

A quantitative study of day–night changes in the spatial distribution of insects in a stony stream

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Summary

1. As many invertebrates are nocturnal, their spatial distribution may change from day to night. This behavioural aspect of their population dynamics has been ignored, but is now examined for the first time by testing the hypotheses: (i) a power function was a suitable model for the spatial distribution of common species of Ephemeroptera, Plecoptera and Trichoptera in a stony stream; (ii) the spatial distribution varied between species but was similar within species for larvae greater and smaller than half-size; (iii) diurnal and nocturnal spatial distributions were significantly different for each species. To ensure that the conclusions were consistent, large samples ($n = 30$) were taken near midday and midnight in April, June and November over 4 years.

2. Twenty-one species were taken in sufficient numbers for the analyses; seven species were too sparse to be included. The first hypothesis was supported. A power function, relating spatial variance (s^2) to mean (m), was an excellent fit in all the analyses ($P < 0.001$, $r^2 > 0.95$), i.e. the spatial variance was density-dependent. The power b , often used as an 'index of aggregation', varied in the range 0.88–2.50.

3. Most analyses supported the second hypothesis. For four species, the difference between the two size groups was just significant ($P < 0.05$), but was due to inadequate data for three species. Large larvae of the fourth species, the caddis *Odontocerum albicorne*, were less aggregated than small larvae at night, and were the only group with a b -value less than one.

4. The third hypothesis was partially supported. The distribution did not change significantly ($P > 0.05$) for nine species; five burrowers in gravel, moss or mud, two highly mobile predators, one sedentary, case-building, Trichoptera species, and one net-spinning Trichoptera species. Aggregation was reduced significantly ($P < 0.001$) at night for four species, all case-building Trichoptera larvae. Aggregation increased significantly ($P < 0.001$) at night, except at low densities, for the remaining eight species, one being a nocturnal predator and the others being herbivorous species; all occurred frequently in night samples of invertebrate drift. Day–night changes in spatial distribution were therefore an essential part of the behavioural dynamics of 12 of the 21 species, and should be investigated in other species, including terrestrial species.

Key-words: aggregation, Ephemeroptera, Plecoptera, Trichoptera, variance–mean relationship.

Journal of Animal Ecology (2002) **71**, 112–122

Introduction

The spatial distribution of animals is an essential part of their population dynamics because it reflects the behaviour of individuals within the population as well as demographic changes (Anderson *et al.* 1982; Taylor *et al.* 1983). Various indices of spatial distribution (also

called indices of dispersion) have been proposed and most are based on different combinations of estimates of the population variance and mean. The simplest approach is therefore to examine the relationship between the spatial variance (s^2) and mean (m). The spatial distribution of individuals in a population can be random ($s^2 = m$), regular, uniform or even ($s^2 < m$), or aggregated, clumped or contagious ($s^2 > m$). As contagious implies that the animals are influencing each other's distribution, and clumped implies an active gathering together, the term aggregation is preferred

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here because it has no implication of causation (Taylor 1984). True population randomness requires that no individual animal can influence others of the same species. It is therefore very rare in nature (Taylor, Woiwod & Perry 1978). Regular distributions are also rare, except in colonial animals or laboratory populations. Aggregation is therefore the most common type of distribution, but the degree of aggregation varies considerably.

The relationship between the spatial variance (s^2) and mean (m) frequently follows a power function (Taylor 1961):

$$s^2 = a m^b \quad (1a)$$

or

$$\ln s^2 = \ln a + b \ln m \quad (1b)$$

where a and b are parameters, with b also serving as an 'index of aggregation'. This model is usually fitted in its linear, logarithmic, form (equation 1b), and was shown to be widely applicable to 444 species of birds, moths and aphids (Taylor, Woiwod & Perry 1980; Taylor *et al.* 1983). It was also applicable to a large number of species of aquatic invertebrates (Downing 1979; Elliott & Drake 1981; Drake & Elliott 1982; Downing & Cyr 1985).

All these analyses show that the parameter b remains constant for the same species in the same environment, but can change with a marked change in the environment and even show a seasonal cycle (e.g. Wratten 1974; Hodgson 1978). It can also change within a life cycle; for example, b increased markedly when larvae of some Trichoptera species aggregated prior to pupation on large stones in streams (Elliott 1981, 1982a,b). The spatial distribution of stream invertebrates may be related to several factors, including their favoured habitat (e.g. surfaces of large stones, shelters under large stones, gravel or mud), their feeding preferences (e.g. herbivore, carnivore, omnivore) and their mobility (e.g. sedentary, slow movers, fast movers). There may be ontogenetic changes in the spatial distribution and, ideally, each instar of aquatic insects should be treated separately. This is rarely feasible (but see Elliott 1981, 1982a,b) and therefore, as a compromise, larvae in the present study were divided into those greater and smaller than half the maximum length attained just before pupation in Trichoptera, and emergence in Ephemeroptera and Plecoptera.

Most stream invertebrates are nocturnal and their increased activity at night often leads to an increase in upstream movements, and in downstream dispersal through the mechanism of invertebrate drift (see reviews by Allan 1995; Rader 1997). An obvious conclusion from all this nocturnal activity is that the spatial distribution of the invertebrates may change from day to night. This aspect of their population dynamics has been ignored, but such changes in spatial distribution

are an important aspect of the fundamental biological process of dispersal by stream invertebrates, i.e. their movement away from their point of origin (Palmer, Allan & Butman 1996). Normally, dispersal is studied over long time scales, but daily changes may be just as important and may provide insight into the ecology of each species. It may be expected that day–night changes in spatial distribution would not occur in sedentary species, or species that burrow in gravel or mud and are thus not exposed to changes in light intensity. Conversely, marked day–night changes would be expected in species living on or near the surface of the stream bed, especially species that are known to be more active at night. These ecological expectations can only be tested by comparing day and night samples, as in the present study.

The present investigation therefore tests the following hypotheses: (i) a power function was a suitable model for the spatial distribution of common species of Ephemeroptera, Plecoptera and Trichoptera in a stony stream; (ii) the spatial distribution varied between species but was similar within species for larvae greater and smaller than half-size; and (iii) diurnal and nocturnal spatial distributions were significantly different for each species, the differences having an ecological basis. To ensure that the conclusions were consistent, large samples ($n = 30$) were taken in different months (April, June, November) over 4 years.

Materials and methods

Samples were taken from Wilfin Beck, a small stream (length 4 km) in the English Lake District. The stream was described in detail by Elliott (1973). The sampling site (latitude 54°20' N, longitude 3°2' W) was in a steep section (fall about 4%) near the mouth of the stream, and was a mixture of riffles and runs with no deep pools. Modal depth ranged from 0.16 to 0.20 m and modal width from 3.0 to 3.7 m for the different samples. The substratum was large stones (diameter up to 0.3 m) over smaller stones and gravel, with sparse clumps of bryophytes on the larger stones and exposed bedrock. The stream was shaded moderately by deciduous trees and leaf packets occurred at the sides of the stream and between large stones in riffles.

Samples were taken near midday and midnight in April, June and November 1966, 1967, 1968 and 1969. To check if sample order affected the results, day samples were taken before night samples in 1966 and 1968, and night samples before day samples in 1967 and 1969. Samples were taken with a Hess–Waters cylindrical sampler (Waters & Knapp 1961), with a net mesh aperture of 0.265 mm and a sampling area of 0.0929 m². The sampling site was 32 m long and was divided by a grid into 1200 sampling units, each with the area of the sampler. To ensure that it was adequately covered by the sampling, the site was divided longitudinally into five strata, each with an area of approximately 22 m², and 12 sampling units

were selected at random from a possible 240 units in each stratum. Six of these units were then allocated randomly to the day sample and six to the night sample. Therefore, each day or night sample was a stratified random sample of 30 sampling units ($n = 30$). Only 2.5% of the site was sampled in the day or night. Once the sampling units were selected, sampling commenced in an upstream direction. The animals were preserved in ethanol, and identified in the laboratory. Before counting, larvae were measured from the front of the head to the tip of the abdomen (to nearest mm), and sorted into those greater than half-size, and those less than or equal to half-size. Half-size was half the mean length of the last larval instar and varied from 3 mm for the smallest species of Ephemeroptera to 9 mm for the largest species of Plecoptera.

Twenty-eight species of Ephemeroptera, Plecoptera and Trichoptera were taken in the samples. The following seven species were too sparse to include in the analyses: Plecoptera, *Chloroperla tripunctata* (Scopoli), *Leuctra hippopus* (Kempny), *L. moselyi* Morton, *Protonemura praecox* (Morton), *Nemoura cambrica* (Stephens); Trichoptera: *Hydropsyche instabilis* (Curtis), *Plectrocnemia conspersa* (Curtis).

Results

Total numbers of the 21 species used in the analyses varied considerably from 438 for *Rhyacophila dorsalis* to 131 675 for *Baetis rhodani*, but their relative abundance was similar in each of the four years (Table 1). For

all these species, the relationship between the spatial variance (s^2) and mean (m) was well described by a power function (equation 1) with estimates of the parameters a and b being provided for larvae greater than half-size, larvae less than or equal to half-size, and both size groups together (Table 2). Equation 1 was an excellent fit ($P < 0.001$) to all data sets and coefficients of determination (r^2) indicated that nearly all the variation in the spatial variance could be explained by variation in the mean, i.e. the spatial variance was density-dependent ($r^2 > 0.96$ for all Ephemeroptera species, > 0.97 for all Plecoptera species and > 0.95 for all Trichoptera species). There were no significant differences between years and therefore the order of sampling (day or night samples taken first) had no effect on the analyses.

EPHEMEROPTERA

Ephemerella ignita provided the only significant difference ($P < 0.05$) between estimates of a and b for the two size groups (Table 2). However, the precision of the estimates for larvae greater than half-size was very poor (note the very wide 95% CL in Table 2). Values for large larvae for either day or night were very similar (arrowed clusters in Fig. 1b) because these larvae were found only in June in each year. Therefore, the difference between the two size groups of this species was probably due to inadequacies in the data.

Comparisons between day and night values revealed two species, *Baetis muticus* and *Caenis rivulorum*, that

Table 1. Total numbers taken in the day and night samples in each year for the twenty-one species used in the analyses (the seven sparse species not used in the analyses are given in the text). Mean density per unit area (0.0929 m^2) can be obtained by dividing each value by 180

	1966	1967	1968	1969
Ephemeroptera				
<i>Baetis rhodani</i> (Pictet)	34 878	32 845	30 300	33 652
<i>Baetis muticus</i> (L.)	403	391	446	416
<i>Ephemerella ignita</i> (Poda)	2 580	2 635	2 520	2 591
<i>Caenis rivulorum</i> Eaton	177	158	189	194
<i>Heptagenia lateralis</i> (Curtis)	617	657	574	650
<i>Ecdyonurus venosus</i> (Fabricius)	2 011	2 109	1 878	2 233
<i>Rhithrogena semicolorata</i> (Curtis)	1 727	1 833	2 129	1 314
Plecoptera				
<i>Perlodes microcephalus</i> (Pictet)	120	125	126	117
<i>Isoperla grammatica</i> (Poda)	251	266	244	236
<i>Siphonoperla torrentium</i> (Pictet)	2 499	2 417	2 784	2 648
<i>Leuctra inermis</i> Kempny	649	608	711	675
<i>Leuctra fusca</i> (L.)	890	841	962	946
<i>Protonemura meyeri</i> (Pictet)	4 231	3 914	3 700	4 087
<i>Amphinemura sulcicollis</i> (Stephens)	2 332	2 183	2 005	2 264
Trichoptera				
<i>Rhyacophila dorsalis</i> (Curtis)	114	119	103	102
<i>Agapetus fuscipes</i> Curtis	166	166	188	165
<i>Hydropsyche siltalai</i> Döhler	923	1 299	1 176	1 152
<i>Odontocerum albicorne</i> (Scopoli)	138	135	152	142
<i>Sericostoma personatum</i> (Spence)	171	162	180	160
<i>Drusus annulatus</i> Stephens	329	357	289	345
<i>Potamophylax cingulatus</i> (Stephens)	935	911	956	918

Table 2. Estimates of the parameters a and b (both with 95% CL) in eqn (1) for larvae greater than half-size, equal to or less than half-size, and of all sizes, together with the ratio of the night and day powers for larvae of all sizes ($b_{\text{night}}/b_{\text{day}}$)

		> half-size		≤ half-size		All sizes		Ratio $b_{\text{night}}/b_{\text{day}}$
		a (95% CL)	b (95% CL)	a (95% CL)	b (95% CL)	a (95% CL)	b (95% CL)	
<i>B. rhodani</i>	Day	1.41 (1.35–1.48)	1.09 ± 0.02	1.45 (1.22–1.73)	1.09 ± 0.04	1.40 (1.36–1.44)	1.10 ± 0.01	1.81
	Night	0.22 (0.21–0.23)	1.97 ± 0.03	0.20 (0.18–0.23)	2.01 ± 0.03	0.21 (0.20–0.22)	1.99 ± 0.01	
<i>B. muticus</i>	Day	1.40 (1.30–1.50)	1.30 ± 0.07	1.38 (1.35–1.41)	1.31 ± 0.03	1.39 (1.37–1.42)	1.30 ± 0.02	1.01
	Night	1.47 (1.31–1.64)	1.36 ± 0.13	1.38 (1.33–1.42)	1.32 ± 0.04	1.40 (1.36–1.44)	1.31 ± 0.03	
<i>E. ignita</i>	Day	1.18 (0.63–2.20)	1.57 ± 0.30	1.68 (1.66–1.71)	1.40 ± 0.01	1.68 (1.66–1.71)	1.40 ± 0.01	1.41
	Night	0.35 (0.02–5.94)	2.50 ± 1.37	1.04 (1.00–1.09)	1.97 ± 0.02	1.05 (1.01–1.09)	1.97 ± 0.02	
<i>C. rivulorum</i>	Day	1.00 (0.94–1.05)	1.23 ± 0.07	1.01 (0.95–1.07)	1.26 ± 0.09	1.01 (0.97–1.04)	1.25 ± 0.07	1.06
	Night	1.01 (0.89–1.15)	1.31 ± 0.18	1.01 (0.93–1.09)	1.32 ± 0.10	1.01 (0.95–1.07)	1.32 ± 0.08	
<i>H. lateralis</i>	Day	0.99 (0.91–1.08)	1.51 ± 0.09	0.90 (0.76–1.05)	1.47 ± 0.12	0.98 (0.91–1.04)	1.42 ± 0.07	1.39
	Night	1.02 (0.97–1.07)	1.97 ± 0.04	1.01 (0.94–1.08)	1.99 ± 0.06	1.01 (0.98–1.05)	1.98 ± 0.03	
<i>E. venosus</i>	Day	1.52 (1.47–1.56)	1.02 ± 0.08	1.39 (1.19–1.62)	1.09 ± 0.08	1.50 (1.45–1.55)	1.06 ± 0.04	1.25
	Night	0.99 (0.95–1.04)	1.32 ± 0.05	1.07 (0.99–1.16)	1.29 ± 0.03	1.00 (0.97–1.03)	1.32 ± 0.03	
<i>R. semicolorata</i>	Day	1.34 (1.29–1.40)	1.12 ± 0.04	1.38 (1.16–1.64)	1.10 ± 0.07	1.34 (1.30–1.39)	1.11 ± 0.02	1.79
	Night	1.33 (0.95–1.87)	1.95 ± 0.30	1.43 (1.23–1.66)	1.97 ± 0.06	1.34 (1.10–1.63)	1.99 ± 0.10	
<i>P. microcephalus</i>	Day	1.02 (0.94–1.12)	1.05 ± 0.11	1.02 (0.77–1.35)	1.10 ± 0.25	1.02 (0.95–1.09)	1.07 ± 0.07	1.01
	Night	0.97 (0.92–1.04)	1.08 ± 0.07	1.00 (0.68–1.47)	1.09 ± 0.37	0.98 (0.93–1.03)	1.08 ± 0.05	
<i>I. grammatica</i>	Day	1.33 (1.27–1.39)	1.10 ± 0.08	1.34 (1.30–1.39)	1.13 ± 0.05	1.34 (1.32–1.37)	1.12 ± 0.03	1.65
	Night	1.25 (1.03–1.51)	1.64 ± 0.28	1.35 (1.28–1.43)	1.96 ± 0.09	1.39 (1.28–1.50)	1.85 ± 0.11	
<i>S. torrentium</i>	Day	1.35 (1.25–1.45)	1.32 ± 0.05	1.40 (1.36–1.44)	1.30 ± 0.01	1.39 (1.37–1.42)	1.30 ± 0.01	1.01
	Night	1.43 (1.30–1.58)	1.29 ± 0.06	1.39 (1.36–1.42)	1.31 ± 0.01	1.40 (1.37–1.43)	1.31 ± 0.01	
<i>L. inermis</i>	Day	1.37 (1.33–1.41)	1.31 ± 0.04	1.36 (1.27–1.46)	1.32 ± 0.05	1.37 (1.35–1.40)	1.31 ± 0.02	0.99
	Night	1.42 (1.34–1.51)	1.31 ± 0.07	1.38 (1.24–1.53)	1.31 ± 0.07	1.40 (1.36–1.45)	1.30 ± 0.03	
<i>L. fusca</i>	Day	1.41 (1.37–1.45)	1.30 ± 0.03	1.38 (1.35–1.41)	1.30 ± 0.01	1.40 (1.38–1.42)	1.30 ± 0.01	0.98
	Night	1.42 (1.33–1.51)	1.24 ± 0.06	1.36 (1.30–1.41)	1.31 ± 0.02	1.42 (1.36–1.47)	1.28 ± 0.03	
<i>P. meyeri</i>	Day	0.98 (0.93–1.04)	1.31 ± 0.03	0.97 (0.90–1.06)	1.31 ± 0.03	0.98 (0.95–1.02)	1.30 ± 0.02	1.31
	Night	0.98 (0.92–1.05)	1.70 ± 0.04	0.95 (0.90–1.00)	1.72 ± 0.02	0.98 (0.94–1.02)	1.70 ± 0.02	
<i>A. sulcicollis</i>	Day	0.98 (0.76–1.26)	1.33 ± 0.22	1.04 (0.91–1.19)	1.29 ± 0.05	1.02 (0.97–1.07)	1.29 ± 0.02	1.32
	Night	0.99 (0.91–1.08)	1.71 ± 0.07	0.95 (0.88–1.04)	1.72 ± 0.03	1.00 (0.97–1.03)	1.70 ± 0.01	
<i>R. dorsalis</i>	Day	1.01 (0.80–1.27)	1.09 ± 0.15	1.03 (0.88–1.20)	1.15 ± 0.23	0.99 (0.91–1.07)	1.08 ± 0.07	1.01
	Night	0.93 (0.73–1.17)	1.05 ± 0.16	1.00 (0.92–1.08)	1.07 ± 0.13	1.00 (0.92–1.07)	1.09 ± 0.06	
<i>A. fuscipes</i>	Day	1.53 (1.35–1.73)	1.21 ± 0.12	1.51 (1.44–1.58)	1.27 ± 0.09	1.52 (1.45–1.59)	1.22 ± 0.06	1.01
	Night	1.44 (1.31–1.57)	1.21 ± 0.08	1.51 (1.48–1.54)	1.22 ± 0.04	1.49 (1.44–1.54)	1.23 ± 0.04	
<i>H. siltalai</i>	Day	1.53 (1.29–1.81)	1.25 ± 0.13	1.50 (1.46–1.54)	1.25 ± 0.02	1.51 (1.46–1.56)	1.25 ± 0.03	1.02
	Night	1.36 (1.24–1.49)	1.31 ± 0.07	1.50 (1.37–1.54)	1.27 ± 0.04	1.43 (1.36–1.50)	1.28 ± 0.03	
<i>O. albicorne</i>	Day	1.43 (1.26–1.62)	1.24 ± 0.12	1.44 (1.30–1.60)	1.25 ± 0.08	1.44 (1.35–1.53)	1.25 ± 0.05	0.85
	Night	1.10 (1.01–1.20)	0.88 ± 0.09	1.20 (1.08–1.34)	1.09 ± 0.08	1.25 (1.16–1.35)	1.06 ± 0.07	
<i>S. personatum</i>	Day	1.41 (1.24–1.62)	1.29 ± 0.15	1.42 (1.31–1.53)	1.28 ± 0.08	1.41 (1.33–1.50)	1.28 ± 0.06	0.84
	Night	1.10 (0.98–1.24)	1.02 ± 0.13	1.19 (1.08–1.30)	1.07 ± 0.10	1.17 (1.09–1.24)	1.07 ± 0.07	
<i>D. annulatus</i>	Day	1.87 (1.79–1.95)	1.48 ± 0.09	1.28 (0.22–7.32)	1.85 ± 1.57	1.88 (1.83–1.93)	1.50 ± 0.04	0.74
	Night	1.19 (1.17–1.22)	1.11 ± 0.04	1.02 (0.26–3.97)	1.24 ± 1.17	1.19 (1.17–1.21)	1.11 ± 0.02	
<i>P. cingulatus</i>	Day	1.94 (1.90–1.98)	1.48 ± 0.02	1.92 (1.88–1.96)	1.50 ± 0.02	1.94 (1.91–1.96)	1.49 ± 0.01	0.74
	Night	1.19 (1.17–1.22)	1.10 ± 0.02	1.20 (1.16–1.23)	1.10 ± 0.02	1.19 (1.18–1.21)	1.10 ± 0.01	

did not change their spatial distribution significantly between day and night ($P > 0.05$ for t -test between day and night values of the parameter estimates of a and b), and hence the ratio of $b_{\text{night}}/b_{\text{day}}$ was close to one (Table 2). This ratio and the degree of aggregation increased significantly ($P < 0.01$) for the remaining five species. For *Baetis rhodani*, *E. ignita* and *Ecdyonurus venosus*, values of a decreased significantly from day to night while values of b increased significantly. Therefore, the degree of aggregation actually decreased at night for the lower densities while increasing at medium to high densities (e.g. Fig. 1a,b). For *Heptagenia lateralis* and *Rhithrogena semicolorata*, values of a did not change significantly from day to night while values of b increased significantly. Therefore, at lower densities the spatial distribution remained close to random during

both day and night, while aggregation increased at night for medium to high densities (e.g. Fig. 1c). These differences were, however, very small and the overall pattern of increasing variance at high density at night was very similar for all five species.

Although the spatial distribution of some species changed from day to night, mean densities did not change significantly (e.g. three species in Fig. 2). However, the precision of the nocturnal estimates of density was poorer than that for the diurnal estimates (cf. 95% CL for day and night mean densities in Fig. 2). This was due, of course, to the increased variance at night, especially at higher densities. Similar results for day and night estimates of mean density were obtained for the different species of Plecoptera and Trichoptera, and therefore further examples will not be shown.

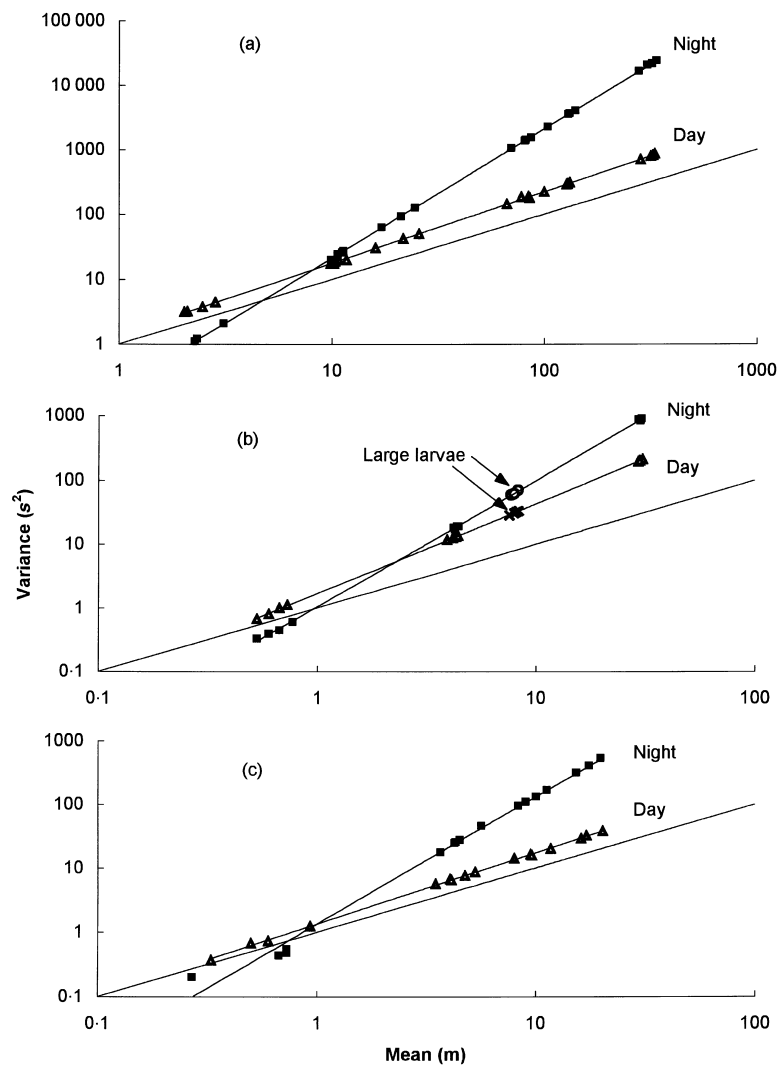


Fig. 1. Relationship between the spatial variance (s^2) and mean (m) for day and night samples with regression lines obtained from equation 1, using the values of a and b for all sizes of larvae in Table 2: (a) *Baetis rhodani* (b) *Ephemerella ignita* (c) *Rhithrogena semicolorata*. Both axes are on logarithmic scales; the line of equality ($s^2 = m$) is given on each figure.

PLECOPTERA

The only significant difference ($P < 0.05$) between size groups was for values of b , but not a , in the night samples of *Isoperla grammatica* and *Leuctra fusca* (Table 2). However, the difference was only just significant and neither value of b was significantly different ($P > 0.05$) from that for both size groups together. As the data points for the larger larvae of both species were close together and their densities were low, the difference between the two size groups was probably due to inadequate data, as was the case for large larvae of *E. ignita*.

Two of the three carnivorous species, *Perlodes microcephalus* and *Siphonoperla torrentium*, did not change their spatial distribution significantly from day to night, and hence the ratio of $b_{\text{night}}/b_{\text{day}}$ was one. The spatial distribution of the very active carnivore, *P. microcephalus*, was close to random in both day and night (Fig. 3a), and larvae of *S. torrentium* were always slightly aggregated (Fig. 3c). Values of a and b for the remaining carnivore, *Isoperla grammatica*, both increased signi-

ficantly ($P < 0.05$ for a , $P < 0.01$ for b) from day to night. The effect of this was similar to that shown by *B. rhodani*, *E. ignita* and *E. venosus*, with a decrease and an increase in the degree of aggregation at lower and higher densities, respectively (Fig. 3b). Two of the four herbivorous species, *Leuctra inermis* and *L. fusca*, did not change significantly from day to night and their spatial distribution was close to random at low densities but became more aggregated as density increased (e.g. Fig. 4a). Values of a for the remaining two species, *Protonemura meyeri* and *Amphinemura sulcicollis*, did not change significantly from day to night, but values of b increased significantly ($P < 0.001$) for both species. The degree of aggregation increased from day to night and also with increasing density (Fig. 4b,c).

TRICHOPTERA

The only significant difference between size groups ($P < 0.05$) was for larvae of *Odontocerum albicorne* in the night samples (Table 2). Large larvae of this species

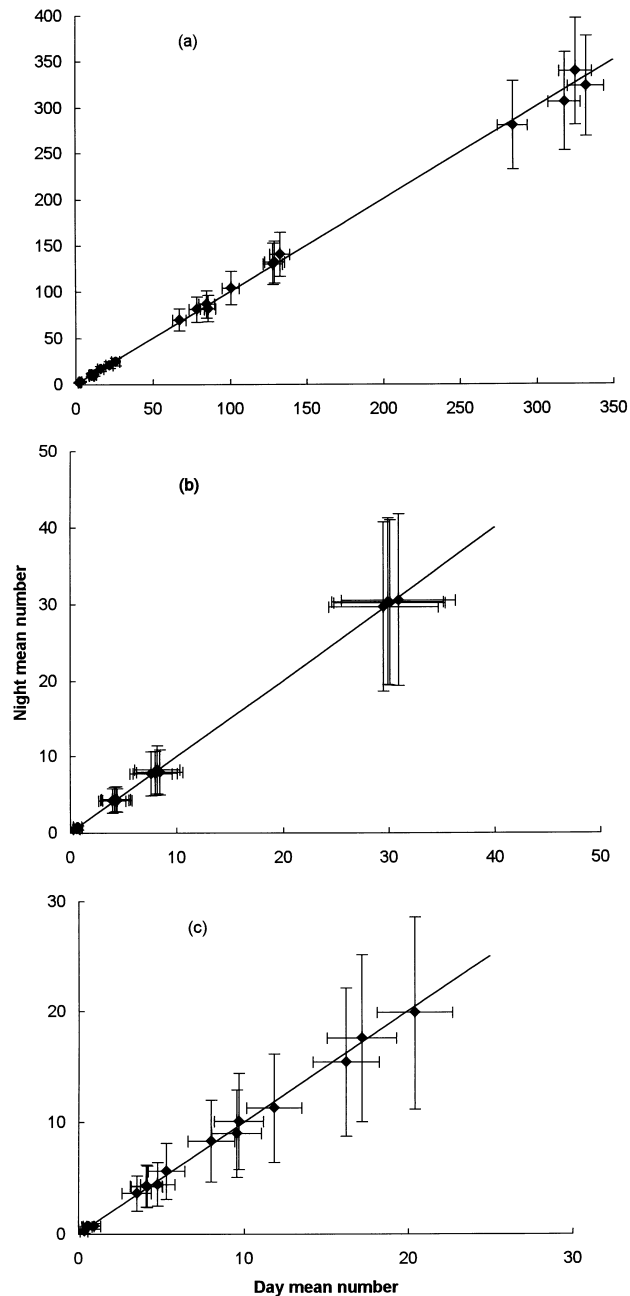


Fig. 2. Relationship between estimates of mean density (m) from the day and night samples with 95% CL for each mean value: (a) *Ephemera ignita* (b) *Rhyacophila dorsalis* (c) *Rhyacophila dorsalis*. The line of equality is given on each figure.

were the only group in all the analyses with a b -value less than one. Their distribution, however, was closer to random rather than regular, because of the a value. This was the only species in the analyses where the difference between size groups was genuine and not due to inadequate data.

The spatial distribution of the very active carnivore, *Rhyacophila dorsalis*, was close to random with no significant difference between day and night samples (Fig. 5a). The rather sedentary case-builder species, *Agapetus fuscipes*, occurred chiefly on the upper surface of large stones and was moderately aggregated with no significant change from day to night. For the net-spinning species, *Hydropsyche siltalai*, the value

of a decreased and the value of b increased from day to night, but both changes just failed to be significant at the 5% level. The close overlap of the day and night values for this species supported the conclusion that the spatial distribution did not change significantly from day to night (Fig. 5b). The remaining four species, *Odontocerum albicorne*, *Sericostoma personatum*, *Drusus annulatus* and *Potamophylax cingulatus*, were all case-builders, and showed a significant decrease ($P < 0.001$) in the values of both a and b from day to night, so that the ratio of $b_{\text{night}}/b_{\text{day}}$ was less than one. These were the only species in all the analyses that showed a significant reduction in aggregation from day to night (e.g. Fig. 5c).

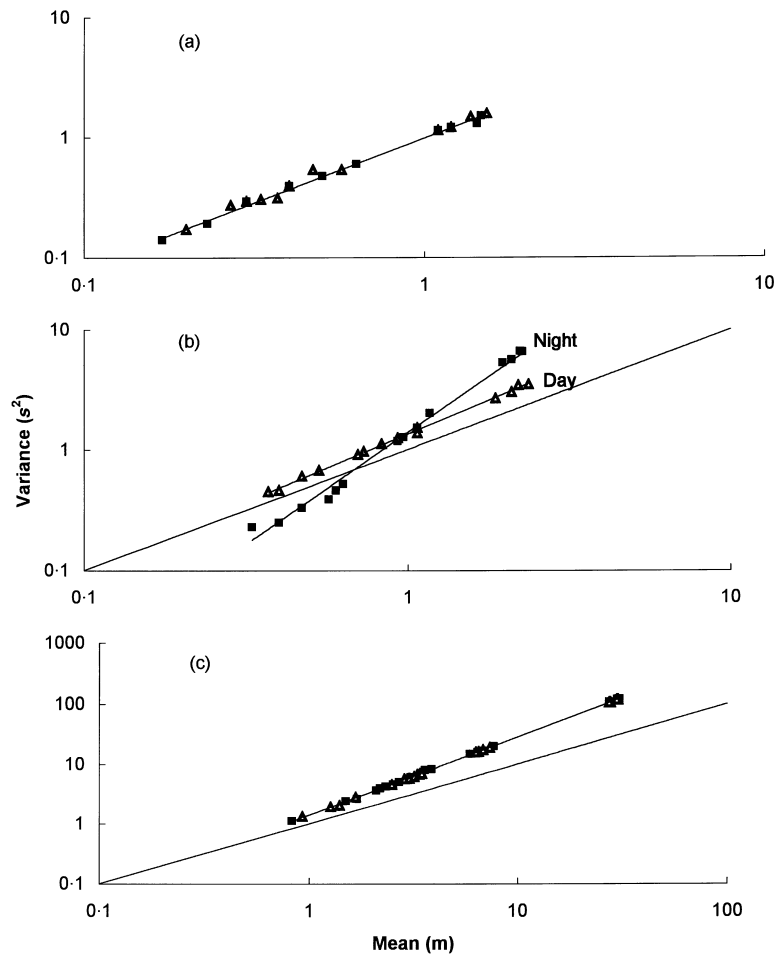


Fig. 3. Relationship between the spatial variance (s^2) and mean (m) for day (Δ) and night (\blacksquare) samples with regression lines obtained from equation 1, using the values of a and b for all sizes of larvae in Table 3: (a) *Perlodes microcephalus*, (b) *Isoperla grammatica*, (c) *Siphonoperla torrentium*. Both axes are on logarithmic scales; the line of equality ($s^2 = m$) is given on each figure except (a) because it would be very close to the regression line.

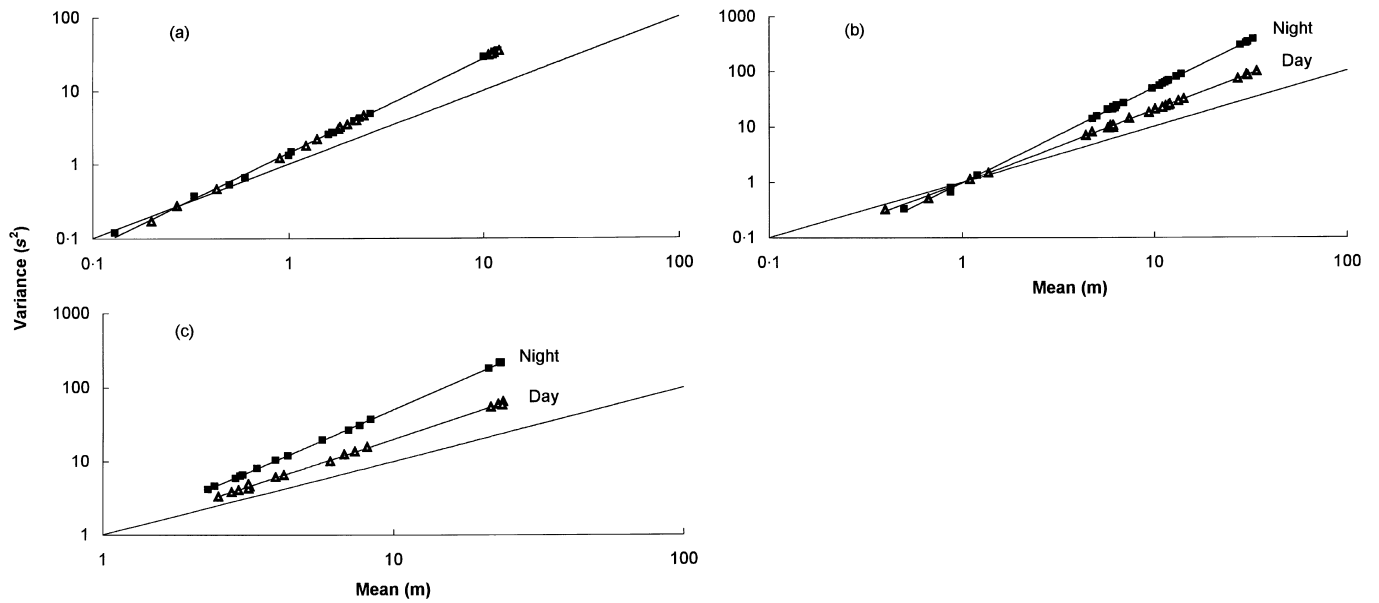


Fig. 4. Relationship between the spatial variance (s^2) and mean (m) for day (Δ) and night (\blacksquare) samples with regression lines obtained from equation 1, using the values of a and b for all sizes of larvae in Table 3: (a) *Leuctra fusca*, (b) *Protonemura meyeri*, (c) *Amphinemura sulcicollis*. Both axes are on logarithmic scales; the line of equality ($s^2 = m$) is given on each figure.

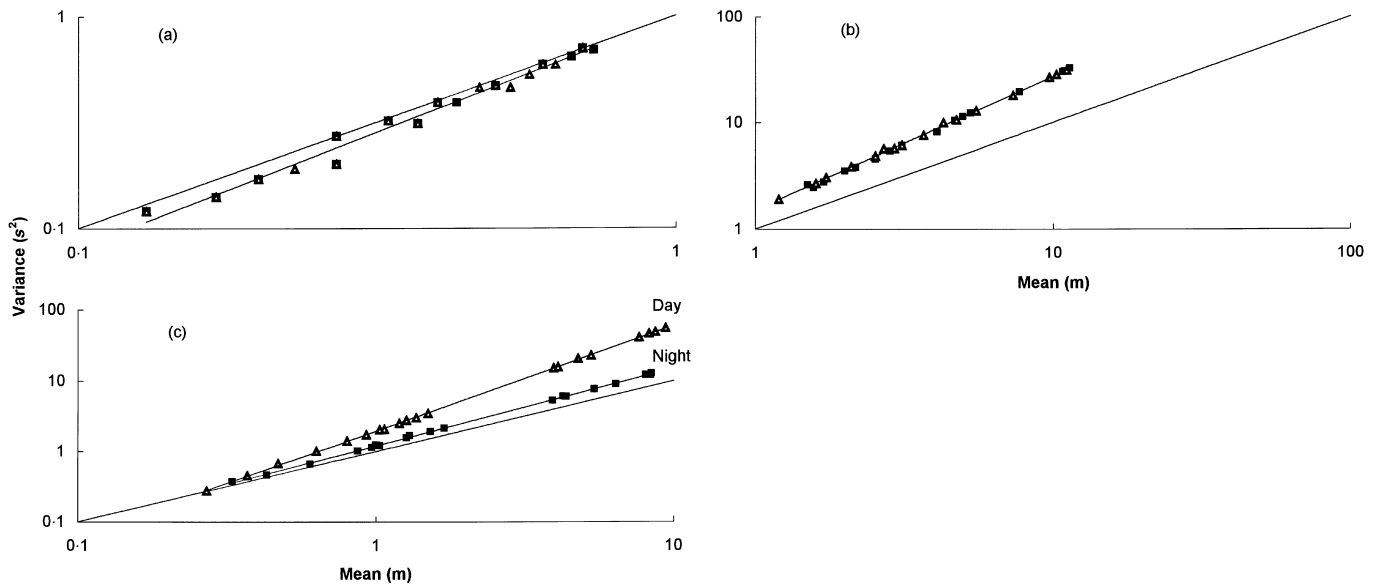


Fig. 5. Relationship between the spatial variance (s^2) and mean (m) for day (Δ) and night (\blacksquare) samples with regression lines obtained from equation 1, using the values of a and b for all sizes of larvae in Table 4: (a) *Rhyacophila dorsalis*, (b) *Hydropsyche siltalai*, (c) *Potamophylax cingulatus*. Both axes are on logarithmic scales; the line of equality ($s^2 = m$) is given on each figure.

Discussion

Of the three hypotheses tested in this study, the first was strongly supported; a power function was an excellent fit to all data sets. The second hypothesis was also supported by most analyses with no significant difference in the spatial distribution of larvae greater and smaller than half-size for each species. Three of the four exceptions were probably due to inadequate data for testing differences, but the fourth, *Odontocerum albicorne*, appeared to be genuine with large larvae being significantly less aggregated than small larvae, but only at night when the larvae are known to be most active (Elliott 1970). The third hypothesis, proposing significant differences between diurnal and nocturnal distributions, was rejected for nine species but supported for the other 12 species.

These differences in spatial distribution were used to divide the 21 species into three groups according to day–night changes in the values of a and b in equation 1 (Fig. 6). Values of a and b for the nine species in the first group did not change significantly from day to night, so that the spatial distribution of these species remained fairly constant (Fig. 6a). Four of these species are burrowers in gravel or moss; *Baetis muticus*, *Leuctra inermis* and *L. fusca* have a long, thin body shape as does their major predator, *Siphonoperla torrentium*, while larvae of *Caenis rivulorum* burrow in muddy gravel (Hynes 1941; Elliott, Humpesch & Macan 1988). It is notable that the spatial distribution of the only predator, *S. torrentium*, in this group was very similar to that of its prey in the group. The case-building Trichoptera species, *Agapetus fuscipes*, grazes on epilithon from the upper surface of large stones and moves very slowly in both the day and night. Its aggregated distribution is obviously due to the larvae being restricted

to large stones. The net-spinning Trichoptera species, *Hydropsyche siltalai*, was aggregated over a wide range of densities, and this probably reflects the limited number of suitable sites for this species to construct its nets (Edington & Hildrew 1995). The two remaining species in this first group, the stonefly *Perlodes microcephalus* and the free-living caddis *Rhyacophila dorsalis*, are both very active predators. Their spatial distribution in both day and night was very close to a random distribution, with values of a and b both close to one (species 3 and 7 in Fig. 6a).

The four species in the second group, *Odontocerum albicorne*, *Sericostoma personatum*, *Drusus annulatus* and *Potamophylax cingulatus*, are case-building Trichoptera species, and all showed significant reductions from day to night in the values of a and b (Fig. 6b). Activity increases at night in all four species and their larvae are essentially nocturnal foragers (Elliott 1969, 1970). Larvae of *O. albicorne* are omnivores while the other three species are herbivores. The present study has shown that during their nocturnal foraging, aggregation of larvae is greatly reduced so that their distribution is close to random with values of a , and especially b , close to one (Fig. 6b). The net product of nocturnal behaviour appears to be a near-random distribution. This does not imply randomness in any specific aspect of behaviour but that, of the many behavioural components that together lead to spatial distribution, those leading to aggregation and those leading to dissociation are evenly balanced (Taylor *et al.* 1980).

The power b increased significantly from day to night for all eight species in the third group, but the value of a decreased significantly for only three species, *Baetis rhodani*, *Ephemerella ignita* and *Ecdyonurus venosus* (species 1, 2 and 4 in Fig. 6c). *Isoperla grammatica* is

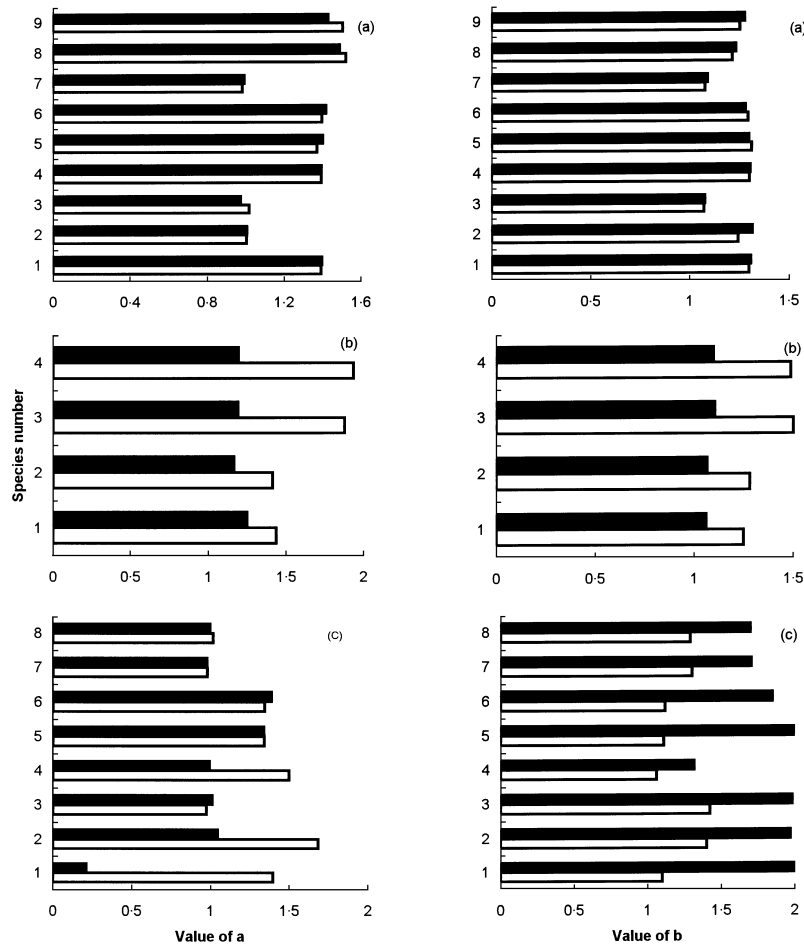


Fig. 6. Values of the constants a and b for day (open bars) and night (black bars) samples arranged in three groups: (a) nine species that did not change their spatial distribution significantly between day and night; (b) four species for which the values of a and b decreased significantly from day to night; (c) eight species for which the value of a or b , or both a and b , increased significantly from day to night. Group one species: 1, *B. muticus*; 2, *C. rivulorum*; 3, *P. microcephalus*; 4, *S. torrentium*; 5, *L. inermis*; 6, *L. fusca*; 7, *R. dorsalis*; 8, *A. fuscipes*; 9, *H. siltalai*. Group two species: 1, *O. albicorne*; 2, *S. personatum*; 3, *D. annulatus*; 4, *P. cingulatus*. Group 3 species: 1, *B. rhodani*; 2, *E. ignita*; 3, *H. lateralis*; 4, *E. venosus*; 5, *R. semicolorata*; 6, *I. grammatica*; 7, *P. meyeri*; 8, *A. sulcicollis*.

the only carnivore in the group and frequently preys on other members of the group. This species is rarely active during the day, most active at dusk and dawn when prey capture is highest, and less active for the rest of the night (Elliott 2000). All eight species are frequently taken in drift samples and also move upstream (see reviews in Introduction). They are therefore highly mobile nocturnal animals that have now been shown to change their spatial distribution from day to night. Although all these species became more aggregated at night ($s^2 > m$) when their densities were medium to high, changes at lower densities were more complex. For *Heptagenia lateralis*, *Rhithrogena semicolorata*, *Protonemura meyeri* and *Amphinemura sulcicollis*, the spatial distribution remained close to random ($s^2 = m$) at low densities, but for *Baetis rhodani*, *Ephemerella ignita*, *Ecdyonurus venosus* and *Isoperla grammatica*, the distribution tended to regularity ($s^2 < m$) at low densities. Therefore the degree of aggregation and the associated changes in behaviour were very strongly density-dependent in these eight species.

The classification of most species was expected from

their ecology. Five of the nine species in the first group are burrowers in gravel, moss or mud, and are thus not exposed to diel changes in light intensity. One is a sedentary, case-building, Trichoptera species. However, the inclusion of a net-spinning Trichoptera species in this group was unexpected because this species is known to change position in response to changes in water velocity (Edgington & Hildrew 1995). The present study does not contradict this observation but simply demonstrates that the degree of aggregation does not change over 24 h. Two other unexpected members of this group were both highly mobile predators that occur on or near the surface of the stream bed. *Perlodes microcephalus* is active during the day, but only below the substratum, and very active from dusk to dawn with a high prey-capture success (Elliott 2000). Nothing is known about the diel activity and feeding patterns of *Rhyacophila dorsalis*, but its similar spatial distribution to *P. microcephalus* suggests that its activity and feeding periodicity may be also similar. Perhaps the near random distribution facilitates the hunting success of these two species and reduces possible intraspecific

competition. The 12 species in the second and third groups were expected to show day–night changes in spatial distribution because their larvae occur on or near the surface of the stream bed, and are known to be active at night. The division into the two groups is linked to their presence in the drift, those in the third group being highly mobile species that frequently occur in nocturnal drift, while the four case–building Trichoptera species in the second group rarely occur in the drift. As the larvae of these four nocturnal species were usually found aggregated under stones during the day, their reduced aggregation when they were active at night was not unexpected. Therefore, with a few exceptions, the ecological expectations summarized in the Introduction were supported by the results of this study.

The power b is often used as an ‘index of aggregation’. In an extensive study of 444 species of birds, moths and aphids, b varied in the range 0.95–3.32 with mean values of 1.68 for birds, 2.07 for moths and 1.97 for aphids, and few values close to, or less than, one (Taylor *et al.* 1980). Values of b in the present study varied in the range 0.88–2.50 for all the analyses, and 1.06–1.99 for the day and night samples with both size groups together (Table 2, Fig. 6). Therefore the values obtained in the present study were well within the range of values reported for terrestrial animals. It would be useful to test the three hypotheses of the present study on terrestrial species. Such work is of practical importance because the variance–mean relationship affects the transformation of data before they can be analysed by some statistical methods (e.g. Healy & Taylor 1962; Elliott 1977; Downing 1979). It also affects the design of sampling programmes when a certain level of precision is required (e.g. Elliott 1977; Downing 1979; McIntyre, Elliott & Ellis 1984).

The 12 species in groups two and three show clearly how the spatial distribution of animals can be affected markedly by the behaviour of individuals within a population, and is not due simply to demographic changes, a point also made by Taylor *et al.* (1983) in response to Anderson *et al.* (1982). Another example of behavioural change is the active aggregation of larvae prior to pupation in some Trichoptera species, this causing a marked change in the variance–mean relationship (Elliott 1981, 1982a, 1982b). As there do not appear to be any other quantitative studies of day–night changes in spatial distribution, it is not known how frequently such changes occur in terrestrial populations, especially for nocturnal species. Such work is needed because there is now enough evidence to show that behavioural changes in spatial distribution are just as important as demographic changes for a clearer understanding of population dynamics.

Acknowledgements

I wish to thank Mrs D. Parr, Mrs W. Harris and Mrs P.A. Tullett for all their help with the sampling. The work

was financed by the Natural Environment Research Council through a grant to the Freshwater Biological Association.

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Received 30 April 2001; revision received 24 September 2001