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Ecology of Iowa *Drosophila* I. Lowland Forest

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We have studied the seasonal abundances of *Drosophila* species collected from a lowland forest community in northeastern Iowa. Eleven species were collected of which six were collected in appreciable numbers (over 20 individuals). One species, *D. affinis*, is dominant until early summer when it virtually disappears and a second species, *D. tripunctata*, becomes dominant. Two other species, *D. falleni* and *D. robusta*, also are very common early in the year and collected much less frequently later. It is hypothesized that temperature is a critical factor in determining these seasonal patterns.
INDEX DESCRIPTORS: *Drosophila* spp., seasonal abundances, lowland forest

An important aim of ecology and evolutionary biology is to understand the temporal and seasonal abundances and the geographical distributions of organisms. These can be studied in various ways depending upon the questions being asked. We are interested in the factors influencing the abundances and distributions of closely related (congeneric) species within and between communities. We are studying the distributions of a group of closely related species native to northeastern Iowa all within the genus *Drosophila* Fallen. This genus is highly polytypic with almost 1500 species described worldwide (Wheeler 1981a) of which 117 occur in the Nearctic Region (Wheeler 1981b). The evolutionary relationships within the genus range from fairly distant (*Drosophila* has been divided into 15 subgenera four of which have over 100 species [Wheeler 1981a]) to very close (there are a number of sibling species pairs known [Patterson and Stone 1952]). It is thus not surprising that *Drosophila* species are quite variable in regard to their ecological preferences and requirements (Carson and Stalker 1951; Patterson and Stone 1952).

The initial focus of our work has been on the seasonal abundances of 11 species which occur in a lowland forest community. We wish to determine the causes of the observed patterns. On a large scale, biogeographic information on distributional patterns is important when speciation is studied and phylogenies are constructed. A survey of Iowa *Drosophila* is particularly important in this regard because the genus is poorly studied in Iowa. Some distributional maps, while having records from neighboring states, leave Iowa blank (e.g. Jaenike and Grimaldi 1983).

On a smaller scale, we would like to know why the *Drosophila* species found within the lowland forest community exhibit different seasonal patterns. For example since a single genus is being studied some of the species are very closely related evolutionarily and probably ecologically. The question arises as to how closely related and potentially competing species can coexist in the same habitat. The answer may lie in competition being reduced because of species differences in daily or seasonal activity patterns. Of particular interest in this regard, two of the species we have collected, *D. affinis* and *D. algonquin*, are sibling species and thus especially closely related. We are looking for ecological factors which may influence observed distributional patterns by looking for ecological correlates of these distributions.

Because of their prevalence, their diversity, and their ease of collection *Drosophila* species are good organisms for evolutionary and ecological studies. Moreover many of the species can be raised in the laboratory. This allows the possibility of testing the importance of hypothesized ecological factors affecting species abundances and distributions under controlled laboratory conditions.

MATERIALS AND METHODS

Drosophila species were collected from a lowland forest community in Cedar Falls, Black Hawk Co., Iowa. Collections began as soon as the flies eclosed in the spring and continued until no more adults were found in the fall. Weather conditions were noted and temperature recorded for each collection. The lowland forest community is in the University Avenue Preserve owned by the University of Northern Iowa. The preserve is a 3.2 h tract of native lowland forest traversed by the Middle Branch of Dry Run Creek. The area was long dominated by American elms until Dutch elm disease struck in the early 1970s. It now consists primarily of box elder, black cherry, hackberry, black walnut, green ash and cork elm. This community was sampled 23 times with collections taken three to five times a month from May to November, 1982, except for August and November when a single collection was made.

Drosophila were attracted to a series of six bait buckets containing a mash of fermenting bananas and bakers yeast. The buckets were on the ground approximately 15 m apart. Collections were made for about an hour in mid-afternoon by periodically placing a net over each bucket and gently tapping the bucket causing the flies to rise into the net. The flies were then transferred to bottles containing Carolina Instant Drosophila medium and brought back to the lab where they were identified. Three keys were used: Sturtevant (1921), Patterson (1943) and Strickberger (1962), with the last key being the most useful. For three species (*D. affinis, D. algonquin*, and *D. athabasca*) the males can readily be distinguished but distinguishing the females is very difficult. For most of the year males of only one species (*D. affinis*) were present and all females collected during this time were assumed to be that species. From 29 August on, when males of more than one species were collected, the females were not separated as to species.

Voucher specimens were preserved and our species designations were checked by Professor Lynn Throckmorton, University of Chicago, and Professor Marshall Wheeler, University of Texas. We attempted to raise all of the species in the laboratory in culture bottles containing Carolina Instant food. No attempt was made to determine specialized rearing conditions for species which did not grow under these conditions.

RESULTS

A total of 11 *Drosophila* species were collected from the lowland forest community. Of these one species, *D. affinis*, was by far the most common, accounting for almost two-thirds of the total sample (1824 individuals). For five other species at least 20 individuals were found and for each of the remaining five species fewer than 10 individuals were found (Table 1).

For the five rarest species it is difficult to know whether we are sampling a resident population or whether they were blown or transported in (perhaps with fruit shipments) from elsewhere. Four of

Table 1. Species abundances of *Drosophila* for the lowland forest community.

Species	Number collected	Percentage of total
D. affinis	1824	62.6
D. falleni	507	17.4
D. tripunctata	280	9.6
D. robusta	171	5.9
D. putrida	65	2.2
Undetermined *D. affinis - D. algonquin* *D. athabasca* ♀♀	25	0.9
D. athabasca	23	0.8
D. quinaria	8	0.3
D. buskii	3	0.1
D. melanogaster	3	0.1
D. algonquin	2	0.1
D. immigrans	1	0.03

the five species (excluding *D. immigrans*) were collected on at least two occasions and one of them (*D. quinaria*) was collected five different times. As the number of separate collections increases so does the probability that we are sampling a resident population.

It is noteworthy that the three rarest species, *D. buskii, D. melanogaster,* and *D. immigrans,* are closely associated with humans and are frequently found in domestic habitats (Patterson and Stone 1952). It is possible that these flies came from nearby refuse dumps or fruit markets. These species are the only three that we found that are known to be closely associated with humans. That they together comprise such a small percentage of our sample (0.24%) is encouraging and demonstrates that we are sampling a natural and not a human-associated population of *Drosophila.*

One of this group of the five rarest species (*D. algonquin*) is a sibling species of the most common species (*D. affinis*). Since these two species are closely related phylogenetically they are likely closely related ecologically as well. It is thus not surprising that only one of the two is found in appreciable numbers. Both of these species are common in the Midwest with temperature apparently playing a critical role in determining which of the two is present in a given area. *D. affinis* has a higher productivity and better competitive ability than *D. algonquin* at warmer temperatures, while at cooler temperatures the reverse is true (Fogleman and Wallace 1980; Fogleman 1982). These data are consistent with the distributions of these two species. *D. algonquin* is a more northern species and is common above about 45° latitude, while *D. affinis,* as in our sample, is very common farther south (Miller 1958).

Of the remaining six species, one (*D. affinis*) is very common while the other five are relatively common (See Table 1). For three of these (*D. falleni, D. tripunctata* and *D. robusta*) over 150 flies were collected and a resident population is clearly present whereas for the other two (*D. putrida* and *D. athabasca*) a resident population is likely. We will discuss the two least common of these five species first.

D. athabasca is closely related to the *D. affinis - D. algonquin* sibling species pair. All three species belong to subgroup b of the obscura group of the subgenus *Sophophora* (Patterson and Stone 1952). *D. athabasca* is one of the most widely distributed *Drosophila* species in North America (Miller 1958) but to our knowledge this is the first time it has been collected in Iowa. Like *D. algonquin* it does better at cooler temperatures (Fogleman 1982). It also seems to do better under moister conditions and is commonly found in the northeastern United States (Miller 1958). Although *D. athabasca* and *D. affinis* are sufficiently different ecologically to coexist in our study area and elsewhere (Miller 1958), in our study area they have population peaks at different times. Ninety-nine percent of *D. affinis* were collected before August while we did not find *D. athabasca* until late August. From late August until sampling ended in November, 23 *D. athabasca* males were collected compared to 8 *D. affinis* males (females could not be separated). These two species are coexisting spatially but coexist temporally only to a limited extent, despite their close phylogenetic relationship, due to different ecological requirements.

D. putrida was collected mainly during the spring and fall with few found during August and none found in September. Although this species is known from states on all sides of Iowa (Patterson and Stone, 1952), to our knowledge this is the first report from Iowa.

Although *D. putrida, D. falleni* and *D. tripunctata* are attracted to banana baits they are at least partly fungus feeders. Since fungal abundance is likely to be a function of rainfall, we hypothesized that within each species there would be a correlation between its relative abundance and the amount of rain that fell during either the day or week previous to each collection. All correlations between the amount of rainfall and species abundance were positive but very small and nonsignificantly different from zero. The hypothesis that there is a correlation between rainfall and the abundance of these fungus feeding species is rejected. It is possible that if we studied strictly fungus feeding species, trapped with mushroom rather than banana bait, this correlation would be significantly positive.

For three of the four remaining most common species almost all of the individuals were sampled before August, ranging from 90% of the total sample in *D. falleni* to 93% in *D. robusta* and 99% in *D. affinis* (Table 2). *D. falleni* had a small fall population peak. *D. affinis* and *D. robusta* exhibit a similar temporal pattern in other areas (Patterson and Stone 1952).

In striking contrast to the above is the pattern of *D. tripunctata* (Table 2). To our knowledge this species was previously unknown in Iowa. Seventy-six percent of the flies of this species were collected from the end of August on. Moreover, *D. tripunctata* was the dominant species during this time, comprising two-thirds of the total number of flies collected. *D. tripunctata* is evidently well adapted to conditions under which the other species are stressed and vice versa.

It is hypothesized that temperature is the major factor influencing the seasonal abundances of these four species. If this is true then the seasonal abundances of the species should be correlated with temperature and moreover the correlation should be opposite in sign for the three early year species (*D. falleni, D. robusta* and *D. affinis*) and the late year species (*D. tripunctata*).

We looked at the correlations within each species between the arc sine of relative abundance versus the average temperature for the week preceeding each collection day and independently versus the temperature of the collection day itself. The relative abundances of the three early year species are all positively correlated with temperature (although only the correlation for *D. robusta* is significant) while that of the late year species, *D. tripunctata,* is significantly negatively correlated with temperature (Table 3). The pattern of correlations in general and the specific correlations of *D. tripunctata* and *D. robusta* are consistent with our hypothesis that temperature is a major factor influencing the seasonal abundances of these species. We are further testing this hypothesis by looking at the survival of *D. tripunctata* and *D. robusta* as a function of temperature under laboratory conditions.

Six of the 11 species we collected grow well on Carolina Instant Drosophila medium and we have established cultures for the following five, *D. tripunctata, D. robusta, D. quinaria, D. buskii* and *D. immigrans.* (We did not establish cultures of *D. melanogaster,* the sixth species).

DISCUSSION

We have collected 11 species of the genus *Drosophila* from our lowland forest study site in northeast Iowa. The large number of species we found is consistent with the known great diversity of

Table 2. Seasonal abundances of the four most common species of *Drosophila* collected from the lowland forest community.

Collection Week	Species *D. affinis*	*D. falleni*	*D. tripunctata*	*D. robusta*
May 9-15	95	0	0	0
May 16-22	524	87	0	1
June 6-12	76	34	6	1
June 13-19	458	200	14	7
June 20-26	121	15	0	25
June 27-July 3	49	0	41	25
July 4-10	156	29	3	30
July 11-17	325	71	0	52
July 25-31	12	21	3	18
August 29-September 4	1[a]	3	29	1
September 5-11	4[a]	11	15	0
September 12-18	0[a]	5	42	0
September 19-25	0	4	39	2
September 26-October 2	0[a]	3	6	0
October 3-9	1[a]	15	14	4
October 17-23	0	4	36	2
October 31-November 6	0	2	2	2
November 7-13	2[a]	3	30	1
Total	1824	507	280	171

[a]Counts represent ♂♂ only (see text).

Drosophila but is almost certainly an underestimate of the true number of species in Iowa for three reasons. First, and obviously, we have only sampled a limited part of the state. As more extensive sampling is done (of more communities and perhaps of other parts of the state) more species should be found.

Second, there is an inherent bias in our sampling technique since we have only collected species which are attracted to fermenting bananas and yeast. Many *Drosophila* species have as their principal food yeasts and associated microorganisms (Carson and Stalker 1951) and it is these species that we most likely will collect. Other *Drosophila* species are only mildly attracted to such bait or find themselves near it by chance, and these will either not be collected or collected in numbers unrepresentative of their true abundance. Some of the species we found in low numbers (see Table 1) may be of this type. This bias should not affect our data on *D. buskii*, *D. melanogaster* and *D. immigrans*, the species associated with humans. They are commonly attracted to banana baits and thus their scarcity in our sample is an accurate indication of their scarcity in our sample area.

It should not be concluded from the fact that we are using bananas as bait that we are only collecting flies which feed on fruits. One of the commonly found species, *D. robusta*, breeds abundantly in the sap exudations of trees (Carson and Stalker 1951) while three others (*D. falleni*, *D. putrida* and *D. tripunctata*) are at least partially fungus feeders. However for these three fungus feeders there is a relationship between being more of an ecological generalist (Lacy 1982) and appearing more often in our collections. Thus the seeming relative abundances of these fungus feeding species may reflect more the differential attractiveness of fermenting bananas to these flies than actual relative abundances.

In order to decrease the sampling bias inherent in our collecting procedures and in order to gain more knowledge on the natural breeding sites of *Drosophila* we are currently collecting various possible foods and bringing them into the laboratory. If these foods are utilized by *Drosophila* for breeding they will contain eggs and other immature stages and we can raise adults from them.

A third bias results from the midafternoon collection time we used. Any species not active at this time will be represented poorly or not at all in our collections.

If these biases have an affect on seasonal patterns within a commonly found species it should be slight since these species are obviously well attracted to our baits. There is however a statistically significant deviation from a one to one sex ratio among collected flies for three of the species. In two there was an excess of males (*D. affinis* before 29 August, 76%, *D. tripunctata*, 63%) while in *D. robusta* there was an excess of females (69%). Similar sex ratio deviations have been previously reported (Carson and Stalker 1951) and most probably reflect differential attractiveness of the bait to the sexes rather than an actual sex ratio imbalance in nature.

On a large scale, we have added to the biogeographical knowledge of *Drosophila* in Iowa. This is particularly important since this genus has been poorly studied in Iowa. All of the species we collected belong to the eastern complex of *Drosophila* species (Patterson and Stone 1952) which is apparently closely tied to deciduous forest such as our lowland study site.

On a smaller scale, we see markedly different seasonal patterns exhibited by different species and for many of these species tempera-

Table 3. Correlations between seasonal abundance and temperature for four species of *Drosophila* from the lowland forest community.

Species	With collection day	With preceeding week
D. affinis	.373	.392
D. falleni	.194	.235
D. tripunctata	−.480[a]	−.527[b]
D. robusta	.411[c]	.425[a]

a $p < .05$
b $p < .01$
c $p \cong .05$ (cut off for significance at .05 is .413)

ture seems to be the major determinant of when a species is found. Two closely related species (*D. affinis* and *D. athabasca*) which show different seasonal patterns are known to differ in their competitive ability and productivity as a function of temperature with *D. affinis* doing better at warmer temperatures (Fogleman and Wallace 1980, Fogleman 1982). In our study the abundance of *D. affinis* is positively correlated (albeit non-significantly) with temperature. *D. athabasca* were collected on too few days to calculate a meaningful correlation of their abundance with temperature. The abundances of two other species, *D. tripunctata* and *D. robusta,* are strongly correlated with temperature but in opposite directions with *D. robusta* doing well when the temperature is high [a situation also reported by Collier (1978)] and *D. tripunctata* doing better at lower temperatures.

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REFERENCES

CARSON, H. L., and H. D. STALKER. 1951. Natural breeding sites for some wild species of Drosophila in the eastern United States. Ecology 32:317-330.

COLLIER, G. E. 1978. Brief ecological notes on *Drosophila* collections from Ithaca, New York. Drosophila Information Service 53:168-169.

FOGLEMAN, J. C. 1982. Temperature effects in relation to the patterns of distribution and abundance of three species in the *Drosophila affinis* subgroup. Ecological Entomology 7:139-148.

———— and B. WALLACE. 1980. Temperature-dependent development and competitive ability of three species in the *Drosophila affinis* subgroup. American Midland Naturalist 104:341-351.

JAENIKE, J., and D. GRIMALDI. 1983. Genetic variation for host preference within and among populations of *Drosophila tripunctata*. Evolution 37:1023-1033.

LACY, R. C. 1982. Niche breadth and abundance as determinants of genetic variation in populations of mycophagous Drosophilid flies (Diptera: Drosophilidae). Evolution 36:1265-1275.

MILLER, D. D. 1958. Geographical distributions of the American *Drosophila affinis* subgroup species. American Midland Naturalist 60:52-70.

PATTERSON, J. T. 1943. The Drosophilidae of the Southwest. University of Texas Publication 4313:46-53.

———— and W. S. STONE. 1952. *Evolution in the Genus Drosophila.* Macmillan Publishing Co., Inc., N.Y.

STRICKBERGER, M. W. 1962. *Experiments in Genetics with Drosophila,* pp. 111-123. John Wiley and Sons, Inc., N.Y.

STURTEVANT, A. H. 1921. *The North American Species of Drosophila,* Carnegie Institute of Washington Publication 301, Carnegie Institution, Washington, D.C.

WHEELER, M. R. 1981a. The Drosophilidae: A taxonomic overview. pp. 1-97. In *The Genetics and Biology of Drosophila.* Vol. 3a. M. Ashburner, H. L. Carson, and J. N. Thompson, Jr., eds. Academic Press, Inc., N.Y.

———— 1981b. Geographical Survey of Drosophilidae: Nearctic Species. pp. 99-121. In *The Genetics and Biology of Drosophila* Vol. 3a. M. Ashburner, H. L. Carson and J. N. Thompson, Jr., eds. Academic Press, Inc., N.Y.