JOURNAL OF FOREST SCIENCE, *57*, 2011 (11): 472–482

Does intraguild predation of *Cosmia trapezina* L. (Lep.: Noctuidae) influence the abundance of other *Lepidoptera* forest pests?

M. Turčáni, J. Patočka†

Department of Forest Protection and Game Management, Faculty of Forestry and Wood Sciences, Czech University of Life Sciences Prague, Prague, Czech Republic

ABSTRACT: The noctuid *C. trapezina* (CT) has been considered an occasional predator of other *Lepidoptera* larvae. Functional/numerical response of predator and/or prey was estimated using 27 years of time-series data from Slovakia and stepwise multiple regression models (SMRM). SMRM were used to examine a possible delayed density-dependent feedback. We constructed 12 order-three autoregressive models [AR(3)] for CT and candidate prey. Independent variables were abundance of *C. trapezina* and abundance of candidate prey in lags 1, 2, and 3. Model variants were: (1) predation on free feeder models (FFM); (2) predation on shelter feeder models (SFM); (3) predation on the sum of 8 species models (S8M); (4) predation on all *Lepidoptera* models (ALM). Models were constructed for three areas (created by grouping sites based on significant correlations among CT populations). Additional comparative models were constructed for another three noctuid species and one geometrid species to compare their regression parameters under the same conditions as for CT. In total, 48 AR(3) SMRM were constructed for comparative species. A negative response of shelter feeders was found in models mainly for CT. We also found the positive response of CT growth rate to abundance of shelter feeders in lag 3 on two out of three models. This pattern was not found for any other comparison of species in the analysis. Possible mechanisms for these results are discussed.

Keywords: *Cosmia trapezina*; intraguild predation; *Lepidoptera* larvae; time series

The oak ecosystem in Central Europe includes more than 200 *Lepidoptera* species (Patočka et al. 1999). Some other authors suggested the presence of even more species, e.g. Csóka (1998) mentioned 292 species, Csóka and Szabóky (2005) reported 308 lepidopteran species belonging to 32 families that feed on oaks in Hungary. Among these are several unusual creatures that are usually competitors for sources of foliage but more or less regularly become also predators. They are represented mainly by the genus *Cosmia*, which includes species known to be occasional predators (in addition to *C. trapezina*, *C. pyralina*, which also lives on oaks although it prefers to feed on *Rosaceae*). Another two species of the genus, *C. diffinis* and *C. affinis*, feed on *Ulmus* spp. *Cosmia trapezina* is a widely polyphagous species feeding on hardwood trees in Europe. Various oak species are preferred host plants in Central Europe. Among these, *Quercus petraea* has been found to be the most preferred (Turčáni et al. 2009). This species does not usually reach great abundance but occasional small-scale outbreaks were recorded in eastern Slovakia during 1998–1999 (Turčáni, unpublished data). In comparison with some other species which feed in the springtime, *C. trapezina* is much larger (average length of mature larva is 36 mm). Considering the length of predicted prey species (17–21 mm), it might be an efficient predator. Larvae of *C. trapezina* are also more robust than are the prey species.

Eupsilia transversa is another entomophagous noctuid species. Entomophagy is known occasionally also in species of the genera *Orthosia* and *Lithophane* (particularly when reared artificially

The work on this research was partially supported by the project of Ministry of Agriculture of the Czech Republic QH71094 "*The use of dendrochronology in reconstruction of fluctuation cycles of nun and gypsy moths in central Europe*".

and with limited space and food supply). However, the incidence of predation in the last two genera is much less frequent than in the genera *Cosmia* and *Eupsilia*. In addition, predation by the tortricid *Zeiraphera isertana* on *Tortrix viridana* was reported by Schuette (1957). Generally, prey selection depends on the size of prey larva and larval feeding habit. Although the prey is generally smaller, *C. trapezina* larvae are able to feed on caterpillars up to their own size in the last instar. Prey often includes, among others, *Tortrix viridana*, *Aleimma loeflingiana* and other Tortricidae; Gelechiidae, *Operophtera brumata* and other Geometridae small to medium in size; and other Noctuidae (sometimes also individuals of the same species) (Patočka et al. 1999). In addition to *Lepidoptera* larvae, *C. trapezina* feeds also on other small insects such as *Aphidina* and *Psocoptera* (Patočka, unpublished data). On cold days, *C. trapezina* often enters into the shelters of *O. brumata*, *T. viridana* and others, consumes them, and then uses their shelter. Information from the literature indicates that this entomophagy is more or less occasional (the fact that the frequency of predation increases with prey abundance shows this to be a functional response). To date, however, no more exacting manipulative experiments focused upon the precise quantification of *C. trapezina* role have been conducted.

There are only a few ambush predators among *Lepidoptera* (Montgomery 1982), and these are known from the Hawaiian Islands (the genus *Eupithecia*, Geometridae). The relationship wherein a competitor for foliage resources is also a predator of its other competitors is considered to be a variant of intraguild predation, or "IGP" (Polis et al. 1989). Relative body size and degree of trophic specialization are two of the most important factors influencing the frequency and direction of IGP. Many IGP predators are also cannibalistic on smaller conspecifics. IGP sometimes increases with decreased abundance of non-guild prey, but at other times it increases with growing density of prey. The relationships between IGP and the relative abundance of guild and non-guild prey needs more study. Finally, IGP is sometimes directed preferentially towards the predator's closest potential competitors (i.e. those with the greatest resource overlap). This may result from direct selection to attack such prey or it may simply be a product of the fact that encounter rates typically increase with similarity of the niche use.

Findings of Arim and Marqueut (2004) suggest that IGP in different groups of predators and prey (i.e. carnivores, omnivores, herbivores, detritivores or top and intermediate species) deviates from the chance expectation so as to indicate that these attributes of species biology are main determinants of IGP persistence. Those authors suggested that IGP satisfies two basic requirements considered important for the trophic structuring of communities. First, its occurrence is not random (it is rather associated with well-defined attributes of species biology). Second, it is a widespread interaction.

Predation on guild members typically yields nutrition and energy gains that should increase growth, reproduction and survival. These gains may be especially important for IGP predators that feed primarily on plants (Polis 1981). While the animals are more than 50% of protein (7–14% N by weight), the plant tissue consists mostly of carbohydrates (with only 0.03–7% N). The resulting reduced competition for local resources should be another benefit for the IGP predator. More precisely, *C. trapezina* usually consumes foliage and it tends to be involved in interspecific competition. Feeding on larvae of other species should have two effects:

(1) *C. trapezina* eliminates part of the prey population and decreases competition. This pattern can scarcely be determined by a pure analysis of time series, because its effect is identical with that of competition.
(2) Feeding on energetically richer food should improve the fertility of females, sperm quality of males, and thus both the quality and quantity (numerical response) of new generations. As this effect should be delayed in time, it could be hidden by other processes taking place within populations.

Whereas specialist predators exhibit both numerical and functional responses to changes in prey density (Gotelli 2001), generalist predators typically demonstrate only a functional response (Linden, Wikman 1983; Weseloh 1990), and particularly when the prey species are not present throughout the entire hunting season. The exact food composition of CT is not known, but estimates that foliage provides the major portion of CT food (Patočka, unpublished data). Because of its high frequency of observed predation, however, the predation is probably quite a general behaviour and thus should be visible from a time series.

IGP systems are often characterized by the presence of indirect relationships among organisms. According to Venzon et al. (2001), in IGP systems it is possible to find apparent competition, interference, induced resistance, indirect defences or avoidance of predation. Maybe that the predation of *C. trapezina* also has indirect effects:

(1) Decreasing the number of shelter feeders and therefore also of shelters. It is known (Lill, Marquis 2003) that the architecture of leaves and the number of shelters are quite important also for other species not primarily making shelters but using them.

(2) The shelter feeders (Hunter et al. 1997) like *T. viridana* are particularly susceptible to intraspecific competition because even minor levels of leaf damage interfere with the integrity of *T. viridana* leaf rolls that are essential for osmoregulation. Predation of *C. trapezina* might be a factor reducing intraspecific competition among shelter feeders.

To use time series for the study of species interactions was suggested e.g. by Hunter (1998). He used time series to analyze interactions between *O. brumata* and *T. viridana* in England. Turchin (1990) suggested that *P*-values of standard regression are sufficiently robust to test for delayed density ($t_{-2,-3}$) effects on per capita rates of growth. However, the significance of rapid (t_{-1}) feedback may be overestimated by simple regression statistics. There is also a debate about the risk from interpreting pure time-series data (Hunter, Price 1998). It is also controversial that there exists a possibility to detect cycles and delayed density dependence (Turchin, Beryman 2000). Hunter and Price (1998, 2000) reanalyzed data and confirmed that density-dependence processes need not necessarily be responsible for the apparent negative feedback. Delayed effects were more important in the present study. Because density dependence is a logical consequence of ecological processes by which populations grow, it is expected in time-series analysis (Beryman 1991; Royama 1997). We therefore used simple regression statistics to identify relationships among species.

Our idea was to analyze abundance time series for *C. trapezina* (as potential predator) and 8 other species (as potential prey) to see if a pattern typical of predator-prey interactions among these species could be detected. The goal of these analyses was to test if observational data would support the *a priori* hypothesis that significant (visible from a time series) predator-prey interaction (expressed by the numerical/functional response of candidate predator/prey) should be detectable.

METHODS

Data collection and management

Sampling of oak *Lepidoptera* was conducted at 20 study sites annually during a period of 27 years (1955–1964 and 1966–1982; data missing for 1965) by Forest Research Institute of Slovakia, Zvolen (group leader J. Patočka) (Fig. 1). Twenty sample branches approximately 0.5 m in length were placed into a bag, cut and beaten against a tray. Samples were taken in mid-May from lower branches of the trees located near the forest edge. Exact sampling dates depended on altitude and annual weather conditions, but generally it was done each year between 10 and 20 May. All *Lepidoptera* larvae were identified to the species level by J. Patočka and counted. In some unclear cases, identification was done after rearing in the laboratory.

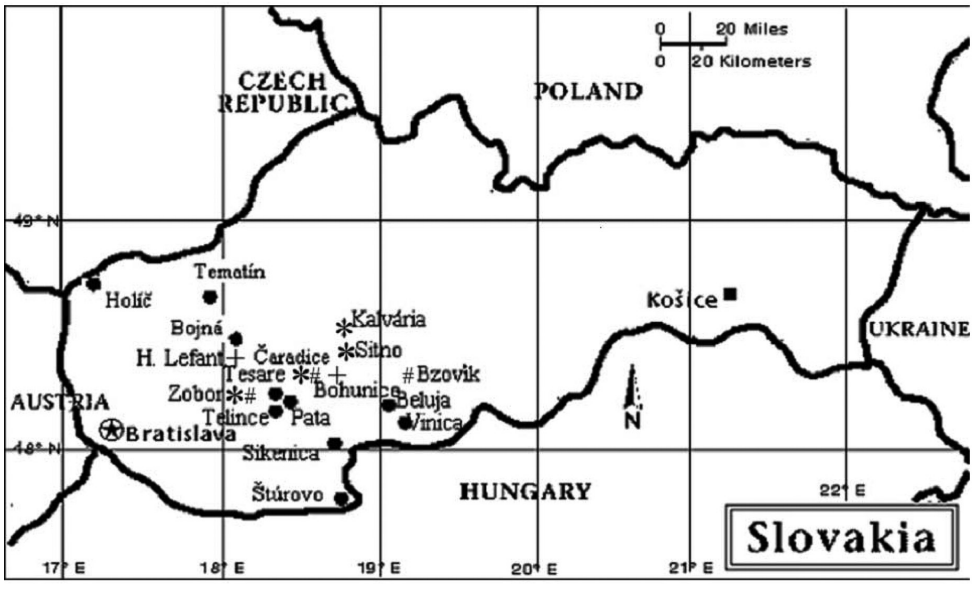

Fig. 1. Location of study sites and model areas A1, A2 and A3 in the Slovakia
*Area 1, #Area 2, *plus # plus + – Area 3

Selection of candidate prey species and study sites for analyses

Selection of potential prey species was based on an analysis by Turčáni (2006) from all 20 study sites and included the following: Tortricidae (shelter feeders) – *Archips xylosteana* (L.), *Eudemis profundana, Zeiraphera isertana*, *Tortricodes alternella*, Geometridae (free feeders) – *Operophtera brumata*, *Erannis defoliaria*, *Larerannis aurantiaria* and *Alsophila aescularia*. Larval counts for each of the eight most likely prey species were summed into time series.

Statistical analyses, preparation of models

Because of low abundance of the candidate predator on individual plots, we compiled data from several study sites. The compilation of closely related sites is based on synchrony among populations of the same species, which has been documented for a variety of taxa (Pollard 1991; Hansk, Woiwod 1993; Ranta et al. 1995; Bjørnstad 2000; Liebhold, Kamata 2000; Peltonen et al. 2002). One characteristic of synchronous dynamics is that nearby locations tend to be more synchronous than do populations separated by long distances. From 20 sites where the survey was done, only 7 related sites situated close to one another and with the highest abundance of *C. trapezina* were selected. Across the entire study period, 15 to 46 larvae of *C. trapezina* were found per site. In total, 164 individuals of *C. trapezina* were found during the study on selected sites. We compiled data in three ways (Fig. 1): Area 1 (A1) included the sites Caradice, Zobor, Sitno and Kalvaria (a group of sites among which *C. trapezina* time series were significantly correlated). Area 2 (A2) included the sites Caradice, Zobor and Bzovik (another group of sites where significant correlations among *C. trapezina* time series were found); Area 3 (A3) included all seven sites: Caradice, Zobor, H. Lefantovce, Bohunice, Sitno, Kalvaria and Bzovik.

We prepared several types of order-three autoregressive models [AR(3)] as follows: Sum of 8 species models (S8M) – all 8 prey species which are the most related to CT according to Turčáni (2006). Free feeder models (FFM) – where only free feeders were selected to compare also differences in the pattern between free and shelter feeders. Shelter feeder models (SFM) – due to some indications that larvae of *C. trapezina* are frequently found in shelters of tortricids, and also of gelechiids (Čapek 1973), we

Table 1. Multiple regression parameters of AR(3) models in Area 1

		$C.t._{T-1}$	$C.t._{T-2}$	$C.t._{T-3}$	$S.F._{T-1}$	$S.F._{T-2}$	$S.F._{T-3}$	$O.ce._{T-1}$	$O.ce._{T-2}$	$O.ce._{T-3}$	$S.F._{T-1}$	$S.F._{T-2}$	$S.F._{T-3}$	$O.cr._{T-1}$	$O.cr._{T-2}$	$O.cr._{T-3}$	$S.F._{T-1}$	$S.F._{T-2}$	$S.F._{T-3}$
Regression coefficients	PCR of predator	−0.7738				−0.383	0.5568	−0.5068						−0.8589		−0.4612			
		(−0.0018)				(−0.0969)	(−0.0221)	(−0.0397)						(−0.0009)		(−0.1135)			
	PCR of prey			−0.607	−0.9308		0.647			−0.9509	−0.779		0.5646	−0.5732			−0.8791		0.4047
				(−0.0597)	(−0.0004)		(−0.0124)			(−0.1838)	(−0.0026)		(−0.0296)	(−0.028)			(−0.0004)		(−0.0532)
Partial R^2 (p−values)	PCR of predator	0.474				0.0653	0.1014	0.2044						0.416		0.0778			
		(−0.0006)				(−0.0969)	(−0.0528)	(−0.0397)						(−0.0016)		(−0.1135)			
	PCR of prey			0.1016	0.3667		0.1076			0.0533	0.3667		0.1076	0.1411			0.3667		0.0997
				(−0.0597)	(−0.0036)		(−0.071)			(−0.1838)	(−0.0036)		(−0.071)	(−0.0356)			(−0.0036)		(−0.0532)

C.t.T−1= Cosmia trapezina abundance in previous year, C.t.T−2= Cosmia trapezina abundance in a year before previous year, C.t.T−3= Cosmia trapezina abundance 2 years before previous year $O.ce._{T-1}$= *Orthosia cerasi* abundance in previous year, $O.ce._{T-2}$= *Orthosia cerasi* abundance in a year before previous year, $O.ce._{T-3}$= *Orthosia cerasi* abundance 2 years before previous year $O.cr._{T-1}$= *Orthosia cruda* abundance in previous year, $O.cr._{T-2}$= *Orthosia cruda* abundance in a year before previous year, $O.cr._{T-3}$= *Orthosia cruda* abundance 2 years before previous year $S.F._{T-1}$= Shelter feeders abundance in previous year, $S.F._{T-2}$= Shelter feeders abundance in a year before previous year, $S.F._{T-3}$= Shelter feeders abundance 2 years before previous year PCR=per capita growth rate

summed also this category. All *Lepidoptera* models (ALM) – in which all *Lepidoptera* found on the sites were included. Patočka (unpublished data) reported direct observations of *C. trapezina* predation on many *Lepidoptera* species, but we had no information about the frequency of predation broken out by species. The abundance of *C. trapezina* was often lower than 1% of the total number of all *Lepidoptera*.

Applied methods

All data in the models were transformed as $\log_{(x+1)}$ and the time series were checked for trends prior to further analyses. Trends were found only occasionally and we continued running the models with non-detrended data. Stepwise multiple regression analysis was applied to the data to examine possible delayed density-dependent feedback processes. The dependent variables in the stepwise multiple regression models (SMRM) were per capita growth rates [$r_t = \ln (N_t/N_{t-1})$] of *C. trapezina* and prey, and the independent variables were abundance of *C. trapezina* and prey at times t_{-1}, t_{-2} and t_{-3}.

We analyzed processes in populations up to 3 lag orders. The decision to analyze greater than 2 lag orders was based on two considerations. First, we analyzed the autocorrelation and partial autocorrelation functions, and there were indications that in the cases of several species included in the study populations it was necessary to go higher than to the second-order density dependence. Second, Royama (1997) formulated three reasons for going higher than AR(2), two of which were applicable for this study: (a) when the realization of density effect is somehow delayed in time, as it should be possible in the case of intraguild predation when the negative effect of the predator on the prey is relatively small and the positive effect of the prey on the predator as expressed by numerical response should appear after several seasons; (b) when the population of a given species interacts with populations of other species (even if there is no delayed effect). In this case, rapid and delayed competition between *C. trapezina* and other *Lepidoptera* should be an interaction making the effect of predation in lag 2 less visible.

Because the pattern of numerical response may not be clear in a time series, we selected also additional *Lepidoptera* species for comparison (all species being approximately of the same size and with similar feeding strategies). Among these, three other noctuid species and one geometrid species were selected for comparative analysis. The noctuid *Conistra vaccinii* and geometrid *Erannis defoliaria* have never been observed to feed on other larvae. *Orthosia cerasi* and *Orthosia cruda* were selected as species observed in rare occasions to hunt other *Lepidoptera* larvae, although we have not directly observed such predation in Slovakia. The same SMRM procedure was also used for the models with comparative species and the selected sites were identical with those for *C. trapezina*. The dependent variables in the regression models with *C. vaccinii*, *O. cerasi*, *O. cruda,* and *E. defoliaria* were the per capita growth rates [$r_t = \ln (N_t/N_{t-1})$] for each of the candidate predator species and preys divided into groups, and the independent variables were abundance of *C. vaccinii*, *O. cerasi*, *O. cruda* and *E. defoliaria* and prey at times t_{-1}, t_{-2} and t_{-3}.

In all cases the boundary level to enter into multiple regression was $P < 0.25$, to leave it was $P < 0.10$. Degrees of freedom were in a range of 21 to 22, depending on the independent factors entering the model.

RESULTS

Characteristics of populations used for building up models

S8M (not represented in Fig., due to high similarity to ALM lines): Linear trends of populations of both *C. trapezina* and candidate prey species were more or less stationary, with a non-significant decline of the prey population during the study period. Abundance of *C. trapezina* according to site accounted for 1.6–7.6% of the abundance of the candidate prey. *FFM* (Fig. 1): Trends were similar to the aforementioned case in all study areas. Abundance of *C. trapezina* accounted for 2.4–8.8% of free feeders. *SFM* (Fig. 2): Trends were decreasing for A1 and A3 in this instance. For this reason, the models were run also with detrended data in these cases. Abundance of *C. trapezina* accounted for 5–55% of shelter feeder numbers. *ALM* (Fig. 2): Because of an outbreak of geometrids in the early 1960's, trends of *Lepidoptera* were slightly but insignificantly decreasing. The proportion of *C. trapezina* in the abundance of all *Lepidoptera* always was lower than 1%.

Models with *C. trapezina* (Tables 1–3)

SFM-AR(3) models: Competition or predator-prey relationship?

Higher abundance of shelter feeders in t_{-3} reflected a higher growth rate of *C. trapezina* in A1 and in A3, thus explaining 10.1 and 15.5% of vari-

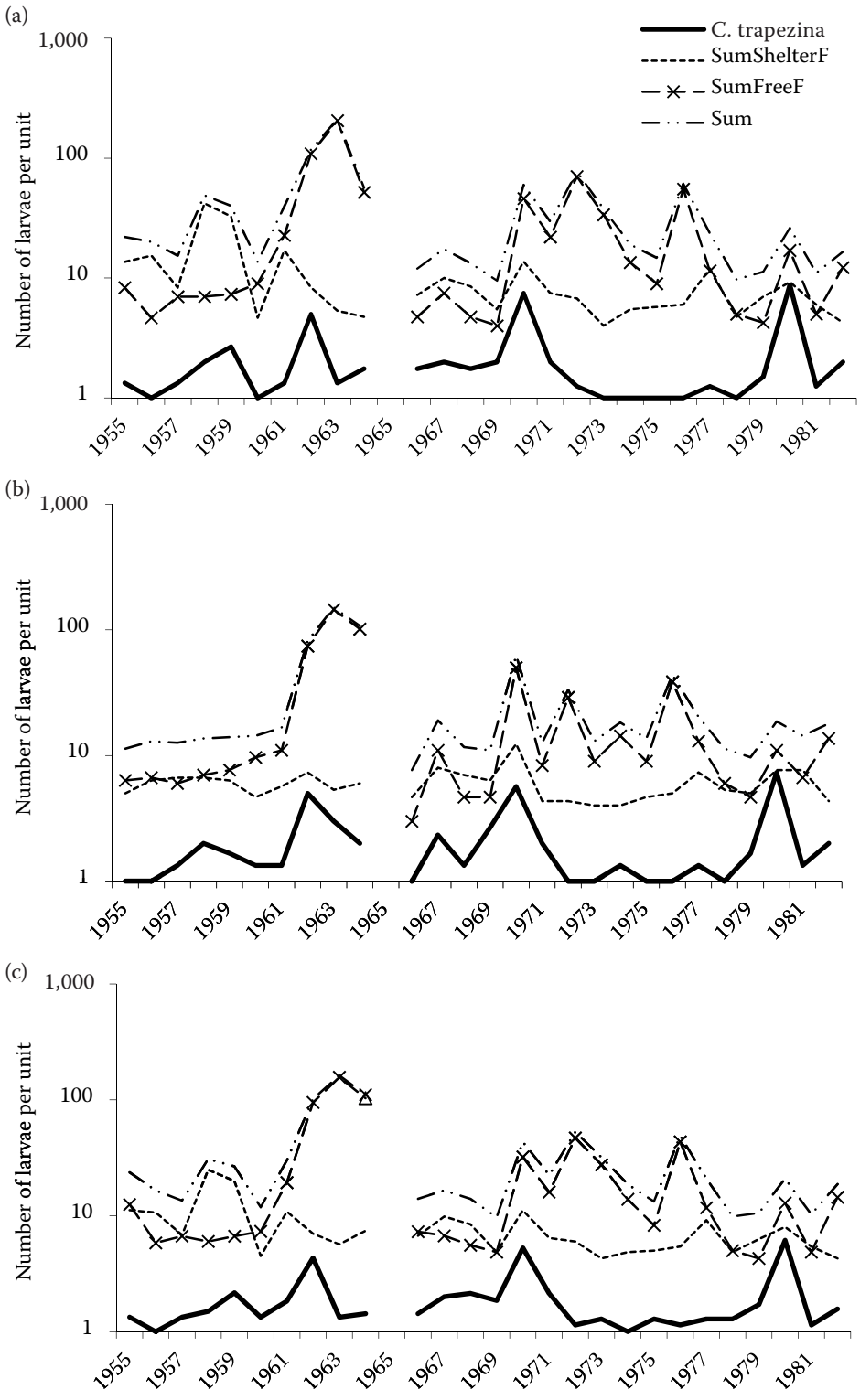

Fig. 2. Fluctuation of *Lepidoptera* groups (larvae per unit) used in models in study area A1 (a), A2 (b) and A3 (c) during study period

ance, respectively, in the growth rate of *C. trapezina* (Figs. 3a, b). This positive feedback of *C. trapezina* could be caused by benefits from predation or by another mechanism unknown to us. In the case of A2, this pattern was not found. By contrast, higher abundance of *C. trapezina* was associated with lower growth rates for shelter feeders in all study areas. At A1 and A3 in t_{-3} the growth rate of shelter feeders explained 10.2 and 14.6%, respectively (Figs. 3c, d), while at A2 in t_{-2} it explained 7.8% of the variance (Fig. 3 e). In this case, the negative feedback of shelter feeders to delayed abundance of *C. trapezina* is an indication of delayed competition between shelter feeders and *C. trapezina* and/or the effect *C. trapezina* predation of the prey population.

Table 2. Multiple regression parameters of AR(3) models in Area 2

		C.t.$_{T-1}$	*C.t.*$_{T-2}$	*C.t.*$_{T-3}$	S.F.$_{T-1}$	S.F.$_{T-2}$	S.F.$_{T-3}$	*O.ce.*$_{T-1}$	*O.ce.*$_{T-2}$	*O.ce.*$_{T-3}$	S.F.$_{T-1}$	S.F.$_{T-2}$	S.F.$_{T-3}$	*O.cr.*$_{T-1}$	*O.cr.*$_{T-2}$	*O.cr.*$_{T-3}$	S.F.$_{T-1}$	S.F.$_{T-2}$	S.F.$_{T-3}$
Regression coefficients (p–values)	PCR of predator	−0.7724						−0.5294	1.5717		−0.183	−0.3799		−0.8902					
		(−0.0024)						(−0.0017)	0		(−0.1271)	(−0.0054)		(−0.001)					
	PCR of prey		−0.294		−0.8291	0.3969			0.8707		−1.125	−0.2856			−0.5102	−0.3019	−1.409		
			(−0.0421)		(−0.0015)	(−0.1896)			(−0.0545)		(−0.0001)	(−0.2398)			(−0.0315)	(−0.2208)	0		
Partial R^2 (p–values)	PCR of predator	0.3915						0.2375	0.3345		0.0385	0.1518		0.4434					
		(−0.0024)						(−0.0054)	(−0.006)		(−0.1271)	(−0.0071)		(−0.001)					
	PCR of prey		0.0781		0.4259	0.0491			0.0618		0.5331	0.0325			0.1001	0.0318	0.5331		
			(−0.1094)		(−0.0013)	(−0.1896)			(−0.1148)		(−0.0002)	(−0.2398)			(−0.0398)	(−0.2208)	(−0.0002)		

Table 3. Multiple regression parameters of AR(3) models in Area 3

		C.t.$_{T-1}$	*C.t.*$_{T-2}$	*C.t.*$_{T-3}$	S.F.$_{T-1}$	S.F.$_{T-2}$	S.F.$_{T-3}$	*O.ce.*$_{T-1}$	*O.ce.*$_{T-2}$	*O.ce.*$_{T-3}$	S.F.$_{T-1}$	S.F.$_{T-2}$	S.F.$_{T-3}$	*O.cr.*$_{T-1}$	*O.cr.*$_{T-2}$	*O.cr.*$_{T-3}$	S.F.$_{T-1}$	S.F.$_{T-2}$	S.F.$_{T-3}$
Regression coefficients (p–values)	PCR of predator	−0.8042				−0.2991	0.6399	−0.4258						−0.8204		−0.464			
		(−0.0007)				(−0.1762)	(−0.0075)	(−0.0703)						(−0.0013)		(−0.1674)			
	PCR of prey			−0.69	−0.9884		0.6559		0.5849		−0.864		0.4527		−0.4927		−1.042		0.4676
				(−0.0135)	(−0.0001)		(−0.0032)		(−0.2339)		(−0.0007)		(−0.0404)		(−0.115)		(−0.0003)		(−0.0302)
Partial R^2 (p–values)	PCR of predator	0.4718				0.0391	0.1553	0.1622						0.4099		0.0609			
		(−0.0006)				(−0.1762)	(−0.0135)	(−0.0703)						(−0.0018)		(−0.1674)			
	PCR of prey			−0.146	0.3993		0.1271		0.039		0.3993		0.1271		0.0661		0.3993		0.1271
				(−0.0135)	(−0.0021)		(−0.0413)		(−0.2339)		(−0.0021)		(−0.0413)		(−0.115)		(−0.0021)		(−0.0413)

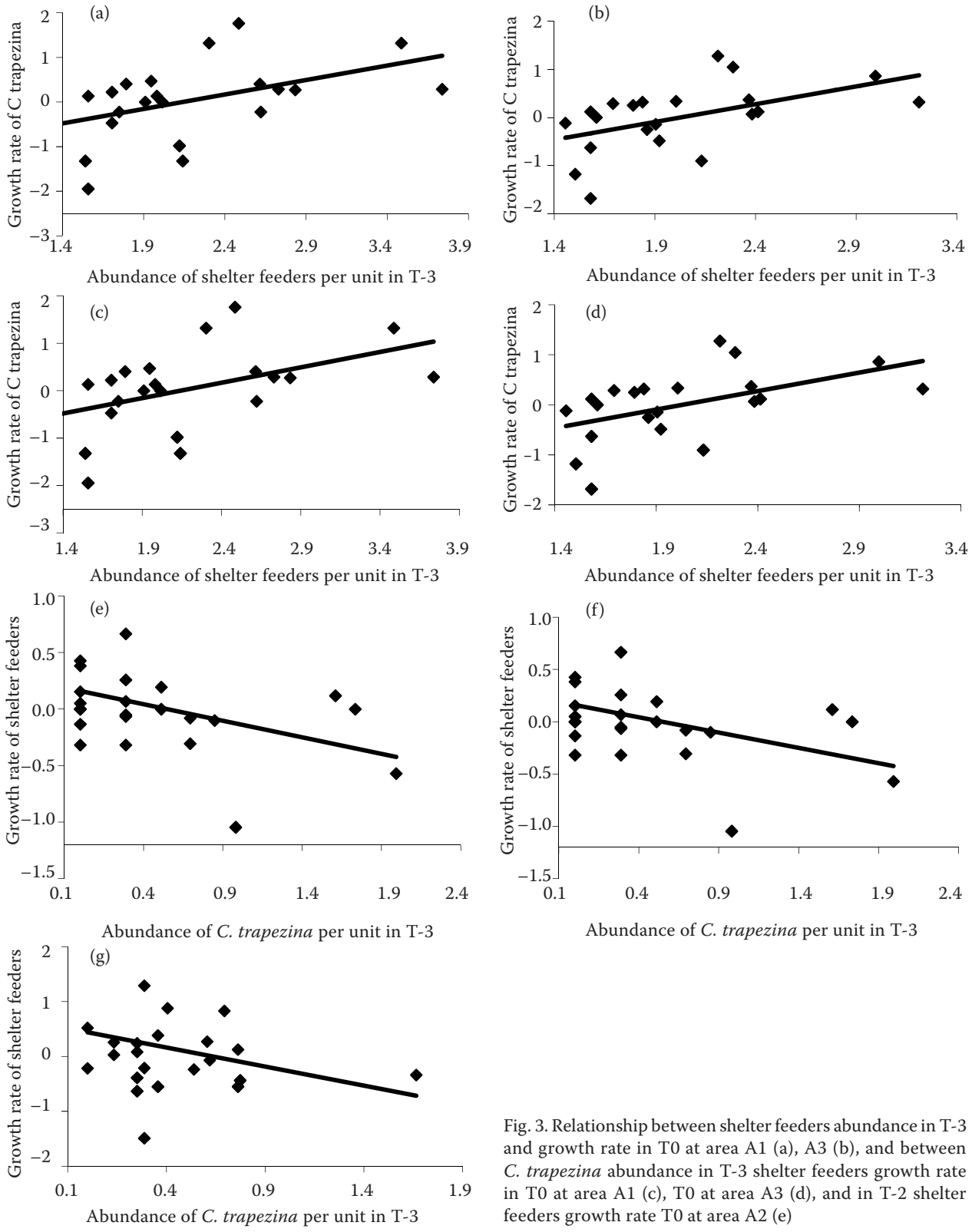

Fig. 3. Relationship between shelter feeders abundance in T-3 and growth rate in T0 at area A1 (a), A3 (b), and between *C. trapezina* abundance in T-3 shelter feeders growth rate in T0 at area A1 (c), T0 at area A3 (d), and in T-2 shelter feeders growth rate T0 at area A2 (e)

Comparative models with *C. vaccinii, O. cerasi, O. cruda* and *E. defoliaria* (Tables 1–3)

In models with *C. vaccinii* we found no patterns as in the case of *C. trapezina*, when delayed competition and/or predation and/or positive effect of candidate prey species on the growth rate of *C. vaccinii* was negligible. In the case of *O. cerasi*, a positive effect of shelter feeders in t_{-1} and t_{-2} is suggested by results at A2 where the higher abundance of all above-mentioned groups of *Lepidoptera* was associated with the higher growth rate of *O. cerasi*. In just one case the abundance of *O. cerasi* in t_{-3} entered into a shelter feeder model explained as

much as 5.3% of the variability in the growth rate of shelter feeders. A higher abundance of *O. cerasi* reflected a lower growth rate for shelter feeders, which should be the result of delayed competition or possible predation. A low abundance of *O. cruda* in t_{-1} generally reflected its own higher growth rate. Higher *O. cruda* abundance in t_{-1} also reflected a lower growth rate of shelter feeders that should indicate direct competition. The analysis of *E. defoliaria* showed results quite different from those for noctuids. The results of several models showed the absence of any regression relationships between abundance in $t_{-1,-2}$ and growth rate. An abundance of *E. defoliaria* several times higher in t_{-2} and t_{-3} reflected a lower growth rate of shelter feeders that suggested delayed competition (predation by *E. defoliaria* has never been seen even in mass artificial rearing and with lack of food). This pattern was found in the groups of shelter feeders and all *Lepidoptera* but not in those of free feeders, thus suggesting that the robust species like *E. defoliaria* is probably a competitor mainly for smaller species using shelters.

In summary, by the comparison of SWRM models of *C. trapezina*, *C. vaccinii, O. cerasi, O. cruda* and *E. defoliaria* we found fluctuation differences between *C. trapezina* and other species. Only in the case of *C. trapezina* models did the higher abundance of this species reflect a lower growth rate of shelter feeders (with only one exception in the case of *O. cruda*). In the models, a higher growth rate for *C. trapezina* reflected a higher abundance of shelter feeders in lag 3. This numerical response in populations of *C. trapezina* (as a candidate predator) should indicate that IGP of *C. trapezina* could be detected to some extent by analyzing time-series data.

DISCUSSION

It is not easy to explain the processes at work in natural populations without precise knowledge of their mechanisms. The best possibility of studying some processes is through manipulative experiments in the laboratory (Hunter 1998). In this case, however, it is almost impossible to incorporate into the experiments all ecosystem variables such as stochastic factors (weather), parasitoids, predators and to conduct the experiments in variable conditions over a long time period. Experiments of this sort are known only from simple systems and are limited to micro- or mesocosms (Jannsen et al. 1998; Venzon et al. 2001). Some authors (Hunter, Price 1998; Turchin, Beryman 2000) agreed with the idea that the time-series analysis cannot by itself identify the mechanism responsible for population fluctuation. Beryman and Turchin (1997) indicated that time series provide us with a diagnostic probe but not a definitive test of hypotheses. Following their recommendations, the time-series analysis can help us to decide which hypotheses should be tested as the first and may thereby save us time, efforts and money.

Because *C. trapezina* feeds not only on prey but also on foliage, the predator-prey system could be hidden by other processes in the populations. Predation not occurring on a massive scale could be underestimated in the mirror of rapid and/or delayed feedback processes, and more precisely by interspecific competition between predator and prey. In spite of the fact that the hunting of smaller *Lepidoptera larvae* by *C. trapezina* is a reality, it is not easy to find evidence of predation in this food web from time series. The results could also be limited by methodology used for data collection (due to high variability between samples). If there is some evidence detectable by using the analysis of time series, the impact of predation could be small and might be overlooked by the statistical methods used.

As mentioned by Hunter et al. (1997), the time-series analysis alone does not provide adequate information to estimate the relative roles of top-down and bottom-up forces in insect populations (Royama 1997). As Hunter et al. (1997) continued, it is only in combination with experimental studies that the importance of processes in populations has been demonstrated. They nonetheless believed that the time-series analysis of data collected at the appropriate spatial scale (i.e. the level of the plant) is a valuable tool – in combination with experiments – for estimating the relative importance of top-down and bottom-up forces for herbivore populations.

Even though we had no information from manipulative experiments focused on the predation of *C. trapezina*, the junior author has many years' experience of directly observing all the species involved in the study. In combination with detailed knowledge of life-history traits (Turčáni et al. 2009) and the possibility to compare several model species, to the best of our knowledge, it is possible to use time-series data to study relationships among individual species. Of course, as we found several times, it is not easy to identify the reasons for regression coefficients and this requires the well-established knowledge of the *Lepidoptera* in the studied community. In spite of the good knowl-

edge of the life-history traits and behaviour of the studied species, we were not able to reach unambiguous conclusions in all cases.

Based on the results, it seems that the relationship of shelter feeders to CT is stronger than is that of free feeders. *C. trapezina* and *O. cruda* had negative effects in relation to shelter feeders, but others did not. The explanation of this fact probably lies in their tendency to predation. *C. trapezina* has a much stronger tendency to predation than do the other three noctuid species. The tendencies of *O. cerasi* and *O. cruda* to predation are only about 20–30% of that of *C. trapezina* (Patočka, unpublished data). A pattern from this low predatory potential of the genus *Orthosia* would be almost invisible in a time series. Only if the abundance of these species were to be much higher, it would be visible. The abundance of *O. cerasi* was lower than that for *C. trapezina* at all 20 sites. In the case of *O. cruda*, abundance at all sites was three times greater than that of *C. trapezina*. At A2, where the effect of *O. cruda* was found, the abundance amounted to only a half of *C. trapezina* abundance and we cannot assess whether or not the pattern was caused by predation.

CONCLUSIONS

The purpose of subjecting the data on *C. trapezina* and in relationship to other *Lepidoptera* to the time-series analysis was to test an *a priori* hypothesis developed from direct observations of these oak insects. The results suggest that populations of the studied species are influenced especially by intraspecific competition, and that this is a general pattern in the populations. The results also suggest that interaction between *C. trapezina* as a predator and some groups of *Lepidoptera* – as prey – is visible in some cases from the time-series analysis. Inasmuch as no relationship was found between *C. trapezina* and *Lymantria dispar*, defoliation by the gypsy moth is not probably influenced by intraguild predation and thus this relationship is not probably visible from dendrochronology studies. Due to a lack of information from life tables or experimental studies, we cannot conclude what the exact mechanisms underlying the population changes for *C. trapezina* and other *Lepidoptera* are like. There remains a possibility that both statistical difficulties and unrecognized exogenous drivers could have resulted in identifying the apparent predator-prey pattern found in the time series. Nonetheless, this time-series analysis provides valuable information for additional manipulative experiments to study the system of intraguild predation among *Lepidoptera* on oaks in Central Europe.

Acknowledgement

We would like to thank the staff of Forest Research Institute (Slovakia) for their efforts during the fieldwork and also the technicians who transferred data from field sheets to an electronic form.

References

Arim M., Marqueut P.A. (2004): Intraguild predation: a widespread interaction related to species biology. Ecology Letters, ***7***: 557–564.

Beryman A.A. (1991): Stabilization or regulation: what it all means! Oecologia, ***86***: 140–143.

Beryman A.A., Turchin P. (1997): Detection of delayed density dependence: comment. Ecology, ***78***: 318–320.

Bjørnstad O.N. (2000): Cycles and synchrony: two historical 'experiments' and one experience. Journal of Animal Ecology, ***69***: 869–873.

Csóka Gy. (1998): Naturally occuring insect defoliators on the oaks in the Hungary. Erdészeti Kutatások, ***88***: 311–318. (in Hungrian)

Csóka Gy., Szabóky Cs. (2005): Cheklist of Herbivorous Insects of Native and Exotic Oaks in Hungary I (*Lepidoptera*). Acta Silvatica et Lignaria Hungarica, ***1***: 59–72.

Čapek M. (1973): The results of study of influence of natural enemies on some oak defoliators during the latency phase. Zvolen, Vedecké práce Výskumného ústavu lesného hospodárstva vo Zvolene: 189–202. (in Slovak)

Gotelli N. J. (2001): A Primer of Ecology. 3rd Ed. Sunderland, Sinauer Associates: 265.

Hunter D.M. (1998): Interactions between *Operophtera brumata* and *Tortrix viridana* on oak: new evidence from time-series analysis. Ecological Entomology, ***23***: 168–173.

Hunter M.D., Varley G.C., Grandwell G.R. (1997): Estimating the relative roles of top-down and bottom-up forces on insect herbivore populations: A classic study revisited. Proceedings of the National Academy of Sciences USA, ***94***: 9176–9181.

Hunter D.M., Price W.P. (1998): Cycles in insect populations: delayed density dependence or exogenous driving variables? Ecological Entomology, ***23***: 216–222.

Hunter D. M., Price W. P. (2000): Detecting cycles and delayed density dependence: a reply to Turchin and Berryman. Ecological Entomology, ***25***: 122–124.

Liebhold A., Kamata N. (2000): Are population cycles and spatial synchrony a universal characteristic of forest insect populations? Population Ecology, ***42***: 205–209.

Lill J.T., Marquis R.J. (2003): Ecosystem engineering by caterpillars increases insect herbivore diversity on white oak. Ecology, ***84***: 682–690.

Linden H., Wikman M. (1983): Goshawk predation on tetraonids: availability of prey and diet of the predator in the breeding season. Journal of Animal Ecology, ***52***: 953–968.

Montgomery S.L. (1982): Biogeography of the moth genus Eupithecia in Oceania and the evolution of ambush predation in Hawaiian caterpillars (*Lepidoptera*: Geometridae). Entomologia Generalis, ***8*** (1): 27–34.

Patočka J., Krištín A., Kulfan, J., Zach P. (1999): Die Eichenschädlinge und ihre Feinde. Zvolen, Institut für Waldökologie der Slowakischen Akademie der Wissenschaften: 396.

Peltonen M., Liebhold A.M., Bjornstad O.N., Williams, D.W. (2002): Spatial synchrony in forest insect outbreaks: roles of regional stochasticity and dispersal. Ecology, ***83***: 3120–3129.

Polis G. A. (1981): The evolution and dynamics of intraspecific predation. ARES, ***12***: 225–251.

Polis G.A., Myers C.A., Holt R.D. (1989): The ecology and evolution of intraguild predation: potential competitors that eat each other. Annual Review of Ecology and Systematics, ***20***: 297–330.

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., Linden H. (1995): Synchrony in population dynamics. Proceedings of the Royal Society of London B, ***262***: 113–118.

Royama T. (1997): Population persistance and density dependence. Ecological Monographs, ***47***: 1–35.

Schuette F. (1957): Übersuchungen über die Populationsdynamik des Eichenwicklers (*Tortrix viridana* L.). Zeitschrift für Angewandte Entomologie–Journal of Applied Entomology, ***40***: 285–331.

Turchin P. (1990): Rarity of density dependence or population regulation with lags? Nature, ***344***: 660–663

Turchin P., Beryman A. A. (2000): Detecting cycles and delayed density dependance: a comment on Hunter and Price (1998): Ecological Entomology, ***25***: 119–121.

Turčani M. (2006): Selected aspects of abundance dynamics of model moth defoliators and possible impact of climate change to that dynamics in the southwestern Slovakia [Habilitation Thesis] Prague, Czech University of Life Sciences Prague: 156. (in Czech)

Turčáni M., Patočka J., Kulfan M. (2009): How do lepidopteran seasonal guilds differ on some oaks (*Quercus* spp.) – A case study. Journal of Forest Science, ***55***: 578–590.

Venzon M., Jansses A., Sabelis M.W. (2001): Prey preference, intraguild predation and population dynamics of an arthropod food web on plants. Experimental and Applied Acarology, ***25***: 785–808.

Weseloh R.M. (1990): Gypsy moth predators: an example of generalist and specialist natural enemies. In: Watt A.D., Leather S.R., Hunter M.D., Kidd N.A.C. (eds): Population Dynamics of Forest Insects. Intercept L.T.D., Andover: 233–243.

Received for publication September 23, 2010
Accepted after corrections August 24, 2011

Corresponding author:
Prof. Ing. Marek Turčáni, PhD., Czech University of Life Sciences Prague, Faculty of Forestry and Wood Sciences, Department of Forest Protection and Game Management, 165 21 Praha 6-Suchdol, Czech Republic
e-mail: turcani@fld.czu.cz