

The effect of host density on the success of commensalistic *Epoicocladius flavens* (Chironomidae) in utilizing streamliving *Ephemera danica* (Ephemeroptera)

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Factors influencing the infestation rate of *Epoicocladius flavens* Malloch on nymphs of the mayfly *Ephemera danica* Müller were analyzed by means of multiple regression. Host density proved to be the most important factor. It is assumed that a differential utilization of the most suitable hosts at different host densities accounts for increased reproductive success and a higher average infestation rate with host density. The relationship between population density and the utilization of the optimal habitat in *E. flavens* is compared to that of a pest species, and is incorporated into a more general theory. A model is formulated exploring the relationship between population size and the probability of a female *E. flavens* of obtaining a mate. The conclusion to be drawn from the model is that the only means by which to increase this probability is by dispersal, since such behaviour will increase the effective population size.

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Факторы, влияющие на скорость заражения *Epoicocladius flavens* нимф поденки *Ephemera danica* проанализированы методом множественной регрессии. Плотность хозяина – наиболее важный фактор. Установлено, что дифференцированное использование наиболее подходящих хозяев при разной плотности хозяев стимулирует размножение и повышает общую интенсивность заражения. Отношение между плотностью популяции и использованием оптимального местообитания у *E. flavens* сравнивали с таковыми у вредителя, результаты включены в общую теорию. При создании модели учтено отношение между плотностью популяции и вероятностью оплодотворения самок *E. flavens*. Из модели вытекает заключение, что единственный способ повышения этой вероятности – расселение, т.к. это может повысить эффективную плотность популяции.

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1. Introduction

Environmental heterogeneity leads to patchiness in the spatial distribution of animal populations and this in turn affects the ability of predators and parasites to find their victims. Therefore environmental heterogeneity influences the outcome of interactions between species. These relationships are very complex, and not easily incorporated into models of population dynamics. Especially the efficiency of parasitoids at exploiting very scattered host populations and their behaviour to avoid complete reproductive failure are difficult to study in the field, and the natural conditions hard to mimic in the laboratory. Since parasitoids, by definition, cause some mortality in the host populations and thereby influence indirectly the extent of their habitat, complexity will increase even more. To provide empirical insight, such relationships may conveniently be investigated in a mutualistic or commensalistic relationship.

An aquatic chironomid, *Epoicocladus flavens* Malloch (= *ephemerae* Kieffer), has proven to be suitable when studying this type of questions. In Europe it lives commensalistically on two mayfly species, *Ephemera danica* Müller and *Eph. vulgata* (L.) (in North America also on mayflies of the genus *Hexagenia*). In earlier accounts the relationship was classified as phoresy, although in the light of present knowledge it would more accurately be termed commensalism. A description of the life history of *E. flavens* follows below.

The present study is mainly concerned with the influence of host density on the success of *E. flavens* in utilizing stream living *Eph. danica*. I also aim at a theoretical model with particular reference to factors allowing the midge to persist at low population densities.

The main body of data derives from samples taken in about 50 separate host-symbiont populations, including thin as well as very dense populations. Such a range of densities would scarcely have been encountered if a single population had been followed through time. However, fluctuations occur in most populations and have essential importance for many interspecific relationships. The approach used here is that density fluctuations of *Eph. danica* can be regarded as a separate factor influencing the degree of infestation by *E. flavens*, provided the number of populations examined is sufficient for average density conditions to be reflected when populations are treated together. In other words, the approach used is to separate factors which influence the deviations from the proposed equilibrium densities of *E. flavens* populations.

2. The life history of *E. flavens*

The life history of *E. flavens* has been described by Svensson (1976, 1979). A few important details will be given below. The nymphs of the two host species in

Europe, one (*Eph. danica*) being exclusively lotic and the other (*Eph. vulgata*) predominantly lenitic, burrow in sandy bottoms with comparatively low organic content. The larvae of *E. flavens* feed on organic particles carried by the respiratory water current produced by the gills of the mayfly nymphs. Such particles settle on the hairy bodies of the hosts and are therefore abundantly available to the midge larvae.

In my main study area, *E. flavens* is generally univoltine. However, the size frequency distribution of larvae from other localities (see below) suggests that there might be a second generation at times. The general morphology of *E. flavens* does not differ in any important respect from those of other orthoclaadiids. Fecundity is about the same in *E. flavens* as in chironomids of similar size. The most remarkable feature in the development of the larva is its stereotypic choice of population site on the fullgrown mayfly nymphs. This may be a mechanism, by which the pupae are carried to the water surface. Laboratory experiments have indicated that the larvae of *E. flavens* are guided by olfactory stimuli to locate the host nymphs.

3. Study area

The investigation was conducted in Skåne, the southernmost province of Sweden. A total of 237 stream localities were visited in May 1976 and 1977, a few weeks before the emergence of *E. flavens* and *Eph. danica*. Of these localities 78 were inhabited by *Eph. danica*, and of these 49 provided enough material for the present study. Five of these were also visited in May/June 1978 and 1979. An additional 34 localities were selected in lakes. Additional information derives from Stampen (55°37'N, 13°35'E), a small stream where more detailed research was conducted from 1973 until 1977 (see Malmqvist et al. 1978, for a description of this stream).

There are considerable regional differences in the water chemistry in Skåne. In the north, several streams are acid, whereas in the south most waters are alkaline due to the limestone bedrock. pH strictly limits the distribution of *Eph. danica*, which has never been recorded in streams with pH < 6.0. It is also sensitive to strong organic pollution, and consequently largely absent from the most densely inhabited parts of the province. Hence, most of the populations of *Eph. danica* and *E. flavens* studied were found in the forested central parts of Skåne.

4. Material and methods

Nymphs of *Eph. danica* with attached *E. flavens* larvae were sampled by means of a hand net. Repeated sampling of all discernible bottom types during a few hours' time at each locality permitted a rough approximation

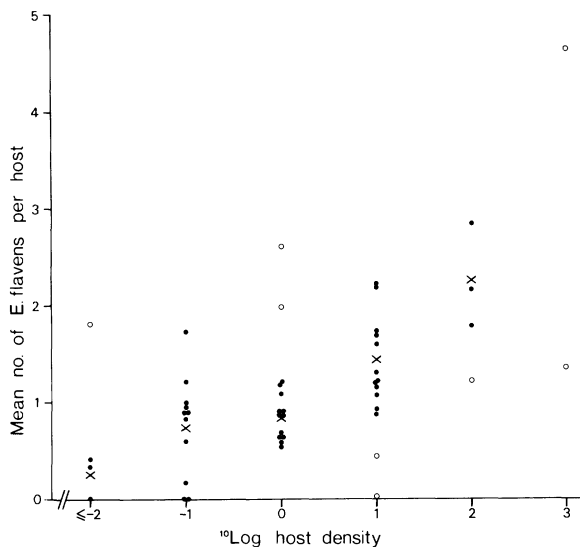


Fig. 1. The relations between infestation rate and host density with other known factors compensated for. Open circles denote values which were omitted in the multiple regression analysis. Crosses represent the means within the host density categories.

of the density of *Eph. danica*, as well as the degree of clumping of the nymphs according to a standardized classification.

All nymphs were preserved in ethanol and brought to the laboratory for subsequent examination. All larvae of *E. flavens* were removed from the nymphs and counted. In addition, the relative number of sessile *Peritrichia* on the nymphs was determined (see Tab. 1).

Environmental variables of potential importance for *Eph. danica* or *E. flavens* were recorded and used in the final analysis.

When calculating the infestation rate, which is defined as the mean number of *E. flavens* per nymph, hosts below 9 mm total body length were excluded, because *E. flavens* is rarely found on this nymph category. This correction may introduce a discrepancy between infestation rate and density of hosts, which include all

nymph sizes. By the time of sampling, small nymphs were abundant at a few localities only, and therefore insufficient to alter the figures produced.

Another potential source of error was the distribution of *Eph. danica* along the streams. Localities having a sparse host population may be assumed to receive drifting nymphs from more densely populated localities, where *E. flavens* is also abundant. When this situation prevailed, the locality was excluded from the analysis. Consequently, most of the samples included have been taken in the upper reaches of watersheds or below impoundments or lake outlets.

In general, more than 50 nymphs have been used for the calculation of infestation rate. However, the rate from 8 of the sparse host populations were based on as few as 20 nymphs. In lakes a careful inspection of at least 100 nymph exuviae for larvae or pupal remnants of *E. flavens* was considered sufficient for establishing whether the species was present or not. The abundance of *Eph. vulgata* in the lakes was not estimated.

The importance of a number of factors on the infestation rate was established by means of a multiple regression analysis. When the infestation rate was transformed to a $^{10}\log$ scale the highest correlation coefficients were obtained. This is probably because of the non-linear relationships between environmental factors and the biological variables (Green 1977). Extreme deviations from the mean infestation rate in each host density category were excluded from the analysis but are presented in Fig. 1.

5. Results and discussion

5.1. Empirical studies

The most important factor influencing the infestation rate of *E. flavens* was host density, which explained 53% of the observed variation (Tab. 2). The other factors together made up 15% of the variation. The effect of aggregation of the host nymphs was insignificant. The correlation between individual variables was weak (Tab. 1). The relatively low correlation coefficients are

Tab. 1. Partial correlation coefficients of variables used in the multiple regression analysis. Significance levels are denoted by asterisks.

	X_1	X_2	X_3	X_4	X_5	X_6
$^{10}\log$ host density ¹	(X_1)	1				
Bottom substrate ²	(X_2)	0.150	1			
Stream width (m)	(X_3)	-0.315*	0.150	1		
Conductivity ³ ($\mu\text{S cm}^{-1}$)	(X_4)	0.288	-0.014	0.107	1	
Relative number of <i>Peritrichia</i> on hosts ⁴	(X_5)	-0.394*	-0.299	0.059	0.392*	1
Stream type ⁵	(X_6)	-0.102	-0.188	-0.152	0.127	0.036
Degree of clumping of hosts ⁶	(X_7)	-0.402**	-0.278	0.129	0.392**	0.566***
						0.344**

1. integer values only, 2. Soft or hard bottom dominating, 3. grouped into the following intervals: 0–200, 200–400, >400 $\mu\text{S cm}^{-1}$, 4. Based on examination of 25 nymphs. Calculations according to Tab. 3, 5. lake or spring fed, 6. Standardized classification: highly clumped, clumped, scattered.

Tab. 2. The influence of various factors on the $^{10}\log$ infestation rate of *E. flavens* on *Eph. danica* as calculated by multiple regression. Significance levels are denoted by asterisks. See Tab. 1 for definitions of the factors.

Factor	R ²	Standardized regression coefficient
$^{10}\log$ host density	0.529***	0.421
Bottom substrate	0.049**	0.215
Stream width	0.029***	-0.302
Conductivity	0.015**	0.286
Relative number of <i>Peritrichia</i>	0.021**	-0.289
Stream type	0.031**	-0.212
Degree of clumping of hosts	0.004 n.s.	0.096
Residual	0.322	

probably a result of the fact that populations are not stable, but fluctuate around a mean.

Two of the variables used in the analysis were included as measures of nutritional conditions, namely conductivity and the relative number of *Peritrichia* on the nymphs. The last mentioned was included because small host nymphs, which carried comparatively few *E. flavens* larvae harbored the relatively largest number of *Peritrichia*. In addition, large nymphs living in streams receiving organic pollutants, and where *E. flavens* was not found, were almost completely covered by the ciliates. The comparatively faster moulting in smaller nymphs, and hence the more frequent elimination of sessile peritrichians, would imply an inverse relationship between the relative number of these organisms and the

size of the nymphs. The fact that the opposite relationship was found suggested that the larvae of *E. flavens* also fed upon the ciliates, so that the lower number on the large nymphs was a grazing effect. Comparisons of the relative number of *Peritrichia* between large and small nymphs from 9 localities showed that small nymphs carried a larger number than did the large nymphs. In 4 cases this difference was significant (Tab. 3). Thus, it might be that the *Peritrichia* are consumed by the midge larvae. Still, however, since conductivity is unaffected by grazing effects it probably provides the best estimate of the nutritional status of the streams. The increase in R² by only 1% due to this variable suggests nutrition to be of minor importance in the present context.

Nymphs on a predominantly stony bottom carried more larvae than nymphs living in a homogeneous soft bottom substrate. This was possibly related to the larger frequency of larvae being dislodged, due to movements of the sand during spates.

In larger streams the larvae may have greater difficulties of locating nymphs, especially since they rely on olfactory stimuli to find nymphs. Hence, one would assume lenitic *Eph. vulgata* nymphs to have comparatively fewer midge larvae. As a matter of fact, *E. flavens* is rarely found in lakes. Of 18 localities in still waters from which adequate material is available only one was inhabited by the species. In running waters, *E. flavens* occurred on 60 localities and was absent from 3. This difference between the two habitat types of course, is highly significant ($p < 0.001$, $\chi^2 = 61$). However, other factors which differ between lotic and lenitic environments could also contribute to the difference observed.

As was indicated above the host size category used by

Tab. 3. The relative number of *Peritrichia* on large and small host nymphs.

Locality	Host size category (mm)	Not detected	Relative number of <i>Peritrichia</i>			Covering most of the body	
			Few	Frequent	3		
		0	1	2			
I	≥ 12		6	8	6	$\chi^2 = 2.42$ n.s.	
	< 12		8	5	12		
II	≥ 12	10	6	4		$\chi^2 = 9.19$ $p < 0.01$	
	< 12	1	7	9			
III	≥ 12	1	11	8		$\chi^2 = 4.95$ n.s.	
	< 12		5	14			
IV	≥ 12	6	10	4		$\chi^2 = 11.28$ $p < 0.01$	
	< 12		7	13			
V	≥ 12	7	11	2		$\chi^2 = 13.98$ $p < 0.01$	
	< 12		9	7	4		
VI	≥ 12	2	8	8	2	$\chi^2 = 3.04$ n.s.	
	< 12	1	7	2			
VII	≥ 12	13	7			$\chi^2 = 0.006$ n.s.	
	< 12	7	4				
VIII	≥ 12	1	7	8		$\chi^2 = 3.73$ n.s.	
	< 12		5	14	1		
IX	≥ 12	5	7	8		$\chi^2 = 5.94$ $p < 0.05$	
	< 12		11	9			

Tab. 4. Environmental characteristics and biological data for 5 populations of *E. flavens*. Wing length measurements and distribution of larval instars derive from samples taken in 1978.

		A	B	Locality C	D	E
Water chemistry (mean annual) } pH		8.31	7.71	7.56	7.28	6.84
	conductivity ($\mu\text{S cm}^{-1}$)	495	492	373	208	148
Water supplied from		spring	lake	spring	spring	lake
Infestation rate ($^{10}\log$ host density)	1977	0.58 (-1)	3.55 (0)	1.85 (3)	1.42 (1)	2.16 (1)
	1978	0.62 (0)	1.42 (1)	1.48 (3)	1.14 (1)	1.81 (1)
	1979	0.82 (1)	4.49 (1)	2.57 (2)	3.04 (1)	2.51 (1)
Female wing length (mean \pm S.D.)		1.554 \pm 0.095	1.550 \pm 0.069	1.521 \pm 0.140	1.510 \pm 0.090	1.594 \pm 0.072
Frequency distribution of larval instars of <i>E. flavens</i> in the beginning of its emergence period	I	0	0	0	0	2
	II	0	3	3	36	28
	III	38	33	35	40	27
	IV	62	64	62	24	43

an *E. flavens* larva prior to pupation (i.e. a small vis à vis a fullgrown nymph) could have a major impact on the emergence success of the midge. Since the flight period of *Eph. danica* is comparatively short, the extent of emergence of the midge outside this period will influence the overall survival of *E. flavens*. In order to elucidate the conditions in different populations of the species, 5 localities (A–E) were chosen. For obvious reasons very thin populations were excluded. Immediately prior to the emergence period most of the larvae were in the last instar at three of the localities while most larvae were in the second or third instar at the other two (Tab. 4). The last mentioned localities are oligotrophic suggesting that nutrition may play a role for the growth rate. Female *E. flavens* from the localities were about equally sized. A significant difference in wing length was observed between D and E only ($p < 0.05$, $t_{\text{two-tailed}} = 2.14$). At Stampen the size of female *E. flavens* decreases rapidly towards the end of

the emergence season (Fig. 2). Since fecundity is related to female wing length (Svensson 1979) it follows that larvae in the second and third instar at the beginning of the emergence period probably have a lower fecundity as adults, than those able to emerge earlier.

Fecundity may also be affected by the probability of mating and hence will be related to population density (see below). In *E. flavens* oogenesis takes two days. In several other species of Chironomidae it is completed at emergence, but species have also been found which, like *E. flavens*, emerge with less developed oocytes (Oliver 1971). The factors which control the development of the oocytes in Chironomidae are unknown. A reasonable explanation for the delayed oogenesis in *E. flavens* may be as follows:

If the probability of becoming mated is low, the midge may have to wait for several hours or even days before encountering an individual of the opposite sex. The energy used for staying alive during this period and for egg maturation probably derives from the same source, namely the trophic tissue because dissection of females of *Epoicocladus* has shown that they do not eat. Hence, an extended flight period might lead to lower fecundity. In some chironomids the eggs become resorbed if the females are not inseminated within a certain time (Downe 1973). In many dipterans the total number of eggs laid is higher after mating, as compared to that in virgins (Engelmann 1970). The flight activity of *E. flavens*, to judge from light trap catches, is probably highest soon after emergence, because the females trapped in this way always had their abdomen elongated as in the pupal stage, and the oocytes were minute. It seems advantageous to delay oogenesis until after mating, because the energy required for flying is then directly available, as compared to the indirect way of gaining energy for this purpose by resorbing already developed oocytes. On the other hand, when the populations are dense and the probability of copulation is high, it is advantageous to have fully developed eggs

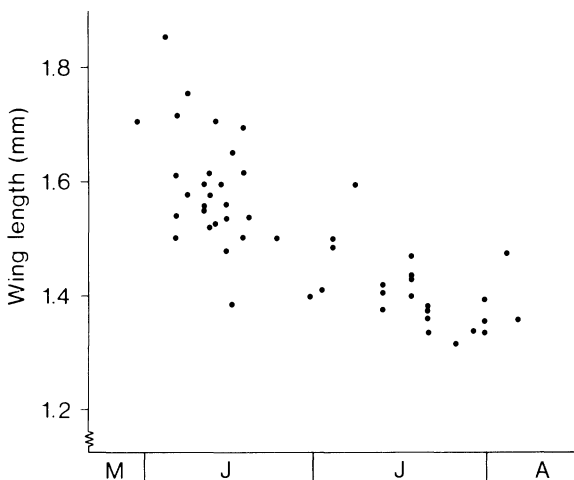


Fig. 2. Female wing lengths of *E. flavens* at Stampen in 1975.

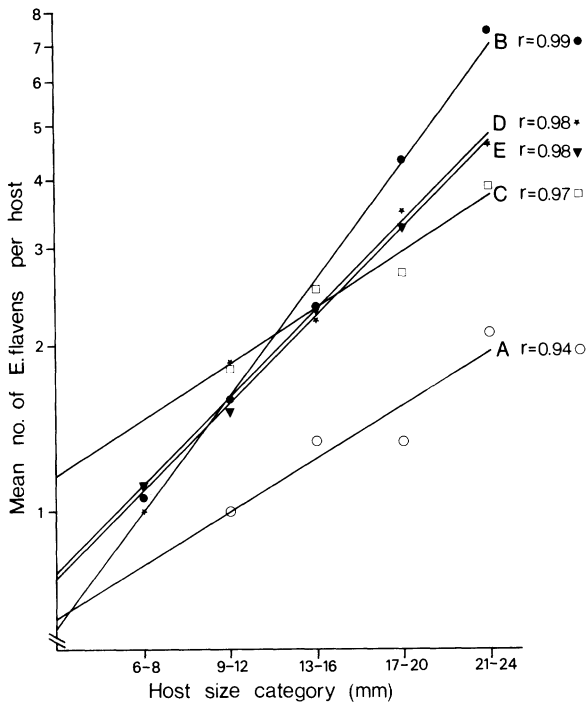


Fig. 3. The relationship between host size and mean number of attached *E. flavens* larvae for 5 populations. Letters refer to Tab. 4.

already at emergence, because this will minimize the time between mating and oviposition and thus the risk of succumbing, for example, to predators before reproduction.

Evidently the average infestation rates in the above populations cannot be directly related to environmental factors and differences in population characteristics as

outlined above. However, they could perhaps interact with such factors as fluctuations and spatial distributions of the host populations to produce the observed levels of infestation.

Recalling the assumption given in the beginning of this paper, that the mean value of the infestation rate within a particular host density category reflects average or equilibrium conditions, the interpretation of the obvious increase in the number of larvae on each individual host in relation to host density as seen in Fig. 1, is that the environmental capacity (*sensu* Milne 1962) for *E. flavens* per unit habitat area increases with the number of available hosts. There are two possible explanations of this change of capacity: (a) the ability of the larvae to find and to make use of the most suitable hosts increases with high host density, and (b) a relationship between the amplitude of fluctuations of the host populations, caused for example, by stochastic changes in the environment, and the average population size of the host population. The latter hypothesis, however, is not supported by the data in Tab. 4.

To test the first explanation I have used data on the populations listed in Tab. 4. The analysis is based on the fact that large host nymphs carry more midge larvae than do small nymphs. The reason for this is that large host nymphs possess a larger surface area suitable for attaching, but also that they supply more food particles to the larvae, and, perhaps most important, that they are much easier to find for the larvae (see below).

Since survival of *E. flavens* may be enhanced on the large nymphs, it would be propitious for a larva always to select as large a host as possible. The relationship between nymph length and average number of attached larvae for 5 populations is illustrated in Fig. 3. To eliminate the direct effect of the difference in mean infestation rate on the relationship, the ordinate has been

Tab. 5. The numerical distribution of *E. flavens* on the hosts, compared with a calculated Poisson and a negative binomial distribution. Localities are those in Tab. 4. The samples from 1979.

Locality	Number of <i>E. flavens</i> per host								χ^2	p-value	
	0	1	2	3	4	5	6	≥ 7			
A	observed	31	19	7	4	1					
	Poisson	28.1	22.2	8.8	2.3	0.5			$\chi^2 = 2.89$	0.5 > p > 0.3	
	neg. binomial	30.7	19.2	8.0	2.8	1.2			$\chi^2 = 0.68$	0.75 > p > 0.70	
B	observed	8	4	8	7	3	2	0	5		
	Poisson	1.3	4.3	7.3	8.1	6.8	4.6	2.5	2.1	$\chi^2 = 44.86$	0.001 > p
	neg. binomial	6.2	7.8	7.0	5.4	3.8	2.6	1.7	2.6	$\chi^2 = 6.64$	0.2 > p > 0.1
C	observed	15	19	22	19	15	6	4	4		
	Poisson	8.3	21.0	26.5	22.4	14.1	7.1	3.0	1.4	$\chi^2 = 12.04$	0.1 > p > 0.05
	neg. binomial	12.3	22.4	23.6	18.7	12.4	7.2	3.9	3.5	$\chi^2 = 2.05$	0.9 > p > 0.8
D	observed	10	20	22	13	10	6	9	7		
	Poisson	5.4	15.6	22.5	21.7	15.6	9.0	4.3	2.4	$\chi^2 = 25.63$	0.001 > p
	neg. binomial	10.3	19.5	20.1	17.0	12.3	8.0	4.9	5.9	$\chi^2 = 4.70$	0.5 > p > 0.3
E	observed	8	8	9	3	1	4	0	2		
	Poisson	4.1	8.8	9.4	6.7	3.6	1.5	0.6	0.2	$\chi^2 = 13.69$	0.05 > p > 0.02
	neg. binomial	7.9	8.7	6.8	4.7	2.9	1.8	1.0	1.2	$\chi^2 = 5.50$	0.25 > p > 0.20

transformed to a $^{10}\log$ scale. As can be seen the slope of the lines varies greatly but the intercepts are about the same. This means that at high mean infestation rate the larger nymphs are preferred, as opposed to a more uniform distribution of larvae among the host size categories at low infestation rates. The distribution of *E. flavens* among the nymphs was best described by a negative binomial distribution (Tab. 5) although in the populations with the lowest infestation rate the distribution was not significantly different from a Poisson. This pattern was caused by aggregation of larvae on the largest nymphs and unexpectedly few larvae on the small nymphs. Notably, the hosts at loc. B were highly clumped, being confined to the edge of the stream. At loc. D, with a steep gradient and a stony bottom, *Eph. danica* was restricted to sandy patches downstream of larger stones and in alcoves. At the other localities the hosts were more uniformly distributed. These observations indicate that the midge larvae, in situations of aggregated host populations, "select" the large nymphs, whereas in more sparse host populations, they settle also on smaller nymphs. These findings support the above explanation for the increased infestation rate with host density. It should be pointed out that the maximum number of larvae observed on a single host in any wild population was much lower than the number that has been kept alive on a single host in the laboratory.

This conclusion differs from the general opinion, documented for several species, that less favourable habitats are used only when the density dependent effects in the optimal habitats make them profitable to exploit (Fretwell 1972, Partridge 1978). The relatively high utilization of a habitat at low population densities is also regarded as a reason why the recovery from especially density-dependent population crashes may be so rapid (e.g. Whittaker and Goodman 1979). However, these interpretations may stem from studies of comparatively dense populations. In very sparse populations, for example, when pest species are below the "building up phase", or in species with limited dispersal capacity, the suboptimal habitat may be more utilized. Thus, the gypsy moth, *Lymantria (Porthetria) dispar* (L.), is found on less preferred host trees after population collapses in the optimal habitats (Leonard 1974). The dispersal in this species mainly occurs in the immature stage and is passive by wind (Leonard 1974), which suggests large losses and a low probability of finding the optimal habitat. That immigration is essential for rapid increases of populations of this species seems clear (Campbell 1976 and references therein). Notably, the outbreak foci for *L. dispar* are open coppices and forest edges along pastures and roads (references in Leonard 1974). The above idea is summarized in Fig. 4.

From both theoretical and empirical studies of biological control substantial evidence has emerged that the spatial distribution of hosts and the searching image

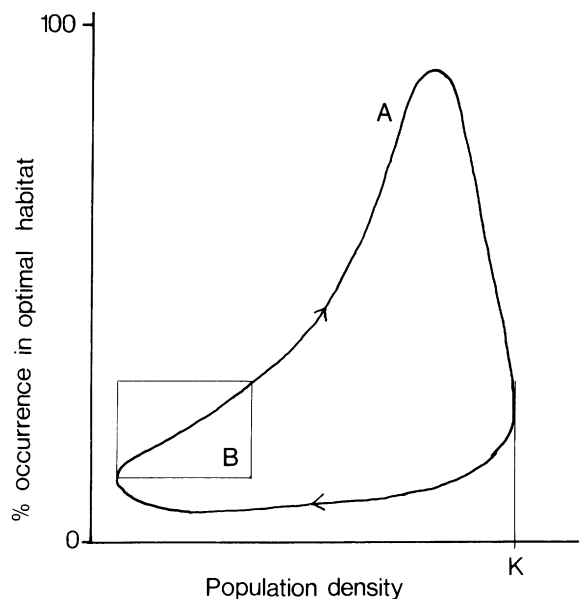


Fig. 4. A model of the relationship between the degree of utilization of the optimal habitat, expressed as percent of total habitat occupied by a population, and the size of the population. The complete cycle (A) is assumed to be found in some insect pest species. Arrows denote the direction of the population cycle when mortality is caused only by intraspecific competition and overexploitation of resources. The rectangle (B) encloses the truncated cycle to be found in some "rare" species, e.g. *E. flavens*. K is carrying capacity.

used by their natural enemies are most important in determining the efficiencies of the latter in reducing the former (Beddington et al. 1978). As was pointed out by Varley (1941) a random distribution of parasites on the hosts is the most likely result of random search. The reverse, however, is not necessarily true (Rogers 1972). For example, if parasite eggs are deposited in areas of aggregated hosts, the resulting distribution will be clumped, even if the parasites search at random. Similarly, if the search is random, but some hosts are rejected for any reason, the final numerical distribution will also be non-random. Usually, two different searching events underlie the observed overall distribution of parasitoids on the hosts. The first concerns the way in which the parasitoids distribute themselves between the patches in which the hosts are to be found. With respect to *E. flavens*, this event may be visualized as the dispersal of the females prior to egg-laying. Secondly, having chosen a certain patch, the parasitoid will exhibit a certain attack distribution; in the case of *E. flavens* the pattern of movements undertaken by the newly hatched larvae to reach the host nymphs.

Assuming a random search within each patch, May (1978) argues that the overall or compound distribution most often will conform to a negative binomial. However, the observed overall distribution does not allow any conclusions as to the searching behaviour of, in this

case, the adult female or the newly hatched larvae (Pielou 1978). It could nevertheless be worthwhile to speculate around the observed compound distributions on the localities investigated. Reasonably, the ability of an egg-laying female to detect aggregates of hosts must be limited, because the value of volatile oviposition attractants as has been found for example in *Aedes* (McDaniel et al. 1979) must be insignificant in running waters, where the current effectively carries odours away. In most of the streams studied it would probably be sufficient to deposit the eggs near the edges, where the majority of hosts are found.

If chemical stimuli are used by the midge larvae to locate hosts, search cannot be random. The increased proportions of exploited large hosts at high densities or in aggregated host populations does not necessarily, however, depend on more active or preferential search. Observations suggest that larvae only accidentally leave their host if this is above a certain minimum size. The following mechanism may account for the observed distributional pattern. If the amount of host substance released by the host which attracts the larva, e.g. a metabolic product, is proportional to the size of the host, the area within which a large host nymph may attract a midge larva is, on average, larger than that for a small nymph, because dilution tends to reduce the concentration with the square of the distance from the source (host). Therefore, the probability of a small nymph attracting a midge larva will be relatively larger at low than at high host densities, provided the size composition of the host population remains the same. The relationship depicted in Fig. 3 will then arise. The above mechanism also implies that the numerical distribution of larvae on all hosts taken together will change from a near Poisson at low host densities to a negative binomial at high host densities, irrespective of the host distribution (although aggregates will promote the tendency). This means that although the searching behaviour of the larvae even if being random will result in a numerical distribution which is either random or clumped depending on the density of the host population.

The reason why the degree of clumping was found to be insignificant in the multiple regression analysis was probably the complexity of this kind of distribution, and consequently the failure of a single parameter to accurately describe its biological importance (e.g. Taylor et al. 1979), especially if the chosen parameter interferes with host density in a non-linear way.

Conclusion

Host density seems to be the most important factor in determining the level of infestation by *E. flavens*. A differentiated utilization of the largest hosts and its effect on the number of adult females produced, is the most likely cause of this pattern.

5.2. A theoretical interpretation of mating success and density

The probability that a midge larva will find a host nymph at different densities defines one of two possible density dependent factors operating below the carrying capacity. The other is the probability of finding a mate when the adults are scarce.

Andrewartha and Birch (1954) calculated the probability of mating for a female tick when the distribution of the tick population on their hosts was gaussian. Rohlf (1969) expanded their model to situations of the ticks being randomly and contagiously distributed on the hosts. His model may be extended to many other populations, one important limitation, however, being the relatively long life span of ticks. When the time available for mating in a female is short, and the maturation of individuals takes place during extended periods, the probability of copulation may be low even under large population densities. This is the situation in several insect populations and it patently applies to *E. flavens*.

At Stampen, adult *E. flavens* from the same generation emerge throughout most of the summer, but the maximum time an unmated adult has been kept alive under laboratory conditions is only four days. Clearly, therefore, a parameter related to the adult life span must be incorporated in Rohlf's model.

His model is built on the following assumptions: (1) The basic adult sex ratio is 1:1. This is the case for *E. flavens*. (2) Successful mating invariably takes place as soon as two individuals of opposite sexes occur on the same day (in the original model: on the same host). This assumption weakens the model. An adjustment which takes into account synchronized emergences without matings is given below. In addition to these conditions I have assumed that the maximum adult life span of *E. flavens* is 4 d (cf. above) and that the pattern of emergence follows a standardized normal distribution, not strictly true under field conditions, and that the emergence lasts for 3 wk (cf. Svensson 1979). The model may, however, be adjusted to account for any other adult life span or pattern of emergence.

If the number of individuals in a population that emerges on a particular day (k) is given by (n_k) , the probability that a female will find a potential mate (p'_{n_k}) can be written

$$1 - \frac{n_k!}{\left[\left(\frac{n_k}{2}\right)!\right]^2} 2^{-n_k} \quad (\text{Rohlf 1969}).$$

If emergence takes place over m days, the probability that a female emerges and finds a male on the first day (p_1) is given by

$$\frac{\frac{n_1}{m} p'_{n_1}}{\sum_{k=1}^m n_k}$$

According to the assumptions given above, individuals which remain unmated after the first day are of the same sex. Since the adults may live for 4 d, one has to consider the probability that they acquire a mate on any of the following 3 d. Thus, the joint probabilities of emergence and mating of a female on the second day (p_2) is given by

$$\frac{\frac{n_2}{m} p'_{n_2} + (1-p'_{n_1}) \frac{n_1}{m} \left(\frac{1-p'_{n_2}}{2}\right) \frac{n_2}{m}}{\sum_{k=1}^m n_k}$$

(where $\frac{1-p'_{n_2}}{2}$ is the probability that unmated individuals from day 2 are of the opposite sex as those left over from day 1).

Similarly, the corresponding probability for the third day (p_3) becomes

$$\begin{aligned} & \frac{\frac{n_3}{m} p'_{n_3} + \left[1 - (1-p'_{n_1}) \frac{n_1}{m} \left(\frac{1-p'_{n_2}}{2}\right) \frac{n_2}{m}\right]}{\sum_{k=1}^m n_k} \\ & + \frac{\frac{n_1}{m} \left(\frac{1-p'_{n_3}}{2}\right) \frac{n_3}{m}}{\sum_{k=1}^m n_k} + \\ & + \left[1 - (1-p'_{n_1}) \frac{n_1}{m} \left(\frac{1-p'_{n_2}}{2}\right) \frac{n_2}{m}\right] \\ & \frac{\frac{n_2}{m} \left(\frac{1-p'_{n_3}}{2}\right) \frac{n_3}{m}}{\sum_{k=1}^m n_k}, \end{aligned}$$

and for the k :th ($K \geq 4$)

$$p_k = p'_{n_k} \frac{n_k}{\sum_{k=1}^m n_k} + \sum_{j=1}^3 (1-p_{k-j}) \frac{n_{k-j}}{\sum_{k=1}^m n_k} \left(\frac{1-p'_{n_{k-1}}}{2}\right) \frac{n_k}{\sum_{k=1}^m n_k}$$

where

$$p_{k-1} = \left[1 - (p_{k-j-1} + p_{k-j-2})\right] \frac{n_{k-j-1}}{\sum_{k=1}^m n_k} \left(\frac{1-p'_{n_{k-1}}}{2}\right) \frac{n_{k-1}}{\sum_{k=1}^m n_k}$$

For large n (with the present distribution of emergence: $n \geq 10$) most of the terms in this series are close to zero. In practice, therefore, p_k reduces to

$$p'_{n_k} \frac{n_k}{\sum_{k=1}^m n_k} + \sum_{j=1}^3 \frac{n_{k-j} n_k}{\left(\sum_{k=1}^m n_k\right)^2} \left(\frac{1-p'_{n_k}}{2}\right)$$

The probability that a female obtains a mate when the population size equals $\sum_{k=1}^m n_k$ thus becomes $\sum_{k=1}^m p_k$. The

effect of population size on $\sum_{k=1}^m p_k$, when the frequen-

cy of emergence follows a standardized normal distribution and lasts for 3 wk, is shown in Fig. 5. I have also constructed the corresponding curve for the situation when the adults mate and die the same day they emerge. In this case

$$\sum_{k=1}^m p_k = \sum_{k=1}^m \frac{n_k}{\sum_{k=1}^m n_k} p'_{n_k}$$

If the males can mate more than once, then $p'_{n_k} = 1 - 2^{1-n_k}$ (Rohlf 1969). The resulting curves describing the relationship between the probability of a female mating and population size, when maximum adult life spans are 1 and 4 d, respectively, are also given in Fig. 5.

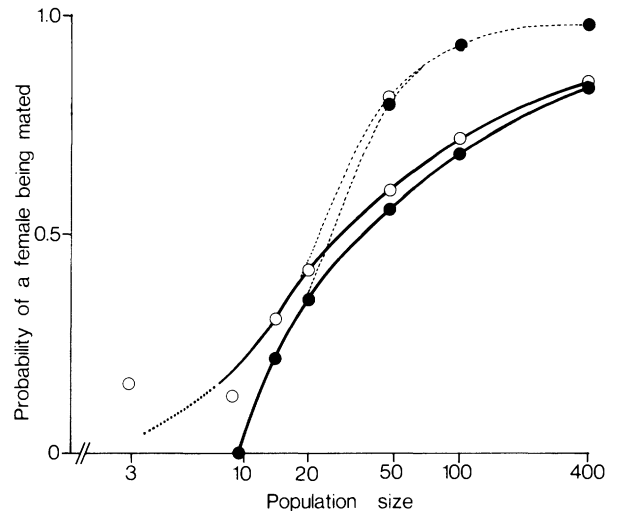


Fig. 5. The effect of population size on the probability of a female becoming mated. Solid lines: when the males mate once. Dotted lines: when the males mate repeatedly. Closed and open circles refer to an adult life span of 1 and 4 d, respectively. The irregular pattern of the curves at low densities reflects the discrepancy between the calculated discrete distribution and the underlying continuous distribution.

The generality of the above formulae can be increased by multiplying p'_{n_k} with a constant C ($0 < C \leq 1$), which denotes the fraction of encounters between pairs which result in successful matings. The value of C is probably higher in a situation of promiscuity, than when males mate only once.

Downe (1973) using an autoradiographic technique, studied the incidence of insemination in laboratory swarms of *Chironomus riparius* Meigen. His data allow the calculation of C for this species. If the midges were allowed to swarm only once, irrespective of the sex ratio, the number of inseminated females was slightly lower than the number of individuals of the sex that was in short supply. The total number of individuals making up the swarm had no significant effect on the fraction of females that were inseminated: this observation seems to justify the above treatment. Using only the results from experiments in which the sex ratio was unity, the calculated average values of C were 0.74 and 0.91 after 1 and 2 swarming periods, respectively. The value of C , however, cannot influence the following conclusions.

5.2.1. Conclusion

If one accepts the assumptions presented above, an obvious interpretation of Fig. 5 is that, in a restricted population, a slight increase in adult life span (from 1 to 4 d) will add very little to an individual's probability of mating. Only at quite low densities is the difference between the resulting curves significant. But at that level the probability of becoming mated is probably insufficient for keeping up with mortality for other reasons, because fecundity is clearly limited in *E. flavens*.

However, as already suggested, the pattern of oogenesis in *E. flavens*, may reflect an optimal use of energy deposits in situations where the probability of finding a mate is low. In terms of range of dispersal, therefore, the difference between an adult life span of 1 and 4 d may be important, because it might considerably increase the area from which the adults are recruited, that is the effective population size (cf. den Boer 1970).

In chironomids and most other Diptera, the adults usually form mating swarms. The formation of such a swarm is facilitated by the use of swarm markers, i.e. landmarks around which the midges gather. It is likely that individuals forming a mating swarm by the use of swarm markers and other visual as well as olfactory signals may be recruited from comparatively large areas so that the effect of dispersed populations is reduced (Downes 1969). The formation of a mating swarm has also been regarded as a mechanism, whereby short-lived chironomids are prevented from leaving the breeding site (reference in Downes 1969). In many species mating seems to occur at the emergence site (Nielsen 1962, Andersson 1974). These apparently contradictory hypotheses may be unified if we regard the mating swarm or the mating site, not as a constant in

space and time, but as a function of population density and distribution. At present, evidence for the validity of this view is lacking.

5.3. Final conclusion

As was concluded above, host density, through a differentiated utilization of the most suitable hosts, may influence the per capita reproductive success. In addition, the pattern of dispersal of adult *E. flavens* may influence the number of eggs per female as well as the prospects of encountering an individual of opposite sex. Dispersal for mating may also, in an indirect way, influence the selection of an oviposition site.

Finally, the importance of the host distribution on the success of *E. flavens* in exploiting *Eph. danica* must be stressed. Although all of the above conclusions bear on analyses of static conditions, nothing but the tendency for *Eph. danica* to form aggregates can explain the very slight increase in efficiency of the symbiont with increasing host density. Or expressed in another way, the average infestation rate at high host densities, obviously far below the carrying capacity, implies a limited ability of the midge larvae to colonize sparse host populations.

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