Stability of natural populations of an aphid, *Uroleucon rudbeckiae*, at three spatial scales

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Abstract—Stability (temporal variability, persistence, resilience) was assessed over 8−13 years for subpopulations, populations, and regional populations of *Uroleucon rudbeckiae* (Fitch) (Hemiptera: Aphididae) in southern Manitoba, Canada. Contrary to expectations, natural populations of this native aphid were not more stable than those of aphids inhabiting crops. Among population parameters, prevalence (proportion of plants infested) proved more effective for quantifying temporal variability than intensity (colony size) or abundance (number of aphids per stem). The parameter "population variability" was a more effective index of temporal variability than the standard deviation of the logarithm or the coefficient of variation. Small differences in temporal variability were detected among populations that varied greatly in size. Population variability declined slightly as spatial scale increased and did not increase consistently over time. Population variability can be considered characteristic of this species in southern Manitoba, having a value of 0.648 ± 0.080 (mean ± standard deviation, $n = 5$, over 8−13 years) on a scale of 0−1, a high degree of temporal variability. Persistence was not related to temporal variability. Subpopulations were less persistent than populations, and one of five populations did not persist. Small populations were more likely to disappear temporarily. No resilience was detected.

Résumé—Nous avons évalué la stabilité (variabilité temporelle, persistance, résilience) sur une période de 8−13 années dans des sous-populations, des populations et des populations régionales d'*Uroleucon rudbeckiae* (Fitch) (Hemiptera : Aphididae) dans le sud du Manitoba, Canada. Contrairement à nos attentes, les populations naturelles de ce puceron indigène ne sont pas plus stables que celles des pucerons qui vivent sur les plantes cultivées. Parmi les variables démographiques, la prévalence (proportion des plantes infestées) s'avère plus efficace comme mesure de la variabilité temporelle que l'intensité (taille de la colonie) ou l'abondance (pucerons par tige). La « variabilité démographique » est un indice plus efficace de la variabilité temporelle que l'écart type du logarithme ou le coefficient de variation. De petites différences de variabilité temporelle peuvent être décelées entre des populations qui diffèrent considérablement en taille. La variabilité démographique diminue légèrement à mesure que l'échelle spatiale augmente, mais elle ne s'accroît pas de façon régulière dans le temps. La variabilité démographique peut être considérée comme une caractéristique de cette espèce dans le sud du Manitoba, avec une valeur de 0,648 ± 0,080 (moyenne ± l'écart type, $n = 5$, sur 8−13 ans) sur une échelle de 0−1, ce qui représente un haut niveau de variabilité temporelle. Il n'y a pas de relation entre la persistance et la variabilité temporelle. Les sous-populations sont moins persistantes que les populations et une des cinq populations ne s'est pas maintenue. Les petites populations sont plus susceptibles de disparaître avec le temps. Aucune résilience n'a été décelée.

[Traduit par la Rédaction]

Introduction

Populations of herbivorous insects are often unstable (Pimm and Redfearn 1988), especially populations of crop pests (van Emden and Williams 1974). Introduction of herbivores without predators and cultivation of crops as monocultures are thought to disrupt natural levels of predation, natural spatial interactions between herbivores and their host

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plants, and natural self-regulation of herbivore populations. "Natural" means under selection locally, prior to the recent rapid environmental change associated with agriculture and the widespread dissemination of organisms as a result of human activities. The link between natural and "stable" has been challenged, however (Connell and Sousa 1983).

Aphids that are pests of annual crops (Way 1967; Jones 1979; Maiteki *et al.* 1986; Bommarco and Ekbom 1996; Lamb *et al.* 1997; Honěk and Martinková 1999; Alyokhin *et al.* 2005) and caught in suction traps over agricultural land (Taylor *et al.* 1980; Redfearn and Pimm 1988) provide examples of instability, often varying in density by many orders of magnitude from year to year. Long-term studies of aphid populations have focussed on the density-dependence of population regulation, not on stability (Wellings *et al.* 1985; Wool 2002; Alyokhin *et al.* 2005; Dixon 2005). However, Cappuccino (1987) observed differences in the stability of two species of *Uroleucon* Mordvilko from the same stands of goldenrod growing in near-monocultures in abandoned fields.

The objective of our study was to assess the stability of populations of a native aphid living on naturally distributed host populations. We expected such aphid populations to be more stable than those on plants growing in monocultures. The size of *Uroleucon rudbeckiae* (Fitch) (Hemiptera: Aphididae) populations on tall coneflower, *Rudbeckia laciniata* L. (Asteraceae), in southern Manitoba, Canada, was measured at five sites over 8–13 years. Both the aphid and its host are native to North America, including Manitoba (Olive 1963; Robinson 1985). This aphid is a monophagous herbivore living in colonies on the tall flower stems of its host, often at or near eye level (Service 1984). It is large and bright red (Olive 1963) and colonies are easily visible. It overwinters as an egg in leaf litter and passes through many parthenogenetic, viviparous generations each year, culminating in a single autumn generation of males and sexual females that lay eggs (Service 1984). During summer both wingless and winged females are produced, the latter being capable of long-distance dispersal. In Manitoba, eggs hatch in May and aphids are active until late September or early October.

In most studies of population stability, including that of aphids, stability is implicitly assumed to be a species-specific trait that can be quantified. Taylor and Woiwod (1980) explicitly concluded that stability is a species characteristic resulting from the density-dependent processes involved in population dynamics. However, the lack of an operational or widely applicable definition limits our ability to quantify the stability of a species. Connell and Sousa (1983) argued that the ups and downs of actual populations must be at the centre of any definition, and emphasized the importance of defining stability in terms of the life history of each species. Grimm and Wissel (1997) recognized that ecological stability has three properties: constancy, persistence, and resilience. Constancy, also termed temporal variability, is the most widely investigated property of stability, but debate continues on the best way to quantify temporal variability (McArdle *et al.* 1990; Heath 2006).

In view of this uncertainty about stability and its role in describing population processes, we examined all three properties of stability and developed operational definitions consistent with the life history of *U. rudbeckiae*. First we assessed potential parameters of population size (abundance, intensity, and prevalence). Next we assessed the utility of various measures of temporal variability (standard deviation of the logarithm, coefficient of variation, and population variability). Then we quantified persistence and resilience and examined the relationships among the properties of stability. We considered three spatial scales (subpopulations, populations, and regional populations) to determine whether estimates of stability apply only narrowly to population processes at a small scale or more widely. Finally, we asked whether population stability is a species trait or results from particular factors that affect population dynamics at one spatial scale.

Materials and methods

Populations

Four natural populations of *U. rudbeckiae* and its host plant, *R. laciniata*, were studied in

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Riding Mountain National Park, Manitoba, Canada. "Natural" refers here to native populations in an environment little affected by humans. The park protects about 10 000 ha of aspen parkland, an ecotone between boreal forest and grassland (Cody 1988). Though surrounded by agricultural land, the park is situated on an elevated plateau and has been little affected by agriculture or forestry (Brook 2009). *Rudbeckia laciniata* occurs in the eastern part of the park, usually at forest edges or in open forest near streams. It is not a dominant member of the herbaceous community anywhere in Manitoba, usually occurring in isolated small patches. The aphid has been found wherever its host plant occurs, although it is often absent from a particular plant patch. The northernmost record of *R. laciniata* is from near the northern edge of the park (Scoggan 1957), and the northernmost record of the aphid is from one of the sampling sites in this study, at the northern edge of the park. A fifth population in a suburban garden in Winnipeg, Manitoba, was included because it was amenable to more intensive observation than those in the relatively remote areas of the park.

The aphid populations in the park included those occurring along parts of four trails: an 860 m long section of Beach Ridges Trail (BR) through a mature aspen forest (51.010N, 100.060W; elevation 400 m), a 2600 m long section of Crawford Creek Trail (CC) through a mature aspen forest (50.997N, 100.065W; elevation 450 m; 1.4 km south of BR), an 800 m long section of Bald Hill Trail (BH) through a mix of meadows and patches of immature aspen forest (50.690N, 99.639W; elevation 710 m; 50 km southeast of CC), and an 1860 m long loop of the Burls and Bittersweet Trail (BB) through a mixed hardwood forest in the floodplain of a stream (50.690N, 99.559W; elevation 400 m; 6 km east of BH).

The fifth population was in the garden of a Winnipeg home (WH), measuring 18 m × 37 m, among mature trees in a riverine forest approximately 200 m from the Red River (49.846N, 97.128W; elevation 230 m; 250 km southeast of BB). The tree composition of the garden was similar to that of the river-bottom forest of BB, but did not include aspen, which dominates the forest at the other sites. *Rudbeckia laciniata* was established in the garden about 25 years ago from seed collected from a single plant growing in the same forest in Assiniboine Park, Winnipeg. The plants grew in four patches, designated A, B, C, and D, established by transplanting a few plants from the original patch (B) and then allowing the patches to expand by self-seeding and runners. Two of the patches were separated by about 4 m (A and B) and partially by a house, whereas the other two patches (C and D) were separated from each other and the others by 10−20 m. No other plant patches occurred in neighbouring gardens. Winged aphids colonized the plants naturally 15 years ago and recolonized some plants annually. The plant patches in the garden were similar in size, spacing, and density to those that occur in the wild. The plants were similar in height and phenology to wild plants and the large predator fauna that attacked the aphids in the garden was similar to that in the park.

Sampling

A census was taken annually. Individual flower stems were searched *in situ* and aphids were counted with minimal disturbance. In four populations all stems were searched and aphids counted, but at BH a subsample of 400−1000 stems was examined because this site usually contained more than 5000 stems. The trails were 1−2 m wide; we searched plants for aphids in a 2 m wide strip on either side of these trails. At BR and CC the census included nearly all of the plants within at least 50 m of the trail because the trails passed through mature forest with an understory that lacked the host plant. At BB and BH many plants were scattered through the forest or meadow more than 2 m from the trails; these plants were not examined. The areas surveyed for plants and aphids were the same each year but varied among sites: CC, 1.04 ha; BR, 0.34 ha; BB, 0.74 ha; BH, 0.32 ha; WH, 0.06 ha. In the early years of the study, small colonies (up to 50 aphids), and in the latter 6 years all colonies, were fully enumerated. The few large colonies were assessed by measuring the total length (cm) of the colony along the stem and flower petioles.

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On average, each 1 cm of colony contained 10 aphids (data not shown).

Populations were assessed in the third week of August. By this time males had begun to appear in some colonies (males are brown rather than red and were usually in the first or second instar), so colonies had almost reached the point where sexual reproduction occurs and eggs are deposited for that year. For 6 years populations were also assessed at the end of June or beginning of July, when flower stems had started to bolt, the first generation of winged dispersers had been produced, and aphid colonies had begun to increase in size on the stems above the canopy of basal leaves. These colonies were easily detected and their presence confirmed that aphids had been able to persist at that site from the previous season. The census of populations in the park took 4−6 days depending on weather and aphid abundance. WH aphids were usually assessed at least weekly. For comparison with the park populations, the dates immediately before the late-spring sampling and immediately after the late-summer sampling were used for WH, because this most southerly population developed more rapidly in spring but produced sexuals a little later than the more northerly populations. BB, BH, and CC were sampled in late summer from 1999 to 2008 but excluding 2004. BR was sampled from 2000 to 2008 except for 2004. WH was sampled each year from 1996 to 2008. Spring samples were taken in the park from 1999 through 2003, with an additional sample in 2007.

At WH the four plant patches were treated as subpopulations; the numbers of plants and aphid colonies in the patches were tallied separately. Three spatial scales were used in the study: subpopulation (*i.e.*, a patch of plants at WH), local population (*i.e.*, WH and the four park sites), and regional population (*i.e.*, an aggregate of the four park populations or all five populations). Temporal (year-to-year) variability and persistence were estimated for each spatial scale.

Estimating population parameters and indices of stability

We considered the aphid a parasite (Bush *et al.* 1997) because it has a single host, many host stems had no aphids, and a small proportion of stems had over 2000 individual aphids. The aphids occupying a single stem were called a colony (infrapopulation; Bush *et al.* 1997). The population parameters used were intensity (number of aphids in a colony), prevalence (proportion of infested stems), and abundance (average number of aphids per plant stem, which equals mean intensity multiplied by prevalence). Density, measured as aphids per unit area, is probably not an ecologically meaningful parameter for this species because the aphid occurs only on its host plant except when dispersing or at the egg stage, so its density depends on the density of plants. Abundance is the parameter commonly used in studies of aphid population dynamics, but given the clumped distribution of aphids on individual host plants, intensity and prevalence provide more information about populations (Rózsa *et al.* 2000).

Three indices of temporal variability were estimated for population parameters: (1) the standard deviation of the logarithm of population estimates (SDL) (Connell and Sousa 1983; Wellings *et al.* 1985; Cappuccino 1987; Alyokhin *et al.* 2005), (2) coefficient of variation of population estimates (CV) (McArdle *et al.* 1990; the untransformed standard deviation divided by the mean and corrected for bias following Sokal and Rohlf 1981), and (3) population variability (PV) (the average of the differences between all pairs of population estimates, where each difference is divided by the larger population estimate of the pair, ensuring that the index is a proportion from 0 to 1) (Heath 2006). SDL has limited value as an index of temporal variability because the standard deviation is related to the mean, thus precluding valid comparisons by analysis of variance of populations with different means (McArdle *et al.* 1990; McArdle and Anderson 2004). Heath (2006) argued that CV is overly sensitive to rare events, inappropriately dependent on deviation from a mean that may not be stable, and inaccurate for short time series. For these reasons PV is the superior index, but CV has the advantage that its standard error can be estimated (Sokal and Rohlf 1981) to facilitate statistical comparisons. Though not an effective index of temporal variability, SDL was

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estimated to allow comparison of *U. rudbeckiae* with aphid species studied previously.

Persistence was measured as the proportion of years in which a subpopulation or population was detected at a particular location. The possibility that aphids were missed cannot be ruled out, but for all subpopulations and four of the five populations every plant was searched individually. For the fifth population, a large sample of plants (up to 1000) was searched for aphids. The aphids are large, bright red, and usually occur in colonies, so they are unlikely to be missed.

No consistently applicable quantitative definition of resilience has been proposed. In the context of *U. rudbeckiae*, a resilient population might decline more slowly after a negative perturbation, or rise more quickly from low abundance after a negative perturbation, than a less resilient one. Our knowledge of environmental factors that cause population fluctuations and of population processes that might facilitate resistance to perturbations are limited, making any assessment of resilience uncertain. To assess whether or not resilience is a factor in the stability of populations, the sequence of peaks and valleys in plots of annual changes of prevalence was examined. The numbers of years from peak to valley and valley to peak were tallied to assess whether lags could be identified that might reflect resilience.

Results

Population parameters and indices of temporal variability

The mean abundance of *U. rudbeckiae* was 3.1 individuals per plant stem (range = 0−22.0, $n = 30$) for five populations sampled in late August over 6 years. Mean intensity was 19.6 aphids per infested stem (range = 2.0−55.2, $n = 28$). Mean prevalence was 0.124, the proportion of stems infested by aphids (range = 0−0.582, $n = 30$). The three population parameters showed positive skewness and kurtosis: 2.64 and 8.16 (abundance); 1.03 and 1.38 (intensity); and 1.67 and 2.70 (prevalence), respectively. Parameters were normalized more effectively by a square-root transformation than by a log transformation. For prevalence, a square-root transformation was more effective than an arcsine or a log transformation. Abundance, but not intensity or prevalence, showed a positive relationship ($P = 0.01$) when the variance was regressed against the mean (log-transformed data) for years, though not for populations ($P = 0.33$), so equality of variances could not be assumed. Taylor's power law was used to further transform abundance data (Southwood 1978) and homogenize variances.

A two-way analysis of variance of transformed data revealed differences in abundance among years ($P = 0.001$, df = 5,20) and among populations ($P = 0.040$, df = 4,20), with an R^2 value of 0.724 for the model. Differences in square-root-transformed intensity were detected among years ($P = 0.021$, df = 5,18) but not among populations ($P = 0.484$, df = 4,18), with an R^2 value of 0.560 for the model. Differences in square-root-transformed prevalence were detected among years ($P < 0.001$, df = 5,20) and among populations ($P = 0.008$, df = 4,20), with an R^2 value of 0.855 for the model. The same findings were obtained with analyses of untransformed data (not reported).

Recalling that abundance = intensity × prevalence, intensity accounted for 44% of the variation in abundance ($r_P = 0.666$, $P < 0.001$, $n = 28$), whereas prevalence accounted for 81% of this variation ($r_P = 0.902$, $P < 0.001$, $n = 30$) (based on transformed data). Intensity and prevalence were weakly correlated ($r_P = 0.436$, $P = 0.020$, $n = 28$). When linear regression was used to identify and exclude outliers and data with high leverage, intensity accounted for 23% of the variation in abundance ($r_P = 0.479$, $P < 0.015$, $n = 25$) and prevalence for 93% ($r_P = 0.965$, $P < 0.001$, $n = 26$). Intensity and prevalence ceased to be correlated ($r_P = 0.268$, $P = 0.186$, $n = 26$). Variation associated with differences among years or populations was greater for prevalence than for abundance or intensity, and prevalence, but not intensity, was highly correlated with abundance. Hence, prevalence was adopted for most subsequent analyses of stability. Prevalence had the further advantage of being available for 48 population-years in the study, whereas intensity was recorded in 30 population-years.

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Table 1. A comparison of three indices of temporal variability, standard deviation of the logarithm (SDL), corrected coefficient of variation (CV), and population variability (PV) (defined in the text), for each of three population parameters estimated annually for populations of the aphid *Uroleucon rudbeckiae* in southern Manitoba over 6 years.

	Abundance			Intensity			Prevalence		
	SDL	CV*	PV	SDL	CV*	PV	SDL	CV*	PV
Index of temporal variability for populations WH, BR, CC, BB, and BH									
WH	0.365	0.880	0.566	0.194	0.475	0.387	0.401	0.846	0.602
BR	0.739	1.318	0.775	0.286	0.653	0.508	0.476	0.928	0.620
CC	1.090	1.671	0.825	0.429	0.704	0.597	0.686	1.387	0.733
BB	0.619	1.418	0.712	0.296	0.789	0.518	0.381	0.795	0.597
BH	2.084	1.720	0.853	0.249	0.442	0.384	1.356	1.725	0.828
Coefficient of variation of indices of temporal variability among populations									
	0.684	0.240	0.153	0.299	0.244	0.216	0.617	0.356	0.150
Pearson's correlation coefficient among indices of temporal variability[†]									
CV	0.793	—	—	0.649	—	—	0.949	—	—
PV	0.794	0.952	—	0.914	0.868	—	0.960	0.999	—

Note: Population parameters are as follows: abundance is the number of aphids per plant stem; intensity is the number of aphids per colony; and prevalence is the proportion of plant stems infested.

*Shown as a proportion rather than a percentage so that indices have similar numerical values.

[†]For intensity estimates, data from 2 of 6 years at BH were excluded because no stems were infested.

A comparison of SDL, CV, and PV showed that temporal variability in intensity was consistently less than variability in abundance or prevalence (Table 1). Based on coefficients of variation of the indices, SDL varied more among populations for each of the population parameters than CV, which in turn varied more than PV (Table 1). The values of these indices for abundance were similar to but usually higher than those for prevalence (11 of 15 cases). PV, by definition, varies between 0 and 1, with average values of 0.75, 0.48, and 0.68 for abundance, intensity, and prevalence, respectively, for the five populations. For abundance, SDL was relatively weakly correlated with CV and PV, and for intensity, SDL was weakly correlated with CV (Table 1). For prevalence, the correlation between CV and PV was remarkably high, therefore the two indices provided similar assessments of temporal variability. For prevalence, both CV and PV were also relatively highly correlated with SDL. The high correlations among SDL, CV, and PV for prevalence further supported the use of prevalence as the main population parameter for subsequent analyses of temporal variability.

Dynamics of aphid prevalence

Over 8–13 years, five aphid populations showed consistent differences in prevalence among populations and substantial fluctuations from year to year (Fig. 1). Average prevalence varied from 0.031 of stems infested at BH to 0.368 at WH (Table 2A). Prevalence was highest at WH and BR, intermediate at CC and BB, and lowest at BH. A two-way general linear model (GLM) for 1999–2008 revealed differences in prevalence among populations ($P = 0.001$, df = 4,31) and among years ($P < 0.001$, df = 9,31), with an R^2 value of 0.701 for the model. A similar result was obtained when prevalence was transformed to normalize the data by calculating its square root, and R^2 rose to 0.828. However, conclusions from the GLM are suspect because the standard deviations of prevalence for populations increase with the mean (Table 2A) and are therefore not homoscedastic. The same is true (data not shown) for standard deviations among yearly estimates, but with a different relationship between standard deviation and mean than for populations. Therefore, Taylor's power law could not simultaneously achieve homoscedasticity for both populations and years. Nevertheless,

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Fig. 1. Temporal variability in prevalence, *i.e.*, the proportion of *Rudbeckia laciniata* stems with aphid colonies, for five populations of *Uroleucon rudbeckiae* sampled in late August of successive years in southern Manitoba.

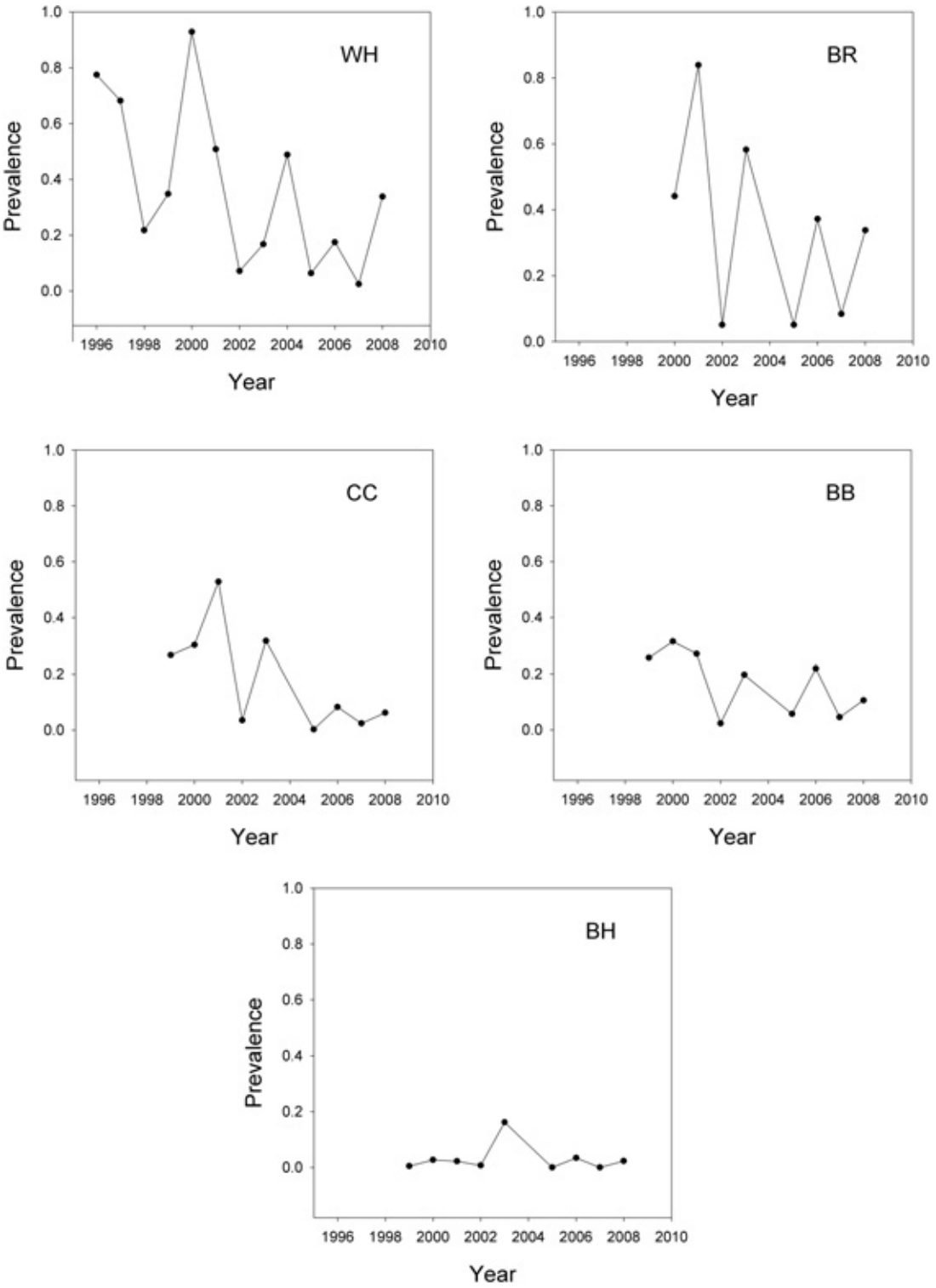

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Table 2. Proportions of *Rudbeckia laciniata* stems infested by *Uroleucon rudbeckiae* (prevalence) (A) and stem counts for five populations of *R. laciniata* (B) surveyed annually for 8−13 years (*n*) in southern Manitoba.

(A) Aphid prevalence.

Population	Period	Mean	SD	*n* (years)	Min.	Max.
WH	1996–2008	0.368	0.290	13	0.025	0.929
	1999–2008	0.311	0.277	10	0.025	0.929
BR	2000–2008*	0.345	0.281	8	0.051	0.839
CC	1999–2008*	0.180	0.181	9	0.003	0.529
BB	1999–2008*	0.165	0.109	9	0.023	0.314
BH	1999–2008*	0.031	0.051	9	0	0.162

(B) Number of plant stems.

Population	Period	Mean	SD	Density[†]	*n* (years)	Min.	Max.
WH	1996–2008	93.2	56.7	—	13	22	188
	1999–2008	113.5	47.8	—	10	42	188
BR	2000–2008*	171.9	127.6	0.20	8	12	394
CC	1999–2008*	1481.6	1791.7	0.57	9	192	5219
BB	1999–2008*	167.1	80.3	0.09	9	66	302
BH	1999–2008*	642.6[‡]	—	>2.00	9	400	1000

*No data were collected in 2004.
[†]Average number of stems per 1 m of trail; not applicable to WH.
[‡]Aphids were counted on a sample of stems because the number of stems exceeded 5000.

Table 3. Pearson's correlation coefficients (*P*) for pairs of *Uroleucon rudbeckiae* populations in southern Manitoba in 1999—2008*, showing the synchrony in the prevalence of aphids (proportion of *Rudbeckia laciniata* stems infested) over 8 or 9 years.

Population	WH	BR	CC	BB
BR[†]	0.802 (<0.05)	—	—	—
CC	0.826 (<0.01)	0.958 (<0.01)	—	—
BB	0.906 (<0.01)	0.940 (<0.01)	0.908 (<0.01)	—
BH	0.392 (>0.05)	0.697 (>0.05)	0.607 (>0.05)	0.579 (>0.05)

*No data were collected in 2004.
[†]Data for 2000—2008.

differences among the three groups of mean prevalence are clearly real because in all 8 years, prevalence at BR was higher than at CC, BB, and BH, and in all 9 years prevalence at CC and BB was higher than at BH. The probability of such strings of difference occurring by chance if estimates were drawn from the same statistical population is <0.005, based on a test of runs (Sokal and Rohlf 1981).

Annual fluctuations in prevalence were highly correlated for WH, BR, CC, and BB (Table 3). The correlation of BH with the other populations was low, probably because its prevalence was less than 0.04 in 7 of 8 years. Nevertheless, prevalence at BH was lowest (0) in 2005 and 2007, when the other populations were also at their lowest prevalence (Fig. 1). When prevalence increased, or decreased, from one year to the next, the direction of change tended to be the same for all populations. Comparing the directions of change from year to year for CC with those for the three other Riding Mountain populations revealed that in 20 of 23 cases, pairs of populations changed in the same direction, which was unlikely to have occurred by

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chance (Pearson's $\chi^2 = 12.6$, $P < 0.001$, df = 1). Comparing WH with all four Riding Mountain populations revealed that in 29 of 31 cases, changes were in the same direction (Pearson's $\chi^2 = 23.5$, $P < 0.001$, df = 1). None of the five populations showed a trend in prevalence from 1999 to 2008 (linear regressions: $P > 0.05$, df = 1,6−1,8), although prevalence for WH tended to decline if the period 1996−2008 was considered (linear regression: $R^2 = 0.309$, $P = 0.049$, df = 1,11). This weak trend may reflect a single year or a few years with high prevalence that occurred early in the sampling period but not since. This possibility was confirmed in 2009, when prevalence of all five populations again rose to levels as high as or higher than those observed early in the study (data not shown).

Annual fluctuations in prevalence were associated with fluctuations in the number of plant stems (Table 2) only at WH (linear regression: $R^2 = 0.447$, $P = 0.013$, df = 1,11). No such relationship was detected ($R^2 < 0.079$, $P > 0.05$) for CC, BB, or BR, and plant stems were not fully enumerated for BH. The trend at WH was due to the three highest estimates of prevalence (Fig. 1) occurring during the first 6 years of the study, when the number of plant stems averaged 41 per year compared with an average of 138 stems per year for the last 7 years of the study. Any effect of stem number could not be separated from a trend in prevalence over time, as described above. Comparisons among populations revealed no relationship between prevalence and the density of plant stems: at BR, with high prevalence, plant density was intermediate; at CC and BB, with intermediate prevalence, plant densities were high and low, respectively; and at BH, with the lowest prevalence, plant density was highest (Table 2B). Differences in prevalence among years and among populations showed no consistent relationship with plant density.

Patterns of prevalence observed for subpopulations (plant patches) at WH were similar to those observed for populations. Over 10 years, subpopulations at WH had an average prevalence between 0.24 and 0.56. Prevalence was usually lowest for subpopulations C and D, intermediate for B, and always highest for A.

Eleven estimates of the mean and standard deviation of prevalence at different spatial scales (four subpopulations, five populations, and two regions) showed that the standard deviation was closely related to the mean ($r_P = 0.946$, $P < 0.001$, $n = 11$). When only the population scale at which the five populations provided independent estimates based on large samples of plant stems were considered, the standard deviation of prevalence also increased with the mean ($r_P = 0.933$, $P < 0.05$, $n = 5$) (Table 2).

Temporal variability as a component of stability

Temporal variability, measured as both CV and PV of the population parameter prevalence, is presented for the subpopulations and populations in Table 4. CV was estimated from square-root-transformed prevalence to normalize data and increase the reliability of confidence intervals. When all pairs of estimates for all three spatial scales were considered, PV was correlated with untransformed CV ($r_P = 0.783$, $P = 0.004$, $n = 11$), but more strongly correlated with CV calculated with square-root-transformed prevalence ($r_P = 0.911$, $P < 0.001$, $n = 11$). Based on 95% confidence intervals, no difference in temporal variability was detected among subpopulations (Table 4). For populations, temporal variability was lower for BB than for CC or BH, and lower for WH and BR than for BH. The range in PV values, 0.565−0.748, reflected real but relatively small differences in the degree of temporal variability, given the large differences in prevalence among them (Fig. 1).

Comparisons of data among the three spatial scales revealed relatively small differences in PV (Table 5). PV for population WH (Table 4) was 13% less than that for, and below the confidence interval of, its four subpopulations (Table 5). Similarly, at the regional scale, PV for RMNP was 9% less than the average PV for its four component populations, though within the 95% confidence intervals (Table 5).

PV was initially erratic when only the first 2 or 3 years of data were accumulated, then stabilized as years were added. This pattern was evident in the longest series of data for

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Table 4. Temporal variability for subpopulations and populations of *Uroleucon rudbeckiae* in southern Manitoba, measured as population variability (PV), *i.e.*, the cumulative average deviation of all pairs of yearly estimates of prevalence, defined as the proportion of *Rudbeckia laciniata* stems with aphid colonies, and as the coefficient of variation (CV) of square-root-transformed prevalence with 95% confidence intervals (CI).

	CV			PV		PV trend over years*		
	CV	CI	*n* (years)†	PV	Duration (years)	Slope	*P*	df
Subpopulation of WH								
A	0.601	0.263	10	0.649	13	0.016	0.114	1,5
B	0.648	0.284	10	0.725	13	−0.006	0.234	1,5
C	0.541	0.237	10	0.635	13	0.008	0.493	1,6
D	0.735	0.322	10	0.729	10	0.016	0.016	1,5
Population								
WH	0.506	0.222	10	0.594	13	0.014	0.002	1,9
BR	0.503	0.246	8	0.615	8	−0.017	0.124	1,4
CC	0.646	0.298	9	0.717	9	0.044	0.016	1,5
BB	0.407	0.188	9	0.565	9	0.010	0.135	1,4
BH	0.932	0.431	9	0.748	9	0.029	0.023	1,5

*Described by the slope of a linear-regression model.
†Data for 3 initial years are excluded because subpopulation D did not exist in those years. Data were available for all subpopulations and populations from 1999 to 2008, except that 2004 was missing for BR, CC, BB, and BH and 1999 was missing for BR.

Table 5. Temporal variability at three spatial scales, measured as mean population variability (PV (mean ± standard error)), where PV is the cumulative average deviation of all pairs of yearly estimates of prevalence, defined as the proportion of *Rudbeckia laciniata* stems with *Uroleucon rudbeckiae* colonies, in southern Manitoba.

Spatial scale	*n*	Duration (years)	PV	95% CI
Subpopulation	4	10–13	0.685 ± 0.025	0.606–0.763
Population	5	8–13	0.648 ± 0.036	0.548–0.747
RMNP* population	4	8–9	0.661 ± 0.043	0.525–0.798
Region†				
RMNP	1	8–9	0.601	
Southern Manitoba	1	8–9	0.581	

*Riding Mountain National Park.
†PV was calculated from the average annual prevalence of aphids for the populations in that region, giving a single estimate of PV for a region.

WH (Fig. 2) and for the other four populations and the subpopulations (not shown). Excluding the first datum for 1996−1997, PV for WH increased by 0.014 ± 0.003, about 1%, each year (linear regression: $R^2 = 0.691$, $P = 0.002$, df = 1,9). No trend over years was observed for subpopulations A, B, and C, but the trend for D was similar to that of WH (Table 4). Among the four park populations, CC and BH showed an increasing trend in PV with time but BR and BB did not (Table 4). PV for the regional group of park populations showed no trend from 2002 to 2008 (slope = −0.004, $P = 0.598$, df = 1,4), and the same was true for the wider region that included WH and the park populations (slope = 0.001, $P = 0.880$, df = 1,4). Although PV increased with the duration of sampling in some cases, no consistent pattern was evident.

Persistence as a component of stability

At the subpopulation scale, persistence (measured as the proportion of years when aphids were present) varied from low in June

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Fig. 2. Cumulative population variability (PV), *i.e.*, the accumulated average deviation of all pairs of yearly estimates from the onset of sampling up to the year shown (see the text), estimated for prevalence (proportion of stems with aphid colonies), for a population of *Uroleucon rudbeckiae* sampled in late August each year from 1996 to 2008 at WH in southern Manitoba.

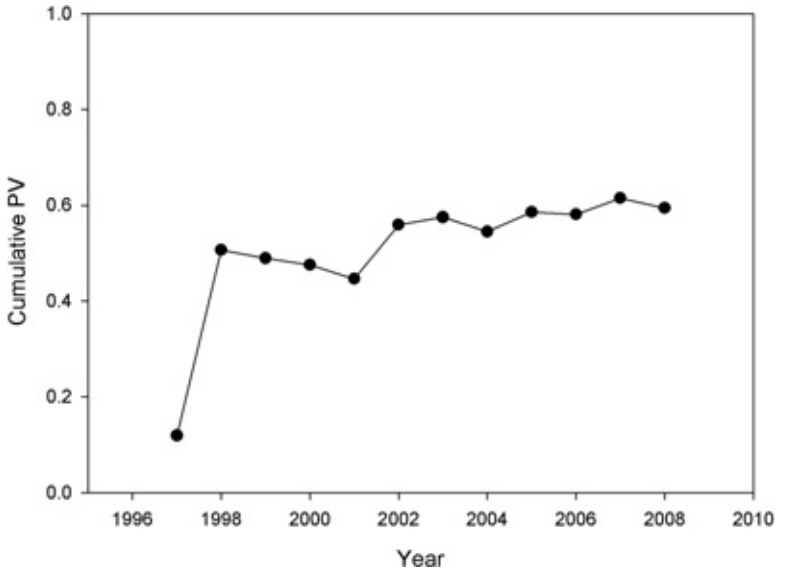

Table 6. Persistence of four subpopulations and five populations of *Uroleucon rudbeckiae* in June (the offspring of aphids that overwintered locally) and late August (onset of the sexual generation) in southern Manitoba, measured as the proportion of years when aphids were detected.

	June		Late August			
	Persistence	Duration (years)	Persistence	Duration (years)	Prevalence	PV
Subpopulation of WH						
A	0.54	13	0.92	13	0.557	0.649
B	0.23	13	0.92	13	0.403	0.725
C	0.08	13	1.00	12	0.241	0.635
D	0.00	10	0.90	10	0.300	0.729
Population						
WH	0.69	13	1.00	13	0.368	0.594
BR	1.00	5	1.00	8	0.345	0.615
CC	1.00	6	1.00	9	0.180	0.717
BB	1.00	6	1.00	9	0.165	0.565
BH	0.00	5	0.78	9	0.031	0.748

Note: Prevalence (the average proportion of stems infested) and population variability (PV), an index of temporal variability, are provided for comparison.

to high in August, with no consistent relationship between June and August levels (Table 6). The subpopulations at WH were consistently less persistent in spring than the overall population at WH, and some subpopulations were not usually present in spring (Table 6). Nevertheless, subpopulations usually had aphids in late August. At the population scale, three of five populations always overwintered successfully and initiated

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a population in spring. Aphids were always present at the onset of the sexual generation in four of the five populations. Aphids in the fifth population (BH) were never observed in spring and were also absent in late August in 2 of 8 years. Therefore, the BH population was less persistent than the other four populations. At the regional scale, aphids persisted throughout the 13 years: they overwintered successfully every year in some of the populations and were present at the onset of the sexual generation every year in all but one population (Table 6).

Persistence from late summer to the following spring was associated with prevalence for subpopulations ($r_P = 0.884$, $P = 0.046$, $n = 4$) but showed no consistent trend in relation to temporal variability (Table 6). At the population scale, BH had low persistence, low prevalence, and high temporal variability, though not appreciably higher than that of CC, which had high persistence. Any relationship between persistence and prevalence was not continuous between spatial scales, however, because populations with relatively low prevalence (CC and BB) had higher persistence than subpopulations with relatively high prevalence (A and B) (Table 6).

Resilience as a component of stability

Over 13 years, three population peaks and three population valleys were identified at WH (Fig. 1). These three fluctuations took 2, 2, and 3 years to drop from each successive peak to the valley and 2, 2, and 1 years to return to the peak. Although the sample of peaks and valleys was limited, the data might be consistent with the hypothesis that population processes delay by a year or two the change in prevalence associated with an environmental perturbation occurring over a single year. On the other hand, environmental perturbations (*e.g.*, unusually cool weather) may last for 2 or 3 years, a possible alternative explanation for the 2- or 3-year intervals between peaks and valleys. Furthermore, the pattern evident at WH was not repeated in the other four populations (Fig. 1). These populations often changed between a peak and a valley within a single year.

Discussion

The abundance of *U. rudbeckiae* varied substantially from year to year and among populations. The range in abundance was at least two and sometimes three orders of magnitude for this aphid living on a patchily distributed perennial herb. The extent of temporal variability was similar to that observed for aphids on herbaceous plants in more disturbed habitats. For two species of *Uroleucon* on a near-monoculture of *Solidago* L. (Asteraceae) in an abandoned field (Cappuccino 1987), temporal variability in abundance was 0.221 and 2.05 (SDL). For three aphid species that are pests in annual potato fields, temporal variability in abundance (SDL) was 0.368, 0.537, and 0.749 (Alyokhin *et al.* 2005). Equivalent estimates of variation in abundance (SDL) for five populations of *U. rudbeckiae* in this study ranged from 0.365 to 2.084, encompassing all but one of the estimates for the other five species. Based on these comparisons of stability among six species from habitats with various degrees of "naturalness", we find no evidence that natural populations of *U. rudbeckiae* are more stable than those in habitats modified to a lesser or greater extent by agriculture.

Although a range of temporal variabilities was detected among these six species, these apparent interspecific differences may not be real, because the measure of stability of the species is the standard deviation of the logarithm of abundance. This measure of temporal variability is unstable when abundance is non-normal, and usually increases with mean abundance, thus precluding a valid comparison using parametric statistics (McArdle *et al.* 1990; McArdle and Anderson 2004; Heath 2006). These theoretical concerns were borne out by the relative lack of uniformity of SDL as an index compared with CV and particularly PV; estimates of SDL for *U. rudbeckiae* populations deviated much more widely than for the other two indices, particularly PV. Furthermore, estimates of temporal variability for most species have been based on samples from a single population, providing no confidence intervals on the estimate for that species. An estimate of

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temporal variability from a single population for each species ensures that apparent differences between species reflect differences among populations rather than among species. These issues are difficult to address retroactively for most of the aphid species that have been studied, but we can ask whether *U. rudbeckiae* has a characteristic degree of temporal variability and at what spatial scale this component of stability should be assessed.

The hypothesis that the degree of temporal variability is a species trait implies that degrees are similar among subpopulations, populations, and spatial scales and remain constant over time. Alternatively, the degree of temporal variability may vary with the dynamics of populations, and therefore patterns are evident among populations or spatial scales that invalidate simple comparisons among species. For example, temporal variability might increase as abundance decreases, because small populations are more likely to collapse or go extinct (Schoener and Spiller 1987). Or temporal variability might decrease as the spatial scale increases, because the independent dynamics of component populations lead to greater evenness at the larger scale (Connell and Sousa 1983). Or the temporal variability of a population might increase over time as a result of the accumulated effects of erratic or long-term cyclical perturbations (*e.g.*, forest succession, outbreaks of lepidopteran defoliators, severe drought) (Pimm and Redfearn 1988).

For *U. rudbeckiae*, temporal variability, measured as PV, was surprisingly uniform among subpopulations, populations, and spatial scales and over time. None of the four subpopulations and only one of the five populations stood out as having a PV that deviated appreciably from those of the others. Temporal variability did decline slightly as spatial scale increased, though not always significantly, as was predicted would be the case as a result of the averaging out of fluctuations of different populations that are asynchronous in their dynamics (Connell and Sousa 1983). That this process had little effect for *U. rudbeckiae* was probably due to the high degree of synchrony in the dynamics observed for the five populations, even though some were widely separated in space. A similar degree of synchrony has been observed for an aphid species inhabiting a tree (Wellings *et al.* 1985), but not for a gall-forming species on a tree (Wool 2002). PV did increase slightly over time, by about 1% per year, for some populations, but not consistently and not at the regional scale. Such a trend, if real, would have no appreciable effect on the estimate of temporal variability for populations, except over long periods of time, because the standard deviation for PV is 12% of the mean.

The population scale provides the most useful estimate of temporal variability for comparing aphid species. The subpopulation scale would differ from species to species because the spatial distributions of their host plants differ. The regional scale is also difficult to define, and in this study was arbitrarily determined by the five populations chosen for study. Thus, we conclude that the temporal variability (PV) in the prevalence of *U. rudbeckiae* in southern Manitoba is 0.648 ± 0.080 (mean $\pm$ standard deviation; $n = 5$ years, over 8−13 years), which, on a scale of 0−1, is high (Heath 2006). Alternatively, measuring temporal variability in terms of year-to-year variation in abundance (mean number of aphids per stem) would increase the estimate to 0.746 ± 0.114 (mean $\pm$ standard deviation; $n = 5$, over 6 years). The temporal variability in prevalence for the same 6 years was 0.676 ± 0.101 (mean $\pm$ standard deviation; $n = 5$, over 6 years), which is not significantly different from that estimated for prevalence over 8−13 years.

Studies of aphid populations have usually focussed on abundance rather than prevalence, and although the numbers of aphids per plant are often reported, the proportion of plants with aphids rarely is. For some aphid species, particularly those on trees, prevalence may reach 1 (Wellings *et al.* 1985), in which case this measure is not useful for assessing temporal variability. Prevalence proved to be an effective measure for *U. rudbeckiae*, however, because relatively few plants (12%, on average) had a colony, and intensity (the number of aphids in a colony (20, on average))

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was less variable than prevalence. Levels of prevalence and intensity probably reflect particular ecological processes, therefore information is lost if they are not recorded separately (Rózsa *et al.* 2000). At present the processes that determine the degree of temporal variability in either prevalence or intensity for *U. rudbeckiae* are unknown, but our study makes clear that the number of aphid colonies is more important than the size of individual colonies in determining temporal variability in aphid abundance.

Temporal variability is only one of three recognized components of stability, the other two being persistence and resilience (Grimm and Wissel 1997). We expected that for *U. rudbeckiae*, temporal variability would influence persistence, with less variable subpopulations and populations being more persistent (Taylor *et al.* 1980). This expectation was not supported by our data. No consistent relationship between temporal variability and persistence was detected, leading to the conclusion that temporal variability and persistence need not be linked. Thus, it is perhaps not surprising that selection for low temporal variability might have little effect on persistence (Sutirth *et al.* 2008).

Prevalence, the proportion of stems with colonies, and perhaps a threshold number of colonies, seemed to be more important in determining persistence than temporal variability. Subpopulations with relatively high prevalence still had relatively few colonies because of the small number of plants in a patch, and were less persistent than populations with similar or lower prevalence but many colonies because plant populations were large. Only one population with very low prevalence, and therefore relatively few colonies at the end of each season, had low persistence. An aphid such as *U. rudbeckiae* is highly dispersive, as is shown by the reinvasion of WH and BH when these populations failed to survive to the following spring. Given the level of dispersal and the tremendous potential for population increase by aphids (Dixon 1985), local extinction may only be likely to occur when the absolute number of colonies drops to a low level, and local stochastic processes eliminate those few colonies. A population with low prevalence, such as BB (16.5% of plants with colonies, on average), can persist because it has relatively low temporal variability and the plant population is large enough to ensure that the absolute number of colonies does not drop below that needed to prevent local extinction. An analogous situation has been observed for species of spiders that disperse to small islands (Schoener and Spiller 1987): species that occurred in small numbers on the islands were less likely to persist than species that were more abundant.

No evidence was found that resilience, the third component of stability, played a role in the stability of *U. rudbeckiae* populations. Populations levels fluctuated rapidly from high to low and back again, suggesting that populations may have reacted immediately to environmental perturbations. On the other hand, many aphid species employ specific density-dependent mechanisms that could contribute to resilience, such as an increase in dispersal or a reduction in fecundity at high density (Way and Cammell 1970; Dixon 1985, 2005). Density-dependent regulation of free-living aphid populations has been demonstrated for some (Wellings *et al.* 1985; Alyhokin *et al.* 2005) but not all aphid species that have been investigated (Wool 2002), although the importance of this density-dependence in reducing temporal variability is not known. For *U. rudbeckiae*, and most aphid species, too little is known about environmental perturbations that might increase variability, or about density-dependent mechanisms that might reduce variability, to speculate on the importance of resilience.

Natural populations of a native aphid living on a patchily distributed herbaceous perennial host plant were highly variable from year to year, and not less variable than populations of endemic or exotic aphids that live on annual crops in monocultures. Subpopulations and populations of *U. rudbeckiae* exhibited at least 10-fold differences in abundance and consistent differences in persistence, showing that they occupied qualitatively different habitats. Nevertheless, for *U. rudbeckiae*, temporal variability was remarkably uniform among subpopulations and populations, among spatial scales,

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and over time. Samples from multiple populations allow temporal variability and its error to be estimated and are sufficiently uniform that it may be concluded that this aspect of stability is characteristic of the species over a substantial region.

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