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Diversity and variability of Lepidoptera populations in urban Brno, Czech Republic

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Urban entomology, Lepidoptera, diversity, stability, variability, light-trap

Abstract. Lepidoptera populations were monitored during 29 years by a light-trap in urban Brno. Compared with other sites in the Czech Republic (Prague-Ruzyně, České Budějovice, Černiš) urban Brno was extraordinarily rich in species, richer than the other Czech sites studied and richer than many British sites in an urban to natural gradient. Variability of the more common species at Brno was as high as that at the ruderal/deteriorated agricultural setting at České Budějovice, and generally higher than that in the wet forest environment at Černiš and much higher than in the park-like/suburban/agricultural setting of Prague. Voltinism had no effect on variability from year to year. Most of the more common species in Brno clearly increased in abundance over the years, unlike those at the other sites. Much of the large diversity at Brno, however, was because of a large number of accidental species, vagrants from elsewhere. When considering only the more common species (≥ 5 individuals per year), however, Brno is among the most species-poor sites. The common species at Brno were mostly tramp species that could take advantage of whatever food and habitat the city had to offer.

Because of strong correlations in abundance between species at one site with conspecifics at other sites over distances of 150–200 km, the abundances in these populations are apparently strongly affected by large-scale processes such as weather, overriding in part large differences between the habitats or by large-scale dispersal of individuals between sites. Significant correlations also existed between conspecifics in these sites in variability as well as in trends in time, with the curious exception of Černiš, the only reasonably natural habitat, suggesting that these parameters are strongly affected by local habitat characteristics.

INTRODUCTION

Taylor et al. (1978) discussed diversity and variability of Lepidoptera in and around urban environments in Great Britain. They showed that maps of the total number of individuals and, especially, of species diversity (measured as the α-diversity index) generally clearly identify urban centers as areas with low numbers and low diversity as compared with surrounding sites. A gradient near London exemplified this trend. At the same time population variability tended to increase with increasing urbanization of the site. A similar trend in diversity was found in Homoptera in Panama (Wolda, 1987), and for beetles in Germany (Klomann, 1975). One would expect urbanization to have such effects. However, such trends were not as obvious for a gradient selected in north-east England (Taylor et al., 1978). Davis (1978) found strong effects of some measures of urbanization on species richness in the greater London area, making clear that the exact structure of the city, the presence of open spaces, of parkland and of gardens, is of prime importance, so that species diversity in one city may be very different from that in another, dependent on the availability of suitable habitats. Taylor (1978) shows urban habitats in general to have a lower insect diversity in Britain. However, there seem to be variants on this theme. In some cities the fauna can be surprisingly rich (Dickman, 1987). Nuorteva (1971) found a much greater bird biomass, but far fewer species, inside the city of Helsinki than in rural areas or in forest. Jacobs (1975) concluded "the multitude of long-term shifts of ecosystems created by man very often reduces species richness and diversity, but probably in as many cases increases it, especially where man creates new diverse structures in a formerly uniform habitat, and maintains these structures in a relatively stable state." To further examine the effects of urbanization on insect diversity, more data from more cities are needed. Unfortunately, outside of the Rothamsted Insect Survey in Great Britain, there is precious little information available. Several interesting studies have been made in suburban and urban environments (Schoof & Savage, 1955; Schoof et al., 1956; Fleet et al., 1978; Owen & Chanter, 1972; Owen D.F., 1976, 1977, 1978; Owen J., 1981, 1991, see Davis (1978) for further references). Rarely, however, were simultaneous similar studies done in other habitats in the same general area that would make comparisons possible. When there are extensive data covering a large number of sites, urban and suburban habitats tend to be avoided, both in insects (Den Boer 1977; Pollard et al., 1986) and in other organisms such as birds (Marchant et al., 1990).

In the present paper we describe the diversity, stability and variability of the moth fauna in urban Brno, studied for 29 years by means of light-trap, and compare the results with light-trap collections of moths from three other sites in the Czech Republic.

METHODS

One of us (JM) has maintained a Jermy-type light-trap (Jermy, 1961 – in Mesch, 1965) on the north- and west-facing balcony of his institute at the Agricultural University in Brno since 1963, and data used here cover the years to 1991 inclusive. The first three years it operated with a 200 W incandescent light bulb, after that with a 125 W mercury-vapor lamp. In 1963 the trap overlooked some experimental fields and an orchard, with an arboretum remnant along the northern limit of the university property. To the north is an arboretum. Over the years several changes have taken place. In 1963 the trap site was towards the edge of the city, but now the area is surrounded by housing developments, generally with gardens, a sport stadium, and industrial plants. On the university area the experimental gardens and orchard were removed to make place for several buildings, erected in 1965 (50 m from the trap), 1980 (50 m), 1985 (200 m) and 1990 (10 m), and the arboretum remnant was removed to widen a street (1965). In the immediate surrounding areas more housing developments were built, a.o. one that replaced agricultural fields (1965) and one on a former military installation (1968), and a large hotel was built in 1988. Pollution of the area also undoubtedly increased over the study period. Lepidoptera caught in the trap were identified to species by JM.

Comparative data were obtained from light-traps in three other sites: 1) A large "bug-zapper" was operated by one of us (IN) on the balcony of his office at the Institute of Plant Protection in Ruzyně near Prague, since 1967 (Novák, 1974, 1983). Data are used here until 1992 inclusive. The trap overlooks a park in front of the institute with agricultural fields nearby. Over the years housing developments of the city of Prague moved closer and closer to the trap site, a nearby wetland was drained and growing fir trees in front of the trap increasingly blocked the visibility of the trap from a distance. A set of 134 species was selected for the study, 19 of which were counted each year, the others each year except 1977–1979. 2) A Jermy light-trap was operated since 1967 by one of us (KS) at České Budějovice in a small garden with deteriorated grasslands, wetlands and agricultural fields nearby. Data are used until 1990 inclusive. 3) A Jermy light-trap also operated by KS since 1981 at Černiš in a wetland forest. Data are used until 1990 inclusive. For further data on the latter two sites see Rejmánek & Spitzer (1982), Spitzer et al. (1984), Jaroš & Spitzer (1987), Spitzer & Lepš (1988) and Wolda et al. (1992). When comparing the diversities at these sites, species from groups of Lepidoptera that were not included in the analysis at all sites, such as many Microlepidoptera counted at Černiš, were ignored.

Except for the discussion on diversity, only the "relatively common" species were considered in the analysis. These are species with a mean abundance of at least 5 individuals per year. As a measure of diversity the index (α) based on the log series was chosen (Fisher et al., 1943) as this seems to be more useful than other popular indices (Wolda, 1983, 1984).

Two variability measures were used, the natural logarithm of the coefficient of variation and the log of the variance of ln[R], where R is y_t/y_{t-1} and y_t is the abundance in year t. The latter measure cannot be calculated if there are zeros in the data. In those cases, zeros were replaced by 0.5 as recommended by Wolda & Marek (1994). Ln(CV) measures overall variability, ln{var(ln[R])} the variability in the changes in abundance from year to year, but generally these two measures are reasonably well correlated (Wolda & Marek, 1994). Trends in time were measured by the (product-moment) correlation coefficient between (log) abundance and time. Results of significance tests with either ln(CV) or these correlation coefficients should be viewed with some caution as the data in a time series of population counts tend not to be independent, making the test, strictly speaking, invalid. Ln{var(ln[R])} usually does not suffer from this problem, but the arbitrariness involved in changing zeros to 0.5 makes a statistical test here too somewhat suspect. However, we are not aware of a better alternative and use the tests anyway. The results should be treated as a guideline rather than as a firm result. The PBLR-test for density dependence (Parametric Bootstrap Likelihood Ratio test, Dennis & Taper, 1993) was also used, as it tests for a "return tendency" towards a stochastic equilibrium (Wolda & Dennis, 1993) and provides important information related to the variability of the data. It examines a fluctuation pattern to see if population size has a tendency to return to a particular range of values. The probability to find statistical significance with this test depend on the length of the data series, so that, in order to compare the different sites, the test was applied here for series of 20 years, which left out Černiš, where only 10 years of data were available.

RESULTS

Species diversity

General statistics on sample size, species richness, and the α-diversity index based on the log-series (Fisher et al., 1943) are given in Table 1. First of all, the extreme power and efficiency of the trap used at Prague is clear. Far more individuals were caught per year than in any of the other sites in spite of the fact that only 134 selected species were monitored. Because all species not included in the list of 134 were ignored, these data could not be used for species diversity estimates. Of the other sites, the Brno samples had the largest number of species and the highest value of α, in total and per year, whether or not the first three years, with the different light source in the trap, were omitted, and even when only the data from the years all sites have in common (1981–1990) are considered. There was a large overlap in species between the sites, in spite of the differences in environment. Of the 407 species observed at Černiš, 90 percent were also found at one time or another at Brno, and the same was true for 81 percent of the species encountered České Budějovice. All the species analyzed at Prague also occurred at Brno. However, when considering only the "common" species (at least 5 individuals per year) the sample from Brno had the lowest count (120). The number of species shared by two sites that were common at both sites was also considerably less. Of the 165 common species at Černiš only 37 percent was also common at Brno, and for České Budějovice this percentage was 52%. Of the 95 species found at all sites, 41 percent were common at all those sites.

TABLE 1. Number of individuals and species of moths in three sites in the Czech Republic as revealed by long-term light-trapping. Plus the number of species shared by two or more of these sites, both for all species and for the species that have at least 5 individuals per year at each site.

	Years	Period	Individ.	Ind./Yr	Spp	Spp/Year	Alpha	Alpha/Yr
All species								
Brno	29	1963–91	280795	9683±1059	639	280.5±6.3	78.0±3.1	55.6
Brno	26	1966–91	269749	10374±1042	625	285.2±5.3	76.5±3.1	55.3
Prague *	23	1967–76,1980–92	752415	32714±1744	134			
Černiš **	10	1981–90	129426	12943±1196	407	274.7±8.3	52.1±2.6	49.7
České Budějovice	23	1967–68,1970–90	140171	6094±610	377	200.7±6.2	47.1±2.4	41.0
Only years 1981–90								
Brno	10	1981–90	91366	9136.6	522	294.5±6.0	73.2±3.2	58.8
Prague *	10	1981–90	312955	31295.5	134			
Černiš **	10	1981–90	129426	12942.6	407	274.7±8.3	52.1±2.6	49.7
České Budějovice	10	1981–90	49093	4909.3	314	190.3±10.7	44.9±2.5	40.4

Species shared. Total/Common

	Common	Brno	Prague	Černiš
Brno	120	—		
Prague *	132	134/88	—	
Černiš **	165	366/62	111/64	—
České Budějovice	121	308/63	112/62	254/75

Species shared by three or four sites

	All Spp.	Common spp.
Brno, Prague & Černiš	110	51
Brno, Prague & České Budějovice	113	52
Brno, Černiš & České Budějovice	236	46
Prague, Černiš & České Budějovice	95	47
All 4 sites	95	39

* Only 134 selected species monitored. All others ignored.
** Microlepidoptera, not monitored in other sites, excluded.

The frequency distribution of abundances (Fig. 1) illustrate a major difference between Brno on one hand and the other two sites on the other. In Brno there not only were fewer common species, but also many more rare species. Only the years shared by all sites (1981–1990) were used here to make the comparison. More than half of the species caught in Brno in those 10 years had an average of less than 1 individual per year ($\ln\{\text{mean}[y]\} \le 0$), while only about one third of the species in the other two sites fell into this category. The relatively high value of the α-diversity index at Brno (Table 1) illustrates these facts. In each and every year in Brno at least some new species were caught, that is species that were never caught before at this site. The lowest numbers of new species were 2 (1978 and 1990), and 3 (1981, 1987, 1989) and in all other years there were more than 3. In contrast, of the 407 species at Černiš (excluding the microlepidoptera) all were already seen at least once in 1986, after only 6 years of trapping, and at České Budějovice the last of the 371 species was already seen in 1981, after 14 years, with no new species at all between 1982 and 1990. This relatively high species turnover at Brno is reflected in the value of the α-diversity index for all years combined being much larger

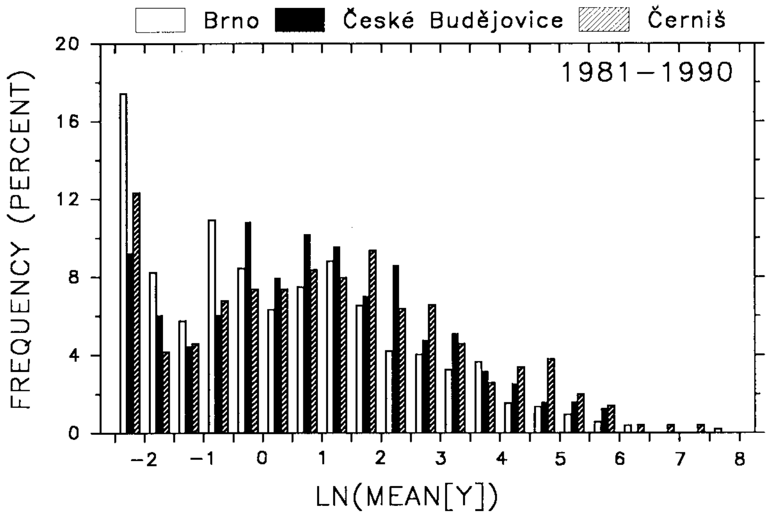

Fig. 1. Frequency distribution of abundances of moth species collected by light-trap over 10 years at 3 sites in the Czech Republic.

than the mean value per year of this index. For the other two sites this difference is much smaller.

In Brno, the quality of the light in the trap was changed after the first three years. Did this affect the catches? Fig. 2 shows the number of individuals and species, plus the α-diversity index for each year for each of three sites. The data for the number of individuals of the moths from Prague were not included here as they reached so much higher abundances that these data would squeeze the data points for the other three sites too far down to the bottom of the graph. The change in light-bulb in Brno occurred between 1965 and 1966. In 1965 the number of species suddenly in Brno suddenly reached an all-time low, but the numbers bounced right back in 1966 and stayed at this level. No clear effect of the changes to the trap was found here. The number of individuals, however, changed abruptly from the lowest value ever in 1965 to a record high in 1966. We have little doubt that part of this steep increase is due to the greater effectiveness of the mercury light-bulb in attracting moths. However, a complicating factor is an outbreak in numbers, precisely in the year 1966, of a number of moth species such as *Amathes c-nigrum*, *Mamestra suasa*, and a number of others, which also undoubtedly contributed to the large number of individuals caught in 1966. As this outbreak subsided, the numbers in the trap decreased again, those they stayed generally slightly above the values found in 1963–65. The effect of the change in light quality was present, but certainly not as strong as the data for 1966 and 1967 suggest. The value of α, which is a combination of individuals and species, had relatively high values in 1963–64, but no change was apparent between 1965 and 1966.

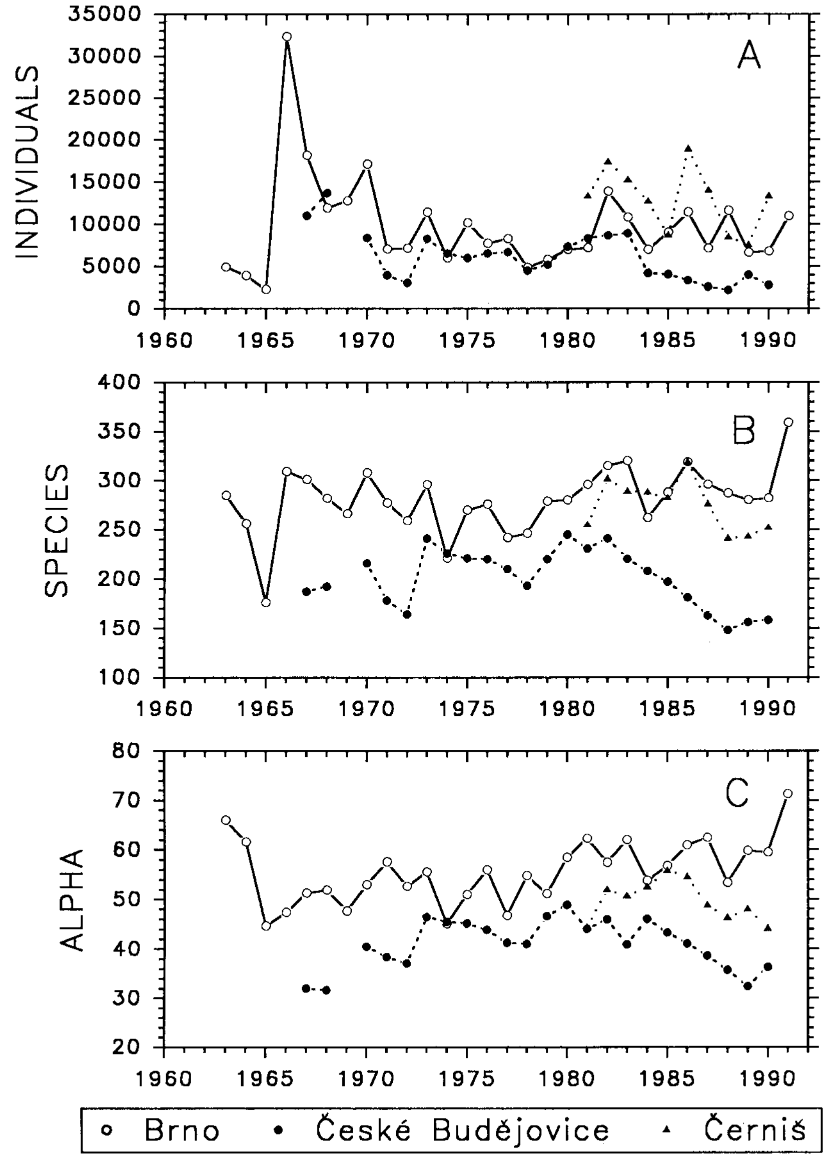

Fig. 2. The number of individuals and of species plus the α-diversity index in each year of operation of the light-trap at three sites in the Czech Republic.

Throughout the paper we will work with all data, including the first three years, but where appropriate the analysis will be repeated with those three years omitted.

Fluctuation patterns

The lines in Fig. 2 for the different sites seem to fluctuate somewhat in synchrony. The correlations between the localities for the years shared between each pair are given in Table 2. All correlations were positive, significantly so except for both species and α in the Brno – České Budějovice comparison. Apparently some factors that affected both the number of moths and species richness were shared by the sites in spite of the fact that, as the crow flies, Brno is some 190 km away from Prague and some 150 km from the other two sites, and that the habitats are very different.

TABLE 2. Correlations between 4 Czech sites in individuals, species and alpha per year, plus, for each site, the correlation of these parameters with time. In each case the number of years monitored simultaneously in both sites is also given.

	Brno	Č. Budějovice	Černiš	Correlation on time		
				1963–91	1981–90	1966–91
Years shared						
Brno	—					
Č. Budějovice	23	—				
Černiš	10	10	—			
Prague	22	21	10			
Individuals, total per year						
Brno	—			–0.175	–0.336	–0.462
Č. Budějovice	0.548	—		–0.620	–0.841	
Černiš	0.428	0.391	—	–0.429	–0.429	
Prague *	0.426	0.327	0.615	–0.160	0.220	
Species, total per year						
Brno	—			0.339	–0.392	0.282
Č. Budějovice	0.025	—		–0.326	–0.956	
Černiš	0.562	0.275	—	–0.475	–0.475	
Alpha, per year						
Brno	—			0.449	–0.115	0.693
Č. Budějovice	0.050	—		0.059	–0.855	
Černiš	0.199	0.498	—	–0.288	–0.288	

* Only 134 species were monitored in Prague.

Fluctuation patterns of individual species that were relatively common in more than one site also tended to show similar fluctuation patterns in these sites. The frequency distribution of correlation coefficients of such species between Brno and the other sites is given in Fig. 3. In all these comparisons the vast majority of the species showed positive correlations between sites. For both the Brno-Prague and the Brno-České Budějovice comparisons, 40 percent of the correlations were significantly positive ($p < 0.05$). For the Brno-Černiš comparison only 10 percent is significant, but in this case there were only 10 years of data to work with.

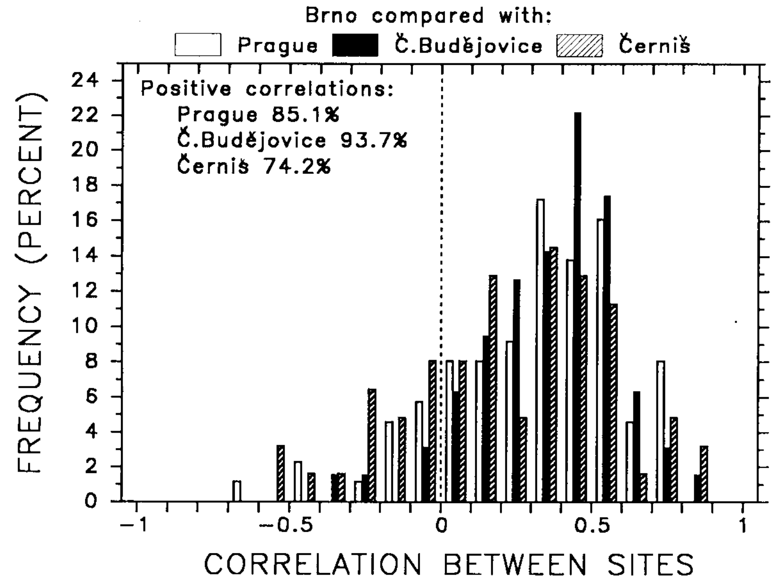

Fig. 3. Frequency distribution of correlations between abundance fluctuation patterns, on a logarithmic scale, of relatively common species shared between Brno and three other sites in the Czech Republic.

Variability

The mean of the log of the coefficient of variation, which measures overall variability, was the lowest in Prague, even lower than at Černiš, while this measure at Brno and České Budějovice had much higher values (Table 3). Ln{var(ln[R])}, which measures variability in changes in abundance from year to year, again showed Prague too be the most stable site with the other sites showing increased variability in the same order as did ln(CV). Now České Budějovice was by far the most variable site while Brno is almost as stable as Černiš. The percentage significant results of the PBLR density dependent test at Prague was much higher than at either Brno or České Budějovice. In summary, in variability Brno was generally comparable to the deteriorated agricultural / wetland site at České Budějovice, while on the average species in Černiš and, especially, Prague tended to be much less variable. The inclusion or omission of the first three years of data in Brno does not affect any of these conclusions (Table 3). Not only was the variability at Prague lower than at the other sites, the fluctuations were also "better behaved" in that a considerably higher percentage of the species showed a significant tendency to return to a stochastic equilibrium as shown by the PBLR test.

Ecologically, the variability from year to year, as measured here, is much more interesting for univoltine species than for species with more than one generation per year. One might expect variability per year to be dependent on voltinism. We compared obligatory univoltine species with others that have two or more 2 generations per year. As Table 4 shows, neither of the two variability measures, in none of the sites, showed significant effects of voltinism, with the possible exception of ln{var(ln[R])} in Prague. However, with eight tests, the formal level of significance should be lowered according to the Bonferroni procedure, putting the threshold at 0.05/8 = 0.006, which makes the one "$p < 0.05$" not significant. Contrary to expectation, voltinism had absolutely no discernable effect on variability. This result seems to be at variance with those arrived at by both Rejmánek & Spitzer (1982) and Spitzer & Lepš (1988), who worked with data from sites also included here, but it should be noted here that they worked exclusively with noctuid moths and had a shorter series of data to work with.

TABLE 3. Mean population variability among common moths from light-trap in four Czech sites. For columns 3–5, sites that share the same letter are not significantly different.

	N	ln(CV)	ln{var(ln[R])}	PBLR 20 Yrs % Signif.
Prague	134	–0.360	–0.325	48.2
Brno, 1963–91	120	–0.075 a	0.083 b	26.5 c (1963–82)
Brno, 1966–91	120	–0.129 a	0.069 b	26.5 c (1966–85)
České Budějovice	121	0.052	0.332	27.3 c
Černiš	194	–0.266	–0.047 b	—

There were significant positive correlations between sites, both in mean abundance and in variability in species that were common in those sites (Table 5). A species that was

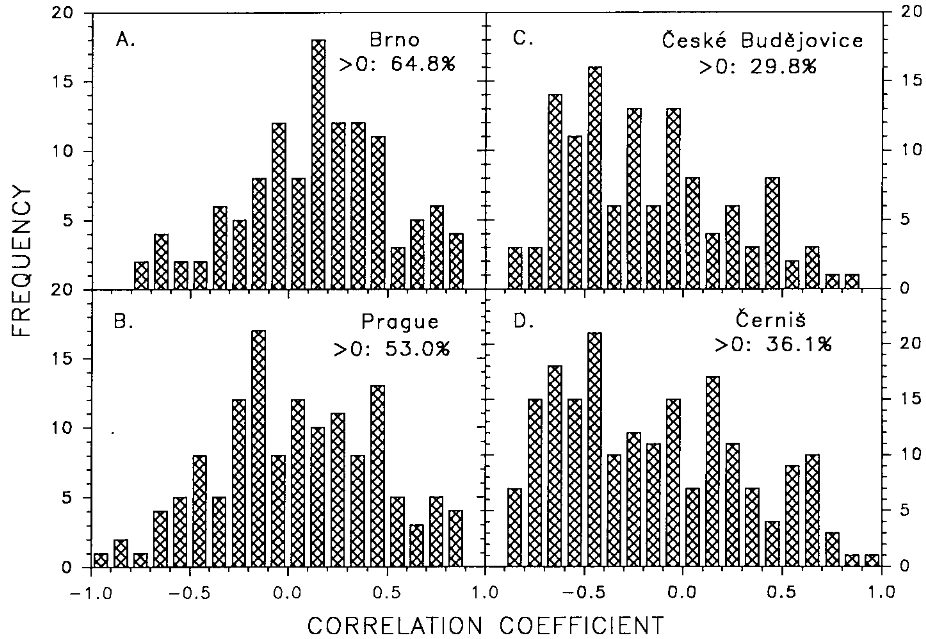

Fig. 4. Frequency distributions of trends in abundance, i.e. correlations between abundance and time, for moths at four sites in the Czech Republic.

variable at one site tended to be also variable at the other sites. The exception here was Černiš, where variability in changes in abundance, ln{var(ln[R])}, was not significantly correlated among the common species shared with other sites, and the correlation in ln(CV) with České Budějovice was not significant either.

TABLE 4. Voltinism and variability of common species (Per year >5 individuals). Mean and standard error of two variability measures for species with one generation vs those with more generations per year. NS = not significant ($p > 0.05$).

	Univoltine	Bi–Polyvoltine	Significance Difference
Prague			
N	87	39	
ln(CV)	−0.352 ± 0.037	−0.340 ± 0.047	NS
ln{var(ln[R])}	−0.367 ± 0.112	−0.112 ± 0.080	$p < 0.05$
Brno			
N	68	37	
ln(CV)	−0.122 ± 0.041	−0.073 ± 0.051	NS
ln{var(ln[R])}	0.034 ± 0.066	0.132 ± 0.088	NS
České Budějovice			
N	57	33	
ln(CV)	0.008 ± 0.044	0.052 ± 0.062	NS
ln{var(ln[R])}	0.230 ± 0.074	0.246 ± 0.108	NS
Černiš			
N	103	40	
ln(CV)	−0.276 ± 0.042	−0.307 ± 0.077	NS
ln{var(ln[R])}	−0.017 ± 0.084	−0.122 ± 0.161	NS

Trends in time

The number of individuals per year decreased at all sites (Table 2), as did the number of species, except in Brno, where this number increased significantly both with and without the years 1963–65. Using only the strictly comparable years 1981–1990, all correlations were negative except for the number of individuals in Prague.

The majority of the relatively common species showed a decrease in abundance over time, both at České Budějovice and at Černiš (Fig. 4, Wolda et al., 1992). Among the selected species at Prague, however, just more than half of the species showed increases over time, and at Brno a majority of 65 percent of the common species increased in abundance (Fig. 4). Especially the difference between the two south-Bohemian sites and Brno is striking. If in Brno the first three years are omitted from the analysis, the percentage increases in abundance drops to 56.1%. This is because the year 1966, with the highest abundance of all years to a large extent because of population outbreaks in a number of species, is now placed at the very beginning of the series. Nevertheless, the majority of species still show increases at a percentage even higher than that at Prague.

There were significant positive correlations between sites in their trends of abundance over time for species that were common in those sites (Table 5). The exception, again, was Černiš, where no significant correlations in trend with any of the other sites was found.

TABLE 5. Between-site correlations of shared species in mean abundance, variability, and trends in time for the years with data in the two sites being compared. In each comparison only species were used that were common in both sites (mean abundance per year > 5). * = correlation significant ($p < 0.05$).

	Brno	České Budějovice	Černiš
ln(mean) abundance			
Brno	—		
Č. Budějovice	0.556*	—	
Černiš	0.292*	0.566*	—
Prague	0.742*	0.610*	0.252*
ln(CV)			
Brno	—		
Č. Budějovice	0.410*	—	
Černiš	0.340*	0.159	—
Prague	0.461*	0.629*	0.437*
ln{var(ln[*R*])}			
Brno	—		
Č. Budějovice	0.236*	—	
Černiš	–0.110	–0.016	—
Prague	0.196*	0.300*	0.227
Correlation on time			
Brno	—		
Č. Budějovice	0.437*	—	
Černiš	0.191	0.078	—
Prague	0.230*	0.249*	–0.060

No significant correlations were found between variability as measured by ln(CV) and trends in abundance. As found before (Wolda et al., 1992), knowing one of the two measures, ln(CV) or the correlation coefficient of abundance on time, has no predictive value for the other. For the variability of change, ln{var(ln[*R*])}, the correlation with trend was just significantly positive, but low, at Černiš ($r = 0.144$) and České Budějovice ($r = 0.195$), but far from significant at Brno ($r = 0.039$) and Prague ($r = -0.033$).

DISCUSSION

Many moth species demonstrated a tendency towards synchronous fluctuations over a large area in the Czech Republic. Total individuals and species per year tended to be positively related (Table 1). There was also a predominance of positive correlations in abundances of individual species between sites (Fig. 3, Table 5). Some of the factors affecting abundance in many species obviously are effective over a large area, irrespective of details of the local habitat, suggesting the importance large-area factors such as weather in the dynamics of these moths, or suggesting large scale movements of many of the species concerned (Taylor & Taylor, 1979; Taylor, 1986). Even variability of these species tends to be correlated between sites as is trends over time (Table 5). However, local habitat characteristics do seem to play an important part here, as in both variability and in trend the populations at Černiš, the habitat among the four sites that is least affected by man, are little or not correlated with conspecifics at the other sites (Table 5).

There is a strong suggestion in the literature, and some good evidence (Taylor et al., 1978; Taylor, 1978), that urbanization, with its adverse effects on the environment for many insects, produces an insect fauna with low diversity and often decreasing species abundances and increasing population variability. There was every reason to expect this same phenomenon to be true in Brno, where during the course of this study more buildings were erected, the amount of open areas decreased, the light-trap site started in 1963 at the edge of the city, but found itself in a more central position as housing developments were constructed, and pollution probably increased. However, the result obtained turned out to be the different. Variability in Brno was indeed high (Table 3), but the number of species found, either in total over the 29 years, or per year, was the highest among the sites compared, at the south Bohemian sites, including even Černiš, a natural area relatively little affected by man's activities. Most common species increased in abundance, often rather strongly so (Fig. 4).

What caused the fauna in Brno to be so rich? Compared with the London gradient from semi-natural forest at the Geescroft Wilderness to the urban site Isleworth in London (Taylor et al., 1978), these Czech sites are all rather rich. Mean α at Geescroft was 35.4, which is lower even than the 41.0 at České Budějovice, the least diverse Czech site, and far lower than the 55.6 at Brno. The other sites in this London gradient were even lower. Diversity values for the urban gradient near and in Manchester similarly are substantially lower than the ones described here. Much of the difference is probably purely geographical, central Europe having a richer moth fauna than the British isles. Perhaps the difference in light-trap design, Rothamsted trap (Taylor, 1968) vs Jermy trap (Mesch, 1965), also had an effect. The difference between Brno and the other Czech sites may also be partly geographical, as southern Moravia does have a richer fauna than southern Bohemia. There is also a difference in design between the trap at Brno and those at the southern Bohemian sites. In Brno, from 1966 onwards a 125W mercury vapor lamp replaced a 200W light bulb used in 1963 through 1965. At Černiš and České Budějovice normal mixed-light bulbs were used throughout. However, as no clear effect of the change in light source on diversity was found at Brno (Fig. 2), it is assumed that the effect of this difference between the sites was also negligible.

In unravelling the problem of the high diversity of the urban Brno samples, one important clue is given in the abundance distribution of the species at Brno (Fig. 1). More than half the species had an average of 1 individual per year or less, while at the southern Bohemian sites only one third of the species were this rare. Unlike the other sites, at Brno species new for the trap showed up every single year during the 29 years of this study. This all points to a large number of accidental species, stray individuals of which enter Brno from outside the city, perhaps aided by the natural updraft of warm air from a city, causing a mild breeze towards the city from surrounding areas (Schmid, 1978). These accidentals caused the overall diversity index to be much higher ($\alpha = 78.0$) than the average diversity index per year ($\alpha = 55.6$). This can be contrasted with samples such as those taken at Bois-de-Chênes in Switzerland (Aubert, pers. comm.), where the diversity index for the total sample ($\alpha = 81.2$) was similar to that found in Brno, but where the mean per year (73.1) was much higher than in Brno. A high percentage of the species found at the other sites were also observed, at one time or another, in the trap in Brno (Table 1). However, when leaving out the rarer species and considering only the more common ones (≥ 5 individuals per year), the picture changed drastically. Now Brno is the least species rich (S = 120), of the same order of magnitude as the relatively poor site at České Budějovice (S = 121), and much poorer than the fauna at Černiš (S = 165) (Table 1). The number of species that were common in Brno and common in another site was rather low. Some of these more common species too may have been accidentals, but ones that, for some reason, have a somewhat higher probability of ending up in the Brno trap.

The second clue is given by the kind of species that are common in Brno. They are mostly tramp species, species that are opportunists and can take advantage of whatever habitats a city has to offer and can thrive and even increase in abundance in the urban environment.

The fauna collected by the light-trap in Brno was rich in species. This might suggest at first glance that Brno provided an excellent habitat for nocturnal Lepidoptera and one might be tempted to conclude that all one has to do to get an environment rich in moths is to eliminate trees and agricultural fields, pave it over for streets, erect buildings, warm them with coal-burning stoves in winter, leaving the moths just some trees along streets and plants and shrubs in small gardens behind the houses, and with a park here and there. This sounds like an absurd conservation strategy, and, of course, it is. It seems likely that the majority of the species caught in the light-trap are accidentals, species that do not have a suitable habitat in the area surrounding the trap in downtown Brno and the species that are common in the trap are mostly opportunists, species that are of minor interest to the lepidopterologist, and are in no need of conservation measures. Species that are threatened and in danger of extinction because of habitat loss, pollution, etc. are not the ones that were common inside the city of Brno.

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REFERENCES

DAVIS B.N.K. 1978: Urbanization and the diversity of insects. In Mound L.A. & Waloff N. (eds): *Diversity of Insect Faunas*. Blackwell, Oxford, London, Edinburgh & Melbourne, pp. 126–138.

DENNIS B. & TAPER M. 1993: Density dependence in time series observations of natural populations: estimating and testing. *Ecol. Monogr.* (in press).

DICKMAN C.R. 1987: Habitat fragmentation and vertebrate species richness in an urban environment. *J. Appl. Ecol.* **24**: 337–351.

DEN BOER P.J. 1977: *Dispersal Power and Survival. Carabids in a Cultivated Countryside.* Misc. Papers 14, Agricultural University, Wageningen, The Netherlands, 151 pp.

FISHER R.A., CORBET A.S. & WILLIAMS C.B. 1943: The relation between the number of species and the number of individuals in a random sample of an animal population. *J. Anim. Ecol.* **12**: 42–58.

FLEET R.R., PIPER G.L. & FRANKIE G.W. 1978: Studies on the population ecology of the smokybrown cockroach, Periplaneta fuliginosa, in a Texas outdoor urban environment. *Environ. Entomol.* **7**: 807–814.

JACOBS J. 1975: Diversity, stability and maturity in ecosystems influenced by human activities. In Van Dobben W.H. & Lowe-McConnell R.H. (eds): *Unifying Concepts in Ecology*. Junk, The Hague, pp. 187–207.

JAROŠ J. & SPITZER K. 1987: *The Lepidoptera of Černiš Wetland in South Bohemia*. South Bohemia Museum, České Budějovice, 42 pp. (in Czech, English abstract).

KLOMANN U. 1975: Bodenarthropoden and Belastungsindikatoren in urbanen Räumen. In Malicky H. (ed.): *Verhandlungen des Sechsten Internationalen Symposiums über Entomofaunistik in Mitteleuropa*. Junk, The Hague, pp. 221–231.

MARCHANT J.H., HUDSON R., CARTER S.P. & WHITTINGTON P. 1990: *Population Trends in Breeding Birds*. British Trust for Ornithology, Tring, U.K., 300 pp.

MESCH H. 1965: Erfahrungen mit Lichtfallen für den Warndienst. *Beitr. Entomol.* **15**: 139–155.

NOVÁK I. 1974: Sexualindex bei Lepidopteren in den Lichtfallen. *Fol. Entomol. Hung. (Suppl.)* **27**: 143–152.

NOVÁK I. 1983: An efficient light-trap for catching insects. *Acta Entomol. Bohemoslov.* **80**: 29–34.

NUORTEVA P. 1971: The synanthropy of birds as an expression of the ecological cycle disorder caused by urbanization. *Ann. Zool. Fenn.* **8**: 547–553.

OWEN D.F. & CHANTER D.O. 1972: Species diversity and seasonal abundance in Charaxes butterflies (Nymphalidae). *J. Entomol.* **46**: 135–143.

OWEN D.F. 1976: Conservation of butterflies in garden habitats. *Environm. Conserv.* **3**: 285–290.

OWEN D.F. 1977: Species diversity and seasonal abundance in Charaxes butterflies (Nymphalidae) in a garden in Northern Nigeria. *Bull. Inst. Fr. Afr. Noire* **39**: 346–350.

OWEN D.F. 1978: Abundance and diversity of bumblebees and cuckoo bees in a suburban garden. *Entomologist's Rec.* **90**: 242–244.

OWEN J. 1981: Trophic variety and abundance of hoverflies (Diptera, Syrphidae) in an English suburban garden. *Holarctic Ecol.* **4**: 221–228.

OWEN J. 1991: *The Ecology of a Garden. The First Fifteen Years.* Cambridge Univ. Press, Cambridge, New York, Port Chester, Melbourne, Sydney, 403 pp.

POLLARD E., HALL M.L. & BIBBY T.J. 1986: *Monitoring the Abundance of Butterflies, 1976–1985.* Nature Conservancy Council, Peterborough, U.K., 279 pp.

REJMÁNEK M. & SPITZER K. 1982: Bionomic strategies and long-term fluctuations in abundance of Noctuidae (Lepidoptera). *Acta Entomol. Bohemoslov.* **79**: 81–96.

SCHMID J.A. 1978: Foreword: The urban habitat. In Frankie G.W & Koehler C.S. (eds): *Perspectives in Urban Entomology*. Academic Press, New York, San Francisco, London, pp. ix–xiii.

SCHOOF H.F. & SAVAGE E.P. 1955: Comparative studies of urban fly populations in Arizona, Kansas, Michigan, New York, and West Virginia. *Ann. Entomol. Soc. Am.* **48**: 1–12.

SCHOOF H.F., SAVAGE E.P. & DODGE H.R. 1956: Comparative studies of urban fly populations in Arizona, Michigan, New York, and West Virginia. II. Seasonal abundance of minor species. *Ann. Entomol. Soc. Am.* **49**: 59–66.

SPITZER K. & LEPŠ J. 1988: Determinants of temporal variation in moth abundance. *Oikos* **53**: 31–36.

SPITZER K., REJMÁNEK M. & SOLDÁN T. 1984: The fecundity and long-term variability in abundance of noctuid moths (Lepidoptera, Noctuidae). *Oecologia* **62**: 91–92.

TAYLOR L.R. 1968: The Rothamsted Insect Survey. *Nat. Sci. Sch.* **6**: 1–10.

TAYLOR L.R. 1978: Bates, Williams, Hutchinson -- a variety of diversities. In Mound L.A. & Waloff N. (eds): *Diversity of Insect Faunas*. Blackwell Scientific, Oxford, London, Edinburgh, Melbourne, pp. 1–18.

TAYLOR L.R. 1986: Synoptic dynamics, migration and the Rothamsted Insect Survey. *J. Anim. Ecol.* **55**: 1–38.

TAYLOR L.R., FRENCH R.A. & WOIWOD I.P. 1978: The Rothamsted insect survey and the urbanization of land in Great Britain. In Frankie G.W. & Koehler C.S. (eds): *Perspectives in Urban Entomology*. Academic Press, New York, San Francisco, London, pp. 31–65.

TAYLOR R.A.J. & TAYLOR L.R. 1979: A behavioral model for the evolution of spatial dynamics. In Anderson R.M., Turner B.D. & Taylor L.R. (eds): *Population Dynamics*. Blackwell Scientific, Oxford, London, Edinburgh, Melbourne, pp. 1–27.

WOLDA H. 1983: Diversity, diversity indices and tropical cockroaches. *Oecologia* **58**: 290–298.

WOLDA H. 1984: Diversidad de la Entomofauna y cómo medirla. *Informe Final IX Congreso Latinoamericano de Zoología*. Arequipa, Peru, 1983, pp. 181–186.

WOLDA H. 1987: Altitude, habitat and tropical insect diversity. *Biol. J. Linn. Soc.* **30**: 313–323.

WOLDA H. & DENNIS B. 1993: Density dependence tests. Are they? *Oecologia* **95**: 581–591.

WOLDA H., SPITZER K. & LEPŠ J. 1992: Stability of environment and of insect populations. *Res. Popul. Ecol.* **34**: 213–225.

WOLDA H. & MAREK J. 1994: Measuring variation in abundance, the problem with zeros. *Eur. J. Entomol.* **91**: 145–161.

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