

COEXISTENCE OF AUSTRALIAN RAINFOREST DIPTERA BREEDING IN FALLEN FRUIT

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SUMMARY

(1) Twenty-eight species of Diptera, including five species of *Drosophila* were reared from fallen fruit collected in subtropical rainforest sites in eastern Australia. The situation was similar to that modelled by Atkinson & Shorrocks (1981). They showed that in discrete and ephemeral breeding sites, coexistence was facilitated if the competitors were aggregated. The aim here was to determine whether aggregation could explain the persistence of this diverse community of flies.

(2) There was little niche differentiation among the flies, many of the species sharing the same kind of fruit. Though there was less overlap over individual fruit items, the dipteran species were not negatively associated as they would be if the low overlap was caused by systematic niche separation.

(3) Low overlap over fruit items would be expected if the fly populations were kept at a low level by density-independent mortality and this might also explain the persistence of a diverse community. There was, however, widespread intraspecific competition, which would not be expected if density-independent mortality was important.

(4) If this guild of flies was maintained by aggregation over discrete and ephemeral breeding sites we would expect low overlap of the species over fruit items, random associations between the species and evidence of intraspecific competition. These were all observed in this guild. Adult flies emerging from the fruits also showed sufficient aggregation to account for their coexistence, as did eggs laid in the wild on artificial breeding sites. The occurrence together of these phenomena suggests strongly that the model of Atkinson & Shorrocks (1981) best explains the coexistence of so many species of Diptera.

INTRODUCTION

Recently, several theoretical studies have suggested that insect species whose larvae live in discrete and ephemeral breeding sites may coexist at equilibrium though the larvae are competing strongly (Shorrocks, Atkinson & Charlesworth 1979; Atkinson & Shorrocks 1981; de Jong 1982). Examples of the kind of breeding site being considered are dung, fallen fruit, fungi and carrion. Coexistence depends on the larvae of the superior competitor having an aggregated distribution over the breeding sites. As long as the inferior competitor is not clumped in the same sites, this ensures that it can survive in breeding sites where the other species is absent or at low density. Atkinson & Shorrocks (1984) have shown that intense aggregation is common among Diptera breeding in fallen fruit. The degree of aggregation is too great to be explained simply by differences in breeding site suitability

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and the main reason for the aggregation seems to be that, though egg-laying females visit sites at random, they leave several eggs at every visit. The competitors do not tend to clump their eggs in the same sites.

There is anecdotal evidence (Elton 1966; Beaver 1977; Atkinson & Shorrocks 1984) that discrete and ephemeral breeding sites support more diverse communities than other kinds of resource. It seems quite possible, therefore, that the processes described above are operating in nature. The aim of this study was to examine some of the properties of one particular group of species to determine whether the discrete and ephemeral nature of the breeding sites was important for their coexistence. The set of species I chose was the guild of larval Diptera exploiting fallen fruit in the subtropical rainforests of Eastern Australia. They are using just the sort of breeding site that appears in the model of Atkinson & Shorrocks (1981) and, in a similar situation, Pipkin (1965) encountered spectacular species diversity among the tropical Drosophilidae of Panama. She commented on how many species regularly shared the same fruits for breeding though they often belonged to the same species group, or even the same sibling set.

Apart from the model of Atkinson & Shorrocks (1981), there are two other major explanations for the persistence of diverse communities in the face of competition for resources (Schoener 1982; Lewin 1983). One explanation says that competition is important in nature and community members have to evolve differences in resource use to minimize the possibility of competitive exclusion. The other says that populations rarely reach the levels at which competition occurs, because, before that happens, their members are eaten by predators or die from natural catastrophes. I will describe the characteristics I expect of communities in which niche differentiation or density-independent mortality are important and contrast those characters with what is expected in a community of insects aggregated over discrete and ephemeral breeding sites.

If this guild of species was being maintained by niche differentiation we would, of course, expect to see evidence of differences in resource use between the fly species. The problem, as in all studies of this kind, is to ensure that the relevant niche dimension has been measured. Among *Drosophila* species, Carson (1971) has claimed that niche differentiation is usually achieved through differences in their breeding sites. Barker (1983) also suggests that larval competition or niche separation is probably more important for community structure than niche separation for food among adults. This is as expected, because the larval stage is when most growth and food consumption takes place and during this time the larvae are confined in one breeding site with little opportunity to escape from competitors. For these reasons, I looked for differences between the fly species in their use of the fruits for breeding. Major differences between the species could account for the persistence of the guild without invoking natural catastrophes, predators or aggregation over discrete and ephemeral breeding sites.

If fly species are kept below carrying capacity by predators or natural catastrophes, there should be no competition, either between the species, or between the members of a single species. If either niche differentiation or aggregation were important, however, we should see evidence of intraspecific competition but not interspecific; members of different species would avoid competition by being in different breeding sites. It is possible to detect the effects of larval competition in the Diptera because, above a certain threshold, increased crowding causes the production of smaller adults (e.g. Bakker 1961; Haupt & Busvine 1968). If, in the field, it can be shown that there is a negative correlation between larval density and adult body size, then the larvae must regularly be at densities above that threshold. When body sizes are severely reduced by crowding, there is some mortality

(Miller 1964) and, even when crowding is not sufficient to cause deaths, any reduction in body size is accompanied by lowered fitness due to extension of the larval period and reduced fecundity (Chiang & Hodson 1950). A negative correlation between larval density and adult body size, therefore, shows that the larvae are suffering the deleterious effects of competition. In some earlier work on field populations of domestic *Drosophila* (Atkinson 1979), I showed that high densities of *D. melanogaster* larvae were associated with reduced body size in the adults of that species and of several other *Drosophila* species sharing the same breeding sites. This technique can therefore detect both intraspecific and interspecific competition.

Finally, in a community in which competitive exclusion was prevented by aggregation over discrete and ephemeral breeding sites, we would expect to find no evidence of niche differentiation or interspecific competition, but we should see intraspecific competition. Most importantly, of course, the members of the community should be aggregated, so I looked for evidence of sufficient aggregation in the fly larvae to explain the coexistence of all the Dipteran species.

Though this overall strategy is not conclusive, I felt that if there was little evidence of niche differentiation, good evidence of intraspecific but not interspecific competition and highly aggregated larval distributions, this would suggest strongly that aggregation over discrete and ephemeral breeding sites explained the number of coexisting species.

METHODS

My main study site was Bruxner Park Flora Reserve, 4 km north of Coffs Harbour on the New South Wales coast. The vegetation is gully rainforest (Baur 1957), intermediate in structure between subtropical rainforest and warm-temperate rainforest. Sampling of the fly larvae was carried out by collecting fallen fruit and rearing the larvae through to maturity. On each collecting occasion I searched all the established pathways within the reserve for fallen fleshy fruits to determine which trees were fruiting. When a collection was made, all the fruit items suitable for oviposition were taken from around the base of a single tree. If there were more than fifty fruits, a small area was completely cleared until fifty items had been collected. Suitable fruits for oviposition were regarded as those with a broken surface into which eggs could be inserted. In practice few fruits were rejected. In October 1981 a single collection was made, of black apple fruits (*Planchonella australis*). In March 1982 collections of fruit were made from two different trees of four separate species. Details of the collections are given in Appendix 1. Also, in March 1982, collections of strangler fig (*Ficus watkinsiana*) and blue olive-berry (*Elaeocarpus reticulatus*) were taken from other rainforest sites in Queensland, Witches Falls National Park, 60 km south of Brisbane and Lamington National Park, 85 km south of Brisbane; both are structurally typical subtropical rainforest (Baur 1957).

After collection, each fruit item was weighed and put in an individual transparent container appropriate to its size. Each container had a floor of moist gravel which was remoistened as it dried out, and was closed with a fine-meshed fabric or a foam rubber bung. The fruits were kept in a constant temperature room at $18 \pm 1^\circ\text{C}$ and were inspected every day for emerged insects. These were removed and stored in alcohol until they could be identified and measured.

For the detection of competition, wing length was chosen as an index of body size because it is a simple and repeatable measurement. It was not considered worthwhile to measure the wings of very small species in which precision would be low, or of the less abundant species

in which the results could not be analysed statistically. Finally, five species were chosen for measurement. In the three *Drosophila* species, *D. immigrans*, *D. pseudotakahashii* and *D. specensis*, and in the chloropid, *Hippelates fergusonii*, the wing length was measured from the anterior cross-vein to the wing tip. In the nematoceran, *Sylvicola dubius*, the measurement was taken from the proximal edge of the discal cell to the wing tip.

The number of adult flies emerging per gram of fruit tissue was used as an indication of the larval density. Of course, this measure is strictly only valid if larval mortality is unrelated to crowding. In laboratory studies of *D. melanogaster* and *D. simulans* this is true except at very high densities (Miller 1964), so adult emergences should at least be correlated with the number of larvae in the fruit.

Aggregation of emerged adults was used as one measure of the aggregation of larvae. Also, during April 1984 in Bruxner Park, an experiment was carried out to look at the aggregation of eggs over a set of more-or-less identical breeding sites. Atkinson & Shorrocks (1984) showed in the laboratory that highly aggregated egg distributions did not require variability in breeding site suitability. This experiment was designed to test that in the field. A grid of freshly cut banana slices (ten rows of six slices) was exposed for 9 h close to a fruiting rusty plum (*Chrysophyllum pruniferum*) tree. Each banana slice was about 1 cm thick and between 2 and 3 cm in diameter and the whole grid occupied an area of 60 × 40 cm. At the end of the exposure period the eggs on each slice were counted with the aid of a binocular microscope.

RESULTS

Niche differentiation

A total of 3362 individuals of twenty-eight dipteran species emerged from all the fruits (Appendix 2), together with three moths and five parasitic wasps. This seems to be another example of discrete and ephemeral breeding sites supporting high species diversity. We would expect the coexistence of so many species to require considerable niche differentiation and a casual inspection of the data suggests that there is some association between fly species and fruit species. For example *Drosophila pseudotakahashii* occurs in good numbers in both collections of rusty plum (*Chrysophyllum pruniferum*), but is absent from both collections of white beech (*Gmelina leichhardtii*). These associations could reflect genuine preferences by the dipteran species for particular fruits, or could be due to the fact that whole collections of fruit may, by chance, entirely miss being visited by a particular species. These two possibilities were resolved by testing whether two collections of the same kind of fruit were more similar in fly species composition than collections of different fruit species. The March 1982 Bruxner Park collections were chosen for analysis because each fruit species was represented by two collections from different trees. The fly species in each collection were ranked in order of abundance and Kendall's rank correlation coefficient (τ) (Southwood 1978) was computed between all pairwise combinations of collections. The average correlation between collections of the same fruit species ($\tau = +0.43$) was significantly greater than that between collections of different fruit species ($\tau = +0.17$) (Mann-Whitney $U_{4,24} = 10$, $P < 0.01$), so the fly species do show consistent differences in fruit preference.

We must now ask whether these different preferences are sufficient to prevent competitive exclusion. McClure & Price (1976) have suggested that, to avoid competitive displacement, two species should have proportional similarity values (Colwell & Futuyama 1971) of less than 0.7 for the critical niche parameter. In Table 1 I have given

TABLE 1. Proportional similarity between dipteran species. Above the diagonal, using fruit species as the basic unit of comparison, below the diagonal, using fruit items as the basic unit

Dipteran species*	2	4	6	10	17	20	21	23	24	25	28
2		0.42	0.97	0.81	0.18	0.20	0.42	0.25	0.04	0.05	0.19
4	0.00		0.42	0.33	0.74	0.78	0.32	0.51	0.04	0.04	0.76
6	0.45	0.26		0.79	0.18	0.20	0.42	0.23	0.04	0.05	0.19
10	0.10	0.03	0.15		0.08	0.11	0.44	0.30	0.04	0.05	0.09
17	0.08	0.19	0.12	0.02		0.90	0.08	0.50	0.03	0.03	0.79
20	0.03	0.12	0.04	0.01	0.36		0.17	0.58	0.11	0.10	0.86
21	0.20	0.09	0.25	0.08	0.04	0.08		0.24	0.57	0.38	0.27
23	0.06	0.04	0.10	0.05	0.25	0.14	0.07		0.17	0.16	0.62
24	0.00	0.00	0.00	0.00	0.00	0.07	0.06	0.02		0.77	0.23
25	0.02	0.00	0.02	0.03	0.00	0.02	0.14	0.04	0.21		0.24
28	0.01	0.19	0.06	0.00	0.12	0.17	0.07	0.06	0.00	0.01	

* Code numbers for the dipteran species are given in Appendix 2.

proportional similarity values for the eleven most common species of fly, taking fruit species as the basic unit of comparison. Fruit species is somewhat confounded with location and date, but, despite this, all the fly species, except *Drosophila pseudotakahashii* and *D. specensis*, have at least one value greater than 0.7, that is, they have at least one potential competitor using a very similar range of fruit species. Competition is not obviously being avoided by the flies using different fruit species as breeding sites.

An alternative to using different fruit species might be to use different fruit items. Each fly species might have a preference for a different stage of decay or a particular microbial composition, irrespective of the species to which the fruit belonged. For example, among the Drosophilidae breeding in the figs of tropical Africa there is a succession of different fly species as decay progresses (Lachaise, Tsacas & Couturier 1982). If there was a succession in these Australian collections, newly fallen fruit would not yield species late in the succession, while in the older fruit we should miss the primary colonizers. We would, therefore, expect fly species to overlap little in fruit items if that was how they achieved ecological separation. A similar low overlap would be expected for any kind of variation in preference among the items. Low overlap over fruit items is not necessarily an indication of niche differentiation, however, because it would also be expected if the species were kept at low density through predation or natural catastrophes, or if the community was being maintained by aggregation over discrete breeding sites. If the low overlap was caused by different preferences we would expect to see an overall tendency for negative associations between the species over fruit items. The other explanations should give no associations, positive or negative. The species should occur together at random.

Table 1 gives values of proportional similarity, taking fruit items instead of fruit species as the basic unit in the calculation. Now, the highest similarity is only 0.45, between *Sylvicola dubius* and an unidentified species of psychodid. Most values are much less than this and are certainly below the figure of 0.7 which McClure & Price (1976) consider necessary for competitive exclusion. We should now test whether the dipteran species are negatively associated, or whether they are assembled at random.

The Barton and David test (Pielou & Pielou 1967) calculates the exact probability of getting the observed number of empty breeding sites in a collection if the species are assembled at random. If there were negative associations among the fly species because of niche differentiation there would be more empty sites than expected. The probability,

TABLE 2. The number of empty breeding sites in each collection, with the probability of getting as few empty, or as many empty assuming the species are randomly associated over uniform breeding sites

Collection*	Number of items	Empty sites	Probability of as few empty sites	Probability of as many empty sites
A	27	2	0.972	0.170
B1	56	40	0.989	0.076
B2	18	1	0.462	0.943
C1	51	26	0.166	0.961
C2	53	22	0.830	0.340
D1	30	14	0.509	0.760
D2	51	18	0.551	0.642
E1	29	0	0.975	1.000
E2	24	1	0.965	0.294
F	59	41	0.787	0.483
G1	65	49	0.999	0.006
G2	24	14	0.999	0.002
G3	33	2	0.983	0.116

* Code numbers for the collections are given in Appendix 1.

calculated on the basis of random assembly, of getting as few empty sites as observed should be low. Table 2 shows that none of the thirteen fruit collections had fewer empty sites than expected. There were, however, two collections (G1 and G2) of strangler fig (*Ficus watkinsiana*) which had many more empty sites than we would expect on the basis of random association among homogeneous fruits. It seems that in these two collections many sites were unsuitable for breeding. The Barton and David test gives no evidence that sites in the other collections are unsuitable, nor is there any sign that the dipteran species can avoid one another by niche differences across fruit items, or, for that matter, by detecting whether fruits are already occupied.

Evidence of competition

For every emerged fly of the five species selected for measurement, we had an index of its body size, of the larval density of its own species and of the densities of all the other potential competitors emerging from the same breeding site. We were, therefore, able to carry out regression analyses of the effect of each species' density on the wing length of every other. A separate analysis was carried out on each species pair in each collection. The dependent variable, wing length is normally distributed, so was not transformed. The analysis was performed on individual wing lengths rather than on the mean of all flies emerging from a fruit item, because large-sample means would tend to have smaller variances than means of small samples, contrary to the assumptions of parametric regression analysis. In some species, individuals of the two sexes differ in wing length, so sex was included as a variable in the regression equation. Each multiple regression was performed stepwise with sex entered before density.

When the regression coefficients for the effect of density on wing length were examined there were forty-six negative coefficients and thirty-five positive. The probability of getting such a departure from 1:1 by chance is 0.187, so there is no convincing overall trend towards the negative relationships that would indicate competition. There is a clear effect, however, when we separate intraspecific analyses from interspecific (Table 3). There is a highly significant excess of negative regression coefficients among the intraspecific analyses, but no trend at all in the interspecific. The difference between interspecific and

TABLE 3. Analysis of the signs of regression coefficients of wing length on density

	Sign of coefficient		χ^2_1
	Negative	Positive	
Interspecific regression	24	28	0.308 N.S.
Intraspecific regression	22	7	7.759 $P < 0.01$
Total	46	35	1.494 N.S.

intraspecific analyses is significant (Heterogeneity $\chi^2_1 = 6.57$, $P < 0.01$). The likely explanation is that intraspecific competition is a potent force in this guild of fruit-breeding flies, but interspecific competition has much less importance.

The widespread occurrence of intraspecific competition is not what we would expect in a community whose populations are reduced by density-independent factors such as predation and climate. That these factors are unimportant, is consistent with other information we have about the community. First, predators within the breeding sites are certainly uncommon. Though many of the Diptera were not identified to species, the families with possibly predaceous larvae, the Empididae, Dolichopodidae and Muscidae, constituted less than 4% of the total emergences. Parasitic wasps were also rare; I reared only five individuals from the collections of fruit. Extremes of climate are uncommon at the latitude of the study sites. In Newfoundland State Forest, 40 km north of Bruxner Park, the mean daily minimum temperature in the coldest month, July, is 7.3 °C and the mean daily maximum in the warmest month, January, is 29 °C (Baur 1957). None of the *Drosophila* species is close to the limits of its range at Bruxner Park (Bock 1976) and I have reared the commonest species in the community, *Sylvicola dubius* from fallen apples collected over 800 km further south, near Melbourne, in Winter (August).

Aggregation of the larvae

Atkinson, & Shorrocks (1983) give details of the distribution of emerged adults from the fruit collections considered in this study. For each of the most abundant fly species in each collection the negative binomial was fitted to the distribution of individuals and values of k were calculated. Figure 1 is a histogram showing the frequency of different values of k . Most are low enough to indicate intense aggregation.

On the grid of banana slices, two kinds of egg were laid. The most abundant were eggs

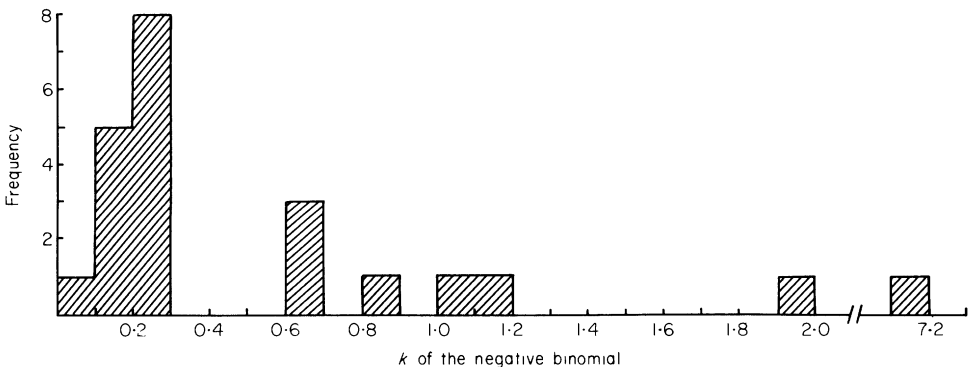


FIG. 1. The frequency distribution of values of k of the negative binomial for the most abundant species in each collection. The data are from Atkinson & Shorrocks (1984).

with two filaments, very similar to those of *D. melanogaster*. These were undoubtedly the eggs of *D. pseudotakahashii*, a member of the *melanogaster* species-group and the only species present in a sweep-net sample taken over the bananas after the experiment was finished. The other kind of egg laid had four filaments and may have belonged to *D. specensis* which was present in sweep-net collections over fallen rusty plums in the vicinity. The negative binomial was fitted to the distributions of each kind of egg separately and the parameter, k , was estimated using the maximum likelihood method of Bliss & Fisher (1953). Chi-squared tests showed that neither distribution departed significantly from a negative binomial. Both were highly aggregated, two-filament eggs having $k = 1.73$ while four-filament eggs had a value of k of 0.27.

DISCUSSION

I have shown that in this community of Diptera there is widespread intraspecific competition, but no evidence of competition between species. I was unable to find significant ecological separation by breeding site, so interspecific interactions are not being avoided through niche differentiation. The dipteran species were, however, aggregated over the breeding sites. It seems worthwhile to examine whether there is sufficient aggregation to explain the coexistence of these species.

I have further explored the properties of the simulation model of Atkinson & Shorrocks (1981) to determine the degree of aggregation necessary for coexistence. The survival of the inferior competitor depends on the competition coefficients as well as on the degree of aggregation. Shorrocks *et al.* (1984) have found that in laboratory studies of *Drosophila* species, most published competition coefficients (thirty-four out of fifty-one) are less than 2 and none is greater than 6. By simulation, I have shown that if the inferior competitor has no detrimental effect on the other species and the competition coefficient for the effect of the superior competitor on the inferior is no greater than 2, then the two species can coexist on a divided resource as long as they are aggregated with k of the negative binomial less than about 1.5. When k is less than 0.5, competition coefficients greater than 6 are required for competitive exclusion; the highest value in the literature was about 6. These broad conclusions are confirmed by analytical methods (R. M. May unpublished). How do these critical values of k compare with those obtained from the dipteran community in Eastern Australia?

Of twenty-two values of k in Fig. 1, twenty are less than 1.5 and fourteen are less than 0.5. For the eggs laid on an array of banana slices. One value of k is slightly over 1.5 and the other is much less than 0.5. It seems that the degree of aggregation in this community is of the order required to explain the coexistence of competing dipteran species.

The reasons for the aggregation seen in this kind of community have been closely examined by Atkinson & Shorrocks (1984). They have shown that it is hard to explain this intensity of clumping by variation in breeding site suitability. The experiment with banana slices, reported in this paper, confirms that eggs can be highly aggregated over fairly uniform breeding sites. There is also little evidence of gregarious oviposition, at least among the *Drosophila* (Atkinson 1983). The aggregation is most easily explained if successful oviposition events are rare, but when they occur, the laying female produces several eggs before searching for a new site. Atkinson & Shorrocks (1984) quoted some evidence from the literature that *Drosophila* species behave in this way. In order to explain the high degree of coexistence, we therefore need to explain why successful oviposition is rare. The three possibilities are that the flies are uncommon relative to breeding sites, that breeding sites

are hard to find for the flies, or, finally, that when sites are found, opportunities for egg laying are scarce. The first two possibilities seem unlikely because fallen fruit at the study sites always attracted many flies. For example, in Lamington National Park, I once counted eighteen visits to a single strangler fig by *D. pseudotakahashii* during a 30 min period. The conclusion must be that few visits lead to successful oviposition. Atkinson & Shorrocks (1984) speculated that the comparative rarity of successful oviposition might be due to disturbance by other flies, especially courting males, and the fact that breeding sites are not suitable for egg laying for very long. Pipkin (1965) found that far more species of *Drosophila* were netted from fallen plant parts than were bred from samples of the same plant parts. She suggested that this was because spatial interference with ovipositing females occurs. Spieth & Ringo (1983) have described the typical behaviour of *Drosophila* females when they visit breeding sites and, apart from describing the problems females have with courting males, they put forward another reason why oviposition may be relatively infrequent. They state that the females must devote the major portion of any visit to feeding, rather than oviposition, because of the nutritional demands of producing numerous yolk-rich eggs. Certainly, egg deposition in *D. melanogaster* is a very hurried event, taking less than a second to complete (personal observation), which suggests that it is important that the flies do not waste time in leisurely oviposition. There is a major requirement for more work on the behaviour of ovipositing flies to establish exactly how limited are the opportunities for egg laying.

We are able, now, to say that everything we have found out about this guild of flies is consistent with there being an important role for aggregation over discrete and ephemeral breeding sites. We cannot, however, reject completely all other explanations for coexistence. In particular, there may be some ecological separation along a dimension I have not measured. Perhaps the larvae can exploit different microhabitats within the same fruit items. Barker (1983), for example, suggests that differences in microflora utilization might explain some of the cases in the literature where breeding sites support two or more *Drosophila* species. However, in this guild of flies we have shown that the species overlap little over fruit items. There would, therefore, be little selection to favour differences in microhabitat. Even if such differences were found, with so little co-occurrence of species, they could be of little importance in structuring the community. It seems probable that the differences in resource exploitation which are observed are not the evolutionary consequences of past competition, but merely reflect the evolutionary histories of the different members of the guild (Connell 1980). Such comments may also apply to the communities of animals exploiting similar breeding sites such as other fruit, fungi, nests, dung and carrion. Elaborate niche differentiation is not necessarily required to maintain their diversity.

ACKNOWLEDGMENTS

I thank the Forestry Commission of N.S.W. and the Queensland National Parks and Wildlife Service for permission to carry out field work, Mr A. G. Floyd who identified some of the fruits, Ian Bock who helped with identification of the fly species, Linda Atkinson who assisted with field work, Peter Parsons for his advice, encouragement and the provision of facilities at La Trobe and John Gibson for providing facilities at the A.N.U. Most of this work was supported by a La Trobe Research Fellowship.

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(Received 8 June 1984)

Collections of fruit with their location and average weight.

APPENDIX 2

[illegible]

19	<i>Drosophila dispar</i> Mather	3												
20	<i>D. immigrans</i> Sturtevant	3	1					3						47
21	<i>D. pseudotakahashii</i> Mather	119	16	60	20	1		81	39		2			13
22	<i>D. serrata</i> Malloch							1		1				
23	<i>D. specensis</i> Bock	25		3	7		5	61	6	3	8	32	28	43
	Chloropidae													
24	<i>Hippelates atricornis</i> Malloch	20	5							1				
25	<i>H. fergusoni</i> Malloch	593						1	2	21		5		
26	Unidentified species							2	4				1	
	Muscidae													
27	Unidentified species	4												
28	Unidentified species	5							1				1	19

* Collections are identified by the same letters as in Appendix 1.