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Ecology of Iowa *Drosophila* II. Lowland Forest and Sand Prairie

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The seasonal abundances of *Drosophila* species collected from a lowland forest community and from a sand prairie community in northeastern Iowa are compared. With some important exceptions, the patterns seen in the lowland forest community were similar to what had been observed in a previous collection (Jennings et al. 1985). Fewer species and many fewer individuals were collected from the sand prairie community, although in general the patterns seen were similar to those of the lowland forest community. Strong evidence of microhabitat differentiation was seen in both communities. In contrast to our previous study, none of the seasonal abundance patterns were significantly correlated with temperature.

INDEX DESCRIPTORS: *Drosophila* species, seasonal abundances, lowland forest, sand prairie

The seasonal abundances and spatial distributions of species native to northeastern Iowa within the genus *Drosophila* Fallen were studied, with special emphasis on understanding seasonal abundance patterns and habitat specificities.

The seasonal abundances of eleven *Drosophila* species from a lowland forest community in Cedar Falls, Iowa, were previously reported (Jennings et al., 1985). Of the 2912 individuals collected, *D. affinis* accounted for 63% of the sample, *D. falleni* for 17%, *D. tripunctata* for 10%, and *D. robusta* for 6%; the remaining 7 species accounted for a total of 4%.

Two basic seasonal abundance patterns were observed for the four most common species. They were either abundant in spring and early summer (*D. affinis*, *D. falleni* and *D. robusta*), with a few individuals collected in the fall (*D. falleni* and *D. robusta*), or were abundant from early summer until fall (*D. tripunctata*). The seasonal abundances of the three early year species were positively correlated with temperature (both with the temperature at the time of collection and, independently, with the average maximum temperature of the preceding week); only for *D. robusta* were the correlations significant. The seasonal abundance of *D. tripunctata* was significantly negatively correlated with temperature. These results are consistent with the critical importance of temperature for many *Drosophila* species (David et al. 1983).

To test the generality of these findings, and to extend our survey to other vegetation communities, in 1983 we re-sampled the same lowland forest community and sampled a sand prairie community. The specific aims of this study were, 1) to determine whether the same general abundance patterns were repeated in the lowland forest community the subsequent year, 2) to study the similarities and differences in the *Drosophila* of two different communities, 3) to determine whether the abundances of any of the species were correlated with an environmental variable, particularly with temperature, 4) to study microhabitat differences within each community, and 5) to examine probable larval/oviposition substrates and to determine daily activity patterns for species in the lowland forest community.

MATERIALS AND METHODS

Drosophila species were sampled from two communities in or near Cedar Falls, Black Hawk Co., Iowa, from April through November, 1983. Sampling began when the adults first eclosed in the spring and continued until no adults were found in the traps in the fall.

The lowland forest community, the University Avenue Preserve owned by the University of Northern Iowa, is a 3.2 h tract of native lowland forest traversed by the Middle Branch of Dry Run Creek. The forest is dominated by box elder (*Acer negundo*), black cherry (*Prunus*

serotina), hackberry (*Celtis occidentalis*), black walnut (*Juglans nigra*), green ash (*Fraxinus pennsylvanica*) and cork elm (*Ulmus thomasii*). The community was sampled 13 times, with three collections taken in May, two in June, July, and September, and a single collection in April, August, October, and November.

The sand prairie community, Cedar Hills Sand Prairie, is 16 h of virgin mixed grass prairie located 13 km northwest of Cedar Falls. The tract is traversed by a moist swale with an adjacent mesic zone dominated by big blue stem (*Andropogon gerardii*) and indian grass (*Sorghastrum nutans*), and a xeric ridge dominated by little blue stem (*A. scoparius*). A few scattered juniper (*Juniperus virginiana*) and Chinese elm (*Ulmus pumila*) saplings occupied the mesic and xeric areas (Crum 1972). The community was sampled 11 times with three collections taken in May, two in June, July, and September, and one in April and August. No collection was made after September 25 in this community.

Drosophila (and other insects) were attracted to a bait consisting of a mash of fermenting bananas and bakers yeast. In each community twelve baited traps (modified from Heim 1978) were hung for 24 hrs from trees at a height 1 to 3 m, and at 15 m intervals. Air temperatures at trap height were recorded at trap placement and recovery. Our previous collections (Jennings et al. 1985) using this mash were from an hour (in the mid-afternoon) of net-capturing flies attracted to the baits, which had been placed in buckets on the ground. A disadvantage of this method was that only flies active at the time of sampling were collected. We recognize a sampling bias in the use of fermenting bananas and yeast as bait; many *Drosophila* species are attracted to this bait but others are not (Carson and Stalker 1951).

The collected flies were brought to the laboratory for identification and counting. Since each trap attracted flies from the nearby vegetation, the contents of each trap were identified separately to give evidence on microhabitat differences in each community. Voucher specimens from our previous collections were used for comparison; flies not readily identified were keyed to species using Strickberger (1962). *D. affinis* and *D. algonquin* males but not females can be readily distinguished. To calculate the overall species composition for these species, for each collection day the females were divided between the two species in proportion to the frequencies of the males. Thus if males of only one species were found during a collection, all females were added to that species. Male frequencies were used for all the data analyses for these species.

To further examine the ecology of these species, two small-scale studies were conducted. First, probable larval/oviposition substrates were collected from the lowland forest, brought into the laboratory, and placed in gauze covered beakers at 20°C, to see if adult flies could be reared from them. Adult flies were also collected directly from natural substrates with aspirators. Second, on 11 June, 8 July, and 2

October, we examined adult daily activity patterns by periodically (every 1 to 2 hours) throughout the day collecting flies from one of the traps in the lowland forest community.

RESULTS AND DISCUSSION

1. Lowland Forest Community

Abundance. A total of 2752 flies belong to twelve *Drosophila* species were collected from the lowland forest community (compared to 2912 flies collected during 1982). The *Drosophila* species composition changed markedly during the season (Table 1). The overall pattern (Table 2) was similar to our previous study (Jennings et al. 1985) but with significant differences. *D. affinis* again was the most common species, accounting for 72% of the sample.

In 1982 three species, *D. falleni*, *D. tripunctata*, and *D. robusta*, were relatively common, with over 150 individuals of each being collected. This year we also collected large numbers of *D. tripunctata* and *D. robusta* but fewer of *D. falleni*. *D. falleni* accounted for 17.4% of the flies collected in 1982 but only 1.5% of the flies collected in 1983. Two other species, *D. algonquin* and *D. putrida*, were relatively rare in 1982 but were much more common in 1983. A particularly striking contrast is that of *D. algonquin*; 2 males were collected in 1982 while 82 males were collected in 1983.

The commonly found *D. affinis* and the rarely found *D. algonquin* are sibling species. This close phylogenetic relationship means that their ecological requirements are probably close as well. Thus it is not surprising that we found large numbers of only one of them. *D. algonquin* is more common than *D. affinis* north of our study area (above 45° latitude) (Miller 1958). At cooler temperatures *D. algonquin* outcompetes *D. affinis*; at warmer temperatures the reverse is true (Fogleman and Wallace 1980, Fogleman 1982).

The species rarely collected in 1982 tended to be rare in 1983 also. *D. buskii*, *D. quinaria*, and *D. immigrans* were found in low numbers both years, although all were more abundant the second year. Two species collected in 1982, *D. melanogaster* and *D. athabasca*, were absent in 1983; *D. melanogaster* was represented by 2 individuals and *D. athabasca* by 23 individuals. In contrast, a few flies of three species which were absent in 1982, *D. duncani*, *D. testacea*, and *D. victoria*, were collected in 1983.

The fact that we found so few *D. buskii*, *D. immigrans*, and *D.*

Table 1. Seasonal abundances of the five most common species of *Drosophila* collected from the lowland forest community. For *D. affinis* and *D. algonquin* the number of males collected is in parentheses.

Collection Day	Species				
	<i>D. affinis</i>	<i>D. tripunctata</i>	<i>D. algonquin</i>	<i>D. putrida</i>	<i>D. robusta</i>
April 21	0	0	6 (6)	0	11
May 13	35 (23)	0	7 (5)	15	5
May 21	0	0	0	0	0
May 29	8 (5)	0	0	2	0
June 12	383 (149)	1	72 (28)	10	0
June 24	579 (183)	3	9 (3)	7	3
July 6	741 (246)	8	0	32	8
July 24	170 (74)	14	0	2	10
August 31	37 (14)	7	0	1	7
September 14	4 (2)	46	71 (40)	5	29
September 25	2 (1)	156	0	57	31
October 16	0	0	0	0	0
November 6	13 (6)	17	0	0	9
Total	1972 (703)	252	165 (82)	131	113

melanogaster is noteworthy. All three species are closely associated with humans and are frequently found in domestic habitats (Patterson and Stone 1952). Thus we are sampling a natural and not a human-associated population of *Drosophila*.

Seasonal patterns. The seasonal abundance patterns of three of the more common species, *D. affinis*, *D. tripunctata*, and *D. falleni*, were similar between the two years. Nearly 97% of *D. affinis* (males) were collected before August (99% in 1982), and, in contrast, almost 90% of *D. tripunctata* were collected from late August through fall (76% in 1982). Many fewer *D. falleni* were collected in 1983 than in 1982; nevertheless the seasonal patterns were similar, with 80% (1983) and 90% (1982) of the flies being collected before August.

The seasonal patterns of *D. robusta* differed significantly between the two years. In 1982, 93% of the individuals were collected before August, while in 1983 only 33% of the individuals were collected during this period. In contrast, in 1983 *D. robusta* showed a marked population peak in September (53% of the total sample; Table 1). High numbers of other species were also collected during September, 1983: *D. tripunctata* (80% of the total sample for this species), *D. algonquin* (49% of the males), *D. putrida* (47% of the total), and *D. falleni* (17% of the total, although most *D. falleni* were collected before August). Two factors which may have accounted for these high September, 1983, abundances were greater precipitation (8.1 vs. 3.7 cm) and higher average maximum temperatures (24.0°C vs. 21.9°C) during September, 1983, than during September, 1982 (U.S. Weather Bureau 1982, 1983).

To determine if ambient temperature might play a role in influencing the observed seasonal patterns, we computed correlations between the relative abundance within each species versus the average high temperature for the week preceding the collection day and, independently, versus the maximum temperature of the collection day itself (all relative abundance frequencies in this and the other analyses are arcsine transformed; Sokal and Rohlf, 1969, pp. 386-387). In doing these correlations no assumption was made that temperature was the only environmental factor that might affect abundances, nor that the exact temperatures used for the correlations were those which the flies experienced. The assumption was made that there was a positive relationship between the temperatures measured and the temperatures that the flies actually experienced; the average high temperature of the preceding week being related to the temperatures the immature stages (larvae) experienced, and the maximum temperature of the collection day itself being related to the temperature at which the adults were active.

None of the correlations is significant; the closest is between *D. affinis* and daily high temperature (0.483, $p = 0.08$). The correlations are (weakly) positive for the three early year species (*D. affinis*, *D. robusta*, and *D. falleni*), in accord with the 1982 results; in 1982 the *D. robusta* correlations were significant. For *D. tripunctata* we found significant negative correlations in 1982. For the current collections not only were the correlations for *D. tripunctata* not significant, but they were essentially zero (0.06 for daily maximum temperature, -0.09 for average weekly maximum temperature). Thus although the general patterns of seasonal abundance in 1983 were similar to those found in 1982, these results suggest that either temperature is much less important than we had previously supposed, or that our measurements of ambient temperature were inadequate descriptors of the temperatures actually experienced by the flies.

Microhabitat heterogeneity. Many *Drosophila* species have different ecological requirements and can discriminate between feeding and/or breeding sites within or between communities (Taylor and Powell 1978, Kekic et al. 1980, Turelli et al. 1984). We thus expected to find evidence of microhabitat heterogeneity for at least some of the species we studied.

In our study microhabitat differentiation would be reflected in a

Table 2. Species abundances of *Drosophila* for the lowland forest community

Species	Number Collected (Males / Females)	Percentage of total
<i>D. affinis</i>	1972 (703 / 1269)	71.7
<i>D. tripunctata</i>	252 (175 / 77)	9.2
<i>D. algonquin</i>	165 (82 / 83)	6.0
<i>D. putrida</i>	131 (70 / 61)	4.8
<i>D. robusta</i>	113 (51 / 62)	4.1
<i>D. falleni</i>	41 (10 / 31)	1.5
<i>D. buskii</i>	28 (12 / 16)	1.0
<i>D. duncani</i>	14 (4 / 10)	0.5
<i>D. quinaria</i>	12 (5 / 7)	0.4
<i>D. testacea</i>	11 (6 / 5)	0.4
<i>D. immigrans</i>	7 (5 / 2)	0.3
<i>D. victoria</i>	6 (2 / 4)	0.2

deviation from the expectation that 1/12 (since we used 12 traps) or 8.3% of the total sample would have been collected in each trap. A significant deviation was found; the percentages range from 20.8% to 3.3% ($X^2=695.7$, 11 d.f., $p<.0001$). All the five most common species (Table 2) were significantly heterogeneous in trap preference (Table 4). None of these species showed the same pattern of trap preference; when the data were broken down by trap none of the correlations were significant between the relative abundances of each species within each trap. These different trap preference patterns are evidence for microhabitat differentiation.

For two of these species (*D. affinis* and *D. robusta*) we have an indication as to the possible causes of the observed trap preference patterns. Almost 24% of the total sample of *D. affinis* came from a single trap, with most of them (23% of the total sample) being collected during June and July. This trap was hung from one of two large cottonwood trees in the forest; the tree was on the margin of the lowland forest community and adjacent to a shrub exhibit. In June and July there were fruiting mulberry trees near this trap; we have collected *D. affinis* adults on mulberry fruit. It is probable that the large number of *D. affinis* found in this trap may have been due to either of these factors.

For *D. robusta*, 23% of the total sample was collected from a trap which was in a stand of conifers and pines and was very close to a stream. Two other traps were placed similarly; we found the second and third largest percentages (13% and 10%) of the *D. robusta* sample in these. *D. robusta* is known to breed in the sap exudations of some trees (primarily elms) (Carson and Stalker 1951), although it is not known to breed in conifers or pines.

Larval/oviposition substrates and daily activity patterns. A number of the species we studied are at least partially fungal feeders (Patterson and Stone 1952; Lacy 1982). We were able to rear many of these (*D. falleni*, *D. putrida*, *D. quinaria*, *D. testacea*, and *D. tripunctata*) from one or more wild fungi collected from the lowland forest. All but *D. quinaria* were also aspirated from one or more fungi. Four species (*D. affinis*, *D. falleni*, *D. putrida*, and *D. tripunctata*) were aspirated from fallen mulberries (*Morus* sp.); *D. tripunctata* was also aspirated from fallen black walnuts (*Juglans nigra*) (Jennings and Seager 1985).

The study of daily activity patterns was done at one trap in the lowland forest. For most of the species we found few or no individuals; for three we found enough to look at the activity pattern. *D. affinis* males (a total of 19) were collected uniformly throughout the day, starting at 7:00 in the morning until dark. In contrast both *D. tripunctata* (14 individuals) and *D. robusta* (5 individuals) were collected in the morning (up until 8:00 for *D. robusta* and until 10:00 for *D. tripunctata*) and evening (at 7:30 for both species). One *D. tripunctata* was also collected at 4:00 in the afternoon.

Table 3. Species abundances of *Drosophila* for the sand prairie community

Species	Number Collected (Males / Females)	Percentage of total
<i>D. affinis</i>	41 (7 / 34)	60.3
<i>D. algonquin</i>	14 (7 / 7)	20.6
<i>D. putrida</i>	6 (2 / 4)	8.8
<i>D. quinaria</i>	3 (0 / 3)	4.4
<i>D. robusta</i>	2 (2 / 0)	2.9
<i>D. falleni</i>	1 (0 / 1)	1.5
<i>D. buskii</i>	1 (1 / 0)	1.5

2. Sand Prairie Community

Abundance and seasonal patterns. The abundance of *Drosophila* at the sand prairie was markedly different from that of the lowland forest in both the number of species and the number of individuals collected. Only 68 flies belonging to 7 species were collected from the sand prairie (Table 3). Remembering that the samples are very small, the abundance patterns were similar to those observed in the lowland forest. Most (71%) of the *D. affinis* males and all *D. falleni* were collected before August. Many of *D. robusta* (100%), *D. algonquin* (71% of the males), and *D. putrida* (50%) were collected during September. Due to the small samples it is impossible to compute temperature vs. abundance correlations as was done with the lowland forest data.

The overall compositions of the two communities, except for one major exception, were similar. As in the lowland forest, the most common species found at the sand prairie was *D. affinis*; *D. algonquin* and *D. putrida* also made up major portions of the overall sample in both communities. Only 2 individuals of *D. robusta*, which was very common in the lowland forest, were found at the sand prairie. Three other species, *D. falleni*, *D. buskii*, and *D. quinaria*, which were less common in the lowland forest were found in low numbers at the sand prairie. Four species which were rare in the lowland forest, *D. duncani*, *D. testacea*, *D. immigrans*, and *D. victoria*, were not found at the sand prairie.

The major exception to this general correspondence between the two communities involved *D. tripunctata*. This species was the second most commonly sampled species from the lowland forest, accounting for over 9% of the total sample. It was not found at the sand prairie. Two substrates which this species uses, mulberries and walnuts, also were not found at the sand prairie (Jennings and Seager 1985). We hypothesize that the absence of *D. tripunctata* from the sand prairie, and perhaps the rarity of some of the other species, may be due to the lack of suitable oviposition sites/larval food sources.

Microhabitat heterogeneity. We also analyzed trap preferences at the sand prairie community. Three of the traps were placed in a stand of trees and three others were placed under solitary trees. Since there were twelve traps, on the average 25% of the flies should be found in

Table 4. Chi-square tests for trap preference heterogeneity for the five most commonly collected species from the lowland forest community. Each chi-square has 11 degrees of freedom.

Species	Chi-square (probability)
<i>D. affinis</i> (males)	292.5 (p<.001)
<i>D. tripunctata</i>	88.1 (p<.001)
<i>D. algonquin</i> (males)	45.3 (p<.001)
<i>D. putrida</i>	24.3 (p<.025)
<i>D. robusta</i>	58.5 (p<.001)

each set of three traps. The traps in the stand of trees accounted for 47.1% of the total sample, and the three traps under solitary trees for 27.9% of the total sample. Clearly the *Drosophila* were concentrated in the stand of trees; the frequency found in the traps under the solitary trees was near the expectation.

In contrast there were four traps placed in the tall grass without any trees nearby. These traps were expected to account for about 1/3 of the total sample; only 13.2% of the flies were found in these traps. We once again see evidence of microhabitat differentiation within a community. The sand prairie is basically a "*Drosophila* desert" with an oasis (the stand of trees).

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