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# SEXUAL ISOLATION AND VARIATION IN MATING BEHAVIOR WITHIN *DROSOPHILA ATHABASCA*

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*Drosophila athabasca* Sturtevant and Dobzhansky 1936 is a member of the *affinis* subgroup (Subgroup b) of the *obscura* group of the subgenus *Sophophora* (Patterson and Stone, 1952). It is widely distributed in the forests of northern North America from Alaska to eastern Canada and southward in the mountains to New Mexico in the west and to Tennessee in the east (Sturtevant and Dobzhansky, 1936; Novitski, 1946). The original description of this species included the recognition of an eastern subspecies, *mahican*, with somewhat lighter pigmentation than the western form. However, Novitski (1946), who studied the salivary gland chromosomes of both western and eastern *athabasca*, found no evidence that the subspecific designation should be maintained for the laboratory stocks at his disposal; neither morphological differentiation nor detectable reproductive isolation distinguished these western and eastern stocks.

*D. athabasca* is rather difficult to maintain in the laboratory, though it sometimes breeds well enough. Yields of flies per culture container vary widely, presumably due to microenvironmental variation, and stocks are frequently lost. By 1954 none remained of the older laboratory strains of *athabasca*, such as those studied by Sturtevant and Dobzhansky (1936), Novitski (1946), and Miller

(1950a, 1951). In recent years a number of new cultures have been established, and attempted crosses between these have shown that a fairly high degree of sexual isolation exists between certain geographically different strains. Moreover, an aspect of mating behavior, duration of copulation, has been found to vary widely in these strains. Although the available information is not sufficient to show the pattern of this variation, the data are presented here on the grounds that they do establish the existence of appreciable intraspecific sexual isolation and mating behavior variation in this widely distributed North American species.

## SEXUAL ISOLATION IN "NO-CHOICE" COMBINATIONS INVOLVING WYOMING AND MICHIGAN STRAINS

In the summer of 1954 new strains were established from collections at the Jackson Hole Biological Research Station near Moran, Wyoming, and at the University of Michigan Biological Station (U.M.B.S.) near Cheboygan, Michigan. To study the inheritance of a mutant character (rough eyes) that appeared in one of the Michigan strains, a few crosses were attempted between mutant Michigan females and normal Wyoming males. None of these produced any progeny. Additional attempts to make the two reciprocal crosses between Wyoming and Michigan *athabasca* also failed, though several strains of each kind were used. (Unfortunately, the mutant strain died out before it could be used in more extensive crosses, so the interlocality crosses had to be performed largely with wild type strains.)

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TABLE 1. Cases of *D. athabasca* females inseminated after 10 or 11 day cohabitations in "no choice" (one kind of female, one kind of male) combinations involving Wyoming and Michigan (*U.M.B.S.*) strains

(The number in parentheses after each combination indicates the number of strain combinations included in the pooled data.)

| Combination                 | Number of females | Females inseminated |          |
|-----------------------------|-------------------|---------------------|----------|
|                             |                   | Number              | Per cent |
| Wyoming ♀ × Wyoming ♂ (5)   | 182               | 136                 | 75       |
| Michigan ♀ × Michigan ♂ (6) | 193               | 133                 | 69       |
| Wyoming ♀ × Michigan ♂ (12) | 242               | 2*                  | 1        |
| Michigan ♀ × Wyoming ♂ (14) | 233               | 0                   | 0        |

\* Adult hybrids accompanied one of these cases.

The existence and degree of sexual isolation were next investigated by way of 10 and 11 day combinations of one kind of female with one kind of male (both intra- and inter-locality) followed by examination of the seminal receptacles of the females for sperms. Females and males were obtained from culture bottles from which flies had been removed no earlier than two days before (*athabasca* has been found to breed no sooner than three days after emergence). Due to variation in culture bottle yields during the time of this experiment it was not considered practical to restrict the combinations always to the same numbers of flies, so the number of each sex was permitted to vary from 5 to 20 per bottle, though the ratio of females to males was always kept close to 1:1. Moreover, mortality of the flies during cohabitation caused some additional variation in the numbers of individuals. An attempt was made to use flies from as many different strains as possible from each locality, since it was expected that if any showed a radical difference from the rest, the difference would be detected and could then be investigated further. However, since there was no strikingly great difference between the results with the different strains, the results have been pooled. All combinations were made in half-pint milk bottles containing standard *Drosophila* food (corn meal-molasses-agar-Tegosept-yeast), the surface of the

food being dusted with sawdust in the hope of preventing the flies from getting stuck. The data were accumulated from November, 1954, through February, 1955, the culture and combination bottles being kept in a room in which the temperature varied from about 17 to 24° C. (as with subsequent cultures and crosses).

Table 1 shows the pooled results of the "no-choice" combinations of Wyoming and Michigan *athabasca*. It can be seen that, although in the intralocality combinations the frequency of females found inseminated was about 75% in the Wyoming strains and 69% in the Michigan strains, none of the 233 Michigan females confined with Wyoming males was found inseminated, and only two out of the 242 Wyoming females kept with Michigan males were found with sperms in their receptacles. Adult offspring (13 females and 5 males) were recovered in one of the two culture bottles in which interlocality insemination was found. Although attempts to mate these to the parent strains and to each other were not successful, the males were found to have fully developed testes containing sperms. More than two years later (1957) this cross was confirmed by successful matings between Wyoming females with a sex-linked recessive mutant gene (bright red eyes) and Michigan males; the daughters were wild type and

sons bright-eyed, and these were fertile when mated to each other.

During this time strains of *athabasca* were obtained from Minnewaukan, North Dakota, and Cedar Lake, Ontario (near the western boundary of the province; this strain kindly furnished by Professor Th. Dobzhansky and Mr. B. Spassky), and these were employed in a few inter-locality crosses. Unfortunately, both these strains were lost before they could be used extensively to study sexual isolation. Nevertheless, both North Dakota and western Ontario strains crossed rather easily with strains from Wyoming, producing numerous fertile hybrids, while neither crossed successfully with the Michigan strains employed. Moreover, as reported below (table 4), the North Dakota and western Ontario *athabasca* were found to resemble the Wyoming strains in copulation time.

*D. athabasca* is known to hybridize in the laboratory with the closely related

species *azteca* (Sturtevant and Dobzhansky, 1936) and *affinis* and *algonquin* (Miller, 1950a). To test the crossability of the available Wyoming (and North Dakota) and Michigan strains of *athabasca* with these other species, cross combinations of these strains with stocks of *affinis* (Florida, Illinois, Nebraska, Tennessee, Texas), *algonquin* (Michigan, Nebraska), and *azteca* (California) were made in the manner already described for the intraspecific combinations. It may be seen in table 2 that, although no interspecific inseminations were found in combinations of *algonquin* and *athabasca*, interspecific inseminations were discovered in combinations of *affinis* females with both Wyoming (and North Dakota) and Michigan *athabasca* males and in all combinations of *azteca* with *athabasca* from the different localities, the frequencies of insemination varying widely from one combination to another but being regularly greater than in the combina-

TABLE 2. *Frequencies of inseminations after 10-day combinations of D. affinis, D. algonquin, and D. azteca, both intra-specific and with D. athabasca*

(The number in parentheses after each combination indicates the number of strain combinations included in the pooled data.)

| Combination  | Number of females | Females inseminated |          |
|--|-------------------|---------------------|----------|
|  |                   | Number              | Per cent |
| <i>D. affinis</i> ♀ × <i>D. affinis</i> ♂ (6)          | 101               | 98                  | 97       |
| <i>D. algonquin</i> ♀ × <i>D. algonquin</i> ♂ (3)      | 106               | 84                  | 72       |
| <i>D. azteca</i> ♀ × <i>D. azteca</i> ♂ (2)            | 106               | 97                  | 92       |
| <i>D. aff.</i> ♀ × <i>D. ath.</i> (Mich.) ♂ (6)        | 121               | 7                   | 6        |
| <i>D. aff.</i> ♀ × <i>D. ath.</i> (Wyo. & N. D.) ♂ (8) | 135               | 39                  | 29       |
| <i>D. ath.</i> (Mich.) ♀ × <i>D. aff.</i> ♂ (7)        | 104               | 0                   | 0        |
| <i>D. ath.</i> (Wyo. & N. D.) ♀ × <i>D. aff.</i> ♂ (4) | 109               | 0                   | 0        |
| <i>D. alg.</i> ♀ × <i>D. ath.</i> (Mich.) ♂ (7)        | 101               | 0                   | 0        |
| <i>D. alg.</i> ♀ × <i>D. ath.</i> (Wyo. & N. D.) ♂ (9) | 114               | 0                   | 0        |
| <i>D. ath.</i> (Mich.) ♀ × <i>D. alg.</i> ♂ (8)        | 107               | 0                   | 0        |
| <i>D. ath.</i> (Wyo. & N. D.) ♀ × <i>D. alg.</i> ♂ (9) | 111               | 0                   | 0        |
| <i>D. azt.</i> ♀ × <i>D. ath.</i> (Mich.) ♂ (5)        | 109               | 50*                 | 46       |
| <i>D. azt.</i> ♀ × <i>D. ath.</i> (Wyo. & N. D.) ♂ (5) | 100               | 8                   | 8        |
| <i>D. ath.</i> (Mich.) ♀ × <i>D. azt.</i> ♂ (5)        | 104               | 2                   | 2        |
| <i>D. ath.</i> (Wyo. & N. D.) ♀ × <i>D. azt.</i> ♂ (5) | 108               | 29*                 | 27       |

\* Certain crosses yielded hybrids, these agreeing as to abnormalities already reported for such hybrids (Sturtevant and Dobzhansky, 1936).

TABLE 3. *Frequencies of D. athabasca females inseminated in three-day "choice" matings (two kinds of females with one kind of male) after seven days of ageing in isolation*

|                                | Homogamic<br>inseminations | Heterogamic<br>inseminations | Chi-square | Isolation<br>index |
|--------------------------------|----------------------------|------------------------------|------------|--------------------|
| Wyo. ♂♂<br>Wyo. ♀♀, Mich. ♀♀   | 67/90 (74%)                | 3/87 (3%)                    | 93.439     | 0.92               |
| Mich. ♂♂<br>Mich. ♀♀, Wyo. ♀♀  | 68/97 (70%)                | 7/98 (7%)                    | 81.068     | 0.82               |
| Wyo. ♂♂<br>Wyo. ♀♀, N. Y. ♀♀   | 85/100 (85%)               | 35/100 (35%)                 | 52.084     | 0.42               |
| N. Y. ♂♂<br>N. Y. ♀♀, Wyo. ♀♀  | 72/100 (72%)               | 24/99 (24%)                  | 46.371     | 0.50               |
| Mich. ♂♂<br>Mich. ♀♀, N. Y. ♀♀ | 79/102 (77%)               | 1/101 (1%)                   | 101.912    | 0.97               |
| N. Y. ♂♂<br>N. Y. ♀♀, Mich. ♀♀ | 62/102 (61%)               | 0/101 (0%)                   | 72.102     | 1.00               |

tions of Wyoming and Michigan *athabasca* with each other.

SEXUAL ISOLATION IN "CHOICE" COMBINATIONS OF STRAINS FROM WYOMING, MICHIGAN, AND NEW YORK

Because the sexual isolation reported here between Wyoming and Michigan *athabasca* was unexpected in view of Novitski's findings (1946), it was considered desirable to investigate the possibility of sexual isolation using strains of this species originating east of Michigan, since the eastern strains of *athabasca* used by Novitski had been obtained from Quebec, New England, New York, and North Carolina. In the summer of 1955 new *athabasca* cultures were established from collections at Cold Spring Harbor, New York.

Preliminary crosses between the New York strains and those from Michigan and Wyoming were made in October and November, 1955; these were 10-11 day "no-choice" combinations similar to those already described except that, since the New York strains were not yet well established, all combinations involved New York males (of various ages) with

females of the other localities. These crosses showed that New York males would mate with both Wyoming and Michigan females. Of 132 Wyoming females kept with New York males, 55 (42%) were found inseminated. Of 82 Michigan females confined with New York males, 5 (6%) were inseminated. Moreover, both these crosses yielded fertile offspring.

Crosses were next performed in which males had their "choice" of two kinds of females. The following procedure was used. Females and males were separated within 24 hours of emergence and kept isolated in culture bottles for 6 days. They were then transferred to vials (still in isolation) and given fresh food. On the 7th day a number of males (varying from 5 to 20) were put in a culture bottle with the same or a similar number of each of two different kinds of females. Since the females from the different localities could generally not be distinguished, one kind regularly had the left wing clipped off and the other kind the right wing, the relationship as to right and left wing being reversed in about half the cases of each combination. Eight different New York strains participated in these crosses. However, due to losses

of strains during the summer of 1955, Wyoming was now represented by only one strain, Michigan by only three. Each locality combination involved several strain combinations. Cohabitations lasted from the 7th to the 10th day, on which females were dissected and their receptacles examined for sperms. Data were collected from March through July of 1956.

Table 3 shows the results of the "choice" combinations. The isolation indexes were calculated according to the method of Charles and Stalker (Stalker, 1942). It may be seen that a high degree of mating preference existed in all cases. The strongest sexual isolation was apparent between New York and Michigan. For instance, no Michigan females were inseminated by New York males, although the "no choice" combinations of the previous fall had shown some insemination in this combination, as well as fertile hybrids. The least isolation existed between Wyoming and New York. However, even in combinations of flies from these localities, there was a fairly high degree of sexual isolation. The combinations of Wyoming and Michigan gave intermediate results. It may also be seen that the frequencies of insemination between Wyoming and Michigan were much higher in these "choice" combinations than had been observed in the "no-choice" matings between strains of these localities the year before.

#### OBSERVATIONS OF MATING BEHAVIOR

Mating behavior was observed in approximately one week old adults in both intra- and inter-locality combinations, the flies having been aged in isolation for six days and then put together in a clean vial on the 7th day. As reported by Miller (1951), courtship in *athabasca* differs from that of the closely related species *affinis* and *algonquin* (Miller, 1950b) in that *athabasca* males usually (though not invariably) extend and vibrate one wing rather than both wings.

However, no significant differences in courtship behavior could be detected between the different strains of *athabasca*. Nevertheless, when females of one locality were combined with males of another, courtship appeared less vigorous and was much less often successful (usually unsuccessful) than in the intra-strain combinations.

Durations of copulation were determined for the existing strains of *athabasca*, as had been done earlier for older strains (lost before the present study began) from Cold Spring Harbor, New York, and Princeton, New Jersey (Miller, 1951). The prevailing temperatures during these observations varied from about 23° C. to 29° C. Nevertheless, although copulation time varied considerably in the different strains (especially the western ones), there was no obvious relationship between temperature and copulation time (such as, for example, was reported for *D. algonquin* by Miller, 1950). Consequently, the data have been pooled without regard for temperatures. The durations of copulations observed are given in table 4, which also includes data from Miller (1951). It may be seen that the durations of copulation were strikingly different between the western and eastern strains of *athabasca*. In the western strains (Wyoming, North Dakota, western Ontario) copulation time was never less than 3' 57", while in the eastern ones (Michigan, New Jersey, New York) copulation time never exceeded 2 minutes. Consistent with the observation of relatively long copulation in the western strains studied here is the report of Spieth (1952) that a Wyoming strain of *athabasca* (Sundance) had 5 observed copulations range from 7' 10" to 10' 5", with a mean of 7' 45", all well within the range of copulation times of Wyoming (and other western) *athabasca* reported here.

An attempt was made to determine durations of copulation in combinations of *athabasca* from Wyoming and New York and in descendants derived from such matings. The results of these ob-

TABLE 4. Durations of copulation in matings of *D. athabasca* within strains from different localities (all first matings of approximately week old adults)

(The number in parentheses after each place name indicates the number of strains contributing to the pooled data.)

| Locality  | Durations   | Mean  |
|---|---|-------|
| Moran, Wyoming (5)  | 3'57", 4'1", 4'15", 4'17", 4'26", 4'54",<br>4'55", 4'58", 5'1" (2), 5'2", 5'16", 5'19",<br>5'20", 5'25", 5'32", 5'38", 5'41", 6'0",<br>6'13", 6'14", 6'15", 6'27", 6'32", 6'41",<br>7'48", 7'56", 8'25", 9'54", 11'3", 11'36" | 6'8"  |
| Moran, Wyoming<br>(mutant strain:<br>"bright eyes")                           | 4'50", 5'29", 6'14", 6'35"  | 5'47" |
| Minnewaukan, N. D. (1)  | 6'50", 7'27", 7'37", 8'25"  | 7'35" |
| Cedar Lake, Ont. (1)  | 4'35", 7'16"  | 5'56" |
| Cheboygan, Mich. (6)  | 1'4", 1'6", 1'9", 1'10", 1'12", 1'19",<br>1'21", 1'33" (2), 1'34" (3), 1'35", 1'40",<br>1'41", 1'47", 1'56", 1'59", 2'0"  | 1'31" |
| Cold Spring Harbor, N. Y.,<br>and Princeton, N. J.<br>(1 each) (Miller, 1951) | 1'12" (2), 1'13", 1'15", 1'23" (2), 1'25"<br>(2), 1'26", 1'27", 1'40", 1'42", 1'48"   | 1'25" |
| Cold Spring Harbor, N. Y. (5)   | 0'32", 0'42", 0'52", 0'56", 0'59", 1'6",<br>1'9", 1'17", 1'25", 1'46"   | 1'11" |

servations are given in table 5. Though the results are rather meager, especially for certain combinations (due to difficulties in getting matings and in getting hybrids between Wyoming females and New York males), they suggest something concerning the basis for the difference of copulation times between the Wyoming and New York strains. The few interlocality matings suggest that copulation time is determined by the male, such as has been reported in certain other species, for example, *D. subobscura* (Milani, 1952). The matings of  $F_1$  females and males and of  $F_1$  males with parent strain females had durations that extended well into the time zone that separated the durations observed for the Wyoming and New York strains—i.e., from 2' to 3' 57". A few facts point to an influence of the male partner's X-chromosome on copulation time. The

few copulations observed between  $F_1$  females and males of the Wyoming female by New York male cross were all longer in duration than any observed involving  $F_1$  males of the reciprocal cross. Moreover,  $F_2$  males that had received the sex-linked recessive mutant gene for bright eyes from Wyoming males mated to New York females (and, consequently, must have had at least part of a Wyoming X-chromosome) had matings that were generally longer than those involving wild-type  $F_2$  males (with New York X-chromosome material) from the same crosses.

#### CROSSABILITY AND MATING BEHAVIOR OF NEW STRAINS FROM WISCONSIN, MICHIGAN, ONTARIO, AND QUEBEC

During the summer of 1956 collections by the author in southern Ontario (Al-

gonquin Park) and Quebec (Gatineau Park, Ste. Anne de Bellevue, Laurentides Park) made possible the establishment of new strains of *athabasca* from these places. Also, Dr. H. D. Stalker of Washington University kindly made available *athabasca* from his collections in northern Wisconsin (Iron River) and Michigan (Iron Mountain), from which new strains were derived. Although these stocks have not yet been used in sexual isolation experiments such as those already described, attempts to hybridize the new strains with the old ones from Wyoming, Michigan (U.M.B.S.), and New York (all possible combinations of new localities with old ones having been attempted) have given difficulties suggestive of such isolation. So far only the following crosses have yielded hybrids (all of which were fertile): Wyoming females by Iron River males; Iron Mountain females by

U.M.B.S. males; Wyoming females by Algonquin Park males, both reciprocal crosses of Algonquin Park by U.M.B.S.; both reciprocal crosses of Gatineau Park by U.M.B.S.: both reciprocal crosses of Ste. Anne de Bellevue by U.M.B.S.; and Wyoming females by Laurentides Park males.

Table 6 shows durations of copulation observed in the recently established strains of *athabasca*. Although the small numbers of observations afford little basis for comparing these strains with each other or with the older ones, it may be seen that the long copulation time characteristic extends into the east, being especially prominent in the easternmost strains (Laurentides Park), and that some strains expressed both long and short copulation times (in particular, certain ones from Iron Mountain and Gatineau Park).

TABLE 5. Durations of copulation in mating combinations of Wyoming and New York *D. athabasca* (one strain from each locality) and of their descendants (all first matings of approximately one week old adults)

| Combination   | Durations   | Mean  |
|---|---|-------|
| Wyo. ♀♀ × N. Y. ♂♂  | 1'3", 1'11"   | 1'7"  |
| N. Y. ♀♀ × Wyo. ♂♂  | 3'55", 4'18", 6'49", 6'56"  | 4'29" |
| F <sub>1</sub> (Wyo. ♀ × N. Y. ♂)<br>♀♀ × ♂♂  | 3'14", 3'21", 5'19"   | 3'59" |
| F <sub>1</sub> (N. Y. ♀ × Wyo. ♂)<br>♀♀ × ♂♂  | 1'9", 1'13", 1'16", 1'18", 1'21", 1'49",<br>1'58", 2'2" (2), 2'16", 2'25", 2'26",<br>2'38", 2'50", 3'9" | 1'59" |
| Wyo. ♀ × F <sub>1</sub> (N. Y. ♀ × Wyo. ♂)♂   | 1'27", 2'6", 2'29"  | 2'1"  |
| N. Y. ♀ × F <sub>1</sub> (N. Y. ♀ × Wyo. ♂)♂  | 2'30", 2'36"  | 2'33" |
| F <sub>2</sub> (N. Y. ♀ × Wyo. br.* ♂)<br>F <sub>2</sub> ♀♀ × "wild" F <sub>2</sub> ♂♂  | 0'14", 1'29", 1'34", 1'42", 2'3" (2),<br>2'28", 2'39", 2'55"  | 1'54" |
| Wyo. ♀ × F <sub>2</sub> (N. Y. ♀ × Wyo. br. ♂)<br>"wild" F <sub>2</sub> ♂♂              | 2'3"  | 2'3"  |
| N. Y. ♀ × F <sub>2</sub> (N. Y. ♀ × Wyo. br. ♂)<br>"wild" F <sub>2</sub> ♂♂             | 2'9", 2'30"   | 2'20" |
| F <sub>2</sub> (N. Y. ♀ × Wyo. br. ♂)<br>F <sub>2</sub> ♀♀ × "bright" F <sub>2</sub> ♂♂ | 2'46", 3'29", 5'15"   | 3'50" |
| Wyo. ♀ × F <sub>2</sub> (N. Y. ♀ × Wyo. br. ♂)<br>"bright" F <sub>2</sub> ♂♂            | 3'54"   | 3'54" |

\* "br." signifies "bright eyes," a sex-linked recessive mutant derivative of Wyoming strain.



TABLE 6. Durations of copulation in matings of *D. athabasca* within strains from different localities (all first matings of approximately week old adults)

Strains established in 1956. The number in parentheses after each place name indicates the number of strains contributing to the pooled data.

| Locality                          | Durations   | Mean   |
|-----------------------------------|---|--------|
| Iron River, Wisconsin (1)         | 4'56", 5'49", 7'34"   | 6'7"   |
| Iron Mountain, Michigan (2)       | 1'25", 1'26", 2'8", 4'12", 5'27"                                      | 2'56"  |
| Algonquin Park, Ontario (2)       | 1'17", 1'30", 1'34", 1'35", 1'39",<br>1'44", 1'45", 2'16", 2'42"      | 1'47"  |
| Gatineau Park, Quebec (5)         | 1'11", 1'24" (2), 1'26", 1'41", 1'56",<br>1'59" (2), 2'32", 4'11" (2) | 2'10"  |
| Ste. Anne de Bellevue, Quebec (5) | 1'20", 1'35", 1'38", 1'58", 2'2", 2'4",<br>2'21"                      | 1'51"  |
| Laurentides Park, Quebec (3)      | 5'56", 7'18", 7'20", 7'59", 10'7",<br>11'44", 20'56"                  | 10'11" |

### DISCUSSION

There are now numerous reports of intraspecific sexual isolation between laboratory strains of *Drosophila* species. Such isolation was reported by Dobzhansky and Koller (1938) between strains of *D. miranda* from California and the state of Washington; by Stalker (1942) between different Ohio strains of *D. americana*; by Dobzhansky (1944) between Mexican and Brazilian *D. sturtevantii*; and by Dobzhansky and Streisinger (1944) (as well as Levene and Dobzhansky, 1945) between strains of *D. prosaltans* from Brazil, Guatemala, and Mexico. Various degrees of intraspecific sexual isolation have been reported, with isolation indexes as high as 0.95 (*D. prosaltans* Brazilian males with Brazilian and Mexican females; Levene and Dobzhansky, 1945). Some negative isolation indexes have been reported (indicating "preference" of males for alien females), as in certain combinations of Brazilian *D. prosaltans* males with Mexican and Brazilian females (Dobzhansky and Streisinger, 1944). The degree of isolation has been found to vary widely with different strains of the same species, the extent of isolation not strictly correlated with geographical origin, as, for example, reported for *D. sturtevantii*

(Dobzhansky, 1944), in which strains from remote localities sometimes showed less isolation than did those from less remote localities.

The sexual isolation data presented here for the *D. athabasca* strains from Wyoming, Michigan, and New York show no essentially different features from those already reported for the other species, though they do establish a rather high degree of isolation within this North American species. The failure of Novitski (1946) to find sexual isolation between his eastern and western strains of *athabasca* suggests that those older strains of this species were much less isolated from each other than were the Wyoming, Michigan, and New York strains on which this report is based.

A high degree of sexual isolation may be taken along with other evidence as a basis for the recognition of sibling species. For example, Dobzhansky (1946) recognized the distinctness of the Brazilian species *D. equinoxialis* from *D. willistoni* on the basis of an almost complete failure of insemination to take place between them in the laboratory. Moreover, no hybrids were detected in the few culture bottles in which insemination had occurred. Though there was a significant (though overlapping) size differ-

ence between these two forms, no reliable morphological criterion for separating individuals of these species was available until Spieth (1949) discovered an internal characteristic (spermatheca tube shape) which differentiated them.

Despite the high interlocality sexual isolation reported here within *D. athabasca*, the available evidence appears as yet insufficient to serve as a basis for subdividing the species into taxonomic categories. In particular, though a very high degree of sexual isolation separates the Michigan strains from the Wyoming and New York strains, some matings of Michigan with the other strains (Wyoming females by Michigan males, Michigan females by New York males) has been found to yield normal, fertile hybrids. Moreover, no clearly recognizable morphological or physiological characteristic has been found to distinguish the strains of the different localities. Although the New York *athabasca* often appeared paler than those from Wyoming and Michigan, this was not always the case and did not afford complete separation from the others. Moreover, the strongly isolated Wyoming and Michigan strains showed no such color difference. Although variation in copulation time serves to distinguish the Wyoming (and other western) strains of *athabasca* from those from Michigan and New York, it does not do so for the strongly isolated Michigan and New York strains. Moreover, observations of matings in new strains from Michigan, Ontario, and Quebec show that some eastern *athabasca* possess the long copulation trait previously found only in the western strains.

In conclusion, it appears that the strains of *athabasca* studied here must represent populations that have undergone a certain amount of genetic divergence concerning mating propensity and behavior. However, the evidence is not yet sufficient to show very well the pattern of this divergence. Additional information is needed on *athabasca* from localities other than those studied here,

and work to obtain this information is in progress.

#### SUMMARY

Several geographically different strains of *D. athabasca* were studied as to sexual isolation and mating behavior. Strains from Wyoming and Michigan showed a marked degree of sexual isolation, though rare matings between Wyoming females and Michigan males did yield fertile hybrids. Strains from New York likewise were strongly isolated from Michigan strains, but some fertile hybrids were obtained between Michigan females and New York males. Wyoming and New York *athabasca* showed some isolation but crossed much more easily in both reciprocal directions than either did with Michigan, producing fully fertile hybrids. The duration of copulation was found to be long (about 4' or more) in western strains of *athabasca* (Wyoming, North Dakota, western Ontario), short (2' or less) in certain eastern strains (Michigan, New Jersey, New York), while other eastern strains (Michigan, Ontario, Quebec) had either a mixture of short and long matings or exclusively long ones (Quebec). Intermediate mating times were observed in the descendants of Wyoming (long) and New York (short) strains.

#### LITERATURE CITED

- DOBZHANSKY, TH. 1944. Experiments on sexual isolation in *Drosophila*. III. Geographic strains of *Drosophila sturtevantii*. Proc. Nat. Acad. Sci., **30**: 335-339.
- . 1946. Complete reproductive isolation between two morphologically similar species of *Drosophila*. Ecology, **27**: 205-211.
- , AND P. C. KOLLER. 1938. An experimental study of sexual isolation in *Drosophila*. Biol. Zentralbl., **58**: 589-607.
- , AND G. STREISINGER. 1944. Experiments on sexual isolation in *Drosophila*. II. Geographic strains of *Drosophila prosaltans*. Proc. Nat. Acad. Sci., **30**: 340-345.
- LEVENE, H., AND TH. DOBZHANSKY. 1945. Experiments on sexual isolation in *Drosophila*. V. The effect of varying proportions of *Drosophila pseudoobscura* and *Drosophila persimilis* on the frequency of insemination

- in mixed populations. Proc. Nat. Acad. Sci., **31**: 274-281.
- MILANI, R. 1952. Variabilita di alcuni aspetti del comportamento sessuale in *Drosophila subobscura*. Symposia Genetica, **III**: 338-380.
- MILLER, D. D. 1950a. Observations on two cases of interspecific hybridization with *Drosophila athabasca*. Amer. Nat., **84**: 81-93.
- . 1950b. Mating behavior in *Drosophila affinis* and *Drosophila algonquin*. EVOLUTION, **IV**: 123-134.
- . 1951. Mating behavior in *D. athabasca* and *D. narragansett*. Drosophila Information Service, **25**: 115.
- NOVITSKI, E. 1946. Chromosome variation in *Drosophila athabasca*. Genetics, **31**: 508-524.
- PATERSON, J. T., AND W. S. STONE. 1952. Evolution in the Genus *Drosophila*. The Macmillan Company, New York.
- SPIETH, H. 1949. Sexual behavior and isolation in *Drosophila*. II. The Interspecific mating behavior of species of the *willistoni* group. EVOLUTION, **3**: 67-81.
- . 1952. Mating behavior within the genus *Drosophila* (Diptera). Bull. Amer. Museum. Nat. Hist., **99**: 397-474.
- STALKER, H. D. 1942. Sexual isolation studies in the species complex *Drosophila virilis*. Genetics, **27**: 238-267.
- STURTEVANT, A. H., AND TH. DOBZHANSKY. 1936. Observations on the species related to *Drosophila affinis*, with descriptions of seven new forms. Amer. Nat., **70**: 574-584.