Rohani et al., 1999).

Diatraea saccharalis (Fabr.) is reported to be the most important sugarcane pest in Brazil, especially in the southeast region (Gallo et al., 1988). As *D. saccharalis* larvae live inside the sugarcane stem, control with pesticides in sugarcane mills has been deemed inappropriate. Biological control of *D. saccharalis* began in 1949 when the 'Amazon fly' *Lydella minense* (Towns.) (Dipt., Tachinidae) was reared and released in sugarcane fields. Another tachinid fly, *Paratheresia claripalpis* (Wulp.), native to South America, was studied in 1942, and in 1950, a third Tachinidae species, *Lyxophaga diatraea* (Towns.) was introduced from Cuba (Gallo, 1980). These three tachinids were reared in sugarcane mill laboratories and intensively released into sugarcane fields. During the 1980s and early 1990s, the most common tachinids reared were *L. minense* and *P. claripalpis*. During 1971–73, the Hymenoptera *Cotesia flavipes* (Cam.) (Hym., Braconidae) was introduced from Trinidad to improve the biocontrol of *D. saccharalis*. However, only in 1974, did mass-production and systematic release of this parasitoid begin (Gallo et al., 1988). In 1978, new *C. flavipes* strains were introduced from India and Pakistan (Macedo, 1978). This is now considered the main biological control agent for *D. saccharalis*, although it has not been entirely efficient and new biocontrol alternatives have been proposed, such as *Trichogramma galloi* (Zucchi) (Hym., Trichogrammatidae) (Botelho et al., 1999).

Studying biological parameters and intraspecific competition between *L. minense* and *P. claripalpis* using *D. saccharalis* as a host under laboratory conditions, Almeida et al. (1986) observed that the mean period for the stages of larva, pupae and adult for *L. minense* was 8.49, 9.27 and 7.16 days, respectively. The mean period for the stages of larva, pupae and adult for *P. claripalpis* was 10.48, 17.06 and 5.08 days, respectively. The mean number of maggots obtained per female for *P. claripalpis* was 374.46 ± 22.61 and 438.86 ± 22.35 for *L. minense*. These authors also observed that the intraspecific competition was stronger for *P. claripalpis* than for *L. minense*. Wiedenmann et al. (1992) observed that under 24 ± 2°C, 50 and 60% of relative humidity, and 14 h of light, the development of *C. flavipes*, from eggs to larval emergence, was 13.8 ± 0.4 days, and 6.6 ± 0.2 days for pupal development. These authors also observed that 4 and 44 h were the minimum and maximum adult longevity of *C. flavipes*, respectively, with survival of 23.8 ± 0.6 h. The mean number of adult *C. flavipes* that emerges from *D. saccharalis* hosts (Gallo et al., 1988) is 50, although this pattern of parasitoid emergence is much variable.

Wiedenmann and Smith (1993) observed the near-linear functional response of *C. flavipes* at low densities of the host *D. saccharalis* in field cages containing corn plants. Although the attack rates were low, this parasitoid was able to find and attack *D. saccharalis* even at the lowest host densities. According to predation theory, these authors argued that the linear response cannot deter host populations once economic densities are exceeded. However, if *C. flavipes* successfully attacks *D. saccharalis* when the host is at low densities, the parasitoid is affecting the latent phase of the host population growth.

The aims of this study were to answer the following questions: Does the form of the synchrony–distance relationship depend on spatial scale? Does spatial scale affect the estimation of temporal population variability? Are spatial synchrony levels related to temporal population variability? In order to understand the causes of synchrony in natural systems, we analysed a data set on *D. saccharalis* and its parasitoids, from a biological control programme in sugarcane fields in the State of São Paulo, Brazil.

2 Methods

2.1 Sampling scheme

In order to control production, sugarcane mill managers concentrate on small areas. These areas are known as 'fields' and 'zones' (contiguous fields). *Diatraea saccharalis* and its parasitoids were sampled at the field level. Almost every day, a group of about five workers went to the sugarcane fields to sample *D. saccharalis* populations and release parasitoids. Currently, at the sugarcane mills studied here, only *C. flavipes* is released. One person for each field walked between rows looking for damaged plants. When they found damaged plants, they removed larvae and put them in plastic dishes with artificial diet. These were taken to the laboratory where *D. saccharalis* larvae and emerged parasitoids were recorded to estimate the percentage of parasitism. Samples were recorded in man-hours. Although samples were taken monthly, they were often not temporally (at the smallest spatial scales) or spatially continuous. Thus, some areas had more samples than others, but the data set showed temporal continuity when analysed at the mill level. This sampling scheme has recently been changed and the description is only valid for the length of time this sampling programme was in use, as described in table 1.

The information available from this data set are: (1) Number of *D. saccharalis* larvae and their parasitoids in each sample; (2) sugarcane varieties at sample time; and (3) sugarcane plant age by number of sugarcane cuts (first cultivation, first cut, second cut, etc. monthly age was only available from São João).

As *D. saccharalis* larval stages susceptible to parasites were present throughout the year, the data set was analysed monthly. When the same field (São João Mill) or zone (Barra

Table 1. *Sugarcane mill basic information*

	Mills	
	Barra sugar mill	São João sugar mill
Data set information dates	03/1984 to 03/1997	05/1982 to 12/1996
Location	São Paulo state, Brazil Latitude: 22°28′42″S Longitude: 48°28′42″W	São Paulo state, Brazil Latitude: 22°25′30″S Longitude: 47°21′34″W
Months with no data (no samples)	01–09/1985	07/1982, 07/1985, 08/1989, 04–06/1990, 09–10/1990, 05/1992, 06/1993, 08/1993, 10–12/1994[1]
Smallest spatial level	Zone (contiguous fields)[2]	Field[2]
Number of zones/fields sampled per month	Maximum: 49; minimum: 7	Maximum: 113; minimum: 2

[1] 1995 and 1996 were completely eliminated from the analysis for presenting a different sample scheme and outlying data, respectively.
[2] Field and zone areas were variable, ranging from 10 to 30 ha and 20 to 60 ha, respectively.

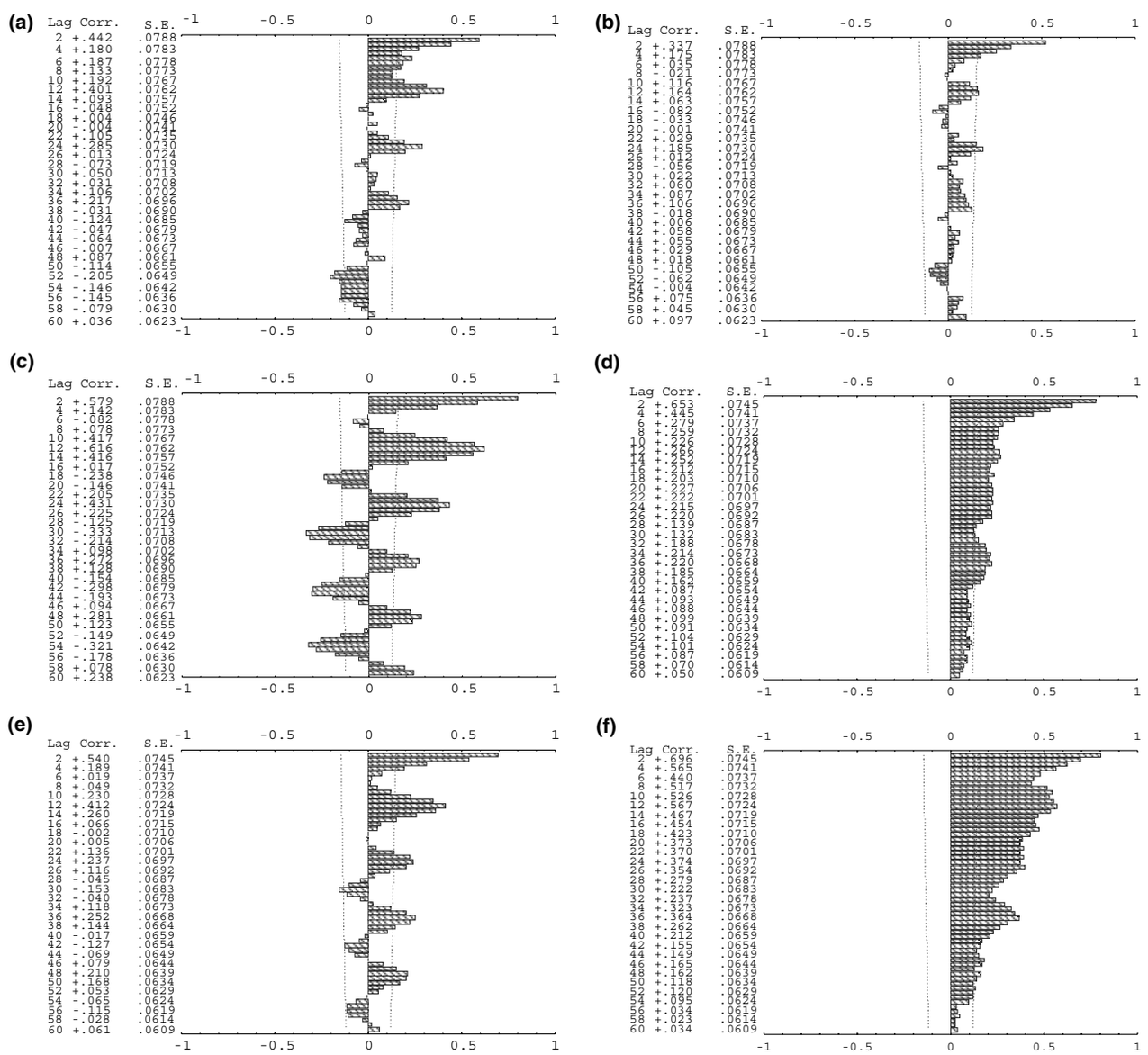

Fig. 1. *Correlograms for* D. saccharalis *(a, d),* C. flavipes *(b, e) and the tachinid (c, f) populations in the Barra Mill and São João Mill with 60 time lags. One time lag corresponds to 1 month. The dotted line in the correlograms show the threshold below which r values are not significant. (a), (b), (c) = Barra mill; (d), (e), (f) = São João mill*

Mill) was sampled more than once per month, only one of the samples was randomly chosen.

2.2 Detecting cycles, measure of synchrony and synchrony–distance relationship

Both of the sugarcane 'Mills', São João and Barra, were subdivided up into the spatial resolution levels. Each mill was subdivided into four areas of similar spatial and sampling dimension denominated 'regional sites'; they were again subdivided into seven areas denominated 'intermediary sites'. The spatial resolution was reduced still further into six farms (groups of zones or fields). Five zones (groups of fields) were chosen which presented longer temporal continuity. These smallest resolution levels were impractical for computing cross-correlation analysis (expressive temporal discontinuity), but were adopted for computing temporal variability.

The log of the species population density was adopted [$\log(xt + 1)$, where xt is the density estimated at month t], because it provided a more accurate normal distribution than raw data. As the areas covered thousands of hectares and the number of samples per month were variable, a density average was calculated for each month. This method was adopted at each spatial scale except for the zone level at the Barra Mill. Tachinid flies were not analysed separately because of frequent zero values. Thus, the term 'species' refers to the *D. saccharalis*, *C. flavipes* and tachinid flies (*L. minense* density + *P. claripalpis* density before data transformation).

Autocorrelation analysis (Royama, 1992) was used to detect population cycles and applied to each species for both mills. Each 'time lag' corresponds to 1 month (a maximum of 60 time lags was adopted here).

As a measure of population dynamics synchrony, 'zero-lag cross-correlation' coefficients were computed between all pairs of sites for each species separately. The number of pairs varied with spatial scale: one for the mills (two mills); six for the regional sites (four at each mill); and 21 pairs for the intermediary sites (seven at each mill). Cross-correlation coefficients were plotted against the distance between each pair of sites. Finally when synchrony was plotted against distance, a Pearson correlation coefficient (Sokal and Rohlf, 1995), or when appropriate, a second-order regression, was calculated for each species and spatial scale. The distance between any pair of sites was calculated as the geographical distance between site centres. These distances were calculated from available maps.

2.3 Population variability and degrees of synchrony

Standard deviation [SD $\log(x + 1)$] of population abundance was calculated at different spatial scales. Average of population variability index was calculated for each species and spatial scale (except for the mills because there was only one value); this gave one value representing temporal variability for each species at each spatial scale. To verify if this measure of temporal variability was subject to bias (McArdle et al., 1990), a multiple regression was computed (Sokal and Rohlf, 1995) taking SD [$\log(x + 1)$] as the dependent variable, and sample size and mean abundance as independent variables.

To study species synchrony, and if this varied between spatial scales, average 'zero-lag cross-correlation' coefficients were calculated and correlation coefficient homogeneity was tested (Sokal and Rohlf, 1995). When the cross-correlation coefficients were homogeneous a new coefficient was estimated representing the scale and species in question.

3 Results

Where autocorrelation analysis was calculated some obvious annual cycles appeared (fig. 1) with exception to *D. saccharalis* and the tachinids in the São João Mill (fig. 1d,f). The tachinid populations presented significantly strong monthly autocorrelation coefficients (fig. 1c,f).

Most of the cross-correlation coefficients were significant (table 2). The lowest significant levels were obtained for *D. saccharalis* (76.2%) and *C. flavipes* (71.4%) at the Barra Mill intermediary level (table 2). In the São João Mill, all cross-correlations were significant independent of species and spatial scale (table 2). Figure 2a, b shows a comparison of cross-correlation coefficients for respective species and spatial scales. Even when 'zero-lag cross-correlation' coefficients were computed between mills (125 km apart), these were significant (fig. 2a,b). Tachinids exhibited stronger synchrony dynamics than *D. saccharalis* or *C. flavipes* at any spatial scale. *Cotesia flavipes* showed the weakest synchronies, except at mill level where *D. saccharalis* was the smallest (fig. 2a,b).

The highest levels of temporal variability [SD $\log(x + 1)$] were obtained at the smallest spatial scales, mainly when compared with the mills (fig. 2c, d). Multiple regression analysis showed that the vast majority of analyses were not dependent on either mean abundance or sample size within each

Table 2. *Zero-lag cross-correlation coefficients for each species at the different spatial scales studied. Each cross-correlation coefficient represents the spatial synchrony for its respective spatial scale*

	Species		
	D. saccharalis	*C. flavipes*	Tachinids
Barra mill			
Region level			
CC (r)	0.39	0.25	0.49
χ^2	1.90	3.29	2.55
Significance (%)	100	83.3	100
Intermediary level			
CC (r)	0.25	0.23	0.36
χ^2	10.47	4.73	19.38
Significance (%)	76.2	71.4	90.5
São João mill			
Region level			
CC (r)	0.50	0.44	0.67
χ^2	3.08	8.38	6.59
Significance (%)	100	100	100
Intermediary level			
CC (r)	0.46	0.38	0.65*
χ^2	14.05	24.30	23.60
Significance (%)	100	100	100

CC (r), cross-correlation coefficient according to the test of homogeneity between correlation coefficients (Sokal and Rohlf, 1995); χ^2, chi-square values (5 d.f. to region and 20 to intermediary level); Significance (%), percentage of significant zero-lag cross-correlation coefficients ($P < 0.05$).

* This value was calculated eliminating the two highest cross-correlation coefficients (18 d.f.). All χ^2 values were not significant ($P > 0.05$).

spatial resolution level (table 3). Consequently, any bias should be small (McArdle et al., 1990). However, when the same analysis was performed across spatial scales, temporal variability was significantly inversely dependent on sample size, with the exception of *D. saccharalis* at Barra and *C. flavipes* at São João (table 4). In these two last cases, temporal variability still increased inversely to cross-correlation as spatial scale decreased (fig. 3). The largest temporal variability was detected at all spatial scales in *C. flavipes* at Barra and in tachinids at São João (fig. 2c,d).

The synchrony–distance relationship revealed different spatial structures depending on species and spatial scale. When synchrony was plotted against distance, two kinds of interesting patterns became apparent: (1) linear decrease with distance (fig. 4a–c), and (2) a U-shape synchrony against distance (for second-order regression, $F = 21.71$; $r^2 = 0.936$; $P = 0.016$) (fig. 4a). Considering only the intermediary level in São João Mill, synchrony did not increase or decrease with distance for any species compared (fig. 4d).

Although this studied data set is not ideal, some aspects encouraged us to continue with the analysis: (1) the highest synchrony levels were achieved by tachinids in both mills at all spatial scales (table 2); (2) *Cotesia flavipes* presented the weakest synchrony levels in both mills at all spatial scales (table 2). We should remember that all species studied here were sampled at the same time and from the same patches. These comparative aspects seem suitable to support the results found here, reinforcing their validity and reducing the undesirable effects concerned with structural problems in the data.

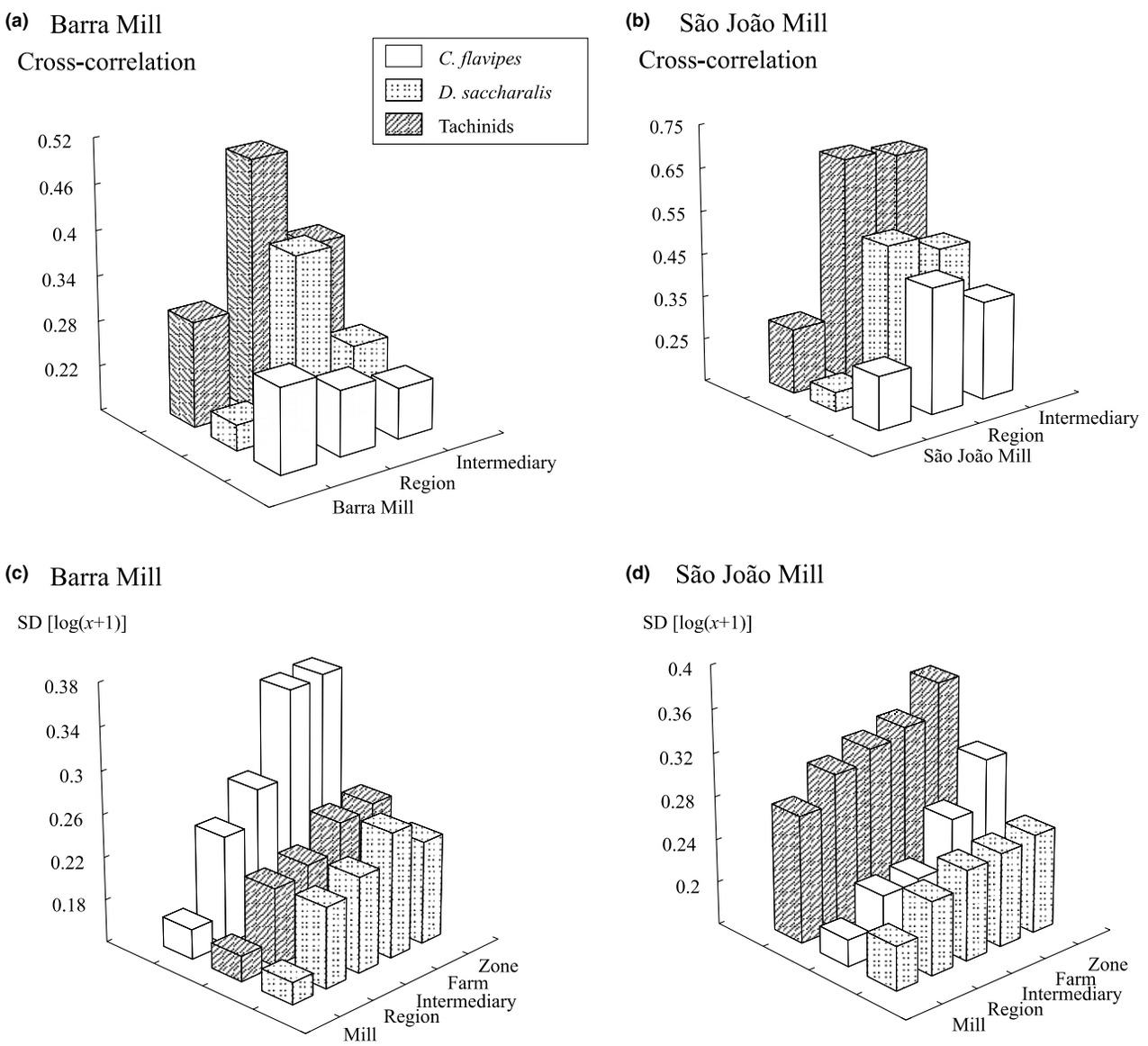

Fig. 2. *Cross-correlation and SD [log(x + 1)] coefficients at three and five spatial scales, respectively. Each bar represents an estimated cross-correlation coefficient [(a), (b)] or an averaged SD [log(x + 1)] index [(c), (d)] of all sites at each spatial scale. The cross-correlation coefficients for the two mills were the same as there was only one pair of populations for each species at this spatial level. (a), (c) Barra mill; (b), (d) São João mill*

Table 3. *Linear multiple regression of temporal variability SD [log(x + 1)] for* D. saccharalis *and its parasitoids. This table gives the t-values of the regression slopes and their significance to each spatial scale in the respective mills*

	D. saccharalis		*C. flavipes*		Tachinids	
	Mean abundance	Sample size	Mean abundance	Sample size	Mean abundance	Sample size
Barra mill						
Zone level (5)						
t	−8.834*	4.812*	0.845	−0.500	4.904*	0.914
P	0.010	0.041	0.487	0.667	0.039	0.457
Farm level (6)						
t	0.425	2.294	1.125	−0.857	8.235*	0.466
P	0.700	0.106	0.342	0.454	0.004	0.673
Intermediary level (7)						
t	−0.276	−1.740	8.854*	−5.717*	1.591	−0.178
P	0.796	0.157	0.001	0.005	0.187	0.868
Region level (4)						
t	−1.659	−3.276	1.802	0.185	10.151	2.083
P	0.345	0.189	0.323	0.884	0.063	0.285
São João mill						
Zone level (5)						
t	−0.329	−0.005	0.129	−0.389	−3.500	−3.215
P	0.774	0.997	0.909	0.735	0.073	0.085
Farm level (6)						
t	−0.559	−0.536	0.683	−0.019	0.711	1.786
P	0.615	0.629	0.543	0.986	0.528	0.172
Intermediary level (7)						
t	−0.697	−0.888	3.678	0.061	−1.115	−0.834
id P	0.524	0.425	0.021*	0.955	0.327	0.451
Region level (4)						
t	−0.204	−0.136	13.704*	2.789	−0.820	0.303
P	0.872	0.914	0.046	0.219	0.563	0.813

* Significant regressions at $P < 0.05$.
The values in parenthesis represent the N values for regressions in each spatial scale.
As there were only two mills, analysis between them was not calculated.

Table 4. *Linear multiple regression of temporal variability SD [log(x + 1)] for* D. saccharalis *and its parasitoids. This table gives the t-values of the regression slopes and their significance across spatial scales in the respective mills. The mean values of temporal variability, abundance and sample size were calculated to leave only one value for each species and spatial scale*

	D. saccharalis		*C. flavipes*		Tachinids	
	Mean abundance	Sample size	Mean abundance	Sample size	Mean abundance	Sample size
Barra mill						
t	−1.377	−2.762	−0.626	−4.306*	0.712	−4.327*
P	0.302	0.110	0.595	0.050	0.550	0.049
São João mill						
t	−3.650	−8.909*	0.823	−2.246	−1.028	−4.864*
P	0.068	0.012	0.497	0.154	0.412	0.040

* Significant values at $P < 0.05$.
N was 5 for all regressions.

4 Discussion

We have empirical evidences suggesting that very different types of dynamics allow populations to exhibit synchrony. Populations showing both strong and weak cycles were synchronous in this study. This is in agreement with other studies (Ranta et al., 1995, 1997a,b), but the different synchrony–distance patterns shown here deserve attention because their shapes are strictly related to spatial scale. This reinforces the idea that spatial synchrony cannot be completely understood independent of spatial scale. A simple change in the spatial scale revealed different synchrony–distance patterns. As an example, in the Barra Mill, *C. flavipes* exhibited both a U-shape synchrony–distance pattern and a linear decreasing relationship depending on the scale adopted (fig. 4a, c). One parasitoid species could be influencing the pattern of synchrony exhibited by another as a result of competition for the same host; there is evidence of competition between *C. flavipes* and *L. minense* (one of the

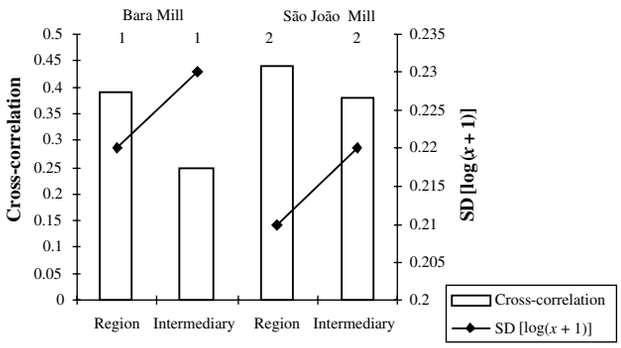

Fig. 3. *Comparison between cross-correlation coefficients and the temporal variability index SD [log(x + 1)] at two spatial scales. When the spatial scale decreases, a decrease in the cross-correlation coefficient was followed by an increase in the temporal variability. (1)* D. saccharalis *at the Barra mill; (2)* C. flavipes *at the São João mill*

tachinid species studied here) in the laboratory (Weir and Sagarzazu, 1998). Thus, competition could be responsible for the spatio-temporal pattern exhibited by the parasitoid species. Although not tested here, we are convinced that multi-species synchrony studies can reveal complex spatial patterns.

Hanski and Woiwod (1993) have argued that regional level synchrony is caused by weather-related environmental stochasticity, which could decrease metapopulation persistence by producing correlated local extinctions. However, samples coming from large areas can average out the small-scale variability leading to a misinterpretation of the extent to which regionally correlated weather patterns produce correlated population fluctuations (Sutcliffe et al., 1996). The decrease in SD [log(x + 1)] with increasing sample area (fig. 2) shows how strongly sampling scale affects the estimation of population variability. Such a decrease in temporal variability may be responsible for the increase in synchrony with the spatial scale.

Spatial synchrony was present in most pairs compared at all spatial scales, even when synchrony decreased with distance. Our study supports the hypothesis that at larger spatial scales (tens and hundreds of kilometres which would average out local heterogeneity), populations would appear to fluctuate in synchrony because of correlations in climatic variations (Thomas, 1991). As density dependence effects were not studied, some unknown patterns may still appear. For example, in the São João Mill, tachinids and *D. saccharalis* had a significant strong monthly autocorrelation index, although they did not exhibit obvious annual cycles (see the Bartlett lines in fig. 1 and the 'zero-lag cross-correlation' values in table 2). Density dependence imposed by the tachinids on the host population could be responsible for the lack of annual cycles found for *D. saccharalis*.

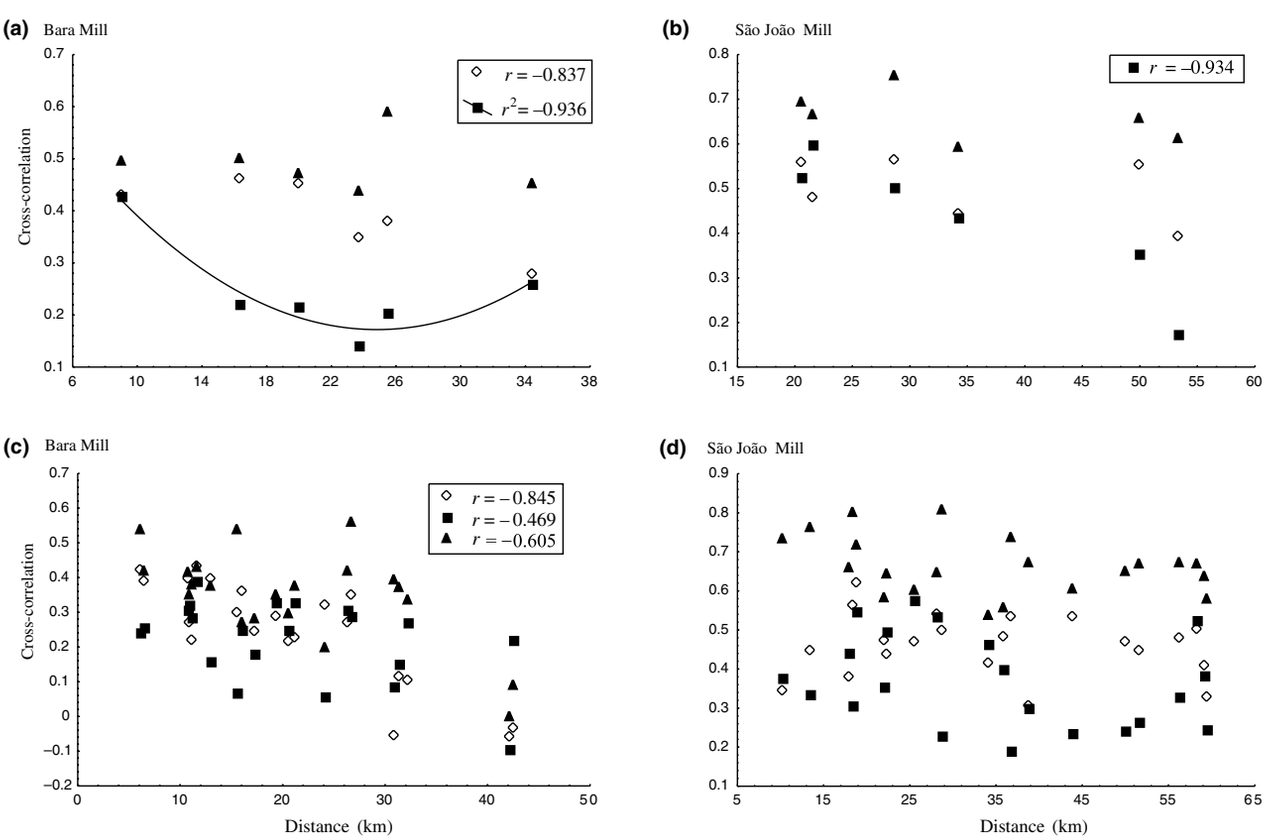

Fig. 4. *The relationship between the dynamics of* D. saccharalis *(◇),* C. flavipes *(■) and tachinid (▲) populations and the distances, for regional (a, b) and intermediary (c, d) sites. Only significant correlation coefficients (Pearson) were shown ($P < 0.05$). In (a), a line was drawn in second-order synchrony–distance relationship with r^2 value indicated ($F = 21.71$ for second-order regression; $P = 0.016$), represented by the equation, $y = 0.794 - 0.050x + 0.001x^2$. (a), (c) Barra mill;(b), (d) São João mill*

The tachinids are native to South America; this could explain the high synchrony values when compared with *C. flavipes*, introduced from Pakistan (Gallo et al., 1988). *Cotesia flavipes* populations would be more affected by regional environmental stochasticity than the tachinids. We have no evidence that parasitoids generate spatial asynchrony in regional host populations, as our results were synchronous at all spatial scales; small data sets at small spatial scales could be responsible for this.

Bottom-up forces, such as food resource quality, and regional weather conditions or environmental stochasticity could be responsible for different patterns at different mills, even when the same species are involved. One difficulty with some of the analysis presented here is that dispersal rates and new habitat colonization rates of these species are poorly or not known (Hall and Green, 1986; Rodriguez-del-Bosque et al., 1990). This kind of information would be valuable, although the distances examined here cover tens of kilometres. The dispersion range of tachinids should be higher than *C. flavipes*; this would explain their higher synchrony levels. Another explanation is that they may be more efficient than *C. flavipes* at finding *D. saccharalis*, maintaining synchrony even when it is scarce in some regions. Although *C. flavipes* has been more intensively released into the sugarcane fields studied here (Botelho, 1992; Macedo et al., 1993), tachinids presented the highest levels of synchrony.

As all species were in synchrony when compared at the Mill level, synchronized general weather conditions may be the reason; this is difficult to corroborate because of the scarcity of weather stations in the area. *Diatraea saccharalis* showed the lowest level of synchrony when compared between mills (fig. 2). The lack of synchronized cycles could explain the small spatial covariance, and the decreasing temporal population trend could affect the significance in the analysis.

The possibility that spatial synchrony may at first decay and then increase with distance, has been previously reported by Ranta et al. (1997a). We have demonstrated that the presence of such a pattern can change depending on spatial scale. The larger spatial scales often obscure the more complex spatial patterns present in smaller ones; however, the opposite can also be true. More studies and experimental designs involving spatial dynamics with more complete data sets from this biological control programme may reveal clearer patterns.

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References

Almeida, L. C. de; Araújo, J. R. de; Botelho, P. S. M.; Degaspari, N.; Araújo, S. M. S. S. de, 1986: Biologia e competição intra-específica de taquinídeos sobre o hospedeiro, *Diatraea saccharalis* em condições de laboratório. Pesq. Agropec. Bras. **21,** 1009–1014.

Bjørnstad, O. N.; Ims, R. A.; Lambin, X., 1999: Spatial population dynamics: analysing patterns and processes of population synchrony. Trends Ecol. Evol. **14,** 427–432.

Botelho, P. S. M., 1992: Quinze anos de controle biológico de *Diatraea saccharalis* utilizando parasitóides. Pesq. Agropec. Bras. **27,** 255–262.

Botelho, P. S. M.; Parra, J. R. P.; Neto, J. F. C.; Oliveira, C. P. B., 1999: Associação do parasitóide de ovos *Trichogramma galloi* Zucchi (Hymenoptera: Trichogrammatidae) e do parasitóide larval *Cotesia flavipes* (Cam.) (Hymenoptera: Braconidae) no controle de *Diatraea saccharalis*, (Fabr.) (Lepidoptera: Crambidae) em cana-de-açúcar. Ann. Soc. Entomol. Brasil **28,** 491–496.

Earn, D. J. D.; Rohani, P.; Grenfell, B. T., 1998: Persistence, chaos and synchrony in ecology and epidemiology. Proc. R. Soc. Lond. B **265,** 7–10.

Elton, C.; Nicholson, M., 1942: The ten-year cycle in numbers of the Lynx in Canada. J. An. Ecol. **11,** 215–244.

Gallo, D., 1980: Situação do controle biológico da broca da cana-de-açúcar no Brasil. An. Soc. Entomol. Brasil **9,** 303–308.

Gallo, D.; Nakano, O.; Silveira-Neto, S.; Carvalho, R. P. L.; Batista, G. C. de; Berti-Filho, E.; Parra, J. R. P.; Zucchi, R. A.; Alves, S. B..; Vendramim, J. D., 1988: Manual de Entomologia Agrícola. São Paulo: Editora Agronômica Ceres.

Hall, D. G.; Green, R. H., 1986: Sampling for the sugarcane borer (Lepidoptera: Pyralidae) in sugarcane. J. Econ. Entomol. **79,** 813–816.

Hanski, I., 1999: Metapopulation Ecology. Oxford: Oxford University Press.

Hanski, I.; Woiwod, I. P., 1993: Spatial synchrony in the dynamics of moth and aphid populations. J. An. Ecol. **62,** 656–668.

Heino, M.; Kaitala, V.; Ranta, E.; Lindström, J., 1997: Synchronous dynamics and rates of extinction in spatially structured populations. Proc. R. Soc. Lond. B **264,** 481–486.

Hudson, P. J.; Cattadori, I. M., 1999: The Moran effect: a cause of population synchrony. Trends Ecol. Evol. **14,** 1–2.

Kendall, B. E.; Prendergast, J.; Bjørnstad, O. N., 1998: The macroecology of population dynamics: taxonomic and biogeographic patterns in population cycles. Ecol. Lett. **1,** 160–164.

Kendall, B. E.; Briggs, C. J.; Murdoch, W. W.; Turchin, P.; Ellner, S. P.; McCauley, E.; Nisbet, R. M.; Wood, S. N., 1999: Why do populations cycle? A synthesis of statistical and mechanistic modelling approaches. Ecology **80,** 1789–1805.

Kendall, B. E.; Bjørnstad, O. N.; Bascompte, J.; Keitt, T. H.; Fagan, W. F., 2000: Dispersal, environmental correlation, and spatial synchrony in population dynamics. Am. Nat. **155,** 628–636.

Koenig, W. D., 1999: Spatial autocorrelation of ecological phenomena. Trends Ecol. Evol. **14,** 22–26.

Korpimäki, E.; Krebs, C. J., 1996: Predation and population cycles of small mammals. BioScience **46,** 754–764.

Lindén, H., 1988: Latitudinal gradients in predator–prey interactions, cyclicity and synchronism in voles and small game populations in Finland. Oikos **52,** 341–349.

Lloyd, A. L.; May, R. M., 1999: Synchronicity, chaos and population cycles: spatial coherence in an uncertain world. Trends Ecol. Evol. **14,** 417–418.

Macedo, N., 1978: New strain of *Apanteles flavipes* was imported to increase its adaptative potential in the Southern Brazil. Entomol. News **4,** 11–12.

Macedo, N.; Araújo, J. R.; Botelho, P. S. M., 1993: Sixteen years of biological control of *Diatraea saccharalis* (Fabr.) (Lepidoptera: Pyralidae) by *Cotesia flavipes* (Cam.) (Hymenoptera: Braconidae), in the state of São Paulo, Brazil. An. Soc. Entomol. Brasil **22,** 441–448.

McArdle, B. H.; Gaston, K. J.; Lawton, J. H., 1990: Variation in the size of animal populations: patterns, problems and artefacts. J. An. Ecol. **53,** 439–454.

Moran, P. A. P., 1953: The statistical analysis of the canadian lynx cycle II. Synchronization and meteorology. Aust. J. Zool. **1,** 291–298.

Paradis, E.; Baillie, S. R.; Sutherland, W. J.; Gregory, R. D., 1999: Dispersal and spatial scale affect synchrony in spatial population dynamics. Ecol. Lett **2,** 114–120.

Pollard, E., 1991: Synchrony of population fluctuations: the dominant influence of widespread factors on local butterfly populations. Oikos **60,** 7–10.

Ranta, E.; Kaitala, V.; Lindström, J.; Lindén, H., 1995: Synchrony in population dynamics. Proc. R. Soc. Lond. B **262,** 113–118.

Ranta, E.; Kaitala, V.; Lindström, J., 1997a: Dynamics of Canadian lynx populations in space and time. Ecography **20,** 454–460.

Ranta, E.; Kaitala, V.; Lundberg, P., 1997b: The spatial dimension in population fluctuations. Science **278,** 1621–1623.

Ranta, E.; Kaitala, V.; Lundberg, P., 1998: Population variability in space and time: the dynamics of synchronous population fluctuations. Oikos **83,** 376–382.

Ripa, J., 2000: Analysing the Moran effect and dispersal: their significance and interaction in synchronous population dynamics. Oikos **90,** 175–187.

Rodrigues-del-Bosque, L. A.; Smith J. W. Jr ; Browning, H. W., 1990: Spatial dispersion patterns of *Diatraea lineolata*, *Diatraea saccharalis*, and *Eoreuma loftini* on corn. Southwest. Entomol. **15,** 291–299.

Rohani, P.; Earn, D. J. D.; Grenfell, B. T., 1999: Opposite patterns of synchrony in sympatric disease metapopulations. Science **286,** 968–971.

Royama, T., 1992: Analytical Population Dynamics. London: Chapman & Hall.

Ruxton, G. D.; Doebeli, M., 1996: Spatial self-organization and persistence of transients in a metapopulation model. Proc. R. Soc. Lond. B **263,** 1153–1158.

Sokal, R. R.; Rohlf, F. J., 1995: Biometry. New York: W. H. Freeman and Company.

Sutcliffe, O. L.; Thomas, C. D.; Moss, D., 1996: Spatial synchrony and asynchrony in butterfly population dynamics. J. An. Ecol. **65,** 85–95.

Thomas, C., 1991: Spatial and temporal variability in a butterfly population. Oecologia **87,** 577–580.

Weir, E. H.; Sagarzazu, L., 1998: Interspecific competition between *Metagonystilum minense* (Diptera: Tachinid) and *Cotesia flavipes* (Hymenoptera: Braconidae) parasitoids of sugarcane borers (*Diatraea* spp., Lepidoptera: Pyralidae). Rev. Biol. Trop. **46,** 1135–1139.

Wiedenmann, R. N.; Smith, J. W. Jr, 1993: Functional response of the parasite *Cotesia flavipes* (Hymenoptera: Braconidae) at low densities of the host *Diatraea saccharalis* (Lepidoptera: Pyralidae). Environ. Entomol. **22,** 849–858.

Wiedenmann, R. N.; Smith, J. W. Jr; Darnell, P. O., 1992: Laboratory rearing and biology of the parasite *Cotesia flavipes* (Hymenoptera: Braconidae) using *Diatraea saccharalis* (Lepidoptera: Pyralidae) as a host. Environ. Entomol. **21,** 1160–1167.

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