

# Natural enemy ravine revisited: the importance of sample size for determining population growth

VOJTECH JAROŠÍK,<sup>1</sup> ALOIS HONĚK<sup>2</sup> and ANTHONY

F. G. DIXON<sup>3</sup> <sup>1</sup>Department of Zoology, Charles University, Prague, The Czech Republic, <sup>2</sup>Research Institute of Crop Production, Prague, The Czech Republic and <sup>3</sup>School of Biological Sciences, University of East Anglia, U.K.

**Abstract.** 1. The population growth of three aphid species, *Metopolophium dirhodum* (Walker), *Rhopalosiphum padi* (L.), and *Sitobion avenae* (F.), on winter wheat, was analysed by regression. The calculations were based on censuses of aphids made in 268 plots at 3- or 7-day intervals for 10 years on leaves and 6 years on ears. The calculations were made separately for each plot each year, then repeated on the pooled data from all plots monitored in a year.

2. At the level of individual plots, no population growth was detected at very low densities. At high densities, the populations grew exponentially and the growth rates did not decrease with increasing aphid density.

3. Significant growth was always detected in the pooled data. These growth rates decreased significantly at the highest densities. Field estimates of the intrinsic rate of increase derived from these data ranged from 0.010 to 0.026 for *M. dirhodum*, 0.0071–0.011 for *R. padi*, and 0.00078–0.0061 and 0.0015–0.13 for *S. avenae*, on leaves and ears respectively.

4. The apparent lack of growth in the individual plots at low densities is attributable to small sample size. It is concluded that the *natural enemy ravine* in the population dynamics of cereal aphids, identified by Southwood and Comins (1976), is a consequence of low population densities at which population increase is undetectable unless very large samples are taken.

**Key words.** Cereal aphids, natural enemy ravine, population density, population growth, sample size.

## Introduction

Aphids can become very abundant on cereals (e.g. Carter *et al.*, 1980; Dixon, 1987). In central Europe, there are three important aphid species colonising winter wheat: *Metopolophium dirhodum* (Walker), which is the dominant species on leaves and avoids the ears, *Sitobion avenae* (F.), dominant on ears but also living on leaves, and *Rhopalosiphum padi* (L.), which colonises the whole plant. The aphids migrate to wheat stands around mid-May, from their winter hosts [*Rosa* spp. (*M. dirhodum*), various Poaceae (*S. avenae*), and *Prunus padus* L. (*R. padi*)]. These aphids colonise the leaves of cereals and, after flowering, except

for *M. dirhodum*, also the ears. The initially very sparse populations grow and reach maximum densities, usually in the last days of June, then decline sharply in abundance.

The population dynamics differ widely between years and stands. Analysis of the population dynamics is complicated because the numbers of immigrant aphids, the length of the period available for population growth, and its rate, are influenced by host-plant cultivar and vigour, microclimate, and natural enemies (Dixon, 1987). A slight dip in a rising curve, or plateaus followed by sudden acceleration, are often observed in the initial phase of population growth (reviewed by Southwood & Comins, 1976). Southwood and Comins attributed this delay in population growth to a *natural enemy ravine*, caused by the activity of polyphagous predators. They concluded that the initial aphid population increase is determined by the balance between the numbers of aphids that invade the crop and the size of the autochthonous population of polyphagous predators.

Correspondence: Vojtech Jarošík, Department of Zoology, Faculty of Sciences, Charles University, Vinicná 7, CZ 12844 Prague 2, The Czech Republic. E-mail: jarosik@mbox.cesnet.cz

Carter and Dixon (1981) offered an alternative explanation: the lack of population growth in the initial phase is attributed to the intermittent nature of aphid immigration, which is amplified by the pre-reproductive delay of the colonising aphids.

The seasonal trends in population increase of aphids on leaves of wheat over a period of 10 years, and over 6 years on ears of wheat in central Europe, are described and analysed. The analysis gave estimates of the intrinsic rate of population increase for these species of aphid. A comparison of the data for separate plots with those for yearly totals across all plots indicated how sensitive the correct interpretation of population dynamics is to sample size. The lack of population growth of cereal aphids at low density, attributed previously to natural enemies (Southwood & Comins, 1976) and aphid migration (Carter & Dixon, 1981), is re-interpreted.

## Materials and methods

Aphid densities were recorded at two localities: (1) At Praha-Ruzyně, central Bohemia (50°06'N, 14°17'E), aphids were counted from 1987 to 1996 on winter wheat grown under standard agricultural conditions, without the use of insecticides. The cultivars sown were Hana, Regina, Viginta, and Zdar. Each year, 5–15 experimental plots of 25 m<sup>2</sup> were established within the wheat stands. A total of 107 plots was investigated. The host plant quality in these plots differed due to variation in soil quality, mineral nutrition, water availability, crop density, cultivar, and variations in weather. (2) At Sedlec, central Bohemia (50°10'N, 14°30'E), aphids were monitored from 1989 to 1994, in small experimental plots established for the routine testing of new cultivars of winter wheat. Aphid counts were made on 161 plots of 54 established and new cultivars, of which only 11 were grown throughout the experimental period. The wheat was sown in a series of 1.4 × 7 m (10 m<sup>2</sup>) plots, in the fourth year of a 10-year crop rotation system, and grown under optimum conditions. Mineral fertilisers were applied at standard doses of 120 kg ha<sup>-1</sup> N, 120 kg ha<sup>-1</sup> P, and 160 kg ha<sup>-1</sup> K. Agricultural practices recommended for wheat growing in the Czech Republic (Špaldon, 1982) were followed except for the application of insecticide.

Aphid counts were made weekly or at 3–4 day (1990) intervals, from before aphid immigration until their disappearance from the crop. On each occasion, 30–300 tillers were examined, depending on aphid abundance. Initially 300 tillers, chosen at random, were sampled but after this sample size was adjusted to maintain a standard error of approximately 25% of the mean number of aphids per tiller (Southwood, 1978). At Praha-Ruzyně, the aphids on leaves (including leaf sheaths) and on ears were recorded separately, except in 1991 when only the numbers on the ears were recorded. The tillers were selected at random at two to five places within each experimental plot. At Sedlec, aphid numbers were recorded at two fixed places within each experimental plot, on a total of 40 or 60 ears.

For each season and each species, the data from individual plots were fitted by linear regression in which population growth was linearised by log transformation of population size  $N$  on leaves or ears, and by expressing time in day-degrees above the lower development threshold of 5°C (Honěk & Kocourek, 1990, Honěk, 1996). The model corresponding to density-independent exponential population growth was

$$\ln[N(DD)] = \ln[N(0)] + rDD \quad (1)$$

where  $\ln[N(DD)]$  is the response variable,  $\ln[N(0)]$  is the intercept,  $r$  is the slope of the regression line and the population growth rate, and  $DD$  is an explanatory variable. The explanatory variable was the sampling date expressed in day-degrees, which was from the beginning of immigration until the peak in aphid abundance. The population growth rate  $r$  is an estimate of the intrinsic rate of increase achieved (Jarošík *et al.*, 1996).

When population densities on individual plots were low, the linear regression (eqn 1) describing the density-independent exponential growth was not significant. Whether the probability of identifying exponential growth increases with maximum aphid density was tested using the presence or absence of significant exponential growth on individual plots as the binary response variable (Cox & Snell, 1989), and the log maximum aphid density on individual plots as the covariate.

To test for deviations from density-independent exponential growth, the square of the explanatory variable was calculated and subtracted from the regression (eqn 1):

$$\ln[N(DD)] = \ln[N(0)] + rDD - rDD^2 \quad (2)$$

If the subtraction caused a significant reduction in deviance, there was evidence of decreased population growth with increasing aphid density (e.g. Crawley, 1993).

Calculations were made each year for each plot using general linear modelling in GLIM (Francis *et al.*, 1994). The calculations were repeated on pooled data from all the plots monitored in a particular year.

The use of log aphid counts and normal distribution of errors in the statistical analyses is preferable to the use of generalised linear models with Poisson or negative binomial distribution of errors (McCullagh & Nelder, 1989). The statistical distributions were tested using aphid counts for 1997 and 1999, years of low and high aphid abundance respectively. The aphid distributions were highly clumped and differed significantly not only from a Poisson but also from a negative binomial distribution. The residual deviances were larger and the explanatory power smaller for the models that used Poisson or negative binomial errors than for the models that used log transformation and normal errors. The adequacy of the log transformation and normal errors was checked further by plotting standardised residuals of the models against fitted values and against explanatory variables, and the ordered residuals against expected order statistics (Crawley, 1993).

## Results

### Population dynamics on individual plots

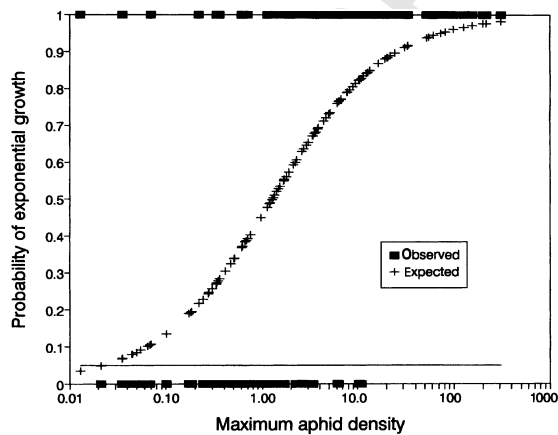
No population growth was detected at very low densities. At higher densities, the populations grew exponentially. The growth rates did not decrease with increasing aphid density.

The probability of identifying exponential growth increased with maximum aphid density. On leaves, the relationship between density and the onset of exponential growth was the same for *M. dirhodum* and *S. avenae* ( $\chi^2=2.17$ , d.f.=2, NS) but significantly different for *R. padi* ( $\chi^2=7.27$ , d.f.=1,  $P<0.01$ ). Exponential growth in *M. dirhodum* and *S. avenae* (Fig. 1) started at a much lower density than in *R. padi* (Fig. 2). The threshold for a 5% probability of the onset of exponential growth was 0.023 aphids per tiller for *M. dirhodum* and *S. avenae* compared with 1.42 aphids per tiller in *R. padi*; however the transition from undetectable population growth to exponential increase was more abrupt in *R. padi* (Fig. 2) than in *M. dirhodum* and *S. avenae* (Fig. 1).

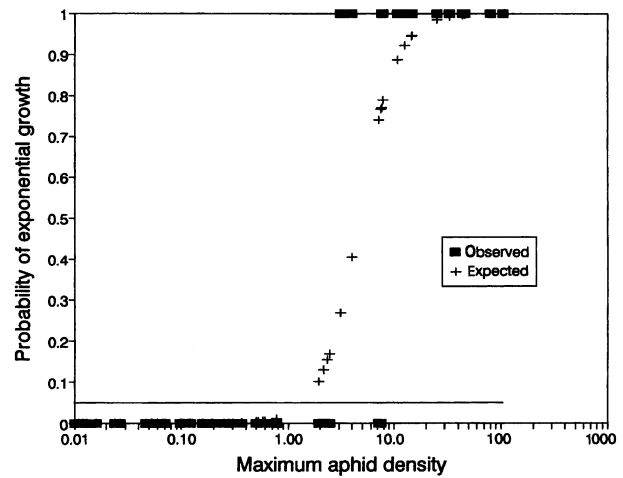
For species that occur on both leaves and ears, *S. avenae* and *R. padi*, the relationship between density and the onset of exponential growth differed on leaves and ears (interaction:  $\chi^2=13.80$ , d.f.=1,  $P<0.001$ ). A highly significant relationship ( $\chi^2=41.74$ , d.f.=1,  $P<0.001$ ) was detected for *S. avenae* on the ears of wheat (Fig. 3). The 5% probability of the onset of exponential growth was 0.44 aphids per ear. By contrast, no significant relationship was detected for *R. padi* on ears ( $\chi^2=1.56$ , d.f.=1, NS) (Fig. 4).

### Population dynamics of pooled data

Significant exponential growth was always detected in pooled data. This is strikingly different from the dynamics



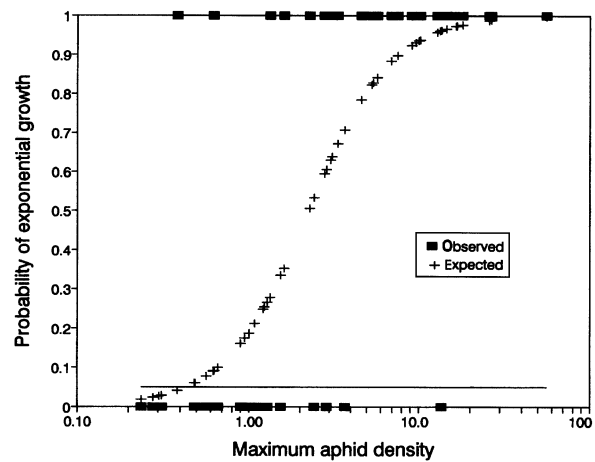
**Fig. 1.** The relationship between the occurrence of exponential growth and maximum aphid density on individual plots for *Metopolophium dirhodum* and *Sitobion avenae* on winter wheat leaves. The horizontal line shows 5% probability of exponential growth and its cross with the expected values shows the aphid density at which the 5% probability is attained.



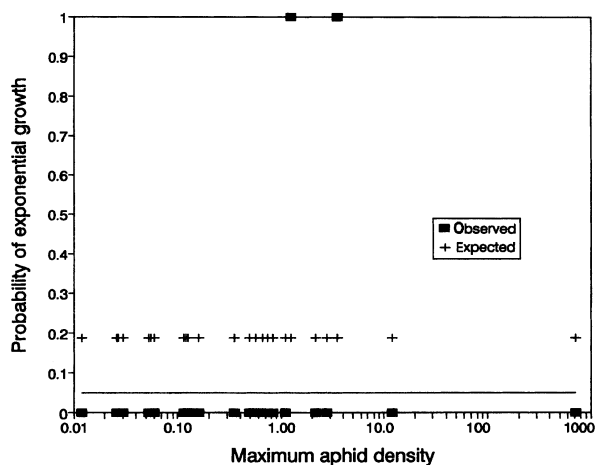
**Fig. 2.** The relationship between the occurrence of exponential growth and maximum aphid density on individual plots for *Rhopalosiphum padi* on winter wheat leaves. The horizontal line shows 5% probability of exponential growth and its cross with the expected values shows the aphid density at which the 5% probability is attained.

on individual plots because significant population growth, indistinguishable from exponential growth, was revealed even at very low densities. The second important difference was that the growth rates decreased significantly at high densities.

Population growth differed significantly between species and years (interaction:  $F=7.16$ , d.f.=12,1253,  $P<0.001$ ). The population growth of *S. avenae* differed significantly on leaves and ears (interaction:  $F=10.41$ , d.f.=7,562,  $P<0.001$ ). The growth rates of individual species also differed significantly between years (*Metopolophium dirhodum*:



**Fig. 3.** The relationship between the occurrence of exponential growth and maximum aphid density on individual plots for *Sitobion avenae* on winter wheat ears. The horizontal line shows 5% probability of exponential growth and its cross with the expected values shows the aphid density at which the 5% probability is attained.



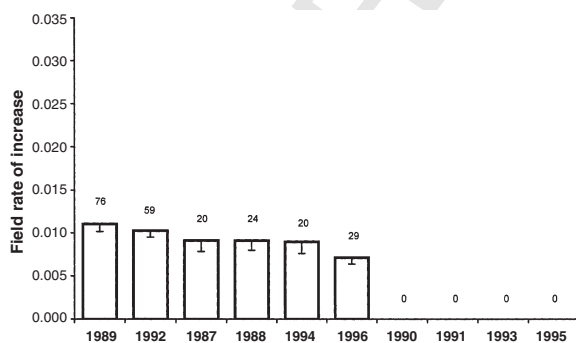
**Fig. 4.** The relationship between the occurrence of exponential growth and maximum aphid density on individual plots for *Rhopalosiphum padi* on winter wheat ears.

$F = 42.87$ , d.f. = 7,463,  $P < 0.001$ ,  $R^2 = 57\%$ ; *R. padi*:  $F = 9.88$ , d.f. = 5,226,  $P < 0.001$ ,  $R^2 = 50\%$ ; *S. avenae*, leaves:  $F = 88.71$ , d.f. = 7,251,  $P < 0.001$ ,  $R^2 = 24\%$ ; *S. avenae*, ears:  $F = 8.67$ , d.f. = 9,320,  $P < 0.001$ ,  $R^2 = 25\%$ ).

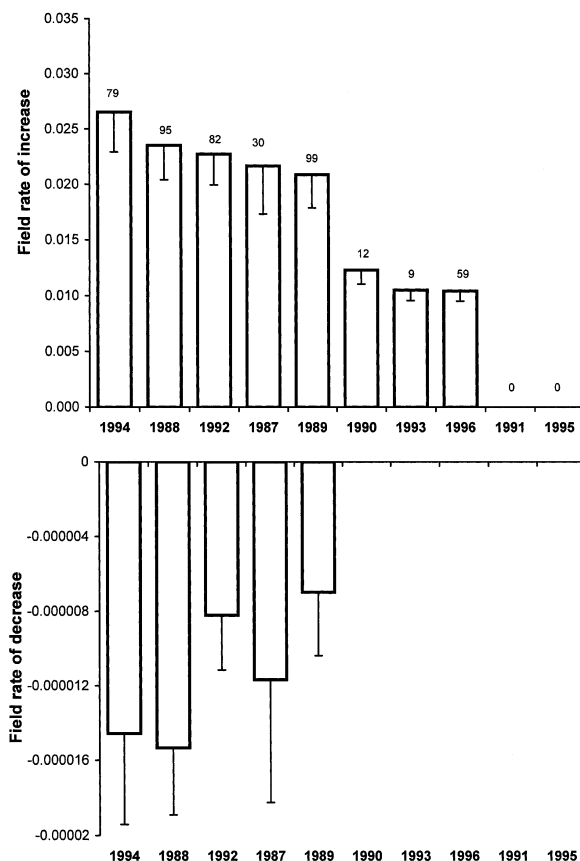
The population growth of *R. padi* was the lowest and the least variable of the three species (this species was absent from samples in 4 of the 10 years (Fig. 5)). The populations increased monotonically in an exponential way. The regression estimates of their intrinsic rate of increases ranged between 0.0071 and 0.011.

*Metopolophium dirhodum* had the fastest population growth on leaves. Its intrinsic rate of increase was between 0.010 and 0.026. Its population growth ( $F = 2.98$ , d.f. = 8,456,  $P < 0.01$ ) decreased significantly with increasing aphid density in seasons with the highest growth (Fig. 6).

*Sitobion avenae* was dominant on the ears but also occurred on leaves. On leaves, the estimates of intrinsic

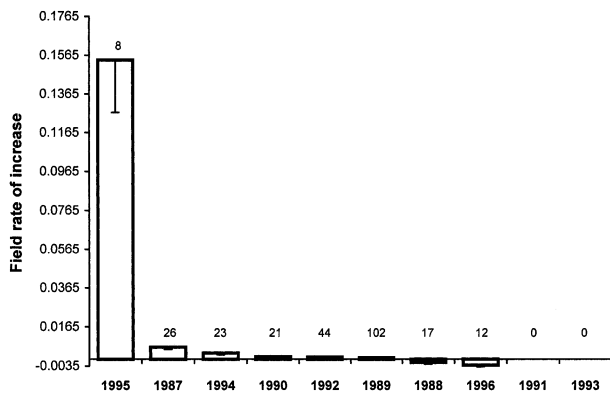


**Fig. 5.** Field estimates of the rate of population increase of *Rhopalosiphum padi* (linear regression slopes of  $\ln$  aphid densities on day-degrees in eqn 2) on winter wheat plants each year from 1987 to 1996. There was no evidence of field rate of decrease (quadratic regression slopes of  $\ln$  aphid densities on day-degrees were not significant). Numbers are the sample sizes, vertical lines are the standard errors.



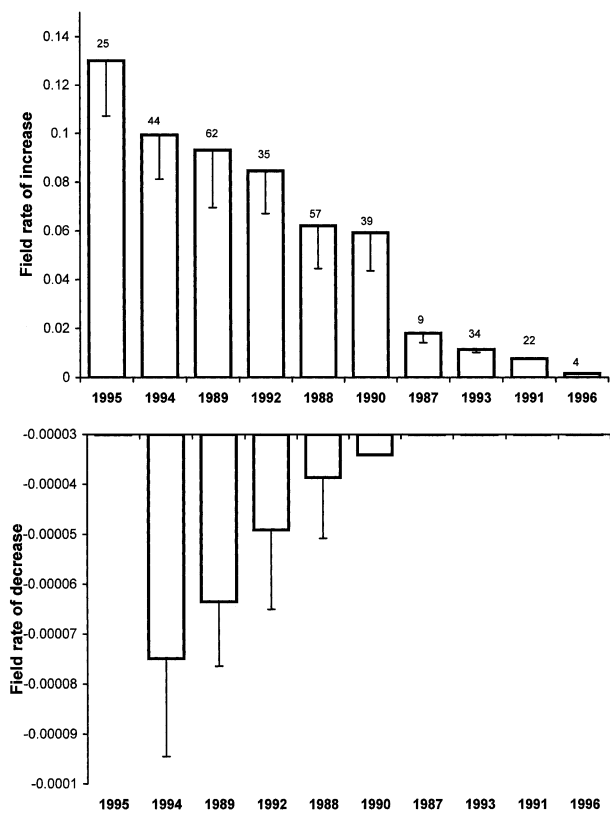
**Fig. 6.** Field estimates of the rate of population increase of *Metopolophium dirhodum* (linear regression slopes of  $\ln$  aphid densities on day-degrees in eqn 2) and field estimates of the rate of population decrease (quadratic regression slopes of  $\ln$  aphid densities on day-degrees in eqn 2) on winter wheat leaves each year from 1987 to 1996. Numbers are the sample sizes, vertical lines are the standard errors.

rate of increase ranged from an extremely high value, 0.15 (1995), to negative values (1988, 1996) (Fig. 7). These extreme values were recorded when abundances were low and therefore likely to be affected by the movement of aphids from leaves to ears. In 1995, this aphid colonised winter wheat very late in the season, and shortly after colonisation moved from leaves to ears. The high population increase thus reflected a massive late spring colonisation rather than population growth. The negative values recorded in 1988 and 1996 reflect the harsh conditions for aphid development that prevailed after the colonisation of wheat (cf. Honěk & Martinková, 1999). The negative growth was a consequence of the time lag between colonisation and population growth, which started after the aphids moved from leaves to ears. The unbiased estimates of the intrinsic rate of increase attributable to population growth on leaves were rather low, ranging from 0.00078 to 0.0061. The estimates did not decrease with increasing density. On the other hand, on the ears of wheat the population growth rate of *S. avenae* was the fastest of all the species.



**Fig. 7.** Field estimates of the intrinsic rate of population increase of *Sitobion avenae* (linear regression slopes of  $\ln$  aphid densities on day-degrees in eqn 2) on winter wheat leaves each year from 1987 to 1996. There was no evidence of field rate of decrease (quadratic regression slopes of  $\ln$  aphid densities on day-degrees in eqn 2 were not significant). Numbers are the sample sizes, vertical lines are the standard errors.

The estimates of the intrinsic rate of increase ranged from 0.0015 to 0.13 (Fig. 8). As for *M. dirhodum* on the leaves, in



**Fig. 8.** Field estimates of the rate of population increase of *Sitobion avenae* (linear regression slopes of  $\ln$  aphid densities on day-degrees in eqn 2) and field estimates of the rate of population decrease (quadratic regression slopes of  $\ln$  aphid densities on day-degrees in eqn 2) on winter wheat ears each year from 1987 to 1996. Numbers are the sample sizes, vertical lines are the standard errors.

those seasons with the highest population increase, there was a significant decrease in population growth rate of *S. avenae* with increasing aphid density ( $F=7.47$ , d.f. = 10,311,  $P < 0.001$ ).

## Discussion

At the level of individual plots, no population growth was detected at very low aphid population densities. For the pooled data, significant growth, indistinguishable from exponential, was revealed even at very low densities. The detection of significant growth using pooled data, when no growth was detectable using data from individual plots, is attributable to the much larger sample size of the pooled data. The sample size on individual plots was 300 tillers/ears at low densities, while the pooled sample sizes ranged from 2400 to 30 600 tillers (average 12 900) and from 1200 to 22 800 ears (average 10 500).

Sample size is important when assessing species abundance (e.g. Krebs, 1989). Using the threshold for a 5% probability of the onset of exponential growth, i.e. 0.023 aphids per tiller for *M. dirhodum* and *S. avenae*, 1.42 per tiller for *R. padi*, and 0.44 per ear for *S. avenae*, a sample size of 300 tillers/ears is clearly insufficient for an accurate assessment of aphid abundance (Ekbom, 1985, 1987; Ward *et al.*, 1985a; Elliott & Kieckhefer, 1986; Elliott *et al.*, 1990). The random population fluctuations that occur at low densities on individual plots are thus attributable to small sample size; they do not mean that these populations are not growing.

The pooled data indicated that *Rhopalosiphum padi* had the lowest, least variable, and monotonically increasing population growth. It is a generalist aphid adapted to cool and humid microclimates (Leather *et al.*, 1989), and does well in dense wheat stands (Honěk, 1991a,b). Its unconstrained exponential growth is probably a consequence of its rapid adaptation to changes in environmental quality and increasing tendency to move within and between host plants. By contrast, the decreasing rate of population growth with increasing density in *M. dirhodum* (the species with the fastest growth on leaves) may be a consequence of its restricted distribution. This species is confined to leaves and is therefore unable to move elsewhere as leaf space becomes limiting.

The slow and monotonical increase of *S. avenae* on leaves may be a response to the cool and humid microclimate that prevails on the leaves of a stand of wheat. *Sitobion avenae* prefers warm, dry conditions (Honěk, 1985), and its rate of population growth is lower on leaves than on ears (Watt, 1979; Acreman & Dixon, 1989; Sengonca *et al.*, 1994). The rate of population growth on leaves did not decrease with increasing population density, probably because of movement to the ears (Holmes, 1988; Chongrattanameteeikul *et al.*, 1991). In contrast, the decrease in the rate of population growth on ears as density increases is attributable to the limited surface area of ears (A. Honěk *et al.*, in prep. a).

The decelerating population growth of *M. dirhodum* on leaves and *S. avenae* on ears, as density increases, is a consequence of intraspecific competition. The intraspecific competition increases in severity as abundance increases and the carrying capacity of the environment is approached. This typically means that either the population becomes crowded within the limited space provided by the plant and/or that the quality of the food resource deteriorates in time as a consequence of aphid feeding and plant senescence. Intraspecific interactions are recorded frequently (Dixon, 1985). Increasing population density results in a decrease in adult body size and fecundity, and induces alate production. These processes decelerate population growth as density increases and thus decrease the maximum abundance attained by a population.

The time lag between colonisation of a stand and population growth, which caused the negative values of population growth of *S. avenae* in seasons with low aphid abundance, conforms with the results of Carter and Dixon (1981). They attributed the population decrease to this time lag rather than a natural enemy ravine (Southwood & Comins, 1976), i.e. the delayed population growth at low density that they attributed to immediate density-dependent predation by polyphagous predators.

The results presented here indicate that a ravine in population dynamics is a consequence of low population density, when population increase is undetectable using small sample sizes. Thus, the ravine is not caused by mortality inflicted by natural enemies (Southwood & Comins, 1976) or by the intermittent nature of aphid colonisation (Carter & Dixon, 1981). It is an artefact of small sample size.

That the ravine could be an artefact of small sample size is dependent on the sample sizes in the studies cited by Southwood and Comins (1976), as evidence for a natural enemy ravine, being small. In the case of Smith and Hagen (1959), it was 200 alfalfa stems; van Emden (1965), 90 mustard plants; and Wratten (1975), 30 stems of winter wheat. Small sample size is also characteristic of the study of Carter and Dixon (1981), in which an alternative explanation for the ravine was proposed (maximum sample size 600 tillers of winter wheat). Parameters used to assess sample size are affected by changes in behaviour and demographic characteristics of aphids, by the environment, and by sample unit size (Taylor, 1984). Therefore, caution must be exercised when using a sample size developed for a particular study (Elliott & Kieckhefer, 1986). Nevertheless, for the species of aphids on cereals, the required sample size for determining aphid densities when populations are as low as they are at the time of the ravine, is more than 500 tillers, in most cases, much more than 500 tillers (cf. Ward *et al.*, 1985a; Elliott & Kieckhefer, 1986; Ekbohm, 1987; Elliott *et al.*, 1990). Moreover, the estimates of sample sizes that should be used at low aphid densities are very unreliable (Ward *et al.*, 1985b). The required sample size for determining densities of less than an aphid per tiller increase rapidly to infinity. Such densities are often typical of the ravine. Therefore, there appears to be no need for an explanation of the ravine in population dynamics of aphids other than small sample size.

Cereal aphid densities in the studies cited in support of the ravine concept were similar to those in this study. This is important because at high densities it is possible to detect the ravine using a smaller sample size. In the study of Carter and Dixon (1981), the densities of *Sitobion avenae* per tiller of winter wheat were 0.073–0.112 and 0.66–3.107 for the first and the second ravine respectively. In the study of Wratten (1975), cited in support of the natural enemy ravine by Southwood and Comins (1976), the densities of cereal aphids on winter wheat over the critical period, from the onset of infestation to 50% anthesis, were about 0.3–4.0 and 0.0–1.0 for *S. avenae* and *Metopolophium dirhodum* respectively. Therefore, there is no evidence from these studies that the ravine might be present when the densities are higher than in this study, and could thus be detected by a smaller sample size.

There is no evidence that polyphagous predators affected aphid population dynamics in this study. Ground beetles (Carabidae) were the dominant guild of polyphagous predators in the study plots (Honěk *et al.*, in prep. b) (however these carabids are mainly seed predators (Honěk *et al.*, in prep. b,c), and their activity density is correlated only loosely with aphid density (Honěk & Jarošík, 2000). Recent results (Bilde & Toft, 1999) suggest that aphids are not the preferred food of carabids, as they have a low nutritional value. The possible role of polyphagous predators as a cause of the natural enemy ravine is thus doubtful, at least in the cereal crops of central Europe.

## Acknowledgements

The work was supported by a grant of GAČR 522/01/0864. V.J. was also supported by MŠMT grant no. J13/98113100004.

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