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Taxonomy, Geographic Distribution, and Ecology of *Drosophila pseudoobscura* and Its Relatives

INTRODUCTION

The flies of the genus *Drosophila* occupy the most important place among the organisms which are used as materials for genetic investigations, and it is no exaggeration to say that since the publication in 1911 of Morgan's classic paper the science of genetics has revolved around *Drosophila* work. Certain species of this genus possess a combination of advantages unrivaled in any other known material: rapid development, great fecundity, hardiness, the ease and relatively small cost with which they can be bred the year round in laboratories, and, finally, the giant chromosomes of the larval salivary glands. The fundamental work was done on *Drosophila melanogaster*; this species is still the best material for the study of the induction of mutations, chromosomal aberrations, and similar problems. It is certainly not, however, the only organism amenable to genetic investigation. For certain problems, for example some problems of developmental genetics where *Drosophila's* small size becomes a disadvantage, other forms are preferable. The mechanisms which control heredity are fundamentally the same in all organisms, no matter to what subdivision of the animal or of the plant kingdom they belong; the principles of genetics are perhaps the most universal of all biological principles. The investigator in genetics is, consequently, free to choose and should choose the organism which offers the most advantage for his study, whether it be in the laboratory or in the field.

For studies on the genetics of natural populations, race formation, and species differentiation, two groups of *Drosophila* species have come to the fore, namely, those related to *D. pseudoobscura* on one hand, and those related to *D. virilis* on the other. As laboratory animals and in the clarity of their chromosomes these species are not much inferior to *D. melanogaster*, and from the standpoint of analysis of natural populations they are superior in certain important respects. *D. melanogaster* is at present nearly cosmopolitan and, at least in the temperate zone, is closely associated with man. Its populations are constantly churned up because of unintentional transport by man. It is known to produce hybrids only with *D. simulans*, and these hybrids are sterile. On the other hand, species related to *D. pseudoobscura* and to *D. virilis* (except *D. virilis* itself) are not intimately associated with man, and within each group there are related species which can be crossed and which produce fertile offspring.

Notwithstanding more than three decades of extensive use of *Drosophila* in genetic studies, the biology of its species, and particularly their life cycles in nature and their ecology, are but little known, and, in fact, have been but little investigated. This deficiency of knowledge is of relatively little moment to the geneticist concerned with these insects only in cultures on a laboratory

shelf. But the genetic phenomena occurring in natural populations are so intimately connected with and conditioned by the biology of the organism that a student of population genetics can ill afford to ignore these connections. The present paper contains a review of the information available on the biology of *Drosophila pseudoobscura* and its nearest relatives, which should serve as a background for the work on the population genetics of these species. Observations made in nature have demonstrated that *D. pseudoobscura* has a very complex biology, many features of which had not been even suspected from many years' acquaintance with the behavior of *Drosophila* flies in the laboratory.

TAXONOMY OF *DROSOPHILA PSEUDOOBSCURA* AND ITS RELATIVES

In 1823 Fallén described a species of *Drosophila* from Sweden which he named *Drosophila obscura* Fallén. The original description is as follows:

Mas & Fem. In truncis arborum, ad Lärketorp Ostrogothiae & Esperöd Scaniae, rarior. E Westrogothia quoque missa a Nobil. D. Gyllenhal.—Magnitudo praecedentis. Caput thorace vix latius: oculis magnis, rotundis, clypeo verticeque obscuris. Antennae breves nigrae: articulo ultimo subtruncato. Seta longa pectinata. Thórax opaco-testaceus, obscurus. Abdomen nigricans. Pedes pallidi. Alae parum l. vix nigredine tinctae.

Sturtevant (1921) called attention to the existence of a species on the Pacific coast of the United States which he regarded as identical with *D. obscura* Fallén. In 1929 Lancefield published an important paper in which he showed that the American representatives of the supposed *D. obscura* are differentiated into two "races or physiological species," which he designated as race A and race B. The crosses between these "races" produce offspring which consists of fertile daughters and sterile sons. Furthermore, the "races" are distinguishable by the chromosome configurations in the males: the Y chromosome of "race A" is J-shaped and that of "race B" is V-shaped. The external morphology of the representatives of both "races" was thought to be identical.

Frolova and Astaurov (1929) found that strains of *Drosophila obscura* Fallén collected in the vicinity of Moscow, Russia, are easily distinguishable from an American strain by their chromosomal complements, male genitalia, body color and body size, and behavior in cultures. The crosses between them failed to produce hybrids. The American form was, therefore, recognized as a species distinct from the European one, and named *Drosophila pseudoobscura* Frolova. Although Frolova and Astaurov were unfamiliar with Lancefield's discovery of the two "races" in the American form, and although the exact geographic origin of their American strain is unknown, the chromosome drawings leave no doubt that the name *D. pseudoobscura* Frolova is properly applicable to Lancefield's "race A."

Systematics of the European representatives of the *obscura* group of species remain even now in a completely unsatisfactory state. Among the Moscow strains which Frolova and Astaurov (1929) had at their disposal there were two groups distinct in their chromosome configurations from each other

and from the American *D. pseudoobscura*. One group had four pairs of V- or J-shaped and one pair of dotlike chromosomes; another group had three pairs of V-shaped, two pairs of rodlike, and one pair of dotlike chromosomes. Which of these chromosome complements belongs to the true *D. obscura* Fallén is unclear. J. E. Collin (*in* Gordon, 1936) described *D. subobscura* Collin from England, differing from *D. obscura* Fallén by larger sex combs in the male, and by a light brownish-gray, completely unstriped thorax in both sexes; it has five pairs of rodlike and one pair of dotlike chromosomes. Buzzati-Traverso (1940) finds in Italy, Germany, and England five species of the *obscura* group, the chromosome complements of which he describes; the names he suggests for them have no standing under the Rules of Nomenclature, since the mimeographed pamphlet containing them is expressly stated not to be a publication. Nothing whatever is known about the occurrence of these or of related forms in Asia, although their presence in at least the northern part of that continent seems very probable on the basis of general zoogeographic considerations.

Lancefield's "race A" and "race B" have been studied in detail. Dobzhansky and Boche (1933) confirmed the sterility of the male "interracial" hybrids, and found two distinct types of Y chromosome in "race A" and two in "race B." Dobzhansky (1935*a*, 1937*c*, 1939) showed that there are at least five types of Y chromosome in A and three types in B, one of these being common to both "races"; it should be noted that strains of A and B which have similar Y chromosomes occur in different geographic regions. The sterility of the male "interracial" hybrids is due to cooperation of at least several, and probably numerous, genes located in all the chromosomes investigated (Dobzhansky, 1936). The viability of the offspring from backcrosses of hybrid females to males of either parental "race" is distinctly lower than that of the pure "races" or of the F₁ hybrids. This lowering of viability was shown to be due to a maternal effect exerted by mixtures of the chromosomes of the two "races" on the cytoplasm of the eggs deposited by the hybrid females, and also to special genes which seem to have no discernible effects on the genetic backgrounds of the pure parental "races" (Dobzhansky, 1935*d*, 1937*a*; Gottschewski, 1940; Mampell, 1941). Thus, although the F₁ females from A × B crosses are themselves fertile, their offspring are reduced in viability to an extent which would probably be fatal under natural conditions. As stated above, the F₁ males are completely sterile.

Comparative study of the giant salivary-gland chromosomes in "races" A and B has disclosed that the gene arrangements in the XR, the second, and especially in the third chromosome are variable from strain to strain within each "race." The XL chromosomes of the "races" differ constantly by a single inversion; the second chromosomes, despite the intraracial variations, also differ by at least a single inversion; the XR chromosomes are usually different, although the so-called "sex ratio" strains of "race B" have the same gene arrangement as the normal strains of "race A"; the third chromosomes may be either similar or different; the fourth and fifth chromosomes are

alike (Tan, 1935; Dobzhansky and Sturtevant, 1938; see also part II in the present publication). Thus, the "races" can always be distinguished by the gene arrangements in their chromosomes. The two "races" present different physiological reaction systems. At 25° C. the development of B takes several hours longer than that of A (Poulson, 1934). At 25° A deposits more eggs than B, at 19° both "races" are about alike in fecundity, and at 14° C. B is distinctly superior to A; at all temperatures the profiles of the egg-laying curves are different in the two "races" (Dobzhansky, 1935c). The longevity of A in the absence of food is greater than that of B (Lilleland, 1938). The two "races" differ slightly in the rate of oxygen consumption during the pupal stage (Dobzhansky and Poulson, 1935). It will be shown below that A occupies warmer and drier habitats than B.

For a number of years all attempts to detect differences in external morphology between the "races" proved unavailing. Genitalia of both sexes were found to be identical by Dobzhansky, and this negative finding was confirmed by G. F. Ferris (oral communication), who kindly consented to re-examine the material. Mather and Dobzhansky (1939) found that the number of teeth in the sex combs is slightly greater in A than in B, and that the wings of B are slightly larger than those of A. Finally, Reed, Williams, and Chadwick (1942) demonstrated that the number of wing beats per unit time during flight is greater in A than in B. This physiological difference also proved to be correlated with a structural one. The authors undertook to calculate a special wing index number, obtained by multiplication of wing area expressed in square millimeters by cubed wing length in millimeters. This index in "race A" was found to vary (in different strains) from 45.7 to 62.8, the average being 55.7, and in "race B" from 68.8 to 76.2, the average being 72.6. In conjunction with the differences in the number of teeth in the sex combs and other characters, this index is probably sufficient to discriminate between A and B on purely morphological grounds.

Because these supposed races are in fact species, although but little differentiated in external morphology, we propose the name *Drosophila persimilis* to replace the inconvenient and biologically meaningless designation "race B." The name *Drosophila pseudoobscura* Frolova is accordingly applicable only to the entity previously designated "race A."¹ The description of the new species follows:

¹ Ginsburg (1940, p. 26) in discussing the race A-race B problem proposes the name "*lancefieldi*₂," which he treats as a subspecific name, without giving either a description or a valid designation or an unequivocal bibliographical reference, as demanded by the Rules of Nomenclature. The name is therefore a *nomen nudum*, and since it is quoted under *D. pseudoobscura* it must be considered an alternative name for *pseudoobscura*. If the name is considered to be correctly proposed, it is obvious from the original wording that it is applied jointly to *D. pseudoobscura* A and B. To make the composite name valid, it must be restricted to one species or the other. We hereby restrict *lancefieldi*₂ to *Drosophila pseudoobscura* Frolova (1929, *Ztschr. f. Zellforsch. u. mikr. Anat.*, vol. 10, p. 212), of which it becomes a synonym. The unfortunate way in which the name *lancefieldi* was proposed leaves no other course. The situation has been discussed with several experts on nomenclature, all of whom have recommended the procedure followed above.

Drosophila persimilis, species nova

♂, ♀. Arista with 7, less frequently with 8 or 6 branches. Antennae brown, third joint darker. Front dark brown, orbits lighter. Middle orbital bristle one-third to one-half as long as the other two. Second oral less than half of the first. Face dark brown. Carina much broadened below, slightly sulcate. Palpi brown. Cheeks narrow, their greatest width about one-fifth the diameter of the eye. Eyes dark red, with short pile. Acrostichal hairs in 8 rows. No prescutellars. Anterior scutellars convergent. Thorax brownish black, mesonotum with 3 indistinct grayish longitudinal stripes, 1 in the middle and 2 in the dorsocentral rows. Scutellum brownish black, its sides frequently paler. Pleurae brownish black. Sterno index 0.7–0.8. Legs yellowish brown, femora infuscate. Apicals and preapicals on the first and second, only preapicals on the third tibiae. Two sex combs in the male; the proximal one has 5 to 7 and the distal 4 to 6 teeth; the mean for the proximal comb is between 5.5 and 6.2 and for the distal one between 4.7 and 5.1 (in different samples). Abdomen brownish black. Wings clear, veins brown. Costal index 2.8; fourth-vein index 1.9. Wing area 2.6–2.8 sq. mm; Reed's wing index 68–76. Body length 2.3 mm.

Testes in young males bright orange-red, ellipsoidal, becoming darker and more elongated with age. Spermathecae cup-shaped, brown, chitinized. Ventral receptacle short and broad, folded once but not spiralized.

Metaphase chromosome group consists of V-shaped X chromosomes, three pairs of rod-shaped, and one pair of dotlike autosomes; in the male, the Y chromosome is large, V-shaped, equal- or unequal-armed. In the salivary-gland cells the middle part of the short limb of the X chromosome (XL), containing approximately the sections from 7 to 12, and the middle part of the second chromosome, containing approximately the sections from 52 to 56, are inverted (these section numbers refer to the standard maps of these chromosomes published by Dobzhansky and Tan, 1936).

Geographic distribution: from central British Columbia to Santa Barbara County, California, and from the Pacific Ocean to the eastern slope of the Sierra Nevada and Cascade ranges. Type locality: Reedsport, Oregon.

Differs from *Drosophila pseudoobscura* Frolova in having a lower average number of teeth in the sex combs, a greater wing area, a higher Reed's wing index, the above-described inversions in the XL and second chromosomes, the V-shaped instead of the usually J-shaped Y chromosome, and in several physiological characters.

It is certain that if any kind of structural difference had been known between *D. pseudoobscura* and *D. persimilis*, they would have been classed as species from the start. Calling them races, and designating them by the letters A and B instead of by Latin names, was an attempt to appease conservative taxonomists who continue to adhere to the purely morphological concepts of species and race. Such a course is neither scientifically consistent nor practically sound. The species is the stage in the process of evolutionary divergence at which an array of populations once actually interbreeding or capable of interbreeding has become split into two or more reproductively isolated arrays. Species exist in nature regardless of whether we can or cannot distinguish them by their structural characters. There is no doubt that the great majority of animal and

plant species differ structurally, and that they can be conveniently, and in most cases readily, recognized and delimited by their morphology alone. But it does not follow that any and all species are recognizable by their externally visible structures.

The following evidence can be adduced in support of the thesis that *D. pseudoobscura* and *D. persimilis* are distinct species in accordance with the definition given above. Individuals belonging to these species show a clear, though not an absolute, sexual isolation (Boche, in Dobzhansky and Koller, 1938). In the laboratory, strains of these species can be intercrossed; interspecific crosses do not go so easily as the intraspecific ones. The F_1 hybrid males are completely sterile. The F_1 females, backcrossed to males of either parental species, deposit numerous eggs; the backcross progenies, however, show a pronounced constitutional weakness. Nevertheless, in the laboratory, it is possible by repeated backcrossing to transfer small blocks of genes of *D. pseudoobscura* onto the genetic background of *D. persimilis*, or vice versa. The question arises whether such gene transfer takes place in nature as well, and if so whether the transfer occurs frequently enough to produce a permanent bridge between the germ plasms of the two natural populations.

The distribution areas of *D. pseudoobscura* and *D. persimilis* are broadly overlapping, and within the zone of overlap representatives of the two species frequently occur side by side. There is, hence, no question of the gene transfer's being precluded merely by geographical isolation. Numerous population samples from localities where the two species occur together have been examined to detect possible individuals which could be identified as interspecific hybrids. No such individuals have been detected. This is negative evidence, to be sure; it is clear that species crosses do not occur frequently, but we cannot exclude the possibility that they take place from time to time. The problem can be approached from another angle: can we detect any evidence that traits normally associated with *D. pseudoobscura* are occasionally present in populations of *D. persimilis*, or vice versa? If hybridization takes place, even though rarely, such "introgression" of one species genotype into the other (Anderson and Hubricht, 1938) might sometimes be observed. Because of the close structural similarity of the two species, we must look to the chromosomes for such evidence. Three possibilities present themselves:

First, a certain type of Y chromosome (type I, Dobzhansky, 1937c) is found in most populations of *D. persimilis* and also in certain populations of *D. pseudoobscura*. Judged superficially, this fact might be taken as evidence of introgression. This chromosome type, however, has never been found in the populations of *D. pseudoobscura* from California, Oregon, and Washington, where it would be expected because of the presence of *D. persimilis*, but only in populations found in southern Arizona, Mexico, and Guatemala, far removed from the range of that species. The type of Y chromosome is similar in appearance in the two species, but it is not impossible that in reality the

chromosomes in question are different. If they are in fact genetically identical, any hybridization must have taken place in the remote past.

Second, the gene arrangement which is normal for the XR chromosome of *D. pseudoobscura* is found in the "sex ratio" strains of *D. persimilis* (Sturtevant and Dobzhansky, 1936b). Could the "sex ratio" condition in *D. persimilis* have arisen through introgressive hybridization with *D. pseudoobscura*? Although the available experimental evidence does not permit a final conclusion, the fact is that the transfer of the XR chromosome of *D. pseudoobscura* onto the genetic background of *D. persimilis* causes sterility rather than the "sex ratio" characteristics.

Third, the gene arrangements found in the XL and second chromosomes of *D. pseudoobscura* have never been found in *D. persimilis*, or vice versa. The "Standard" gene arrangement in the third chromosome occurs, however, in both species and in the same geographical region. It will be shown in the following section that this gene arrangement is phylogenetically very old and may have been present in the ancestral species from which both modern ones developed. In the same way, the occurrence of "weak" and "strong" races in both *D. pseudoobscura* and *D. persimilis* (Dobzhansky, 1937a and unpublished data) is more likely a survival of the elements from which the sterility mechanism found in the hybrids between these species has been constructed than a result of introgressive hybridization.

To summarize: although we cannot assert that *D. pseudoobscura* never hybridizes in nature with *D. persimilis*, this hybridization is certainly not frequent enough to constitute a channel for a regular gene exchange. These two forms have reached specific distinction. An objection may still be raised against giving them separate names. After all, the systematic nomenclature has been devised primarily for a practical purpose: labeling specimens. The distinctions between *D. pseudoobscura* and *D. persimilis* are admittedly of a kind which not only does not permit a museum worker easily to distinguish pinned specimens, but is difficult even in living individuals, unless breeding experiments or cytological examination are resorted to. This objection fails to take into account that the methods of systematics have, though slowly, changed in the past, and are at present quite different in different groups of organisms. The time is not remote when entomologists described species entirely on the basis of external structures visible in dried specimens with the aid of a hand lens. Only over the protests of conservatives have the characteristics of the genitalia, which frequently demand examination of dissected and cleared internal organs under a microscope, become an accepted criterion of species distinction in many genera and families. Species of some flatworms, nematodes, and annelids are not distinguishable without microtome sections. Bacteriologists would hardly yield to the suggestion that they distinguish species not by culturing them on artificial media, but by observations on the appearance of the organisms in unstained preparations.

It happens that the characteristics of the chromosomes and the breeding behavior furnish the safest method for distinguishing *D. pseudoobscura* and

D. persimilis. We are far from offering the preposterous advice that henceforward all entomologists should examine the chromosomes of their species before describing them. The methods of systematics in any given group are determined by the level which the knowledge of this group has attained and by the uses to which this knowledge is being put. Species of *Drosophila* are being used as material for studies not only, and even not mainly, by museum systematists. To call *D. pseudoobscura* and *D. persimilis* "races" is confusing not only to geneticists, but also to those systematists who are interested, for their own purposes, in the results of genetic work.¹

The third North American species of the *obscura* group is *D. miranda*, described by Dobzhansky (1935*b*). It differs from *D. pseudoobscura* and from *D. persimilis* in certain details of morphology, in breeding habits, and in the chromosome structure. The genitalia are identical. The body color, and especially that of the legs, is darker. The body size is larger, and specimens caught in nature are usually recognizable by their size, although specimens of *D. miranda* reared from starved larvae may be smaller than those of *D. pseudoobscura* or *D. persimilis* which have developed on abundant food. The proximal sex combs have 6 to 10 (average 8.4) teeth, and the distal ones 5 to 8 (average 5.8) teeth. The development of *D. miranda* takes longer than that of either *D. pseudoobscura* or *D. persimilis*, and the sexual dimorphism is greater: in the same culture the males frequently begin to hatch only after all the females have hatched. *D. miranda* is sensitive to high temperatures (25° C. being sublethal), and somewhat sluggish in its movements.

The metaphase chromosomes of *D. miranda* females are indistinguishable from those of its relatives, but the males have an odd chromosome number (9) instead of the even one (10). This is due to the singular X¹-X²-Y heterochromosome mechanism in this species (Dobzhansky, 1935*b*; MacKnight, 1939). Examination of the salivary-gland chromosomes reveals that a large number of changes in the gene arrangement have taken place during the evolutionary process which have led to the separation of *D. miranda* from the ancestral *D. pseudoobscura*-*D. persimilis* stock. A fact of considerable interest is this: in the three chromosomes in which such comparisons are possible, the gene arrangement of *D. miranda* is one inversion step closer to that of *D. pseudoobscura* than to that of *D. persimilis* (Dobzhansky and Tan, 1936).

Males of *D. miranda* show a pronounced aversion to mating with *D. pseudoobscura* and *D. persimilis* females, and vice versa. The sexual isolation be-

¹ A suggestion has been made that forms of *Drosophila* which behave as species but are scarcely or not at all distinguishable in conventional museum specimens be designated as subspecies rather than species. This would make confusion worse confounded. The museum systematist would not be benefited thereby, because he is just as interested in determining the subspecies as he is in knowing the species to which his specimens belong. More important still, the usage of the subspecies category has at last reached a certain stability; subspecies are genetically distinct subdivisions of species which replace each other in space. Unless we believe that species exist in nature only if we can distinguish them with the aid of conventional methods, there is no reason to avoid calling a species a species.

tween *D. miranda* and *D. persimilis* is somewhat stronger than that between *D. miranda* and *D. pseudoobscura* (Dobzhansky and Koller, 1938). No natural hybrids have been found. In the laboratory, the crosses of *D. miranda* females to males either of *D. pseudoobscura* or of *D. persimilis* produce hybrids of both sexes, whereas the reciprocal crosses produce only females and a few exceptional males (Dobzhansky, 1937b). The F₁ hybrid males have rudimentary testes and are always sterile. The hybrid females deposit numerous eggs which, with rare exceptions, produce no larvae; this result is due to grave disturbances in the behavior of the polar bodies and in cleavage (Kaufmann, 1940). Gene exchange between *D. miranda* and its relatives is completely impossible in nature.

Drosophila pseudoobscura, *D. persimilis*, *D. miranda*, and their little-known Old World relatives form a compact *obscura* species group within the subgenus *Sophophora* of the genus *Drosophila*. Another equally close-knit group within the same subgenus, the *affinis* group, has been revised by Sturtevant and Dobzhansky (1936a) and by Sturtevant (1942). It includes six known representatives: *D. affinis*, *D. algonquin*, *D. azteca*, *D. athabasca*, *D. narragansett*, and the rare *D. seminole*, all of which occur in North and Central America. The two species groups appear to be ecologically very close, although their geographic areas tend to be mutually exclusive (see below). Only a few of the characters which differentiate the *obscura* and the *affinis* groups need be named here. In the former the acrostichal hairs in front of the dorso-central bristles are arranged in eight rows, in the latter in six rows; in the former the males have two sex combs and ellipsoidal testes, in the latter one well developed and one rudimentary comb and spiral testes; the ventral seminal receptacle in the females of the *obscura* group is shorter than in the *affinis* group. Hybrids may be obtained between *D. athabasca* and *D. azteca* (Sturtevant and Dobzhansky, 1936a), between *D. athabasca* and *D. algonquin*, and between *D. athabasca* and *D. affinis* (Miller, 1939, 1941). These hybrids are sterile, except the female hybrids from the *D. algonquin* ♀ × *D. athabasca* ♂ cross, which are slightly fertile. No hybrids at all are obtainable between the representatives of the *obscura* and *affinis* species groups. Other species groups of *Sophophora* (Sturtevant, 1942) are obviously too remote from *obscura* to be relevant to the present discussion.

GEOGRAPHIC DISTRIBUTION

Three species of the *obscura* group occur in North America, and five, possibly more, are found in Europe and, perhaps, in Asia. Virtually nothing is known about the distribution of the Old World species; that of the American species is relatively well studied (fig. 1).

Drosophila persimilis occurs from Vancouver Island and central British Columbia to south-central California, and from the Pacific to the eastern slope of the Sierra Nevada and Cascade ranges. It is also found in the Coso and Panamint ranges. The northernmost localities in which the species has

been found are Campbell River on Vancouver Island (about 20 miles from the mouth, alder grove along a creek); forest near 150-mile House, British Columbia; and an alder grove near a stream, about 10 miles northeast of

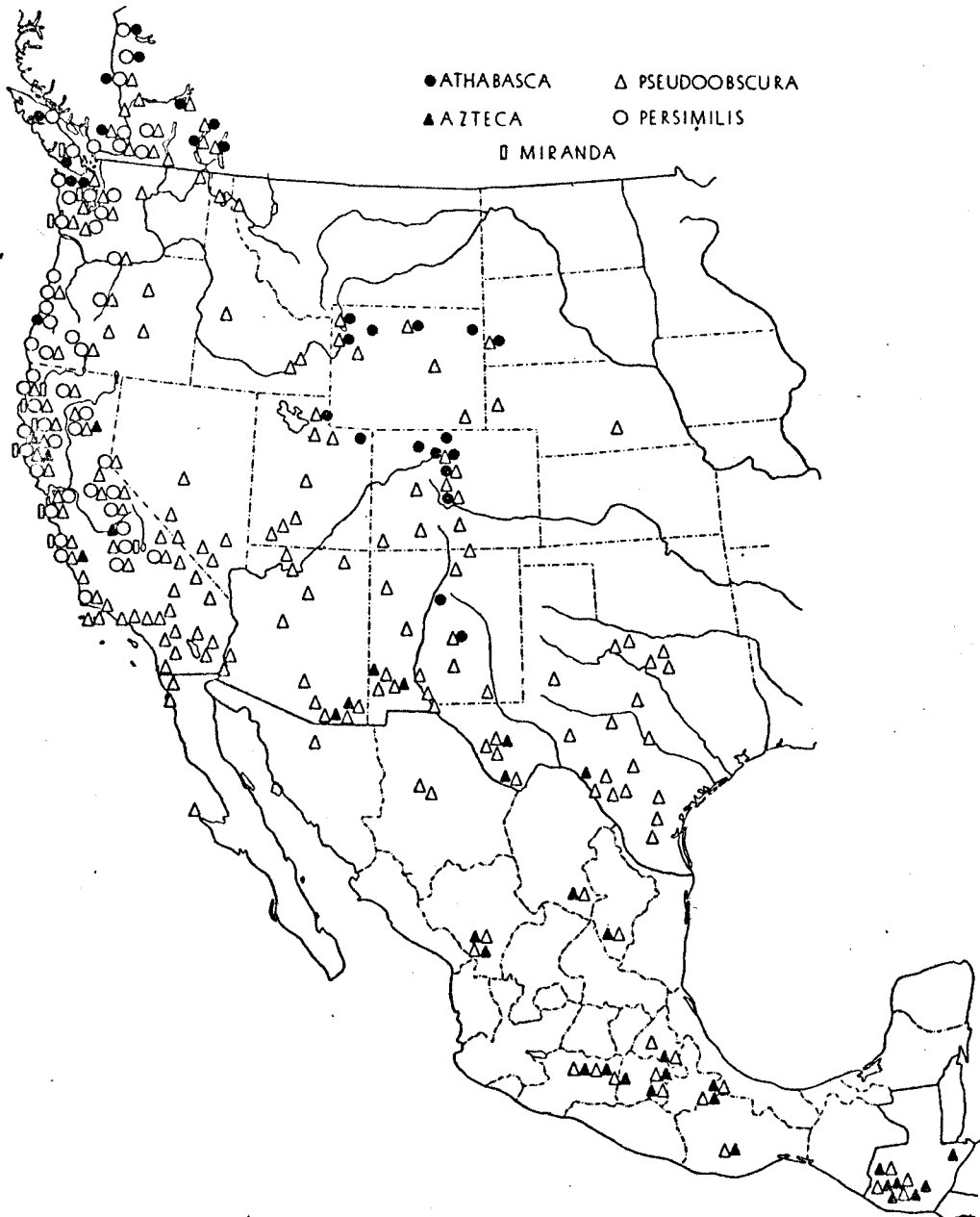


FIG. 1. The known geographic distribution of *Drosophila pseudoobscura*, *D. persimilis*, *D. miranda*, and *D. azteca*, and the southwestern part of the distribution of *D. athabasca*.

Quesnel, British Columbia. Along its northern boundary, *D. persimilis* is replaced by *D. athabasca*, a representative of the *affinis* species group. *D. athabasca* is the commonest species of the genus in Alaska, where it has been found very abundant near Chitina, also at Juneau, Ketchikan, and

Gravina Island; it becomes less common in more southerly regions. Thus, *D. athabasca* is much commoner than *D. persimilis* at Campbell River, 150-mile House, and Quesnel, British Columbia. Slightly farther south, at Cowichan Lake on Vancouver Island, at Cape Flattery and Brinnon, Olympic Peninsula, Washington, and at Pavilion, British Columbia, *D. athabasca* is less common than *D. persimilis*. Farther south, *D. athabasca* has been found only at Reedsport, Oregon. This type of replacement of one form by another along a boundary line which does not coincide with any clear geographic barrier is frequently observed in subspecies of the same species, but it is not common where full species are concerned. It is easy to demonstrate that *D. athabasca* and *D. persimilis* are not subspecies of the same species: no intermediates between them are found in the territory in which they occur together. Although in general adapted to different environmental optima, these two species are ecologically sufficiently similar to tend toward mutual exclusiveness. *D. persimilis* is very common along the Pacific coast from the Olympic Peninsula, Washington, to San Francisco Bay, California. In this region it occurs literally within the sound of the ocean surf, as well as in the mountains. As one proceeds eastward, away from the ocean, into the inner Coast Ranges, the species becomes less frequent. It is very common in the Cascade Range, including the eastern slope thereof (e.g., near the source of the Metolius River, Oregon). In the Sierra Nevada of California, *D. persimilis* is characteristically an inhabitant of the forests at higher elevations. Thus, it has been recorded as common at Manzanita Lake, Mount Lassen National Park; relatively frequent at Deer Creek southwest of Mount Lassen, at Lake Tahoe, at Tuolumne Meadows, Yosemite National Park, and at Mariposa Grove; and again very common in the higher parts of the Sequoia National Park. On the eastern slope of the Sierra Nevada it is common at Mammoth Lakes and in Lone Pine Canyon at the base of Mount Whitney. The southeasternmost known localities are the Coso Range and the southern part of the Panamint Range, in the Death Valley region, California. In the Coast Ranges south of San Francisco Bay the species is relatively uncommon; it has been found on the Monterey Peninsula between Pacific Grove and Carmel, in the pine-oak woodland of the Santa Lucia Mountains northwest of the Tassajara Hot Springs, and, finally, at Nohojui Park, Santa Barbara County. Its southern boundary is, hence, not adequately known. No collecting has been done in the cross ranges which connect the Sierra Nevada and the Coast Ranges at the south (e.g., the Tehachapi Range, Mount Pinos). In southern California the species appears to be wholly absent.

The distribution area of *D. pseudoobscura* (fig. 1) is much wider than that of *D. persimilis*, and the former apparently includes the latter. The only locality from which a rather extensive sample of the population has been analyzed and in which *D. persimilis* but not *D. pseudoobscura* was found is Prairie Creek Redwood Park, near Orick, California. No *D. pseudoobscura* has been found, however, on Vancouver Island, or at Pavilion, 150-mile House, or Quesnel, British Columbia. It is, therefore, probable that *D. pseudoobscura*

does not extend so far north as *D. persimilis*, but more material is necessary to settle this question. The northernmost known localities of *D. pseudoobscura* are Brinnon and Seattle, Washington, and Yale, Princeton, Merritt, Lytton, Kamloops, Lake Shuswap, Arrowhead, Nakusp, and Kaslo, British Columbia. Farther south, *D. pseudoobscura* and *D. persimilis* occur side by side, but an analysis of their distribution makes it strikingly apparent that the former becomes more and more predominant as one moves from regions with a cool and humid oceanic climate to those with a warmer but more continental climate. Thus, *D. pseudoobscura* is generally rare along the coast north of San Francisco Bay, commoner in the valleys between the outer and inner Coast Ranges, still commoner in the lower reaches of the Sierra Nevada, and the only occupant of the territory east of the Sierra Nevada save for the restricted populations in the Coso and Panamint ranges. Altitudinally, *D. pseudoobscura* is more common at lower and *D. persimilis* at higher elevations. Thus, a sample taken in the pine-oak-madroño belt at about 3000 feet on Mount Yollo Bolly (inner Coast Range, California) consisted predominantly of the former, and a sample in white fir at 6000 feet on the same mountain gave mainly the latter species. In the Sierra Nevada, a sample at Camino, approximately 4000 feet, gave only *D. pseudoobscura*, whereas at Lake Tahoe, 6200 feet, *D. persimilis* is more abundant. In the Sequoia National Park, *D. pseudoobscura* is predominant below 5000 feet, but above 6000 feet both species are equally frequent or *D. persimilis* takes the lead.

Outside the region where *D. pseudoobscura* and *D. persimilis* occur together, the distribution area of the former extends eastward to the Rocky Mountains and Texas and southward to Mexico and Guatemala. In the Rocky Mountains of British Columbia, *D. pseudoobscura* is gradually replaced northward and eastward by *D. athabasca*, the manner of the replacement being the same as described above for *D. persimilis* and *D. athabasca*. A similar replacement occurs in Idaho, Wyoming, Utah, and Colorado, as shown by the following list of localities based on the collecting done by the collaborators of J. T. Patterson and by Th. Dobzhansky. In this list P stands for *D. pseudoobscura* and A for *D. athabasca*, and the figures indicate the number of specimens in the samples collected.

Idaho. Mountains northeast of Boise: P numerous, A none. Pocatello: P 32, A none. Coeur d'Alene: P numerous, A none.

Montana. Bitterroot Mountains near Thompson Falls: P numerous, A none.

Wyoming. Grand Teton National Park: P 5, A 341. Yellowstone National Park: P 6, A 17. Cody: P none, A about a dozen. Big Horn Mountains: P rare, A common. Sundance: P none, A some. Jackson Canyon: P 19, A none. Casper: P 33, A none.

South Dakota. Black Hills: P 33, A 1 (Patterson); P 4, A numerous (Dobzhansky).

Utah. Wasatch Range near Liberty: P 70, A none. Ogden River: P 42, A 9. Cottonwood Canyon southeast of Salt Lake City: P 497, A none. Uinta Mountains near Soapstone: P 17, A none. Uinta Mountains north of Vernal: P none, A 5.

Colorado. Park Range near Columbine Lodge: P none, A 22. Cache la Poudre Canyon near Mishawauka: P none, A about a dozen. Grand Lake: P none, A numerous. Estes Park: P 10, A 12 (Patterson); P 32, A 24 (Dobzhansky). University Camp: P rare, A common. Mount Campbell: P 35, A none. Manitou: P 168, A 1. Colorado Springs, North Cheyenne Park: P 12, A none. Pikes Peak, tree line (about 11,500 feet, the highest collecting locality for the species): P 7, A none. Walsenburg: P 148, A none.

Nebraska. Ponderosa pine forest near Scottsbluff: P some, A none. Gibbon (collected by A. H. Sturtevant): P 1, A none.

New Mexico. Patterson informs us that single females of *D. athabasca* have been collected by G. B. Mainland and R. B. Wagner on July 5 and 7, 1942, at Sulfur Canyon, Sandia Mountains, Bernalillo County, and at Middle Bonita Canyon, Lincoln County. These two localities constitute the southern extremity of the distribution area of the species.

A. P. Blair's collecting in eastern Oklahoma failed to disclose *D. pseudoobscura* there, and the very extensive collecting of Patterson and his colleagues in Texas shows that the eastern boundary of the species in that state is close to the line Wichita Falls—Plano—Fort Worth—Arlington—Florence—Georgetown—Aldrich near Austin—San Antonio—Three Rivers—Alice—Falfurrias. Here it comes in contact with the westernmost extensions of the ranges of two species of the *affinis* group, *D. affinis* and *D. algonquin*. In the forested zone of the western United States *D. pseudoobscura* is by and large the commonest species of the genus, except in the marginal territories discussed above and near man's habitations. In central and southern Mexico and in Guatemala, on the other hand, *D. pseudoobscura* is seldom the predominant species in any climatic or altitudinal belt, and where it does occur it shares the region with *D. azteca*, a member of the *affinis* group (fig. 1). In these countries *D. pseudoobscura* is apparently not found below 5000 feet, and it ranges to at least 10,000 feet (Río Frío, Puebla, Mexico). This range corresponds to the "temperate" and partly to the "cold land" (*tierra templada* and *tierra fría*). Here this species seems to avoid living in the depth of the forest (which it by no means avoids in the United States), and is characteristically found in somewhat drier habitats on the margins of the woods, on slopes covered with sparse tree vegetation, and partly in the brushland. *D. azteca* has the same preferences, but it appears to occur both at lower and at higher elevations than *D. pseudoobscura*. An individual of what was almost certainly *D. azteca* (which, however, was not brought alive to the laboratory) was found on the forested hills above Quirigua, Guatemala, on the edge of a tropical rain forest. *D. azteca* has also been found on the slopes of the volcano Agua at about 8000 feet, and among the pine barrens east of Guatemala City, where *D. pseudoobscura* has not been found.

As would be expected in view of the great extent, both horizontally and vertically, of the distribution range of *D. pseudoobscura*, it occurs in a variety of habitats. In part of the distribution area which lies in the United States it is found wherever trees of any kind grow. Oak and ponderosa pine forests

seem to support the densest populations, but good collections have been made in localities where the only trees were either aspen, or alder, or willow, or piñon pine, or juniper. For some years *D. pseudoobscura* was believed to be attached to forests. Hence its distribution in the southwestern United States, where forests occur on mountain ranges separated by stretches of desert, was regarded as discontinuous. Indeed, as a rule, no *D. pseudoobscura* can be collected during the summer months in desert or semidesert localities in California or Nevada. In March 1936, however, a fair collection was made in the dry course of Gila River, northeast of Yuma, Arizona, where mesquite bushes were the only treelike plants. In May 1938 a few individuals were found among desert vegetation in the higher part of the Mojave Desert (Granite and Ivanpah Mountains), and in the Colorado Desert (Chocolate Mountains, Orocopia Mountains). W. P. Spencer found a single individual at Mesquite Springs, Death Valley. In the spring of 1941, following a winter of abundant precipitation, K. J. Mampell and C. Epling made a series of collections in the Mojave and Colorado deserts (Chuckwalla Mountains, Desert Center, Borego Valley, and Bagdad in California; Yuma, Castle Dome, Tucson, and Sonoita in Arizona). The desert vegetation may, therefore, support populations of *D. pseudoobscura* which may reach considerable densities in the spring season of favorable years. Nevertheless, it would be misleading to describe the distribution of *D. pseudoobscura* in the southwestern United States as perfectly continuous. In the same region the montane forests support larger, denser, and more flourishing populations than the deserts do. Furthermore, in summer, when forest-dwelling populations are most numerous, the desert populations are in eclipse. The desert populations are at their peak when the breeding season in the mountains has barely begun. Freedom of migration from mountain to mountain across the desert stretches is necessarily restricted. The desert colonies may be regarded as exploring parties which have penetrated a less congenial environment.

The distribution area of *D. miranda* is included within that of *D. persimilis*, and hence also that of *D. pseudoobscura* (fig. 1). The species was first described (Dobzhansky, 1935*b*) from Lake Cowichan, Vancouver Island, and mountains near Brinnon, Olympic Peninsula, Washington. An early collection from Seattle contained an individual which might have been *D. miranda*, but subsequent collecting failed to find this species there. Next, *D. miranda* was discovered in Lone Pine Canyon, on the eastern slope of Mount Whitney, California; in this locality it is not rare, and has been collected in three successive years. Astonishingly enough, Lone Pine Canyon is the only locality in the whole Sierra Nevada where the species is known to occur. Rather extensive collecting in the Sequoia National Park, which lies just to the west of Mount Whitney, as well as in other parts of the range has failed to disclose its presence. In 1940 the species was recorded from Willapa Bay, Washington, and from Orick, Coffee Creek, Weott, Mendocino, Big Basin, and the Monterey Peninsula, California. Although it has not been recorded from Oregon, it appears probable that *D. miranda* is distributed more or less continuously

along the Pacific coast from Vancouver Island to the Monterey Peninsula. The Sierra Nevada locality seems, however, to be completely isolated from the main body of the species, a fact which suggests that it was more widely distributed in the past than it is now. Judging by its present distribution, *D. miranda* prefers the humid, cool, and equable oceanic climate even more than does *D. persimilis*.

The distribution areas of the American representatives of the *obscura* group are encircled by those of species belonging to the *affinis* group, except where the former are bounded by the Pacific Ocean (fig. 1). Thus, the area of the *obscura* complex taken as a whole is sharply discontinuous: the three American species are isolated from their European and possible but as yet unknown Asiatic relatives. In the *affinis* group, *D. narragansett*, *D. seminole*, *D. affinis*, and *D. algonquin* occur in the eastern United States, the two species last named coming in contact with *D. pseudoobscura* in Texas. *D. athabasca* extends from the Atlantic to the Pacific Ocean; the peculiar replacement of *D. pseudoobscura* and *D. persimilis* at their northern boundaries by *D. athabasca* is described above. The southwestern boundary of *D. athabasca* (fig. 1) is roughly a crescent projecting southward along the Pacific coast (Vancouver Island, Olympic Peninsula, Reedsport in Oregon) and along the Rockies (southward to Colorado and New Mexico), and receding northward in the intermontane region. The species is not known to occur in south-central British Columbia or in eastern Washington.

The distribution of *D. azteca* with relation to that of *D. athabasca* and of the species of the *obscura* group is of interest as a possible source of information on the history of the latter. Be it noted that *D. azteca* is a rather close relative of *D. athabasca*, and is capable of producing sterile hybrids with it. Yet the distribution areas of these two species are separated by those of the *obscura* group, and nowhere, so far as is known, come in contact. In Mexico and Guatemala the distribution of *D. azteca* seems to be continuous, at least in the mountains, but in the United States this species has been found only in several widely separated localities. The southernmost of these (Arizona: Huachuca Mountains, Ramsey Canyon, Cave Creek in Chiricahua Mountains; New Mexico: Glenwood, Silver City; Texas: Davis Mountains, Chisos Mountains, Bracketville; we are greatly obliged to J. T. Patterson for these interesting records obtained by his collaborators) are almost certainly a direct extension of the Mexican part of the distribution area. *D. azteca* has also been found, however, in several scattered localities in California: at Stony Creek and Deer Creek in the Sierra Nevada, and at Pinnacles National Monument, Sebastopol, Hopland, and Guerneville in the Coast Ranges (see fig. 1; the last four localities are based on collections of A. H. Sturtevant). It is virtually certain that further collecting will detect *D. azteca* in other localities in California; nevertheless, there is little doubt that its distribution in California is not continuous. It has been wholly absent from very large samples from Mount San Jacinto and from the Death Valley region, and many smaller but still fairly extensive samples from many localities in California, Nevada,

and northern Arizona. It may be noted that *D. azteca* seems to be not rare in those California localities in which it has been found. The northwesternmost extremity of the distribution area of *D. azteca* (Hopland, California) is not very far removed from the southwesternmost extreme of the area of *D. athabasca* (Reedsport, Oregon), but there remains a gap between them which is not known to be bridged. Similarly, the separation of these two species at the east is also not very wide: *D. azteca* occurs in southern Arizona, southern New Mexico, and southwestern Texas, and *D. athabasca* in the Rocky Mountains as far south as central New Mexico (fig. 1). The combined distributions of *D. azteca* and *D. athabasca* almost encircle those of *D. pseudoobscura*, *D. persimilis*, and *D. miranda*.

HABITAT AND FOOD

The standard technique of collecting *Drosophila pseudoobscura* and its relatives in their natural habitats is by attracting them to baited traps. The traps used by us were either half-pint milk bottles or paper drinking cups with a layer of fermented banana on the bottom. In favorable localities and at favorable seasons, several thousand individuals can be taken in a single evening in a territory of about an acre, some traps yielding as many as 200 flies. Under such conditions *Drosophila* populations reach very high densities. Yet if no bait is exposed, these flies are very seldom seen. The favorite collecting method of entomologists, "sweeping" with a collecting net on grass and foliage, catches none, at least in the daytime, when "sweeping" is usually practiced. The normal habitat of the fly is well concealed, and must be learned by a slow process of inference.

By using this method of baited traps in the vicinity of Berlin, N. W. and E. A. Timofeeff-Ressovsky (1940a) found that species of the *obscura* group were continuously distributed over the territory sampled, with scattered nuclei of greater population density. By contrast, *D. melanogaster* and *D. funebris* were found in disjunct islands around compost heaps, fruit and vegetable stores, and the like. We have found that the distribution of *D. pseudoobscura* is like that of its European relatives. Although continuous in distribution, it varies in density seemingly in accord with different microenvironments. Table 1 shows the numbers of individuals in traps exposed at Saunders Meadow, near Idyllwild, California, in June 1942. The traps were arranged in a straight line at 20-meter intervals. Traps A to G stood in a ravine densely shaded by *Pinus ponderosa* and *Libocedrus decurrens*, along which flowed a small stream; traps H to K were on the forest margin, among large oaks (*Quercus Kelloggii*); traps L to O extended onto an open grassy meadow.

Clearly, traps I to K were most productive, and A to E and M to O least frequented. Traps exposed near large oak trees, especially those injured by insects and by woodpeckers, have proved to be consistently productive in different regions. Traps exposed in meadows surrounded by forest are consistently underpopulated, although by no means empty. In these respects, the

data in table 1 may be regarded as characteristic of a much larger body of data, although the relative scarcity of *D. pseudoobscura* in traps A to E in the shaded ravine may have been caused by competition with *D. occidentalis*,

TABLE 1

NUMBERS OF FLIES IN TRAPS EXPOSED IN A SHADED RAVINE (A TO G), ON A FLAT AMONG LARGE OAKS (H TO K), AND ON A MEADOW (L TO O)

Date (1942)	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O
June 5	3	1	9	0	7	8	8	15	11	29	80	10	7	4	1
June 6	6	6	7	1	4	5	3	5	2	14	29	5	1	1	0
June 8	7	5	10	4	6	4	10	11	19	33	43	8	3	3	2
June 10	2	7	0	0	3	8	9	4	11	19	52	7	3	2	11
June 11	5	1	1	1	5	2	5	4	3	17	23	8	6	1	2

	1	2	3	4	5	
	105	78	88	31	82	
6	7	8	9	10	11	12
74	88	53	67	60	114	59
13	14	15	16	17	18	19
99	71	105	93	181	92	66
20	21	22	23	24	25	26
60	66	117	96	97	61	66
27	28	29	30	31	32	33
80	87	101	60	94	38	26
34	35	36	37	38	39	40
68	58	28	22	27	55	38
	41	42	43	44	45	
	79	57	29	21	40	

FIG. 2. Numbers of individuals of *Drosophila pseudoobscura* in each of 45 traps arranged checkerboard fashion 20 meters apart on June 18 to 24, 1941, at Keen Camp, California. Note the differences in the intake of the different traps.

which in this particular locality is very abundant and came to the traps by hundreds. Where the latter species is not so prevalent, *D. pseudoobscura* is very common in densely forested habitats. Figure 2 gives the numbers of flies caught on seven successive days (June 18 to 24, 1941) in each of 45 traps

arranged checkerboard fashion at 20-meter intervals near Keen Camp, Mount San Jacinto, California. Day after day some traps gave high yields of flies, while others were less productive. The productive traps nos. 1, 2, 3, 11, 15, 16, 17, 18, 22, 23, 24, 29, and 31 all stood near large pine trees (*P. ponderosa*), on a forest floor covered with a layer of pine needles. Traps 32 to 45 stood in brushland of *Artemisia tridentata* with scattered pines; these traps yielded fewest flies. The remainder of the field was covered with bushes of *Ceanothus cuneatus*, *Rhamnus californica*, and *Artemisia tridentata*, and scattered pines; the fly yield varied from high (no. 13) to low (no. 4). A similar discontinu-

61 21 41 89 48 82	36 7	36 18 34 122	78 26 97 115	58 12 39 74	9 4	5 1 6 21 15 42
11 0	17 4	37 8	25 11	35 10	8 5	10 7
16 6 7 28	9 5	15 11 16 31	57 20	52 22 46 127	11 13	14 16 33 34
16 1 7 13	38 9	29 10	20 20 39 44	17 4	12 6	34 9 48 43
5 3 15 44	87 9	56 14 42 62	27 13	36 10 18 109	13 19	7 7 11 38
35 3	20 4	40 2	16 4	56 23	37 15	9 3
42 12 17 58 52 53	18 2	63 33 81 96	38 14 61 73	55 13 24 68	35 8	48 10 39 105 36 51

FIG. 3. Numbers of individuals of *Drosophila pseudoobscura* in different traps exposed in June 1942 near Idyllwild, California. Further explanation in text.

ous distribution was observed on the field schematically represented in figure 3 (near Idyllwild, California). The traps yielding many flies stood near oak or pine trees; the unproductive traps were mostly in grassy meadows. Again and again it has been observed that traps exposed near trees, especially old and diseased ones, are well attended, and those in brush or meadowland relatively unproductive. The height of the trap above the ground makes little difference, at least in the forest. For example, Alexander Sokoloff placed a series of traps on the trunk of a pine tree from the ground level to about 40 feet; all traps yielded approximately equal numbers of flies. But direct sunlight is decidedly unfavorable.

Since the data point to a connection between the flies and tree vegetation,

a series of "sweepings" with a collecting net on tree trunks was undertaken in July 1942 near Idyllwild, Mount San Jacinto. It yielded several dozen *D. pseudoobscura*, mostly on oaks (*Quercus Kelloggii*), but also on old pines. Therefore, at least some flies take refuge during the daytime in the crevices of oak and pine bark.

The natural food of *D. pseudoobscura* is little known. A. H. Sturtevant found numerous larvae of this species and of *D. persimilis* feeding on the fermenting sap of a wild grapevine (*Vitis californica*) in a forest in Sonoma County, California. The vine had been injured with an ax, and the sap was dripping on the forest floor. G. Mainland informs us that he has observed adult *D. pseudoobscura* congregating on fruits of a species of *Opuntia* in southern New Mexico. These fruits contained larvae of an undetermined species of *Drosophila*. In the summer of 1941, however, our attention was directed by Pierre Miller to an extraordinary diseased specimen of *Cedrus deodara* in Beverly Hills, California. This tree was suffering severely from a "slime flux," a bacterial infection. Fermenting sap was oozing as froth at various points on the trunk, and the odor of yeast was perceptible several feet away. As it flowed down the bark, this frothy sap became concentrated into a kind of white jelly, resembling library paste. As it dried at the periphery and on the ground or in the crotch of a branch, it took on the consistency and color of moist brown paper. Adult *Drosophila* were abundant around the tree and numerous larvae were to be seen beneath the jelly rather than within it, creeping along the moist crevices of the bark. Their pupae were conspicuous in the drying papery parts. When put into half-pint bottles, these larvae and pupae eventually matured, and from them were recovered numerous adults of the three species most commonly collected in this region: *D. pseudoobscura*, *D. simulans*, and *D. hydei*.

These observations show that the larvae of *D. pseudoobscura* can feed and mature on the fermenting sap of bleeding trees and in decaying fruit. Whether this is its only, or even its normal, food remains to be decided. At first sight, this seems unlikely. In the arid Southwest flourishing populations can be found in coniferous and mixed forests which in midsummer are extremely dry, and in which neither decaying fruits nor fermenting sap seem to be available. W. P. Spencer has suggested (oral communication) the possibility that in such environments the species may breed in the soil of the forest floor on a diffuse food supply of decomposing plant particles, this breeding taking place only during the seasons when sufficient moisture is available in the soil. The populations found during the dry season are, then, the survivors of the spring brood and will themselves breed in the fall months. This hypothesis has been carefully tested. Although the possibility that some larvae may develop in the soil is not excluded, it seems probable that this is not the norm. In the first place, the flies are known to reproduce and hatch during the course of the dry season (see below). Furthermore, analyses of the fly crops show that the flies have access to supplies of concentrated foods even in the apparently dry forests.

In the summers of 1941 and 1942, at Keen Camp and at Idyllwild, California, flies were attracted to the usual banana traps, but were caught before they had time to ingest the bait. Their crops were dissected at once and the contents examined under a compound microscope. We are greatly indebted to V. P. Sokoloff, of the Citrus Experiment Station, Riverside, who made agar-plate cultures and determined some of the microorganisms thus obtained. Only about 10 per cent of the flies caught had their crops nearly or completely empty and collapsed. Since the contents of the crop pass into the gut within about 24 hours after the ingestion of the food (this point has been determined by experiment), few of the flies had gone foodless for 24 hours or more before being caught. The rest had their crops more or less distended with food. Some flies had their crops filled with practically a pure culture of a single species of microorganism; more frequently the crops contained mixtures of several species. Furthermore, the crop contents varied greatly from fly to fly, even among individuals caught simultaneously at the same collecting station. At least 99 per cent of the nonliquid crop contents were bacteria, yeast cells, and mold spores, named in the order of frequency. The remainder were occasional spores of such fungi as *Diplodia*, *Cladosporium*, *Helminthosporium*, rusts or smuts, and amorphous particles of some indeterminate organic matter. A great variety of yeast forms were found, differing in size and shape of the cells and in manner of growth. One very characteristic form suggests *Saccharomyces farinosus*, but was not very common (found in 4 crops among nearly 200 dissected). Some cells resembling *Oidium* and *Leuconostoc* were also found. Among the bacteria, large and small, single and chain-forming, Gram-positive and Gram-negative cocci were encountered, as well as a variety of rodlike forms of diverse sizes, some Gram-positive and some Gram-negative, either motile or nonmotile. An apparently undescribed species of *Sarcina* gave agar-plate cultures which, in the laboratory, attracted *Drosophila* (V. P. Sokoloff, written communication).

Media of high carbohydrate content seem to be required for the development of many of the microorganisms commonly found in the fly crops. A search for these media in the forest was undertaken, but met with only indifferent success. Moist places were found on the bark of some oaks which had evidently bled earlier in the season; moist decaying areas were found in the crotches of dead branches of others, and under the bark of dying trees and in hollow stumps there were some moist masses of debris produced by wood- and bark-boring insects. Only a single *Drosophila* larva was found in such places, and it was injured in the process of extraction and could not be determined. An examination of the microflora of these materials revealed the presence of forms, both bacteria and yeasts, which appeared to be similar to those found in the fly crops. The possibility that the flies may breed on live trees in the abandoned burrows of wood-boring insects has been suggested, but could not be checked. It is obvious that more observations are necessary to solve the problem regarding the food of *Drosophila pseudoobscura* and *D. persimilis*.

ATTRACTIVE RADIUS OF BANANA TRAPS

Because *Drosophila pseudoobscura* is collected with the aid of banana traps,¹ it is desirable to know from what distance the flies visiting these traps come. A knowledge of this point may help to clarify the problem of the distance traveled by flies in nature in their quest for food. The striking inequalities in the intake of different traps exposed only short distances apart (Dobzhansky, 1939, also table 1 and figs. 2 and 3 above) suggest that the visitors to a given trap are drawn from a limited territory in its immediate vicinity. On the other hand, the fact that traps in a variety of microenvironments are visited to some extent suggests that the attractive radius of a trap may be fairly large, since it is difficult to suppose that the flies are omnipresent. The following experimental procedure was devised by Bruce Wallace and Th. Dobzhansky.

In June 1942, 49 traps were arranged checkerboard fashion (fig. 3), 20 meters apart, in a pine-oak woodland near Idyllwild, California. Approximately 300 meters from this experimental field, a control field with 10 traps located roughly in a circle about 10 meters apart was arranged. On the evenings of June 24 and 26 collections were made from all the traps. The numbers of flies caught are shown in the upper left-hand corners of the squares in figure 3. On June 25 and 28 only the alternate traps were exposed on the experimental field. Consequently, the number of traps was 16 instead of 49, but the distances between them were 40 instead of 20 meters. The slanting numerals in the middle of the squares in figure 3 show the numbers of flies caught on these days. Finally, on June 29 and 30 only 9 traps, 60 meters apart, were exposed on the experimental field; the numbers of flies are shown in the lower right corner of the squares in figure 3. The 10 control traps were, of course, exposed on each of the six evenings. To make the treatment of all the traps equal, the fly collections were made in all the traps simultaneously, by several observers starting and completing the counts by the watch. The average numbers of flies collected per trap are shown in table 2.

The numbers of flies varied greatly on different days, in the experimental as well as in the control traps. This variation was probably due chiefly to weather conditions (fewer flies come on cool days; see below). More important for our present purpose is the fact that when the traps on the experimental field were spaced 20 meters apart, they caught fewer flies than the control traps, whereas traps located 40 or 60 meters apart caught more flies than the controls. This is shown best by the ratios of the fly numbers in the experimental control traps (the right-hand column in table 2). These ratios were significantly higher when the experimental traps were spaced at 40 or 60 meters than when they were located 20 meters apart; the 40- and 60-meter

¹ Fermenting banana is, of course, not the only substance which attracts the flies. Decaying cantaloupes are at least equal to banana in attracting power. Decaying fruit and vegetables and fermenting liquids of many kinds are commonly visited. *D. pseudoobscura* is only occasionally found on kitchen refuse, and other species, particularly *D. simulans*, *D. melanogaster*, and *D. hydei*, are evidently much superior to it in these environments.

spacings did not differ significantly from each other. It follows that traps 20 meters apart interfere with each other, but those at 40 or 60 meters show no such interference. Since the control field was in a territory more favorable for the flies (denser trees) than the experimental field, the fact that the control traps, though only about 10 meters apart, had more flies than the experimental traps does not contradict the above conclusion.

The objection may be raised that comparing the average numbers of flies in all the traps on the experimental field is unfair. Indeed, different traps on the experimental field of 49 were not equally well attended (see fig. 3). To cope with this objection, the data for June 24 and 26 were recalculated taking into account only those traps which stood in the positions which were subsequently occupied by the traps spaced at 40 or at 60 meters. The average numbers of flies in the 16 traps corresponding to those used on June 25 and 28 are: for June 24, 35.56 ± 5.44 ; for June 26, 13.06 ± 1.97 . The average numbers

TABLE 2
NUMBERS OF FLIES PER TRAP ON THE EXPERIMENTAL AND THE CONTROL FIELDS

Date (1942)	Number of traps	Distance between traps (m.)	Flies per trap		Ratio Exper. : control
			Experimental	Control	
June 24	49	20	30.8 ± 2.8	39.1 ± 4.5	0.79 ± 0.12
June 26	49	20	10.4 ± 1.1	14.1 ± 0.7	0.73 ± 0.08
June 25	16	40	20.3 ± 4.8	22.5 ± 2.4	1.30 ± 0.25
June 28	16	40	69.1 ± 8.8	40.3 ± 5.0	1.72 ± 0.31
June 29	9	60	44.8 ± 8.0	35.7 ± 2.7	1.25 ± 0.24
June 30	9	60	57.3 ± 9.8	43.6 ± 4.6	1.32 ± 0.26

of flies in the 9 traps corresponding to those used on June 29 and 30 are: for June 24, 38.00 ± 7.60 ; for June 26, 12.67 ± 2.88 . The ratios experimental:control are, therefore, 0.91 and 0.97 for June 24, and 0.93 and 0.90 for June 26. Comparing these ratios with those for traps spaced at 40 and at 60 meters (table 2), we find that the ratios for traps at 20 meters are smaller than unity, and for traps at 40 and 60 meters greater.

The most reasonable view is that the probability of a fly's coming to a trap (or to a natural food source) is a function of the distance between them. Most of the flies in the immediate neighborhood of a trap will be attracted to it, and fewer and fewer of the flies at greater distances will come. The absolute attractiveness of a trap will, of course, depend on the nature and quantity of the bait, on the species and physiological condition of the flies, on weather, and on the presence or absence of other sources of attraction in the environment. Therefore, the above data are valid only for *D. pseudoobscura* and only for midsummer conditions on Mount San Jacinto. Under these conditions, the effective attractive radius of a banana trap for *D. pseudoobscura* is hardly more than 30 meters.

DIURNAL PERIODICITY

Under laboratory conditions, species of *Drosophila* seem to be more or less equally active whenever observed. Geneticists who may have worked for many years with them in laboratories are therefore often unaware of the fact that in nature these insects display striking differences in behavior at different times of the day. As early as 1933, when one of the writers first attempted to collect *D. pseudoobscura* and *D. persimilis* in the mountains of California, it was found that by far the most effective time to expose the traps was shortly before sunset or shortly after sunrise. In summer, particularly, it was found that the arrival and disappearance of the flies both night and morning was frequently quite abrupt. N. W. and E. A. Timofeeff-Ressovsky (1940a) have also reported that near Berlin, *D. melanogaster*, *D. funebris*, and species of the *obscura* group are most active during the morning and evening, and scarcely appear at midday and during the night. Our own observations have established a similar behavior for *D. simulans* and for members of the *hydei* group.

A diurnal cycle typical for *D. pseudoobscura* on a warm, cloudless day of early summer on Mount San Jacinto is represented in the upper part of figure 4. The data are based on the output of 10 traps exposed in an open yellow pine forest at Keen Camp, elevation 4300 feet. No flies came between sunrise and 7 A.M.; the temperature during that time rose from 42 to 54° F. A temperature of about 50° F. (10° C.) is apparently limiting for *D. pseudoobscura*: below that, no flies appear. Between 7 and 10 A.M. flies were coming, the maximum abundance being observed around 8 A.M. None came between 10 A.M. and 5 P.M. Another sharp maximum occurred at about 6:30 P.M. Darkness fell shortly after 7 P.M., and the flies left the traps very abruptly: none were left by 7:30 P.M. Another cycle, observed on August 17, 1942, at Bluff Lake, San Bernardino Mountains, California, elevation between 7300 and 7400 feet, is shown in the lower part of figure 4. In this case, 13 traps were exposed in *Pinus contorta*-*Abies concolor* forest; the amplitude of temperature change was less than on the day discussed above; sunshine alternated with cloudiness. Some flies were present from sunrise on; the morning maximum came around 8 A.M.; from 10 A.M. to 4 P.M. the flies were rare, but at no time were the traps completely deserted; another, and very sharp, maximum was observed at 5:45 P.M.; flies were still abundant at the time of the apparent sunset, at 6:15 P.M.; very few remained at darkness, 6:45 P.M., and none were present at 7:05 P.M. The two cycles shown in figure 4 are astonishingly similar, despite the differences in elevation of the collecting localities, temperature, humidity, and cloudiness. The following differences between the cycles may, however, be noted: (a) the flies at Keen Camp appeared later in the morning, probably on account of the lower temperature; (b) some flies at Bluff Lake were active at midday; we hope to show below that this is probably ascribable to the cloudiness.

Any attempt to analyze the causation of the diurnal cycles is confronted with

a difficulty inherent in the observational, as contrasted with the experimental, method. Obviously, several variables are changing in the fly environment during the day: light, temperature, humidity, wind, cloudiness, etc. The changes in these variables are neither independent nor subject to our will. The only recourse is to compare the behavior of the flies on different days, at different seasons and places. This we have attempted to do, and the following data

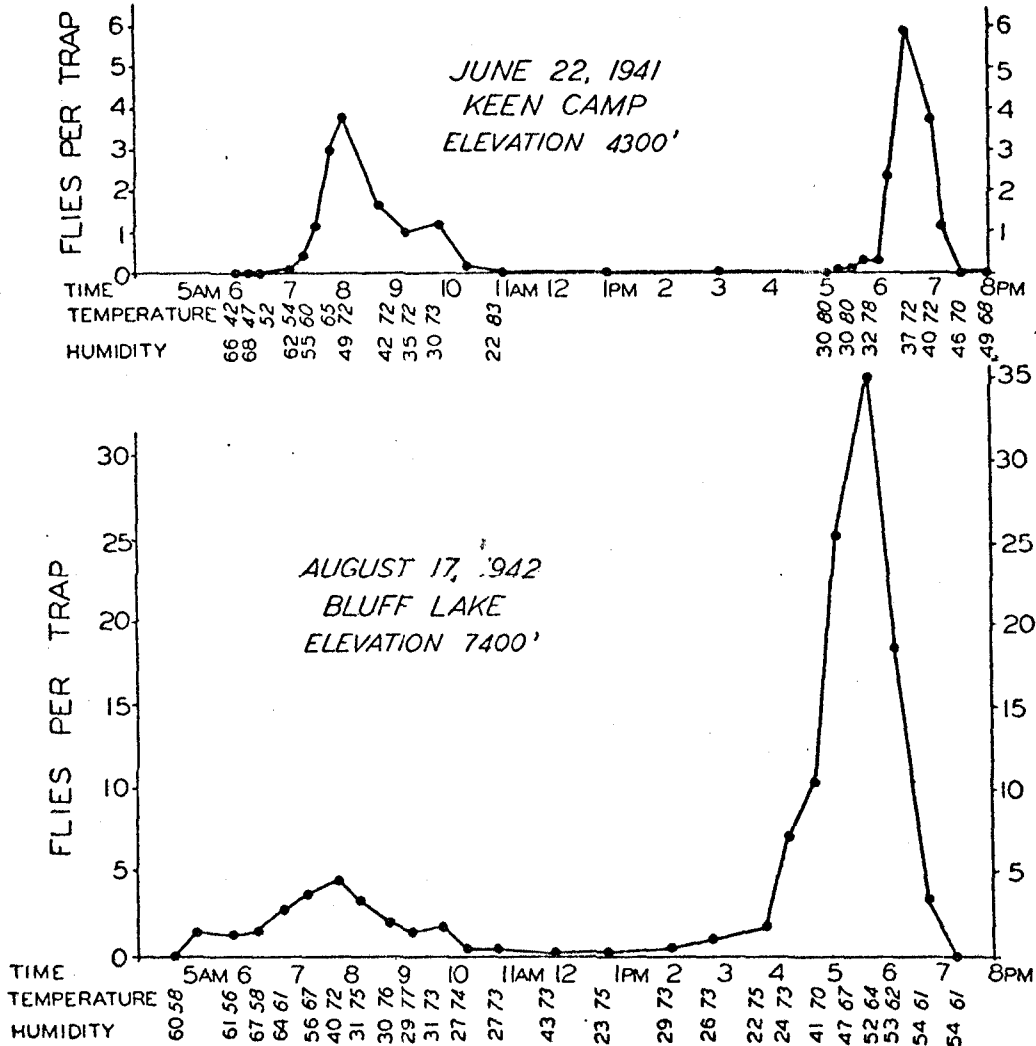


FIG. 4. The diurnal periodicity in the activity of *Drosophila pseudoobscura*

are samples of the material collected. For several years we entertained the hypothesis that temperature and humidity are the primary factors which evoke the activity of the flies during the morning and evening hours; at present we are inclined to believe that light intensity is the primary factor, temperature and humidity being less important.

After analysis of all the data available, the following facts of behavior seem to be established. The invariable rule to which no exceptions have so far

been found is that no flies are active during the hours of darkness, from dusk to dawn. By "activity" we mean in this discussion the flight in search of food which leads the flies to enter traps. Flies have been trapped through a range of relative humidity from 11 per cent to nearly 100 per cent. Although most have been trapped within the range from 30 to 50 per cent, it seems probable that this is merely a reflection of the greater prevalence of days with this range in the parts of southern California where the major part of the work was done. If the temperatures at which collections have been made are held constant for intervals of 5° and the numbers of flies are plotted for different percentages of relative humidity, or if the relative humidity is held constant for intervals of 10 per cent and the numbers of flies are plotted for different degrees of temperature, no preference appears for any combinations of temperature and humidity, whether all stations are included, both morning and evening maxima or either alone, or whether stations are treated separately. Flies have been trapped through a range of temperature from 47.5 to 90° F. If numbers be considered, however, it appears that more have been trapped between 60 and 80° ; yet here again, this result seems only to reflect the number of days with these temperatures when recordings were made. If the diurnal maxima of abundance alone are considered, the total range of humidity at which they were recorded is 23 to 71 per cent, and the total range of temperature 55 to 87° . The latter, recorded at Andreas Canyon, is close to the highest temperature at which any flies have been collected, the former not much above the lowest. Only a single fly was caught below 50° F.

At a given collecting station, the numbers of flies encountered on successive days may vary greatly, but, unless clouds or rain intervene, the times of the appearance and disappearance of the flies change but slowly. Figure 5 shows the numbers of flies that came to traps on the afternoons of June 24 to 30, 1942, at Idyllwild (fig. 5 and table 2 describe different aspects of the same experiment). June 26 was cool; the temperature changed from 66° F. at 5:25 P.M. to 56° at 7:05, and the relative humidity from 49 to 69 per cent; the average number of flies per trap was 10.9. June 24 was warmer and drier (73° and 31 per cent at 5:15 P.M., 58° and 50 per cent at 7:15 P.M.); the average number of flies per trap was 32.2. June 28 was still warmer, but less dry (80° and 30 per cent at 5:00 P.M., 61° and 64 per cent at 7:05 P.M.); the average number of flies rose to 58.0. June 30 was the warmest day (81° and 26 per cent at 5:15 P.M., 63° and 54 per cent at 7:05 P.M.); the average number of flies fell to 49.6. Despite these variations, the flies appeared in appreciable numbers at about 5:30 P.M., reached maximum abundance between 6 and 6:30, and disappeared shortly after 7 P.M. on each of these four days (fig. 5).

The independence of the time of appearance, of maximum abundance, and of disappearance of the flies as regards temperature, and the dependence of the number of flies coming to traps on temperature, and possibly on humidity, was observed repeatedly whenever collections were made at the same station on a series of successive cloudless days. Flies come to traps at their customary time, unless the temperature falls to or below 50° F. The possibility that

there may exist also an upper limit of temperature tolerance will be discussed below. Rain and cloudiness change the situation completely. This was observed for the first time in July 1935 in Cimarron Canyon, New Mexico. After a brisk thunderstorm, *D. pseudoobscura* came abundantly from noon until 2 P.M., disappeared thereafter, and returned shortly before sunset. *D. persimilis* and *D. pseudoobscura* have repeatedly been trapped during the day on the coast of northern California, where fog or cloudiness is the rule in summer. From July 23 to August 8, 1941, flies were collected every after-

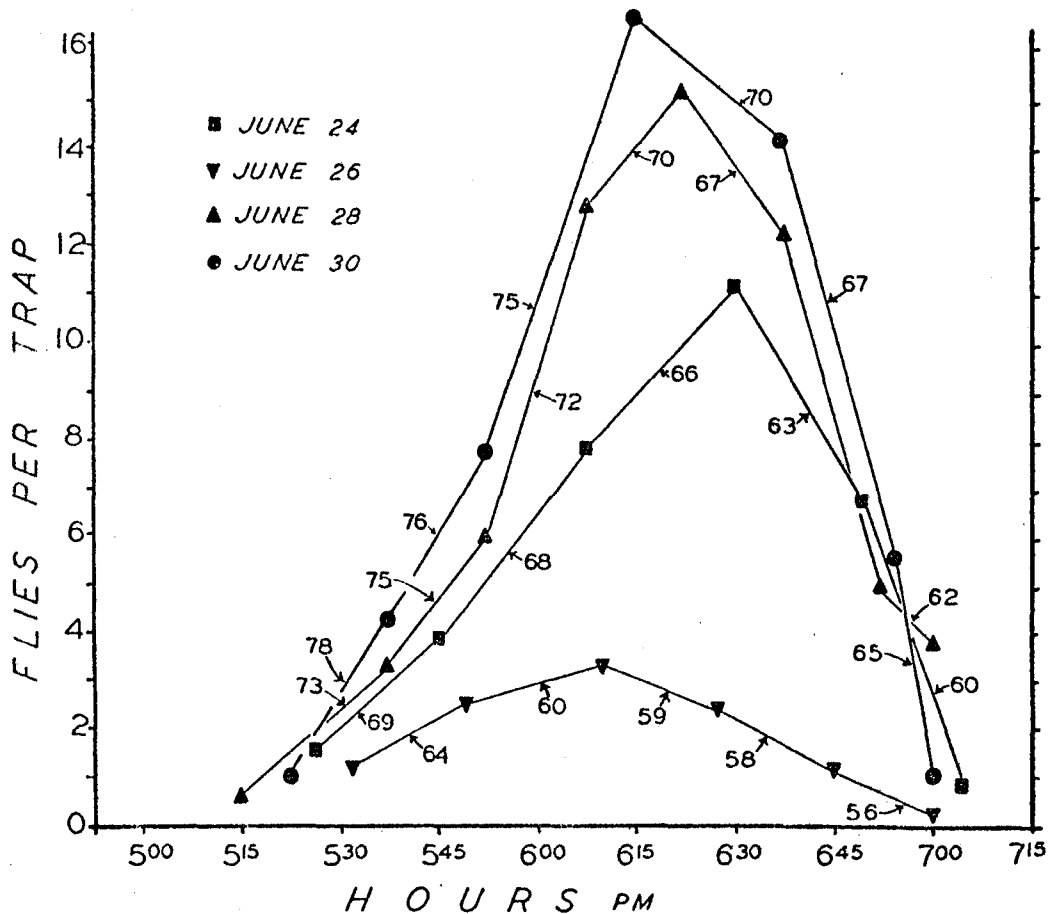


FIG. 5. Numbers of flies attracted to traps on days with different temperatures

noon on the same experimental field at Keen Camp, California. Most of these days were cloudless, and the flies appeared regularly at about 5:00 to 5:30 P.M., reached maximum abundance between 6:10 and 6:45, and disappeared after dark between 7:10 and 7:20 P.M. July 25 was, however, cloudy, and the maximum abundance of the flies was observed at 5:30 P.M. Rain fell on August 7; the flies were about equally abundant from 3:45 (when the experiment started) to 6:10 P.M., and disappeared at 7:05 P.M. Following a long drought, the day of August 9, 1942, was cloudy at Idyllwild. A mist fell around 5:20 A.M., and again at noon, and it rained from 4 P.M. on. On this day *D. pseudoobscura* was abundant from 5 to 9 A.M., rare but still present from 9 A.M. till noon,

and again abundant from noon till 4 P.M. On the clear day of August 12, the flies were abundant from 4:45 to 8 A.M., absent from then till 5 P.M., and present again till about 7 P.M., on the same part of the experimental field on which such different behavior had been observed only three days previously (table 3).

Since cloudiness and rain increase the humidity, usually lower the temperature, and cause the flies to come to traps at any time during the daylight hours, it seemed plausible to ascribe to these factors the evocation of the activity of the flies. As pointed out above, other data are inconsistent with this hypothesis. Since cloudiness has also the effect of diminishing the

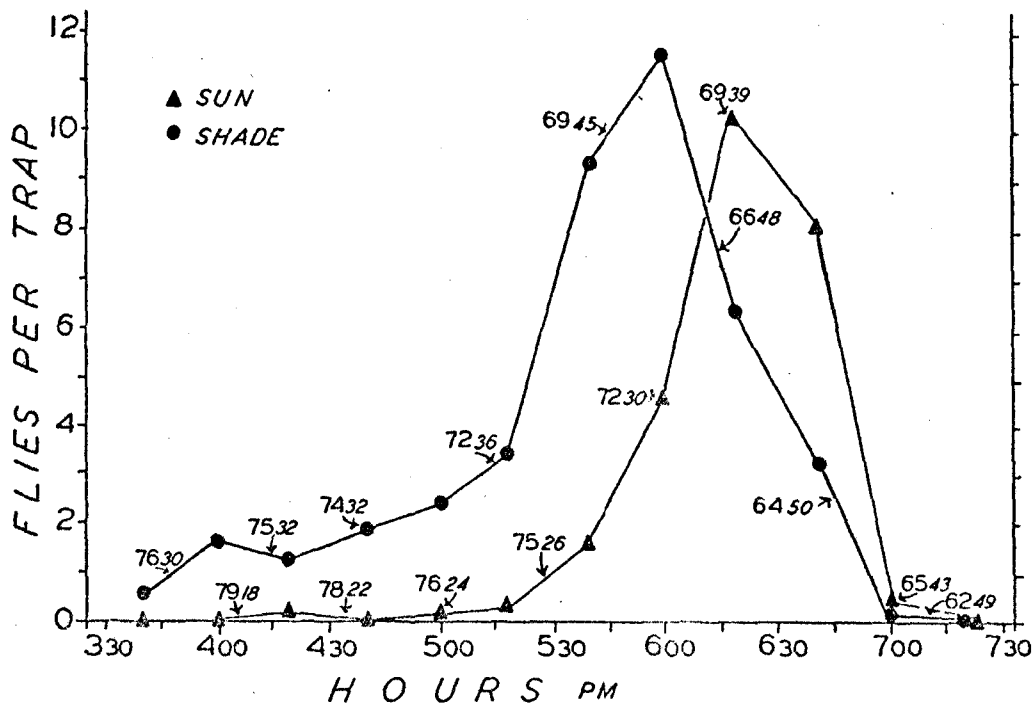


FIG. 6. Numbers of flies which came to traps exposed in a shaded ravine and on sunlit slopes near Idyllwild, California, on July 30, 1942. Larger numerals, temperature in °F.; smaller (slanting) numerals, relative humidity in per cent.

intensity of sunlight, the facts so far presented do not necessarily contradict the view that light intensity is the primary factor determining *Drosophila's* activity. To test this view, the following observations were made. On the afternoon of July 30 a series of 15 traps was exposed in a ravine well shaded by a dense growth of ponderosa pine and *Libocedrus decurrens* at Saunders Meadow, Mount San Jacinto. Another series of 15 traps was exposed simultaneously on the sunlit slopes of the same ravine in a sparse stand of *Pinus Coulteri*, *P. ponderosa*, and *Quercus chrysolepis*. Although the second series of traps was protected from direct sunlight by the shadows of the tree trunks, the light intensity in their surroundings was obviously greater than in the shaded ravine. Temperature and humidity readings were made both in the ravine and on the slopes. The results are presented in figure 6. The observa-

tions were repeated in the same setting on August 12 during the whole day; this time, however, only 10 traps were exposed in each series, and temperature and humidity readings were taken only in the ravine; the results are presented in table 3. Another repetition fell on the rainy day of August 9, with the results given above. The data in figure 6 and table 3 show concordantly that in a well shaded area *D. pseudoobscura* remains active at all daylight hours even on clear days, whereas no flies come to traps in more open areas except in the morning and the evening. To be sure, the morning and evening maxima are observed in the shaded area as well, but here they are not so sharp as they are in the open. It may be noted that the temperature in the shaded area

TABLE 3

NUMBERS OF FLIES PER TRAP OBSERVED AT DIFFERENT TIMES OF THE DAY ON AUGUST 12, 1942, IN A SHADED RAVINE AND ON SUNLIT SLOPES

Time (A.M.)	Temp. (°F.)	Humidity (%)	Flies		Time (P.M.)	Temp. (°F.)	Humidity (%)	Flies	
			Shade	Sun				Shade	Sun
4:45	58	77	0	1.3	12:10	75	40	0.3	0
5:05	57	82	1.3	12.3	1:05	74	40	0.1	0
5:30	57	75	1.9	4.8	2:00	74	36	0	0
6:00	57	75	1.4	2.4	3:10	74	40	0.2	0
6:30	58	70	1.1	2.6	4:00	73	44	0.3	0
7:05	59	72	0.2	1.1	5:15	71	60	2.9	0.3
8:05	67	70	2.4	1.3	5:45	67	62	4.0	3.8
9:00	70	60	1.5	0	6:15	68	62	4.0	3.8
10:00	75	44	0.1	0	6:45	63	71	0.7	2.1
11:00	74	40	0.1	0	7:30	62	73	0	0

was 3 to 4° F. lower and the relative humidity 10 to 15 per cent higher than in the open area. Figure 5 and other data show, however, that even greater temperature and humidity fluctuations affect only the abundance, not the times of appearance and disappearance of the flies.

Another way to test the relative effects of light and weather on the daily periodicity is to observe the times at which the flies are active in the same locality in different seasons of the year. Still another way is to compare the behavior of the flies at the same season, and preferably on the same day, in localities at different elevations and hence with different temperature and humidity regimes. Obviously, only cloudless or nearly cloudless days are suitable for such comparative observations. Andreas Canyon is a locality lying at the foot of Mount San Jacinto, elevation about 800 feet. Table 4 shows the numbers of flies coming to traps at different hours of the day in that locality; temperature records (Fahrenheit) are also shown in table 4. The flies are common at Andreas in winter and spring, very scarce in late summer. January 11, 1942, was cloudy; flies came to traps from morning till sundown, without a definite maximum. On March 13 a strong wind arose in the afternoon and no flies appeared. Other days recorded in table 4 were clear. In

September, October, May, and June flies were coming to traps only in the mornings and the evenings. In May the evening maximum of abundance of flies was observed around 5:30 P.M., the temperature at that time being 72°; in September the evening maximum came around 5:00 P.M., temperature 88°; in October the maximum was at about 4:00 P.M., temperature 68°. Clearly, the evening maxima come at very different temperatures, and, we may add, at different humidities. With the advent of short winter days, in November and December, the morning and evening maxima approached each other to such an extent that only a short period in the middle of the day showed no activity on the part of the flies. In winter, however, the flies appear late and disappear early. On December 7 the first fly came at 8:30 A.M., which is later than the end of the morning activity in September, and the last fly was observed at 4:30 P.M., which is the time when flies just begin to come to traps in September, May, and June. The temperature during the evening maximum of abundance of flies in November was 66-67° F., and in December 62°. The evening maxima come, therefore, at temperatures from 62 to 88°. Morning maxima are generally less definite, but the data in table 4 record them at temperatures from 58 to 66° F. Meteorological data for Riverside, California (about 40 miles from Mount San Jacinto) show that the morning twilight in June begins at about 3 A.M., sunrise is at 4:45 A.M., sunset at 7:20 P.M., and the end of the evening twilight at 9 P.M.; in December the morning twilight comes at 5:40 A.M., sunrise at 7:10 A.M., sunset at 4:45 P.M., and the end of the evening twilight at 6:20 P.M. Even more interesting and pertinent are the data for light intensity at different hours of the day and at different seasons. The light intensity has been measured in terms of gram-calories per square centimeter of horizontal surface. The intensities between 10 and 30 gram-calories are observed between 6:40 and 8 A.M. and between 5:15 and 6:40 P.M. on June 21, and between 8:50 and 11:15 A.M. and between 1:30 and 4:10 P.M. on December 23. We are indebted to the University of California, Citrus Experiment Station, Riverside for these meteorological data. The hypothesis that the activity of the flies is determined by the light intensity seems to be on the whole consistent with the known facts.

Comparison of the times of appearance, maximum abundance, and disappearance of the flies in localities at different elevations is made difficult by the seasonal variations in their abundance. At low elevations the flies are scarce in summer, whereas at high ones they are not to be found in winter. We have tried to assemble data for Andreas Canyon (elevation 800 feet), Piñon Flat (4000 feet), and Keen Camp (4300 feet), all within 10 to 15 miles of one another on Mount San Jacinto. Occasional observations have been made also in divers other localities. The tabulation on page 33 summarizes some of the data on the hours of the afternoon at which the maximum of abundance of flies is observed, and on temperatures (Fahrenheit) prevailing at these hours.

The maxima as well as the arrival and disappearance of the flies tend to come at the same time, despite differences in elevation, temperature, humidity, and environment generally at the different stations. At Piñon Flat, however,

the maximum tends to occur a little later than at Andreas Canyon and Keen Camp. This is not clearly shown in the above data, but it has been observed repeatedly. This delay is probably significant, because this station is but little shaded from the setting sun; Andreas Canyon has a high mountain lying to the west of it, and it passes into shade long before sunset; Keen Camp is forested and is also shielded on the west by a mountain range. Whether these facts are sufficient to explain the behavior of the flies at Piñon Flat is not quite clear, but in any case the data as a whole are consistent with the hypothesis that the activity of the flies is determined by light rather than by temperature or humidity.

In the summers of 1941 and 1942 flies marked with a mutant gene or with a spot of paint on the thorax were released at Keen Camp, Piñon Flat, and Idyllwild. (These experiments are described in the following section.) These

HOURS OF THE AFTERNOON AND TEMPERATURES (F.) AT WHICH MAXIMUM ABUNDANCE OF THE FLIES HAS BEEN OBSERVED

Dates	Andreas		Piñon		Keen	
	Time (P.M.)	Temp. (°F.)	Time (P.M.)	Temp. (°F.)	Time (P.M.)	Temp. (°F.)
June 15-17, 1941.....			7:00	72	6:30	70
Sept. 9, 1941.....	5:00	78	6:00	74	6:00	76
Oct. 3, 1941.....	4:00	68	5:30	62	4:00	63
Nov. 8, 1941.....	3:30-4:00	67	4:00	62	3:30-4:00	67
Dec. 6-7, 1941.....	4:00	62	4:00	55
Jan. 10-11, 1942.....	3:30	67	3:30	62
Apr. 2-3, 1942.....	5:00	78	5:30	68
May 2-3, 1942.....	5:30	72	6:00	66	5:30	63

flies, and their ancestors for several generations, were bred in regular culture bottles in the laboratory. For several consecutive evenings after the liberation of the marked flies, traps were exposed in the neighborhood of the point of release, and the numbers of the marked and wild flies which came to these traps were recorded. These experiments have revealed an astonishing fact: at least at Keen Camp and at Idyllwild, the laboratory-grown flies fell almost immediately into the diurnal cycle characteristic of the wild flies in the same locality. Sometimes for a day or two after the release the marked flies began to arrive in the traps about half an hour before the wild flies did, but on the following days there was no observable difference between the behavior of the marked and the wild flies. Similar experiments conducted at Piñon Flat in July 1942 suggested that in the hot and arid midsummer climate of that locality the laboratory-grown flies did not adjust themselves quite so successfully as they did in the milder environments of Keen Camp and Idyllwild. At any rate, only a small fraction of the liberated marked flies were recaptured, and those which came to traps did so mostly before the wild flies ap-

peared. As indicated above, there is some reason to suspect that the diurnal cycle of the flies at Piñon Flat is somewhat different from that in other parts of Mount San Jacinto. Only experiments can determine to what extent the diurnal periodicity of the flies is inborn and to what extent it is induced by the environment during the fly's development. It is also possible that there may exist geographic races or ecotypes which have somewhat different periodicities; this possibility must be left open.

This hypothesis, that light is the principal causal factor which determines the diurnal periodicity of the flies, explains the data better than any other which we have been able to contrive. Aside from the indications of a peculiar behavior of flies at Piñon Flat (see above), there is only one fact which seems inconsistent with this hypothesis. This is the fact that more time elapses between sunrise and the morning maximum of abundance of the flies than between the afternoon maximum of abundance and sunset (fig. 4, tables 3, 4). The light intensity, of course, increases from morning to noon and decreases from noon to sunset. The light intensity which permits the flies to be active must be greater in the morning than in the afternoon. The reacting material, the fly, is evidently not the same at different times of the day.

SEASONAL CYCLES

The distribution areas of *Drosophila pseudoobscura* and *D. persimilis* are so extensive, both horizontally and vertically, and accordingly embrace such a range of climates, that the seasonal cycles must of necessity be different in different parts of their specific areas. Systematic observations have been made by the writers on the cycles of *D. pseudoobscura* on Mount San Jacinto in California and by J. T. Patterson in Texas, chiefly at Aldrich, near Austin. The writers' observations were made in four localities, namely Andreas Canyon, Piñon Flat, Keen Camp, and Idyllwild.

The first-named locality is a palm oasis at the mouth of a perennial stream which debouches onto the Colorado Desert near Palm Springs. The elevation is approximately 800 feet. The slopes are clothed with the sparse, shrubby vegetation characteristic of the Colorado Desert. The oasis itself is made up of palms (*Washingtonia filifera*), willow (*Salix lasiolepis*), sycamore (*Platanus racemosa*), and poplar (*Populus Fremontii*). The ordinary daylight range of temperature during the winter months, except on rainy days, varies roughly from 50 to 75° F., and of relative humidity from 20 to 60 per cent. During the summer months, the site comes under the influence of the desert drought, although this effect is ameliorated in the immediate vicinity of the stream because of the tree cover. The ordinary daylight range of temperature then varies roughly from 65 to 95°, and of relative humidity from 20 to 60 per cent.

The second locality, Piñon Flat, is found on the desert side of the mountains at an elevation of 4000 feet. The climate shows greater extremes of temperature than at Andreas. Light snowfall is occasional in winter; the ordinary range of daylight temperature is from 40 to 65° F., and of relative humidity from 20 to 50 per cent. The corresponding ranges in summer are

60 to 90° and 20 to 60 per cent. The vegetation is an open woodland of piñon (*Pinus monophylla*) and juniper (*Juniperus californica*) interspersed with scrub oak (*Quercus dumosa*) and *Rhus ovata*. A thin layer of duff is found beneath the pines and oaks.

The third locality, near Keen Camp (Hurkey Creek), lies at an elevation of 4300 feet at the lower margin of the yellow pine zone. The principal cover is an open but well developed forest of *Pinus ponderosa* with shrubs of *Artemisia tridentata*, *Ceanothus cuneatus*, and *Rhamnus californica*. The duff is fairly thick, especially around the bases of trees. Rainfall is higher than at Piñon Flat, and several inches of snow cover the forest floor during the winter. Observations of temperature and humidity have been made only from May to November, inasmuch as the flies are not found during the winter months, unless perhaps on exceptionally warm days. During this period the ordinary range of daylight temperatures is from 40 to 75° F. in November

TABLE 5
OCCURRENCE OF *Drosophila pseudoobscura* IN DIFFERENT MONTHS

Locality	J	F	M	A	M	J	J	A	S	O	N	D
Andreas Canyon	-	x	X	X	x	.	.	.	-	-	-	-
Piñon Flat	-	x	x	X	X	x	.	.	-	-	-	-
Keen Camp	o	o	o	-	x	X	X	x	-	-	-	o
Idyllwild					x	X	X	x				
Aldrich	172	131	512	1113	562	2	6	0	1	62	144	231

- few flies or none.
- fairly abundant.
- X maximum.
- x increasing to or decreasing from the maximum.
- o unknown, but probably none or only occasional.

and May and from 50 to 90° in July and August. The corresponding humidity is 25 to 80 per cent.

Idyllwild, at an elevation of 5300 feet, is located well within the yellow pine forest, the principal trees being *Pinus ponderosa*, *Libocedrus decurrens*, *Quercus Kelloggii*, and the most abundant shrubs species of *Arctostaphylos*. It lies on the coastal side of the mountains, with a general exposure to the west. The climate is in general similar to that of Keen Camp, but being at a higher elevation and more subject to coastal influences, Idyllwild has a greater rainfall and snowfall, and the relative humidity is generally higher.

It is apparent from the above description that the four localities form a climatic gradient up the mountain, and, as judged from the nature of the vegetation, a gradient which roughly approximates the climatic gradient from the Colorado Desert northward into the Sierra Nevada. The occurrence of the flies in the San Jacinto localities, and also at Aldrich in Texas, is shown in table 5.

From this table (see also table 4 for detailed data at Andreas Canyon) it will be observed that the maximum population shifts from March and April

at Andreas Canyon to June and July at Keen Camp and Idyllwild. It is possible that at the latter station the flies persist in abundance into August as well. The data shown for "Aldrich" were obtained by systematic collecting by J. T. Patterson; the cycle suggested by his figures is similar to those of Andreas and Piñon Flat (to which his locality is more similar climatically) and somewhat intermediate between them. At the same time, his data are illustrative of the relative frequencies which we have observed at Mount San Jacinto. According to Patterson, the species is relatively uncommon in Texas. Two trips to central Mexico, made by the senior author in September (end of the rainy season) and in March (the dry season), showed the population at the former time to be only slightly less than at the latter. At Wildrose Canyon (Panamint Range, Death Valley), large numbers of flies have been repeatedly obtained in May and early in June, but only a few flies were found later in June and in early October. Although comparable in climate and vegetation with Piñon Flat, this station lies at an elevation of 7900 feet and is under snow in winter.

Although the seasonal maxima are relatively constant with reference to the time of year, they fluctuate from year to year in numbers caught, and hence presumably in population density. Climatic factors seem clearly causative of this type of fluctuation. The degree to which the population of a given region seemingly contracts and expands is apparently a function partly of rainfall. The winter of 1940-1941 was unusually wet. Not only was *D. pseudoobscura* relatively plentiful on the Colorado and Mojave deserts during the late winter and spring, being collected there many miles from tree vegetation, but at Piñon Flat, for example, the population was still abundant in July and even in August. On the other hand, the winter of 1941-1942 was more than usually dry and was followed by a dry summer during which the flies were quite scarce in July at Piñon Flat.

Abundance of flies at a given season does not necessarily mean that the flies are breeding at that time. At first glance, as was pointed out above, it seems improbable that sufficient suitable places could be found in summer in the dry forests of southern California for the larvae to exist long enough to mature. The fact that adult flies find sufficient food almost daily during this period might or might not mean that the source of supply is such that the larvae could also feed. Fortunately, we have direct proof that flies breed throughout the summer. On June 9, 1941, 2000 laboratory-grown flies homozygous for the recessive mutant gene orange (bright-red eye color) were liberated at Keen Camp. During the following week many orange-eyed flies visited the traps which had been exposed in the vicinity of the point of release; copulating pairs were observed which consisted of orange or wild, and of both orange and wild partners. Traps were exposed again from July 23 to August 8 in the same neighborhood, and during that time 41 orange-eyed flies were collected. These orange flies, however, were not the survivors of the flies released in June, but young individuals which had hatched in the wild; their age was established by inspection of their reproductive organs (see below). Again, on June 16, 1942, 3297 orange flies were released, this time at

Idyllwild. Many orange and mixed copulating pairs were seen during the following week. On July 12 to 15, traps were exposed about 400 meters from the point of release, and 5 young orange flies were captured.

The age of a fly can be judged to a certain extent by its appearance. Flies less than 12 hours old are pale, with bright eyes and semiopaque wings. Such flies never come to traps. Old flies differ from younger ones in having some of the macrochaetae broken, the edges of the wings torn, and the abdomens shriveled. Such flies are observed from time to time. The condition of the reproductive organs, however, is a better measure of the biological age than the external appearance. When females are hatched their ovaries consist of the terminal chambers only; this we shall refer to as age I. At temperatures around 22° C. and with ample food, growing oöcytes appear in a day or two (age II), and mature eggs on the 3d to 7th day. Ovaries of florid females 3 to 20 days old (age III) are loaded with mature eggs, but in old females most

TABLE 6
AGE OF FLIES COLLECTED AT IDYLLWILD, CALIFORNIA

Date	Females				Males			
	I	II	III	IV	I	II	III	IV
June 3.....	0	10	32	0	0	20	3	0
June 9.....	0	15	14	0	1	12	3	0
June 17.....	2	6	13	0	2	22	3	1
June 19.....	3	27	16	1	8	37	7	0
July 5.....	2	23	25	4	3	14	29	2
July 15.....	1	16	45	1	1	7	22	0
July 24.....	4	21	22	0	3	33	37	0

egg strings have regressed and only a few mature eggs are present (age IV). From the time of hatching to about 4 days, males have transparent orange-red, broadly ellipsoid testes (age I). During the following week or two, the testes elongate but remain orange-red (age II); elongation progresses and a dark-red opaque coloration develops, first in spots and then over the whole organ (age III). Males a month old have sickle-shaped dark-red testes (age IV). The speed of these changes depends on temperature, food, and probably other factors. Starving females may not have ripe eggs when 10 days old. The characters just described measure the biological rather than the chronological age, especially in females. Nevertheless, a young fly is distinguishable from a florid or an old fly. Samples of flies were collected from time to time at Idyllwild in the summer of 1942 for inspection of the external characters and of the reproductive organs. The data are summarized in table 6.

The rapid dwindling of the numbers of orange flies captured on successive days after their liberation suggests that the average longevity of the flies in nature is very much less than their longevity under laboratory conditions. This fact and the age determinations, despite all the uncertainties of the latter,

make the conclusion inescapable that young flies constantly appear throughout the summer, at least at Idyllwild and at Keen Camp. The apparent scarcity of the flies in midsummer at Andreas and at Piñon Flat, however, raises the question whether they breed in midsummer at these localities as well. Since the summer temperatures there are high, the intake of traps should be a fair measure of the population density. It is conceivable, however, that too high a temperature and too low a humidity may cause the flies to be quiescent, just as temperatures below 50° F. are known to do. Some observations suggest that this may indeed be the case. Two morning and three evening collections on July 9 to 11, 1942, at Piñon Flat produced only about a dozen flies. On July 15 a local cloudburst drenched the locality. The evening collection on July 17 produced 199, and on July 18, 151 flies in 61 traps. Were most of these flies present before the rain? Dissection of a sample of flies caught on the 18th has made this extremely doubtful: among the females 2 were of age I, 12 age II, and 9 age III; among the males 7 were of age I, 12 age II, and 9 age III. At least some of the wild flies were freshly hatched. These observations were made in connection with experiments, to be described, in which orange-eyed flies were released and their capture was attempted on the days following. The proportions of orange flies recaptured were abnormally small, before as well as after the rain referred to, but those which were found had traveled farther from the point of release than they had traveled at lower temperatures in corresponding experiments at Idyllwild. This fact suggests that the flies are not completely quiescent at Piñon Flat during the summer, and it appears probable that rain somehow hastens the hatching of the flies from pupae. A spurt in the abundance of flies after a rain has also been observed at Keen Camp (August 1941), and many of the flies which appeared after the rain were shown by dissection to have been very young.

The number of generations per year is difficult to determine. In the laboratory a fly may remain alive long enough to meet not only its children but even its grandchildren; nevertheless we have evidence that the longevity of a fly in nature is usually only a fraction of its potential life span. At least in California, the temperatures of the habitat change greatly from day to night; precisely what these temperatures are is unknown, and the duration of the fly's development at fluctuating temperatures is also conjectural, since laboratory experiments are usually made at constant temperatures. Under such conditions, the estimates of the number of generations can at best be only approximate. Assuming the length of a generation under summer conditions at Keen Camp or Idyllwild to be 3 weeks at the minimum, and in spring and autumn 4 to 6 weeks, the flies can hardly produce more than seven generations per year in these localities, and probably less. If the breeding at Andreas Canyon is continuous throughout the year, ten generations per year in that locality is not an unlikely estimate; about half of these generations would develop during the summer shrinkage of the population. Since even in natural habitats, however, the flies may live for several weeks, the average number of generations per year may be only half of the above estimates.

MIGRATION

Any species, race, or genotype tends to increase its distribution area. In the case of *Drosophila*, the movements of the adult fly (the movements of larvae are negligible) may cause an individual to leave its progeny at some distance from the place where this individual itself was born. The distance probably varies from individual to individual and from species to species, but no matter how small it may be in one generation, the progeny of a pair, if it survives, will spread in the course of time. Moreover, from time to time some individuals may be transported passively, by wind or other agencies, over distances far greater than those which an individual could cover by means of its own organs of locomotion. Although the net result of both active and passive migration is to increase the distribution area, the two processes must be studied by different methods, because of intrinsic differences between them. The active spread produces a constant pressure on the boundaries of the distribution area, but an ecologically unsuitable barrier may cancel the result of this pressure. Passive migration is probably irregular and sporadic, but it may suddenly accomplish conquests of large areas inaccessible to active spread. Considered historically, migration also presents two different aspects. In terms of short intervals of time a species may be very sedentary, and yet it may be capable of spreading widely over long periods; on the other hand, relatively mobile forms may have their distributions fixed by specialized adaptation to conditions which exist only in a geographically limited area.

Some information is available on the passive transport of *Drosophila*. Glick (1939) in Louisiana has collected insects from an airplane at different altitudes. He records one specimen of *D. melanogaster* at 200 feet, 1 specimen of an undetermined *Drosophila* at 200 and 2 at 1000 feet, 5 specimens of *Scaptomyza adusta* (a representative of Drosophilidae) at 200, 1 at 500, 2 at 1000, and 1 at 3000 feet, 5 specimens of *Scaptomyza* sp. at 200, 3 at 1000, 2 at 2000, and 1 at 3000 feet, and 10 specimens of undetermined Drosophilidae at 200, 3 at 500, 2 at 2000, and 1 at 3000 feet. Whether or not these insects were alive at the time of capture is unknown, and if they were, they might or might not have been capable of reproduction after their aerial journey. Although no *D. pseudoobscura* or its relatives were recorded (these species do not occur in Louisiana), their passive transport by wind is nevertheless a possibility. There is also indirect evidence that this possibility is to be reckoned with, at least in terms of historical spread of the species. As was stated above, *D. persimilis* is common at intermediate and high elevations in the Sierra Nevada. But this species has also been found in the Coso Range and in a part of the Panamint Range, both of which lie to the east of the Sierra. These ranges are typical desert mountains, and their environment is not at all characteristic of the territory inhabited by *D. persimilis*. Other ranges in the Death Valley region are inhabited by *D. pseudoobscura* but not by *D. persimilis*. Deep desert valleys lie between the Sierra Nevada and the Coso and Panamint ranges. One can suppose either that *D. persimilis* in the Coso and Panamint ranges is a relic

of more continuous distribution in the remote past, or that this species is occasionally blown by winds eastward over the Sierra Nevada, where it is common, and has succeeded in establishing a few outposts on the desert ranges of the Death Valley region, the environment of which is on the whole adverse to the welfare of this species.

N. W. and E. A. Timofeeff-Ressovsky (1940a, b, c) have been the pioneers in experimental studies on rates of active migration in species of *Drosophila*. The technique used by these investigators has been to release known numbers of laboratory-grown individuals of *D. melanogaster* and *D. funebris*, marked by easily identifiable mutant characters, at the center of a rectangular experimental field measuring 70×90 or 110×110 meters. On the first and the following days after the release of the marked individuals, from 63 to 121 baited traps have been exposed checkerboard fashion around the point of release, and the marked and the wild flies which came to these traps have been recorded and again released at the point of capture. The rate of movement in *D. melanogaster* and *D. pseudoobscura* proved to be so low that experimental fields of the sizes indicated above were sufficient to contain all, or at least a majority, of the released flies for up to two weeks.

Experiments on migration rates in *D. pseudoobscura* have been conducted in the summers of 1941 and 1942 at Keen Camp, at Idyllwild, and at Piñon Flat, Mount San Jacinto, in collaboration with Bruce Wallace, Harlan Lewis, Alexander Sokoloff, Mrs. N. P. Dobzhansky, Miss R. Mirsky, and others. The resulting data, together with a mathematical analysis by Sewall Wright, will be published elsewhere; here only a summary of the conclusions reached to date can be given. The experiments were started with the technique of Timofeeff-Ressovsky only slightly modified, but this technique proved to be completely unsuitable for our species. The released marked flies (the mutant orange, which produces a bright-red eye color, was used in most experiments; in other experiments wild flies were caught, marked with a tiny spot of "platinum" nail polish on the thorax, and released again) reach the margins of an experimental field 70×70 meters in size, and pass beyond the margins, in one day after the release. Fields four times this size (140×140 meters) were tried without success. *D. pseudoobscura* is evidently much more mobile than its congeners studied by the Timofeeff-Ressovskys. The reason why all the released flies must be contained within the perimeter of an experimental field is simple: the rates of the fly's movements are arrived at by computing the variances of the distributions of the marked flies on the field. If some flies escape beyond the confines of the field, the variances will be grossly underestimated. Owing to the limitation in the number of observers, the checkerboard-like plan of the experimental field had to be abandoned. Instead, from 60 to 70 traps were arranged in two lines intersecting at right angles in the middle; the marked flies were released at the intersection. With traps spaced 20 meters apart, such cross-shaped experimental fields were built with arms up to 340 meters long. The marked flies, however, reached the ends of the arms of the cross in a few days after the release. As soon as this happened,

the plan of the experimental field was modified: two of the four arms of the cross were sacrificed and the other two arms were extended by adding traps at their ends. Linear files of traps up to 1080 meters long were built in some experiments.

Theoretically, the movements of the released marked flies in a uniform two-dimensional medium may be expected to obey one of the three following rules: (1) The flies may move at random, somewhat in the fashion of particles undergoing Brownian movement: the direction of motion during a given time interval will be independent of the direction during the preceding or the succeeding time intervals. If so, the variance of the distribution of the flies on the experimental field should increase in proportion to the time elapsed after the moment of their release at the center of the field. (2) The flies may move away from the densely populated areas into the more sparsely populated ones, or vice versa. Since in most experiments 2000 to 4000 marked flies were released at one point, the central part of the experimental field is temporarily overpopulated. If the flies can discern population density gradients and direct their movements accordingly, the variances will increase more rapidly at the beginning than at the end of each experiment, or vice versa. (3) The flies may possess a "homing instinct," known to exist in many vertebrates and also in tsetse flies among insects (Jackson, 1940). Each individual fly may establish a territory to which its movements will be largely confined. The marked flies will range more or less widely over the field until they establish their home ranges, whereupon their movements will be much more restricted. The variances will grow rapidly at the beginning of the experiment, and will be nearly stationary after the home ranges have been established.

Discrimination among the three possibilities outlined above is made difficult by disturbing influences encountered in the experiments. Outstanding among these influences are the temperature variations observed from day to day in practically every experiment. As shown by the variances of the distributions of the flies observed on different days, the flies travel much more extensively at higher than at lower temperatures. This necessitates a study of the relation between variance and temperature. The daily increment of variance increases exponentially with increase of temperature. If the logarithms of the increments of variance are plotted against the temperatures observed at the times of the maximum activity of the flies on the days when collecting has been made, the data for temperatures above approximately 60° F. seem to fall on a straight line. The few observations made at temperatures below 60° F., however, do not fall on the same line. This may mean either that some of the observations are accidentally inexact, or that the movements of the flies have different temperature coefficients below and above 60° F. Since we cannot decide which alternative is true, regression coefficients have been computed, with the aid of a method suggested by Wright, for the data including and excluding the observations at temperatures below 60° F. These regression coefficients are respectively $y = 3.13122 + 0.04950 x$, and $y = 2.87409 + 0.0719 x$, where y is the logarithm of the increment of variance in meters

per day, and x is the temperature in degrees Fahrenheit above 60° . The two equations give, of course, two sets of expectations for the increase of variance in the actual experiments. A comparison of the expected and the observed values leads to the conclusion that the data favor, on the whole, the hypothesis that the movements of the flies are random (the first of the three hypotheses outlined above). The third hypothesis ("homing instinct") is excluded; the second hypothesis (movement along density gradients) is unlikely, although it is possible that some slight tendency to escape overpopulated regions is present.

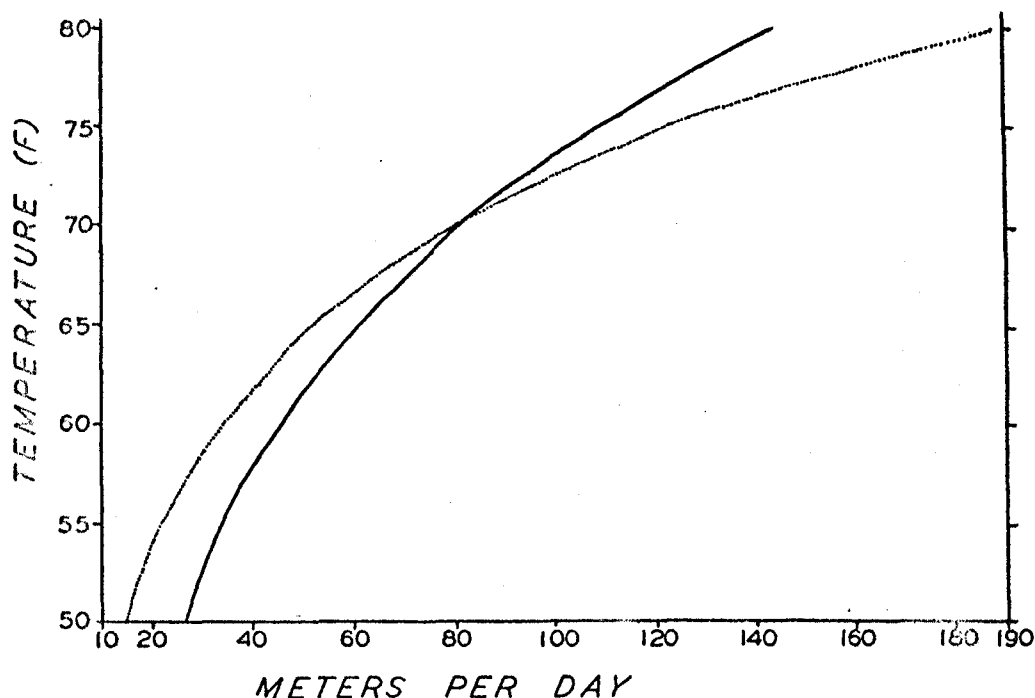


FIG. 7. The mean distances from the point of release traveled by *Drosophila pseudoobscura* at different temperatures. The two lines correspond to the two sets of expectations mentioned in the text.

The average distance traveled by the flies per day can be deduced from the daily increments of variance of their distributions on the experimental fields. As shown by Wright (unpublished), the average distance equals approximately 1.253 standard deviations per day; the standard deviation is, of course, the square root of the variance. Figure 7 presents the average distances in meters per day (abscissae) plotted against the temperatures in degrees Fahrenheit (ordinates). Two lines are shown in this figure, corresponding to the two possible sets of expectations mentioned above. At about 70° F. the two expectations coincide, indicating that the flies travel 81 meters per day on the average. At 80° the distance traveled turns out to be 144 or 188 meters; at 60° , 46 or 34 meters; and at 50° , 26 or 15 meters. The situation at the lower temperatures is obviously least satisfactorily known; this is the result of the fact that a majority of the experiments were conducted in midsummer,

when temperatures ranged around 70° F. at the times of the maximum daily activity of the flies, only a single experiment having been started at 56°.

It is plain that we have succeeded in determining at best only the order of magnitude of the daily movements of *D. pseudoobscura*. Yet even such information, inexact as it is, is valuable for an understanding of the breeding structure of natural populations. The Timofeeff-Ressovskys (1940a, b, c) have, unfortunately, published no data on the temperatures at which their experiments on the movements of *D. funebris* and *D. melanogaster* were conducted near Berlin, Germany. Assuming that the temperatures during their experiments were somewhat lower on the average than during ours, the conclusion is still inescapable that the distances traveled per day by *D. pseudoobscura* are ten or more times as great as those traveled by *D. funebris* or *D. melanogaster*. With similar absolute population densities per unit area, *D. pseudoobscura* will, therefore, have a larger genetically effective population than these other species. In a continuously inhabited territory there will be much less opportunity for isolation by distance with *D. pseudoobscura* than with *D. funebris* or *D. melanogaster*. Nevertheless, as compared with other insects, some of which have been observed to make flights of several miles per day, *D. pseudoobscura* must be regarded as a relatively sedentary organism. If an organism which moves at random in a uniform two-dimensional medium travels on the average a distance r per day, in n days it will have traveled on the average not the distance rn , but only $r\sqrt{n}$. Suppose, then, that at a temperature of about 70° F. individuals of *D. pseudoobscura* born or released at a given point reach in a day, on the average, the periphery of a circle with a radius of 80 meters centered on the point of birth or release. If the temperature remains constant, a circle with a radius of 160 meters will be reached in 4 days, and a circle with a radius of 400 meters in 25 days. It is to be emphasized that these are the *average* distances, and some individuals will undoubtedly move farther and others much less far from the starting point. The important conclusion is that with such rates of migration, the interchange of genes and other genetic variants between populations residing several miles apart may be slow enough to permit a racial differentiation of such populations and preservation of racial differences from swamping due to hybridization. This is, indeed, what is observed (Wright, Dobzhansky, and Hovanitz, 1942; see also part II in the present publication).

SUMMARY

1. Three species of the *Drosophila obscura* group occur in North America. They are: *Drosophila pseudoobscura* Frolova, *Drosophila persimilis* Dobzhansky and Epling, and *Drosophila miranda* Dobzhansky. *D. persimilis* is a name here proposed to designate the entity previously known as "*Drosophila pseudoobscura* race B." Evidence is presented to demonstrate that *D. persimilis* is, despite the paucity of structural differences, specifically distinct from *D. pseudoobscura*. Species is defined as "the stage in the process of evolutionary diver-

gence at which an array of populations once actually interbreeding or capable of interbreeding has become split into two or more reproductively isolated arrays."

2. The distribution area of *D. pseudoobscura* extends from British Columbia to Guatemala and from the Pacific Ocean to the Rocky Mountains and Texas; that of *D. persimilis*, from British Columbia to California and from the Pacific to the Sierra Nevada-Cascades mountain chain; that of *D. miranda* is confined to the Pacific coast from Vancouver Island to Monterey, with an apparently disjunct colony in the Sierra Nevada.

3. The food of the adult *D. pseudoobscura* consists chiefly of yeast and bacteria gathered probably from fermenting tree sap and similar sources. The food of the larvae is unknown, but is probably the same as that of the adult.

4. On sufficiently warm cloudless days the flies come to traps only at certain hours after sunrise and immediately before sunset. At other times they seek shelter in crevices of tree bark and similar places. The hypothesis that the diurnal periodicity is determined by changes in light intensity during the day fits the available data better than any other hypothesis which we have been able to contrive.

5. The seasonal cycles in *D. pseudoobscura* are different in different parts of its distribution region. Some of these cycles are described.

6. Experiments on the rates of active migration in *D. pseudoobscura* have been made. In reasonably uniform two-dimensional environments the flies move at random rather than follow density gradients. No "homing instinct" or "territoriality" is present. If the temperature at the time of the evening maximum of activity of the flies is close to 70° F., the average distance from the starting point traveled by the flies per day is approximately 80 meters. The migration rate grows or diminishes exponentially with changes in temperature. The observed migration rates seem to be small enough to permit racial differentiation in populations residing only a few miles apart in a continuously inhabited territory.

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