REVIEW

Screwworm Eradication in North and Central America

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Screwworms, Cochliomyia hominivorax *(Fig. 1), have been eradicated from the USA and now have a tenuous hold only in the Yucatan peninsula of Mexico, where control programmes based on massive release of sterile males have recently been initiated. Sterile male release operations are now underway in Guatemala and proposals have been made to extend the eradication procedures south to the Darien Gap in Panama. It is planned to extend the barrier zone to Belize and Guatemala later this year. This article reviews the progress and operational obstacles of the screwworm eradication programme.*

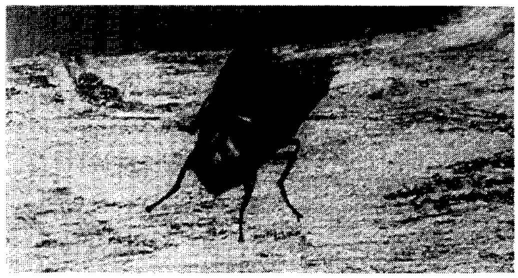

Fig. 1. The Screwworm fly, Cochliomyia hominivorax.

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Screwworms, *Cochliomyia hominivorax* (Diptera: Calliphoridae) have been eradicated from vast areas where they once were endemic the year round, thereby freeing the continental USA from seasonal risk of infestation. Eradication in Mexico west of 93° latitude was recently declared[1] and now less than 230 000 km² of Mexican territory remain at risk to screwworms. This accomplishment confirms the robustness of the sterile insect release technique (SIT) proposed by Knipling[2] and first demonstrated by Baumhover and colleagues[3] (Box 1). It is testimony also to the planning of the Joint Mexico-American Commission and the perseverance and skill of thousands of Mexican workers. Much of the story is set forth by programme personnel in a recent publication[5].

Screwworms are obligate parasites of mammals that cause primary myiasis in pre-existing wounds. The larvae from a single oviposition can kill smaller animals, and superinfections can kill mature cattle. Humans can also be infected and even killed[6]. Screwworm control by chemical methods and animal husbandry was expensive, short term, and relatively ineffective before SIT first was brought to bear on the problem in the southeastern USA (Fig. 2)[7].

Myiasis begins when egg masses of up to 450 eggs (350 on average) are oviposited on wounds. Flies may develop and lay subsequent egg batches at a temperature-dependent rate provided that sufficient wounds are available. Screwworms are highly fecund and migration is an important component of their population ecology[8]. Although fly densities tend to be low on average, the fly populations are highly aggregated and local populations may be quite numerous[8]. This has an important bearing on the outcome of sterile male releases, for there is no evidence that released males search out population centres of native flies or that wild females disperse to avoid brother–sister matings.

Before the advent of SIT, the geographical range of screwworms in the USA extended seasonally and discontinuously from North and South Carolina westward to California. Screwworm foci were present in Iowa, Illinois, Minnesota, South Dakota, Utah, Wisconsin, and other midwestern and western states, usually in mid and late summer[9,10]. In winter, populations were confined to Florida and the southern portions of Texas, Arizona, New Mexico and California in addition to Mexico[11–13] and countries south to Argentina.

The annual case incidence in Texas (Fig. 3a) provides an index of abundance since 1962. A further index is provided by case reports from Arizona and New Mexico (Fig. 3b). A case represents a sample of larvae, usually those larvae hatching from a

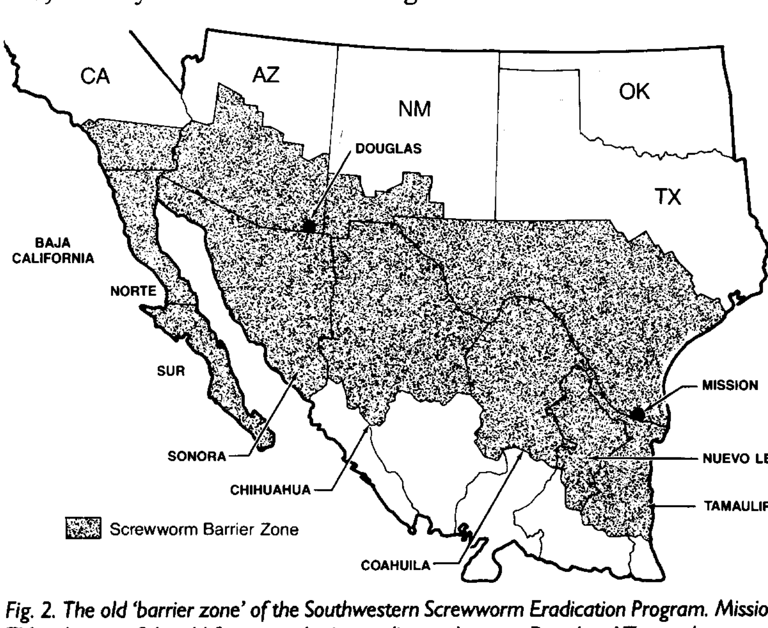

Fig. 2. The old 'barrier zone' of the Southwestern Screwworm Eradication Program. Mission, TX is the site of the old factory and primary dispersal centre. Douglas, AZ was also a packaging and dispersal centre. Baja California, Sonora, Chihuahua, Coahuila and Tamaulipas are the northern frontier states of Mexico and the border is indicated.

Box 1. How does the Sterile Insect Technique Work?

The sterile insect technique (SIT) involves release of large numbers of sterilized insects to compete with the wild insects for mates. Wild females mated with sterile males fail to produce offspring.

The working of the SIT can be illustrated by the following equation:

$$W_{n+1} = \left[\left(Wn \times \frac{Wn}{Wn + (R \times C)}\right) + M\right] \times I$$

where: W is the number of wild individuals of any one sex (an equal sex ratio is assumed so the first W_n in the equation refers to egg-laying females and the others refer to males); n and $n+1$ refer to generations, assuming that successive generations do not overlap. R is the number of sterile released males and C is their competitiveness, defined as the relative probability of a released male mating compared with that of a wild male – this depends on its mating behaviour and on whether it is released in the right place to find females. However, density-dependent or frequency-dependent matings may occur, so that C would vary inversely with R. This behaviour has been detected in tsetse flies[4] and seems to hold for sterile screwworm fly releases (E.S. Krafsur, unpublished). M is the number of immigrant females, assumed to arrive already inseminated with fertile sperm and unwilling to mate again. (The monogamous behaviour of female screwworms is thus an adverse factor for the working of SIT, contrary to the earlier belief that it was essential for success. This belief arose because it was not realized that radiation doses up to a few kilorads act by inducing dominant lethal mutations, not by inactivating sperm, so that when a female is mated to both a fertile and a sterile male it lays a proportion of fertile eggs.) I is the tendency of the population to increase or decrease e.g. due to seasonal factors and density-dependent factors. When $I = 1$ and $R = 0$ then each newly eclosed female would breed one mature daughter – the population would remain stable.

In this equation, released sterile females are omitted because their presence would be neutral, unless they somehow affected male competitiveness.

This equation shows that if R is constant over successive generations there would be accelerated collapse towards eradication as the R : W ratio progressively improved. However, this would be prevented if (1) M is not zero, i.e. there is a high rate of immigrant females, or (2) I increases because of density-dependent effects or (3) C declines because the release pattern consistently fails to find certain localized wild populations.

single egg mass. Cases were submitted by stockmen and veterinarians to Veterinary Services, Animal-Plant Health Inspection Service, USDA, for species identification. Postage-free mailers were provided to the public for this purpose[14], and responses to cases were inversely density-dependent[15] – the rate of submissions (samples submitted/cases claimed) falling off as case loads increased. Collections began in 1962 and became effective in 1963 (Ref. 16, 17). The spatial and temporal pattern of cases since 1978 suggests that only larvae generated by fertile immigrant females or by their F_1 adult progeny have been detected in the USA. No screwworms have been found since August 1982 and searches continue. Knipling conservatively estimated in 1984 (Ref. 5) that the cost:benefit ratio in USA of screwworm eradication was 1:10, and that the benefits will continue to accrue indefinitely. Costs and benefits to Mexico for 1986 were estimated to be 10.3 and 37.9 million pesos, respectively (US$1≃1000 pesos).

Mass-reared screwworms were sterilized as 5-day old pupae with ^{60}Co and after adult emergence, both sexes were released[7]. Beginning in 1975 irradiation was performed with ^{137}Cs and the minimum radiation dose applied was 5500 rads. Females so treated invariably fail to undergo vitellogenesis and so do not oviposit. Sterile fly dispersions in the old 'barrier zone' included highly endemic areas[13] of the frontier states of Mexico (Fig. 2). Typically, releases in Mexico would be made in winter and spring, and continue so long as the USA remained free of substantial screwworm populations. USDA aircraft were loaded in Mission, Texas (Fig. 4) and Douglas, Arizona. Year-round sterile fly production and releases in Mexico began in late 1976 (Ref. 1). Case reports in the old 'barrier zone' of Mexico are summarized in Fig. 3c and suggest that the Mexico programme became effective in 1979. Eradication south to a new barrier at the Isthmus of Tehuantepec (Fig. 5) planned by agreement between Mexico and the United States in 1972 (Ref. 18) was declared in December

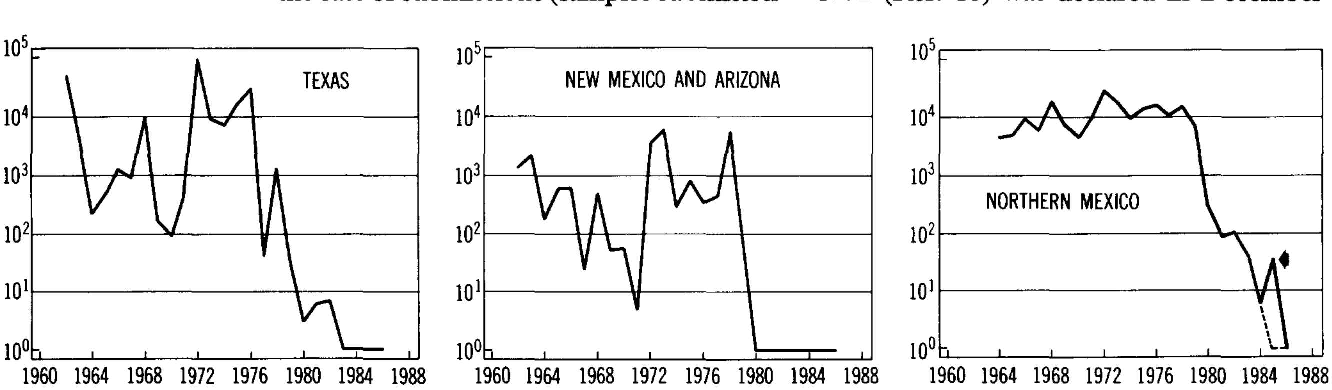

Fig. 3.(a) Annual laboratory-confirmed screwworm case reports from Texas. Cases are logarithmically transformed [log(cases+1)]. No cases have been detected since 1982. (b) Annual case reports from Arizona and New Mexico. No cases have been discovered since 1979. (c) Annual case reports from the northern states of Mexico, including Baja California Norte, Baja C. Sur, Sonora, Chihuahua, Coahuila, Nuevo Leon, and Tamaulipas. The arrow points to an episode of sabotage in which a six-week outbreak of screwworms occurred along a principal highway in Tamaulipas (32 cases) and San Luis Potosi (111 cases). Evidence suggests the deliberate release of unirradiated flies. The dotted line shows the trend when the 32 Tamaulipas cases in 1985 are not plotted. No autochthonous screwworms have been detected since 10 August 1985, but 2 cases were intercepted in San Luis Potosi in November 1985 in animals transported from Southeastern Mexico.

1984 (Ref. 1). This extraordinary achievement represents a far greater undertaking than the Florida[7] and southwestern USA campaigns.

Present Status

Recent events are set forth in Table 1, which shows case reports in the states immediately to the west of the barrier zone, in the present barrier zone, and east of the barrier zone where systematic fly releases began in 1986. The recent decline in screwworm cases in the barrier occurred even though sampling effort increased, as is demonstrated by the increased number of non-screwworm cases. It seems that the Republic of Mexico should soon be entirely free of screwworms.

Table 1. Myiasis case reports in regions of Southern Mexico, 1976 to 31 October 1986. The gap in reports from mid 1978 to early 1983 reflects transfer of livestock inspectors to states where eradication procedures were most intense. The non-screwworm cases provide an index of sampling effort.

Year	Screwworm cases	Non-screwworm cases
West of barrier: Veracruz, Oaxaca (166 107 km^2)		
1976	4820	516
1977	6502	451
1978	3584	88
1983	1113	222
1984	532	708
1985	6	565
1986	0	283
Barrier: Chiapas, Tabasco (99 752 km^2)		
1976	4243	79
1977	6242	101
1978	3143	118
1983	556	60
1984	1872	279
1985	273	534
1986	226	709
East of barrier: Campeche, Quintana Roo, Yucatan (139 810 km^2)		
1985	1157	87
1986	369	182

Eradication Strategy

Early surveys[13] had shown the geographical and seasonal distribution of screwworms in northern Mexico, where they were highly endemic. Much of Mexico is mountainous with high plateaux[19] and winter temperatures may be limiting in the north[13]. Nevertheless, screwworm eradication in Mexico was bound to be more difficult than in the USA because of the huge area to be treated, the continuous presence of stable populations in the tropical and subtropical lowlands, and difficult logistics and communications. Extensive, isolated valleys also exist and were thought to harbour screwworm populations that could have been reproductively isolated and therefore refractory to the sterile insect technique.

The eradication strategy was essentially one of 'overkill'[1,20,21], relying principally on the production of tremendous numbers of sterilized flies. Important programme components included public education, an extensive livestock inspection programme in areas undergoing sterile fly treatment, and now stringent inspection of all animals transported to screwworm-free areas from the new barrier zone.

Transported livestock are inspected, dipped or sprayed at five stations in the barrier zone, which are manned with Mexican Army as well as Commission personnel. Suspect animals are quarantined and the seemingly uninfested accompanying animals are reinspected at their destinations. This strategy was employed also in the Florida and southwestern USA campaigns, but the effort, organization, and effectiveness necessary in Mexico was very much greater. In particular, the logistics of maintaining US-made machinery and equipment, of importing and transporting up to 500 tons of food products monthly for rearing screwworms, and aerial distribution of up to 600 million sterile flies weekly over vast and remote areas, demanded a high level of skill and organization not necessary in the USA programmes. It required three years to appreciate and overcome problems in the establishment of the enterprise (see Box 2).

Field Operations

Three distribution centres were established at the outset of the Mexico programme, in Tampico, Guadalajara, and Tuxtla Gutierrez[20] (Fig. 5). Radiosterilized pupae were transported initially by modified DC-6 aircraft and later by refrigerated truck to these centres, where they were packaged, held until about 90% of the pupae had emerged, loaded onto aircraft, and aerially distributed. Aeroplanes were hired from private contractors when it

Fig. 4. Production plant for sterile screwworm flies at Mission, Texas, now held on standby but capable of producing around 200 million sterilized flies per week.


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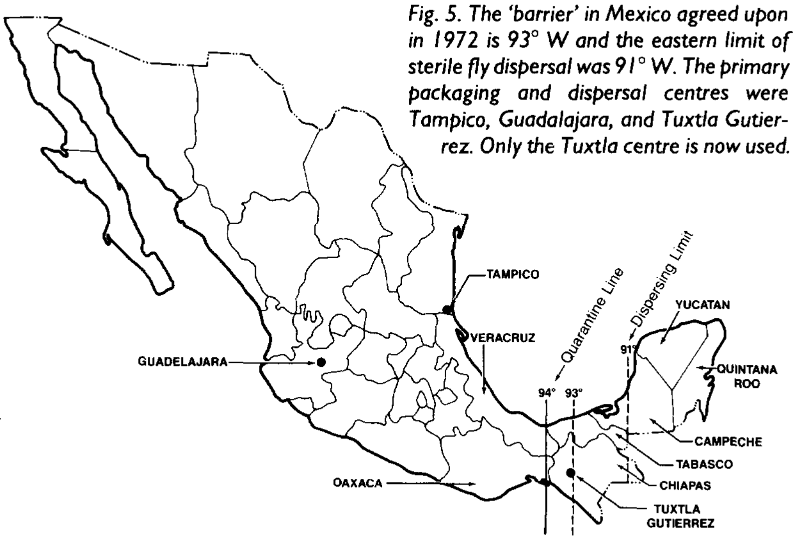

Fig. 5. The 'barrier' in Mexico agreed upon in 1972 is 93° W and the eastern limit of sterile fly dispersal was 91° W. The primary packaging and dispersal centres were Tampico, Guadalajara, and Tuxtla Gutierrez. Only the Tuxtla centre is now used.

Box 2. Early Problems in the Mexican Campaign

Flies produced in 1977 and 1978 were released in the old barrier zone, Baja California and Veracruz. Results were not as hoped, despite the combined production of up to 600 million sterile flies per week from the Mission and Tuxtla plants. Clearly, more than massive numbers of sterile flies is required to achieve excellent results[15]. Pineda-Vargas, Co-Director of the programme, identified difficult communications and transportation exacerbated by overly tight central control from Commission headquarters in Mexico City, problems that were solved in part through administrative reorganizations and devolution of control to regional headquarters and distribution centres[1]. Also, new tactics were adopted. In 1979 resources were concentrated for a 'frontal' assault from the north and successive 'critical lines' were established and moved south and east as eradication proceeded.

Other problems in screwworm production and distribution arose in Mexico, including biological and logistic problems in rearing screwworms, in transporting the irradiated pupae, and distributing the sterile adults[22,23]. At maximum production, the Tuxtla plant consumed 500 tons of dry food products monthly and 680 000 gallons of water daily, to formulate the liquid diet[24] for screwworm larvae. Its chief components had to be imported from USA; uneven product availability and inevitable transportation delays required that a three-month supply be maintained at Tuxtla. Screwworm larvae are particularly sensitive to the quality of spray-dried bovine blood and powdered egg, which degrade with time. Furthermore, any contamination of bovine with porcine blood made larval media slightly toxic, and high bacterial counts also have important effects on the fitness of larvae. The most obvious phenotypic effect of inadequate diet is small body size – size of adults is the single readily identifiable component of 'competitiveness'[25].

The substrate upon which the liquid diet is applied was changed in 1983 from linters cotton to cellulose acetate blankets after unpublished work by D.D. Wilson in Mission had shown its superior properties in producing larvae[22,26]. Seemingly trivial changes in construction or composition of the release cartons also have profound consequences[23]. Boxes might not open after dispersal from aircraft, insecticidal contamination in recycled paper caused losses, ventilation holes of improper size would adversely affect temperatures within or allow escapes.

Research that materially aided eradication was summarized by Whitten[26] and included the development of a chemical screwworm attractant and a new trap design that improved the efficiency of monitoring both native and released screwworm adults. In addition, incorporation of gelling agents in the diet of first instar larvae reduced the labour requirements and the amount of liquid diet necessary to raise screwworms. Much of the screwworm research programme of the USDA Agricultural Research Service, however, involves a perpetual search for evidence of premating and postmating reproductive isolation among screwworms of different geographic origins. The possibility of parthenogenetic reproduction is evaluated and continuous research on strain development also is performed. The time consuming and expensive task of strain development is performed because of the prevalent view that colonised insects become increasingly adapted to factory conditions. Programme officials refer to this adaptation as 'deterioration' and presume that such strains become progressively less competitive than their wild cousins[22,23,27].

became clear in 1976 that changes in sterile fly release tactics were necessary[15,23,28]. Up to 70 single and twin-engine aircraft were used, and navigational aids were adopted in 1983 that permitted more precise targeting of sterile flies than was possible when navigation was entirely visual.

Sterile fly releases were routinely made over large areas twice weekly; flights were made in early morning to minimize heat stress on the released flies. Between 800 and 3100 flies (of both sexes) were released per km^2, distributed from parallel lanes set 3.2 km apart on any one flight. These lanes were offset by 1.6 km on the subsequent flight, thereby maximizing the chances of placing sterile males near breeding sites[15,28,29]. Local reports of screwworms governed the eradication tactics. District veterinary officers were empowered to establish distribution subcentres and provided with sufficient authority, inspectors, sterilized pupae, pilots, and aircraft. Special grid releases could be superimposed on the routine 'blanket' grid, and additional releases were made over watercourses and local outbreak centres.

Hypothetical 'critical lines' were established progressively southward during the course of the eradication campaign. These lines, of which the first was erected in January 1981, extended from the Gulf of Mexico to the Pacific coast. Indigenous screwworm populations were considered eradicated in the area behind the line (north or west, depending on longitude), and any screwworm cases detected were considered as evidence of a successful recolonisation (with the exception of infestations in transported animals). Extraordinary measures were taken to find and eliminate any related infestations by concentrating livestock inspectors, instituting quarantine procedures and carefully targeting sterile fly releases in the area. A six-month period must elapse in which no screwworm cases are found before a State can be declared officially screwworm free.

Large numbers of livestock inspectors were necessary to provide information on screwworm distribution and abundance and to obtain participation of the agricultural community. Up to 540 inspectors performed sampling, educated stockmen and helped to develop public awareness of the eradication programme. Screwworm cases had to be solicited in Mexico far more than in the USA, where an adequate network of roads and highly developed state extension services existed. Also, many Mexican stockmen do not consider screwworms to be economically as serious as do US stockmen. In September 1986, 249 inspectors were employed (see Box 3).

Is eradication real?

Of course, it is impossible to prove a negative. Thus it is a formal (if unlikely) possibility that undetected screwworms persist, scattered in low densities or as isolated, relict populations[32]. We consider the possibility of such populations to be small because screwworms are highly fecund, and an average female at eclosion produces about 135 female progeny in her adult lifetime (E.S. Krafsur, unpublished). Furthermore, the generations overlap constantly and there is no diapause so cases should appear whenever screwworms are present and temperatures sufficient to allow flight and oviposition (about 16°C)[11]. Sampling of adults or their ovipositions show highly aggregated or contiguous distributions[8], and previously inseminated females demonstrate an enormous propensity for dispersal[30,33], at least in semi-arid environments. These life history features generate the 'boom and bust' population dynamics shown by screwworms. Furthermore, the clinical severity of screwworm infestation, together with the active seeking of cases by stockmen and programme inspectors make it exceedingly unlikely that local outbreaks would go undetected for long.

Future Extensions

Maintenance of a barrier in its present location requires sterile fly dispersions over an area of approximately 158 000 km² (Fig. 5). This task was said to require 150 million flies per week. Also, an expensive inspection and quarantine programme must be maintained, and the eventual annual cost was stated to be US$50 million[34]. More recent estimates put the combined cost to Mexico and the USA at US$15 million. The maintenance costs and risk of reinfestation could both be minimized by applying eradication procedures progressively southwards, to the Darien Gap in Panama, an area of only 12 000 km² (Fig. 6). Annual appropriations by the US Congress for screwworm eradication to the Southwest Screwworm Eradication Programme and to the Joint Mexico-American Commission are provided in Table 2. The modest research expenditures are not included. The relative US and Mexican contributions are fixed by treaty at 80%–20% respectively and were decided on the basis of the relative sizes of the national livestock industries.

Clearly there is no conceptual or operational reason why the programme cannot be extended southwards to Panama[34]. The remaining obstacles facing the project would seem to be political, because seven

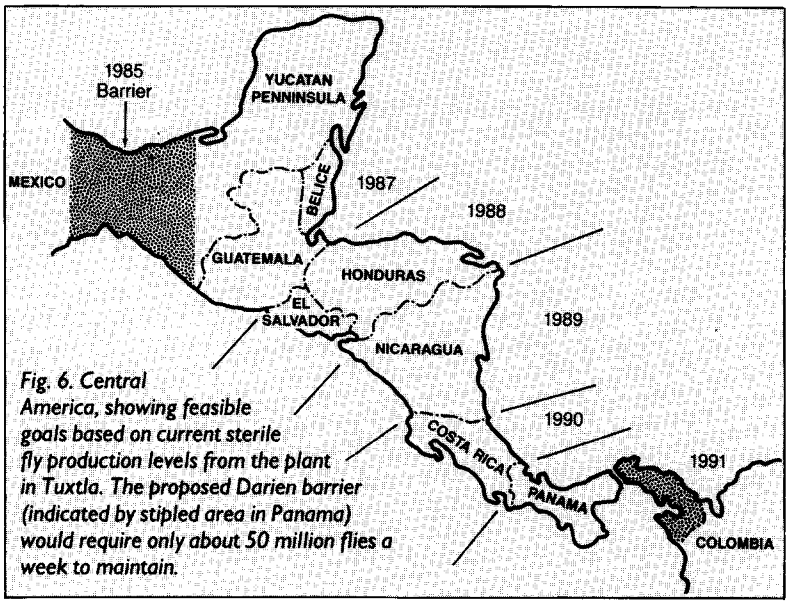

Fig. 6. Central America, showing feasible goals based on current sterile fly production levels from the plant in Tuxtla. The proposed Darien barrier (indicated by stipled area in Panama) would require only about 50 million flies a week to maintain.

Box 3. The Role of Livestock Inspection and SIT in Mexico

It may be considered that intensified livestock inspection, not SIT, was the principal determinant of screwworm eradication. Clearly helpful to eradication, livestock inspection results in preventive treatment and increased epidemiological information to programme managers. It seems however, that the case submission rate (reported/actual) in Mexico (Table 1, Fig. 3c) was less than in USA (Fig. 3a, b). Discovery and killing of developing larvae in wounds alone therefore would count little towards eradication. Moreover, surveys[13,30] and ecological studies using sentinel sheep to collect ovipositions from wild screwworms[8,29] show that average screwworm densities in Mexico were certainly no less than in the USA, so it cannot be concluded that case submissions in Mexico testify to less numerous natural populations than once obtained in USA.

Estimates of sterile mating frequencies between released factory males and native females in Mexico were made before and during the eradication campaign (Ref. 27, 29, C.J. Whitten, unpublished, and unpublished data from the Joint Mexico-American Commission for the Eradication of Screwworms), usually with the object of evaluating newly synthesized strains for field effectiveness. The sterile mating estimates provide evidence that SIT was efficacious in Mexico, as is suggested by the accompanying tabulation. These sterile mating rates are fully comparable to earlier estimates from Texas, Tamaulipas, Florida and Curacao[29].

Sterile mating frequencies in Mexico and Guatemala

State	Year	Strain[a]	Release Rate[b]	Population Density[c]	Percent Sterile Matings[d]
Veracruz	1975	FF8	193	5.00	23.3
Sinaloa	1979	DE-9	279	3.00	71.4
Veracruz	1980	Sinaloa	346	5.44	55.1
Chiapas	1981	V-81	268	10.30	18.6
Guerrero	1982	A-82	?	8.69	41.3
Yucatan	1983	Oaxaca-83	?	8.31	49.8
Yucatan	1984	A-82	270	3.77	44.7
Yucatan	1984	VF-84	246	4.52	52.8
Guatemala	1986	CH-85	356	13.88	21.5

[a]Strain designations refer to state or nearest town where founding stock originated e.g. V-81 is Veracruz in 1981, A-82 is Arriaga (Chiapas) 1982, VF-84 is Villa Flores (Chiapas) 1984. FF8 was derived from south Texas stocks in 1973. DE-9 originated from Tamaulipas. CH-85 is from Chetumal (Quintana Roo) (see Ref. 22, 26, 29 and 31 for reviews of strain histories)
[b]Release rate in units of sterile males per km² of treated area
[c]Target population density in units of egg masses per pen per week. Pens contained wounded, sentinel sheep
[d]As estimated from hatchability of ovipositions on wounded sentinels

Box 4. Did SIT Really Eradicate Screwworms?

Some commentators have challenged the notion that eradication is feasible or in fact accomplished. Richardson and colleagues contend that nominate screwworms represent a complex of more or less reproductively isolated species[35]. They advocate complex patterns of host selection among species (curiously analogous to certain Hawaiian drosophilid flies) and claim cytological, morphological and ecological evidence in support. But study of five electrophoretic loci in diverse populations from USA, Mexico, El Salvador, and Costa Rica show similar allele frequencies (Ref. 34 and C.J. Whitten, unpublished). Comparative studies on male genitalia from screwworms representing a great many geographic regions provide no evidence of specification[36,37]. The polytene chromosomes of hundreds of flies from diverse areas were homosequential and without evident structural polymorphisms[38], and careful study of mitotic and meiotic chromosomes does not confirm any of the earlier claims of chromosomal diversity[39]. These studies[38,39] employed isofemale lines (lines established from single-pair matings in the field). Hybrids between most lines also were examined. Furthermore, sterile mating frequencies in the field between irradiated males and native females in Curacao, Florida, Texas, and Mexico from 1954 to 1982 show no evidence of assortative mating – contrary to what would be expected if target and release populations were incompatible for any reason[29].

Changes in the factory stocks of flies bred for sterilization and release were made in 1966, 1971, and nearly every year thereafter. This was done to minimize factory adaptation and presumptive loss of field competitiveness[22,23,27,35]. Field evaluation of newly synthesized strains has been performed in most years since 1973. The results, in terms of sterile matings between released males and native females, do not seem to show detectable strain effects (Ref. 29 and E.S. Krafsur, unpublished). Similarly, no relationship was detected between the geographic origin of strains and sterile mating rates among target populations in different regions[29,31]. Examples include flies originating from Texas dropped on Curacao[3], Florida flies dropped on Texas and Texas flies dropped on Tamaulipas and Veracruz.

It has also been advocated that screwworm abundance is only depressed because of continental changes in climate, and that scattered, undetected populations may exist, waiting only for a return of warmer winters and moister, cooler summers[40] before expanding to former densities. The literature is replete with reference to the presumed decisive effects of climate on annual flux in screwworm abundance[17,41]. Yet few reports have offered data to support the contention that screwworm populations are favoured by exceptionally wet, warm weather and depressed by exceptionally winter cold or summer dry weather.

Experimental work[42] confirmed Parman's[11] arduously estimated overwintering threshold temperature of 10°C. Mean December, January and February temperatures fall below 10°C at a line about 30°N (i.e. north of San Antonio). Winter temperatures of 10°C or more occur south of San Antonio even in exceptional years[31,43]. Variation from year to year in screwworm abundance in Texas shows no statistically significant association with mean winter, spring or autumn temperatures or rainfall. Only summer temperatures were significantly associated with summer screwworm abundance in 5 of 7 climatological divisions of Texas. Although much of the seasonal change in abundance clearly is related to temperature, annual changes in screwworm abundance cannot reasonably be attributed to climate.

Indeed, the virtual disappearance of screwworms in USA since 1980 correlates with the effectiveness of sterile fly releases in Mexico, as is demonstrated by comparison of Fig. 3a and 3b with Fig. 3c. Moreover, examination of available temperature records from Oaxaca and Yucatan shows no biologically significant change in mean winter temperatures since 1936. There are thus no grounds for supposing that climatic changes have aided screwworm eradication in detectable ways.

sovereign countries must reach agreement with the Mexico-American Commission and establish their own organizations to promote screwworm detection and eradication. Already progress has been made. The original agreement called for a barrier centred at 93°W. Sterile fly liberations extended eastwards to 91°. This agreement was amended on 2 April 1986 to permit extension of eradication procedures to the states of Campeche, Quintana Roo and Yucatan (Fig. 5). The amendment also provides for negotiations and agreements with Central American countries and Panama, and in December 1986 it was officially agreed to begin eradication procedures in Guatemala.

Meanwhile, programme managers must remain aware that screwworms have the capacity to return to Mexico and the USA. After eight years of highly effective suppression, screwworm populations exploded in 1972 in the southwestern USA (Ref. 1). As perception of risk to screwworm attack declines, the livestock industry and animal health authorities become increasingly less likely to detect a return of screwworms in good time, allowing re-establishment of the species. In addition, there is an appreciable risk of the Tuxtla factory suddenly ending production because of social unrest or earthquake. A new factory in Panama would reduce this risk. Meanwhile, the old Mission plant (Fig. 4) remains on standby, ready to resume production of sterile flies, although flies are not currently maintained in Mission because of the chance of escapes. An 'insurance' colony is maintained by the USDA Agricultural Research Service in

Table 2. Annual US appropriations for screwworm eradication in USA and Mexico. The relative US and Mexican contributions were fixed at 80%–20% of the totals expended in Mexico[a]

Year	Amount (US$)	% For US Programme[b]
1962	2 771 700	100
1963	2 771 700	100
1964	2 806 200	100
1965	3 456 200	100
1966	4 158 400	100
1967	4 667 700	100
1968	5 091 500	100
1969	5 209 300	100
1970	6 188 000	100
1971	6 856 400	100
1972	6 825 500	100
1973	9 847 300	93.2
1974	18 537 300	53.3
1975	21 924 000	51.5
1976	24 475 000	61.1
1977	29 768 000	46.9
1978	34 984 000	43.3
1979	35 653 000	44.0
1980	36 607 000	38.0
1981	43 055 000	15.4
1982	46 086 000	3.9
1983	48 900 000	2.6
1984	49 500 000	–
1985	37 133 000	–
1986	31 589 000	–
1987	28 396 000	–

[a]Data from National Programs Staff (Screwworm), International Programs, USDA-APHIS-VS, Hyattsville, Maryland
[b]Included programme expenses in the Mexican states of the old barrier zone

Fargo, North Dakota, where a hostile climate would ensure the rapid extinction of any local screwworm escapes.

The successful conclusion of the Mexican campaign reaffirms the efficacy and strength of SIT. The achievement of the Joint Commission is enhanced when consideration is given to the population biology of the screwworm fly and its great reproductive potential. The sterile insect technique remains a credible tool for the eradication of other pest insect species from large areas (see Box 4).

References

1 Pineda-Vargas, N. (1985) *Misc. Publ. Entomol. Soc. Am.* 62, 12–15
2 Knipling, E.F. (1955) *J. Econ. Entomol.* 48, 459–462
3 Baumhover, A.H. *et al.* (1955) *J. Econ. Entomol.* 48, 462–466
4 Rogers, D.J. and Randolph, S.E. (1985) *Annu. Rev. Entomol.* 30, 197–216
5 Graham, O.H. (1985) *Misc. Publ. Entomol. Soc. Am.* 62, 1–3
6 Dove, W.E. (1937) *J. Econ. Entomol.* 30, 29–39
7 Baumhover, A.H. (1966) *J. Am. Med. Assoc.* 196, 240–248
8 Krafsur, E.S., Hightower, B.G. and Leira, L. (1979) *J. Med. Entomol.* 16, 470–481
9 Laake, E.W. (1944) *J. Econ. Entomol.* 37, 319
10 Laake, E.W. (1950) *J. Econ. Entomol.* 43, 387–389
11 Parman, D.C. (1945) *J. Econ. Entomol.* 38, 66–76
12 Lindquist, A.W. and Barrett, W.L., Jr (1945) *J. Econ. Entomol.* 38, 77–83
13 Hightower, B.G. *et al.* (1966) *J. Econ. Entomol.* 59, 416–420
14 Bushland, R.C. (1985) *Misc. Pub. Entomol. Soc. Am.* 62, 12–15
15 Krafsur, E.S. and Garcia, L. (1978) *J. Med. Entomol.* 14, 687–697
16 Bushland, R.C. (1975) *Bull. Entomol. Soc. Am.* 21, 23–26
17 Novy, J.E. (1978) in *The screwworm problem* (Richardson, R.H., ed.), pp. 19–36, U. Texas Press, Austin
18 United States Department of State (1972) Treaties and Other International Acts Series 7438. 8 pp.
19 Bonine, M.E. *et al.* (1970) *Atlas of Mexico* 138 pp. Bureau of Business Research, U. Texas, Austin
20 Reichard, R.E. (1985) *Misc. Publ. Entomol. Soc. Am.* 62, 28–30
21 Whitten, M.J. and Foster, G.G. (1975) *Annu. Rev. Entomol.* 20, 461–476
22 Marroquin, R. (1985) *Misc. Publ. Entomol. Soc. Am.* 62, 31–40
23 Hofmann, H.C. (1985) *Misc. Publ. Entomol. Soc. Am.* 62, 41–48
24 Gingrich, R.E., Graham, A.J. and Hightower, B.G. (1971) *J. Econ. Entomol.* 64, 678–683
25 Hightower, B.G., Spates, G.E. and Garcia, J.J. (1972) *J. Econ. Entomol.* 65, 1527–1528
26 Whitten, C.J. (1985) *Misc. Publ. Entomol. Soc. Am.* 62, 16–21
27 Krafsur, E.S. and Hightower, B.G. (1979) *J. Med. Entomol.* 16, 33–42
28 Krafsur, E.S. (1978) *Proc. Entomol. Soc. Wash.* 80, 164–170
29 Krafsur, E.S. (1985) *Bull. Entomol. Soc. Am.* 31, 36–40
30 Hightower, B.G. (1969) in *Insect ecology and the sterile male technique*, pp. 25–31, International Atomic Energy Agency, Vienna
31 Krafsur, E.S. (1985) *Entomol. Exp. Appl.* 37, 297–305
32 Krafsur, E.S. *et al.* (1986) *Nature* 323, 495–496
33 Hightower, B.G., Adams, A.L. and Alley, D.A. (1965) *J. Econ. Entomol.* 58, 373–374
34 Snow, W.J. *et al.* (1985) *J. Med. Entomol.* 22, 353–360
35 Richardson, R.H., Ellison, J.R. and Averhoff, W.W. (1982) *Science* 215, 361–370
36 Gagne, R.J. and Peterson, R.D. (1982) *Ann. Entomol. Soc. Am.* 75, 574–578
37 LaChance, L.E. *et al.* (1982) *Science* 218, 1142–1143
38 Dev, V., LaChance, L.E. and Whitten, C.J. (1986) *J. Heredity* 77, 427–434
39 LaChance, L.E. and Whitten, C.J. (1985) *Ann. Entomol. Soc. Am.* 79, 792–798
40 Readshaw, J.L. (1985) *Nature* 320, 407–410
41 Graham, O.H. and Hourrigan, J.L. (1977) *J. Med. Entomol.* 13, 629–658
42 Flitters, N.E. and Benschotter, C.A. (1968) *Ann. Entomol. Soc. Am.* 61, 65–67
43 Krafsur, E.S. (1987) *Med. Vet. Entomol.* 1, 71–80

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Genetics and Trypanotolerance

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Genetic resistance to disease and its use in domestic livestock usually ranks last, if at all, amongst preferred disease control measures – usually preceded by measures such as chemotherapy, vector control and vaccination. Thus, interest in genetic resistance is often a reflection of dissatisfaction with other control strategies, and the current emphasis on trypanotolerant cattle in Africa is just such a case. Eighty years of tsetse fly eradication programmes have had little impact on tsetse distribution[1,2], although recent research with odour baited targets impregnated with insecticide brings hope for the future[2]. The search for a vaccine has proved more arduous than anticipated[3] and the number of drugs available for therapy and prophylaxis is limited.

In the search for alternative solutions to the problem of African trypanosomiasis, attention has recently focused on genetic resistance – a subject normally covered by immunologists or veterinarians[3–7]. In this article, Rosemary Dolan discusses the concept from the geneticist's viewpoint.

Variation between cattle breeds in response to tsetse challenge has been recognized since the beginning of this century. In 1904 dwarf humpless shorthorn cattle from the tsetse belts of Benin, were imported into Zaire[8] and the first descriptions of trypanotolerance in West Africa reached the literature in 1906[9,10]. In East Africa the presence of humped cattle immune to trypanosomiasis in the Koalib area of Sudan was first reported in 1913[11].

Following these early reports, differences between cattle breeds in the face of tsetse challenge have been a recurrent observa-