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Gypsy Moth Control with the Sex Attractant Pheromone

Mass trapping or permeation of the air with pheromone can prevent male gypsy moths from finding mates.

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The gypsy moth [*Porthetria dispar* (L.)], a serious defoliator of forest, shade, and orchard trees in northeastern United States, is spreading rapidly to the South and gradually to the West and threatens to become a national problem.

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There is deep division among scientists, administrators, environmentalists, and public officials about whether its spread can be stopped or should be stopped. On some occasions we read of citizens and township officials begging for relief from the moth's depredations; at other times it is claimed that after the initial flareup damage can be small, and that we should learn to live with the insect and find ways to minimize the damage rather than attempt to halt expansion of the present infestation. The way in which the gypsy moth problem has been handled has been criticized (*1*), but the critics have not come up with practical and ecologically acceptable solutions.

In this article we describe the problem and discuss the possibilities of using the recently identified sex pheromone of the gypsy moth (*2*) to combat this insect.

History

The gypsy moth, a native of Europe, Asia, and North Africa, was brought to Medford, Massachusetts, in 1869 for the purpose of producing silk for local industry; unfortunately, some insects accidentally escaped. The moth became established, but was largely unnoticed until 20 years later when there was a devastating population explosion. The following comment of a local resident is typical (*3*): "In 1889 the walks, trees and fences in my yard and the sides of the house were covered with caterpillars. I used to sweep them off with a broom and burn them with kerosene, and in half an hour they were just as bad as ever. There were literally pecks of them. There was not a leaf on my trees. . . . The stench in this place was very bad."

Though local infestations were gradually brought under control by natural forces and such efforts as burning egg masses, treating them with creosote, banding trees to catch the caterpillars, and spraying or dusting with chemicals such as lead arsenate, spread of the moth into new areas continued. For a long time the moth was confined to New England, but the cost was high—averaging $1.7 million a year for the 33 years preceding 1940 (*4*). When DDT (dichlorodiphenyltrichloroethane) became available in the late 1940's, it served as a powerful weapon against the insect (*5*); but its use was phased out after 1958, and the pest has spread rapidly as far south as Virginia. Widely scattered finds of the insect have been made recently in North and South Carolina, Alabama, Florida, Ohio, and Wisconsin.

The Moth and Its Threat to the Environment

The gypsy moth has one generation a year. In the Northeast the larvae or caterpillars emerge from overwintering eggs in late April or early May (usually over a period of 2 to 4 weeks) and begin to feed on suitable hosts. Although oak, willow, poplar, speckled alder, basswood, gray birch, river birch, and apple are favored, many other trees and ornamentals are attacked, including evergreens. Many young caterpillars spin down on silken threads that break off and act as sails (*6*), allowing the wind to carry the tiny insects off, usually for a few hundred meters but sometimes for more than 40 kilometers away (*7*), where they may start new infestations. The caterpillars feed voraciously on leaves, normally passing through five and six instars (molts) for the males and females, respectively, and attaining a length of 4 to 7 centimeters. In late June or early July they change to the pupal stage, usually for 10 to 14 days. The brown adult male moths, which start emerging from pupation before the females, are strong fliers and are capable of mating several times. The off-white female, with its abdomen filled with eggs, does not fly. To lure the male for mating, she releases a sex attractant, which the male detects with great sensitivity; he then flies upwind to find the female (*8*). The female normally mates once, and then lays from 100 to 800 eggs in a buff-colored, hair-covered mass, from which the larvae merge the following spring. Adult moths do not feed and they live only a short time after mating. Damage by the insect is thus limited to the larval stage.

The efficient means by which the sexes find one another for mating and propagation, the large number of eggs laid, and the voracious appetite of the larvae account for the explosive population buildups of this insect and the great harm it does. A single 5-cm caterpillar eats about 0.1 square meter (1 square foot) of leaf surface a day (*9*). A single defoliation has been known to kill white pine, spruce, and hemlock (*10*). Two successive defoliations can kill most hardwoods (*10*). As an example, 3 years after the use of sprays was banned in the Morristown (New Jersey) National Historical Park in 1967, a survey showed that one-third of the park's oak trees, average age 100 years, had been killed by gypsy moth defoliation (*9, 11*). With oak forming the natural ground cover of much of the Northeast, the ecological implications are inescapable.

In 1970, this pest defoliated 800,000 acres of forest. In 1971 this figure rose to 1.9 million acres (1 acre is equivalent to 0.4 hectare). Although noncommercial forests and parks have suffered most, commercial forests of the Appalachian and Ozark mountain ranges and of the South are now threatened.

Cities and towns are not spared. The complaint of one resident of Shirley, New York, was quoted in the *New York Times* (*12*): "Our children cannot go out. Our pools are finished for the summer. It's a question of survival —the caterpillars or us."

Current Control Measures

Intensive efforts have been made in the past to solve the gypsy moth problem by the use of natural biological agents, and many species of parasites and predators have been imported and released for this purpose (*13*). Native parasites and predators also attack the pest at various stages. Vertebrates feeding on it include white-footed mice, cuckoos, blackbirds, and grackles. Among the invertebrates *Calosoma* beetles kill the caterpillars and a chalcid wasp, *Ooencyrtus kuwanai*, parasitizes the eggs.

Attempts are being made to develop means of using a virus causing "wilt disease" in the larvae to suppress populations (*14*). Also, a strain of *Streptococcus faecalis* and a commercially available bacterial insecticide, *Bacillus thuringiensis*, are being investigated for control (*15*).

Carbaryl (Sevin), the insecticide now most frequently used against the gypsy moth, is applied at the rate of 1 pound (0.45 kilogram) of active material per acre to prevent large infestations from killing trees. Egg counts are made before the insecticide is applied to determine if the population density is sufficient to cause defoliation (*16*). The cost of effective treatment with insecticide averages $3 to $5 per acre for a season, and the time at which the insecticide is applied is critical.

The foregoing measures are meant to minimize the damage caused by the moth rather than to eliminate it, and none is considered capable of doing more than slowing the moths' rate of spread. With the insecticides now available there is little hope of our preventing the spread of the pest throughout its potential range, which may include western forests.

Left to its own devices, the gypsy moth would probably continue to spread at its rather slow natural rate. In recent years vastly increased trade and traffic have enhanced greatly the chances of artificial spread of the moth, particularly because egg masses or pupae can pass undetected on mobile homes and camping trailers. Federal-state quarantine measures have been able to minimize artificial spread, but they have been ineffective in preventing local natural movement.

Authorities face two immediate problems in combating the moth. One is to prevent excessive damage in areas of severe infestation (defoliation of commercial forests and highly valued shade trees and harassment of residents by the caterpillars). Present plans call for an integrated approach involving various combinations of the control methods cited. These plans include more extensive use of traps baited with the sex attractant to detect new infestations and to assess moth abundance in known infestations. The number of moths trapped can be used to signal the need for application of pesticides and other control measures; the use of pesticides can then be made more efficient and restricted to those areas where treatment appears necessary, thus minimizing pollution from this source.

The other problem, more pressing at the moment, is to prevent further spread of the pest by finding and eliminating light or incipient populations beyond the areas now generally infested.

Now that the highly potent sex attractant pheromone of the gypsy moth, *cis*-7,8-epoxy-2-methyloctadecane or disparlure (*2*), is available in ample quantities, means of using it to prevent spread of the pest are being intensively investigated. Because action of disparlure is very highly specific to the gypsy moth and it is effective in very low concentrations, its use is expected to pose no hazards to people and to be ecologically acceptable from all standpoints.

Disparlure in Detection and Survey

The isolation, identification, and synthesis of disparlure culminated a search for this attractant pheromone that started at Harvard University in the 1920's (*17*) and was taken up by the U.S. Department of Agriculture (USDA) in 1940 (*18*). As a crude extract of the last two abdominal segments of the female (called a tip), the sex lure was used in traps to detect moth infestations since the 1940's (*19, 20*). Female pupae were laboriously collected in the field and the tips clipped into benzene 24 hours after the females emerged. The tips were extracted with benzene, the solution concentrated, and the extract hydrogenated to stabilize the lure (*18, 21*). Survey traps were baited with extract equivalent to ten tips.

In 1960, the sex attractant of the gypsy moth was reported to be 10-acetoxy-7-hexadecen-1-ol (called gyptol) (*22*); a homolog called gyplure (12-acetoxy-9-octadecen-1-ol) was also reported to be active (*23*). Both compounds were later found to be inactive (*24*), and use of the natural extract of the moth was resumed.

Collections of tips frequently had to be made in distant countries (Spain, Yugoslavia, French Morocco) because moth populations available in the United States, especially when DDT was used extensively, were often low or uncertain. Costs of collections to bait the 60,000 survey traps used by USDA and the states were about $25,000 a year. Bioassay and chemical analysis indicated that the last extract of tips collected for the USDA in Spain in 1969 contained the equivalent of about 0.2 nanogram of sex pheromone per tip.

Table 1. Numbers of insects captured with attractant aged 1, 6, and 12 weeks (*25*).

Amount of attractant per trap (μg)	Approximate age of attractant (weeks) 1	6	12
*Natural extract**			
	11	6	0
Disparlure†			
1.0	127	146	138
0.1	155	109	126
0.01	88	90	40
0.001	69	20	7

* Equivalent to ten tips per trap, the amount used in standard survey traps. † Trioctanoin, 5 mg, added as keeper in each trap.

In 1969, the sex pheromone of the gypsy moth was identified and synthesized (*2*). One of our first preparations of disparlure was a 30-gram lot. At the rate the USDA had been using attractant to bait its traps, this amount was enough for the next 50,000 years. The eventual cost of disparlure is estimated at 30¢ per gram.

With a synthetic lure readily available, survey traps are now being baited with 100 micrograms of disparlure to increase detection efficiency. This tiny quantity is about 50,000 times the amount of lure present in traps baited with the extract of insects collected in Spain in 1969. But the greater amount of lure used is only part of the story. Disparlure is formulated with "keepers," which are volatile or nonvolatile diluents, to regulate its volatilization (*25*) and thereby prolong the action of the lure. A variety of these compounds were tested, and the best (trioctanoin) was used in the traps. Typical data, given in Table 1, show the great superiority of the disparlure-trioctanoin combination over the natural moth extract in both intensity of attraction and persistence (*25*). In 1970, baited traps were set out in mid-April, early June, and mid-July, that is, 12, 6, and approximately 1 week, respectively, before the flight of the moth. In this way aged and fresh materials were compared simultaneously under identical conditions. Traps containing 1.0 and 0.1 μg of disparlure at the three different ages were so effective they were actually saturated with moths in the moderately infested test area because of the low trap capacity (about 20 moths maximum). Traps with as little as 1 ng of disparlure plus 5 milligrams of keeper still caught moths after being exposed for 12 weeks in the field.

The Animal and Plant Health Service of the USDA and the cooperating state agencies currently use a weather-resistant cylindrical cardboard trap 5 cm in diameter and 10 cm long with clear plastic ends having 2.5-cm openings. Males responding to the disparlure (on a cotton wick) enter the traps and get stuck on a gummy material within. In intensive surveys the traps are placed at ⅞-mile (1.4-kilometer) intervals in lines about 1 mile apart (1.6 kilometers). The spacing of survey traps that will provide assurance of detecting new infestations at the lowest practicable level has not yet been determined with the new lure.

In the 1970 survey, hundreds of traps baited with 1 to 10 μg of disparlure were interspersed among thousands of traps baited with the natural extract; reports from the states in which the traps were used showed that captures per trap with disparlure were 9- to 37-fold greater than those with the natural lure.

In 1971, survey traps baited with 20 μg of disparlure plus keeper were used for an entire season for the first time. The fact that gypsy moths were found in many outlying areas where they had never been found before is no doubt due in part to the high degree of efficiency of the new lure. Furthermore, about $50,000 a year was saved because the new traps, unlike the old ones, did not require rebaiting in midseason.

The high potency of the lure and its exceptional persistence greatly exceeded our expectations, and the use of disparlure as a control measure began to appear feasible.

Disparlure for Control

The major objective in the proposed use of the sex pheromone is to prevent male moths from finding females and mating, thereby preventing their propagation. The proposed techniques are regarded as suitable only for light incipient populations, such as those now being found in areas where the moth has recently spread in the mid-Atlantic, southern, and midwestern areas of the United States. If high populations can be suppressed by other means, the attractant can then be employed to maintain suppression or to eliminate infestations.

To exercise control, the pheromone must disrupt communication between the sexes. Toward this end two methods are under investigation. One method consists of luring males to their destruction in some simple but suitable trapping device, and the other consists of "confusing" males with pheromone vapors dispensed into the atmosphere.

The information needed for the traps to be used effectively includes (i) an assessment of the attractant power of the pheromone in traps as opposed to the attractant power of the competing virgin females in the natural populations; (ii) the number and distribution of traps required relative to the number and distribution of gypsy moths in the population to be controlled; and (iii) the growth rate of gypsy moth populations, which determines the degree of control required to reduce their numbers.

To apply the confusion method, it will be necessary to provide a sufficiently high vapor concentration to prevent normal responses or proper orientation of males to the pheromone produced by the females. As with traps, the degree of mating inhibition required to achieve suppression of populations will depend on the insects' normal potential for increase in the absence of control.

An understanding of the dynamics of an insect population is basic to the development of suitable strategies for its control, regardless of the methods employed. Such understanding is particularly important in the use of the sex pheromone as a means of control.

The gypsy moth may spread by two means. Young larvae can become airborne and drift for some miles before settling on host plants in a new site (*7*), and the insect can be carried to new sites by the movement of egg masses or other immature stages on vehicles or timber, or by other means of transport (*9*). Adults of the larvae spread by air can be expected to be scattered downwind in a somewhat random fashion. The males must then locate the scattered individual females, and the nonflying mated females will each deposit a cluster of eggs. Therefore, beginning in year 2, the larvae and subsequent adults will tend to exist in colonies. Insects emerging from individual egg masses transported to uninfested areas will similarly tend to exist in such colonies.

The rate of growth of gypsy moth populations has been a subject of study by entomologists for some years. While each female is capable of depositing several hundred eggs, insect mortality is naturally high, and few of the potential progeny survive to mate. In one study, there was a 6.4-fold average increase in the population per generation (*26*); in another study there was a 7.5-fold increase (*27*). Although the rates of population increase can be expected to vary from place to place and from year to year, they are likely to be higher in low-density populations than in moderate- to high-density populations because of the suppression forces that are dependent on population density. Some segments of a population may increase at a higher-than-average rate, while the rate of increase of other segments may be less than average. From the standpoint of developing effective control methods, it seems prudent to assume rates somewhat higher than average to ensure that the suppressive measures used will be sufficiently effective to achieve near-maximum results. Therefore, we propose a tenfold rate of increase as being a reasonable growth rate for incipient gypsy moth populations in favorable environments.

With this rate of increase per generation (or year), we would expect a population to grow as shown in Table 2, until it reaches a density that will be adversely affected by normal density-dependent suppression forces. The projected rate of increase would lead to substantial defoliation in localized areas by year 6 or year 7. Thus, to avoid damage, a population has to be suppressed at an earlier period in its growth.

If the tenfold growth rate were realistic, the reproductive capability of 90 percent of an incipient population would have to be nullified each year merely to keep the population from increasing. The reproductive potential of each generation would have to be reduced more than 90 percent if elimination were to be achieved.

Early detection of new gypsy moth infestations is vital to the successful use of the attractant to suppress or eradicate new infestations. Studies are required to correlate the data obtained from trapping with the size of incipient populations. The assessment of population sizes in absolute numbers will be vitally important in estimating the number of pheromone traps required to achieve suppression or elimination.

Mass Trapping to Eliminate Gypsy Moth Populations

The principles of insect suppression through the use of sex pheromone traps were developed by Knipling and McGuire (*28*) who used models of postulated insect populations. The validity of these principles was confirmed by recent field-trapping studies on the boll weevil (*29*) and the red-banded leaf roller (*30*).

The parameters that influence the absolute efficiency of such traps in practical control are many. Because of the continuous release of the synthetic pheromone from traps as opposed to the intermittent release of the pheromone by the females, the traps should be considerably more efficient than the females in attracting males. The efficiency of trapping could, however, be limited in large-scale trapping programs where the traps are distributed at random over large areas while concentrations of males and females are emerging from colonies. The dispersal of adult males, following emergence and before they seek females, could minimize this effect. Although it is not possible to give accurate estimates of the effects of all the parameters on the efficiency of a trapping system, it is possible to estimate with reasonable confidence the general magnitude of the results that would be expected from the use of various ratios of traps to competing females.

In the calculations that follow we will assume that each trap is as attractive as a single unmated female. This assumption is probably conservative for the gypsy moth. Thus, Fig. 1 shows that disparlure-baited traps containing from 1 to 6 μg of the pheromone in 5 mg of trioctanoin caught approximately the same numbers of males as did traps baited with single virgin females (*31*). Because the use of 100 to 500 μg of disparlure in each trap is contemplated, the attractant power of a trap should be substantially greater than that of an unmated female.

The height of the traps relative to the height at which virgin females emerge could influence the competitiveness of the traps. Traps dispersed by air are apt to drop to ground level. Since the numbers of males captured by traps placed at 0, 3, 6, and 12 feet (1 foot is equivalent to 0.3 meter) above ground were 27, 22, 34, and 16, respectively (*20*), traps on the ground can be expected to be effective in capturing male moths. However, some means of suspending traps at different heights above ground could assure greater competition with females in the environment and a greater reduction of the moth population.

The results of the studies shown in Table 1 indicate that the traps will probably retain their attractant power throughout the emergence and mating period of the moths.

The longevity of females is an important consideration in male annihilation techniques. If females are unable to mate on a given day because males are absent, they may survive to the next day and be successful in luring a male. The longer the time that mating can be prevented, the more likely it becomes that the females will die before they can mate and deposit fertile eggs. A natural mortality rate of 25 percent of the unmated female population each day has been assumed in population suppression models for other insects (*28*). This figure seems reasonable for the gypsy moth since the average life expectancy of unmated females is less than 1 week (*3*). With a mortality rate of 25 percent per day, an uncontrolled insect population will stabilize at a level approximately four times the daily emergence rate (*28*). If a high percentage of females cannot mate each day because the males have been captured in traps, there will be a gradual accumulation of unmated females, and the ratio of traps to unmated females will decline steadily until the unmated female population stabilizes. The shifting ratio of traps to competing females must be taken into account and allowances made in estimating the number of traps needed for various natural population densities.

Traps suitable for a mass-trapping program of the gypsy moth can be of simple design and can be produced at low cost. Because their usefulness will probably be limited to low populations, trapping devices large enough to hold two or three males should be adequate. The cost of such traps, including pheromone and adhesive to snare the moths, is estimated at 2¢ each. The cost of distributing traps in wooded areas will probably be considerable, but should be no higher than that of applying pesticide sprays. (Studies to improve the efficiency of available trap designs and distribution systems are under way.)

Utilizing the various elements discussed, we will develop population models to indicate the effects of mass trapping on incipient populations of

Table 2. Rate of increase per generation (or per year) in a population of gypsy moths in a favorable environment. A tenfold rate of increase per year is assumed, as is the presence of a single mated pair in year 1.

Successive years	Number of adults in population
1	2
2	20
3	200
4	2,000
5	20,000
6	200,000

the gypsy moth. Starting with a hypothetical population 3 years after its origin from ten single isolated egg masses distributed over a 10-square-mile area (1 square mile is equivalent to 259 hectares), we can expect 100 males and 100 females at each location. Although the total population of 1000 males and 1000 females would normally be expected to emerge over a period of several weeks, we will further simplify the model by assuming that emergence occurs during a 10-day season. This stipulation will make the expected results more conservative since a given number of traps competing with the same number of insects emerging over a period of 20 days would be essentially twice as effective in preventing mating because half as many insects per day would emerge. This model could be representative of small established colonies; for a population originating from larvae airborne

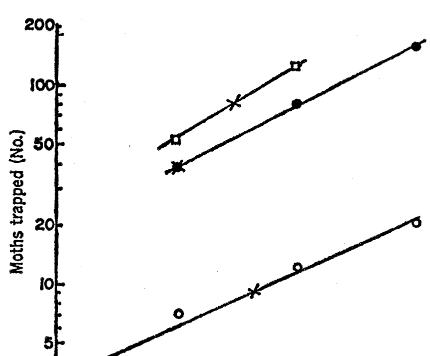

Fig. 1. Numbers of released moths captured in traps baited with live virgin females (crosses) compared with the numbers captured in traps baited with several concentrations of disparlure in three simulated field tests (data of different tests designated by squares and by closed and open circles). One female moth is equivalent to 1 to 6 μg of disparlure in 5 mg of trioctanoin (*31*).

from a heavily infested area, the model would be similar except that the insects would tend to be randomly distributed throughout the 10-square-mile area. Although the distribution of traps in relation to the distribution of unmated females can be expected to influence the efficiency of the traps, the theoretical effect of traps will be calculated without regard to this spatial factor.

A total of 5000 traps in the 10 square miles (500 traps per square mile) will be provided to compete with the 1000 unmated females in the area, and we will make the following assumptions: (i) The insects emerge at the rate of 100 males and 100 females per day. (ii) Each trap is equal to a virgin female in attractant power. (If the traps are more competitive, for example, three to five times as competitive as females, the number of traps required could, of course, be reduced.) (iii) The mortality factor is 25 percent per day for both the males and females. (iv) Females mate once and then are no longer attractive to the males. (v) The males can mate once per day on each day during their lifetime. (vi) Unmated females, as well as the traps, are attractive continuously during the mating period. (Since the "calling period" of the female is not continuous, this would be another conservative assumption that could compensate for unknown factors that might make expectations too liberal.)

The calculated effects of the hypothetical trapping program are shown in Table 3. The ratio of traps to unmated females starts at 50 : 1. Because the unmated females accumulate while trap density remains constant, the ratio of traps to unmated females drops to about 14 : 1 by day 10. With this ratio, the degree of mating inhibition is still theoretically 93 percent, which is adequate for the suppression of a population having a net potential increase rate of 10.

In an uncontrolled population the degree of mating success is assumed to be 100 percent, so that 1000 females mate. In the controlled population the total number of females expected to mate is 54. Therefore the overall suppression due to the capture of males is 94.6 percent, or approximately 95 percent.

If the level of suppression is 95 percent (the figure is rounded to simplify calculations) and there is a tenfold net increase in the population, during the following year one would expect the population to decline by one half. With

Table 3. A model showing the theoretical effects of traps baited with disparlure being used to intercept males before they can mate with females in an incipient population. The number of females mating in an uncontrolled population would be 1000; the total number of females mating in the controlled population is 54. Thus mating is controlled by 94.6 percent (*32*).

Day	No. of traps	Unmated females	Males	Ratio of traps to unmated females	Males captured (No.)	Matings (No.)	Unmated females remaining	Daily suppression (%)
1	5000	100	100	50:1	98	2	98	98
2	5000	174	102	28.7:1	99	3	171	97
3	5000	228	102	21.9:1	98	4	224	96
4	5000	268	103	18.7:1	98	5	263	95
5	5000	297	104	16.8:1	98	6	291	94
6	5000	318	105	15.7:1	99	6	312	94
7	5000	334	105	15:1	98	7	327	93
8	5000	345	105	14.5:1	99	7	338	93
9	5000	354	105	14.1:1	99	7	347	93
10	5000	360	105	13.9:1	99	7	353	93

the same number of traps and an emerging population of only half the original number per day, a theoretical ratio (traps to unmated females) of 99 : 1 would be achieved initially, and the overall reduction in mating would be 97.5 percent in year 2. In year 3 the population should be reduced an additional 75 percent to give an emergence rate of about 12 moths of each sex per day. Again, with the same number of traps, the initial ratio of traps to virgin females would rise to about 400 : 1, and the population should be practically eliminated during year 3.

The increasing efficiency that is characteristic of the pheromone trapping system as the population declines is analogous to the effects obtained when sterile insects are released for insect control (*33*).

For the model shown in Table 3 we used an isolated population and did not take into account the larvae that would continue to invade trapped areas adjacent to existing high populations. In actual suppressive programs conducted in areas adjacent to high populations, at least 5000 traps per square mile would probably be employed. The extra traps (ten times the number in the hypothetical model) would be expected to provide adequate compensation for larval incursion, localized concentrations of emerging females, and unknown factors not taken into account in the model.

The use of biodegradable traps and innocuous adhesives should pose no hazards to people or to animals, although the presence of large numbers of such traps in populated areas may be objectionable from an esthetic standpoint. Preliminary toxicological tests indicate that disparlure has very low mammalian toxicity.

New finds of the moth or of egg masses well outside the generally infested area would also have to be dealt with. The placement of traps by hand or aircraft drops in and around the areas of such finds should be a simple and inexpensive means of preventing the moth from becoming established.

Monitoring Results of Trapping with Pheromone

A major problem in the control or elimination of pests is the assessment of the results obtained by the suppression efforts. This is particularly true when pest populations are low, and the methods used for detecting the pest are not very efficient. Fortunately, disparlure provides an excellent means of detecting the gypsy moth. Nevertheless, when widely scattered incipient populations occur and efforts are made to eliminate or keep the populations suppressed, measurements of the effects of such containment programs are generally uncertain or unreliable.

Pheromone traps used for suppression have a built-in system for monitoring the results of their use. This aspect is worthy of discussion because the data obtained by trapping relative to the degree of control of the moth can readily be misinterpreted. In contrast to the conclusion that most people would come to, the greater the number of moths caught per trap, the more unsuccessful will be the control system. The validity of the foregoing statement can be illustrated with some simple hypothetical examples.

If 100 traps, each equal in attraction to a female, were in operation in an area having 1000 males and 1000 unmated females on a given day, one would expect the traps to capture 1/11 or 91 of the males, which amounts to 0.91 male per trap. The females would attract 10/11 of the males and 909 matings would result. When the average rate of capture per trap per day approached (or exceeded) one, as in the example given, at least 90 percent of the females would be expected to mate, and no significant suppression could be expected.

If the moths that were captured were well distributed and on a given day 100 traps captured 0.1 male per trap, we could, by applying the same reasoning, calculate that approximately 90 percent of the males were captured and that 10 males (and consequently 10 females) were in the area. This may be considered satisfactory control, but it is hardly enough to accomplish suppression.

With only occasional moths being taken in a large number of traps and the captured moths being well distributed, the degree of control should be high. For example, an average capture rate of 0.01 male per trap per day would suggest a reduction in mating of approximately 99 percent, enough to effectively suppress populations of low density.

In the foregoing discussion we emphasize the need for monitoring a high proportion of traps to ascertain the progress of suppression programs, especially when capture rates are low. The capture of large numbers of moths per trap indicates that the number of competing females must also be high, and we cannot expect control to be effective. Should the trap be made equivalent in attraction to many females, then somewhat higher average rates of capture could still be consistent with a high degree of control. The attraction of traps baited with pheromone has not yet exceeded by more than several times the attraction of competing unmated insects.

"Confusion" Method

If the atmosphere is permeated with disparlure, or if many individual sources of the chemical are distributed in an area, the ability of male moths to locate females in that area is greatly impeded, presumably because the synthetic sex odor is everywhere and is indistinguishable from the natural female scent. Furthermore, the odor reception system of the males may become saturated or habituated and thereby insensitive or less sensitive to the attractant as a result of continuous exposure to it. The so-called "confusion" method, originally suggested in 1960 (*34*), has shown promise in small trials with some insect species (*35*), but has not yet been fully investigated for any insect. The mechanism of action in confusing the males and the influence of population density on effectiveness of the method have not been established.

In 1971 two tests of the confusion method were conducted with laboratory-reared gypsy moths before the mating flight. The results were encouraging (*36*). In the more pertinent test, pieces of disparlure-treated paper measuring 0.06 square inch (0.4 square centimeter) were uniformly distributed by aircraft over 40-acre plots; about 5000 pieces of paper were used per acre, containing in all less than one drop (20 mg) of disparlure per acre. This would represent about 3.2 million pieces of treated paper and about 12.8 grams of the attractant per square mile. Males released periodically in these plots were unable to find special traps containing unmated females or disparlure (about one trap per acre) for 6 days. In contrast, males were captured by such traps in untreated plots. During the next release of males, 21 days after dropping the disparlure-treated papers, some males were captured by the traps containing females or disparlure within the treated area; however, the number caught was still two-thirds less than the number captured in the untreated plots.

If we assume that the receptors of the males were not adversely affected by the pheromone and that the males continued to search for females, the presence of the artificial sources of pheromone can be regarded as a "numerical confusion" method. We believe that during the first 6 days of the test, each treated piece of paper had a great amount of attractant power, and in view of the many sources of the attractant (5000 papers per acre) from which the lure emanated, the males were repeatedly diverted from the few females (one per acre) or the disparlure-baited traps (also one per acre). By the 21st day the attraction of the treated papers apparently had declined sufficiently to allow some males to locate traps containing females or disparlure.

If the many sources of the synthetic attractant confused the males because of numerical superiority, we would expect this technique to be more effective against low than against high populations. If the average population per square mile is as low as 100 of each sex and if there are 1 million artificial sources of the attractant, each fully competitive with a female, the initial ratio of attraction would be 10,000 : 1. If the average population is 1000 males and 1000 females, the ratio would drop to 1000 : 1. With a population of 10,000 of each sex, the ratio would drop to 100 : 1. If we assume that the males respond to the pheromone sources, the efficiency of the technique will depend largely on the average number of responses that the males will make in their lifetimes. When first released in the presence of the lure, males become highly excited, a condition that is likely to hasten their demise. Also, continuous exposure to the pheromone does appear to dull their response.

Although we have much to learn about the mechanism and efficiency of the confusion method, we are encouraged in this new approach by the finding that mating was inhibited for 6 days with a released insect population corresponding to 1000 per square mile, and that some inhibiting action persisted for 21 days. Two key questions are: How many sources of the lure and what amount of the artificial attractant will be required? How can the confusion effect be prolonged to encompass the entire duration of the mating flight? Although the main mating flight usually lasts 10 to 14 days, some insects appear before and after this period. We estimate that the confusion period should continue for 4 to 5 weeks, provided the sources of the lure are distributed to coincide with the start of moth flight. This time is indefinite and varies from year to year depending upon local climatic conditions. It is therefore important to achieve maximum persistence of the attractant so that applications can be made well in advance of the beginning of adult emergence.

Persistence of the lure can be increased by starting with much larger amounts (for example, 1 gram per acre), by multiple applications, and by improved formulations. It might be possible to include microencapsulated lure, various chemical diluents (keepers), additives to employ chemical stability, or to use lure carriers other than paper. Chemical analyses and laboratory bioassays of various formulations, aged or exposed under simulated conditions (rain, weathering), are being made to select the most persistent formulations for field testing.

Lure-treated papers falling on trees eventually drop to the forest floor, undoubtedly aided by wind and rain. Disparlure, known to be vulnerable to acid, may be degraded by contact with the usually acid forest floor. The effectiveness of papers falling in low spots or under forest debris is also diminished because the heavy attractant vapors have little tendency to rise and spread. Means of suspending the lure in the trees (for example, disparlure on strings or mixed with a sticker) are therefore needed to improve both the stability of the lure and effectiveness of the confusion method.

If, in the final stage of finding a female, males become oriented with the aid of sight, as suggested by Doane (*37*), visual factors could also influence the effectiveness of the confusion method. The likelihood of males coming within visual range of females would be increased at high population densities. However, it seems reasonable to assume that at low densities, vision alone would not be a major detection mechanism for the gypsy moth. The existence of a very powerful pheromone in this species lends credence to this probability.

While we believe that the practical application of the confusion technique, when perfected, will probably be limited to low populations, we must not overlook the possibility of using pheromones to block vital physiological or behavioral processes in insects through fatigue or other mechanisms. Such effects, if they could be achieved and sustained, would probably be independent of density of the natural population.

The confusion method, even if substantial amounts of disparlure are required, should be much less costly to apply than insecticides and, because of the lure's highly selective action, should avoid the hazards often associated with the use of broad-spectrum insecticides. As much as 5 grams of lure per acre at a cost of approximately 30¢ per gram would still be within the cost range of insecticides now required for effective control.

Discussion

Scientists engaged in research on the use of sex pheromones for insect control are fully aware that much more information than is now available is needed before the best techniques for their use can be formulated. However, research—basic, applied, and theoretical—on the synthetic pheromone of the gypsy moth has advanced to the stage that federal and state agencies are prepared to undertake pilot experiments designed to test the feasibility of suppressing or preventing the spread of this pest (*38*). Because it appears that the effectiveness of disparlure will be governed by the density of the gypsy moth populations, it seems doubtful that disparlure alone will be of benefit where the pest is already causing damage of economic proportions. Yet there are millions of acres of forest and shade trees south and west of the currently infested areas where the pest has not yet become established. There is no reason to assume that the pest cannot and will not spread to forested environments in virtually all parts of the nation and create the same havoc in many other areas as is now experienced in the Northeast unless appropriate countermeasures are applied.

There is good reason to hope that it will be possible and practical to develop a pheromone technology for containing the spread of the gypsy moth. Populations of the insect in advance of the currently infested areas are still generally scattered and are of low densities. The attractant provides an excellent method of early detection, even though the vastness of the area to which the pest might spread makes early detection a difficult and costly program. Isolated infestations can be expected to consist of very few insects, the number of insects in a single incipient infestation being unlikely to exceed 2000 within 4 years of its origin. Infestations of this size, if well delineated, would be well within the range that can be suppressed by pheromone traps or possibly by the confusion system. A critical requirement will be the detection of infestations as soon as possible and the delineation of their exact location by intensive trapping so that the pheromone can be used with maximum effect and efficiency.

If we include the year of initial spread by larval drift, there should be a period of about 3 years during which individual foci of infestations do not consist of more than 200 adult insects. However, in an area that might be 50 miles in advance of well-established populations, there could be hundreds or even thousands of such small incipient populations. Within a year or two the same situation might exist in other areas 25 to 50 miles still further west or south. On the other hand, if pheromone traps or some other system of pheromone utilization were put into operation where natural larval spread had not yet occurred, and if spread by other means was still minimal, the pheromone would have to compete only with scattered moths or with small colonies of perhaps 20 insects each. Under such circumstances as few as 100 traps per square mile might be adequate to prevent the establishment of the pest, although at least 1000 traps per square mile would be contemplated in actual practice. Thus, the advantage of early protective action in the form of a pheromone-treated barrier is readily apparent. In areas closer to the general infestation where small incipient populations might have existed for 1 or 2 years, 500 or more traps per square mile might be adequate, but at least 5000 traps per square mile should be employed. The cost of such a protective barrier should not be prohibitive; present estimates are $100 for 5000 traps and $100 for dispersing them. Thus chances seem good that the immediate spread of the pest into new areas could be largely halted for $200 per square mile. The cost of chemical control would probably be in the order of $2000 per square mile, and it is doubtful that presently available chemicals could halt spread of the moth.

The possibility of traps being used to eliminate incipient populations already existing immediately in advance of the generally infested areas should not be discounted. If the cost of traps and their distribution is as low as anticipated, their use could be less costly than chemical control even if they were distributed at a rate as high as 25,000 per square mile. The cost of this number at 2¢ each would be $500 per square mile, and the cost of application might not be much higher than that of applying fewer traps. Large numbers of traps are likely to overwhelm incipient populations even in the 3rd or 4th year of their becoming established. Furthermore, where localized populations are too high to yield to this suppression, the traps might prevent a general buildup of the insect throughout the area, and populations too high to be controlled in this manner might be delineated and dealt with by other means. Moreover, the existence of a barrier of densely distributed traps should make the more lightly treated protective barrier ahead of it more effective.

The use of the pheromone to halt or delay the unrelenting spread of the moth would give us time to explore other ecologically acceptable ways to cope with the higher populations found in established infestations. There would also be time to perfect techniques for mass rearing and release of sterile male moths to control small isolated infestations, especially in heavily populated urban centers and much-used recreational areas where large numbers of traps might be considered objectionable. The sterile male technique should prove complementary to the use of pheromone traps, which could be particularly effective in suppressing moths in more extensive rural areas. As with the pheromone, population suppression by the release of sterile males would be effective chiefly against low-density moth populations or higher populations that could be reduced to low levels by other means.

The containment of the gypsy moth, if proved feasible by the methods proposed, will be a major undertaking and the cost will be high, probably amounting to several million dollars each year. However, such costs would have to be balanced against the tens of millions of dollars in annual losses of our timber resources that seem inevitable if the pest is allowed to spread unchecked. The esthetic values of our forests and shade trees must also be taken into account.

There is the tendency today for some ecologists to oppose any pest suppressive measures on the assumption that the measures employed, or even the elimination of the pest itself, will upset the ecology of the area under treatment; often no distinction between native and alien pests is made. In response to such views, we note that should containment be achieved by the use of the pheromone disparlure, supplemented by the use of sterile moths in special areas, implementation of such measures should be without hazard and be completely acceptable from an ecological standpoint. In contrast, even without economic considerations, there is reason for us to have grave concern over the harmful ecological effects of the gypsy moth if this alien pest is left to spread to the limits of its range and become a permanent resident throughout the forest ecosystems of the country.

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The following equation summarizes the calculations:
$$M_n = \frac{[m + SM_{n-1}] \cdot [f + S(F_{n-1} - M_{n-1})]}{T + [f + S(F_{n-1} - M_{n-1})]}$$
where M_n is the number of matings on day n, m is the number of males, and f is the number of females emerging each day; F_n is the number of unmated females on day n [or $F_n = f + S(F_{n-1} - M_{n-1})$], D is the number of days in the mating season, S is the survival rate per day, and T is the number of traps. Thus $\int_1^D M_n$ gives the total number of matings in the controlled population, and fD is the number of matings in the uncontrolled population.
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Social Institutions and Nuclear Energy

Alvin M. Weinberg

Fifty-two years have passed since Ernest Rutherford observed the nuclear disintegration of nitrogen when it was bombarded with alpha particles. This was the beginning of modern nuclear physics. In its wake came speculation as to the possibility of releasing nuclear energy on a large scale: By 1921 Rutherford was saying "The race may date its development from the day of the discovery of a method of utilizing atomic energy" (*1*).

Despite the advances in nuclear physics beginning with the discovery of the neutron by Chadwick in 1932 and Cockcroft and Walton's method for electrically accelerating charged particles, Rutherford later became a pessimist about nuclear energy. Addressing the British Association for the Advancement of Science in 1933, he said: "We cannot control atomic energy to an extent which would be of any value commercially, and I believe we are not likely ever to be able to do so" (*2*). Yet Rutherford did recognize the great significance of the neutron in this connection. In 1936, after Fermi's remarkable experiments with slow neutrons, Rutherford wrote ". . . the recent discovery of the neutron and the proof of its extraordinary effectiveness in producing transmutations at very low velocities opens up new possibilities, if only a method could be found of producing slow neutrons in quantity with little expenditure of energy" (*3*).

Today the United States is committed to over 100 × 10^6 kilowatts of nuclear power, and the rest of the world to an equal amount. Rather plausible estimates suggest that by 2000 the

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