Geographical Distributions of the American Drosophila affinis Subgroup Species[1]

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The *Drosophila affinis* subgroup belongs to the *D. obscura* group of the subgenus *Sophophora* Sturtevant. Except for one European species, *D. helvetica* Burla, 1948, the subgroup consists of eight American species: *D. affinis* Sturtevant, 1916; *algonquin* Sturtevant and Dobzhansky, 1936; *athabasca* Sturtevant and Dobzhansky, 1936; *azteca* Sturtevant and Dobzhansky, 1936; *dobzhanskii* Patterson, 1943; *narragansett* Sturtevant and Dobzhansky, 1936; *seminole* Sturtevant and Dobzhansky, 1936; and *tolteca* Patterson and Mainland, 1944. The closeness of relationship of these species is attested to not only by their morphological similarity but also by the fact that it has been possible in the laboratory to derive certain interspecific hybrids: *athabasca* x *azteca,* both reciprocal crosses (Sturtevant and Dobzhansky, 1936); *algonquin* ♀ x *athabasca* ♂ (Miller, 1939); *affinis* ♀ x *athabasca* ♂ (Miller, 1941); and *azteca* x *tolteca,* both reciprocal crosses (Patterson, 1954). Moreover, female *algonquin-athabasca* hybrids are fertile (Miller, 1941), as are both sexes of hybrids between *tolteca* ♀ ♀ and *azteca* ♂ ♂ (Patterson, 1954).

Since the *affinis* subgroup was first identified (Sturtevant and Dobzhansky, 1936), the distributions of the member species and their incidence in collections have been reported both in reports on cytological and genetic variation in the species, and in reports on *Drosophila* collecting and species distributions — for example, Dobzhansky and Sokolof (1939), Miller (1939), Patterson (1943), Patterson and Wagner (1943), Dobzhansky and Epling (1944), Patterson and Mainland (1944), Novitski (1946), Spiess (1949), Patterson and Stone (1952), Williams and Miller (1952), Levitan (1954), and Buzzatti-Traverso and Scossiroli (1955). These reports (and unpublished data) have not only led to extensions of previously known geographical ranges, but also have given better ideas of the limits of distribution of some of the species and of the relative frequencies of two or more of the species collected together. It is the purpose of this paper to summarize information on the distributions of the American members of the *affinis* subgroup, using published records and the unpublished data of the author and several other collectors.

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THE DISTRIBUTION MAP

Figure 1 shows the places at which the eight American members of the *affinis* subgroup have been collected. Specimens have mostly been individuals attracted to bait (usually fermenting banana) exposed in wooded areas. Identifications have ordinarily been based on males only, since females of these closely related species are usually difficult to distinguish. Two of the species, *dobzhanskii* and *seminole,* have each been reported from one locality only, as is designated on the map by the initial letters of these species names. On the other hand, fairly large geographical distributions are indicated for the remaining six species, as is discussed in the following paragraphs.

D. affinis is widely distributed in the eastern United States from the western Great Plains to the Atlantic coast. The species extends north as far as a line from central Minnesota to southern Quebec. Although collecting has been uneven over the eastern United States, there seems to be no reason to doubt that *affinis* is more or less continuously distributed throughout this area, especially since it has proven to be abundant in collections over most of this range (as is shown in the tables, below). Sturtevant and Dobzhansky (1936) described a *D. affinis* subspecies, *iroquois,* distinguished from typical *affinis* by somewhat darker pigmentation and reported from Massachusetts, New York, New Jersey, and Mississippi. Since this form has not been distinguished in most collections of this species, no attempt has been made to show its distribution here.

The distribution of *algonquin* broadly overlaps that of *affinis* but is distinct from it. The western boundary of the range of *algonquin* appears similar to that of *affinis.* However, *algonquin* has not been reported from the extreme southeastern part of the United States; its

southeastern boundary seems to lie near a line from southern Texas to New Jersey. The northern limits of distribution of *algonquin* would seem from the map to be similar to those of *affinis*. As is shown in Table I and further discussed below, however, *affinis* is rare in this region, while *algonquin* is often abundant. This is particularly true near the Great Lakes and the St. Lawrence River. This suggests that the actual northern boundary of the range of *algonquin* may lie well to the north of the northernmost points recorded on the map for this species.

D. athabasca has a much wider distribution than either of the other species just discussed and is, indeed, one of the most widely distributed native *Drosophila* species of North America. As is shown on the map, the range of *athabasca* extends from central Alaska to eastern Canada and to New England, southward along the Pacific coast to central Oregon, south in the Rockies to New Mexico, and

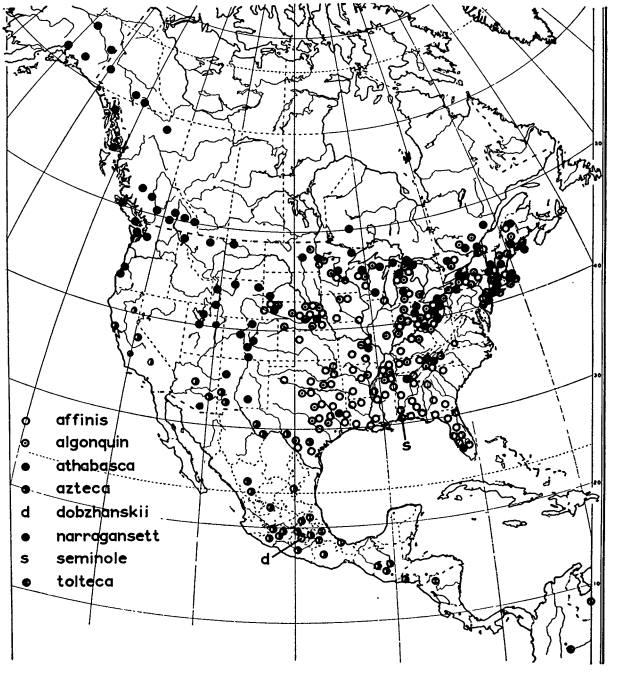

Fig. 1.—Map showing the collection localities of the eight American species of the *Drosophila affinis* subgroup. For the reason discussed in the text, *D. athabasca* is not shown at St. Louis or in Mississippi or Alabama, though the data of Tables I and III have been left unchanged as to the presence of the species in those places. (Goode's Series of Base Maps, No. 102; copyright 1937 by the University of Chicago.)

south in the Appalachians to the Great Smokies of Tennessee and North Carolina. *D. athabasca* must be much more widespread in Canada than the map shows it to be, since the species has been found to be very common at nearly all Canadian collecting localities, and these places, though widely scattered, are restricted to only a small part of that country.

Some features of the distribution of *athabasca* are doubtful. For example, the southward extent of this species along the Atlantic coast is uncertain, due to a lack of collecting records south of New York and New Jersey, where the species has been reported to be common (see Tables III and V). The question of whether *athabasca* occurs in the central and southern Middle West involves an uncertainty of another kind, a possible misidentification of *affinis* as *athabasca* in some of the collections. Males of *athabasca* are distinguishable from *affinis* and *algonquin* males by the sex combs (as illustrated in Sturtevant and Dobzhansky, 1936). The large size of the *algonquin* sex combs and their orientation nearly parallel to the axis of the first tarsal segment make males of this species especially easy to distinguish from males of the other two, both of which have small sex combs oriented at a greater angle with respect to the tarsal segment axis. On the other hand, the identification of males as either *affinis* or *athabasca* appears to have caused some difficulty in places where *affinis* presumably exists without *athabasca* or with very few of the latter species. The presence of *athabasca* in Nebraska was shown to be doubtful by Miller (1955), who proposed a sex comb index for separating males of *affinis* and *athabasca* according to the length of the sex comb relative to the length of the first tarsal segment. On this basis the conclusion of Williams and Miller (1952) that *athabasca* existed in this state is suspected of being incorrect, so the map does not show this species in Nebraska. A similar difficulty of identification may have been experienced by Carson and Stalker (1951), who reported *athabasca* as well as *affinis* at St. Louis, Missouri. These workers have kindly made available to this author both pinned and living specimens from the St. Louis area, and so far none of these has been determined to be *athabasca,* though *affinis* and *algonquin* were clearly present in their collections. On this account, *athabasca* has not been shown on the map as occurring in Missouri, and similarly it has been omitted from certain points southeast of St. Louis (Mississippi and Alabama localities, Table I) where it was recorded as present in the unpublished collection data of Dr. H. D. Stalker, although the Table I and Table III data furnished by Drs. Carson and Stalker have been left unaltered as to the presence of this species at St. Louis and the Mississippi and Alabama localities. Reports of *athabasca* in the Great Smokies of Tennessee and North Carolina are undoubtedly correct, since laboratory cultures of this species from that area have been successfully used in breeding experiments with members of the species from elsewhere (e.g., by Novitski, 1946). As a consequence of omitting *athabasca* from the lower Middle West the distribution of this species

shown on the map differs from that given in the paper of Buzzatti-Traverso and Scossiroli (1955), who showed *athabasca* to extend southward to a boundary lying across the southern plains from New Mexico to eastern Tennessee.

The original description of *athabasca* included the recognition of an eastern subspecies, *mahican* Sturtevant and Dobzhansky, 1936, characterized by paler pigmentation than that of typical *athabasca,* and reported from New Hampshire, Massachusetts, and New Jersey. Novitski (1946) concluded that laboratory stocks of *mahican* were not distinctly different from other stocks of *athabasca* in this respect and, consequently, disregarded the subspecific designation in his consideration of the species. The present author has observed that some *athabasca* collected at Cold Spring Harbor, New York, were definitely lighter than members of the species from elsewhere, including other eastern localities (Michigan, Ontario, and Quebec). However, since most collection records for this species do not include reference to the pigmentation characteristics on which recognition of *mahican* is based, it has seemed best to ignore the subspecific designation in this paper also. It should be interesting to investigate further the variation of pigmentation in eastern *athabasca.* Other evidence of intraspecific variation in *athabasca* has come from studies of sexual isolation between different geographical strains (Miller, 1958); stocks from Michigan have shown a high degree of isolation with respect to cultures from Wyoming and New York, which showed less isolation with respect to each other, but hybrids produced from successful interlocality crosses were fertile.

Figure 1 shows that *azteca* has a geographical distribution extending from northern California to Guatemala. This range appears discontinuous in places, perhaps partly due to a scarcity of collections, but probably in part due to an actual interruption of the distribution of this forest-dwelling species by the deserts of northern Mexico and the southwestern United States. *D. azteca* slightly overlaps the distributions of *affinis* and *algonquin* in southern Texas. However, it has not so far been shown to overlap the range of *athabasca* in the southern Rockies. In southern Mexico *azteca* overlaps the ranges of *dobzhanskii* and *tolteca.* Regarding the latter species, Dr. M. R. Wheeler informs the writer that *tolteca* is generally collected at lower elevations than *azteca,* suggesting some ecological isolation between these two species in their zone of overlap.

D. narragansett has a wide distribution in the eastern United States, with a range resembling very much that of *affinis.* However, unlike the other widespread *affinis* subgroup species of eastern North America, *narragansett* is very seldom common in collections in which it does occur (though in certain months it has been rather common at St. Louis, as is shown in the data of Carson and Stalker given in Table III). Consequently, data on the distribution of this species have been more difficult to evaluate than have been those of related species, and the sudden appearance of *narragansett* in certain remote collec-

tions has been rather surprising. For example, *narragansett* was not reported in Nebraska by Williams and Miller (1952), but it has since turned up in this state as a few individuals at Lincoln in the collections of Dr. Weeks (Table III) and at Chadron State Park in the collections of Miller, Sulerud, and Williamson (Table I). Dr. H. D. Stalker sent the author several specimens of this species collected at St. Petersburg, Florida, in December, 1952. Since the remoteness of that locality from previous collecting points made it seem that the specimens might not actually be *narragansett* (for example, might possibly belong to *seminole,* which *narragansett* would seem to resemble, according to Sturtevant and Dobzhansky, 1936), an attempt was made to cross females of the derived St. Petersburg strain to males of a *narragansett* stock from Amherst, Massachusetts, which had been provided by Dr. P. T. Ives of Amherst College. Since this cross yielded fertile progeny, it was concluded that the St. Petersburg form represented true *narragansett.*

D. tolteca is distributed from Mexico to the South American countries of Colombia and Venezuela. South American strains provided by Dr. M. R. Wheeler were tested by reciprocal crosses to the Nicaraguan strain by Mr. Stewart Ensign, who found that these crosses all gave fully fertile offspring and, hence, concluded that the Colombian and Venezuelan strains represented *tolteca.* The apparent discontinuous nature of the distribution of *tolteca* may well be due to a scarcity of collections in Central America.

The existence of the *affinis* subgroup elsewhere in South America remains doubtful. Duda (1927) reported *D. affinis* from Paraguay. Although it was suggested by Sturtevant and Dobzhansky (1936) that this report might involve an error of locality identification, our present knowledge of the existence of *tolteca* in northern South America makes it seem more likely that a member of the *affinis* subgroup does occur as far south as Paraguay[1].

RELATIVE FREQUENCIES OF "AFFINIS" SUBGROUP SPECIES IN EASTERN NORTH AMERICA

The four species *affinis, algonquin, athabasca,* and *narragansett* have been collected together in many places in eastern North America. Data on the relative frequencies of these species in collections should be useful for drawing conclusions concerning the centers and boundaries of their distribution areas, and for understanding their ecological relations as revealed by seasonal variation in relative frequencies and variation from place to place within the same area. Tables I - V present relative frequencies of these four species (among themselves) at various collecting localities in the eastern United States and Canada. In the majority of cases the species frequencies

[1] Recently Dr. M. R. Wheeler of the University of Texas has provided the author with a culture of what seems to be *D. tolteca* from Coroicó, Bolivia (collection of M. Wasserman).

TABLE I.—Frequencies and sex ratios of *D. affinis, algonquin, athabasca,* and *narragansett* in collections in eastern North America. Data from localities at which collections were made during no more than one month of the year or for which collecting data for more than one month were pooled.

Place and Date (Collector)	No. of flies	Species ratio of males: *aff. alg.-ath.-narrag.* (percent)	Sex ratio
NORTH OF 45° N. LATITUDE (WEST TO EAST)			
Halstad, Minn. (Sulerud) Summer, 1957	274	26-66-8-0	1:3.1
Little Falls, Minn. (Stalker) August, 1956	110	9-84-7-0	1:1.6
Iron River, Wis. (Stalker) August, 1956	120	1-53-34-0	1:2.8
Iron Mountain, Mich. (Stalker) August, 1956	216	0-17-83-0	1:2.1
Petoskey, Mich. (Stalker) August, 1956	212	3-33-64-0	1:2.3
Univ. Mich Biol. Sta. (Miller) July, 1954	1194	2-74-24-<1	1:0.9
Algonquin Pk., Ont. (Miller) August, 1956	274	1-16-83-0	1:0.8
Gatineau Pk., Que. (Miller) August, 1956	203	0-13-87-0	1:1.4
Ste. Anne de Bellevue, Que. August, 1956 (Miller)	144	1-62-38-0	1:2.2
Laurentides Pk., Que. (Miller) August, 1956	216	0-0-100-0	1:0.5
BETWEEN LATITUDES 40° AND 45° N. (WEST TO EAST)			
Chadron State Pk., Nebraska June, 1957 (Miller, Sulerud, Williamson)	252	98-2-0-<1	1:2.2
Keokuk, Iowa (Stalker) June, 1956	107	98-2-0-0	1:0.8
Crawfordsville, Ind. (Stalker) June, 1956	68	96-4-0-0	1:0.7
Plainwell, Mich. (Stalker) August, 1956	88	79-13-8-0	1:2.4
Windham, Vt. (Spiess, 1949) June-August, 1946	99	(19-4-76-0)	
Braintree & Cambridge, Mass. July-Sept., 1946 (Spiess, 1949)	150	(10-40-50-0)	
Penobscot Bay, Me. (Spiess, 1949) June, 1946	50	(0-8-92-0)	
BETWEEN LATITUDES 35° AND 40° N.			
Hopkinsville, Ky. (Stalker) June, 1956	149	100-0-0-0	1:0.7

TABLE I—(*continued*)

Place and Date (Collector)	No. of flies	Species ratio of males: *aff. alg.-ath.-narrag.* (percent)	Sex ratio
SOUTH OF LATITUDE 35° N. (WEST TO EAST)			
Austin, Texas (Wheeler)			
March, 1946	370	97-3-0-0	1:0.6
February, 1953	184	95-5-0-0	1:2.3
Collections of April, 1946 (Stalker)			
Mississippi			
Corinth	132	86-4-7-3	1:2.6
Alabama			
Hartselle	86	92-0-1-7	1:6.2
Lacon	23	91-0-9-0	1:22.0
Twin Oaks	62	95-0-5-0	1:14.5
Oak Park	96	96-0-4-0	1:47.0
Verbena	29	97-0-3-0	1:28.0
Montgomery	38	97-0-3-0	1:37.0
Orion	26	100-0-0-0	1:12.0
Troy	86	100-0-0-0	1:5.6
Ozark	19	100-0-0-0	1:8.5
Abbeville	80	99-0-1-0	1:7.0
Georgia			
Elison	324	100-0-0-0	1:1.6
Leory	201	100-0-0-0	1:2.4
Albany	262	100-0-0-0	1:1.2
Mitchell Co.	38	100-0-0-0	1:6.6
Thomasville	53	100-0-0-0	1:2.1
Florida			
Monticello	215	100-0-0-0	1:1.7
Madison	30	100-0-0-0	1:4.0
Wellborn	31	100-0-0-0	1:5.2

are based on males only (except for the data of Spiess, 1949, in Table I). Sex ratios (the species pooled for both females and males) are also included in the tables. Although all the data have been handled in essentially the same way, it seemed desirable to segregate the records in the separate tables according to the nature and extent of the information afforded.

In the majority of cases, collections were performed in a locality for only a short while (usually less than a month) during a single year, or else collection data of longer periods were pooled, thus giving no indication of possible seasonal variation at the locality. Such data have been incorporated into Table I, where they are arranged geographically in categories based on latitude zones and listed from west to east within each category. It may be seen from this table that the

relative frequencies of the four species varied greatly from place to place.

D. affinis, though generally rare north of 45° N. latitude, was usually the most common of these species throughout the eastern United States, reaching 100 percent in the extreme southeastern part of its range. *D. algonquin* may be seen to have had its highest frequencies in the north, exceeding 50 percent at places in Minnesota, Wisconsin, Michigan, and Quebec. Moreover, its frequency was consistently high at Rochester, New York (Table III). *D. athabasca* was also most frequent in the north, exceeding 50 percent at points in Michigan, Ontario, Quebec (where it reached 100 percent in the Laurentides Park), and New England. It was also the most common species at Englewood Cliffs, New Jersey (Levitan, 1954; Table III), and at all elevations in the Great Smokies near Gatlinburg, Tennessee (Table IV). *D. narragansett* was rare or absent in these collections, though it reached 7 percent at Hartselle, Alabama.

Table I also shows variation of sex ratio in the pooled data for these species. Deviations from a 1:1 sex ratio have often been

TABLE II.—Frequencies and sex ratios of *D. affinis, algonquin, athabasca,* and *narragansett* in collections in Ohio. Unpublished data of Professor W. P. Spencer and associates. Data pooled for different places within each latitude range and for different years of collection (1936 to 1947).

Places	No. of flies	Species ratio of males: *aff.-alg.-ath.-narrag.* (percent)	Sex ratio
Latitudes 41°-42° N. Counties: Defiance, Ottawa, Cuyahoga, Williams, Ashtabula Mahoning.	980	49-44-6-0	1:1.8
Latitudes 40°-41° N. Counties: Mercer, Champaign, Marion, Crawford, Richland, Ashland, Licking, Wayne, Holmes, Muskingum, Stark.	20,122	77-15-8-<1	1:2.2
Latitudes 39°-40° N. Counties: Butler, Hocking, Athens.	3,955	91-6-3-<1	1:3.1
Latitudes 38°-39° N. Scioto County.	1,162	96-<1-4-<1	1:2.7

reported in *Drosophila* collections, for example, by Levitan (1954), whose Englewood Cliffs, New Jersey, collections included a large proportion of *affinis* subgroup specimens. Table I shows that greater or less inequalities of males and females generally existed in these *affinis* subgroup species, with the deviations sometimes in one direction and sometimes in the other but most often involving an excess of males. There is no clearly evident geographical pattern for these ratios, except for the fact that the most extreme deviations from a 1:1 ratio were reported in the various localities in Alabama, where collecting was done in April, 1946, by Dr. H. D. Stalker, who informs the author that a number of those collections were made during the middle of rather hot, dry days.

Table II summarizes the extensive collection data of Professor W. P. Spencer and associates in Ohio. These data were accumulated over the years 1936 to 1947 and during various months of those years (though mainly June, July and August) and in numerous places (though most often in the vicinity of Wooster). The data have been pooled in categories based on 1° latitude bands across the state. It may be seen that *affinis* was always the most abundant of the four *affinis* subgroup species, with *algonquin, athabasca,* and *narragansett* having lower frequencies in descending order. The frequencies of *affinis* and *algonquin* clearly varied inversely with respect to each other from north to south, *affinis* having a rising gradient of frequencies (49 percent to 96 percent) in that direction, *algonquin* a descending gradient (44 percent to less than 1 percent). These variations of frequency are consistent with the general impression given in Table I that *affinis* becomes more common as one proceeds southward; *algonquin* is more abundant in the north, especially near the Great Lakes.

Table III represents collections from places at which the data of the diffeernt months and/or seasons of one or more years were segregated. The frequencies of *affinis* and *algonquin* show clear seasonal variations at Lincoln and St. Louis. In the 1947 collections at Lincoln *affinis* started out with a relatively low frequency in the spring, rose to a maximum in the summer, and became less frequent in the fall, while *algonquin* had rather high frequencies in the spring and fall and a lower one in the summer (Williams and Miller, 1952). The 1952 data from Lincoln show the same sort of frequency relationship for these species, but the frequencies of *algonquin* in that year were much lower than in the corresponding months of 1947. The data of 1953 and 1955 at Lincoln show still different frequencies of these species in the month of May. It should be added, however, that the collections of the different years were made at different collecting sites, a fact which may have contributed to the year to year differences. The St. Louis data of Drs. Carson and Stalker (unpublished) are complicated by the possibility that *affinis* may sometimes (or often) have been mistakenly reported as *athabasca.* Nevertheless the frequencies of *algonquin* — the identification of which is not doubtful — and of specimens identified as *affinis* appear to have followed much the same

TABLE III.—Frequencies and sex ratios of *D. affinis, algonquin, athabasca,* and *narragansett.* Data from localities for which collections were recorded separately for different months of one or more years.

Place and Dates (Collector)	No. of flies	Species ratio of males: *aff. alg.-ath.-narrag.* (percent)	Sex ratio
Lincoln, Nebraska (Williams and Miller, 1952)			
1947 (Williams)			
May	243	43-57-0-0	1:4.8
June	107	77-23-0-0	1:1.3
July	2,266	79-21-0-0	1:1.5
August	1,562	72-28-0-0	1:1.5
September	404	31-29-0-0	1:1.8
October	116	30-70-0-0	1:1.5
1952 (Miller)			
May	147	85-15-0-0	1:0.8
June	105	96-4-0-0	1:0.8
July	171	99-1-0-0	1:0.8
August	50	100-0-0-0	1:1.2
September	149	97-3-0-0	1:1.6
1953 (Miller, Weeks)			
May	331	64-35-0-1	1:3.7
1955 (Miller)			
May	122	73-27-0-0	1:2.7
St. Louis, Missouri (Carson and Stalker, unpublished; males only)			
1946			
February	(188)	0-100-0-0	
March	(695)	1-95-1-5	
April	(203)	5-70-8-17	
May	(2,374)	8-38-53-1	
June	(796)	30-21-21-0	
July	(788)	16-2-81-0	
August	(1,667)	30-1-69-0	
September	(400)	37-7-56-0	
October-November	(270)	7-51-41-0	
December	(258)	3-25-72-0	
1947			
May	(574)	6-32-61-1	
June	(302)	12-27-62-0	
September	(406)	14-14-61-0	
October	(983)	11-7-82-0	
Rochester, New York (Miller)			
1941			
June	538	4-93-2-1	1:4.2
July	959	3-95-2-0	1:3.1
August	324	5-92-3-0	1:2.5
Englewood Cliffs, New Jersey (Levitan, 1954; *ath.* & *narrag.* together)			
1948			
May-June	1,435	13-8-79	1:3.9
August-October	1,960	12-4-84	1:3.0
1949			
March-April	531	1-13-87	1:2.1
May-June	1,452	1-6-93	1:2.0

sort of pattern of seasonal variation reported for these species at Lincoln. The Rochester, New York, data for June through August of 1941 are remarkable in that they show uniformly very high frequencies of *algonquin*. The Englewood Cliffs data (Levitan, 1954) show that in each of the two years *algonquin* was more abundant in collections early in the season than it was later.

Table IV is a presentation of unpublished collecting data of Drs. Carson and Stalker at different elevations in the Great Smoky Mountains of Tennessee. Here *narragansett* was not reported and *algonquin* had uniformly low frequencies at the different altitudes. The identifications of *affinis* and *athabasca* may be considered more reliable than those of the St. Louis data of Table III, since *athabasca* is definitely known from the Great Smokies. It may be seen that *athabasca* was reported as the most common of these species at all elevations and from a minimum frequency at 1400 ft. it was shown to have a rising gradient of frequencies with increasing altitude, reaching a 99 percent maximum at the highest elevation, 6,000 ft. Conversely, the frequencies of *affinis* decreased with increasing altitude from 1400 to 6000 ft.

Table V is based on data from collections of the author at Cold Spring Harbor, New York, during three weeks from mid-August to early September, 1955. These data have been segregated from the rest because the collection effort was divided more or less equally between two rather different sites, and between mornings and evenings, and these different sites and collecting times gave certain differences (in some cases significant) of species frequencies (*affinis* and *athabasca*) and sex ratio. Site A was a rather wet (springs and almost marshy surroundings) situation just north of the Long Island Biological Association laboratories. Site B was a relatively dry, sloping, well-drained location near the buildings of the Carnegie Institution of Washington and the Long Island Biological Association, approximate-

TABLE IV.—Frequencies and sex ratios of *D. affinis, algonquin,* and *athabasca* collected at different elevations in the Great Smoky Mountains near Gatlinburg, Tennessee, in July, 1947. Unpublished data of Drs. H. L. Carson and H. D. Stalker.

Elevation (feet)	No. of flies	Species ratio of males: *affinis-algonquin-athabasca* (percent)	Sex ratio
1,000	120	16-1-83	1:2.8
1,200	258	30-1-69	1:4.4
1,400	468	41-1-59	1:2.8
2,000	1,137	22-1-78	1:2.3
3,000	1,089	15-1-84	1:2.4
4,000	1,330	12-1-88	1:2.4
5,000	276	5-0-95	1:2.6
6,000	201	1-0-99	1:2.1

ly 1000 ft. south of Site A. Table V shows that *affinis* was invariably less common at Site A than at Site B and, conversely, *athabasca* always more common at Site A than Site B. Moreover, application of the Chi-square test showed the frequencies of these two species were significantly different at the two localities not only for the totals of morning and evening collections for the entire period but also for the separate weeks of the collecting period. In addition, the frequencies of *affinis* and *athabasca* differed in the morning and evening collections, especially at Site A, where *affinis* was always more common in the evening than in the morning, *athabasca* more common in the morning than in the evening, with the difference in relative frequencies of these species between mornings and evenings being highly significant in the entire collection totals and in the totals for the first week (though not in those of the second and third weeks). It may also be seen from Table V that the sex ratio varied from place to place and time to time. Some of the sex ratio differences were calculated to be significant. A highly significant sex ratio difference between the two localities was found in the morning collections of the first week, and the morning collections of the second and third week showed significant differences between sex ratios at the two sites, but the differences were in the opposite direction from that of the first week! At Site A in the third week there was a highly significant difference between morning and evening sex ratios.

DISCUSSION OF THE INCIDENCE AND DISTRIBUTION OF "AFFINIS," "ALGONQUIN," AND "ATHABASCA" IN EASTERN NORTH AMERICA

The geographical range of a *Drosophila* species may well be considered to be a dynamic entity, as was emphasized, for example, by Carson 1955), who stressed the dynamic nature of intracontinental boundaries of a species range. Within the region covered by such a species there must be much variation in population density, depending on variation of the environment from place to place within this area. Moreover, with changes of the environment (seasonal, year to year), the *Drosophila* populations should change rather rapidly, since these insects have short life cycles and the adults presumably do not live very long. The distribution boundaries of such a species should likewise fluctuate, except inasmuch as they are fixed by natural barriers, such as an ocean. With changing environmental conditions a species may sometimes extend itself into previously unoccupied territory, sometimes withdraw from a region, possibly leaving isolated subpopulations behind.

There are many difficulties in the way of getting a very accurate picture of the geographical distribution of a *Drosophila* species. For one thing, the data on which such a picture is based must necessarily come from numerous sources, representing the collections of various investigators at different times and places. The records may be complicated by difficulties of species identification. Since collections

TABLE V.—Frequencies and sex ratios of *D. affinis, algonquin,* and *athabasca* in collections at Cold Spring Harbor, New York, 1955. Data separated according to week, collecting area, and time of day. Descriptions of collecting areas given in text.

Week Collecting Area Time of Day	No. of flies	Species ratio of males: *aff.-alg.-ath.* (percent)	Sex ratio
First week (13-19 August 1955)			
Site A			
Morning collections	245	38-1-61	1:1.1
Evening collections	292	58-1-41	1:1.5
Site B			
Morning collections	96	66-1-33	1:3.6
Evening collections	96	75-0-25	1:1.9
Second week (20-26 August 1955)			
Site A			
Morning collections	257	39-1-60	1:2.1
Evening collections	196	45-3-52	1:1.7
Site B			
Morning collections	28	73-0-27	1:1.2
Evening collections	34	88-0-12	1:2.4
Third week (27 August - 2 September 1955)			
Site A			
Morning collections	145	48-5-47	1:3.7
Evening collections	298	54-4-42	1:1.7
Site B			
Morning collections	111	72-7-21	1:2.2
Evening collections	211	73-<1-27	1:1.9
Entire Collecting Period (13 August - 2 September 1955)			
Site A			
Morning collections	647	41-2-57	1:1.8
Evening collections	786	53-3-44	1:1.6
Site B			
Morning collections	235	69-4-27	1:2.4
Evening collections	341	75-<1-25	1:2.0

will have been made in different years and different seasons, the combined data can hardly be considered to afford anything like a synoptic picture of a species distribution. Moreover, only rarely will collections at the same locality be sufficiently prolonged to give an idea of seasonal or year to year changes. The difficulty due to seasonal variation may, however, be somewhat counterbalanced by the fact that, especially in northern latitudes, most collecting will have been concen-

trated in summer months, when it might be expected that the *Drosophila* populations are at a maximum.

The already mentioned seasonal variation of relative frequencies of *affinis* and *algonquin* at Lincoln and St. Louis (Table III may well represent a general relationship of these species at places where they coexist, though the actual freqeuncies may vary considerably from place to place and year to year (as is also indicated in the table). In the cooler parts of the year, *algonquin* is relatively abundant, sometimes even more common in collections than *affinis,* though in most of the collections at Lincoln and St. Louis *affinis* (or *affinis* plus *athabasca* at St. Louis?) was the more common species. This relationship seems consistent with the fact that *algonquin* is generally a more northern species than *affinis,* with much higher frequencies than *affinis* at the northernmost places where they are found together. On the other hand, one might wonder whether *algonquin* could be collected in those southern localities where it has not been found if collecting were conducted during the coolest part of the year, at least in years of unusually cool weather.

As mentioned earlier, most of the collecting on which this report is based was done by exposing bait, usually fermenting banana, and collecting from the flies attracted to the bait. This introduces another variable: presence and absence of species and variation of relative frequencies of the species (and of the sexes) in collections may well have been influenced not only by the numbers of the different kinds in the population but also by differential mobility of the different kinds of flies to the bait. In addition to this factor of differential mobility there are possibly environmental factors which influence the collecting. These include temperature, illumination, humidity, wind, and the nature and condition of the bait. It has not generally been the practice to secure data on such environmental factors at the times of collection.

The collections at Cold Spring Harbor (Table V) give some insight into the possible influence of environmental factors on the collection of the *affinis* subgroup species. Unfortunately, these collections, which were made to obtain *athabasca* for experimental work, were not accompanied by the taking of records on ecological conditions, so only a general idea of the circumstances attending the collections can now be had. As already mentioned, Site A had more moisture than Site B. It is also true that mornings generally gave the impression of a higher humidity than evenings, judging from the heavy dew often encountered on the vegetation in the mornings but not in the evenings. As was already pointed out, Table V shows that *athabasca* was invariably more common at Site A than at Site B and, moreover, that at Site A *athabasca* was always more common in the mornings than in the evenings. The difference between the species frequencies at the two collecting sites could, of course, have been due to a more abundant breeding of *athabasca* at Site A than at Site B (and conversely for *affinis*). The evidence of morning-evening differ-

ences in the frequencies of the two species at Site A would seem to mean that the diurnal variation of environmental conditions, perhaps largely a change of humidity, influenced differentially the mobility of the two species to the bait, the movement of *athabasca* being favored by a high relative humidity. Hence the over-all higher frequency of *athabasca* at Site A may have been due to a greater mobility of *athabasca* at Site A. Information on the actual breeding sites of these two species at Cold Spring Harbor or similar places would be most interesting. Inasmuch as variation in sex ratio in the different collections at Cold Spring Harbor may be taken as significant, it likewise suggests a differential influence of the environment on the mobility of the two sexes to the bait.

Although the *affinis* subgroup species *affinis, algonquin,* and *athabasca* are together the most abundant native *Drosophila* species of eastern North America, very little is known about their ecological relations, in particular, their breeding sites. These species are, however, regularly found in forests, and there is some evidence of their association with trees and other plants of the forests. Sturtevant (1921) writes that *affinis* is not rare about bleeding trees, and in Sturtevant and Dobzhansky (1936) it is stated that Sturtevant collected members of the *affinis* subgroup by sweeping a net over tree trunks and obtaining specimens on bleeding trees. Carson and Stalker (1951) reported that at St. Louis *affinis* was found breeding in small fruits, and *athabasca* (though possibly *affinis?*) in fleshy fungi, slime fluxes of red oak, and in small fruits, though the frequencies with which these breeding sites were encountered were so low that it seemed that these very common species must have had other more important natural breeding sites. Wheeler (as reported in Patterson and Stone, 1952) reported *affinis* breeding in the sap of a bleeding wild grapevine in Texas. In the summer of 1956 the present author bred a single *D. algonquin* female out of a fleshy fungus collected in Algonquin Park, Ontario.

In spite of uncertainties as to the faithfulness with which the available data reveal the geographical distributions of *affinis, algonquin,* and *athabasca,* some tentative conclusions on these distributions may be drawn, with speculations on some details of the distributions and the probable factors responsible for the distributions.

Judging from its high relative frequencies (with respect to *algonquin*) during the summer at Lincoln and St. Louis (Table III), *D. affinis* seems to be primarily a species of the southeastern United States, generally favored by high temperatures and/or other summer conditions. The western limit of its range appears to lie close to the western boundary of the Great Plains and may well be very irregular, following the vegetation along river bottoms, as is reported for *D. robusta* by Carson (1955), though, unlike *robusta,* no such natural breeding site as the American elm (which harbors *robusta*) is known. Collection records are too meager to serve as a basis for describing the western boundary of this species. With respect to other members of

the *affinis* subgroup, *affinis* is relatively very frequent even in the westernmost part of its range (Chadron State Park, Nebraska, Table I). However, with respect to the more distantly related *D. pseudoobscura* (*obscura* subgroup of the *obscura* group), *affinis* diminishes in frequency westward across Nebraska while *pseudoobscura* increases (a similar relationship exists in Texas; Patterson and Wagner, 1943). As mentioned earlier, *affinis* diminishes in the north so as to be rare relative to *algonquin* and/or *athabasca* in a zone extending from Minnesota to Quebec and New England. The high relative frequency of *affinis* at Halstad, Minnesota, with respect to other places north of 45° N. latitude (Table I) and the somewhat low frequencies of *affinis* in New England with respect to places farther west between 40° and 45° suggest that the northern boundary of this species is oriented in a northwest-southeast direction rather than east and west (though the species has not yet been reported from North Dakota, perhaps because of a scarcity of collections).

D. algonquin appears to be a northern species with its greatest abundance in the Great Lakes and St. Lawrence region. In general its frequencies diminish to the west, south, and east of this area (Tables I and II), but even remote from this region (Lincoln and St. Louis) it reached high frequencies in the cooler months of the year (Table III). As already mentioned, the western boundary of *algonquin* appears similar to that of *affinis*. In the east (Quebec, New England) it decreases with respect to *athabasca*. This may be true in the north as well, but a lack of collections in Canada north of the Great Lakes makes it impossible to show this. In other directions it decreases with respect to *affinis*. Low frequencies of this species in such southeastern and southern points as Gatlinburg, Tennessee (Table IV), and Austin, Texas (Table I), suggest that the species approaches the margin of its distribution near those places, as does the absence of reports of this species in the extreme southeast (Table I). Though it remains to be investigated, there would seem to be a reasonable possibility that the southeastward extent of this species is limited by the southeastern boundary of the hardwood forests and that the species is excluded from the southeastern evergreen forests of the Atlantic and Gulf coasts (judging from the limits of these forest regions shown in Braun, 1950).

D. athabasca is an inhabitant of the boreal forests of Alaska and Canada, but it extends southward well out of this region. In eastern North America this was the only species of the subgroup collected in the boreal forest of the Laurentides Park, Quebec (Table I), but in the mixed or hardwood forests where it was otherwise collected in the east it was invariably obtained along with other species of its subgroup. Its probable absence in most of the Great Plains and in the lower Middle West has already been mentioned. In the eastern United States and adjacent Canada its highest relative frequencies have been in the northern Great Lakes region, lower Ontario and Quebec, New England, and at high elevations in the Great Smokies, suggesting a preference for cool, damp situations, such as is also sug-

gested by its high frequencies at Site A at Cold Spring Harbor and in the morning collections at that location (Table V).

It would be desirable to have more collection records in which the *affinis* subgroup species were distinguished, both at new localities and at different times of the year. Eventually it may be hoped that important natural breeding sites of these species will be discovered. Knowledge of these should help in the evaluation of the variations in abundance of these species from place to place and from time to time.

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