

Breeding Site Specificity in the Domestic Species of *Drosophila*

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Summary. The emergences of domestic *Drosophila* species from fruits and vegetables in a market are analysed by partitioning the species diversity. Confidence limits are determined for the components of diversity.

Despite some coexistence of different species within the same breeding site, ecological differences between them are revealed. Partitioning of the breeding sites is more important than partitioning of the season. *D. melanogaster*, *D. simulans*, and *D. subobscura* are specialised on fruits and *D. busckii* on vegetables. *D. immigrans* and *D. hydei* are less specialised. The coexistence is explained by reference to ecological theory.

Introduction

Carson (1971) has suggested that 'the major specificity of the ecology of *Drosophila* relates to the niche in which the female of the species deposits her eggs'. Unfortunately, statements about the unspecialised use of breeding sites by the domestic species have been based upon the range of food items used rather than their frequency of use (Shorrocks, 1977). This paper examines more detailed quantitative records obtained from a fruit and vegetable market 4 km southeast of the centre of Leeds.

The market consists of four large unheated buildings, each 75 m × 35 m in area, separated by roadways and surrounded by an extensive open space.

Large quantities of discarded fruits and vegetables are always present around the market buildings and the adults of seven species of *Drosophila* are trapped in the area (Atkinson, in prep.). Six species can be described as cosmopolitan domestic species, these being *Drosophila busckii* Coquillet, *D. funebris* (Fabricius), *D. hydei* Sturtevant, *D. immigrans* Sturtevant, *D. melanogaster* Meigen, and *D. simulans* Sturtevant. The seventh, *D. subobscura* Collin, is a common woodland species in Britain (Shorrocks, 1975) but is often found in domestic habitats (Basden, 1954; Shorrocks, 1974).

Methods

Each week from 28.4.1976 to 27.10.1976 a sample of discarded fruits and vegetables from the market was brought back to the laboratory. The interiors of the market buildings were not sampled because regular access was difficult; therefore, the sampling was confined to the open space within 20 m of the buildings. Random sampling of the breeding sites was impracticable owing to the large amount of material, so a representative sample was achieved by bringing in at least one item of each fruit or vegetable species found and, in the case of the more common species, several items in different stages of decay. When the collection was returned to the laboratory the items were placed separately in glass jars with the tops covered with nylon fabric. The jars were then placed in an outdoor insectary and were examined at least three times a week. Any emerged flies were removed and identified.

Results

A total of 437 potential breeding sites were investigated, of which 180 yielded *Drosophila*. The numbers of *Drosophila* emerging from each species of breeding

Table 1. Numbers of each *Drosophila* species emerging from each species of breeding site

Breeding sites	<i>D. busckii</i>	<i>D. funebris</i>	<i>D. hydei</i>	<i>D. immigrans</i>	<i>D. melanogaster</i>	<i>D. simulans</i>	<i>D. subobscura</i>	Total flies	Number of breeding sites
Apple <i>Malus pumila</i>	1		1	6	1429	290	162	1889	75
Apricot <i>Prunus armeniaca</i>					51	20		71	5
Aubergine <i>Solanum melongena</i>				20				20	5
Banana <i>Musa</i> sp.				17	237	65	35	354	27
Cabbage <i>Brassica oleracea</i>	1	1	2					4	1
Carrot <i>Daucus carota</i>				7	3	1		11	4
Cauliflower <i>Brassica oleracea</i>	74							74	4
Celery <i>Apium graveolens</i>	1	4						5	3
Courgette <i>Curcubita pepo</i>	13			12				25	4
Cucumber <i>Cucumis sativa</i>		1		2				3	5
Grapefruit <i>Citrus paradisi</i>			14	75	490	2	28	609	15
Lemon <i>Citrus limon</i>	4	7	26	60	218	7	14	336	32
Lettuce <i>Lactuca sativa</i>	41		33	47			3	124	5
Mango <i>Mangifera indica</i>			11		3			14	1
Marrow <i>Curcubita pepo</i>						3		3	2
Melon <i>Cucumis melo</i>	15		124	39	97	4		279	15
Onion <i>Allium cepa</i>				29	5	32	13	79	12
Orange <i>Citrus aurantium</i>	1	2	35	151	789	73	31	1082	59
Peach <i>Prunus persica</i>			1	27	606	64	5	703	31
Pear <i>Pyrus communis</i>					23	65	9	97	22
Plum <i>Prunus domestica</i>				7	315	62	43	427	47
Potato <i>Solanum tuberosum</i>	24							24	9
Strawberry <i>Fragaria</i> sp.					4			4	6
Tomato <i>Solanum lycopersicum</i>			17	87	127	32	30	293	47
Yam <i>Dioscorea</i> sp.			131		163			294	1
Total	175	15	395	586	4560	720	373	6824	437

Table 2. Numbers of each *Drosophila* species emerging from all breeding sites collected each month

Month	<i>D. busckii</i>	<i>D. funebris</i>	<i>D. hydei</i>	<i>D. immigrans</i>	<i>D. melanogaster</i>	<i>D. simulans</i>	<i>D. subobscura</i>	Total flies	Number of breeding sites
April	0	0	0	0	0	0	0	0	14
May	24	0	0	0	262	39	3	328	48
June	76	4	29	28	1974	244	61	2416	83
July	73	1	259	362	815	129	57	1696	77
August	2	5	89	65	713	199	70	1143	83
September	0	5	18	122	796	109	25	1075	75
October	0	0	0	9	0	0	157	166	57
Total	175	15	395	586	4560	720	373	6824	437

site are shown in Table 1. In Table 2 the emergences are classified according to the month in which the breeding site was brought into the laboratory.

Niche Dimensions

The relative importance of different breeding sites and seasonal changes to the community structure was investigated by partitioning the species diversity (Levins, 1968; Shorrocks, 1975). Diversity was measured using the Shannon and Weaver (1949) formula,

$$H = - \sum_{i=1}^n p_i \ln p_i$$

where p_i is the frequency of species i . If a component of diversity, j (e.g., season), is divided into n categories (e.g., months), then the between-category contribution to diversity is equal to the total diversity minus the within- or mean-category diversity.

$$H_{\text{between}} = H_{\text{total}} - \frac{1}{n} \sum_{j=1}^n H_n = \frac{1}{n} \sum_{j=1}^n (H_{\text{total}} - H_n).$$

When dealing with individual breeding site items as categories, p_i was known and the Shannon and Weaver formula could be used. For other components of diversity, such as breeding site species or season, p_i could only be estimated from a sample. In these circumstances a modified formula (Hutcheson, 1970) was used,

$$H = - \left(\sum_{i=1}^n \hat{p}_i \ln \hat{p}_i \right) + (s-1)/2N$$

Table 3. Niche analysis for *Drosophila* emergences

Niche component	<i>H</i>	95% confidence limits
Within-breeding-site items	0.38	0.33–0.43
Between-breeding-site items, within species	0.23	0.17–0.28
Between-breeding-site species	0.37	0.25–0.49
Total between breeding sites	0.60	0.39–0.80
Between months	0.22	0.14–0.30
Apparent interaction (breeding sites and months)	-0.05	
Total	1.15	

where \hat{p}_i is the proportion of species i in the sample, s is the number of species being sampled, and N is the sample size.

Since both between- and within-category diversities are means, standard errors of these means can be computed. To use these standard errors to estimate the significance of components of diversity we need to know the distribution of H . Bowman et al. (1971) have shown theoretically that the distribution of H is asymptotically normal and Heip and Engels (1974) have demonstrated empirically that the diversities of samples of copepods as measured by H are normally distributed.

Table 3 shows the analysis for niche components of *Drosophila* species. The smallest pure component was between months, which was significantly smaller than the within-breeding-sites component at the 5% level ($t=2.3$) and was also smaller than the total between-breeding-sites component at the 1% level ($t=4.7$). Partitioning of the season is evidently less important in the community than partitioning of breeding sites.

The total between-breeding-site diversity is made up of a larger component due to partitioning of breeding site species and a smaller component due to the partitioning of different items of the same species, and the difference between them is not significant. There are, then, differences between the items, possibly in the state of decay, as well as differences between the species, which lead to exploitation by a range of *Drosophila* species.

The within-breeding-site component of diversity is a measure of coexistence. It makes a significant contribution to the total *Drosophila* species diversity, indicating that partitioning of the breeding sites is not rigorous enough to entirely separate the species.

The term labelled apparent interaction in Table 3 is the sum of two terms, the real redundancy and the real interaction between season and breeding site. The magnitude of these two terms cannot be determined in this type of analysis. The real redundancy is a positive term that measures the non-orthogonality of dimensions and the real interaction is a negative term that measures the extra diversity accounted for by taking both dimensions together. Real redundancy in this analysis would mean that different breeding sites were found in different months. Real interaction would mean that the *Drosophila* species were using different breeding sites in different months. The sum of the two

terms in this case is negative and so there is a small apparent interaction. If the sum were positive there would be apparent redundancy.

The magnitude of the real redundancy can be estimated by carrying out a diversity analysis on breeding site species in which the between-months component of diversity is a measure of non-orthogonality. When this was done the total breeding site species diversity was 2.72 of which only 0.07 or 2.5% was between months. Thus most breeding sites occur in all months and the two dimensions are effectively orthogonal. Since the real redundancy is very small and the apparent interaction in Table 3 is very small then the real interaction must also be small. The *Drosophila* species do not then change their breeding sites significantly during the season.

Breeding Sites

The breeding site species were compared with respect to *Drosophila* species emerging using Raabe's percentage similarity (Southwood, 1966). Percentages for each breeding site species were weighted according to the number of *Drosophila* emerging and combined to give the dendrogram in Figure 1.

There are two main groups of breeding sites revealed by the analysis, a group of vegetables (lettuce-celery in Fig. 1) and a group containing all the fruits but also some vegetables (apple-onion). Within the second group some taxonomically related breeding sites are closely associated in the analysis. The three *Prunus* species plum, peach, and apricot are very similar in their *Drosophila* fauna as are the three *Citrus* species, lemon, orange, and grapefruit. The second group (apple-onion) can be divided again into a group of nine closely associated fruits (apple-strawberry) and a group of mostly vegetable-like breeding sites (tomato-onion), which do not form a group in the analysis but will be considered separately. The justification for this is that none of these vegetable-like breeding sites seems to undergo the alcoholic fermentation characteristic of fruits. Fruits have a low pH that favours the growth of yeasts rather than the bacteria that are the common spoilage agents of vegetables. Pears are the only fruits that commonly undergo bacterial spilage, and these are associated with veget-

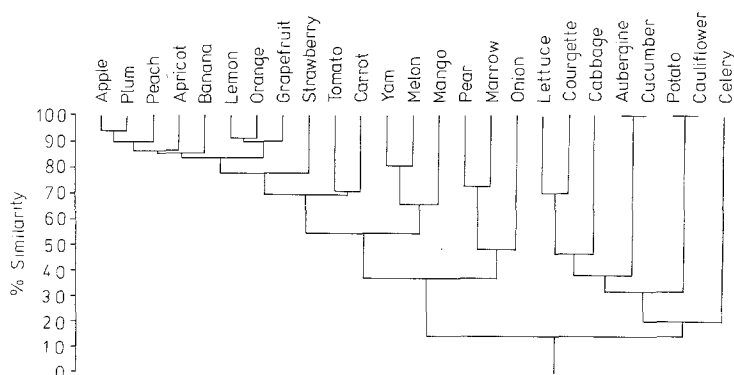


Fig. 1. Dendrogram of breeding sites clustered according to percent similarity of *Drosophila* emerging

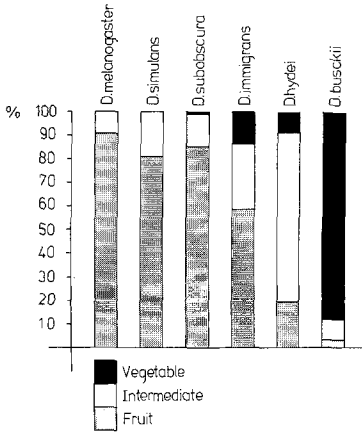


Fig. 2. Percentage of *Drosophila* of each species emerging from the three breeding site groups

able-like breeding sites in the analysis (Jay, 1970). The breeding sites are divided, then, into three groups; fruits (apple-strawberry), vegetables (lettuce-celery), and an intermediate group (tomato-onion). *D. funebris* is excluded from the following analyses because too few data were available.

Figure 2 is a histogram showing the proportion of each *Drosophila* species emerging from the free different breeding site groups. It appears that *D. melanogaster*, *D. simulans*, and *D. subobscura* are specialists on fruit, *D. busckii* is a specialist on vegetables while *D. immigrans* and *D. hydei* are intermediate.

The degrees of specialisation of the species were examined in more detail by computing their niche breadths on breeding sites. The niche breadths were measured using a derivation of Simpson's index (Levins, 1968; Shorrocks, 1974).

$$B_i = \frac{1}{n \sum_{h=1}^n p_{ih}^2}$$

where p_{ih} is the proportion of species i in category h . The niche breadth was computed for each *Drosophila* species using breeding site groups, breeding site species, and individual breeding site items as categories. A *Drosophila* species with a narrow niche on breeding site groups has a restricted number of breeding site species available to it and so will have a narrow niche on breeding site species even if it is entirely unselective within a group. To investigate the selectivity within groups, the niche breadth across breeding site species was calculated separately for each breeding site group and weighted according to the number of *Drosophila* individuals of that species emerging from that group. The weighted mean of these niche breadths gives emphasis to the preferred group of that *Drosophila* species. It is a measure of niche breadth on breeding site species independent of the niche breadth on groups.

Niche breadth across breeding site items is similarly dependent on niche breadth across breeding site species and so the niche breadth on items is calculated separately for each breeding site species and the weighted mean determined. The results are shown in Table 4.

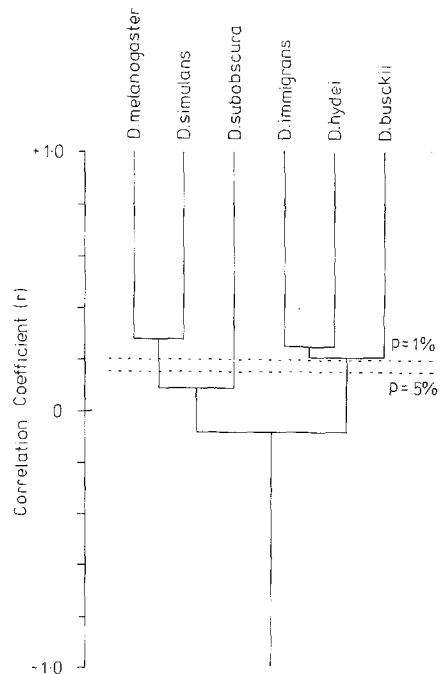
The niche breadths may represent selection of breeding sites by the *Drosophila*

Table 4. Niche breadths

Categories	<i>D. melanogaster</i>	<i>D. simulans</i>	<i>D. subobscura</i>	<i>D. immigrans</i>	<i>D. hydei</i>	<i>D. busckii</i>
Mean breeding site items	0.14	0.09	0.05	0.14	0.47	0.41
Mean breeding site species	0.53	0.37	0.35	0.36	0.29	0.35
Breeding site groups	0.40	0.48	0.45	0.76	0.60	0.43

or differential survival by the larvae or both. *D. immigrans* and *D. hydei* have the broadest niches on breeding site groups, reflecting Figure 2. On breeding site species *D. melanogaster* is the least specialised within its preferred group. On the other hand *D. hydei*, despite being broad-niched on groups, is relatively specialised on species. On breeding site items *D. hydei* and *D. busckii* are very much broader-niched than the other species, which may be selecting items for the state of decay or microfloral composition.

The associations between *Drosophila* species within breeding site items were investigated. The number of flies of each species emerging from each item was transformed to logarithms and the product moment correlation coefficient was calculated between all pairs of species. The species were clustered according to the weighted variable group method (Sokal and Sneath, 1963) and the resulting dendrogram is shown in Figure 3. There are two significant groups at the 1%

**Fig. 3.** Associations between the *Drosophila* species on individual breeding site items

level. *D. melanogaster* and *D. simulans* are significantly associated and *D. immigrans* and *D. hydei* are significantly associated with *D. busckii*.

Season

Figure 4 shows the maximum and minimum temperatures recorded twice a week throughout the season and, for each species of *Drosophila*, the number of flies emerging from the breeding sites brought in each week. *Drosophila* emerging from a breeding site picked up in a given week will not necessarily have come from eggs laid in that week, but allowing for this error and assuming that survival from egg to adult remains constant throughout the season, the emergences in Figure 4 reflect the distribution of oviposition through the season. The breeding seasons of the species overlap considerably but there are differences in their time of peak egg laying. *D. melanogaster* and *D. simulans* have two peaks, one in mid-June and the other at the beginning of September. *D. hydei* and *D. immigrans* have their peak in mid-July, though these peaks may be peculiar to the single season studied.

To investigate the relationship between temperature and oviposition, the product moment correlation was calculated between mean weekly temperature and the weekly emergences from Figure 4, transformed to logarithms. The results are shown in Table 5. There is a significant positive correlation for *D. melanogaster*, *D. simulans*, *D. immigrans*, and *D. hydei*, suggesting that their breeding is most strictly limited by temperature or another environmental variable correlated with it. McKenzie (1975) has shown that oviposition of *D. melanogaster* is very slow at 12°C in the laboratory and increases with temperature up to

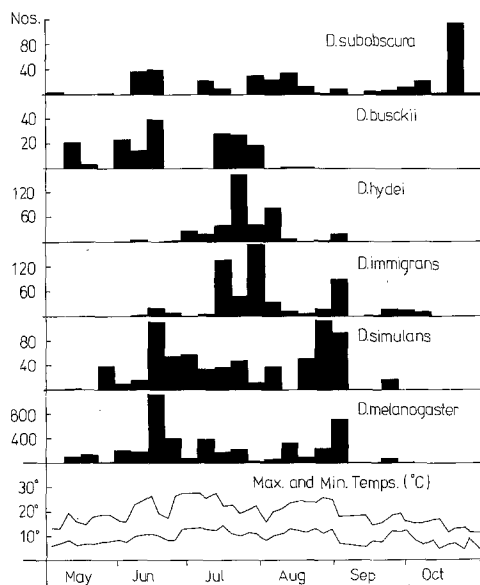


Fig. 4. Emergences of *Drosophila* from breeding sites collected each week together with twice weekly maximum and minimum temperatures

Table 5. Product moment correlation (r) between mean weekly temperature and oviposition

<i>Drosophila</i> species	r	Significance
<i>D. melanogaster</i>	+0.68	$P < 0.01$
<i>D. simulans</i>	+0.77	$P < 0.01$
<i>D. subobscura</i>	+0.12	n.s.
<i>D. immigrans</i>	+0.52	$P < 0.05$
<i>D. hydei</i>	+0.57	$P < 0.01$
<i>D. busckii</i>	+0.21	n.s.

20°C. He also found that in a field population larvae and pupae are not found at temperatures below 14°C. These temperatures fit the breeding season of *D. melanogaster* in Leeds quite well. The emergences of *D. subobscura* in Figure 4 remain fairly constant throughout the season and continue into October after the other species have stopped egg laying. This species, unlike the others that evolved in various tropical or sub-tropical areas, is a native of Europe. It is less adversely affected by temperatures and less able to exploit high summer temperatures than the cosmopolitan species.

Discussion

Sturtevant in 1921 described the larvae of *D. busckii* and *D. funebris* as general scavengers feeding on rotten potatoes, excrement, etc., while most common species prefer decaying fruit. *D. hydei* is described as intermediate between the two types. Shorrocks (1977) has emphasised the fundamental ecological division in *Drosophila* between those that use decaying substrates as breeding sites and those that use substrates undergoing alcoholic fermentation. In the domestic habitat fruits undergo alcoholic fermentation but in the vegetables other forms of decay predominate. As we have shown *D. melanogaster*, *D. simulans*, and *D. subobscura* are fruit specialists, *D. busckii* is a vegetable specialist while *D. immigrans* and *D. hydei* are able to use both types of breeding site, thus confirming the qualitative statement of Sturtevant.

Despite the partitioning of breeding sites that occurs, the analysis of diversity confirms considerable coexistence of different cosmopolitan *Drosophila* species within single breeding site items. Budnik and Brncic (1974) suggest that this phenomenon is fairly common in nature. They found *D. pavani* feeding in the same rotting fruits as some of the domestic species. This coexistence occurs because ovipositing females of domestic species show less selectivity in their choice of breeding sites than many wild species (Pipkin et al., 1966; Heed, 1971). Even at a fruit market the species of fruit available for breeding are fairly unpredictable and in the domestic niche generally, the probability of an ovipositing female finding a breeding site of the same sort as it developed in must be extremely small. MacArthur and Pianka (1966) have predicted that low expectation of finding a particular resource and increasing similarity of resource types demands generalisation. Evidently breeding site species in the domestic niche are similar enough and unpredictable enough to favour genera-

lisation. The difference between fermenting fruits and decaying vegetables, however, is so great that most of the domestic species have specialised on one or the other.

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