

# Spatial dynamics and cross-correlation in a transient predator–prey system

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## Summary

1. We examined spatiotemporal data in a transient, seasonal system involving a specialist predatory beetle, *Carcinops pumilio* (Erichson), and its prey, larval *Musca domestica* L.

2. Prior to beetle colonization, larval fly populations were highly spatially structured, but as adult predatory beetles immigrated and colonized the field, the beetles became increasingly clustered at local spatial scales, causing spatial decorrelation in the dynamics of their prey. Larval flies appeared to regain local clustering as beetle abundance approached a carrying capacity with the prey population.

3. During exponential population growth, beetles were generally strongly negatively cross-correlated with their prey at local spatial scales.

4. We were able to simulate these spatially–extended interactions in a predator–prey coupled map lattice model. We used this model to investigate the effects of global and local prey reproduction, in the presence and absence of global stochasticity, on predator and prey spatial structuring and cross-correlation.

5. The work shows in a uniquely detailed fashion how the transition from eruptive pest abundance to regulation by a specialist predator is associated with a transition in spatial structure.

*Key-words:* coupled map lattice, interspecific covariance, nonparametric spatial covariance function, predator–prey interactions, spatiotemporal dynamics.

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## Introduction

The synchrony and spatial correlation of population dynamics has been widely debated since Elton's study on population cycles in the Canadian lynx (1924). Much attention has been placed on two important causes of synchrony: the Moran effect (i.e. regional abiotic stochasticity) and dispersal (Royama 1992; Ranta *et al.* 1997; Bjørnstad, Ims, & Lambin 1999). A number of studies have also focused on the role of trophic interactions on synchronization and, more generally, on spatial pattern formation (Ims & Steen 1990; Hassell, Comins, & May 1991; Bascompte & Solé 1995), and recent empirical studies support the notion that both synchronization and desynchronization can result from trophic interactions (Maron & Harrison 1997; Ims & Andreassen 2000; Bjørnstad *et al.* 2002). In

parallel, great theoretical stride has been made in studies of spatially extended consumer–resource systems (Hassel *et al.* 1991; Wilson & Hassell 1997; Wilson *et al.* 1999; Keeling, Wilson, & Pacala. 2000). Much of that work, however, focused on the stationary (asymptotic) dynamics that will have little relevance to highly seasonal or disturbed ecosystems. Hastings & Higgins (1994) furthermore argued that long-term dynamics might be irrelevant to understanding a system because stochastic disruptions are frequent relative to the return times of spatiotemporal system, and Hastings (2001) suggested that understanding the dynamics of transients can play a key role in understanding the structure of natural systems. Also, secular changes in host demography can defy the notion of stationarity (Grenfell, Bjørnstad, & Kappey 2001). Transient dynamics may thus be the rule rather than the exception.

Agricultural systems, most of which are relatively short-lived, involve seasonal reestablishment of the community and internal system changes from season-to-season. Also, control interventions targeting insect pest populations can be frequent, exacerbating the

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transience of the dynamics. Natural systems exhibit similar characteristics, in which communities may continuously re-establish themselves due to disturbances or phenology. In that context, studies of spatial structure and cross-correlation in transient populations of both insect pests and beneficial species would augment our understanding of their intricate relationship (Winder *et al.* 2001). This is a critical issue in agricultural systems since control tactics against insect pests are largely motivated by the potential for insecticide resistance (e.g. Alstad & Andow 1995), possible effects on nontarget organisms (e.g. Flexner, Lighthart, & Croft 1986), and concerns of food quality (e.g. Food Safety Act of 1990, Great Britain; Food Quality Protection Act of 1996, United States). We studied the spatiotemporal dynamics of a predator-prey system through the invasive phase of the predator. We describe the pattern of spatial aggregation (and segregation) of the prey and the predator through the spatial (cross-) correlation functions at several snapshots in time, and find a significant shift in spatial dynamics. The shift is consistent with an exploratory couple-map lattice model of the system.

## Materials and methods

### FIELD SITES AND SAMPLING REGIMES

Spatiotemporal abundance data of larval house flies, *M. domestica*, and a predatory beetle, *C. pumilio*, were collected from two poultry production facilities in Juniata and Lancaster Counties, Pennsylvania (Sites 1 and 2, respectively). *M. domestica* populations in accumulated hen manure can reach remarkable levels; for example, Tobin (1997) observed > 4000 third instars in 200 g samples during peak fly abundance. Not surprisingly, nuisance and public health problems are often associated with poultry operations. *C. pumilio* adults and larvae are naturally occurring and effective predators of fly eggs and early instars, and adult beetles, for example, can each consume > 50 eggs and immatures per day (Geden & Axtell 1988).

Temperatures inside facilities were maintained within the hen thermoneutral zone (20–24 °C) by fans located at evenly spaced intervals on both sides of the facility. The fans are primary ports of entry and egress for *M. domestica* and *C. pumilio*. At Site 1 (14 × 79 meters), we collected 108 samples per week for 8 weeks, and then biweekly for the next 8 weeks. Sampling at Site 1 began 5 days (25 November 1996) following manure removal, although clean-out was not complete and ~5% of the manure volume, accumulated over ~10 months, was left in the facility. For the duration of the sampling period (November–March), outside weather conditions in central Pennsylvania, whose monthly mean temperatures were < 5 °C, negated immigration. At Site 2 (16 × 160 m), we collected 162 samples per week for 10 weeks. Sampling began 90 days following manure clean-out on 3 April 1997. In

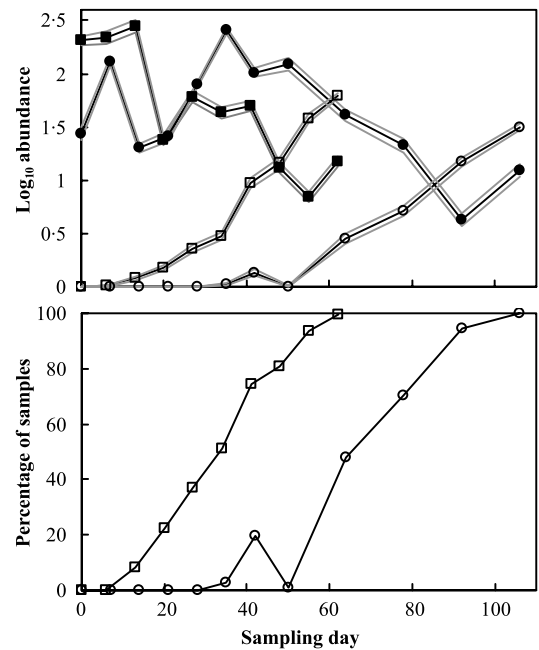


Fig. 1. Mean (and standard error lines) of abundance of larval flies (solid shapes) and adult beetles (open shapes) at Sites 1 and 2 (circles and squares, respectively) (top graph), and the corresponding percent of samples containing at least one *C. pumilio* adult (bottom graph).

this case, the manure was completely removed and the facility chemically sterilized following clean-out. Although the facilities differed in their clean-out schedules, predator population growth increased at statistically the same rate in both facilities (Tobin, Fleischer, & Pitts 1999; Fig. 1), and the initial sampling value of *C. pumilio* adults was 0 in both facilities. Samples were taken from spatially referenced locations and weighed, generally ranging from 100 to 200 g. Sub-samples were taken from each sample to measure moisture, and third instar *M. domestica* and adult *C. pumilio* were counted and expressed as  $\log_{10} + 1$  abundance per 200 g of dry manure matter.

At hen thermoneutral zone temperatures, the fly generation time is an average of 23 days, with roughly 13 days spent during the egg and larval stages (Lysyk & Axtell 1987). Developmental history of *C. pumilio* over a range of temperatures is not well known; however, Morgan, Patterson, & Weidhas (1983) reported that at 26 °C, average beetle generation times were approximately 40 days, with 22 days spent as egg and larvae. [For comparison, fly eggs and larvae require ~8 days to complete development at 26 °C (Lysyk & Axtell 1987)]. This system may thus go through many generations per year, and our temporal length of our study includes at least 2–4 fly and 1–2 beetle generations.

### PREDATOR-PREY SIMULATIONS

We used the discrete-time density-dependent Lotka–Volterra model as the basis for simulating predator-prey

dynamics of an idealized fly beetle system. Local predispersal dynamics of predator ( $P$ ) and prey ( $N$ ) abundance at time  $t$  and spatial location  $i$  were

$$N'_{i,t+1} = (N_{i,t}) \exp\{r(1 - N_{i,t}) - \theta_{i,t} - aP_{i,t}\}, \quad \text{eqn 1}$$

$$P'_{i,t+1} = (N_{i,t})\{1 - \exp(-aP_{i,t})\}, \quad \text{eqn 2}$$

where  $r$  is prey growth rate, and  $a$  is the predator-prey interaction strength that represents system productivity (Murray 1993). The primed vectors on the LHS represent predispersal local abundance (e.g. Hassell *et al.* 1991). Stochasticity (local and global) in prey dynamics were added according to

$$\theta_{i,t} = \{(1 - \rho_\theta)(U_{i,t}) + \rho_\theta V_t\}, \quad \text{eqn 3}$$

where  $\rho_\theta$  is the global correlation in the stochastic forcing. Both  $U_{i,t}$  and  $V_t$  were sequences of independent zero-mean Gaussian random variables with variance  $\sigma = 0.1$  (see Bjørnstad 2000). Environmental stochasticity was thus assumed to be temporally independent yet possibly spatially correlated. Because of the transient nature of our field system, we simulated 30 generations of spatiotemporal dynamics, realized according to Eqns (1–3) in  $30 \times 30$  coupled map lattices with absorbing boundaries. Prey and predator abundance were thus represented as  $900 \times 1$  matrices,  $N$  and  $P$ , respectively. Following local dynamics, half of the individuals were assumed to disperse to the four adjacent cells according to

$$N_{t+1} = D \times N'_t, \quad \text{eqn 4}$$

$$P_{t+1} = D \times P'_t, \quad \text{eqn 5}$$

where  $D$  is the  $900 \times 900$  dispersal matrix with 0.5 along the diagonal and 0.125 at entries linking neighbours, and  $\times$  denotes matrix multiplication. Initial prey was assumed to be randomly distributed at low abundance according to a uniform distribution from [0,1]. To investigate transient spatiotemporal dynamics following predator colonization, initial predator abundance was random over ~5% of the cells and zero elsewhere.

The rate of prey growth,  $r$ , was held fixed at 1.5, and was chosen to represent the reproductive capacity of *M. domestica*, in which females can each oviposit ~400 eggs (Fletcher, Axtell, & Stinner 1990), yet avoiding complex population dynamics (May 1974; Ruxton 1994). The predator-prey interaction parameter,  $a$ , was set at 1.5. Although the values of these parameters were somewhat arbitrarily chosen, we used them as a starting point for investigating transient, spatiotemporal predator-prey dynamics. [In accompanying studies (Tobin 2002; Tobin & Bjørnstad, unpublished), we detailed the consequence of nonlinear dynamics and the strength of the predator-prey interaction parameter on transient patterns in theoretical predator-

prey populations.] Because house fly adults are quite mobile, we further compared the effects of local and global prey reproduction on spatiotemporal dynamics. The former assumes that local prey populations influence local abundance at the next time step, while the latter accounts for the field-wide fly abundance to influence local dynamics due to fly dispersal capability. We thus simulated predator-prey dynamics with both local (eqns 1–2) and global [through substitution of  $N_{i,t}$  with a time-specific field-wide mean abundance in eqns 1–2] prey reproduction. We also simulated dynamics in the presence and absence of regional correlation in stochasticity (i.e.  $\rho_\theta = 0$  or 0.3; cf. eqn 3).

#### SPATIAL SIMULATION AND ESTIMATION

We simulated the coupled map lattice and conducted subsequent analyses using S-Plus (Mathsoft 2000) on a 250 CPU Linux cluster operated by the Center for Academic Computing – Numerically Intensive Computing Group of The Pennsylvania State University. Spatial structure in predator and prey populations, and their interspecific covariance, was estimated using a nonparametric spatial covariance function in S-Plus (Mathsoft 2000) on the PC-Cluster. This function uses a smoothing spline to measure the correlation between the density of pairs of samples over a continuous function of the distance separating samples, without assuming any functional form *a priori* (Bjørnstad & Bascompte 2001; Bjørnstad & Falck 2001). Let  $\delta_{ij}$  be the Euclidean distance between spatial locations  $i$  and  $j$ , and  $\rho_{ij,t}$  be the spatial correlation in prey or predator abundance,  $z_i$  and  $z_j$ , at the two locations at time  $t$ ,

$$\hat{\rho}_{ij,t} = \frac{(z_{i,t} - \bar{z}_t)(z_{j,t} - \bar{z}_t)}{\frac{1}{M} \sum_{a=1}^M (z_{a,t} - \bar{z}_t)^2}, \quad \text{eqn 6}$$

where  $M$  is the total number of local populations and  $\bar{z}_t$  represents the field-wide mean abundance at time  $t$ , so that the denominator represents the spatial variance of the population. Letting  $\rho_t(\delta)$  be the expected spatial correlation between abundances as a function of distance,  $\delta$ , the spatial covariance function can be estimated from nonparametric regression of  $\rho_{ij,t}$  against  $\delta_{ij}$  according to

$$\tilde{\rho}_t(\delta) = \frac{\sum_{i=1}^M \sum_{j=i+1}^M K\left(\frac{\delta_{ij}}{h}\right) \rho_{ij,t}}{\sum_{i=1}^M \sum_{j=i+1}^M K\left(\frac{\delta_{ij}}{h}\right)}, \quad \text{eqn 7}$$

where  $K$  is a kernel function with bandwidth,  $h$ , that defines curve smoothness (Härdle 1990; Hall & Patil 1994). We used a spline function as an equivalent kernel and 15 degrees of freedom for the spline estimation.

We estimated the spatial cross-correlation between prey and predators as a function of distance,  $\tilde{C}_t(\delta)$ , defined as

$$\tilde{C}_t(\delta) = \frac{\sum_{i=1}^M \sum_{j=1}^M K\left(\frac{\delta_{ij}}{h}\right) \omega_{ij,t}}{\sum_{i=1}^M \sum_{j=1}^M K\left(\frac{\delta_{ij}}{h}\right)}, \quad \text{eqn 8}$$

where  $\omega_{ij,t}$  denotes the spatial cross-correlation in abundance of the prey abundance at location  $i$  and time  $t$ , and the predator abundance at location  $j$  according to

$$\hat{\omega}_{ij,t} = \frac{(N_{i,t} - \bar{N}_t)(P_{j,t} - \bar{P}_t)}{\sigma_N \sigma_P}, \quad \text{eqn 9}$$

where  $\sigma$  denotes the space-time variance in prey ( $N$ ) and predators ( $P$ ) (Bjørnstad & Bascompte 2001; cf. eqn 6). We used the bootstrap method (1500 replications) to generate confidence limits around the estimated nonparametric covariance function from field data. We erected 95% confidence intervals as the 0.025% and 0.975% quantiles of the bootstrap distribution (Efron & Tibshirani 1993; Bjørnstad & Falck 2001). For our theoretical system, we derived sampling distributions from a Monte Carlo distribution of 1000 replicated simulations of the transient predator-prey system. Although we focused on estimating local aggregation (i.e. local spatial autocorrelation) for fly larvae and adult beetles, and their local segregation (i.e. local spatial cross-correlation between flies and beetles) because it generally dictated the range of spatial structure – greater deviations from 0 in local correlation resulted in longer ranges of spatial continuity – we also estimated spatial correlation over a range of lag distance.

## Results

### SPATIAL ESTIMATION IN FIELD DATA

Temporal dynamics of larval flies and adult beetles, and the percent of samples containing at least one

*C. pumilio* adult, are presented in Fig. 1. Because of different hen management schedules between the two sites, sampling dates of key events, such as initial beetle colonization, differed yet the overall dynamics were similar. Field-wide fly populations prior to predatory beetle establishment were high, with means often exceeding 200 third instars per 200 g sample, but were drastically reduced in concert with beetle logistic growth. Tobin *et al.* (1999) reported that once adult beetles were detected from samples, the rates of predator population growth were statistically the same between the two sites.

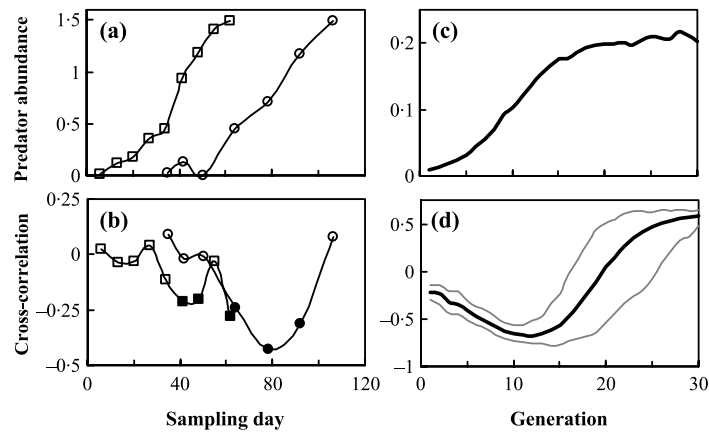
Estimates of local aggregation (estimated by the spatial correlation at distance lag = 0; e.g. Bjørnstad & Bascompte 2001) of larval flies prior to beetle establishment were fairly similar between the two sites and indicated significant clustering (Table 1). During beetle population growth and establishment, beetles became increasingly aggregated. Concurrently, fly larvae became decorrelated at local spatial scales (Table 1). Predatory beetles and larval prey were locally segregated (i.e. negative cross-correlation) during rapid beetle population growth. This spatial segregation between predator and prey was observed at both field sites and appeared to be linked to predator abundance – during rapid beetle population growth, beetles and larval prey were segregated at local scales, but as predators approached a carrying capacity, the cross-correlation tended towards no correlation or positive correlation (Fig. 2 A and 2B).

The transition in spatial dynamics also occurred over a range of lag distance. This is exemplified in Fig. 3, which shows the behaviour of the spatial correlation function at Site 2 for fly larvae, adult beetles, and their interaction over both sampling week and lag distance. Initially, larval flies were highly aggregated over scales > 10 meters, while the initial immigrants of predatory beetles were only weakly autocorrelated. The inverse was true when beetles were rapidly increasing in abundance. However, as a carrying capacity is reached,

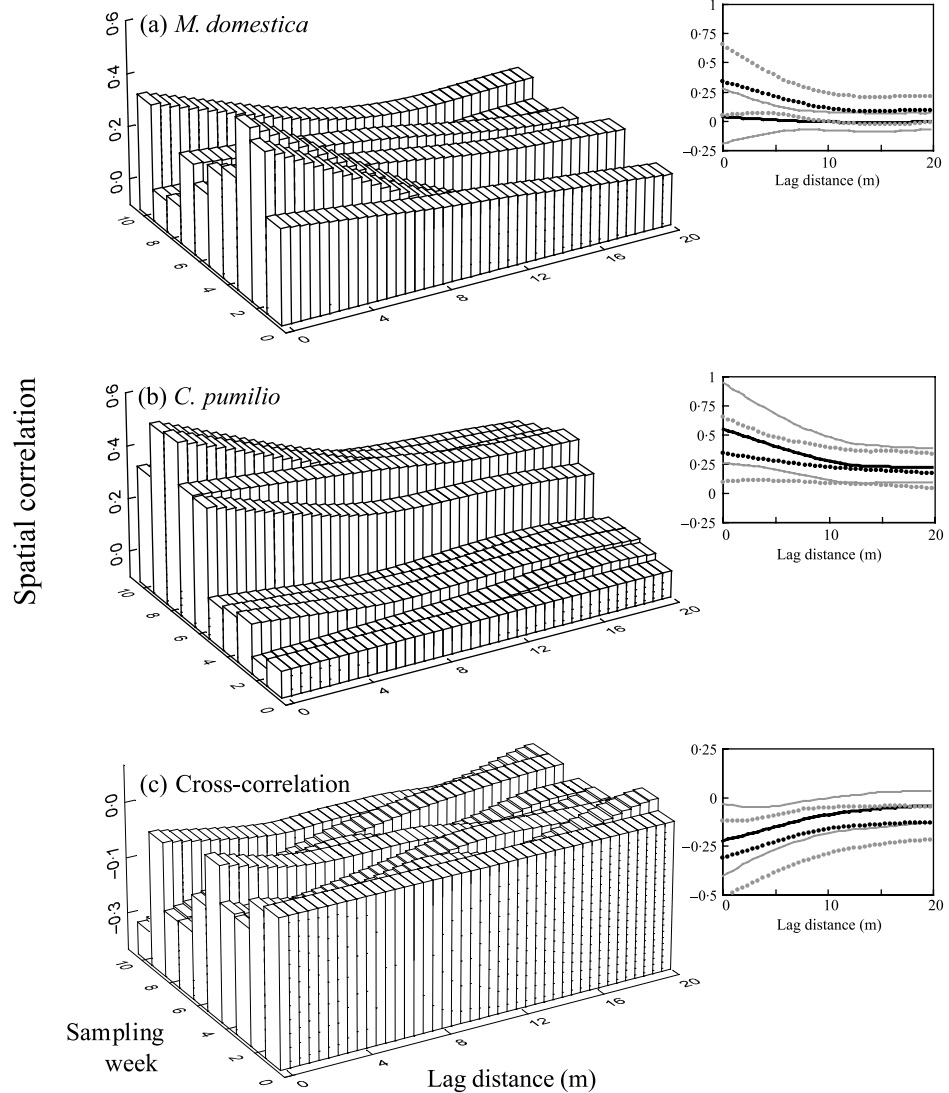
**Table 1.** Estimates of local aggregation (spatial correlation at lag distance = 0) in third instar house flies and adult predatory beetles (95% bootstrapped CI)

Week	Site 1		Site 2	
	Flies	Beetles	Flies	Beetles
1	0.36 (0.01, 0.86)	NA	0.26 (0.03, 0.56)	NA
2	0.35 (0.04, 0.77)	NA	0.50 (0.24, 0.80)	-0.03 (-0.14, 0.01) <sup>NS</sup>
3	0.49 (0.15, 0.93)	NA	0.54 (0.26, 0.87)	0.09 (-0.14, 0.41) <sup>NS</sup>
4	0.42 (0.03, 0.89)	NA	0.32 (0.03, 0.67)	0.07 (-0.18, 0.33) <sup>NS</sup>
5	0.22 (-0.15, 0.65) <sup>NS</sup>	NA	0.28 (-0.04, 0.66) <sup>NS</sup>	0.05 (-0.17, 0.33) <sup>NS</sup>
6	0.36 (0.03, 0.81)	0.08 (-0.10, 0.49) <sup>NS</sup>	0.17 (-0.09, 0.44) <sup>NS</sup>	0.39 (0.14, 0.67)
7	0.46 (0.06, 0.92)	-0.21 (-0.52, -0.01) <sup>NS</sup>	0.24 (-0.01, 0.54) <sup>NS</sup>	0.39 (0.11, 0.73)
8	0.48 (0.98, 0.06)	-0.02 (-0.13, 0.01) <sup>NS</sup>	0.04 (-0.22, 0.29) <sup>NS</sup>	0.55 (0.24, 0.96)
9	–	–	0.02 (-0.20, 0.27) <sup>NS</sup>	0.54 (0.24, 0.98)
10	0.23 (-0.16, 0.66) <sup>NS</sup>	0.10 (-0.34, 0.67) <sup>NS</sup>	0.35 (0.08, 0.68)	0.34 (0.10, 0.69)
12	0.01 (-0.40, 0.41) <sup>NS</sup>	0.28 (0.11, 0.59)	–	–
14	0.20 (-0.08, 0.58) <sup>NS</sup>	0.22 (0.05, 0.56)	–	–
16	0.40 (0.05, 0.79)	0.37 (0.13, 0.66)	–	–

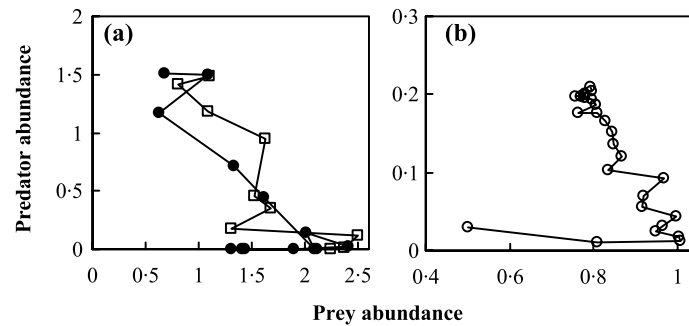
<sup>NS</sup>, Not Significant. NA, prior to collection of beetles from samples.



**Fig. 2.** Relationship between predator abundance at Sites 1 and 2 (A, circles and squares, respectively), and the respective mean local segregation between predators and prey (B). Solid shapes indicate significant cross-correlation estimates, whereas open shapes denote nonsignificant estimates. Comparatively, predator abundance in our theoretical system (C) is shown with the respective mean local cross-correlation (D; 95% confidence intervals are indicated by light grey lines).



**Fig. 3.** Spatial correlation in prey (A), predators (B), and their interaction (C) across lag distance and sampling week. Insert figures are the spline correlograms at Weeks 8 (black line) and 10 (black circles) with corresponding 95% CI (grey lines and circles).



**Fig. 4.** Phase plots of  $\log_{10}$  abundance of larval house flies and predatory adults beetles at Sites 1 and 2 (A, circles and squares, respectively), and phase plot of synthetic predator and prey abundance (B). Initial conditions for all sets are characterized by low predator abundance.

the spatial structure of beetles decreases both locally and over a range of lag distance, while the corresponding structure of fly larvae increases both locally and over a range of lag distance to a similar level as adult beetles (Fig. 3).

#### THEORETICAL SPATIAL ESTIMATION

The transient dynamics of theoretical predator and prey populations bore considerable resemblance to our field data (Fig. 4) [Note, though, that our initial parameters for the theoretical model had predators and prey oscillating around an equilibrium ratio of 1 : 4, respectively, as opposed to the approximately 1 : 1 ratio observed in fly beetle dynamics. This is a trivial consequence of the somewhat arbitrary choice of parameters in our model system.]

Theoretical spatial segregation between predators and prey are depicted in Fig. 2(D), with notable similarities between the strategic model and empirical data. There were periods of local segregation induced by predator establishment and growth. Also, the local cross-correlation increased from negativity to roughly zero as predators approached a stable level, and values continued to increase to stable positive values as predator-prey dynamics stabilized around an attractor (Fig. 2C,D). Comparatively, this pattern of spatial segregation corresponded well with the increasing

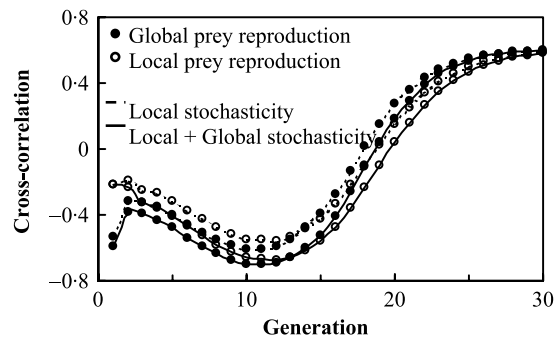
predator abundance observed in field data, although we do lack empirical evidence of significantly positive cross-correlation during the stabilization of predators and prey during the late stable phase.

Estimates of local spatial segregation between predators and prey using different prey production strategies (i.e. global or local) in combination with the presence and absence of global stochasticity are represented in Fig. 5. The dynamics were similar for all cases and demonstrated periods of segregation that corresponded to predator colonization. Global prey reproduction tended to result in asymptotic levels of cross-correlation in 3–5 fewer generations than local reproduction, while global stochasticity yielded somewhat more negative levels of local cross-correlation (Fig. 5).

#### Discussion

Research on the ecology of infectious disease shows that control interventions, such as vaccinations, can lead to asynchrony or synchrony depending on details of natural history (Rohani, Earn, & Grenfell 1999; Bjørnstad 2000). In the former case, persistence may be enhanced while in the latter case, it may not, showing how spatiotemporal dynamics are critical for ecological consequences of human interventions. The analogy to systems where insect pests are managed through control interventions in integrated pest management is thus apparent. Spatial dynamics are also increasingly recognized as having diverse effects on local temporal dynamics (Keeling *et al.* 2000), motivating a range of new questions about how spatial pattern affects temporal processes.

In field data, the level of local aggregation exhibited a characteristic density-dependent shift through time (Table 1, Fig. 1). Prey were initially high in abundance and locally aggregated, while predators were initially very low in abundance and did not significantly differ from spatial randomness. This is intuitive, as initial prey populations result from large clutch sizes of rapidly developing eggs laid gregariously by adult flies (Lysyk & Axtell 1987; Stafford & Bay 1994). In contrast, the immigration of predatory beetles occurs more slowly than of their prey, clutch sizes are roughly 10-fold



**Fig. 5.** Mean local spatial segregation between synthetic predators and prey with global or local prey reproduction, coupled with either local stochasticity or local and global stochasticity.

smaller, and development of beetle immatures occurs almost three times as slowly (Morgan *et al.* 1983). It is still unknown exactly how these beetles colonize poultry production facilities. Geden, Stoffolano, & Elkinton (1987) observed that adult beetles shifted from negative to positive phototaxis when food sources were depleted due to, for example, overcrowding, which suggested a mechanism for emigration. Also, Tobin *et al.* (1999) observed a temporally consistent spatial trend in beetle dynamics that emanated from one area of the facility, suggesting a singular immigration event in space and/or time. Overall, as predators increased in abundance, they became increasingly aggregated, resulting in decreased prey abundance and prey aggregation.

Over broader spatial scales, the interplay between abundance and synchrony has been observed, for example, in bird populations, with the more abundant species tending to be more synchronous; however, this relationship did not exist across spatially unique populations of the same species (Paradis *et al.* 2000). In our field data, prey appeared to regain local clustering as their density approached an equilibrium with predator density (Table 1, Fig. 1). It is possible that *C. pumilio*, an effective predator that can consume > 50 fly immatures each day (Geden & Axtell 1988), caused local decorrelation of prey if dispersal of beetles was limited. Indeed, Geden *et al.* (1987) observed that adults rarely engaged in flight unless food sources were depleted over several days. During beetle exponential population growth, however, local clustering of both species may have been maintained through the formation of patches that were, in essence, spatially segregated.

Our theoretical model of a predator-prey system provided temporal dynamics of abundance similar to field data (Fig. 4), and cross-correlation estimates showed that predators and prey is consistently predicted to be spatially segregated during the transient phase (Fig. 2D). All sets of data, whether empirically based or theoretically derived, revealed that the transition in spatial cross-correlation between predators and prey could be linked to increasing population growth of a natural enemy (Fig. 2), whether prey reproduction was locally or globally governed, or whether or not prey and predator populations were subject to global stochasticity (Fig. 5). In essence, the transition from eruptive pest abundance to regulation by a specialist predator was thus associated with a transition in spatial dynamics.

Developing a sound theoretical model based on empirical evidence is a first step toward gaining insight into transient predator-prey population cycles. In the future, we intend to investigate patterns of local spatial aggregation and cross-correlation across a wider range of parameter values in theoretical dynamics. In particular, since many agricultural and other anthropogenic systems are transient, environmental factors, particularly weather, may not play as large a role in inducing spatial structure as they do in perennial systems (Royama 1992; Ranta *et al.* 1997). For instance, the relative roles of regional stochasticity and dispersal in

inducing long-term regional synchrony in six forest insect species have been recently examined, with the former being the dominant process (Peltonen *et al.* 2002). However, it is not known what their respective contributions would be in more transient systems. Dispersal ability, for example, has been shown to play an important role in influencing spatial structure in single and interacting species (Hassell *et al.* 1991; Sutcliffe, Thomas, & Moss 1996; Keeling *et al.* 2000; Bjørnstad & Bascompte 2001).

Understanding spatial structure in transient systems has several rewards. In agriculture, a comprehensive understanding of the spatial and temporal dynamics of not only the herbivore pest species, but also its natural enemies, should facilitate our understanding of the nontarget effects of pest control tactics to beneficial species, and the potential of pest species to develop resistance to these tactics. In particular, one potential application involves site-specific management in agriculture, in which a cropping system is differentially managed in space and time. Although this approach has shown much promise in more stationary processes, such as when managing and optimizing soil properties, using this approach to manage spatially and temporally dynamic insect populations could be problematic unless the factors that influence spatial structure are better understood.

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