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32. D. A. Story and V. M. Bryant, Jr., Eds., "A preliminary study of the paleoecology of the Amistad Reservoir area" [report to National Science Foundation (1966), pp. 65-667].
33. V. M. Bryant, Jr., and H. J. Shafer, in (*9*), p. 22.
34. No attempt was made to break up the Holocene flood record according to distinct phases of climatic fluctuation. Patton and Dibble (*13*) address this problem in the Arenosa Shelter slackwater record by performing discrete time-series analyses on floods occurring within the various climatic phases of the Texas Holocene. Our tributary mouth sites all fall within the same climatic interval, a xeric phase which extends back about 2300 years. Climatic fluctuations are significant only when the entire Holocene flood record is examined, such as at the Arenosa Shelter. We are investigating the effects of climatic fluctuations on paleoflood frequency.
35. R. C. Kochel, R. A. Johnson, R. J. Wayland, *Va. Acad. Sci.*, in press.
36. We thank H. Mills, R. J. Everett, G. C. Marshall, C. Hunt, T. M. White, T. Hayre, J. Martin, H. Hunt, L. Billings, Jr., J. Skiles, M. Rose, W. King, D. Rowland, W. J. Thompson, A. O. Baker, T. J. Jarrett, D. Duncan, F. Ingram, and the E. Hinojosa family for hospitality and access to land along the Pecos and Devils rivers. P. C. Patton and B. L. Kochel assisted in the fieldwork. D. S. Dibble and P. C. Patton provided discussions and data for the Arenosa Shelter. S. Valastro, Jr., offered advice on interpreting radiocarbon dates. We are grateful to P. E. Smith for the loan of a field vehicle and to B. L., D. E., and the late R. I. Kochel for assistance. L. R. Beard, P. C. Patton, A. J. Scott, and E. L. Lundelius provided useful reviews of this manuscript. This work was supported by grant EAR 77-23025 from the National Science Foundation. Support for manuscript preparation was provided by the Geology Foundation, University of Texas at Austin.

Autocidal Control of Screwworms in North America

R. H. Richardson, J. R. Ellison, W. W. Averhoff

"Screwworm" is a name given to the larvae of several species of blowflies (Calliphoridae) which lay their eggs on or near open wounds of warm-blooded animals. Soon after they hatch, the first-instar larvae of the dipteran parasites enter the wound and feed on fluids from the living tissue, causing myiasis (*1*). Mature, third-instar larvae drop from the wound and pupate in the soil. Adult female blowflies often lay their eggs on the navels of newborn livestock, pets, and wild game. The feeding larvae enlarge the wounds which thus attract more ovipositing females (*2*). Unchecked infestations cause death of even an adult host as a result of physical damage or secondary infections.

Summary. The larva of the blowfly *Cochliomyia hominivorax*, also known as the screwworm, eats the living flesh of cattle and sheep and other warm-blooded animals. A program to eradicate the screwworm in the United States was initiated in the 1950's. The program was very effective until 1968, but severe screwworm outbreaks occurred in 1972 to 1976 and in 1978. Although the program has again been effective since 1979, the possibility of outbreaks recurring in the future has highlighted the need for a broader understanding of the pest. Studies of screwworm populations in the United States and Mexico indicate that much of the genetic diversity of this insect is distributed among sympatric non-interbreeding populations. A new approach may be required to retain the effectiveness of the control program and to prevent a serious outbreak from threatening the economic viability of the U.S. livestock industry.

A program to eradicate screwworms [*Cochliomyia hominivorax* (*sensu latu*)] in the southern United States was initiated by the U.S. Department of Agriculture (USDA) in the 1950's. This program, which depended on an autocidal technique—the release of sterile blowflies—was completely successful in Florida, where eradication of the screwworm during 1958 and 1959 cost $10 million. In 1962 the program was expanded into Texas and the Southwest, with sterile flies being dropped from airplanes in a band two to several hundred kilometers wide along the U.S.–Mexico border (*3*, *4*). Suppression of screwworm populations was highly effective until 1968, and again in 1979 to the present. However, there were several severe outbreaks in the intervening years. Our studies of screwworms in the United States and Mexico have led us to believe that because of the genetic complexity of the screwworm populations the present approach to controlling the pest should be reexamined.

Background

Periodic outbreaks of screwworms did not become a serious problem in livestock (*5*) in the United States until the late 1800's, when there was a large increase in the number of cattle in the Southwest. New cattle trails and the construction of railroads and windmills (*6*) after the Civil War made markets and water more accessible and allowed Texas to become blanketed with cattle (*7*, *8*). The windmills were used to fill waterholes so that even in periods of drought water was usually available (*9*). A similar year-round water supply was achieved in areas of adequate seasonal rainfall by constructing earthen ponds.

The great increase in cattle led to increasing outbreaks of screwworms which, by the turn of the century, were becoming an annual curse on ranches in central Texas and along the Gulf Coast (*10*). It also led to severe overgrazing and fewer prairie fires (*11*) and, consequently, changes in the distribution of certain plants. For example, the chaparral in southwestern Texas and northeastern Mexico became a thorn forest of woody legumes, as did the central and southern Gulf Coast regions of Texas. Deer replaced the antelope as the dominant game animal, as cattle had replaced sheep (*12*). Since screwworm flies feed on the nectar of such legumes (*13*, *14*), and since, like cattle and deer, the flies are associated ecologically with watercourses, the flies, cattle, and deer were generally in close proximity and screwworm populations could rapidly expand.

According to Dobie (*8*), the importation of British cattle and the improved nutrition of the breeding stock also contributed to the increase in screwworms. Earlier, sparse winter grazing followed by spring growth of vegetation stimulat-

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ed estrous cycles in feral cattle. The wild (black) cattle and Longhorns usually gave birth to their calves the following winter, before adult blowflies arrived from their overwintering areas below the winter freeze-line, or while local populations were still small. However, the crossbred herds gave birth year-round, so that oviposition sites became constantly available and the screwworms began to replace the plains wolf (the lobo, *Canis lupus*, not the coyote, *C. latrans*) as the major predator of newborn calves (*15*).

Ecological changes caused by the increase in cattle also occurred on either side of the U.S.–Mexico border from Texas to California. In addition to the overgrazing, barbed wire fences became common after World War I. Sheep had usually been kept in flocks on open ranges tended by shepherds, but when the ranges were fenced the sheep were not as closely observed (*16*). Thus screwworm-infested wounds were less likely to be treated and the larvae could complete their life cycles.

While the pest was becoming worse in Texas and the Southwest, it was also being transported to the Southeast. Screwworm-infested cattle were moved from Texas to Florida in the early 1930's, where the screwworm flies could survive the winters in the southern part of the state. From here there was an annual northward expansion of screwworm populations along the Atlantic seaboard, where the pest caused economic losses that were estimated in 1958 to amount to \$20 million per year (*2*).

The screwworm populations in the southwestern United States also migrated northward each spring as the frost line receded. Some years they reached the Canadian border, but usually they reached about midway across the United States (the 40th parallel). They caused many millions of dollars of damage annually to domestic livestock, game animals, and pets (*3*).

History and Effects of the Autocidal Program

The sterile male method of insect population suppression and local extinction was conceived by Knipling in the late 1930's (*17*). This method requires the rearing of large numbers of an insect pest which are then sterilized by radiation and released among wild populations. The induced dominant lethal mutations prevent viable embryos from forming. For the sterile males to be effective, they must pass seminal fluids to the wild females or these females will remate (*18*), thus there must be no interference with the mating and insemination process. Sterile females also contribute to the suppression and elimination of the wild population (*19*), since fertile males that mate with sterile females are, in effect, partially removed from the reproductive population. The sexually active irradiated flies that are released must prevent complete replacement of the wild individuals—that is, the death rate of the wild population must exceed the reproductive rate.

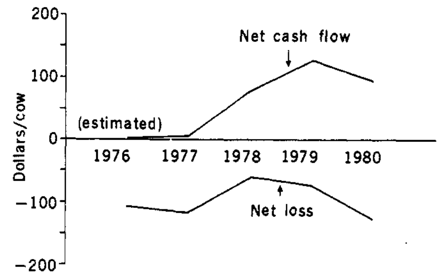

Fig. 1. Financial summary of traditional cattle ranching operations [data from (*24*)]. Net cash flow is the difference between short-term operating expenses and cash income. It includes, for example, the costs of feed, hired labor, veterinary care, equipment repair, fuel, and taxes. Cash income is principally from the sale of animals. The net cash flow must remain positive with very rare short-term losses for a rancher to stay in business. Extended drought, extraordinary taxes, screwworm outbreaks, and similar hazards can lead to bankruptcy. Net loss shows the long-term effect of being unable to replace equipment or achieve a return on capital investment.

From 1890 to 1933, entomologists had recommended a variety of trapping and husbandry practices to control what they thought was the screwworm fly (*10*). Although the taxonomic distinction between the saprophytic fly (*Cochliomyia macellaria*, also a blowfly) and the parasitic screwworm fly *C. hominivorax* was known in Argentina in 1915 (*1*), this distinction was not recognized by North American entomologists until 1933 (*20*). *Cochliomyia macellaria* was easily cultured on rotting meat, but *C. hominivorax* at first had to be cultured on living animals. It was not until Bushland and Hopkins (*21*) developed a technique for culturing screwworms on ground beef that sufficient numbers could be produced to make the sterile fly technique practicable.

The sterile fly technique was first used for screwworms on the islands of Sanibel and Curaçao, where the species (*C. hominivorax*) was successfully eliminated. The USDA then attempted to eradicate the screwworm in the southeastern United States, focusing on the overwintering populations in Florida. These populations had recently been introduced from northeastern Mexico and Texas (*22*).

After the screwworms were eradicated in Florida, more ambitious plans were laid by the livestock producers in Texas, with support from producers in New Mexico, Arizona, California, Oklahoma, Louisiana, and Arkansas. They collected funds to build facilities for rearing millions of screwworm flies to be sterilized and released, and thereby enabled the USDA to begin an expanded screwworm control program (*3*, *23*).

This program in Texas represented a biologically radical departure from the previous programs (*17*). First, instead of attempting to eradicate the screwworm in the United States, the USDA aimed to prevent an annual expansion of the Mexican screwworm populations into the United States without intentionally affecting the permanent populations in Mexico. Second, the permanent populations in Mexico, from which the screwworms to be suppressed were derived, were predictably heterogeneous.

In spite of these biological differences and the less than perfect control, the program was sufficiently successful to lead to striking changes in the livestock industry. Control of screwworms in the United States had the effect of reducing the labor required in livestock production as well as reducing the seasonal changes in the supply of animals. This savings in labor and better market control were instrumental in the livestock industry's survival during the period of price instabilities and labor force displacement since the 1960's (*15*, *24*). However, the reduced need for labor meant that many cowboys moved to urban jobs. Now, after 20 years the industry would be hard put to find sufficient numbers of livestock handlers experienced in getting animals out of the brush using horses, dogs, or helicopters, should a severe screwworm outbreak again make the close observation of animals necessary.

It has been estimated that the relative financial benefits of the screwworm control program were about 113 times its cost up to 1974 (*25*); an even greater benefit/cost ratio has been obtained since then. However, these advantages have not prevented a decline in the profits in cow-calf ranching, on which the livestock industry depends (Fig. 1) (*24*). The average cash flow in the Southwest in 1979 was \$160 per cow, but if one considers the long-range investment, including the ownership costs, the average cow cost the rancher about $75 that year. For 1980, the loss was about $125, and in 1981 the loss may be worse, even in the absence of screwworm outbreaks. Only five cases of screwworms were reported in the United States in 1981, and Baja California was declared free of screwworms on 6 December 1981. Nevertheless, significant outbreaks occurred less than 200 kilometers from the U.S.–Mexico border.

The USDA factory for rearing screwworm flies at Mission, Texas, was closed on 1 January 1981. Since then all sterile flies have been reared at a factory near Tuxtla Gutierrez, Chiapas, Mexico. After several labor-management disputes and technical problems were settled, production at this factory reached its design capacity of 500 million flies per week in October 1981. Concentrated releases of sterile flies are now routinely made in central Mexico approximately south of a line from Tampico west to 125 kilometers north of Mazatlan. The plan has been to eradicate screwworms north of the Isthmus of Tehuantepec, but recent indications suggest that the location of the barrier zone might be moved further south into Central America.

Screwworms also occur in South America, causing considerable loss to livestock in Brazil and Argentina, for example. Although we are unaware of plans for an autocidal progam in South America, research on the genetics of screwworms is being conducted in Brazil. Other species have been introduced into Brazil from Africa and have caused losses, especially in coastal areas (*26*).

A synthetic blowfly attractant, which was developed to supplement the autocidal technique, is used in a screwworm adult suppression system (SWASS) in combination with an insecticide. It has been effective in northern areas, but it is almost totally ineffective in southern Mexico. Entomologists hoped to use the SWASS technique for initial treatment in local outbreaks, but the variable results have been disconcerting.

Forewarnings of Genetic Diversity Among Screwworm Populations

The first indication that some screwworm populations might be resistant to eradication came from experiments in the 1950's. On Sanibel Island, a weekly release rate of 75 flies per square kilometer (200 per square mile) was effective in controlling the local screwworm population. In Curaçao the release rate had to be quadrupled (*17*). When control efforts turned to Florida, eradication of the fly in one small area required about 3500 flies per square kilometer (*22*). Population suppression also faltered on several occasions in other parts of the Southwest. In a field test in southern Tamaulipas, Mexico, the weekly release rate was raised from the usual 150 to 400 flies per square kilometer to almost 4000 per square kilometer before sterility was adequate for eradication. In 1971, a screwworm population in the area of the Little River, Arkansas, resisted all attempts of eradication, although the population did not expand. This population was eventually eliminated by freezing weather (*17*). In an attempt to control populations on the island of Viequez in 1972, less than 50 percent of the wild flies mated with sterile males in spite of weekly releases of more than 7500 flies per square kilometer; however, control was achieved when a different strain of screwworm fly was used (*27*). In a field test conducted in Tamaulipas in 1979, sterile flies of strain 009, a factory-reared population, were ineffective in suppressing the wild population. The Aricruz strain eventually was effective, probably because it was genetically related to one of the types found in this area (*28*). Common release rates in the program today are between 600 and 1500 flies per square kilometer.

The Screwworm Outbreak of 1978

Many factors can reduce the effectiveness of an autocidal control program. Nonuniformity in the distribution of the sterile flies is one such factor, and this may be caused by excessive distances between the flight paths of the airplane or by excessive distances between the points of container release. Another factor that influences a control program's effectiveness is the quality—that is, health and age—of the sterile flies. Genetic differences among strains can affect both the robustness of the flies and their acceptability as mates to the wild population.

Each of the severe screwworm outbreaks in the United States in 1968, 1972, 1975, 1976, and 1978 followed periods of more effective suppression (Fig. 2). Favorable weather for screwworms and reduced care of livestock were two of the explanations given for these outbreaks. Warm, moist weather accentuates any inherent problems associated with a control program and was certainly an important factor in these outbreaks, as was the reduced ability of ranchers to adequately inspect their animals and treat infested wounds. However, these somewhat simple explanations overlook other, more significant, factors (*29*).

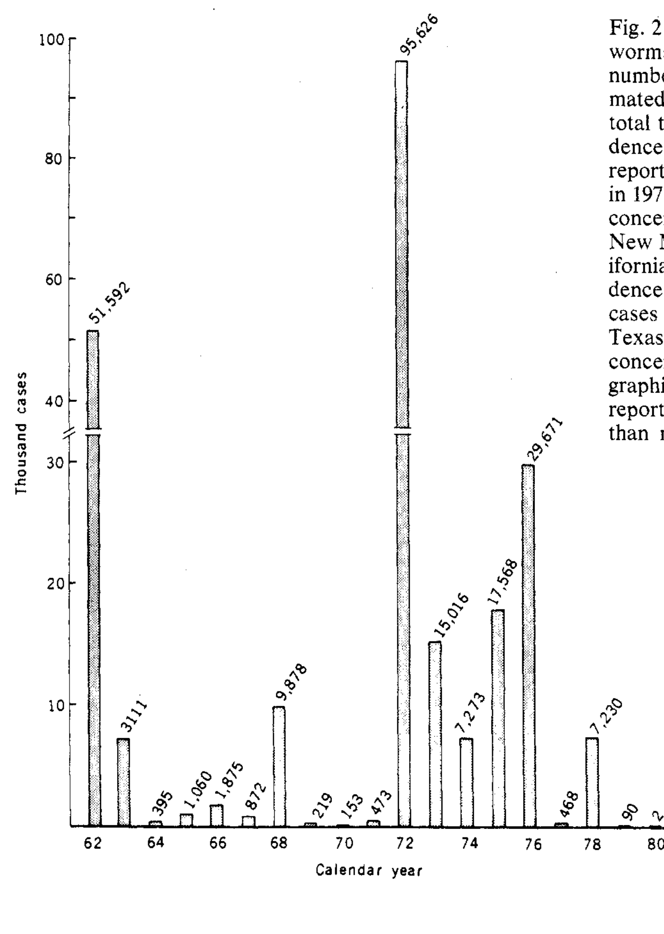

Fig. 2. Reported cases of screwworms in the United States. The number of cases reported is estimated to be 1 to 5 percent of the total that occur. When the incidence is highest, the percentage reported declines. For example, in 1978 the outbreak was largely concentrated in west Texas, New Mexico, and Arizona. California had a moderate incidence, and early in the season cases were reported in south Texas. Since the outbreak was concentrated in a particular geographic region, the percentage reported probably was lower than might be expected had it been uniformly distributed. The reporting of cases in northern Mexico is not reflected in these statistics. Although only two cases were reported in the United States in 1980 and five in 1981, a number of cases were reported in both northeastern Mexico and northwestern Mexico in spite of the intensive distribution of sterile flies and use of the SWASS technique.

In 1978, when we began sampling larvae from infested wounds of cattle, horses, and dogs in Arizona and New Mexico, sterile flies of the 009 strain were being released weekly at a rate of several thousand per square mile, but the population remained uncontrolled. It soon became evident that the local screwworms were different from those in Texas, an observation that was confirmed by metaphase chromosome karyotyping and allozyme analyses. Not only were the wild populations genetically different from those (strain 009) being released, but they were also composed of several geographically overlapping, but genetically isolated, types (Fig. 3). Parts of their home ranges in Mexico have now been determined (see Fig. 4).

We found primarily five types of screwworms in 1978: types D, F, and J in west Texas; types A, B, and F in New Mexico; types A, B, and D in Arizona; and types A and D in California (see Fig. 3) (*30*). Karyotypes of a few other types were also found, but these accounted for less than 15 percent of the samples. Types A and B were intermixed in southwestern New Mexico and southeastern Arizona. Some multiply infested wounds contained both types A and B. Type A was the widespread "western type" whereas type F was the widespread "eastern type" that was also responsible for most of the screwworm outbreaks in west Texas. In eastern New Mexico, types A and F were broadly overlapping in their distributions. The only other karyotype of note found in the United States that year was type J, which occurred only in west Texas and has not been collected since. Types A and F were the most destructive screwworms. Wounds infested with these types typically contained 100 to 300 sibling larvae either as a primary infestation or as subsequent infestations in previously infected wounds.

Types A and B had different reproductive strategies (*29, 31*). Females of type B tended to oviposit small clutches of eggs which caused wounds with small numbers of larvae. Furthermore, they preferred fresh wounds; we found larvae of this type only among the oldest instars in a wound, or in wounds with larvae of a single instar. We postulated that this type of screwworm was responsible for the ranchers' observations that some infestations healed when all the larvae dropped out, even though the wound was untreated. Since treating wounds is laborious and exposes animals to risk of further injury, the ranchers often delayed treatment of some wounds and then discovered that no treatment was necessary.

Genetic patterns and mating structure of the screwworm population in 1978. The chromosomes of screwworms can readily be differentiated. The X and Y chromosomes are conspicuously different from each other and there are differences in several autosomes (Fig. 5). Although correct identification of a karyotype (*32*) can be tedious, hybrids heterozygous for several chromosomes of different morphologies can easily be detected (Fig. 6). The process of normalizing karyotypes removes real differences in the total genome length such as caused by heterochromatic additions or dele-

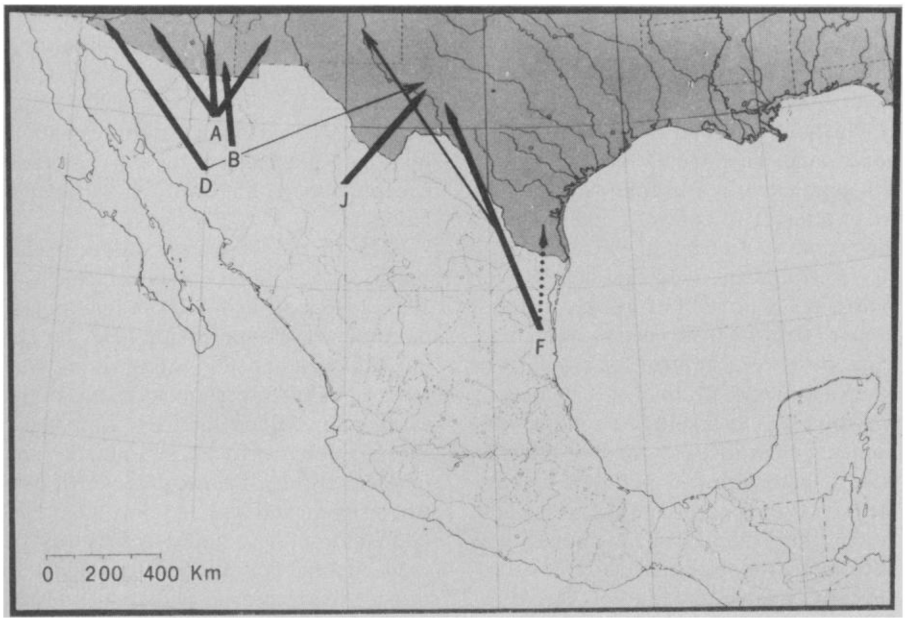

Fig. 3. The possible origins of five types (*28*) of screwworms found in the United States in 1978. By comparing this figure with Fig. 4, which shows locations of permanent populations in Mexico, one can determine patterns of invasion. There was apparently little east-west movement, which is the shipping pattern for livestock. The few isolated cases (thin arrows) may have been related to human activity.

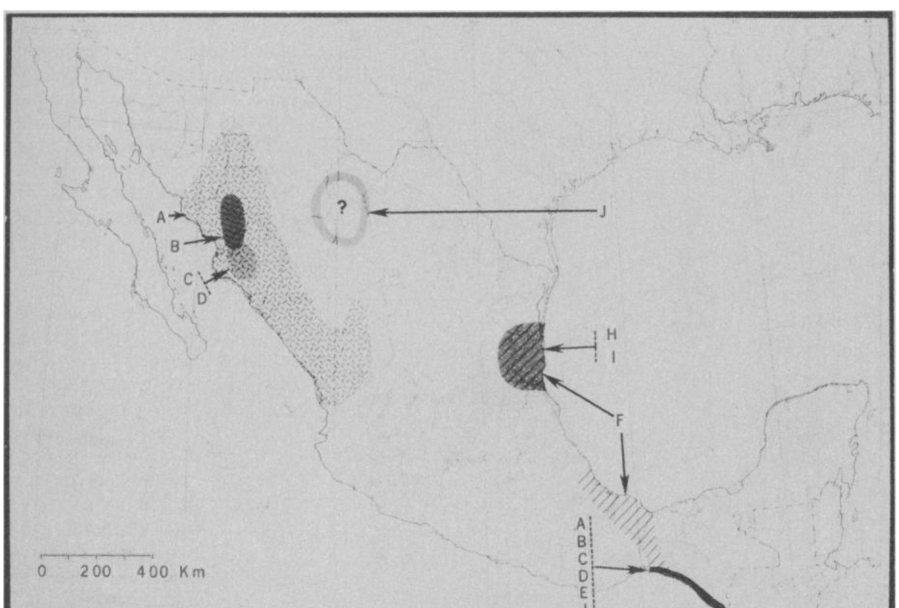

Fig. 4. The known distribution of types of screwworms in four regions of Mexico where collections have been made. There are four types present along the northwestern coast of Mexico. These types may be distributed along the entire Pacific coast of Mexico, because the same four and two additional types were found in extensive collections from the Pacific coast of Chiapas in southwestern Mexico. Collections in 1981 in this area also added another type (I) formerly known only from northeastern Mexico, indicating that the southern range may contain most of the types found in Mexico, western or eastern. Genetic diversity within types so distributed is to be expected.

tions. Thus the differences seen in a hybrid cell are much more striking than the differences seen by comparing normalized karyotypes.

In studying the genetics and systematics of different screwworm populations in 1978 we observed extensive polymorphisms in allozyme loci and quinacrine-bright bands of metaphase chromosomes (*33*). In all the populations we studied the genetic variation was equivalent to that in *Drosophila* and many other outbreeding species (*34*). In only one sibship obtained in more than 500 independent collections with more than 2500 individuals examined have we found evidence of hybridization among types. Since a sibship represents the progeny of a single wild female, her mating with a male of a different type cannot be said to indicate a significant breakdown of genetic isolation. However, the sibship that we observed is noteworthy because it contained triploid individuals, diploid heterozygotes and, in addition, diploid individuals that were probably produced parthenogenetically (*35*) (Fig. 6B).

Most of the protein variations and some of the heterochromatic chromosome bands occur in homozygous as well as heterozygous screwworms. The presence of heterozygotes indicates extensive interbreeding of various genotypes, but does not imply the absence of subpopulations that are genetically isolated provided they contain the same variations within as between subpopulations. However, some of the chromosome variations, including total lengths and centromere positions, are found only in homozygous wild types. The absence of heterozygous screwworms with these differences implies the presence of noninterbreeding subpopulations (gamodemes) with genetic differences between them that are not found within.

Genetic differences segregating in a single panmictic population occur with a predictable frequency in heterozygotes (*36*). If a population has a breeding structure consisting of two or more subpopulations, the frequency of heterozygotes is reduced in proportion to the genetic diversity among the subpopulations [Wahlund effect (*37*)]. When the populations are maximally differentiated (allele frequencies are zero in one subpopula-

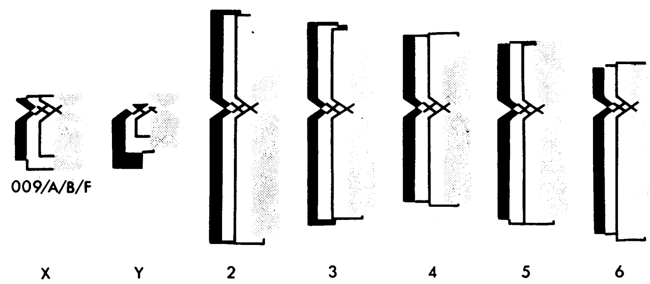

Fig. 5. The karyotype of the factory-reared strain 009 compared with the karyotypes of three types present in the United States in 1978. The karyotype of 009 differs significantly in Y chromosome length from all of the wild types present in the United States in 1978. It seems to be closest in karyotype to type B: compare the X chromosomes and chromosomes 2 and 5. Types A and F, however, differed extensively from 009 in the length of the X chromosome and in the arm lengths of several autosomes. We found no wild screwworms that matched the karyotype of type 009, and we assume this type to be extinct or a result of long-term culturing and mongrelization.

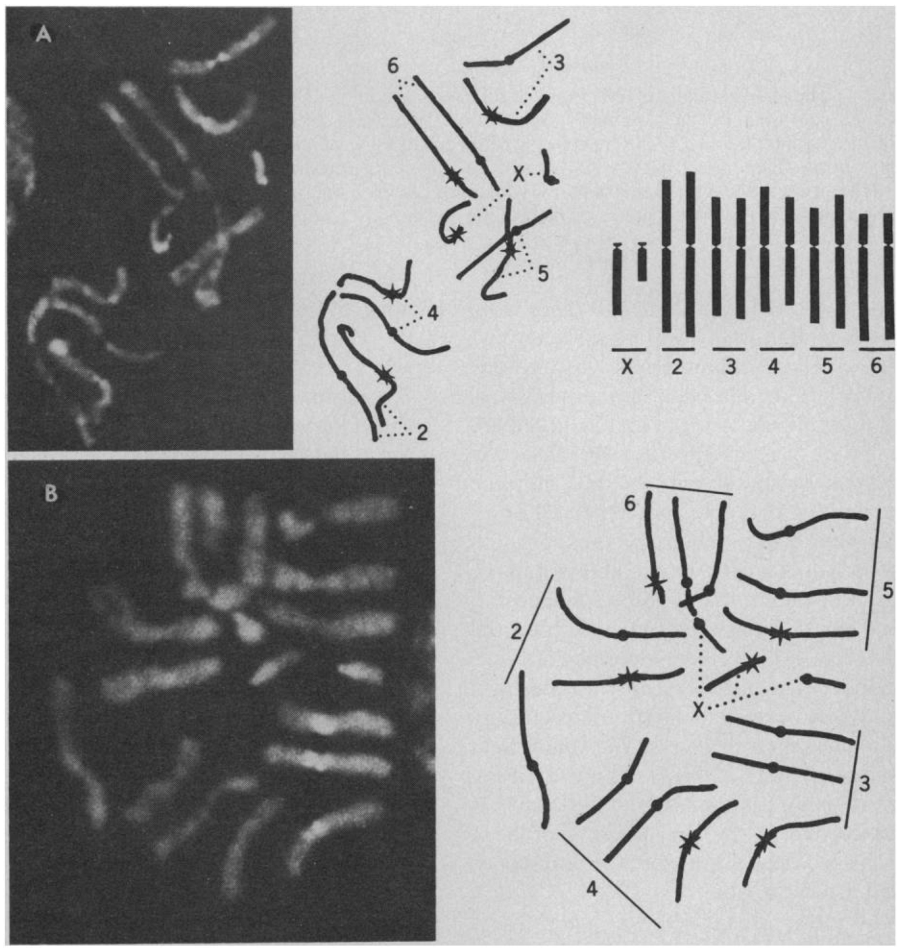

Fig. 6. Karyotypes of hybrids. (A) Photomicrograph and diagram of a karyotype originally identified as type A from southeastern New Mexico. The strain was cultured in the research facilities at Mission, Texas. The karyotype was prepared from an individual after three generations of culture, and shows evidence of hybridization with another type of screwworm, probably type I from northeastern Mexico. The starred centromeres in the diagram indicate chromosomes putatively from type I, and the round centromeres indicate type A. Note the striking size difference between the two X chromosomes. Other differences between the chromosome arms and their Q-band patterns are evident in chromosomes 2, 3, 4, and 5. Chromosome 6 appears to differ only in Q-band pattern in these two populations. (B) A micrograph of a triploid individual from an extraordinary sibship collected in Chiapas. This is one of two triploid individuals that had two type F genomes (indicated in the diagram by a dot at the centromeres) and one type I genome (indicated by a star at the centromeres). Chromosome 6 is not easily discernible in this micrograph, but chromosomes 2, 3, 4, and 5 and the three X chromosomes are clearly visible. Differences can be found in heterochromatic distribution (chromosome 3), centromere placement (chromosomes 4 and 5), and in overall length (the X chromosomes and chromosome 4). We interpret this karyotype as being from a type F diploid egg fertilized with a type I sperm. Other individuals in the same sibship included homozygous type F females that probably developed parthenogenetically, and male and female heterozygotes that had one haploid set of type F and one haploid set of type I. The chromosomes are mitotically paired, and this pairing allows one to determine homologies unambiguously. A type I chromosome is labeled here as chromosome 5 on the basis of somatic pairing with type F chromosome 5, although it would be considered a chromosome 4 according to criteria used for chromosome identification (*32*). Likewise a chromosome 5 of type I (here listed as 4 I) pairs with chromosome 4 of type F. Thus the classification methods have resulted in an underestimate of the chromosome differences between types.

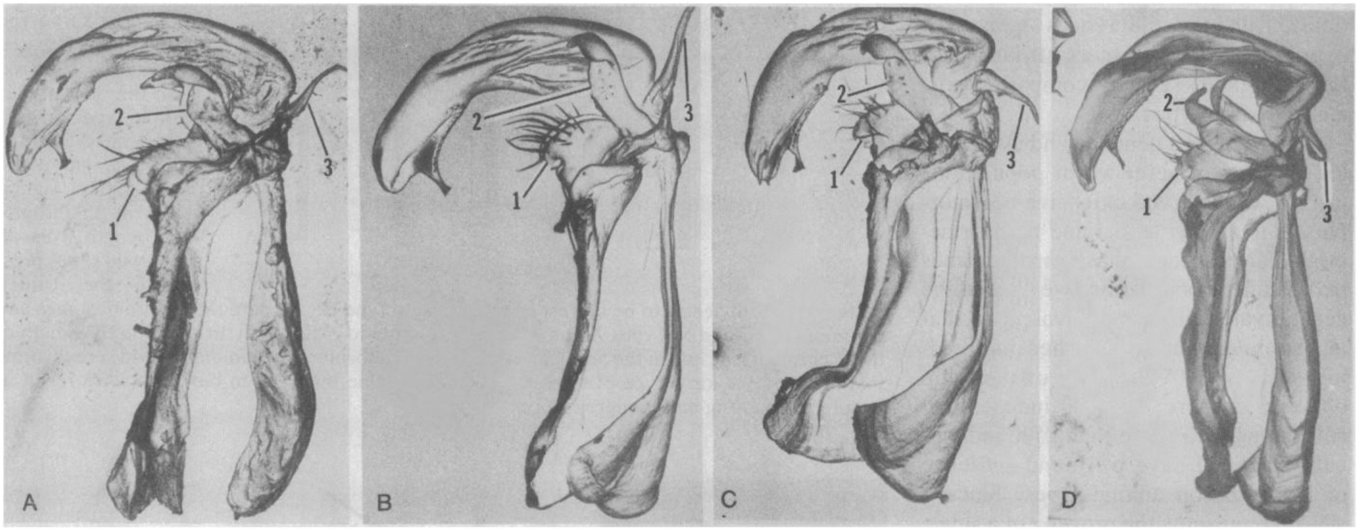

Fig. 7. The male genitalia of four types of screwworm adults. (A) Type 009, the factory-reared strain in 1978. (B) Type A. (C) Type B. (D) Type F. Differences in these types include 1, the bristle pattern, size, and morphology of the gonopods; 2, the length, width, and characteristic positioning of the parameres; and 3, the morphology and positioning of the epiphallus. There are also characteristic differences in the morphology of the hypandria. The curl of the epiphallus in type F is characteristic, but is accentuated by drying the specimen during its preparation. All images (×105) were taken with an ISI Super III scanning electron microscope in the secondary emission mode. The specimens were sputter coated with approximately 0.02 micrometer of platinum/iridium.

tion and one in another) and there is no cross-mating, there will be no heterozygotes. These characteristics enable one to specify membership of any individual in a subpopulation; the loci involved are referred to as diagnostic (*38*). Thus, the genetic variation may be polymorphic where heterozygotes are observed or diagnostic where heterozygotes are absent. The karyotypic characters that we use to characterize types are diagnostic, and on this basis we have defined the different types of screwworms (*28*).

In certain instances polymorphic loci may also be used to differentiate subpopulations when there is a Wahlund effect at two or more loci (*39*). Analyses of the electrophoretic variation in allozymes is concordant with the differentiation of types of screwworms, but the differences are not diagnostic.

In other instances we have found structural differences in the chitinized parts of the male genitalia of the screwworm flies. We found no intermediate forms among the wild specimens nor among the direct offspring from wild females cultured in the laboratory. Intermediate forms of the male genitalia have been observed, however, in laboratory-derived hybrids and in cultures maintained in the laboratory. [We believe the changes in laboratory cultures are due to contamination of the cultures, and in some instances have confirmed this to be the case (*40*) (Fig. 6A).] For example, Fig. 7 shows the internal male genitalia from three wild types and from type 009, the factory-reared strain that was being released in 1978. The differences evident among these types are generally found only among different, closely related species.

To date we have identified, on the basis of karyotypes, nine types of screwworms, five of which reached the United States in 1978 (A, B, D, F, and J). The other types have been found exclusively in Mexico (Fig. 4). No type is defined solely on the basis of Y chromosome diversity because heterozygotes are not expected. However, once a type has been distinguished and is found to have a distinctive Y chromosome, this chromosome becomes a useful key character. In each of types A and F there are two types of Y chromosomes. These have been considered to be polymorphisms within these types, although the two types show little or no geographic overlap (sympatry). Whether the Y chromosomes really do indicate different types of screwworms remains to be determined.

Since 1978 we have found types C and D in southern Sonora, Sinaloa, and Chiapas, and type E in Chiapas. Infestations of these types caused less damage to the host animal than types A and F and produced little or no drainage from the wounds. We found cattle with such wounds in New Mexico and Arizona, but not Texas. This may reflect differences in the screwworms, host conditions, weather, or other factors. We also observed that ranchers in Mexico sometimes did not make an effort to treat infested wounds from which we had collected larvae, and that the screwworm-infested wounds in cattle in southern Mexico lacked an odor. Whereas cowboys in the United States generally locate hidden infested animals by an odor that is detectable 100 meters or more downwind, we could detect no such odor even at 3 centimeters in wounds infested by types C, D, or E in Mexico.

Type H has been found to date only in northeastern Mexico. Type I, that we originally found with type H, was first suspected when studies with starch gel electrophoresis failed to reveal a characteristic larval esterase band for *Est-C*. Although all of these types of screwworms were collected from both cattle and sheep, type H was commonly found in cattle, whereas type I was routinely collected from sheep. Type I also has a unique electromorph band segregating for phosphoglucose isomerase.

Karyotypes of older screwworm populations. A karyotype of *C. hominivorax* was first published by Kaufman and Wasserman (*41*). The larvae from which the karyotypes were prepared were cultured from screwworms originally collected in Texas. From time to time newly caught flies were added to the culture (*42*). At a later time samples from the culture were supplied to Boyes, who published a revised karyotype (*43*). Photographs of metaphase chromosomes of screwworms that were, presumably, also collected in Texas, were subsequently published by LaChance *et al.* (*44*), and from these photographs we have drawn a third karyotype (Fig. 8). These three karyotypes differ from one another and, in view of recent results, some of the differences should be noted.

The drawing by Kaufman and Wasserman shows an X chromosome that approaches the length of the smaller autosomes. Boyes' karyotype shows small changes in autosome measurements, but a decrease of 50 percent in the length of the X chromosome from the Kaufman and Wasserman drawings. The karyotype shown in the micrograph of LaChance *et al.* (*44*) shows still other differences, suggesting that a third type was in culture at the time of his study. We have found no screwworms with karyotypes similar to those found by Kaufman and Wasserman (*41*) or by Boyes (*43*), but the karyotype of type I, which occurs in northern Tamaulipas, is similar to that described for the strain used by LaChance *et al.* (*44*). These data suggest that there have been 11 types of screwworms studied in North America. The screwworm population recently eradicated from Baja California was not sampled for genetic analysis. In view of the large areas of Mexico from which no samples have been obtained, and the difficulties experienced in the screwworm eradication program in Puerto Rico and the United States from 1968 to 1978, there must certainly be more than 11 types of screwworms contributing to the complex breeding structure and genetic diversity of the screwworms that became established or caused outbreaks.

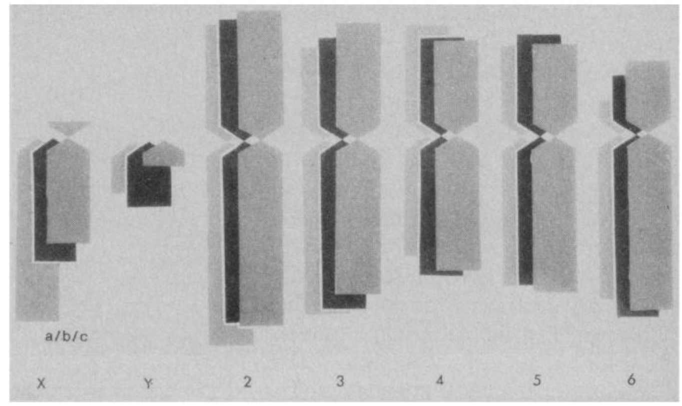

Fig. 8. Screwworm karyotypes from previous studies: (a) Kaufman and Wasserman; (b) Boyes; and (c) LaChance *et al.* The karyotype drawn from LaChance *et al.* (*44*) is similar to that of type I, differing only in its Y chromosome. The karyotype of Boyes (*43*) is different from any encountered in this study, but is probably most closely related to type F. The differences between the karyotype of Kaufman and Wasserman (*41*) and all other karyotypes included in this study exceeds all differences otherwise observed.

Preliminary results of a field test. A strip approximately 200 by 25 kilometers in Chiapas, Mexico, bounded on three sides by the Pacific Ocean, Guatemala, and the coastal mountain range, was identified as a location to test the effectiveness of sterile flies of a known type on a complex screwworm community. The screwworm population in the area was comprised of seven types—A, B, C, D, E, F, and I (Fig. 4). Sampling in 1980 and early 1981 indicated no significant differences among frequencies of types of screwworms with time.

For the test we used two laboratory strains, a "narrow based" strain, RGM-6, derived from a wild pair of type F flies, and a "broad based" USDA strain, V-81, formed by forced crosses of samples of three types. Most of the samples were composed of type F with a small number of types A and B. The test area was divided into three plots, one on each end receiving either sterile flies from V-81 (southeast end) or RGM-6 (northwest end). The area in the middle (buffer zone) did not have flies released in it, but the results suggest that there were extensive movements into the buffer zone from both treated areas. The release rate for the 8 weeks of the test averaged about 85 flies per square kilometer, a rate comparable to that used in the first successful field test in 1951 on Sanibel Island, Florida (*17*).

Results in both of the treated areas were very similar and have been combined (Fig. 9). By the end of the test, type F was absent (reduced from 39 to 0 percent), type D had more than tripled to become the most common (increased from 16 to 52 percent), and type I had increased tenfold (2 to 20 percent). The overall density of the community had remained stable. The increases in types D and I illustrate "species releases," and reveal a strong genetic isolation between type F and types D and I. The persistence of other types shows their genetic isolation from type F, and illustrates the ineffectiveness of a genetic mismatch between sterile flies and wild flies. However, higher release rates would probably have affected some of these populations.

Implications of the Genetic Diversity of Screwworms

How the eradication process has worked. How has the screwworm eradication program been so effective with so many reproductively isolated and genetically differentiated populations? We discuss here some possible explanations that seem to be consistent with the results of our studies of screwworm populations in the United States and Mexico, along with some inferences about the previous populations from available records.

Theoretically, sterile flies that are maintained above some critical ratio with a natural population will cause that population to decline to extinction in a few generations. Sterile flies maintained below the critical ratio will only suppress the population if the natural regulation of that population is density-dependent and sterile and wild flies are competing. The critical release rate must maintain the critical population ratio. The critical ratio depends in part on the effective mating of sterile flies with fertile flies. Under ideal conditions the theoretical critical number of sterile flies is about 25 percent of the carrying capacity, giving a critical ratio of 1 to 4. Preferential mating among wild flies increases the critical ratio (*45*).

Since actual release rates are far above natural densities of screwworm flies, a ratio of sterile to fertile flies is always greater than one, and somtimes greater than 100. Behavioral (prezygotic) isolating mechanisms may be overpowered by unnaturally high densities of sterile flies. If intermating restrictions were among the main factors contributing to the separation of the different types of screwworms, a limited amount of cross-mating would be expected, particularly at high densities. However, the growth dynamics of an outbreak also modify the effectiveness of sterile flies. Whether or not the critical ratio could be obtained would depend on (i) the natural rate of population growth, since a slow rate would tend to increase the numbers of sterile flies by fertile matings; (ii) the sterile flies being released before the natural expansion of the population was advanced (pre-logarithmic phase); (iii) the availability and distribution schedule of sterile flies; and (iv) the strength of the isolating mechanisms at high population densities and the proportions of sterile flies (the net effect of which would be the "effective release ratio").

There are many ways in which the effectiveness of irradiated flies may be reduced, and sexual discrimination against the sterile flies is to be expected when the type released differs from the wild types. For example, a higher death rate or lowered mating vigor reduces the effective release ratio for a given release rate. Although the isolation may be overcome in many instances by sufficient densities of irradiated flies, in some instances high density alone has been inadequate to suppress populations.

The existence of multiple types of screwworms was slow to threaten the effectiveness of the eradication program in the Southwest. The original objective was to eradicate screwworms from the United States and prevent reinvasion by maintaining a barrier zone of sterile flies. With respect to the geographic range of screwworms, however, only the northern margin of the permanent population was targeted for suppression. The diversity of the pest and the relation between diversity and species range was not known. Since only one or a few types surged northward in most years, the presence of different types was not obvious. If one considers that karyotypes found in the 1960's are now absent and that the control program was effective until 1968, it appears that the earlier populations of screwworms were exterminated. They must have been confined to the barrier zone along the U.S.–Mexico border where the sterile flies were released. Populations of any endemic types of screwworms on various Caribbean islands might also have been completely eradicated as a result of autocidal control programs.

One may postulate that screwworm populations increased in density and extended their summer ranges because of the disturbances in the ecological system from about 1890 to 1940. After the expansion, one or a few types became dominant. After the control program started in the Southwest, the dominant types were gradually suppressed and other types replaced them, similar to D replacing F in the Chiapas field test (Fig. 9). The residual pest population then became a mixture with previously rare types being more common. This pattern would be similar to the tenfold increase in type I in the Chiapas field test (Fig. 9). Thus, the success of the program would become more haphazard, depending on an adequate match with the dominant type (or types) in any given area in a particular season.

As the eradication program expanded and other locally dominant populations were suppressed, the diversity of the pest (that is, the expressed diversity) increased. As was observed for types D and I in the field test in Chiapas, we postulate that outbreaks of screwworms occurred in northern Mexico and extended into the United States when either (i) a dominant type was suppressed, permitting the increase of a previously minor type, or (ii) when a more southern type

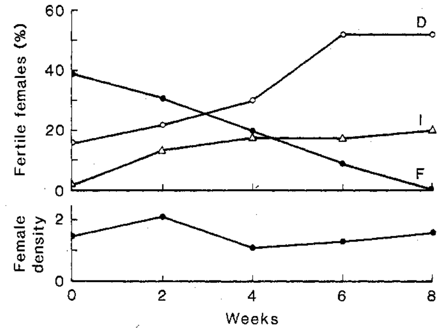

Fig. 9. Changes in proportions of types when an area was treated with type F sterile flies. The test was conducted along the Pacific Coast in southwestern Chiapas and included the release of sterile flies for 8 weeks, during which the overall sterility was very low, but there were profound changes in the composition of the mixture. Type F disappeared, whereas types D and I increased. The balance of the mixture was not statistically different from initial proportions. The total screwworm population was relatively stable, as measured by average numbers of egg masses that were collected per pen of sentinel sheep per day.

moved northward to incorporate a niche of the previous occupants. If the sterile flies did not match the new occupants sufficiently to achieve a critical ratio, the population could expand as soon as the conditions were appropriate. A lag to allow further adaptation to the extended niche, or until there was an especially suitable growing season, might be expected in either case.

Instead of changes in the composition of the wild population being suspected, deterioration of the cultured population was often blamed for the loss of control. This resulted in new collections being made. A rematch was achieved since the new flies collected, cultured, sterilized, and released usually represented the dominant types causing the outbreak. However, a single type might be the predominant pest one time, whereas more than one type might cause the losses another time. In the latter case a single interbreeding population in culture would have only a limited effect when sterilized and released on a mixture of types. With few data available the USDA considered new procedures.

Considerable attention was given to the collection and formation of the screwworm populations to be cultured (*46*), funds being available for the culture of only one factory population. The USDA intended to expand the program to eradicate screwworms to the Isthmus of Tehuantepec, and suspected that geographically diverse populations would be encountered. It was thought that a genetically diverse culture would better match populations over a wide area, and that there might be some degree of hybrid vigor from greater heterozygosity in the cultured population (*46*). However, our findings indicate that the natural diversity was much greater among types than within types, and that collections in different areas often resulted in cultures derived from hybridization between types. Such a culture matched nothing in nature, and usually required high release rates (*47*). Nevertheless, the V-81 strain used in the Chiapas field test illustrated that a small amount of mongrelization would not necessarily impair effectiveness.

We also found evidence for another possibility (Fig. 6A) (*48*). Because of the degree of genetic isolation among the types in culture, contamination of a culture with different purebred types could lead to a mixed culture of mongrel and purebred individuals—a closer approximation to the natural diversity. Indeed, the continual mixing of the culture without forced crossing was routine in the earlier phases of the eradication program, and may have been an important reason for the changes in karyotypes reported by Kaufman and Wasserman (*41*), Boyes (*43*), and by LaChance *et al.* (*44*), as well as for the early effectiveness of the program.

Reinvasion of the United States. Figure 3 shows the types of screwworms that invaded the United States in 1978, and their likely origins (or nearest known localities) in Mexico. Contrary to the more localized types, the widespread types (A and F, and possibly I; see Fig. 4) are polytypic in their Y chromosome, and the distribution of the different Y chromosomes varies from north to south. Although we consider populations to be interbreeding if we cannot verify that they are isolated, these widespread types may still be mixtures that are noninterbreeding.

If these types are, in fact, mixed rather than polymorphic, another possibility must be considered. Southern types may not be adapted to northern conditions. Type I has not been found outside of Mexico since the studies of LaChance *et al.* (*44*). We drew the karyotype (Fig. 8) from only a single cell shown by LaChance *et al.* and cannot be sure that it is identical with the type I we described in Chiapas. Furthermore, the Chiapas type I is polymorphic, containing individuals identical in karyotype (and seemingly in their allozyme profile) to those in Tamaulipas as well as individuals differing primarily in their Y chromosome. The risk of serious screwworm outbreaks in the United States may have been reduced in the past 3 years, because of the successful elimination of the types adapted to the more northern regions of Mexico from which flies may naturally spread to the United States in a single season. If this is the case, a few years may elapse before other screwworm niches are extended into the eradicated zone, possibly by introductions from southern Mexico, or from elsewhere, such as Africa or South America.

If there is no such differentiation of northern and southern types, reinvasions may occur at any time as a result of movements of cattle in trade or ranching operations (in spite of inspection and quarantine efforts in Mexico) or as a result of residual pockets of flies within the area supposedly eradicated. The Texas Animal Health Commission has a program to alert livestock producers to screwworm outbreaks, but the ability to control such an outbreak is questionable.

The distribution of the infested animals reported in the United States and northern Mexico in 1980 and 1981 suggests that the mode of reintroduction of the screwworm is likely to be by way of human activities. Therefore, the geographic regions with screwworm populations threatening the United States need not be those nearest our borders. The sources of reinfestation are likely to be screwworm populations in regions with a significant amount of animal traffic into the United States or northern Mexico. Inspection and early warning plans are important in preventing reinfestations and in facilitating rapid responses to reinfestations when they occur.

Any response to an outbreak will be handicapped because all sterile flies are produced at the factory in Chiapas, 1500 kilometers south of Texas. If the types of screwworms causing the outbreak are genetically different from those in culture, the sterile flies released may not be able to suppress them. Thus, we believe the ultimate success of screwworm control will depend on the availability of a mass culture facility in the United States, where an adequate nucleus of skilled personnel will be able to respond quickly to an outbreak by releasing effective sterile flies. At the present such a capability does not exist.

Current strategy is to use the SWASS technique in the area of an outbreak and to follow this treatment with release of the strain being cultured in Chiapas. However, chemical approaches are inefficient on low-density, scattered populations, and blowflies from southern Mexico are unlikely to respond to the SWASS attractant. Little is known about the degree of specificity required for an attractant to be effective with different types of screwworms.

Total eradication of the screwworm may have unexpected ecological consequences. For example, deer populations in south Texas increased rapidly after the control program became effective in the 1960's, and caused serious crop damage. After eradication of a sexually reproducing (and controllable) screwworm type, the possibility of there being a species release of a parthenogenetic type is an unknown risk (*35*).

Although it seems prudent to continue the present plan to eradicate screwworms from northern Mexico to the Isthmus of Tehuantepec, it may not be to the economic advantage of the United States to use resources for eradicating the pest in Central America or the northern countries of South America. Mammal shipments into the eradicated zone of Mexico or the United States frequently originate in other countries (for example, exotic game is imported from Africa). Although control of the screwworm in countries from which mammals are imported deserves consideration, limited resources should probably now be concentrated on preventing reintroduction and preparing effective responses to screwworm outbreaks. Failure to protect the livestock industry is a threat to the agricultural economy of the nation.

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16. P. W. Turner, personal communication. See also the *Grazing Industry Papers* (*7*). The "drift fences" constructed in the late 1800's and running east and west prevented livestock from "drifting" southward during the winter. The fencing of cattle began when Herefords, Shorthorns, and other stock were imported and the open range was converted to private ranches. Sheep areas were fenced much later, especially after World War I.
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28. We use the term "type" in this article to refer to what might otherwise be called gamodeme. The term gamodeme has the advantage of avoiding the controversial application of species to populations that are partially or completely reproductively isolated [J. S. L. Gilmour and J. Heslop-Harrison, *Genetica* **27**, 147 (1954)]. In the case of screwworms, the term has only been used thus far for populations that do not appear to intercross in nature. Although such populations can be hybridized in forced conditions, many are sympatric and genetically differentiated to such an extent that they may be formally recognized as different species. As a result of the differences in response to the release of sterile flies of one type by a mixture of different types shown in Fig. 9, it can be said that experimentally type F is a different species from types D and I.
29. The USDA officials focused on the logistics of the eradication program, attributing the outbreaks to "problems with execution." For ex-

ample, the release of sterile flies in Sonora in 1978 was limited and there was a 2-week delay in release early in the season in Arizona, aggravating the severity (*45*). Also, flight lanes were widely spaced because of an aircraft shortage, but local releases were made where infestations were heavy.
30. Types D and A have similar autosome and X chromosome karyotypes, but very different Y chromosomes. Whether or not heterozygotes of these types could be distinguished with routine analysis is debatable, but we refer to them as separate gamodemes because of the subtle differences in their autosomes.
31. This difference in screwworm behavior, which was pointd out by R. Bond, L. Shannon, and G. Moore (personal communication), was not noted by USDA officials even though it served as the basis for the ranchers' postponement of treatment of infested cattle.
32. The screwworm chromosomes initially were arranged according to the convention with *Drosophila* chromosomes, with the X and Y being first, followed by the autosomes in descending order of size. However, when the first screwworm karyotypes were prepared the factory strain (type 009) was used as a standard and it became evident that to compare homologous chromosomes between different types some criterion other than size would be necessary. The X and Y are easily determined in all types. The longest chromosome in the genome (invariably a metacentric or submetacentric) became chromosome 2; the only chromosome with extraordinary fluorescence on each side of the centromere after staining with quinacrine became chromosome 3; chromosomes 4, 5, and 6 were assigned by designating chromosome 4 as the most nearly metacentric of these three; chromosome 5 as the most nearly metacentric of the remaining two; and chromosome 6 as the most nearly telocentric of the chromosomes. Applying these criteria to the Kaufman and Wasserman karyotype, our chromosome 2 is their chromosome 6, our 3 is their 5, our 4 is their 3, our 5 is their 4, and our 6 is their 2. In the Boyes karyotype, our 2 is his VI, our 3 is V, 4 is II, 5 is IV, and 6 is III. In both cases, the X and Y chromosomes are in agreement with our designations. See Fig. 6B and (*35*), where our designations of chromosomes 4, 5, and 6 misnamed homologous chromosomes; the comparison between types when the correction is made shows greater karyotypic diversity. Our designation may have biased the karyotypes toward similarity among karyotypes in other instances as well.
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35. We have recently found cytological evidence for parthenogenesis in one sibship from Chiapas, Mexico. This sibship included triploid individuals resulting from fertilization of a diploid type F egg with a type I sperm, diploid female individuals that were homozygous for type F chromosomes, and diploid male and female individuals that were heterozygous for type F and type I karyotypes. The most plausible explanation for these observations is that the maternal parent produced both diploid and haploid eggs. The diploid eggs resulted in both the triploid individuals (with fertilization) and parthenogenetic diploid development of type F females. The haploid eggs, when fertilized, developed into the heterozygous males and females.
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48. Cultured populations generally contain some homogametic types that match wild types, but they could be selectively reassembled after mongrelization, or they could be contaminants. Since we have been monitoring the populations cultured for release [R. H. Richardson, J. R. Ellison, W. W. Averhoff, *Autocidal Control of Screwworms in North America: Effects of Genetic/Taxonomic Complexity* (Genetics Institute, University of Texas, Austin, January 1981)] we have detected the appearance of types that were not originally included among collections crossed; presumably the cultured population was contaminated with other types being cultured. Male genitalia as well as chromosomes show the mixing, and the "introgression" of the mongrelized and contaminated culture.
49. This article is adapted from the Plenary Paper presented at the Genetics Society of America annual meeting, Boulder, Colo., 18 August 1980. Funds for this research were given by The Perry Foundation, Southwest Animal Health Research Foundation, Texas Sheep and Goat Raisers Association, University of Texas at Austin, Department of Energy, and USDA. We thank H. Q. Sibley, P. Turner, T. Priestly, and R. Peeples for assistance and encouragement. Numerous individuals made the research possible, including cooperators in Texas: staff of the Texas Animal Health Commission; in New Mexico: R. Bond, J. Cooper, H. Hopson, D. Liesner, L. Locklar, J. Raush, B. Thompson, G. Thornton, J. L. Wiley; in Arizona: J. Barney, C. E. Dockter, J. P. Elsworth, C. Hilbers, R. Lucas, G. Miller, J. Moore, T. Pfister, J. W. Pickerel, R. Proper, R. W. Riggs, J. Rogers, J. Savoini, L. Shannon, L. Sullivan, J. Weinheimer; in California: El Cajon Veterinary Clinic staff, W. J. Dedrick, D. Fly, E. T. Henry, and F. Scharf. Information and cooperation were given by many USDA personnel, including APHIS and ARS staff in Mission, Tex., Tuxtla Gutierrez, Chiapas, Mexico, and Fargo, N.D. We give special thanks to R. C. Bushland, E. F. Knipling, W. Klassen, M. E. Meadows, B. Hightower (deceased), E. Judy, B. Sudlow, D. Hopkins, G. Gassner, and D. Neilson. Members of the Mexico-American Commission for the Eradication of the Screwworm have been especially helpful in Mexico, most notably N. Pineda, M. Vargas, and A. Martinez.