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## Roles of dispersal, stochasticity, and nonlinear dynamics in the spatial structuring of seasonal natural enemy–victim populations

Received: 5 May 2005 / Accepted: 23 July 2005 / Published online: 9 September 2005  
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**Abstract** Natural enemy–victim systems may exhibit a range of dynamic space–time patterns. We used a theoretical framework to study spatiotemporal structuring in a transient natural enemy–victim system subject to differential rates of dispersal, stochastic forcing, and nonlinear dynamics. Highly mobile natural enemies that attacked less mobile victims were locally spatially segregated from each other when governed by approximate linear dynamics. In contrast, in nonlinear dynamical systems, such as cyclic populations, interacting species achieved local aggregation with each other regardless of dispersal rates, and aggregation was enhanced specifically when highly mobile enemies attacked less mobile victims. These patterns of spatial aggregation held under varying levels of stochastic forcing. This work thus shows a range of dynamic spatial patterns in interacting-species models, and how spatial aggregation between natural enemies and victims can be achieved in locally unstable populations that are linked through dispersal.

**Keywords** Predator–prey interactions · Spatial aggregation · Nonparametric spatial covariance function · Coupled map lattice

### Introduction

Participants in a natural enemy–victim system exhibit a range of spatially and temporally dynamic metapopula-

tion structure. Describing such spatiotemporal patterns is a central problem in ecology and is paramount to understanding the underlying processes that govern such dynamics (MacArthur 1972; Steinberg and Kareiva 1997). In particular, there has been much recent interest in exploring the space–time properties of seasonal populations (Saravia et al. 2000; Winder et al. 2001; Tobin and Bjørnstad 2003, Labra et al. 2003), which can apply to, for example, pest outbreaks and invasions of exotic species. In many respects, understanding these seasonal and more transient systems may be more critical in developing ecological paradigms, as stochastic disruptions, such as habitat fragmentation or the invasion of new species, can be frequent relative to the return times of long-term spatiotemporal systems (Hastings and Higgins 1994; Hastings 2001). We previously examined the spatial dynamics and cross-correlation in a transient predator–prey system within both an empirical and theoretical context, and observed that the transition from eruptive pest abundance to regulation by a specialist predator was associated with a transition in spatial structure (Tobin and Bjørnstad 2003). In this paper, we extend this work by addressing the roles of dispersal, stochasticity, and nonlinear dynamics on patterns of spatial aggregation and segregation in seasonal predator–prey populations.

Regional stochasticity [i.e., the Moran effect (Moran 1953)] and dispersal have been argued to play important roles in mediating the spatiotemporal dynamics of an individual species (Hassell et al. 1991; Ranta et al. 1998; Hudson and Cattadori 1999; Peltonen et al. 2002). Dispersal can induce synchrony in populations because it links neighboring populations, while spatially correlated climatic forcing can cause populations to behave similarly over large scales. Peltonen et al. (2002) argued, in a study of several forest insects and associated climatic data, that on a landscape scale, regional stochasticity was the dominant force in synchronizing populations. However, theoretical studies have suggested that ecological interactions that produce nonlinear dynamics, such as through limit cycles or chaos, can affect the level of synchrony in populations whether

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dispersal or the Moran effect dominates (Ranta et al. 1998; Bjørnstad et al. 1999; Bjørnstad 2000). Ripa (2000) furthermore contended that dispersal could only be a synchronization force when local dynamics were close to unstable, while Lande et al. (1999) showed that dispersal can increase the level of synchrony in populations that were weakly regulated and when the scale of dispersal was less than the scale of the correlation to the stochastic event.

Although many past studies in spatiotemporal ecology have centered on single-species dynamics, much attention is also given to the space–time dynamics of age-trophic interactions, particularly those involving natural enemies and their victims (Hassell et al. 1991; Bascompte and Solé 1995; Maron and Harrison 1997; Wilson and Hassell 1997; Wilson et al. 1999; Ims and Andreassen 2000; Keeling et al. 2000; Bjørnstad et al. 2002; Tobin and Bjørnstad 2003). Past theoretical work studied the spatial cross-covariance between natural enemies and victims to show, depending on dispersal ability, a high degree of within-patch synchrony, or spatial lag between the two (Bjørnstad and Bascompte 2001). In nature, lagged spatial responses have been observed in the dynamics of two aphid prey species and a generalist predator, in which the spatial pattern of the latter was more often than not positively associated with the spatial patterns of aphids at the previous time step, whereas the inverse was observed for that of the prey (Winder et al. 2001). Because of the importance of the dynamics of spatially extended, multitrophic interactions in ecological theory and practice, we studied the roles of potential factors in the spatial structuring of such populations.

Our primary objective was to examine space–time dynamics in a predator–prey system during the colonization phase of the predator. We were particularly interested in the joint effects of dispersal ability, non-linearity, and stochasticity on this type of space–time interaction to elucidate the mechanisms and/or processes that govern predator–prey seasonal dynamics. We examined the effects of differential rates of dispersal on patterns of spatial auto-covariance and cross-covariance. We subsequently explored the degree of spatial aggregation or segregation between predator and prey when local dynamics were approximately linear or nonlinear in the presence or absence of regional and local stochasticity. In this paper, we show that the dispersal ability of interacting species can influence the local spatial aggregation depending on details of temporal dynamics.

## Materials and methods

### Natural enemy–victim model

We used the discrete-time density-dependent Lotka–Volterra model as the basis for simulating dynamics. Local pre-dispersal dynamics of predator ( $P$ ) and prey

( $N$ ) abundance at time  $t$  and spatial location  $i$  were calculated according to:

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

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

where  $r$  is prey growth rate, and  $a$  is the predator–prey interaction strength (Murray 1993). The parameter  $a$  was held fixed at 2.25 to maximize predator efficiency (Tobin 2002). The primed vectors on the LHS represent pre-dispersal local abundance. Stochasticity (local and global) in prey dynamics were added according to:

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

where  $\rho_\theta$  represents 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  $\sigma$  (cf. 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 Eqs. 1, 2, and 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, individuals were assumed to disperse to the four adjacent cells according to:

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

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

where  $D$  is the  $900 \times 900$  dispersal matrix and  $\times$  denotes matrix multiplication. Values of the dispersal matrix were assigned according to the desired level of dispersal ability. For example, in the case when half of individuals remain and half disperse, then the values in  $D$  are 0.5 along the diagonal and 0.125 at each of the four entries that link the neighboring cells. 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  $\sim 5\%$  of the cells and zero elsewhere. We simulated this system, and conducted subsequent analyses, in S-Plus (Mathsoft 2000) on a 250 CPU Linux cluster operated by the Center for Academic Computing—Numerically Intensive Computing Group of Pennsylvania State University.

### Estimation of spatial covariance

We used the nonparametric spatial covariance function to measure local spatial structure for each species and their interaction (Bjørnstad and Falck 2001). This approach 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. We used 30 equivalent df, which were determined by the square root of the total number of cells in the coupled map lattice, in the spline estimations using spline as an equivalent kernel. We derived Monte Carlo distributions of 500 replicated simulations of the 30-generation seasonal predator–prey system, and erected 95% confidence intervals as the 0.025 and 0.975% quartiles of the distribution (Efron and Tibshirani 1993). We focused on estimating “local” spatial clustering (i.e., the spatial auto-correlation function as the distance between pairs of sampled values approaches 0) because it generally dictated the range of spatial structure—greater deviations from 0 in local correlation resulted in longer ranges of spatial continuity—but we also estimated spatial correlation over a range of lag distance; however, for reporting, we will focus on the local spatial covariance as a surrogate for defining spatial pattern.

### Dispersal in approximate linear and nonlinear dynamics

The range of dispersal rate, from 0 (no dispersal) to 1 (all individuals disperse), was partitioned into 0.1 intervals. We then estimated the local spatial cross-covariance function for each combination of predator and prey dispersal rate and at each generation when assuming linear dynamics ( $r$  in Eq. 1 = 1.5) and two-phase limit cycles ( $r = 2.5$ ). For these simulations, the variance of the 0-mean random stochastic component ( $\sigma$  used for  $U$  and  $V$  in Eq. 3), was fixed at 0.1, and  $\rho_\theta$  was fixed at 0.3 (Tobin and Bjørnstad 2003). A summary of these variable and parameter combinations is presented in Table 1.

### Joint effects of dispersal and stochastic forcing

Based on results from varying dispersal rates in the preceding section, we used fixed dispersal rates of predators and prey to explore spatial cross-covariance

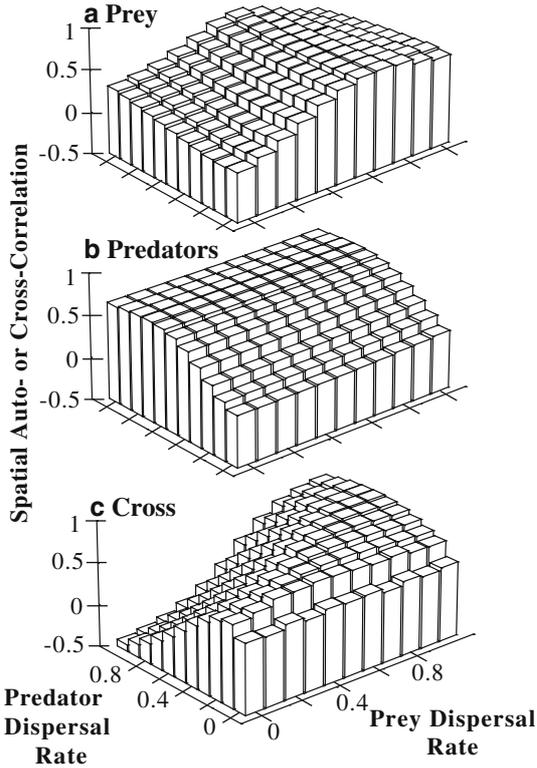
when the dynamics were approximately linear and nonlinear, and when the level of stochastic forcing is altered. We used a system of “highly mobile” prey, in which 75% of individuals disperse evenly to one of four adjacent cells, with “less mobile” predators, in which 25% disperse, and a system of the inverse. For these two systems, we estimated the local spatial cross-covariance function at each generation under linear dynamics ( $r = 1.5$  in Eq. 1), two-phase limit cycles ( $r = 2.5$ ), quasiperiodicity ( $r = 3.0$ ), and chaos ( $r = 3.5$ ). We also used both systems of predator–prey dispersal abilities when governed by two-phase limit cycles ( $r = 2.5$ ) to explore the strength of the stochastic component by using values of  $\sigma$  of 0, 0.05, 0.1, 0.5, and 1 when  $\rho_\theta = 0$  and 0.3. A summary of these variable and parameter combinations is presented in Table 1.

## Results

Different combinations of prey and predator dispersal rates influenced the local spatial auto-covariance for each species and their interaction (cross-covariance) when dynamics were assumed to be linear and when the temporal dynamics were at equilibrium (i.e., asymptotic) (Fig. 1). For each individual species of predator and prey, dispersal enhanced local spatial clustering, which in turn extended the range of spatial structure. When considering the local spatial aggregation between predators and prey, however, the results were more complex. Highly mobile predators that attacked less mobile prey resulted in very low levels of local cross-correlation. For example, when predators and prey disperse at a rate of 0.75 and 0.25, respectively, the local asymptotic cross-correlation was  $-0.07$ , whereas for the inverse conditions, the local asymptotic cross-correlation was 0.61 (Figs. 1, 2). However, during the establishment phase of predator dynamics, the behaviour of the cross-covariance function was similar regardless of predator–prey dispersal rate combination (Fig. 2). It is

**Table 1** Combinations of values used in simulations (500 simulations, 30 generations of the seasonal predator–prey system over a  $30 \times 30$  coupled map lattice) to estimate generation-specific local spatial cross-correlation.  $\rho_\theta$  Global correlation in the stochastic forcing

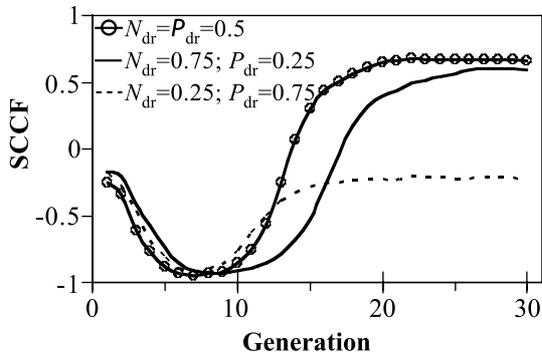
Dispersal	Values (Eqs. 4, 5)	Dynamics (Eq. 1)	Stochasticity (Eq. 3)
Predator and prey	0 to 1 by 0.1	Linear ( $r = 1.5$ ) Cyclic ( $r = 2.5$ )	$\sigma = 0.1$ ; $\rho_\theta = 0.3$
Predator and prey	0.25, 0.75	Linear Cyclic Quasiperiodic ( $r = 3.0$ ) Chaos ( $r = 3.5$ )	$\sigma = 0.0$ $\sigma = 0.1$ ; $\rho_\theta = 0.0$ $\sigma = 0.1$ ; $\rho_\theta = 0.3$
Predator and prey	0.25, 0.75	Cyclic	$\sigma = 0.0$ $\sigma = 0.05$ ; $\rho_\theta = 0.0$ $\sigma = 0.1$ ; $\rho_\theta = 0.0$ $\sigma = 0.5$ ; $\rho_\theta = 0.0$ $\sigma = 1.0$ ; $\rho_\theta = 0.0$ $\sigma = 0.05$ ; $\rho_\theta = 0.3$ $\sigma = 0.1$ ; $\rho_\theta = 0.3$ $\sigma = 0.5$ ; $\rho_\theta = 0.3$ $\sigma = 1.0$ ; $\rho_\theta = 0.3$



**Fig. 1** Local asymptotic spatial auto-covariance in prey (a) and predators (b), and their cross-covariance (c), over a range of predator and prey dispersal rates when governed by approximate linear dynamics

furthermore interesting to note that the temporal dynamics, represented by phase plots, revealed similar temporal patterns across predator–prey dispersal rate combination during both the phase of predator establishment and at equilibrium (Fig. 2).

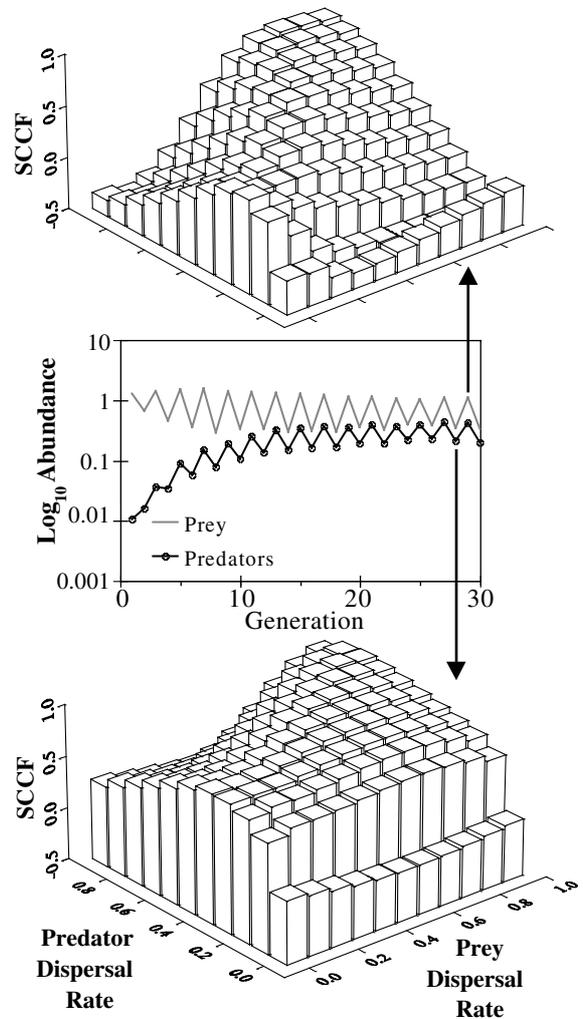
When using a prey growth rate to approximate two-phase limit cycles (e.g.,  $r = 2.5$ ) to study the effects of prey and predator dispersal, we observed consequent cycling in the pattern of the local spatial cross-correlation



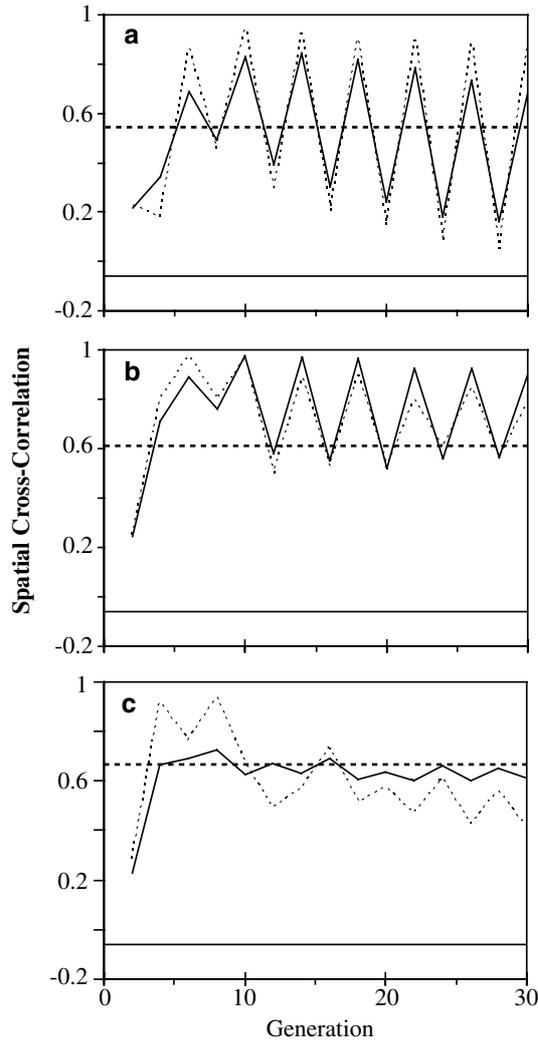
**Fig. 2** Dynamics of the local spatial cross-covariance (SCCF) between predators and prey at selected combinations of prey ( $N_{dr}$ ) and predator ( $P_{dr}$ ) dispersal rates when populations are governed by approximate linear dynamics

tion across the range of dispersal rate combinations (Fig. 3). The dynamics of the cross-covariance function over time, using the dispersal rate combinations of 0.75 for prey and 0.25 for predators as well as the inverse, showed similar patterns in other systems assumed to be nonlinear; that is, in these nonlinear systems, the spatial aggregation between predators and prey was enhanced, during alternating time steps—relative to linear-approximated systems—when predators had the greater dispersal capacity (Fig. 4).

The level of stochasticity (i.e., the variance of  $U$  and  $V$ , cf. Eq. 3) also influenced the dynamics of local spatial cross-covariance when using the above-mentioned predator–prey dispersal rate combinations and two-phase limit cycles (Fig. 5). The presence or absence of regional correlation to stochasticity (i.e.,  $\rho_\theta$  in Eq. 3) had negligible influence on the local spatial covariance

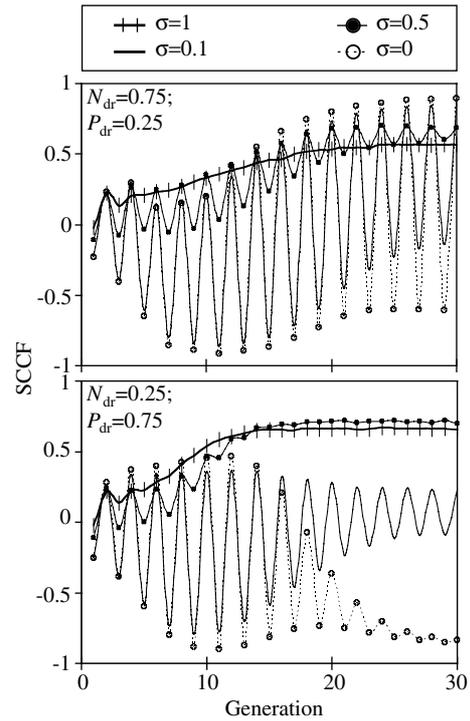


**Fig. 3** Changes in local spatial aggregation (SCCF) between predators and prey over a range of dispersal rates and when populations are governed by two-phase limit cycles. Note the fluctuations in spatial patterns in which the local cross-covariance is enhanced when both populations are in the decline phase of their cyclic dynamics



**Fig. 4** Local spatial aggregation (SCCF) between mobile predators (dispersal rate=0.75) and less mobile prey (dispersal rate=0.25) (*solid lines*) and the inverse (*dashed lines*) in **a** two-phase limit cycles, **b** quasiperiodicity, and **c** chaos. The *horizontal lines* indicate the degree of spatial aggregation at equilibrium under the same dispersal strategies (by *line type*) when the system is governed by approximate linear dynamics

because stochasticity was still expressed at local scales even in the absence of any regional correlation. When prey have the greater dispersal capacity, the pattern of spatial aggregation between interacting species was similar across levels of stochasticity, though there were far greater amplitudes of the cross-covariance function over time in less variable environments (i.e., little to no stochasticity). However, when predators have the greater dispersal capacity, varying the level of stochasticity led to divergent patterns. We observed that environmental stochasticity was a necessity for local spatial aggregation between predators and prey while the lack of it resulted in their local spatial segregation (Fig. 5). However, since we focused our attention primarily in cyclic populations, more work is needed to determine the effects of stochasticity on spatial



**Fig. 5** Local spatial aggregation (SCCF) between predators and prey under differing dispersal strategies in cyclic populations ( $r=2.5$ ) and under varying levels of stochasticity ( $\sigma$ )

structuring in populations governed by approximate quasiperiodic and chaotic dynamics.

## Discussion

For each individual species, high rates of dispersal enhanced their respective local spatial clustering as previously reported within both an empirical and theoretical context (e.g., Molofsky 1994; Sutcliffe et al. 1996; Ranta et al. 1998; Kendall et al. 2000; Peltonen et al. 2002). However, highly mobile predators that attack less mobile prey can lead to interesting effects on local spatial cross-correlation, resulting in asymptotic negative spatial cross-correlation when governed by linear dynamics. Given highly mobile predators and density-dependent prey dynamics, low prey abundance at one time iteration coupled with high predator abundance would result in the inverse at the next iteration, whereby prey numbers increase exponentially due to the loss in predator abundance from high dispersal. When prey are mobile and are attacked by limitedly dispersing predators, prey that immigrate into a lattice cell occupied by few predators would rapidly increase in abundance in the absence of predators, but their increase in population could lead to increases in predator abundance when they do finally immigrate into the cell. This theoretical observation is consistent with findings in nature in a two-prey-generalist predator system (Winder et al. 2001).

This concept of spatial patterns essentially lagging through time has been previously proposed as a source of traveling waves by Bjørnstad and Bascompte (2001), who based this argument on the fact that the spatial cross-covariance, or measure of spatial aggregation (or segregation), affects host population dynamics. We strengthen this proposition with this work by demonstrating the effects of predator–prey dispersal abilities on local spatial dynamics during the colonization phase of the predator. The concept of negative local spatial cross-covariance does pose interesting questions in ecological applications. For example, in conservation biology, there is warranted concern regarding the potentially inimical role that enemies, particularly nonnative ones, play on the dynamics of their victims, particularly for those that are native (Sinclair et al. 1998; Schneider 2001). Also, biological control applications are greatly dependent on space–time overlap between natural enemies and their target prey. These results suggest that there are important consequences in the degree to which natural enemies, whether the result is desirable or not, can affect host dynamics based explicitly on their respective ability to disperse.

The effects of differential rates of prey and predator dispersal differed depending on whether the system was governed by approximately linear or nonlinear dynamics. In the former, there was segregation between predators and prey when highly mobile predators attacked less mobile prey, while in the latter the level of local aggregation between the two was substantially higher. Even when chaos was assumed, there was aggregation between the two interacting species at a local scale, though on a regional level, populations are usually not (Bjørnstad 2000; Tobin 2002).

Extreme oscillations in local predator and prey populations have previously been observed, both empirically and theoretically (Rosenzweig 1971, 1972; Pascual et al. 2001). Given that natural enemies that are more mobile than their prey can be successful in limiting prey abundance in nature (Winder et al. 2001), it is reasonable to assume that adequate spatial and temporal overlap can exist between the two when dispersal rates greatly differ. We suggest that prey and predator populations, in the absence of patches, could be cyclic, quasiperiodic, and even unstable, and still allow spatial and temporal overlap. In fact, some have argued that local population stability of natural enemies and prey is not necessarily a prerequisite for persistent host–parasitoid interactions providing that on a regional level, the population was divided into semi-independent subpopulations linked through dispersal (Crowley 1981; Murdoch et al. 1985; Adler 1993).

These results are conceptually similar to those reported by Ripa (2000), who argued, albeit at a regional level, that dispersal in a single-species space–time model was only effective in increasing synchrony when local dynamics were unstable. Ranta et al. (1998) also reported that cyclic populations could be synchronized through dispersal. Here, we show that locally, predators

and prey can be aggregated in space under nonlinear dynamics, including chaos; however, single- and interacting-species models have shown that on regional levels, chaotic populations are difficult to synchronize regardless of dispersal (Allen et al. 1993; Heino et al. 1997; Tobin 2002).

We have shown that the dynamics in a spatially extended predator–prey system can lead to a variety of emerging spatiotemporal patterns. Highly mobile natural enemies, that attack fairly sessile prey when governed by approximately linear dynamics, resulted in asymptotically negative local spatial cross-correlation, whereas when differing dispersal rates were coupled with exogenous dynamics, we observed a high spatial and temporal overlap between the two. Future work should investigate the role that differential prey and predator dispersal rates play in inducing regional spatial correlation in cyclic and populations.

**Acknowledgements** We thank Akiko Satake and Alexei A. Sharov for comments on earlier versions of this manuscript, and the Pennsylvania State University Center for Academic Computing—Numerically Intensive Computing Group. This research was supported by the USDA Forest Service, Northeastern Research Station.

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