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## Aggregated breeding dispersion of *Drosophila* species reared from Cornelian cherries (*Cornus mas*) and plums (*Prunus domestica*).

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Six *Drosophila* species emerged from twelve samples of Cornelian cherries gathered from the lawn under one Cornelian tree at each of two locations. They were compared to *Drosophila* flies from plums. The largest number of species emerging from a cherry was four, and the largest number of flies, all species pooled, was 17. Every large sample was overdispersed, suggesting aggregation. Two methods were chosen for assessing aggregation. The first was to fit a negative binomial distribution to the data, the second to demonstrate density-dependence of dispersion. In view of a model of coexistence (ATKINSON & SHORROCKS, 1984) the data were also checked for independence of dispersion between species. Association cannot be ruled out. Dissociation was prominent in some combinations of paired species.

Keywords: aggregation, dissociation, oviposition, larval performance, *Drosophila*.

### INTRODUCTION

Many species of *Drosophila* breed in a variety of resources (e.g. SHORROCKS, 1982) and often two or more species emerge from a resource item as small as a berry. We examined whether these species compete as they develop and if so, what is the outcome. An aggregation model of coexistence predicts that two species may coexist for a long period despite strong competition under two conditions. They must share an ephemeral and divided breeding resource, and their dispersion over the breeding items must be aggregated independently of each other (e.g. SHORROCKS *et al.*, 1979; ATKINSON & SHORROCKS, 1981, 1984). In a number of papers the model was extended to systems with many species and applied to empirical data from several species (ATKINSON, 1985; SHORROCKS, 1990; SHORROCKS & ROSEWELL, 1987; SHORROCKS *et al.*, 1990).

Here we examine own data against this theory. We reared *Drosophila* flies in September 1990 from Cornelian cherries (Kornelkirsche, samples 4 and 5, BURLA & BÄCHLI, 1991b). We first checked for aggregated breeding dispersion of each species, then for the independence between the species, and thirdly for evidence of competition.

Cornelian cherries were chosen as breeding resources because in a preliminary report they were one of the fruits which yielded the largest number of flies and the most species (BURLA & BÄCHLI, 1991b). Resource partitioning can be ruled out as the cherries are small, but competition for food seems likely. The cherries are present in the fall in very large numbers at many places and can be collected easily. The Cornelian tree is native in Southern Europe and warm parts of Central Europe, where it grows in forests. North of the Alps it is rare in the wild, but common in gardens. We collected the fruit items in gardens, which had the disadvantage that most emerging flies belonged to species common in domestic environments.

A small sample of plums was included to obtain comparable data from the larger plums (Zwetschge, sample 4, BURLA & BÄCHLI, 1991b).

## MATERIAL AND METHODS

*Collection and laboratory work*

Cornelian cherries were collected from the lawn beneath a Cornelian tree in two comparable yards. The Gockhausen site was 100 m from a forest, and the Pfaffhausen site 230 m. Both localities are on the outskirts of Zürich, Switzerland. Ten samples were taken in Gockhausen and two in Pfaffhausen, totalling 886 cherries. In eight of the samples the state of maturity of the fruit was noted. The flesh of ripe fruit is bright scarlet and solid. It then turns pale and soft, and mould may grow on it. A sample of 180 ripe cherries pulled from the twigs failed to produce a single fly. We therefore assume that *Drosophila* females lay eggs only on Cornelian cherries which have fallen.

The number of cherries collected was a small fraction of those on the lawns. Both yards had two Cornelian cherry trees, and others grew in neighbouring yards. The cherries are superabundant from the end of August through mid October. Although we did not apply a scheme of random sampling, we took pains to gather cherries randomly.

The volume of a Cornelian cherry ranged from roughly 1 to 2 cm<sup>3</sup>, and the stone was about a fourth of this. Most of the remainder was pulp, the resource exploited by *Drosophila* larvae.

To compare yields from larger fruit items, 30 fallen plums were collected at the same time in Gockhausen, beneath a small group of domestic plum trees which bordered the road opposite the yard with the Cornelian tree. About half the plums were picked from the gutter, the others from the undergrowth. They all were ripe and had variable amounts of damage. The average volume of an intact plum ranged from roughly 4 to 10 cm<sup>3</sup>.

The fruit was sprayed against mould with a Nipagine solution (30 g of Nipagine was dissolved in 10 ml of ethanol and 15 ml of this solution was added to 1 liter of tap water to produce the spray). Thereafter each fruit item was separately placed in a glass tube on a piece of blotting paper. The tubes were kept in a stock room, at a constant 18 °C, 80 % relative humidity and a LD 12:12 light period. The tubes were inspected every third day for emerged flies. When mould developed on a fruit, it was sprayed again with Nipagine (mixture as above). Flies which hatched late were only included if they could be ruled out as offspring of those which hatched earlier. The flies were preserved in 80 % ethanol for subsequent species and sex identification and measurement. After 40 or more days the fruits were discarded.

*Aggregation*

Aggregated dispersion implies overdispersion. We demonstrate overdispersion in a sample by the ratio V/M (V for variance and M for mean), for the number x of flies emerging from a single fruit. The term (N-1)•V/M is distributed like chi-square with N-1 degrees of freedom.

ROSEWELL *et al.* (1990) used the negative binomial distribution for assessing aggregation in a sample. They computed the maximum likelihood estimate of the parameter k following BLISS & FISHER (1953). We estimated k in the same way, separately by sample, for the two most frequent species.

When computing a goodness of fit chi-square after fitting a negative binomial to a sample, high classes of x (the number of flies emerged from a fruit) are cur-

rently pooled if the expected frequency falls below 1. In doing this, the highest, and most impressive, values of  $x$  are sacrificed, thus weakening subjective evidence for aggregation. The estimate of the parameter  $k$  is strongly influenced by the proportion of those fruits from which no flies emerged ( $x = 0$ ). Typically, this proportion is low in abundant *Drosophila* species, and high in rare ones. Thus, different species cannot be easily compared on the basis of  $k$  alone. SHORROCKS & BINGLEY (1990) showed that the class of  $x = 0$  is heterogeneous. A fruit may be found or not by an egg laying female, and if found, it may be accepted or avoided. We were unable to make this distinction in the present study.

We used the power function  $V = a \cdot M^b$  for demonstrating density dependence of aggregation in a comparison of samples (TAYLOR *et al.*, 1978). In logarithmic form the function becomes a linear regression formula, with  $\log(a)$  as the intercept of the regression line and  $b$  as the slope of it.

### *Independence between species*

We used the Spearman rank correlation to test whether those species which emerged from the same cherry were, on the whole, associated or dissociated. Each species was successively paired with every other species. Using BONFERRONI's rule, significance level becomes 0.005. For a joint evaluation of all samples (13 at most) in each cell in Tab. 8, we considered the ratio between positive and negative correlation coefficients, and used the binomial distribution to assess the probability of the observed ratios occurring by chance.

### *Regression*

Thorax length was entered as a dependent variable in a linear regression to check whether larval crowding had an effect. The numbers of conspecific and of alien flies which hatched from the same cherry were used as independent variables. The analysis was run separately for each species and sex.

## RESULTS

### *General*

*Drosophila* flies emerged from 547 out of 886 Cornelian cherries, a success rate of 61.7 % (Tab. 1). Six species were recorded, one (*D. subsilvestris*) in negligible numbers. *D. melanogaster*, *D. simulans* and *D. immigrans* are domestic species and the other three are wild. The long established species *D. melanogaster* was much less abundant than the latecomer *D. simulans*. *D. subobscura* dominated the wild species. More flies per fruit item were obtained in Gockhausen than in Pfaffhausen (samples 5 and 6), and more from overripe than ripe fruit. It did not seem to matter which day sampling took place between early and late September. Overripe fruit items may be more attractive to egg laying females than ripe ones, perhaps because of a more progressed stage of fermentation, or because they are exposed longer on the ground, with increased probability of becoming infested by *Drosophila* once or several times. The low frequency, or absence, of the domestic species in Pfaffhausen (Tab. 1, samples 5 and 6) is remarkable, as the places are similar in many respects. However assemblages of *Drosophila* species commonly vary a lot from place to place, often for no obvious reason (BURLA & BÄCHLI, 1991a).

Tab. 1 - Survey of raw data. Twelve samples of Cornelian cherries, in chronological order, and one sample of plums. Samples 5 and 6 are from Pfaffhausen, the others from Gockhausen. Columns from left to right: sample number; day in September 1990; N, number of cherries per sample; maturity state of cherries, if noted; N\_y, number of cherries which yielded flies; total number of emerged flies per sample, separate by *Drosophila* species: sim, *simulans*; mel, *melanogaster*; imm, *immigrans*; sub, *subobscura*; obs, *obscura*; ssi, *subsilvestris*.  $\Sigma$ , total number of flies per sample.

sample	date	N	state	N_y	sim	mel	imm	sub	obs	ssi	$\Sigma$
1	3	43	rotten	37	165	5	6	34	6		216
2	3	57	ripe	22	27	2		11	2		42
3	3	43	rotten	34	98	8	6	30	4		146
4	3	57	ripe	15	48			4	13		65
5	8	75		21	1			30	1		32
6	8	75		27	9	2		25	2		38
7	14	68	rotten	50	114	6	1	15	3		139
8	14	68	rotten	49	136	3	3	10	1		153
9	24	100		74	167	2		19		1	189
10	24	100		81	241	6	2	13	3		265
11	24	100		64	115		4	18	3		140
12	29	100		73	238	8	3	16	3	1	269
$\Sigma$		886		547	1359	42	25	225	41	2	1694
plums		20	30		124	8	4	18			154

The number of species which emerged from a Cornelian cherry varied from 1 to 4 (Tab. 2). While most fruits yielded one species only, many yielded more and thus coexistence of larvae of different species was common. The number of flies which emerged from a cherry, all species taken together, is seen in Tab. 3. Many numbers are large, suggesting that the nutritive value of a cherry is high. From six Cornelian cherries a second generation of *D. simulans* emerged 25 or more days

Tab. 2 - Number of fruit items from which S *Drosophila* species emerged, for each sample.

S	number of sample of Cornelian cherries												$\Sigma$	plums
	1	2	3	4	5	6	7	8	9	10	11	12		
0	6	35	9	42	54	48	18	19	26	19	36	27	339	4
1	19	19	14	10	20	25	36	42	58	64	51	58	416	22
2	14	3	18	5	1	1	13	5	16	13	12	12	113	4
3	3		2				1	1	2		4	1	17	
4	1													1

after collection. In one cherry, three *D. simulans* emerged in the first generation and 25 in the second, thus increasing the maximal number of flies emerged from one cherry to 28. Thus not all first generations exhaust the resource.

The number of unexploited cherries is remarkable. Most fruit is typically available only during short periods in a year, and then in such abundance that far from all is exploited.

Only four species emerged from the plums (Tab. 1). No more than two species coexisted (Tab. 2). The largest number of flies which emerged from a plum was 26 (Tab. 3). The dominant species, *D. simulans*, comprised just over 80 % of the total, as in cherries.

Tab. 3 - Number of fruit items from which x *Drosophila* flies emerged (species pooled), for each sample.

x	number of sample of Cornelian cherries												plums
	1	2	3	4	5	6	7	8	9	10	11	12	
0	6	35	9	42	54	49	18	19	26	19	36	27	5
1	4	8	9	6	14	20	18	15	30	15	29	19	7
2	5	9	6	2	4	5	8	13	19	17	18	14	6
3	5	5	4	4	2	1	10	8	7	22	10	10	2
4	3		2	3	1		7	5	5	11	1	8	2
5	5		1	1		1	1	3	6	5	4	6	
6			2				4	1	2	5		7	1
7	2		10					1	3	3		3	
8	7		2				1		2	1			
9	1		1					1		1	1	1	1
10			1								2		1
11			1				1	1		1		1	2
12	2										1		
13	1							1			2		
14	1		1										1
15													
16													
17	1												
...													
25													1
26													1

#### Assessing aggregated dispersion

The number of flies which emerged from a cherry is listed for the two most frequent species in Tab. 4 and 5, and for three rare ones in Tab. 6. Fifteen frequency

arrays were considered sufficiently long for estimating the parameter  $k$  and fitting a negative binomial distribution. The value of  $k$  was lower than 1 in 11 out of the 15 arrays, demonstrating aggregated distribution. The fit was not satisfactory in four frequency arrays (samples 4 and 11 in Tab. 4 and samples 2 and 3 in Tab. 5). Seve-

Tab. 4 - Number of fruit items which yielded  $x$  specimens of *D. simulans*, for each sample. The total number of fruit items per sample is given in Tab. 1. M, mean; V, variance; V/M, variance ratio; bold numbers indicate values significantly larger than 1;  $k$ , parameter of the negative binomial distribution;  $X^2$ , goodness of fit chi-square from fitting a negative binomial distribution; bold numbers indicate fit at  $p < 0.05$ . In sample 4 the Chi-square was computed on the basis of  $k_1$  (BLISS & FISHER, 1953).

x	number of sample of Cornelian cherries												plums
	1	2	3	4	5	6	7	8	9	10	11	12	
0	12	42	15	39	74	70	25	22	31	19	42	35	13
1	8	8	9	5	1	2	20	15	32	17	33	15	3
2	3	3	5			2	6	12	15	21	13	16	2
3	3	3	5	9		1	6	8	6	21	5	5	2
4	3	1	1	4			5	3	5	10	3	8	2
5	1		1				1	2	5	3	2	6	2
6	1		1				2	1	2	5		8	
7	4		3					2	2	1	1	2	
8	2		2				2		2	1			
9									1		1	1	
10	1								1		1	2	1
11	1							1				1	2
12	2		1						1		1	1	
13	1												
14													
15													1
16													
17	1												
...													1
21													
...													1
25													
M	3.84	0.47	2.28	0.84	0.01	0.12	1.68	2.00	1.67	2.41	1.15	2.38	4.13
V	19.4	0.9	8.23	1.96	0.01	0.24	4.97	6.27	3.74	4.22	2.92	7.75	42.5
V/M	<b>5.05</b>	<b>1.89</b>	<b>3.62</b>	<b>2.32</b>	1.00	<b>2.02</b>	<b>2.96</b>	<b>3.14</b>	<b>2.24</b>	<b>1.75</b>	<b>2.5</b>	<b>3.26</b>	10.3
k	0.70	0.40	0.77				0.92	1.02	1.41	3.18	1.17	0.82	0.34
$X^2$	<b>16.0</b>	<b>1.89</b>	<b>12.2</b>	28.8			<b>12.8</b>	<b>8.73</b>	<b>7.64</b>	<b>8.38</b>	63.6	<b>14.1</b>	<b>30.6</b>

ral short arrays suggest that Poisson distributions would fit them. A satisfactory fit was computed in six arrays from Table 5. However, in all of them the observed frequency of class  $x = 1$  was lower than expected, while in the class with the highest number of  $x$  the observed frequency was higher than expected. Hence, it appears that those samples were just too small to reject the hypothesis of randomness, and thus are considered irrelevant.

The fit by a theoretical distribution is considered significant if the value of  $X^2$  is lower than a critical  $\chi^2$  looked up in a table with  $p = 0.05$  and the respective degree of freedom (df). df is equal to  $N-3$  in a negative binomial distribution and  $N-2$  in a Poisson distribution for an array with  $N$  classes ( $x = 0, 1, \dots$ ).

Tab. 5 - Number of fruit items which yielded x specimens of *D. subobscura*. Second row from bottom: goodness of fit chi-square from fitting a Poisson distribution (Pd); bold numbers indicate fit at  $p < 0.05$ . Otherwise as in Tab. 4.

x	number of sample of Cornelian cherries												plums
	1	2	3	4	5	6	7	8	9	10	11	12	
0	24	50	27	53	55	54	58	63	83	89	86	86	20
1	13	4	9	4	13	18	6	2	15	9	10	12	6
2	2	2	3		5	2	3	1	2	2	4	2	4
3	1	1	1		1	1	1	2		2	4	2	
4	1		3		1								
5	2												
M	0.79	0.19	0.70	0.07	0.40	0.33	0.22	0.15	0.19	0.13	0.18	0.16	0.47
V	1.65	0.34	1.36	0.07	0.62	0.36	0.35	0.34	0.2	0.16	0.23	0.18	0.53
V/M	<b>2.08</b>	<b>1.75</b>	<b>1.95</b>	0.95	1.55	1.08	<b>1.60</b>	<b>2.29</b>	1.03	1.19	<b>1.28</b>	1.10	1.14
k	0.83	0.19	0.63		0.66		0.27						
$\chi^2$ Pd	<b>6.23</b>	7.53	9.45		<b>6.31</b>	<b>1.67</b>	7.86	13.7	<b>0.21</b>	<b>2.66</b>	6.94	<b>0.96</b>	
$\chi^2$ nb	<b>4.61</b>	7.63	6.07		<b>0.81</b>		<b>0.79</b>						

The density dependence of aggregation is seen in Fig. 1. As expected, the log of the variance (V) increases linearly with the log of the mean (M). The 24 samples (12 per species) seem to almost fit into a common relationship, suggesting that these

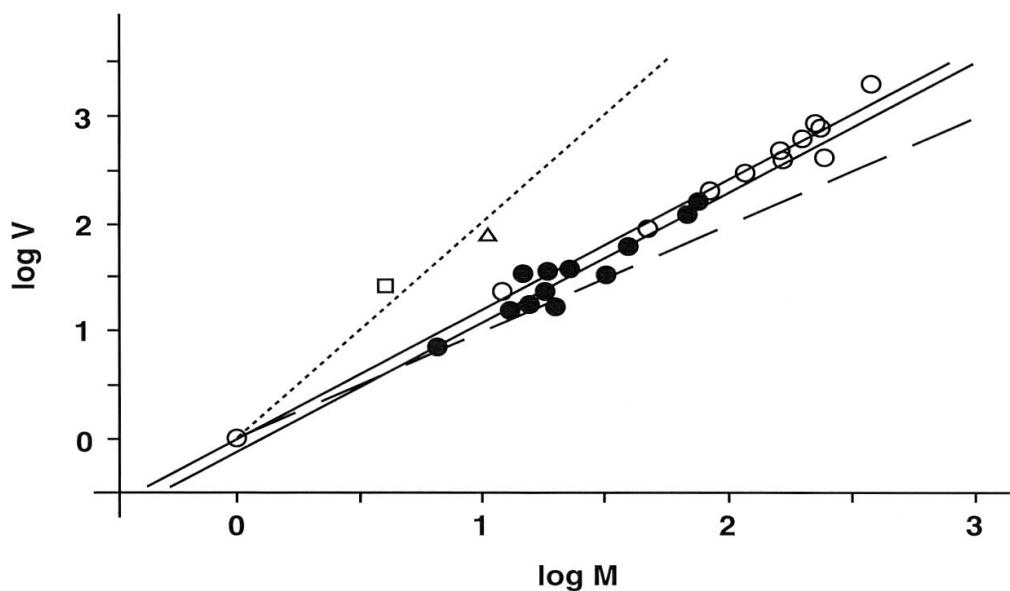


Fig. 1 - Linear regression of log variance (V) on log mean (M) after TAYLOR *et al.* (1978), for *D. simulans* (open circles) and *D. subobscura* (solid circles). The functions are:

$$\begin{aligned} \log V &= 0.003 + 1.201 \cdot \log M \text{ in } D. simulans, \text{ and} \\ \log V &= -0.143 + 1.222 \cdot \log M \text{ in } D. subobscura. \end{aligned}$$

The respective regression lines are close to each other and almost parallel. The slope of each is larger than 1,  $p < 0.001$ . Each circle stands for a sample of Cornelian cherries. Isolated square: *D. simulans* reared from plums. Isolated triangle: *Chymomyza amoena* reared from chestnuts and acorns (BURLA & BÄCHLI, 1992). Two reference lines, one with slope  $b = 1$  (hatched) and another with  $b = 2$  (stippled), are drawn.

species have the same, or a similar, spatial behaviour. Although both slopes are significantly larger than 1, they are smaller than most of those recorded for other species (TAYLOR *et al.*, 1978), possibly because they relate to small, homogeneous samples. Slopes computed from pooled samples may be larger (SEVENSTER, 1992). Another cause could be the small size of the Cornelian cherries, which could have an effect on female oviposition behaviour, or could lead to food limitation. The value from the sample of the larger plums, indicated by an empty square in the plot, is clearly isolated from the samples of the cherries.

Subjective evidence of aggregation is obtained from the four *D. immigrans* reared from plums (Tab. 6). They jointly emerged from a single plum (together with 21 *D. simulans*).

Tab. 6 - Number of fruit items which yielded x specimens of the less abundant species *D. melanogaster*, *D. immigrans* and *D. obscura*. All samples which yielded *D. melanogaster* are mentioned. Samples of the other two species with fewer than 2 specimens per Cornelian cherry were omitted. Two columns refer to species reared from plums.

x	D. melanogaster sample number, Cornelian cherries										plums	D. immigrans cherries			plums	D. obscura cherries		
	1	2	3	6	7	8	9	10	12	1		2	4	1		3	11	
0	38	55	38	73	62	66	98	95	94	29	37	55	46	29	37	37	96	
1	5	2	2	2	6	1	2	4	4		1		4		3		1	
2					3		1		2		1	1	2			1		
3											1				1		1	
4														1				
5										1		1						

Tab. 7 - Number of Cornelian cherries yielding the different combinations of *Drosophila* species in each sample.

sample	number of Cornelian cherries yielding:							3 species					4 species															
	1 species	2 species	3 species	4 species	mel	sim	imm	sub	obs	ssi	mel	mel	sim	sim	sim	sim	sim	sim	sim	sim	sim	sim	sim	sim	sim	mel	imm	sub
1	1	12	5					1		1	1	10	2		1	1	1	1	1							1		
2		13	5	1				1	1		1	1																
3	1	10	1	2				3				13	1	1		1												
4		4	3	3								1		4														
5			19	1								1																
6	1	4	19	1				1					1															
7		32	5					4	1	1	4	2																
8		41	1					1			3	1																
9	1	54	3	1				1			14																	
10		64						3		1	8	1																
11		45	5								1	9	3															
12	1	49	1	5	1	1		3		2	6	1																
$\Sigma$	5	328	1	71	9	2		18	3	6	69	15	2			3	4	3	5	2						1		
plums		14		7				1		1	3																	

*Testing for independence of dispersions*

Most cherries yielded only one *Drosophila* species (left part of Tab. 7), suggesting independence, if not dissociation, between species. Fewer cherries yielded 2, 3 or 4 fly species (other three parts of Tab. 7).

The correlation coefficients between paired species are given in Tab. 8. A positive coefficient indicates association, a negative one dissociation. In pairwise com-

Tab. 8 - Spearman rank correlation coefficient  $r$  for pairs of species (10 large cells), and in each cell for each sample (left column of numbers). Coefficients differing from zero at  $p < 0.005$  are marked with an asterisk.

<i>D. simulans</i>	1	-0.004				
	2	-0.195				
	3	0.133				
	4	-0.460				
	7	0.108				
	8	0.335				
	9	-0.025				
	10	0.084				
	11					
	12	0.151				
	plums	0.284				
<i>D. immigrans</i>	1	0.360	1	0.003		
	2		2			
	3	0.134	3	-0.029		
	4		4			
	7	-0.055	7	0.038		
	8	0.477*	8	0.290		
	9	0.094	9			
	10	-0.041	10	0.220		
	11		11	-0.108		
	12	-0.064	12	-0.157		
	plums	-0.040	plums	0.176		
<i>D. subobscura</i>	1	-0.139	1	-0.485*	1	-0.061
	2	0.064	2	-0.731*	2	
	3	-0.361	3	-0.091	3	-0.189
	4	-0.208	4		4	-0.536
	7	-0.010	7	-0.547*	7	-0.074
	8	-0.073	8	0.091	8	0.276
	9		9	-0.127	9	
	10	0.062	10	-0.049	10	0.163
	11		11	-0.259	11	0.110
	12	0.100	12	-0.249	12	-0.104
	plums	-0.154	plums	-0.590	plums	-0.154
<i>D. obscura</i>	1	-0.114	1	-0.005	1	-0.100
	2	-0.073	2	-0.269	2	
	3		3		3	
	4		4		4	
	7	0.163	7	-0.100	7	-0.038
	8	-0.031	8	-0.167	8	-0.031
	9		9		9	
	10	0.285	10	-0.016	10	-0.026
	11		11	-0.031	11	-0.041
	12	-0.064	12	-0.052	12	-0.044
	<i>D. melanogaster</i>	<i>D. simulans</i>	<i>D. immigrans</i>	<i>D. subobscura</i>		

parisons of domestic species there is just one sufficiently significant coefficient, between *D. melanogaster* and *D. immigrans*, in sample 8. As it is the only case out of 26 comparisons of two domestic species, there is very little evidence for association. On the other hand, dissociation is prominent in the comparison of *D. simulans* and *D. subobscura*. In the respective cell the coefficient is significantly smaller than zero in three out of ten samples. There are 9 negative coefficients obtained from 10 samples. Using a binomial distribution and assuming equal proportions of both signs, the probability of 9 : 1 occurring is less than 0.01. The sign test also provides evidence of dissociation between *D. simulans* and *D. obscura*, *D. immigrans* and *D. obscura* as well as *D. subobscura* and *D. obscura*, at  $p = 0.01, 0.02, 0.06$ , respectively. Hence, dissociation occurs between wild and domestic species, and among wild species.

Two samples involving 12 out of the 14 specimens of *D. subobscura* reared from plums contribute subjective evidence of dissociation: four plums yielded just one of them (and no other species), four other plums just two. Also, each of the two specimens of *D. subsilvestris* emerged from a cherry alone.

#### *Effects of crowding on larval performance*

Two or more larvae exploiting the same Cornelian cherry might grow into smaller adults than those laid alone. Also, the sex ratio might differ from 1 : 1 if the two sexes are not equally resistant to crowding. If either of these effects can be demonstrated, it would provide evidence for harmfulness of crowding.

In 23 out of 28 regressions of thorax length on density the slope was negative, thus the thorax of the fly is shorter as more flies emerge from the same cherry. Only six out of the 23 negative slopes were significantly lower than zero. However, none of the five positive slopes was significantly larger than zero. In a binomial distribution, the numeric ratio of 23 : 5 is expected to occur in less than 1 % of the trials, assuming both signs are equally probable. It might be wrong to include very small slopes into the comparison, although some differ significantly from zero. If we only consider the slopes with absolute values larger than 0.1, the ratio between the numbers of negative and positive signs becomes 17 : 1. This, too, allows us to reject the hypothesis of equal probability. Hence, larval crowding decreases adult body size. This is more convincing in large than in small cherry samples, and more in plum than in cherry. Twelve out of 23 negative slopes can be attributed to intraspecific effects, eleven to interspecific. However, five out of the six significant instances involve effects of alien flies, and only one such instance involves effects of conspecific flies.

The data fail to show a consistent effect of crowding on sex ratio. Summed over all samples, there were 705 female and 578 male *D. simulans* counted, representing a proportion of 55 % females. There were 23 female and 15 male *D. melanogaster*, representing 61 % females. The sexes in the remaining species were more or less equally frequent. The two most extreme ratios of females to males in a single cherry were 10 : 2 and 0 : 6, both *D. simulans*. The most extreme ratio for *D. subobscura* was 0 : 5. Sex ratio did not appear to be affected by the presence or absence of another species in the same fruit. Nor was it affected by the number of conspecific flies hatching from the fruit. Similar inconsistencies were seen in other species.

#### *Parasitoid wasps*

The only other insects emerging from the fruits were 32 braconids, *Asobara tabida* NEES, and 53 cynipids, *Leptopilina heterotoma* (THOMSON). The former emer-

ged from 22 cherries and the latter from 24. There were three instances of both species emerging from a single cherry. The number of days which elapsed between collecting a cherry and emergence of a wasp, ranged from 22 to 38 for the braconids (mode 25) and 22 to 43 for the cynipids (mode 33). The frequency distribution of emerged wasps per day within these ranges was much narrower in the latter than in the former.

Six out of the 46 fruits which yielded wasps also yielded a fly. A *D. subobscura* and a braconid emerged from each of three cherries, a *D. subobscura* and a cynipid from another. A *D. simulans* and a cynipid emerged from one cherry and a *D. simulans* and two braconids from another.

#### DISCUSSION

The analysis of our data suggests the following:

- Aggregation seems to be the rule, but becomes significant only in abundant species, a minority in the wild.
- The frequency dependence of aggregation seems to be about the same in *D. simulans* and *D. subobscura*, although the former is domestic and the latter wild, and although the latter is much less frequent in domestic habitats than the other.
- Associated dispersion between coexisting species cannot be ruled out entirely.
- Dissociated dispersion between species was rather common.

Aggregated dispersion of the present type might have several causes (e.g. BLISS & FISHER, 1953, ATKINSON & SHORROCKS, 1984). Contagious oviposition is one. According to ATKINSON & SHORROCKS (1984), females lay eggs in clutches. KÜNZLI (1986, see BURLA *et al.*, 1987) watched female *D. subobscura* laying eggs on Deadly Nightshade fruit (*Atropa belladonna*) exposed in an observation chamber. Females spent at least three minutes on a fruit item. They often stayed on the side of the fruit item after laying an egg on it and chased other females away when they approached. Females were seen to lay between one and five eggs on a fruit item before they moved on. Only then would other females add eggs to the same item. A fruit item appears to be more attractive the more eggs it already contains. Egg clusters are commonly derived from more than one female. The observations provide evidence that females choose breeding items and stick to this preferred site. They also provide evidence for contagious oviposition. This also explains why not all fruit items in a patch are equally exploited for breeding, even if all are in the same state of maturity. Another cause of aggregated breeding dispersion might be unequal fruit quality. ATKINSON & SHORROCKS (1984) mention this but assign little importance to it. However, PFAENDLER (1984, see BURLA *et al.*, 1987) observed that the number of eggs laid on a fruit item by a group of female *D. subobscura* depended on its state of maturity and decay. In nature it also depends on the presence and accessibility of a fresh humid wound in the fruit item left after it falls from the pedicel. Female *Drosophila* in this study were unable to cut through an intact fruit skin. While oviposition by *D. melanogaster* seemed to be encouraged by a rough surface on the culture medium in the laboratory (ATKINSON, 1983), it is doubtful whether this roughness would similarly affect free-living species laying eggs on Cornelian cherries.

The highest slope in the logarithm of the power function was 1.83 when computed from *Drosophila* (ROSEWELL *et al.*, 1990), but is only about 1.2 in our data. Equally low b values were reported for "field experiments" (SHORROCKS & ROSE-

WELL, 1987, ROSEWELL *et al.*, 1990). According to HANSKI (1989), a low  $b$  value suggests "mortality due to intraspecific competition in the most abundant species".

There is association between species if particular fruit items are attractive to more than one species, or if oviposition in one species stimulates other species. This may happen if species have similar preferences, and at the same time tend not to avoid each other.

Dissociation may have several causes. It may result from unequal preferences of species when they choose breeding sites. It may also be caused by avoidance of fruit items already occupied by another species. Alternatively, the presence of larvae of one species might be detrimental to larvae of coexisting ones. It is likely that selection favours avoidance between potentially competing species.

Reduction of body size under crowding, as demonstrated in the present study, was also observed, among others, by KÜNZLI (1986), ATKINSON (1979), GRIMALDI & JAENIKE (1984) and KREBS *et al.* (1992). It could be an effect of competition. The present study did not assess larval mortality, but KÜNZLI (1986) observed that the proportion of flies which emerged from a fruit diminished with the number of eggs deposited on it, and could drop to less than 10 %.

The results support the view that competition is a significant factor in spatial dispersion. The issue has been much debated. For instance, SHORROCKS *et al.* (1984) and ATKINSON (1985) attribute little importance to competition as long as breeding dispersions are aggregated. HANSKI (1981) insists on the contrary. HUGHES (1980) showed that food limitation is not a necessary condition for competition.

Strong aggregation may be advantageous even in the absence of competing species of the same genus. Evidence for this was obtained by rearing *Chymomyza amoena* from chestnuts and acorns collected from forest sites where they were abundant (BURLA & BÄCHLI, 1992). In Switzerland, *C. amoena* is almost the only drosophilid to exploit these nuts for breeding. There were 575 unproductive nuts, but 12 yielded 1 *C. amoena*, 2 yielded 2 flies, 2 yielded 3 flies, 2 nuts yielded 9 flies and 1 yielded 14 flies. The corresponding  $k = 0.02$  indicates very strong aggregation. The *C. amoena* data are represented by a triangle in Fig. 1. However, they are pooled from many samples, which may lead to overinterpretation of aggregation (SEVENSTER, 1992).

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#### ZUSAMMENFASSUNG

In zwei Vororten von Zürich wurden unter einem Baum von *Cornus mas* insgesamt 886 Kornelkirschen aufgelesen. Aus diesen schlüpften im Zuchtraum innert eines Monats 547 Imagines aus 6 Arten von *Drosophila*. Die Häufigkeitsverteilung von Früchten, die, getrennt nach *Drosophila*-Art,  $x = 0, 1, 2, \dots$  Fliegen ergaben, folgte bei den zwei häufigsten Arten einer negativen Binomialverteilung. In der logarithmierten "power function" (TAYLOR, 1978) streuen die Proben bei beiden Arten eng um eine Gerade, deren Steigung von etwa 1.2 gesichert grösser als 1 ist. Beide Verfahren belegen aggregierte Dispersion.

Unser Befund passt zu einem theoretischen Modell, wonach zwei oder mehr Arten trotz Konkurrenz nebeneinander bestehen können, falls bei jeder Art die Häufigkeitsverteilung ihrer Nachkommen über diskrete und vergängliche Ressourcen aggregiert ist, unabhängig von den anderen Arten (ATKINSON & SHORROCKS, 1981, sowie folgende Schriften dieser Autoren und ihrer Mitarbeiter). Während unsere Daten aggregierte Verteilungen enthalten, war die Unabhängigkeit zwischen Arten nicht durchwegs nachweisbar. Ausser Andeutungen von Assoziation gab es Fälle von Dissoziation.

Aggregierte Dispersion dürfte vom Eilegverhalten beeinflusst oder hervorgebracht sein. Aus frühe-

ren Beobachtungen im Laboratorium wissen wir, dass Weibchen von *D. subobscura* bis zu 5 Eier auf eine Frucht abgeben und andere Weibchen noch Eier hinzufügen. Wenn sich verschiedene Arten bei der Eiablage meiden, entsteht Dissoziation, sonst Assoziation.

Es gibt zwei Hinweise auf mögliche Konkurrenz zwischen Larven, die sich gemeinsam in einer Frucht entwickeln. Zum einen war die Körpergrösse (gemessen wurde die Thoraxlänge) im Durchschnitt desto kleiner, je mehr Fliegen aus einer Frucht schlüpften. Zum anderen lässt die geringe Steigung der Regressionsgeraden in Fig. 1 vermuten, dass Konkurrenz im Spiel war.

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