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Interspecific synchrony among foliage-feeding forest Lepidoptera species and the potential role of generalist predators as synchronizing agents

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While synchrony among geographically disjunct populations of the same species has received considerable recent attention, much less is known about synchrony between sympatric populations of two or more species. We analyzed time series of the abundance of ten species of spring foliage feeding Lepidoptera sampled over a 25-year period at 20 sites in the Slovak Republic. Six species were free-feeders and four were leaf-rollers as larvae. Twenty-nine percent of interspecific pairs were significantly synchronous and correlations were highest among species exhibiting similar feeding strategies. Similar patterns of interspecific synchrony have been previously demonstrated in several other taxa, and the synchronizing effects of weather and/or specialist predators have been proposed as mechanisms. As an alternative explanation, we explored a model in which two species within the same feeding guild were synchronized by the functional response of generalist predators. In this model, species remained unsynchronized in the complete absence of predation or when predatory pressures were applied to only one species. Pairs of prey species projecting relatively similar search images to predators were more highly synchronized than species with relatively different search images. Prey handling time only influenced synchrony when it was very high relative to the total time prey was exposed to predators. Our model's prediction of greater synchrony among species that project similar search images to predators was in agreement with our field study that showed greater synchrony among species sharing similar larval feeding strategies and morphologies.

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Synchrony among populations of the same species has been documented for a diversity of taxa (Pollard 1991, Hanski and Woiwod 1993, Ranta et al. 1995a, b, Bjørnstad 2000, Liebhold and Kamata 2000, Paradis et al. 2000, Peltonen et al. 2002). One characteristic of synchronous dynamics is that nearby locations tend to be more synchronous than populations separated by long distances. This pattern has inspired two hypotheses regarding the causes of spatial synchrony: 1) synchronization via movement of members (or predators) among populations or 2) synchronization of populations via the effects of spatially synchronous stochastic effects (i.e. weather, Ranta et al. 1995a, b, Bjørnstad et al. 1999). These two processes are apparently capable of producing identical patterns of synchrony and therefore, without additional information it is often difficult to differentiate

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their relative importance, though for some organisms dispersal can be effectively ruled out (Grenfell et al. 1998, Koenig 1999, Peltonen et al. 2002).

Less information exists about the extent of synchrony among populations of different species. There are some reports of synchronous population fluctuations in tetraonid birds (Ranta et al. 1995b, Lindström et al. 1996), small mammals (Small et al. 1993, Norrdahl and Korpimäki 1996), and insects (Miller and Epstein 1986, Raimondo et al. 2004). As in the case with intraspecific synchrony, the causes of interspecific synchrony are rarely clear. Hypotheses include synchronization through the effects of common stochastic effects, such as weather (Lindström et al. 1996, Hawkins and Holyoak 1998, Myers 1998, Watson et al. 2000) and synchronization through the numerical responses of shared predator populations (Ydenberg 1987, Marcström et al. 1988, Ims and Steen 1990). While synchronization due to specialist predators has been demonstrated in both empirical and theoretical studies of small mammals (Ydenberg 1987, Ims and Steen 1990, Norrdahl and Korpimäki 1996), identifying specialist predators as synchronizing agents will only be applicable if prey dynamics are significantly influenced by specialist predators.

In contrast to small mammals, the population dynamics of lepidopterous insects appear to be much more strongly influenced by generalist predators (Hassell 1978, Price 1997). Where specialist predators exhibit both numerical and functional responses to changes in prey density (Gotelli 2001), generalist predators typically demonstrate only a functional response (Linden and Wikman 1983, Wesloh 1990), particularly when prey species are not present throughout the entire predator hunting season. The latter scenario is exemplified by Lepidoptera in the spring foliage feeding guild and their generalist predators such as birds and small mammals. Early ecologists suggested that species within a feeding guild may be regulated as a whole, rather than as individual species, through shared predation pressure (Hebert et al. 1974, Comins and Hassell 1976). This concept, originally termed "apparent competition", results when prey species that are not in direct competition affect each other's populations through a functional and/or numerical response of a shared predator (Holt 1977).

Despite the widely recognized importance of generalist predators, little is known about their role in synchronizing their prey. In this study, we quantified patterns of synchrony among populations of ten different oak-feeding Lepidoptera species over a 25-year period at 20 different sites in the Slovak Republic. Although no data on predation were available, we also investigated the role of generalist predators as synchronizing agents using a simple two prey model and demonstrated that the functional response of a generalist predator is capable of inducing synchrony among prey populations. We also used this model to study how relative prey palatability and handling time affected synchronization.

Synchrony in time series of oak-feeding Lepidoptera populations

We analyzed data collected by the Forest Research Institute, Zvolen, Slovakia (part of former Czechoslovakia). Insect counts were made from 1955–1964 and from 1966–1982 in early May, (usually between May 10th and 15th), at 20 sites throughout the Slovak Republic (Fig. 1). The size of forest stands in which sites were located varied from several hectares to several hundred hectares. Lepidoptera were collected from each site by placing nets around 20 lower canopy branches (about 0.5 m long representing about 100 leaves) of 20 trees of *Quercus* spp. at the forest edge. Netted branches were cut and subsequently beaten over a sheet and all Lepidoptera dislodged from the branches were identified and counted (Patoèka et al. 1962, 1999). Samples were collected from the same sites each year. The 10 most abundant species, representing four families, were selected for the analysis. Of these species, five were primarily free feeders as larvae and four were leaf-rolling larvae (Table 1). The ln-transformed abundance of each species was used to generate a time series for each site (Fig. 2).

We evaluated synchrony among all possible pairs of the ten species. Synchrony among each pair of species was quantified using the cross-correlation of ln-transformed abundance of the two species at the same site, averaged across all sites. To score the statistical significance of the average correlation, a bootstrap confidence interval was generated for each comparison by resampling (1,000 iterations) and recalculating the average correlation (Bjørnstad et al. 1999). This method compensated for the lack of independence among sites. Since measuring interspecific synchrony among the 10 species involved a total of 45 separate comparisons, α levels were adjusted using a Bonferroni correction. Based on the corrected α level, the pairwise 99.9% confidence interval was used to determine the statistical significance of the correlations. Correlations were considered significant if the confidence interval did not include zero. Statistical tests for correlation between autocorrelated time series such as these are fraught with problems (Buonaccorsi et al. 2001) but the methods used here were conservative and spurious correlations were thus unlikely.

Thirteen species pairs (29%) had significantly positive correlations and no pairs had significant negative correlations (Table 2). The significant correlations occurred primarily among species pairs within a family or feeding group. Within the family Geometridae, all species pairs were synchronized with the exception of

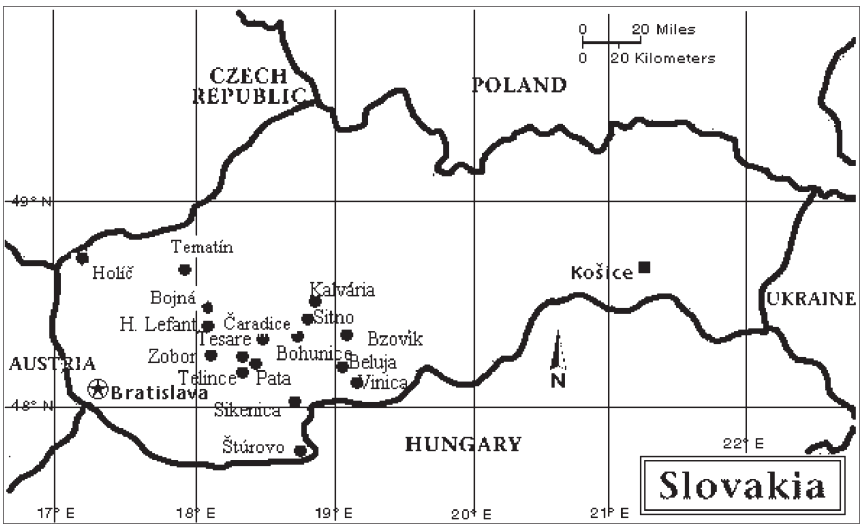

Fig. 1. Location of study sites within the Slovak Republic.

Alsophila aescularia (Denis & Schiffermüller) with *Erannis defoliaria* Clerck and *Operophtera brumata* L. The Noctuid, *Orthosia cruda* Denis & Schiffermüller was significantly correlated with all geometrid species. All tortricid species pairs were significantly correlated within the family sans *Tortrix viridana* L. with *Archips xylosteana* L. and *Eudemis profundana* (Denis & Schiffermüller). The only free feeder/leaf-roller pair that was significantly correlated was *E. defoliaria* and *Aleimma loeflingiana* L. (Tortricidae). *Lymantria dispar* L. (Lymantriidae) was not significantly correlated with any other species in the study.

Each species was classified as either "free" or "concealed" based on the mode of larval feeding. Every possible pair of species was thus designated as either representing the same or different feeding groups. A Wilcoxon rank test was used to determine if there was a significant difference in the correlation of species pairs in the same and different feeding groups (Conover 1999).

Table 1. Study species and primary larval feeding habit.

Species	Family	Larval feeding
Archips xylosteana L.	Tortricidae	leaf roller
Aleimma loeflingiana L.	Tortricidae	leaf roller
Tortrix viridana L.	Tortricidae	leaf roller
Eudemis profundana (Denis & Schiffermüller)	Tortricidae	leaf roller
Alsophila aescularia (Denis & Schiffermüller)	Geometridae	free
Operophtera brumata L.	Geometridae	free/web leaves
Agriopis aurantiaria Hübner	Geometridae	free
Erannis defoliaria Clerck	Geometridae	free
Lymantria dispar (L.)	Lymantriidae	free
Orthosia cruda (Denis & Schiffermüller)	Noctuidae	free

Based on this test, interspecific correlations were significantly higher among species pairs in the same feeding group than among species pairs in different feeding groups ($W = 433$, $n = 24$, $m = 21$, $P = 0.006$). Fifty-seven percent of species in the same feeding group had significant correlations, where only 4% of species in different feeding groups were synchronized.

Modeling the role of generalist predators as synchronizing agents

The model system was idealized as a guild of foliage-feeding Lepidoptera and their generalist predators, such as birds and/or small mammals. Individual prey species are present for only a short period of the predator hunting season and in the model, predator recruitment is unaffected by the prey species abundance. The predators, therefore, exhibit only a functional response to the changes in prey density and no numerical response (Holling 1965, Real 1977, Wesloh 1990). This is a realistic system since generalist predators have repeatedly been shown to significantly influence the population dynamics of forest insects (Campbell et al. 1983, Atlegrim 1989, Elkinton et al. 1996, Floyd 1996, Greenberg et al. 2000).

For simplicity, the model included only two prey species. We assumed that prey dynamics were primarily determined by a second-order density dependent process (different from predation) combined with environmental stochastic effects. This was a reasonable representation since partial autocorrelation functions of over half of the log transformed Lepidoptera time series (described above) had significant negative lag 2 correlations, typical of an AR(2) process (unpubl.). Indeed, Turchin (1990)

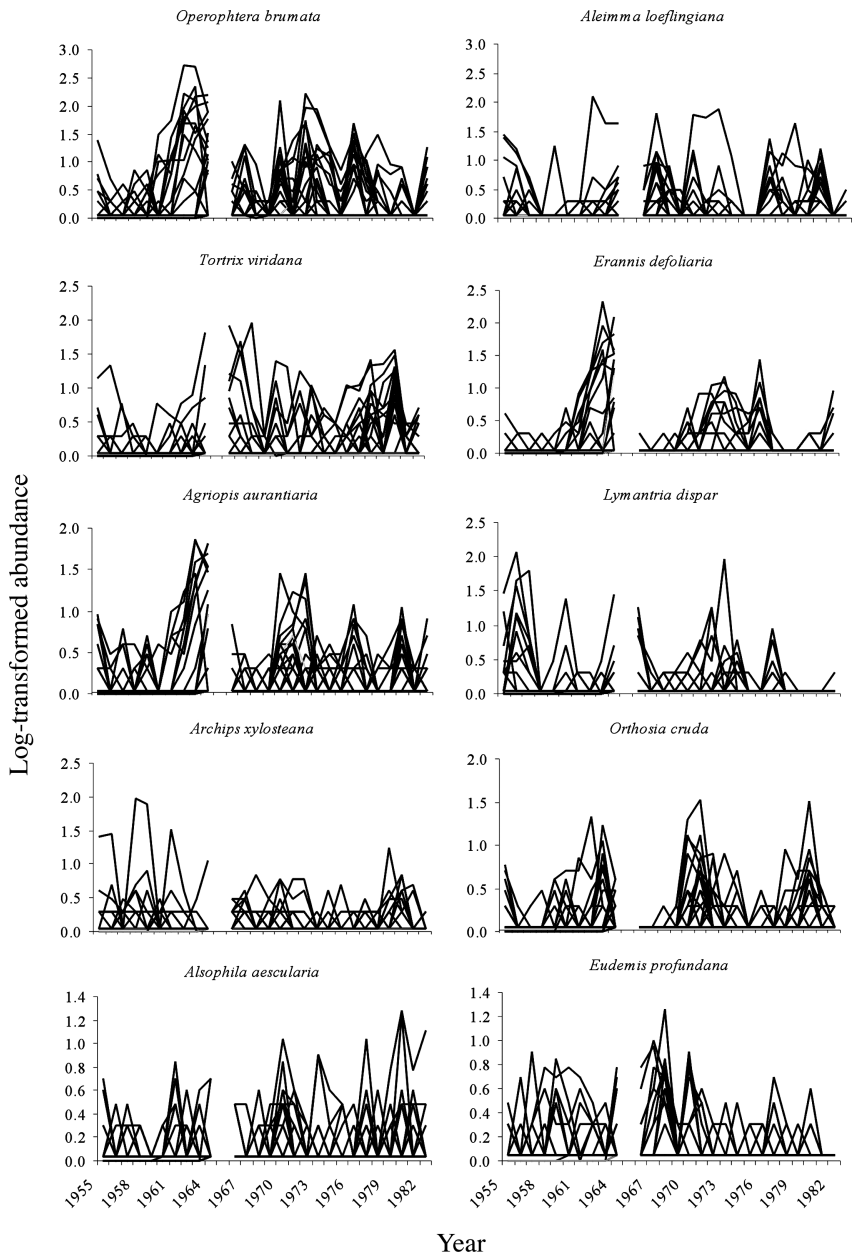

Fig. 2. Time series of the 10 study species on 20 sites throughout the Slovak Republic from 1955 through 1982.

analyzed log transformed time series of 14 forest insect species and found that their dynamics were mostly characteristic of AR(2) processes. In the absence of predation, individual prey dynamics were thus described by the second-order model (Turchin 1990):

$$N_{1,t+1} = N_{1t}\exp(r_1 + a_1 N_{1,t} + a_2 N_{1,t-1} + \varepsilon_{1,t}) \quad (1a)$$

$$N_{2,t+1} = N_{1t}\exp(r_2 + b_1 N_{2,t} + b_2 N_{2,t-1} + \varepsilon_{2,t}) \quad (1b)$$

where $N_{1,t}$ and $N_{2,t}$ were the densities of the two prey species at times t. The parameter r is the intrinsic rate of increase and a and b are parameters that determine the dynamics of species 1 and 2, respectively. The parameters were assigned values of $r_1 = r_2 = 0.6$, $a_1 = b_1 = 0.04$, $a_2 = b_2 = -0.09$ to create oscillating dynamics. The stochastic variable, $\varepsilon_{i,t}$, had a mean and standard deviation of (0, 0.01) and was uncorrelated between the two prey populations to remove the synchronizing effect of shared environmental stochasticity (Moran 1953).

A type II predator functional response was modeled using Holling's (1959) disc equation for two species.

Table 2. Average cross-correlation coefficients for interspecific comparisons are presented in the upper portion of the table. The lower portion of the table contains the 99.9% confidence interval for each species pair. Cross-correlations in bold are significant at the $\alpha = 0.001$ level.

	Free feeders						Leaf rollers			
	A. aurantiaria	*A. aescularia*	*E. defoliaria*	*O. brumata*	*L. dispar*	*O. cruda*	*A. loeflingiana*	*A. xylosteana*	*E. profundana*	*T. viridana*
A. aurantiaria		**0.17**	**0.49**	**0.47**	0.06	**0.38**	0.15	−0.03	0.14	0.08
A. aescularia	(0.01, 0.37)		0.04	0.11	0.04	**0.17**	0.08	0.10	0.09	0.09
E. defoliaria	(0.16, 0.73)	(−0.08, 0.25)		**0.53**	0.05	**0.21**	**0.25**	−0.08	0.15	−0.06
O. brumata	(0.24, 0.67)	(−0.05, 0.30)	(0.29, 0.78)		−0.03	**0.28**	0.15	−0.07	0.08	0.02
L. dispar	(−0.07, 0.21)	(−0.08, 0.17)	(−0.11, 0.25)	(−0.13, 0.09)		0.06	0.06	0.08	−0.02	0.00
O. cruda	(0.19, 0.55)	(0.06, 0.30)	(0.03, 0.37)	(0.11, 0.44)	(−0.12, 0.29)		0.07	0.11	0.04	0.05
A. loeflingiana	(−0.02, 0.38)	(−0.05, 0.23)	(0.04, 0.44)	(−0.02, 0.34)	(−0.09, 0.23)	(−0.10, 0.23)		**0.22**	**0.27**	**0.23**
A. xylosteana	(−0.16, 0.13)	(−0.05, 0.24)	(−0.21, 0.12)	(−0.22, 0.05)	(−0.05, 0.23)	(−0.05, 0.26)	(0.01, 0.48)		**0.18**	0.13
E. profundana	(−0.02, 0.34)	(−0.10, 0.30)	(−0.04, 0.44)	(−0.04, 0.19)	(−0.13, 0.12)	(−0.10, 0.23)	(0.06, 0.55)	(0.02, 0.34)		0.01
T. viridana	(−0.07, 0.24)	(−0.05, 0.27)	(−0.16, 0.04)	(−0.11, 0.19)	(−0.12, 0.12)	(−0.07, 0.20)	(0.04, 0.43)	(−0.01, 0.29)	(−0.19, 0.23)	

The number of each prey species removed from each population by the predator was determined by (Murdoch 1973):

$$N_{1a,t} = \frac{\gamma_1 N_{1,t} T}{1 + \gamma_1 h_1 N_{1,t} + \gamma_2 h_2 N_{2,t}} \quad (2a)$$

$$N_{2a,t} = \frac{\gamma_2 N_{2,t} T}{1 + \gamma_1 h_1 N_{1,t} + \gamma_2 h_2 N_{2,t}} \quad (2b)$$

where $N_{ia,t}$ was the number of prey removed from the population of species i at time, t, h_i was the handling time of each species, and T represents the predation pressure. The model assumes that both prey species are exposed to the predator for the same amount of time and during the same time of the year, thus T was the same for both prey species in each time step. Since there was no predator numerical response to prey populations in this model, T was assigned a random normal deviation (mean = 0.05, standard deviation = 0.01) to incorporate variation in generalist predation populations and include a range of predator abundance (Turchin 2003). Predator search rate of each prey species, γ_i, was unique for each time step and was determined by the relative densities of each prey species modified by a constant search image (θ_i) such that:

$$\gamma_{1,t} = \frac{\theta_1 N_{1,t}}{(\theta_1 N_{1,t} + \theta_2 N_{2,t})} \quad (3a)$$

$$\gamma_{2,t} = \frac{\theta_2 N_{2,t}}{(\theta_1 N_{1,t} + \theta_2 N_{2,t})} \quad (3b)$$

where $\gamma_{1,t} + \gamma_{2,t} = 1$. The model simulated the removal of each of the prey species by predators during each time step by linking the predator functional response (Eq. 2) to prey dynamics (Eq. 1) so that the populations projected as:

$$N_{1,t+1} = N_{1t}\exp(\gamma_1 + a_1 N_{1,t} + a_2 N_{1,t-1} + \varepsilon_{1,t}) - N_{1a,t} \quad (4a)$$

$$N_{2,t+1} = N_{1t}\exp(\gamma_2 + b_1 N_{2,t} + b_2 N_{2,t-1} + \varepsilon_{1,t}) - N_{2a,t} \quad (4b)$$

Model simulations were first conducted over 500 generations and 500 replicates using a range of θ_i values in the sequence (0 to 0.08 by increments of 0.002) to assess the effects of search image only. For these simulations, handling time was held constant at 0.001. To determine the combined effects of search image and handling time, similar simulations were conducted over a range of θ_i values in the sequence (0 to 0.03 by increments of 0.01) and h_i values in the sequence (0.0015 to 0.1365 by increments of 0.015) for all possible combinations of θ_i and h_i. In both simulations, each replication began with a pair of prey species with initial populations set in complete anti-phase ($N_{1,0} = 10$, $N_{1,1} = 8$, $N_{2,0} = 10$, $N_{2,1} = 12$). For each replication, the first 200 generations were removed prior to obtaining correlation coefficients between the time series of the two prey species to remove any artifactual, transient dynamics and allow predation

pressures to synchronize the populations. An average correlation coefficient was calculated from 500 replications for each combination of θ_i in the first set of simulations and for all combinations of θ_i and h_i in the second set of simulations.

In the absence of shared predation, both prey populations maintained independent dynamics and drifted in and out of synch (Fig. 3a). In general, when predators did not have a search image for both prey species (when either θ_1 or θ_2 was 0) one or both of the predator search rates, γ_i, reduced to zero and the correlation between the two prey populations approached zero (Fig. 4). When predators removed prey from both populations ($\theta_1 > 0$ and $\theta_2 > 0$), predation had a synchronizing effect on the prey populations (Fig. 3b). Relative search images projected by the two prey species had a clear effect on the level of synchrony that occurred. Two prey species projecting equal search images were highly synchronized over all values of θ greater than zero, however populations were less synchronized when the two prey species had values of θ that were relatively distant from each other (Fig. 4). These results suggest that for prey species to be synchronized by generalist predators, they must share a similar degree of preference by the predator; otherwise the hunting time of the predator is consumed by the species with the greater search rate independent of prey density. This presumably results from the predator "favoring" one species over most density values. Holling's (1959) type III functional response models this effect, in which predators switch from a preferred prey species to an alternate prey species when the preferred species reaches low densities. This functional response occurs when a predator cannot hunt with equal efficiency for different prey species and devotes more time to the preferred species (i.e. the species with the greater search image) (Abrams and Matsuda 1996).

The level of synchrony decays further when a prey species with a relatively high search image also has relatively high handling time, or when both species with

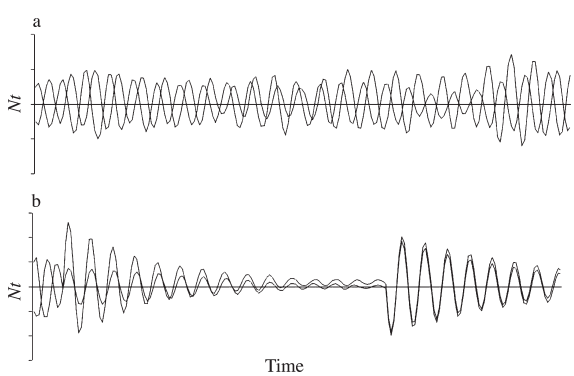

Fig. 3. (a) Two prey species in the absence of predation, (b) two prey species synchronized by the functional response of generalist predators ($\theta_1 = \theta_2 = 0.005$; $h_1 = h_2 = 0.02$).

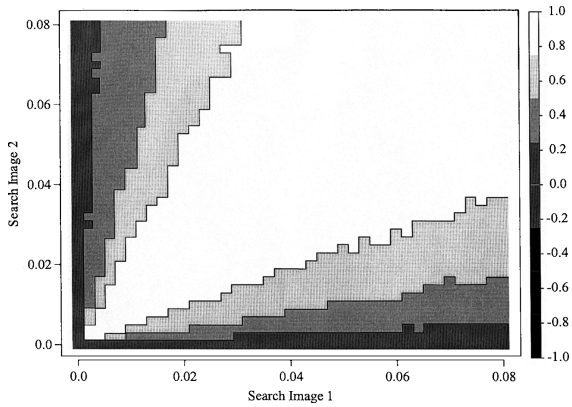

Fig. 4. Level of synchrony between two prey species projecting various search images. Handling time ($h = 0.001$) is constant. The gray scale for each search image combination is the average (of 500 iterations) cross-correlation of the two prey species' time series.

relatively similar search images each have high handling time (Fig. 5). The time spent handling prey reduces the time available to search for prey (Holling 1965). Therefore, if the prey species triggering a relatively higher search image requires more time to consume, the reduced search time results in lowered predation pressure that is not sufficient to synchronize populations. However, the values of handling time used in this simulation were unrealistically high compared to T, the total time prey species were exposed to predators (approximately 27–80% of total T to handle one prey). At more realistic values of h (<1% of total T) variations in handling time had no effect on synchrony. Although handling time may change with learned efficiency associated with higher densities (Murdoch 1973), this effect was not modeled in this study.

Discussion

Our model demonstrated that for any two sympatric species with population dynamics driven by similar but independent density dependent processes, predation by a shared generalist predator is capable of synchronizing the dynamics of the two species. These results demonstrate that predation by generalist predators is a possible cause of interspecific synchrony, in addition to numerical responses by specialist predators and shared stochastic (i.e. weather) effects.

Our model predicted that generalist predators will induce greater synchrony among sympatric prey species populations that project relatively similar search images. In the case study of oak-feeding caterpillars in the Slovak Republic, species within the same feeding group demonstrated greater synchrony than species in different feeding groups. Species within the same feeding guild exhibit relatively similar behavior (Mason 1987)

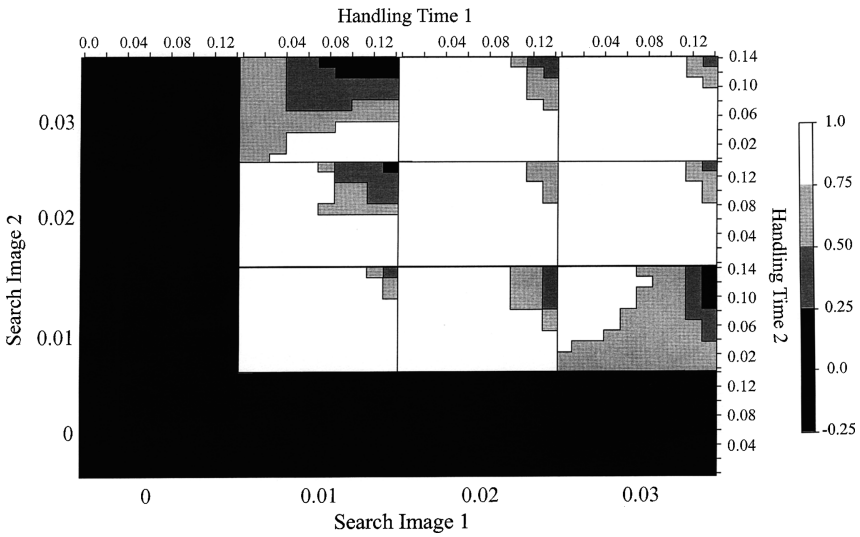

Fig. 5. Simulation results of a 2-prey/generalist predator system. Each large box represents various values of search image for prey species 1 and 2 and are labeled by the primary x and y-axes of the entire grid. The smaller grids within each large box represent varying values of handling time and are labeled by the secondary x and y-axes. This figure represents every combination of 4 values of search image and 10 values of handling time for 2 prey species (1600 combinations). The gray scale for each search image/handling time combination represents the average (of 500 iterations) cross-correlation of two prey species' time series.

and have converged on an adaptive morphology that maximizes performance within their life history strategy. Leaf-rolling larvae are generally of smaller size with reduced setation and prolegs, and spend the majority of their time as larvae living within the leaf shelter where they feed (Stehr 1998). These larvae would presumably project a search image that is very different from that of free-feeding larvae, which are generally larger, more mobile, and spend more time exposed to their predators. We can expect, therefore, that morphological and behavioral adaptations to a feeding niche would cause larvae within a feeding group to project relatively similar search images to a generalist predator compared to species in different feeding groups.

One exception to our findings was the lack of synchrony of *L. dispar* with other species within the free-feeding group. Although *L. dispar* converges with other free-feeding larvae in its behavior and many morphological features, it is a unique species in our study in that it possesses dense setation over much of its body, possibly projecting a different search image to predators. Lack of correlation between *L. dispar* and other species may also have been due to its unique dynamics compared to all other species. As an outbreaking species, populations of *L. dispar* periodically reach high- density extremes, the causes for which are not entirely known (Liebhold et al. 2000, Turcáni 2001). Therefore, periodic outbreaks of *L. dispar* may prevent synchronization of gypsy moth with populations of other species within a similar feeding niche.

Nomadic specialist predators have previously been implicated as causes of synchrony among allopatric populations of the same species by concentrating in patches of high density and reducing the prey density within these patches to the average density of a larger area (Ydenberg 1987). The guild-level synchronization of sympatric herbivore species by generalist predators demonstrated by our model functions in a similar manner, in which resident generalists concentrate on the prey species of higher density, reducing predation pressure on the prey species of lower density. This behavior is described by the predator functional response and an indirect interaction between prey species: an increase in density of one prey species decreases the predator functional response to the other, in turn increasing the density of the other prey (Abrams and Matsuda 1996). When predators also experience a positive numerical response to prey densities, prey species can indirectly depress each other ("apparent competition") by increasing the abundance of shared predators, which leads to prey species fluctuating in antiphase of each other or synchronous fluctuations with a time lag (Holt 1977, Abrams et al. 1998). In Holt's (1977) original model of apparent competition, numerical responses outweighed functional responses, thereby resulting in asynchronous dynamics of prey species. Our hypothesis of guild-level synchrony by generalist predators assumes that predators experience only a functional response to prey density, thereby resulting in prey synchronization.

Very little work regarding interspecific synchrony has been conducted and the theoretical groundwork is limited to models of nomadic specialist predators (Ims and Steen 1990). However, interspecific synchrony among specific groups of sympatric foliage feeding Lepidoptera (such as reported here) has been documented in earlier studies (Miller and Epstein 1986, Raimondo et al. 2004). Though our model demonstrates that the shared functional response by generalist predators may be the cause of the interspecific synchrony

observed in our data, we cannot exclude other possible mechanisms. Climatic factors can have both direct and indirect effects on insect populations (Martinat 1987) and have been implicated as a causal mechanism of interspecific synchrony (Small et al. 1993, Hawkins and Holyoak 1998, Myers 1998). Since sympatric species are exposed to the same random weather effects, this mechanism is likely to contribute to interspecific synchrony; however, it seems unlikely that this would cause greater levels of synchrony among species sharing similar feeding strategies as observed in the field data. Weather may also synchronize different species based on life history characteristics such as pupation strategy. All of the geometrids included in this study pupate in the soil over long periods of time; *A. aurantiaria*, *E. defoliaria* and *O. brumata* pupate underground during summer and fall months and the pupae of *A. aescularia* remain underground during summer, fall, and winter. The totricids used in this study pupate for only 1–2 weeks on the foliage, with the exception of *A. loeflingiana*, which pupates in the soil similarly to geometrids. Since *A. loeflingiana* was significantly correlated with all other torticids and with only one geometrid, synchronization by weather effects on the pupal stage is not strongly supported by our results.

Koenig (2001) associated interspecific synchrony of birds with diet categories but found only a weak relationship between synchrony and diet, concluding that other factors were integral in synchronizing populations. Bottom up factors, such as foliage quality, may have an influence on Lepidoptera dynamics and may be pursued as a possible synchronizing mechanism in future studies. Since all the species in this study feed on oak, this does not offer an alternative hypothesis capable of explaining the distinct difference in the synchrony of Lepidoptera with similar and different feeding groups. Rather, we expect that the synchronous dynamics observed in time series of oak-feeding Lepidoptera (Fig. 2, Table 2), as well as similar patterns of synchronous dynamics observed in the dynamics of other insect herbivores (Miller and Epstein 1986, Raimondo et al. 2004) could result as the combined effects of both synchronous stochastic effects (i.e. weather) and generalist predators.

Most predator–prey models simplify the complex multi-species interactions that operate in actual food webs. The system of forest Lepidoptera and generalist predators modeled here addresses the premise that generalist predators do not focus hunting on a single species, but are sensitive to a particular range of search images (Tinbergen 1960). Based on the results of our model, prey species within a range of search images are hunted with relatively equal efficiency by the generalist predator and in turn, are synchronized by the functional response of the predator. Using foliage-feeding Lepidoptera as an example, species projecting relatively similar search images are represented by species within a feeding guild, and may be viewed by generalist predators as one type of food choice. Although this model offers some insight into how guilds of generalist predators might impact the dynamics and synchrony among herbivores, data on predator impacts in specific communities are needed before the importance of generalist predators as synchronizing agents can be completely evaluated.

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