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Larval niche differences between the sibling species, *Drosophila montana* and *D. littoralis* (Diptera) in northern Finland

Jouni Aspi (1996)

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Differences in larval substrate, or in the spatial and temporal occurrence of larvae between two closely related and ecologically similar *Drosophila* species were investigated. Vials containing homogenised tissue of water lily stems or birch phloem wetted with sap were exposed for oviposition in two habitats during two time periods. A logit analysis of the field emergence data suggested significant niche differences between the species. The logit model best explaining the species composition among emerging adults included an interaction between habitat and substrate, and also an interaction between habitat and exposure period. The differences between the species were, however, small and the species overlapped broadly with respect to each of the studied niche dimensions. The distribution of emerging flies among the yellow water lily vials appeared to fulfill the assumptions of a theoretical model for aggregation-mediated coexistence, i.e. the distribution of flies was aggregated among vials in both species, and there was no interspecific correlation in the numbers of flies emerging from the vials.

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1. Introduction

The boreal *Drosophila virilis* species association consists of four closely related sibling species (*D. lummei* Hackman, *D. littoralis* Meigen, *D. ezoana* Takada & Okada and *D. montana* Stone, Griffen & Patterson). The phenology and spatial distribution of adults of these species in the field is very similar, and they form a compact group distinct from the other drosophilids in northern Scandinavia (Lumme *et al.* 1978, 1979, Aspi *et al.* 1993).

Although there are only slight differences among these species in their adult ecology (Lumme *et al.* 1978, 1979, Aspi *et al.* 1993), they may differ in other life stages. In *Drosophila* the major specificity of the ecology seems to relate to the breeding sites in the larval stage (e.g. Carson 1971, Krebs *et al.* 1993). There is only scanty information available about female oviposition and on larval feeding sites among these species. In general the species of the *D. virilis* group are classified as sap breeders, the known breeding sites being sap and the decaying phloem tissue of some deciduous tree species (e.g.,

Carson 1971, Spieth 1974, Shorrocks 1982, Watabe & Peng 1991). During the previous fieldwork in the boreal area (Aspi *et al.* 1993) we have been able to breed a few adults of *D. littoralis* and *D. montana* from the phloem tissue of birch and yeast growing on birch sap fluxes, and also from the rotting stems of yellow water lily, *Nuphar lutea*. At least these two species seem to share the breeding substrates.

Drosophila species using identical breeding resources may differ in the spatial or temporal use of these resources (Kaneshiro *et al.* 1973, Lachaise *et al.* 1982, Nunney 1990). The distribution of adult flies during the breeding season may provide indirect evidence about spatial differences in breeding sites of *Drosophila*. Among the boreal *D. virilis* group there seem to be, however, no large differences in the spatial distribution of ovipositing females (Lumme *et al.* 1979, Aspi *et al.* 1993). All these species feed and mate in close proximity to water. Only *D. montana* is not as strictly restricted to habitats with high humidity as the other species (Lumme *et al.* 1979, Aspi *et al.* 1993). The main breeding season of boreal species of *D. virilis* group is in early spring, and is very short, limiting the possibility of temporal niche differentiation (Lumme *et al.* 1978, Aspi *et al.* 1993). However, Aspi *et al.* (1993) reported differences in the seasonal mating schedules between the three most common species of the *D. virilis* group, which may in turn also indicate temporal differences in occurence of larvae.

The use of similar breeding substrates can lead to interspecific competition and exclusion of competing species. Coexistence of competing *Drosophila* species in spatially homogenous environments may sometimes be promoted by differences in life-history (Sevenster & van Alphen 1993a, 1993b; see also Davis & Hardy 1994). However, there seem to be no large differences in life-history characters among the boreal *D. virilis* group species (Lumme *et al.* 1978, Aspi *et al.* 1993).

The exclusion of competing species will not always occur if the resources are patchy and ephemeral. Several authors have suggested theoretical models (Shorrocks *et al.* 1979, Atkinson & Shorrocks 1984, Hanski 1981, 1983, Ives & May 1985; see Hanski [1987] and Shorrocks [1990] for reviews) in which an inferior competitor can coexist with a superior one if the competing stages are aggregated among the discrete and ephemeral resource patches, and if intraspecific aggregation exceeds interspecific aggregation. Under these conditions interspecific competition is more intense among the superior species than among the inferior one. Since earlier observations indicate that the natural breeding sites of *D. virilis* group species are discrete and ephemeral (i.e. wounds in birch bark and rots in stems of yellow water lily), the aggregation-mediated competition model may allow their coexistence even if the breeding niches are similar.

The aim of this paper is to examine whether *D. littoralis* and *D. montana* have a different oviposition preference for the two known breeding substrates and in spatial and temporal distribution of larvae in the field. The aggregation model of coexistence is also considered in light of the distribution of larvae among resource items.

2. Material and methods

2.1. Substrate preparation

Baits from decaying plant material were prepared to resemble the natural breeding substrate of the species (see e.g. Offenberger & Klarenberg 1992). The plant materials used were: 1) phloem tissue of birch (*Betula pubescens*) peeled from young trees, dried, homogenised and moistened with birch sap, and 2) tissue of underwater stems of the yellow water lily (*Nuphar lutea*) homogenised into a pulp. After a period of rotting and fermenting, each substrate batch was mixed thoroughly and frozen. For the field study, 10 ml of thawed birch phloem tissue or 5 ml of yellow water lily pulp was dispensed directly into plastic vials (75 mm deep, 27 mm diameter). Different volumes of the two substrates were used to keep the carbohydrate content of the vials similar.

2.2. Exposure of substrate vials for oviposition in the field

The fieldwork was carried out near Kemi, Finland, along the River Iso-Ruonaoja (E27 Grid number 7292:394, 65°40′N, 23°35′E; see Aspi *et al.* 1993 for a detailed description). In earlier trappings all members of the riparian guild have been found, with *D. littoralis* the most common followed by *D. montana*, *D. lummei*, and *D. ezoana* respectively.

The oviposition vials were placed in white 2-litre plastic buckets (14.5 cm deep, 15.5 cm diameter) containing a 5 cm layer of moistened sand. Two vials of birch phloem and two of yellow water lily were randomly half-submerged in a square in the sand layer. The buckets were placed in two

habitats: on the river shore, or in a forest five metres from the river bank (Fig. 1).

Substrate vials were exposed for oviposition (and also for natural microbe contamination) for two different periods: 12 replicates between 12 May and 31 May (early season), and 12 replicates between 22 May and 5 June (late season) in 1992. These time limits covered the whole reproductive period of overwintered females (Aspi *et al.* 1993). Although the latter period was shorter, the accumulated temperature sum above 5° C (below which the activity of flies ceases) was rather similar for both, 91.5 daily degrees in the early season and 115.7 in the late season. Overlapping periods were used to increase the number of flies per vial, since in preliminary experiments the number of flies emerging per vial had been fairly low.

After exposure, the vials containing the substrate were plugged and taken back to the laboratory. The vials were kept outside in a ventilated cage, where the ambient temperature was quite similar to that of the original breeding site. The contents of the vials were moistened regularly with distilled water. All emerging flies were collected and identified to species.

2.3. Niche metrics and aggregation analysis

Emergence data was used to calculate niche breadth for different niche dimensions and niche overlap between species. All niche metric calculations were carried out on Krebs' (1989) NICHE program. Niche breadth for substrate, season and habitat usage for each species was estimated using Levins' standardised niche breadth (scale from 0 to 1.0) formula (e.g. Krebs 1989):

$$\text{eq. 1. } BA = (B-1)/(n-1),$$

where: BA = Levin's standardized niche breadth, B = Levin's original measure of niche breadth, n = number of possible resource states.

[Levins' original measure of niche breadth is calculated from the formula:

$$\text{eq. 2. } B = 1/(\Sigma pj2),$$

where: B = Levin's measure of niche breadth, pj = Proportion of individuals found in resource state j].

Niche overlap between the species was calculated using Morisita's index of overlap (e.g. Krebs 1989):

$$\text{eq. 3. } C = (2\Sigma pijpik)/\{\Sigma npij[(nij-1)/(Nj-1)] + \Sigma npik[(nik-1)/(Nk-1)]\}$$

where: C = Morisita's index of niche overlap between species j and k, pij = Proportion resource i is the total resources used by species j, pik = Proportion resource i is the total resources used by species k, nij = Number of individuals of species j that use resource category i, nik = Number of individuals of species k that use resource category i, Nj, Nk = Total number of individuals of each species in sample, (i.e. $\Sigma ni_j = Nj$, $Snik = Nk$).

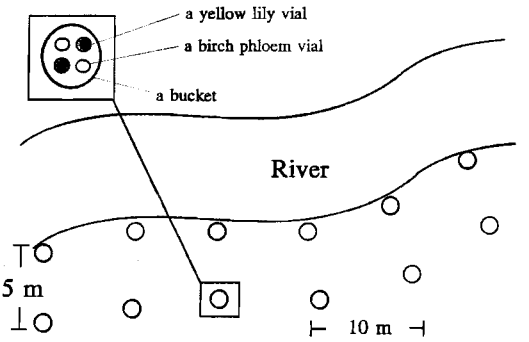

Fig. 1. Schematic representation of the experimental design.

This measure of overlap ranges from 0 (no resources used in common) to 1.0 (total overlap).

Morisita's index was calculated for uncombined data using each vial as a different "resource" category, and also for each measured niche dimension (habitat, substrate and exposure period). For this analysis the twelve replicates within habitats (i.e. shore and forest) were combined, as were the data from the two vials containing the same substrate within the buckets.

The significance of niche differences was analysed statistically by subjecting the emergence data to a logit analysis (Christensen 1990), where the species of an emerging fly was the response variable, and substrate (birch vs. yellow water lily), exposure period (early vs. late), and habitat (shore vs. forest) were the explanatory variables. Logit regression was further used to analyse the temporal difference in emergence dates between the species. For this analysis, the two exposure periods were pooled, emergence data from all vials was combined within sixteen two-day periods, and curve-fitting for the number of emerged flies in each species was carried out by the least-square principle (Jongman *et al.* 1987) and the date (Julian day from the beginning of the experiment) as the explanatory variable. The GLIM statistical package (e.g. Aitkin *et al.* 1990) was used to fit the logit models and to determine the parameters for least square regression.

If the distribution of flies among the resource items is random, the distribution of emerging adults should follow a Poisson distribution. Departure from the Poisson distribution was tested using the index of dispersion test (Krebs 1989, p. 76). The aggregation pattern of the larvae among the vials was further analysed by using comparable measures of both intraspecific and interspecific aggregation as suggested by Ives (1988, 1991). These measures are based on the mean and variance of the larvae in the vials as censused by the number of emerging adults. Intraspecific aggregation is measured by J, the proportionate increase in the number of conspecific competitors experienced by random individual relative to a random distribution. It is calculated by:

eq. 4. $Ji = [(Vi/xi) - 1)/xi)]$,

where: Ji = measure of intraspecific aggregation for species i, xi = mean of the number of larvae per vial in species i, Vi = variance of the number of larvae per vial in species i.

When individuals are randomly distributed, $Ji = 0$, whereas a value of $Ji = 0.5$ indicates a 50% increase in the number of conspecifics expected in a vial (e.g. Shorrocks & Sevenster 1995). Interspecific aggregation is measured by C, which measures the proportionate increase in the number of heterospecific competitors relative to a random association (Ives 1988, 1991). It is calculated by:

eq. 4. $Cij = Covij/xixj$,

where: Cij = measure of interspecific aggregation between species i and j, $Covij$ = covariance between species i and j, xi = mean of the number of larvae per vial in species i, xj = mean of the number of larvae per vial in species j.

When $Cij = 0$ then species i and j are independently distributed across vials, when $Cij > 0$ then species are positively associated and when $Cij < 0$ then species are negatively associated.

For estimating the relative strength of intra- and interspecific aggregation on the number of competitors with which a larva shares a resource, Ives (1991) has proposed a quantity A, calculated by:

eq. 5. $Aij = [(Ji + 1)(Jj + 1)]/(Cij)^2$,

where: Ai_j is a measure of relative strengths of intra- and interspecific aggregations for species i and j, and Ji, Jj, and Cij as above. When intra- and interspecific aggregations are equal then $Aij = 0$, and when $Aij > 0$ then intraspecific aggregation is stronger than interspecific aggregation (e.g. Jaenike & James 1991, Shorrocks & Sevenster 1995, Sevenster 1996).

3. Results

3.1. Niche metrics for *D. montana* and *D. littoralis*

Adults of only two species, *D. littoralis* and *D. montana* were obtained from the vials exposed for ovipositing in the field. The mean number of flies per vial was 0.656 (Median = 0) for *D. littoralis* and 2.23 (Median = 0) for *D. montana*.

Species composition was not independent with respect to the explanatory variables (i.e. exposure period, habitat and substrate) (Table 1). The best fitting logit model included an interaction between habitat and substrate, and also an interaction between habitat and exposure period ($\{HS\}\{HP\}$). This model was the only adequate representation of the data, as adding an interaction between substrate and exposure period (i.e. model $\{HS\}\{HP\}\{SP\}$) did not significantly improve the explanatory power of the model ($\Delta G_{(1)} = 0.849; p > 0.1$).

The total niche overlap between species estimated by using each vial as a different "resource" category was fairly high (0.631). The univariate niche statistics showed an even broader overlap than that with respect to each studied niche dimension (Table 2). Both species had a lower niche breadth for breeding substrate than for other factors. *D. littoralis* exhibited a more variable breeding-site niche than *D. montana*. Although yellow water lily pulp produced more specimens of both species, *D. littoralis* was relatively more abundant in birch phloem pulp than *D. montana*. Overlap between species by substrate was, however, high. The interaction between substrate and habitat (Table 1) was due to fact that two species appeared to have the minimum substrate niche breadth in different habitats (Fig. 2). The niche widths of *D. littoralis* in shore and in forest were 0.600 and 0.498, and those of *D. montana* 0.127 and 0.242, respectively (Fig. 3).

The adult emergence data indicated that *D. montana* larvae were almost equally abundant

Table 1. Logit analysis of the factors influencing the overall species composition. The abbreviations for the factors are: H = habitat (shore vs. forest), S = substrate (birch phloem tissue vs. water lily) and P = exposure period (early vs. late).

Model	*G*	*df*	*p*
{HS}{HP}{SP}	4.943	1	0.026
{HS}{HP}	5.792	2	0.055
{HS}{SP}	0.843	2	0.004
{HP}{SP}	9.238	2	0.010
{P}{HS}	11.562	3	0.009
{S}{HP}	9.611	3	0.022
{H}{SP}	14.894	3	0.002
{H}{S}{P}	15.818	4	0.003

Table 2. Niche metrics for the dimensions studied between two boreal *Drosophila virilis* group species.

	Breadth		Overlap
Dimension	*D. montana*	*D. littoralis*	
Exposure period	0.880	0.833	0.999
Habitat	0.991	0.728	0.909
Substrate	0.204	0.684	0.976

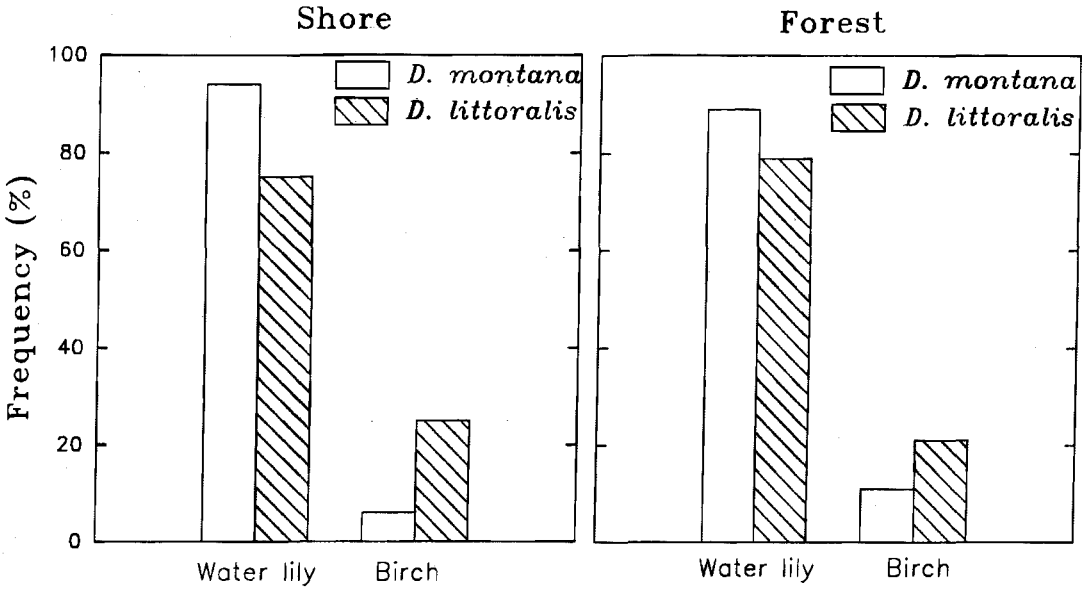

Fig. 2. Percentage of adults emerged from the two substrates in the two habitats studied. N = 63 for *D. littoralis*, N = 214 *D. montana*.

in both habitats, whereas *D. littoralis* was relatively more abundant on the river bank. The narrower habitat niche of *D. littoralis* caused the lowest degree of niche overlap in this dimension. The interaction between habitat and exposure period appeared to be almost solely caused by *D. littoralis* (Fig. 3), which was concentrated on the river bank during the early exposure period (niche breadth 0.198). In the late exposure period, when this species was more abundant, it was also found in the forest (niche breadth 0.943). No large differences were detected in the relative abundance of *D. montana* in different habitats in the two exposure periods (niche breadths 0.995 and 0.989 for early and late exposure periods, respectively).

Niche overlap of the species on the basis of the two exposure periods was large. The degree of temporal overlap between the species was also assessed for the sixteen two-day emergence periods, and this niche overlap showed a lower value (0.718). This distribution of emerging adults differed significantly between the species ($G_{(7)} = 49.39$; $p < 0.001$), and in the least-square analysis Gaussian response curve gave a good fit for the number of emerged flies with respect to emergence day both in *D. littoralis* and in *D. montana* (Fig. 4). The observed daily frequencies of inseminated females did not differ significantly from the values given by the fitted curves (goodness of fit tests gave $G_{(11)} = 13.28$ in *D. littoralis*, $G_{(12)} = 16.36$ in *D. montana*: $p > 0.1$ in both cases). The Gaussian response curve parameter t, which is a measure of the emergence amplitude (range of emergencies is about $4t$; see e.g. Jongman *et al.* 1987) was quite similar for both species: 4.4 for *D. montana* and 4.6 for *D. littoralis*, indicating no large differences in the amplitude of adult emergences. On the other hand, the parameter u, i.e. the day that gives the maximum (see e.g. Jongman *et al.* 1987) for *D. montana* was 25.0 and for *D. littoralis* 29.9 revealing a difference of about five days in the mean times of emergence. To test whether this difference between the species was significant, the emergence data from both species was pooled, and species was also used as an explanatory variable as well (together with the day of emergence) in a logit regression model with a Gaussian response curve. Excluding species variable, this model significantly decreased the explanatory power of the model ($G_{(1)} = 103.26$; $p < 0.001$) and confirmed that the difference in emergence dates between species was significant.

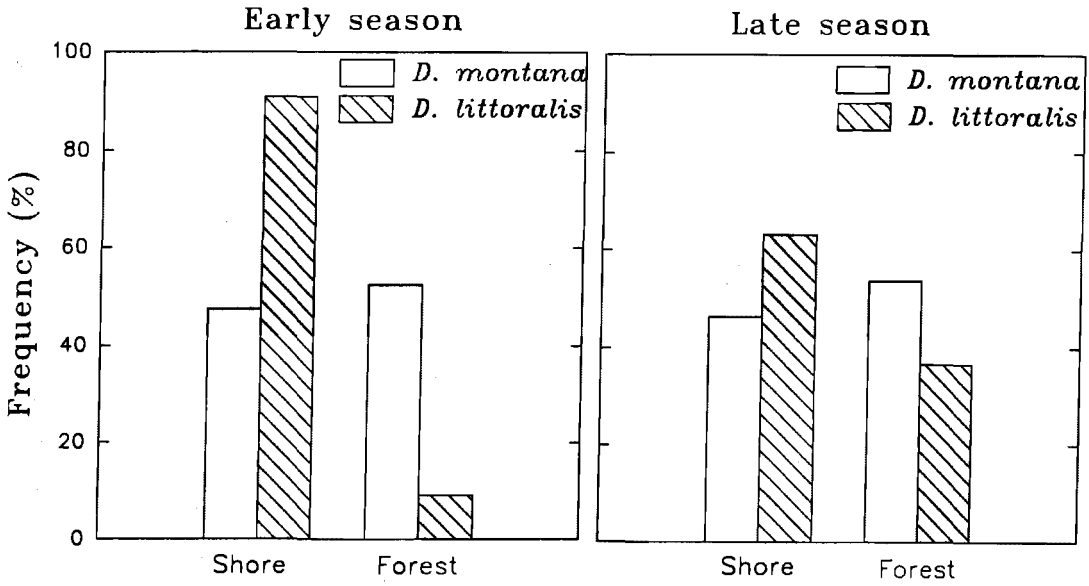

Fig. 3. Percentage of individuals emerging from the two habitats during the two exposure periods. Number of specimens as in Fig. 2.

3.2. Intra-and interspecific aggregation

Because the birch phloem produced a low number of flies in both species, the aggregation pattern of larvae among vials was only analysed for yellow water lily vials. The early exposure period samples did not allow goodness-of-fit tests due to low number of flies emerged, and the data from both periods was combined. To avoid spurious positive covariance between species due to double zero vials (i.e. vials in which both species were absent), these vials were excluded from the analysis (see e.g. Worthen & McGuire 1988, Shorrocks *et al.* 1990).

The larvae appeared to be aggregated among the yellow water lily vials. Distribution of the emerging adults differed significantly from the Poisson distribution in both *D. montana* ($\chi^2_{(26)} = 143.4$; $p < 0.001$) and *D. littoralis* ($\chi^2_{(26)} = 140.1$; $p < 0.001$) (separate tests for the late exposure period gave similar conclusions in both species and were not reported). The intraspecific aggregation parameter (J) was positive in both species, and it was somewhat larger in *D. littoralis* ($J = 2.487$) than in *D. montana* ($J = 0.628$).

The interspecific aggregation parameter was slightly positive ($C = 0.521$), but not statistically significant (Spearman rank correlation: $r_S = 0.040$; $N = 27$; $p > 0.1$), indicating that the vials producing many *D. montana* were not the same as those yielding many *D. littoralis* (see Fig. 5). The interspecific aggregation parameter (C) was smaller than either of the intraspecific aggregation parameters, and the measure of the relative strength of intra- and interspecific aggregation (A) was 2.454, indicating that the effect of intraspecific aggregation on the number of competitors a larva shares a resource with was stronger than the effect of interspecific aggregation.

4. Discussion

The number of flies emerging per vial was low compared with the number of mature females collected in the study site (see e.g. Aspi *et al.* 1993, Aspi & Lankinen 1992). There are several possible reasons for the low number of emerging adults. First, this may reveal that the principal breeding sites of these species are not birch phloem or yellow water lily. However, extensive rearing attempts have been made in the study area, and only the ones used in this study have produced emerging adults. A more probable reason for the low number of emerging adults may be that the females may have

had problems with finding the vials, since the amount of substrate used in the field experiment was rather small. Yet another possibility is that the imitated substrates did not support larval development as well as their natural breeding substrates do.

The observed differences in the adult spatial and temporal distribution of *D. littoralis* and *D. montana* (Lumme *et al.* 1979, Aspi *et al.* 1993) were also reflected in the temporal and spatial occurrence of larvae. With respect to the proximity of water, adults of *D. montana* have a wider niche than *D. littoralis* (Lumme *et al.* 1979, Aspi *et al.* 1993). Correspondingly, the larvae of *D. montana* appeared to be more abundant than *D. littoralis* in the less moist habitats. In northern Finland *D. montana* females tend to copulate about one week earlier than *D. littoralis* females (Aspi *et al.* 1993). The difference in the adult emergence maxima in the present experiment appears to be about the same, *D. montana* emerging about five days earlier than *D. littoralis*.

Some interactions between habitat and the other explanatory variables affecting the species composition among emerged flies were confirmed during the study. The interactions may be due to differences in environmental conditions between the habitats and also between the exposure periods. Krebs & Barker (1992) and Arthur & Cassey (1992) have described how such changes in temperature or relative humidity and wetness of substrate may affect competitive relationships of other closely related *Drosophila* species under laboratory conditions.

The present results confirm that at least two species belonging to this species group (*D. littoralis* and *D. montana*) partially share the same breeding niche, and may be potential competitors. I was not, however, able to show that there is competition between the species. Despite overlapping resources, environmental factors may well keep the population densities at such a low level that there is no competition at the larval stage at all. In fact, competition in *Drosophila* has been demonstrated in only a few cases in natural conditions in the wild (Grimaldi & Jaenike 1984, Atkinson 1985, Jaenike & James 1991).

The level of niche partitioning seems to be low with respect to any of the studied niche dimensions between *D. littoralis* and *D. montana*. However, the estimate for niche overlap using each vial as a different resource category was smaller (0.631) than

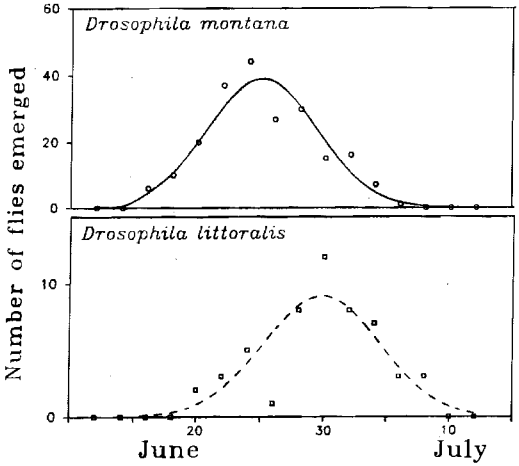

Fig. 4. Number of individuals emerging from the field-kept vials during the season. The solid and broken lines represent the fitted number given by logit regression. Number of specimens as in Fig. 2.

that for separate niche dimensions (0.999–0.909). This may be partly due to random effects, since vials were nested units within the studied niche dimensions. On the other hand, it may also indicate that the egg-laying females may perceive the 'habitat' on a much finer scale than that of forest or river bank. This explanation is also supported by the fact that the probability of the best fitting logit model (including interaction between habitat and substrate, and also an interaction between habitat and exposure period) was low ($p = 0.055$). Accordingly, more detailed studies on the environmental requirements of egg-laying females among boreal *D. virilis* group species are needed.

In their survey of *Drosophila* studies Rosewell *et al.* (1990), Shorrocks *et al.* (1990), and Shorrocks & Sevenster (1995) found that individual species almost without exemption exhibit aggregated distributions, and that associations between species were generally low. However, Worthen & McGuire (1988), Nunney (1990) and Jaenike & James (1991) reported that the numbers of emerging adults are often correlated between species belonging to the same species group.

D. montana and *D. littoralis* belong to the same species group (*D. virilis* species group). However, on the basis of emerging adults the species distributions were aggregated, and the effect of intraspecific aggregation on the number of competitors the lar-

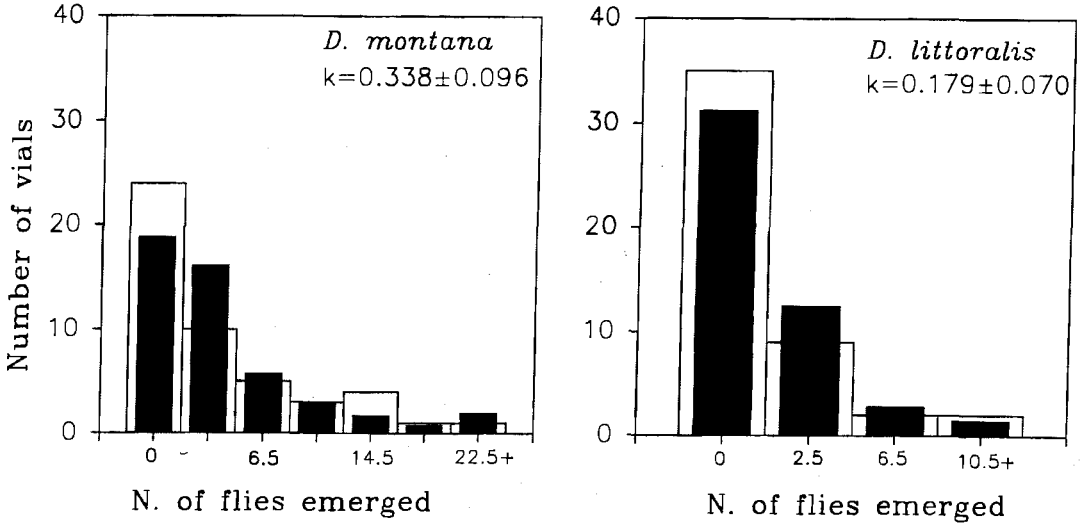

Fig. 5. Association between the numbers of flies emerging from the yellow water lily substrate vials in *Drosophila montana* and *D. littoralis*.

vae shared a resource which appeared to be stronger than the effect of interspecific aggregation. Given that the distribution of the emerging adults represented the original distribution of eggs, the requirements of aggregation models of coexistence seemed to be fulfilled in the present case. This mechanism promotes coexistence of these two species even in a competitive situation.

The observed clumped distribution of individuals within the species over the resource items seems to be problematic, because this can cause food competition among siblings. Several reasons for aggregated distributions of individuals have been suggested. Firstly, clumping can be initially advantageous to larvae (for a survey of advantages, see Stamp 1980): for example, chewing into food item may be more successful in groups. Sjerps *et al.* (1993) have recently suggested a theoretical model, in which clumping is advantageous during the initial growth of larvae, but disadvantageous later. They showed that several factors, like the size of eggs supply and the patchiness of suitable oviposition items, can contribute towards egg clumping.

Secondly, in *Drosophila* the mating behaviour may have some importance on the aggregation of eggs. In general drosophilid mating takes place in fly aggregations on suitable feeding and breeding sites (Spieth 1974, Spieth & Ringo 1983). These aggregations may not be randomly dispersed among the resource items. In *D. virilis* species group, Bartelt *et al.* (1986) have described existence of special aggregation pheromones, which attract both sexes of these species, and may accordingly cause non-random courtship aggregations. Because leaving an aggregation and searching a new breeding site is costly, *Drosophila* females may tend to lay their eggs at the same sites where they have mated. Even though laying eggs in these sites may be costly in terms of intraspecific competition, it may still cost less than leaving the site and possibly losing a suitable feeding or ovipositing resource.

Thirdly, Shorrocks *et al.* (1979; see also Atkinson & Shorrocks 1984, Shorrocks & Rosewell 1987) have proposed a model, in which ovipositing females visit breeding sites randomly, lay eggs at a constant rate while on a site, and have a constant probability of leaving the site. This kind of egg-laying behaviour would lead to independent and aggregated distribution of species among resource items. This was the pattern observed in *D. littoralis* and *D. montana* on the basis of adult emergences. However, it have been questioned whether this mechanism of aggregation can lead to coexistence of the competing species (Green 1986, 1988; Sevenster 1996; see also Shorrocks & Rosewell 1988).

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