

ERADICATION AND PEST MANAGEMENT

Judith H. Myers

Departments of Zoology and Plant Science, Centre for Biodiversity Research,
University of British Columbia, Vancouver, British Columbia, Canada, V6T 1Z4;
e-mail: myers@zoology.ubc.ca

Anne Savoie and Ed van Randen

Department of Biological Sciences, Simon Fraser University, Burnaby, British
Columbia, Canada, V5A 1S6

KEY WORDS: screwworm, boll weevil, gypsy moth, Mediterranean fruit fly, codling moth,
fire ant, area-wide management

ABSTRACT

Eradication is the elimination of every single individual of a species from an area to which recolonization is unlikely to occur. Cost-benefit analyses of eradication programs involve biases that tend to underestimate the costs and overestimate the benefits. In this review, we (a) highlight limitations of current cost-benefit analyses, (b) assess eradication strategies from biological and sociological perspectives by discussing particular cases of successful and failed eradication efforts, and (c) briefly contrast eradication and ongoing area-wide control as pest management strategies. Two successful eradication programs involve the screwworm and cattle ticks. Gypsy moth and medfly eradication programs have not been successful, and subsequent captures of insects recur in eradication areas. In situations where heterogeneity of land use patterns make it difficult to prevent reinvasion of the pest, education and area-wide suppression are probably more realistic goals than eradication.

INTRODUCTION

Eradication is the elimination of every individual of a species from a geographic area that is sufficiently isolated to prevent reinvasion (53). Twenty years have

passed since the *Bulletin of the Entomological Society of America* recorded a debate on eradication (23, 36, 53, 60). Subsequently, more eradication programs have been initiated, but perspectives on whether or when eradication is the appropriate goal remain divided. In principle, eradication should be carried out when long-term costs of damage and/or control exceed short-term costs of successful and permanent elimination. However, most of the relevant biological parameters are unknown, and costs and benefits do not affect all people equally. In fact, the biological endpoint of the ability to eliminate a species is only one component of the equation. Eradication is not necessarily more efficient than ongoing lower-level control efforts.

Most eradication efforts are targeted at introduced pests, with the objective of either removing these species from all or part of their new range or preventing their further spread. For insect pests, eradication techniques include release of sterile males, which results in many mated females producing nonviable offspring; spraying with insecticides, including biological insecticides (bacteria, virus, or fungus); use of bait attractants for monitoring or control; and habitat manipulation. In 1989, Dahlsten & Garcia (15) edited a volume that provides an overview of eradication concepts as well as case histories of projects on the Japanese beetle (*Popillia japonica*), the whitefringed beetle (*Graphognathus* spp.), the Dutch elm disease (*Ceratocystis ulmi*), the citrus blackfly (*Aleurocanthus woglumi*), the oriental fruit fly (*Dacus dorsalis*), the citrus canker (*Xanthomonas campestris* pv. *citri*), the imported fire ants (*Solenopsis richteri* and *Solenopsis invicta*), the date palm scale (*Parlatoria blanchardi*), the gypsy moth (*Lymantria dispar*), and the yellow fever mosquito (*Aedes aegypti*). Some of these projects are revisited and updated here.

In this review we (a) highlight limitations of current cost-benefit analyses, (b) assess eradication strategies from biological and sociological perspectives by discussing particular cases of successful and failed eradication efforts, and (c) briefly contrast eradication and ongoing suppression as pest management strategies.

ECONOMIC ANALYSIS OF ERADICATION PROGRAMS

Among the most serious agricultural pests are introduced insects and weeds (18). Following the discovery of an exotic species that has the potential to become a pest, eradication is often prescribed. If eradication is successful, no further expenditure on control will be necessary (16). This is a powerful economic argument. However, it cannot be assumed that after successful eradication, control of other species of pests will not be necessary. For example, winter moth, *Operophtera brumata*, an introduced moth in Canada, is just one of several lepidopterans that attack apple trees. Spray programs for other

caterpillars continue even when biological control of winter moth is successful (62).

A strong justification for attempting eradication of a newly recognized exotic species is the threat of export restrictions on potentially contaminated crops or goods. The first country to discover or report an exotic species may be subjected to restricted trade. The response is to begin a program to eliminate the new pest.

Cost-benefit analyses are used to evaluate potential eradication programs (24, 42). Although the cost-benefit analysis is conceptually simple, conducting a rigorous analysis is extremely difficult because identifying and comparing the costs and benefits of all actions and inactions becomes increasingly unmanageable as the interest groups affected proliferate (44). A proper cost-benefit analysis assumes that: 1. all significant consequences can be enumerated in advance; 2. meaningful cost and benefit judgments can be produced; 3. the often disparate costs and benefits can be compared to one another; 4. people really know how they value different consequences today and how they will value them in the future; and 5. people want to maximize the difference between expected benefits and losses (16, 24, 42, 63).

Benefits from Eradication

The benefit of an eradication program is usually measured as the sum of the losses to individual growers, producers, and marketers that would be averted by the eradication project (16). These benefits are almost always overestimated for the following reasons.

LACK OF SCIENTIFIC DATA In the case of an exotic organism, there is little empirical evidence on which to base the probability of establishment, the potential distribution if it becomes established, or the severity of its impact in the new environment (42). Local extinctions of small isolated populations may be more frequent than originally thought (30, 52a, 66). Therefore, some newly introduced species may become extinct without applied programs. Factors that control the distribution and abundance of species are often not well documented, and therefore the evaluation of the potential impacts of a species in a new habitat must be subjective.

POTENTIALLY BIASED DECISION PROCESS The evaluation of the pest is almost exclusively done by the affected industry and its support services. Often the cost of the proposed eradication program is paid by a government for the benefit of an industry. For example, the spray program to eradicate the Asian form of the gypsy moth from Vancouver, British Columbia, in 1992 was funded by the federal government, but it was rationalized as necessary to prevent the establishment of a forest and urban pest (personal observation). If a forest or agricultural industry is not required to contribute to the program, its members

are more likely to be advocates of eradication. Once eradication attempts begin or quarantine regulations are put in place, the process for discontinuing these procedures is frequently unspecified. The decision-making process is intrinsically biased toward eradication attempts (16).

POTENTIALLY BIASED EVALUATION The economic evaluation of the impact of an exotic species concentrates primarily on the immediate effects on producers. This approach has been criticized by Fischhoff (24) and LeVeen (42). Although a new pest can reduce farm yield, the actual cost to growers and to society will depend on the distribution of the loss among producers. If the pest is relatively widespread, the law of supply and demand can adjust the price of the commodity. How the cost is adjusted to demand depends on the elasticity of the price. In agricultural systems, loss in output can actually increase revenues to producers (42). If the pest does not influence all producers equally, those who manage to grow their crops pest-free will enjoy a large profit. Eradication would not benefit these producers, and they may see a reduced profit if eradication were successful (24). Including the dynamic adjustments of the entire system in the impact analysis can substantially reduce the potential gains of eradication (42).

Costs of Eradication

In contrast to benefits, biases in procedures often underestimate the costs of proposed eradication programs. Too often, only the direct costs such as immediate outlay for personnel, materials, and equipment are included (16), whereas harder to measure probabilistic costs are omitted (63). Some examples follow.

ESCALATING COSTS FOR KILLING THE LAST INDIVIDUALS Eliminating the last 1–10% of the population may demand equal expenditures of time, energy, and money to that required for the first 90–99% and therefore be more expensive per insect killed. Although population reduction can “buy time” by slowing the spread and/or the initial outbreak of an introduced species, each and every female capable of reproducing must be removed for eradication to be complete.

COSTS OF UNANTICIPATED IMPACTS ON OTHER ASPECTS OF SOCIETY Different groups may value potential “pests” in different ways. For example, fire ants may usually be annoying to humans but may also be valued by some growers as predators of plant pests, and pest control personnel may benefit from continued control efforts (29, 69).

COSTS OF MONITORING POPULATIONS AND INITIAL REDUCTION Costs for monitoring may go up when densities have been reduced and/or the costs of reducing populations before the eradication program is initiated, as in a sterile male control program, may be omitted or underestimated. New procedures may be required for monitoring populations at low density.

COSTS OF POTENTIAL REINTRODUCTION The costs of preventing or managing potential reintroductions must be estimated and included in the cost-benefit analysis. Stricter quarantines and other exclusion tactics may have to be implemented to decrease the probability of reintroduction.

COSTS OF PUBLIC RELATIONS The cost of public relations in establishing an eradication program can be substantial, even if producers are not taxed to support the program. Public concern about the use of insecticides, even biologically based insecticides, and about environmental ramifications of eradication must be recognized. Information must be disseminated and consultation carried out in a responsible manner by those agencies proposing the eradication program. This process can be very expensive.

THE COST OF POTENTIAL LAWSUITS The probability of potential lawsuits must be considered in estimating the costs of an eradication program. For example, in California, the State Medfly Project was sued by Santa Clara County and several other cities in both state and federal courts (26). More than 14,000 claims were filed for damage to automobile paint, and the eventual payout for these claims cost the state of California \$3.7 million.

RISKS TO HUMAN HEALTH The risks of the eradication program to human health must be estimated in some way, although this is very difficult. For example, some individuals can suffer health problems just from the stress of being in an area undergoing an aerial spray. This cost is sometimes trivialized by proponents of the program but should be considered of equal importance to other health costs.

COSTS OF HUMAN ERROR The costs of human error in reducing the success of an eradication program must be considered. Although we can never be certain that we have enumerated all of the imaginative ways in which people can make mistakes, an attempt must be made to factor in the costs of errors. A good example of human error is the case of the accidental release of 100,000 fertile medflies in California during the 1980 sterile insect release (SIR) program (46).

Societal costs and benefits must be included by governments and industry in justifying and planning an eradication program, and this process must be open to public scrutiny.

SUCCESSFUL ERADICATION PROGRAMS

Klassen (34) lists 42 species for which eradication has been attempted. Of these, he scores 9 as failures, 10 as examples of some success (gypsy moth is included in this category), and 21 as successes. On this list of successes are

Africanized bees, *Apis mellifera*, and Mediterranean fruit fly, neither of which have proven to be permanently eradicated from North America. A difficulty in evaluating eradication projects is finding the data for critical analysis of the programs that have been declared as successful. Below are some of the better documented examples.

Screwworm

The eradication of the New World screwworm, *Cochliomyia hominivorax*, is a classical study in insect control and involves both the eradication of a species from an area where it was established, and eradication following an introduction to an exotic habitat. Screwworm flies lay eggs in wounds on mammals and cause major economic losses to cattle producers in infested areas. The initial programs to eradicate the screwworm are reviewed in several papers (38, 61a). The eradication of the screwworm was achieved through a sterile insect release (SIR) program. Millions of male flies were reared, sterilized, and released. Females that mated with sterilized males produced unviable young, and this led to a decline in the population.

Between 1958 and 1960, screwworm were eradicated from Florida at a cost of \$11 million. By 1966, the last enzootic population was eliminated from the southeastern United States. There followed a program to push back the edge of the screwworm distribution in Mexico and Central America. Its eradication from the United States and Mexico was reported to have been achieved in 1991 and is estimated to have cost \$750 million (61). Efforts continue to eradicate the screwworm from Central America, with successful eradication from Belize in 1992, from Guatemala in 1993, from El Salvador in 1994, and from Honduras in January 1995. By April 1995, the number of cases of screwworm attack in Nicaragua had dropped to 4% of previous levels (25).

A relatively recent test for the sterile male technique occurred when the New World screwworm was discovered in Libya in 1988. The flies are believed to have entered the country with a shipment of sheep from South America. By August 1990, when the first shipments of sterilized flies were made to Libya from production facilities in Mexico, the screwworm outbreak covered 26,000 km² (41). By February 1991, 28 million sterilized flies per week were being shipped from Mexico and released in Libya, and by May 1991, this number increased to 40 million sterile males per week. The last wound caused by a screwworm was seen in April 1991, and eradication was declared to have been achieved in October 1991 (3, 61). The potential role of weather on the reduction of screwworm populations in Libya was evaluated by Krafur & Lindquist (41). This analysis showed that, while winter temperatures in the highlands were too cold for fly survival, in coastal areas winter temperatures were above

the threshold for fly survival. Simulations indicated that the reduction of fly density and eventual eradication of screwworm could be attributed to the releases of sterile males. This successful eradication program cost approximately \$82 million (3).

A characteristic of the screwworm that may make it susceptible to eradication with the sterile male technique is its association with mammals, which makes its distribution easier to monitor. Although refuge populations can exist among wild mammal populations, major populations are likely to be associated with herds of domesticated animals. Other characteristics that might contribute to successful control are that screwworm flies can be trapped and they are easily reared and sterilized in the laboratory. The distribution, behavior, and genetics of screwworm flies are well characterized. Eradicating a species on the edge of its range may also provide an advantage. The screwworm is primarily a tropical insect and climatic factors may periodically reduce populations on the edges of its range. The screwworm program has shown the potential of the sterile male procedure and has undoubtedly, through its success, influenced other proposed eradication projects.

Citrus Canker

Although this example does not involve an insect pest, the eradication of citrus canker, *X. campestris* pv *citri*, is an important example of a successful eradication program aimed at a non-indigenous pest. First discovered in Florida in 1913, this bacterial pathogen is an obligate parasite of the citrus family with major effects on grapefruit, sweet orange, and lemon. The disease causes direct damage to fruit, and continued exposure to the disease will kill a tree. In areas of the world where the disease is well established, such as Asia, India, and Latin America, control is difficult, and canker is a continual economic concern (1).

The eradication program for citrus canker was initiated in 1914 and lasted until 1943. The program involved the destruction by burning of all infected and suspected hosts. More than 250,000 fruit-bearing trees and 3 million nursery trees were destroyed, and an untold amount of money, inconvenience, and heartache were required to eradicate this disease (1). Undoubtedly, true eradication, where all individuals were destroyed, was accomplished in the southeastern United States (48, 71).

The reasons for success can be attributed to six major factors. First, an aggressive eradication program was initiated within a few years of the introduction of the disease. Second, the pathogen is an obligate parasite and cannot survive for long without host material. Third, the pathogen is unable to move independently and depends on the movement of infected host material by humans. Fourth, the pathogen is an introduced parasite of an introduced crop,

thus both the bacteria and host are isolated from parent populations. Fifth, the pathogen has a very restricted host range and requires specific environmental conditions to infect hosts. Sixth, the eradication program was undertaken by highly motivated individuals, and in many cases the citrus growers themselves carried out the eradication efforts. These conditions made eradication possible (48), but even so, this program required 30 years of persistent effort.

Unfortunately, in 1984, despite strict quarantines, a new strain of the disease was introduced into Florida. Immediately a new series of eradication measures went into effect and 17 million nursery and young orchard trees were destroyed by the end of 1985 (1). Subsequently, the new strain was discovered to be much less virulent than the previous one, and eradication is considered to be unwarranted (48, 67).

This situation demonstrates how eradication may be feasible when an entire population can be managed and an effective control exists. But even with these highly favorable conditions, eradication required 30 years and cost tens of millions of dollars. Whereas quarantine combined with low pest mobility excluded this pest for an extended period, reintroductions remain difficult to prevent. Citrus canker was intercepted 2603 times at US ports of entry between 1973 and 1978, and reintroduction did occur in 1984.

Cattle Tick

Eradication of cattle tick, *Boophilus annulatus*, is a notable example of the successful elimination of an established pest. Ticks infected with protozoan parasites that cause cattle tick fever were introduced into the United States on Spanish cattle during the time of initial colonization by Europeans. However, only in 1889–1890 did scientists firmly establish that certain fever-causing diseases in cattle were transmitted by cattle ticks (34).

In 1906, an eradication campaign began that involved livestock owners, state officials, and US Department of Agriculture (USDA) specialists. The program involved three tactics. First, some pastures were rendered tick-free by excluding all host animals until the ticks had starved to death. The second and more common tactic was to retain the livestock on the infested pastures and to disinfect the animals at regular two-week intervals by immersion in an arsenic solution that killed the engorged female ticks. Third, interstate movement of tick-infested cattle was prohibited through quarantine. The campaign to eradicate cattle ticks from the United States is the most sustained, extensive, coordinated area-wide attack ever made against an arthropod pest. The tick was removed from over a million square kilometers during a period of 34 years. The tick is confined to the lower Rio Grande River in Texas, where reinfestation occurs via animal movement from Mexico. Thus, continual control of fringe populations is required (34).

Tsetse Fly in Nigeria

Tsetse fly, *Glossina palpalis palpalis*, is another example of the local eradication of an insect that attacks mammals, including humans (54). This program integrated the use of traps and insecticide-impregnated targets (7700 cm² blue cloth screens) to initially reduce the populations of flies along rivers and streams. Sterile males were released when the population was reduced sufficiently to achieve a ratio of 10 sterile males to 1 wild male. This release led to the final eradication. The insecticide-treated targets were useful in reducing populations in marginal habitats and helped to prevent reinvasion of areas from which flies had been eradicated. In this situation, the distribution of the flies appeared to be associated with riparian areas, and a combination of techniques was used first to reduce and then to eradicate the flies.

Oriental Fruit Fly in the Okinawa Islands

Another successful eradication project was the removal of oriental fruit flies, *D. dorsalis*, from several of the Okinawa islands (40). This project was based on the attraction of male flies to a lure, methyl eugenol, which was applied with a toxicant to an absorbent material. Five years were required to eliminate the populations on the islands. This project was feasible because an effective lure was available to attract the male flies and isolation greatly reduced immigration to the areas of successful eradication.

Summary of Successes

Klassen (34) summarized some of the factors that are associated with successful eradication (Table 1). Certainly, organisms with restricted distributions either through host or habitat specificity or geographical isolation are more likely to be successfully eradicated. The ability to modify the availability of hosts may be important, as in the examples of citrus canker and cattle ticks. However, many eradication projects have not been successful. Below we consider some

Table 1 Factors that may influence the success of an eradication program (modified from Ref. 34)

-
-
1. Early detection and rapid initiation of an eradication program against an exotic species
 2. Poor adaptation of species to new location (edge of range)
 3. Lack of genetic variability and no development of resistance or behavioral change
 4. Host or habitat specificity
 5. Low reproductive rate and few (one) generation(s) per year
 6. Efficient and inexpensive monitoring techniques for low densities
 7. Powerful suppression methods—sterile male, insecticide baits, effective insecticide
 8. Public conviction that species is of potential economic importance
 9. Effective education program
-

ongoing eradication programs and the characteristics that have slowed their success.

ONGOING ERADICATION PROGRAMS

Eradication of Established Pests

Whether established pests are suitable for attempted eradication is extremely controversial. Justification of eradication programs against established pests is usually based on the long-term environmental and economic benefits. For example, Knipling (36) pointed out that, if the boll weevil (*Anthonomous grandis*) or the tsetse fly (*Glossina* spp.) could be eradicated from critical areas, the direct and indirect economic benefits that would accrue would amount to billions of dollars in just a few decades and would greatly reduce the environmental contamination associated with insecticide use.

Eradication programs of abundant and widespread pests commonly prescribe intensive and extensive insecticide treatments to reduce population densities prior to a SIR program. The cost of the SIR program is usually so high that it needs to be amortized over a long period of time for the costs and benefits to balance. Rabb (60) expressed concern that long amortization schedules involve less reliable predictions because ecological, economic, and sociological factors vary in unpredictable ways with time.

BOLL WEEVIL The boll weevil entered Texas from Mexico in 1892 and within 30 years had spread throughout the entire cotton belt of the southern United States to become a key pest, causing an estimated 8% loss of yield (56). In 1958, the National Cotton Council called for increased research and development to provide the technical expertise for eradication of this pest (34). By early 1968, Knipling concluded that sufficient advances had been made to justify a full-scale eradication experiment. One year later a special study committee on boll weevil eradication was formed and recommended a site in Mississippi for a trial eradication (57).

The pilot Boll Weevil Eradication Experiment was conducted in 1971–1973 in southern Mississippi, Alabama, and Louisiana. The eradication area had a radius of 40 km and was surrounded by three buffer zones that extended the radius to about 120 km. A five-step program was carried out in the eradication zone while the normal in-season control was carried out in the three buffer zones. The five-step plan included (a) normal in-season insecticidal control; (b) reproduction-diapause control of the boll weevil in the fall, which included habitat destruction and insecticide application to limit the number of overwintering individuals; (c) trapping in the spring with trap crops that were then destroyed and pheromone traps; (d) early-season insecticide application at the

pin-head stage before populations became damaging, and (e) release of sterile males (33, 56, 57). Overall, the trial was largely successful in severely suppressing boll weevil populations. However, whether eradication was achieved in the core area is very doubtful. At the termination of the project in 1973, two completely different conclusions were drawn. The Technical Guidance Committee concluded that it was technically and operationally feasible to eliminate the boll weevil as an economic pest in the United States (see 35). In contrast, the Entomological Society of America Review Committee (9) stated its reservations concerning any massive eradication undertaking without further research to refine suppressive techniques.

In 1978, amid much political maneuvering and controversy, a new trial eradication program was started in Virginia and North Carolina; it was intended, if successful, to be extended westward in phases to eradicate the boll weevil from the United States. Optimistic projections for this program were based on the improvements to the technologies of mass rearing and sterilization, as well as the legislated dedication of the participants (57). A two-step process was planned. In the first year, populations were to be reduced to a low level through heavy insecticide treatment and cultural control measures. In the second year, the reduced populations were to be eliminated with the use of pheromone attractants, sterile male releases, and limited chemical applications. In the core area, during the second year, one infestation was detected, and this was attributed to reinvasion (37). Knipling (37) concluded that the basic technology was advanced to the point that isolated boll weevil populations could be eradicated and that continuous populations could be rigidly managed on an area-wide basis.

Full-scale eradication programs were then initiated in the western United States (California and Arizona) and in North and South Carolina (39). The eradication zone in the southeast was expanded in 1987 to include Georgia, Florida, and Alabama. The program has been associated with a decrease in the application of insecticides for boll weevil and a concurrent increase in yield (22), but whether true eradication has been achieved in these areas is doubtful.

The boll weevil program exemplifies some general observations regarding the eradication of a long-established species. The boll weevil is a highly mobile pest that possesses the ability to increase dramatically from low levels to damaging levels in a short period of time. The boll weevil also overwinters in hedgerows, forest litter, and other foliage near production fields, and such overwintering populations serve as reservoirs from which reintroductions to cotton fields will occur (13). These characteristics ensure that 100% kill will be extremely difficult to achieve and, when reintroductions from reservoirs occur, that the pest's high mobility and fecundity will lead to frequent population escapes. This was certainly the case in both the 1971–1973 and 1978–1980 eradication experiments in which reinfestations were discovered. In addition,

eradication was not claimed for the full-scale programs, despite almost a full decade of effort.

Even if eradication were successful, the release of secondary pests previously controlled by spray programs directed at boll weevil may occur. For example, European corn borer (*Ostrinia nubilalis*), soybean looper (*Pseudoplusia includens*), and stink bugs (*Euchistus servus* and *Acrosternum hilare*) became more prevalent in the southeastern United States during the time of the full-scale eradication programs (45). On the other hand, reduced insecticide use following eradication could allow more successful natural or biological control of other insect species.

Although the economic benefits of boll weevil eradication can be documented, referenda to decide on whether new programs should be initiated have often failed (32). Opposition appears to be based on loss of freedom in decision-making by landowners and apprehension about the role of the state. Interestingly, the opinions of landowners are not apparently influenced by their concerns for environmental issues associated with eradication programs. Area-wide management and eradication programs have been common for cotton pests, and these are listed in Reference 45 and reviewed in Reference 33.

CODLING MOTH IN BRITISH COLUMBIA The codling moth, *Cydia pomonella*, is a pest of apples in most parts of the world. It was the target of a small-scale eradication effort in the 1970s in a relatively isolated valley in British Columbia, Canada, the Similkameen Valley (59). The goal was to reduce populations of codling moth so that chemical control would not be necessary for at least several years. Prior to the release of sterile males, elimination of refuge populations of moths is necessary. Neglected apple trees in the vicinity must be cut down or sprayed. To initially reduce codling moth populations and therefore to maximize the ratio of sterile to wild moths, preliminary insecticide sprays are used. Fallen apples that could be a source of overwintering moths must also be destroyed. In this pilot project, the release of sterile males over 3 years after the initial reduction of populations with insecticides reduced the codling moth to near extinction (58). Further control was not necessary for 2 years in most locations. However, the cost of this program even with the 2 years without control was over two times the cost of chemical control. Although populations could be reduced to low levels, eradication was not possible, and reinvasion of codling moths from other areas occurred.

Approximately 20 years later, an extensive sterile male codling moth control program has been mounted in British Columbia. This program was initiated following an economic analysis that did not consider the potential of other possible controls of codling moth such as mating disruption (4a) or the use of granulosis virus as a spray (28a) and that underestimated the costs of prerelease

sanitation—spraying and removal of abandoned orchards. This program was recently reviewed while still in progress (9a). The program assumes that eradication of the codling moth using the SIR technique is feasible and that SIR offers the potential for eradication. In this case, eradication is defined as the elimination of this insect species as a pest of commercial apple production. The preferred goal is the elimination of codling moth from the Okanagan Valley of British Columbia, but this outcome is probably not feasible. Though the economic benefit-cost ratio is unfavorable, the advantages of a healthier environment and sustainable pest management favor the SIR program.

In the first two years of release (1995–1996), sterile males were not sufficiently active in the early spring to be competitive with wild males. In 1996, populations of codling moth were low in all areas, which made it difficult to evaluate the impact of the SIR program, but some indicators were positive. The success of this program is threatened by shrinking budgets for agricultural programs and by the difficulty of carrying out region-wide “eradication” in an area of heterogeneous land use with urban areas, abandoned orchards, and multiple jurisdictions including land belonging to native Americans.

THE IMPORTED FIRE ANT Two South American species of fire ants, the red fire ant, *S. invicta*, and the black fire ant, *S. richteri*, have been the focus of controversial eradication and control efforts since the 1950s (17, 43, 70). The black fire ant was originally introduced to Mobile, Alabama, in 1918, and the red fire ant sometime between 1933 and 1945. The spread of these two species became noticeable in the late 1940s and was rapid during the 1950s. Currently, their distributions cover 106 million hectares (ha) and extend from southern North Carolina through southern and eastern Texas (69). The painful stings of fire ants and their invasion of urban settings have made them the focus of massive control efforts. Whether the species are agricultural pests is debated (17, 29), but their nasty habit of nesting in electrical equipment, their impacts on wildlife and native ant species, and their negative impacts on humans in parks and recreational areas cause them to be public enemy number one in some areas of the South.

Efforts to stop the spread of the fire ants through quarantine and eradication of new populations were associated with widespread use of broad-spectrum insecticides. In 1957, an eradication campaign funded by federal and state governments began with the aim of removing the ants from North America (17). Dieldrin and heptachlor were used in these initial eradication programs, but soon the persistence and environmental side effects of these toxic chemicals were recognized (8). Between 1957 and 1961, a million hectares were sprayed with persistent toxic insecticides at the cost of \$15 million, and only temporary relief was provided from the red fire ants. In the years following, two insecticides were

developed for killing ants, mirex and ferrimamicide, and these were primarily used with baits. The environmental persistence, side effects on mammals and fish, and the toxic breakdown products of these insecticides led to their being banned (17). By 1989, eradication efforts had gone on for 26 years at the cost of \$200 million dollars, and the fire ant problem was worse than ever. The elimination of native species of ants by the fire ant control programs facilitated the reestablishment of the fire ants when control procedures stopped. Davidson & Stone (17) proposed that the resistance of fire ants to control efforts called into question the eradication philosophy. Political forces, particularly during the 1950s, played an important role in the development of the fire ant eradication programs (64), and it was suggested that the aggressive attempts to control the imported red fire ant may have been associated with the general "anti-red" attitude of the US government of the time (17).

Eradication of Recently Introduced Insects

Eradication of introduced pests is often recommended based on the assumption that the new species will do one or all of the following: (a) increase the costs of production and marketing, (b) pose important health risks (e.g. yellow fever mosquito, *A. aegypti*), (c) cause extensive environmental damage (e.g. gypsy moth, *L. dispar*), (d) lead to trade embargoes and quarantines (e.g. Mediterranean fruit fly), and (e) increase the use of chemicals and other costly controls (34, 65). Such eradication attempts are usually in response to reports of entry at ports, at borders, or through the mail system (16). The tools for such eradication commonly include detection, aerial and ground spray programs, fumigation, and toxic food and lure baits (12). Continued exclusion of a pest is increasingly less reliable as a potential tool as human population density and mobility increase. Most introduced species were spread by humans (14, 16).

Factors that may influence the potential for eradication of introduced species include the time of detection following introduction, the rate at which an eradication program is mounted, and the degree to which the introduced species is adapted to the new environment (34). Unfortunately we rarely understand the factors limiting the distribution and abundance of species well enough to predict the probability of establishment. An interesting example is the brown-tail moth, *Euproctis chrysorrhoea*, which was introduced to North America at approximately the same time as the gypsy moth. This species rapidly spread in the northeastern United States, whereas the gypsy moth was rather slow to spread following its introduction. However, now the brown-tail moth is restricted to small isolated coastal populations while the gypsy moth continues its spread across North America (55, 68). In some cases, populations of introduced insects decline following initial outbreaks, but without biological control or continued suppression (4, 52). In fact, natural extinctions of small

populations of introduced species may contribute to the apparent success of eradication programs. For example, widespread pheromone trapping identified 76 locations in which the gypsy moths occurred in British Columbia, Canada, prior to 1992. Of these, only 27 persisted in subsequent years as indicated by trap catches (52a), and the remaining 49 apparently went extinct.

When dealing with an introduced species, an important judgement must be made that often is based more on politics than on biology: Is the species established and relatively widespread, or can eradication totally eliminate the species from the new area? This judgement can be influenced by which agency is responsible for exotic species before establishment (e.g. those responsible for quarantine), versus after establishment (e.g. agriculture and forestry agencies or private industry). Before establishment is conceded, eradication is the goal. Once establishment is declared, containment or control are the aims. After an exotic species is declared to be established, trade embargoes may be imposed on goods that could be contaminated by the offending species (27). Therefore, periodic declarations of successful eradication can be advantageous. Two ongoing eradication programs of introduced species are described below.

GYPSY MOTH IN NORTH AMERICA The gypsy moth was first targeted by organized eradication efforts in the United States in the late 1800s. However, despite these efforts, the pest has continued to spread and is now perhaps the most notorious forest pest in North America. Eradication has been abandoned in the infested areas of the northeastern United States and Ontario, Canada. Now only suppression is attempted in sites of high density and areas in which particularly strong interactions with people are likely. But many states at the edges of the spreading invasion have continued to pursue eradication and carry out programs designed to slow the spread of gypsy moth (47).

A well-documented example of invasion and attempted eradication comes from the history of the gypsy moth in Michigan (21). Gypsy moth was first identified in Michigan in 1954, and aerial spraying with DDT over the next 9 years resulted in "successful" eradication. In 1966, a "new" infestation was reported in the same area, and this time carbaryl was used to eradicate the moth. By 1973, monitoring efficiency was improved through the development of disparlure, an improved synthetic gypsy moth sex pheromone. In that year, 1828 moths were captured over an extensive area including the previously treated zones. Eradication was again initiated, this time using carbaryl and diflubenzuron, and after 3 years, the Michigan Department of Agriculture reported considerable progress toward eradication, with 4 counties reporting complete eradication. By 1980, the pheromone lure used in traps was further improved, and now gypsy moth was found in 37 counties (20, 21, 28). Eradication programs continued, and over 16,000 ha were sprayed between 1980 and

1984. However, by 1984 the gypsy moth had spread to 73 of the 83 counties in Michigan (21). Eradication programs sponsored by the Michigan Department of Agriculture were stopped for the Lower Peninsula, although the federal government continued to fund eradication in the Upper Peninsula, along the edge of the distribution. Gypsy moth populations reached outbreak proportions in 1992 (47). An earlier simulation study had predicted that suppression of populations at the time of outbreak would be more cost effective than continued eradication attempts (50, 51). Since 1989, Michigan has sponsored public education programs that focus on the biology of the gypsy moth and the least disruptive control measures. These programs emphasize learning to live with the pest (47) and are the antithesis of the information programs preceding eradication. To persuade the public to support eradication efforts, threatening scenarios of possible impacts of the introduced insect are usually presented (2, 10, 11).

Several important conclusions can be drawn from this example of the gypsy moth in Michigan. First, despite eradication attempts, gypsy moths continued to spread and probably persisted in Michigan since they were first reported in 1954. Second, as the trapping technology used in the monitoring program improved, new populations were more likely to be discovered. Similar advances in technology led to the identification of the Asian strain of the gypsy moth in the Pacific Northwest. The Asian strain may have been present in North America since the last outbreak in Russia in 1981, when ships carrying egg masses were discovered in Vancouver, Canada. But Asian gypsy moths were only recognized as a distinctive form in 1992, when surveys were first conducted for this strain and techniques were available for distinguishing the European and Asian strains. Third, reintroductions of the gypsy moth are inevitable. There is no such thing as a "one-time" eradication effort, and reintroductions can have serious implications to the assessment of the costs and benefits of continued eradication programs. Finally, as long as the costs of eradication are borne by state and federal governments, many people will support the need for the program. However, if homeowners and forest companies are asked to pay for the program, reassessment of its value may occur (49).

MEDITERRANEAN FRUIT FLY IN CALIFORNIA The history of the detection and eradication of the Mediterranean fruit fly (medfly) in California has been summarized recently by Carey (5, 6). The first medfly captures in California were in 1975, when 77 flies were captured in the Los Angeles area. No further captures were made until 1980, when 5 more flies were captured at another site in the Los Angeles Basin and 195 flies were captured in Santa Clara County 650 km to the north. The latter led to a massive eradication campaign, with application of malathion sprays and baits to 2000 square km. Eradication was declared to be successful on September 21, 1982, following the \$100,000 program.

In 1989, 25 medflies were captured in the eradication zone. A sterile fly program was initiated, and eradication was declared the next year. Again, in 1992, over 100 flies were captured in the original eradication zone. This pattern suggests that, after eradication programs, small medfly populations remain that are not identified because the lure used in the baits is not efficient enough to detect low populations (31). An interesting pattern is revealed by the trapping of medflies in northern and southern California; in both areas large numbers of flies were trapped in 1981, 1989, and 1992. This trap catch suggests the presence of a widespread established population that periodically increases, perhaps in association with favorable climatic conditions, to densities sufficient to be detected by the trapping program. Another interesting observation is that 95% of medfly catches are during the summer and autumn, with only 5% in the winter and spring (5). This seasonal pattern of catches might be a factor that influences the declaration of successful eradication.

Carey (5) made the following assumptions in predicting the outcome of the medfly invasion: (a) the medfly is established in California and is not dependent on reintroduction, (b) current eradication programs using sterile males or localized spraying of malathion bait will fail, (c) new and effective technology for eradication will not be developed in the near future, and (d) the medfly will not go extinct by chance. The conclusion that the medfly is established in California is controversial (19, as cited in 5) but has implications for designing future detection and control programs. The highest number of trapped flies in California was in 1993. This indicates that, even with extensive eradication programs that are undoubtedly suppressing populations in some locations, there has been an overall increase in the number of flies in other areas. A major problem with interpreting trapping data is the lack of information on how many traps are monitored each year. Therefore, one must interpret numbers cautiously because, once flies are found in an area, trapping intensity may increase.

Comparison of Mediterranean Fruit Fly and Gypsy Moth Programs

There are similarities between the so-called eradication programs directed at the exotic species medfly and gypsy moth in western North America. In both situations, trade restrictions are the major threat that dictates continued eradication efforts. The pattern of insect catches in the trapping program varies from year to year with 1982–1983, 1986, and 1989–1992 as the years in which many new populations were recognized for the gypsy moth in British Columbia, and 1975, 1981–1982, 1989, and 1992–1993 as years of high medfly captures in California. In both cases, insects are often caught subsequently in areas in which eradication was considered to have been successful (5). Based on the

results of annual pheromone trapping for gypsy moths in British Columbia, moths have been caught subsequently in five of eight "eradicated" areas. These observations indicate that it is very difficult to eradicate a species once it has reached sufficiently high densities to be trapped, and they also suggest that variation in the climate or some biotic factor may be associated with years in which few or no captures are made. What is not easy to evaluate is the impact of attempted eradication programs on slowing the spread of the exotic species and in delaying the need for regular control procedures or acceptance of the insect damage. Because there are no controls for these "eradication experiments," we cannot adequately estimate what the economic impacts would have been if no eradication had been attempted.

ERADICATION VERSUS AREA-WIDE MANAGEMENT

As indicated by the quotation at the beginning of this paper, the word eradication is value-laden. It implies that the technology, finances, and willingness to accept side effects are sufficient to eliminate a species from a geographic area. An alternative—area-wide management—fits more comfortably into a sustainable paradigm for pest control. However, area-wide programs are not always accepted by landowners. Three problems associated with the establishment of regional pest management are (a) unequal pest control demand among land owners, (b) determination of the size of the management group, and (c) determination of the cost-sharing arrangements (7). Mobile insects such as bollworms and boll weevils can be suppressed at lower cost on a regional level than on individual farms. However, there can be other economic ramifications of successful programs. The eradication program for the boll weevil in North and South Carolina led to an increase of cotton production because it made it feasible to plant marginal areas to cotton. Increased production can reduce the price of a crop and therefore the value of eradication or area-wide suppression (7).

Education must be a part of eradication or area-wide management programs. However, these large programs often seem to be developed by government agencies that act as advocates rather than educators. As evidenced in the boll weevil situation in Louisiana, there can be a mistrust of government (32) and rejection of a program in a referendum even though it is justified by economic evidence. Great pressure often exists to declare successful eradication following an extensive and expensive control program such as with the Mediterranean fruit fly in California (6). Population density data are rarely published during eradication programs, and monitoring may stop once eradication is declared. There is also a tendency to use the word "eradication" when it is obvious that the resources available for the program and the heterogeneity of land use are such that every individual of the pest has not been removed. Declaring eradication as

the goal may create false expectations. Area-wide suppression is a much more realistic goal. A reduction in both pesticide use and secondary environmental impacts are good indicators of the benefits of successful programs, in addition to the reduced impact of the pest.

ACKNOWLEDGMENTS

We appreciate the comments and suggestions of Jennifer Ruesink on this paper.

Visit the *Annual Reviews* home page at
<http://www.AnnualReviews.org>.

Literature Cited

1. Agrios GN. 1988. *Plant Pathology*. San Diego: Academic. 3rd ed.
2. Anonymous. 1992. Final environmental impact report: gypsy moth, *Lymantria dispar* (L.) eradication program in California. Sacramento, CA: Calif. Dep. Food Agric. 160pp.
3. Anonymous. 1992. *The New World Screwworm Eradication Programme: North Africa 1988–1992*. Rome: Food Agric. Org. UN. 192 pp.
4. Beirne BP. 1975. Biological control attempts by introductions against pest insects in the field in Canada. *Can. Entomol.* 107:225–42
- 4a. Cardé RT, Minks AK. 1995. Control of moth pests by mating disruption: successes and constraints. *Annu. Rev. Entomol.* 40:559–85
5. Carey JR. 1996. The future of the Mediterranean fruit fly *Ceratitis capitata* invasion of California: a predictive framework. *Biol. Conserv.* 78:35–50
6. Carey JR. 1996. The incipient Mediterranean fruit fly population in California: Implications for invasion biology. *Ecol.ogy* 77:1690–97
7. Carlson GA, Wetzstein ME. 1993. Pesticides and pest management. In *Agriculture and Environmental Resource Economics*, ed. GA Carlson, D Zilberman, JA Miranowski, pp. 268–318. Oxford: Oxford Univ. Press
8. Carson R. 1962. *Silent Spring*. Boston: Houghton Mifflin. 368 pp.
9. Comm. Entomol. Soc. Am. 1973. The pilot boll weevil eradication experiment. *Bull. Entomol. Soc. Am.* 19:218–21
- 9a. Compton R, Maskerine S, Isman B. 1996. *SIR program review, final report*. APA Consulting Group. 44 pp.
10. Counc. BC Plant Prot. Advisory. 1985. *Understanding the Gypsy Moth Threat*. Vancouver, BC
11. Cram SA. 1990. *Gaining Support for British Columbia's Gypsy Moth Wars 1978–1988: A Case Study in Public Relations*. Victoria, BC: BC Minist. For.
12. Crooks E, Havel K, Shannon M, Snyder G, Wallenmaier T. 1983. Stopping pest introductions. In *Exotic Plant Pests and North American Agriculture*, ed. CL Wilson, GL Graham, pp. 239–59. New York: Academic
13. Cross WH. 1983. Ecology of cotton pests with special reference to the boll weevil. In *Cotton Insect Management with Special Reference to the Boll Weevil*, ed. RL Ridgeway, EP Lloyd, WH Cross, pp. 53–70. Washington, DC: US Dep. Agric.
14. Czerwinski C, Isman MB. 1986. Urban pest management: decision-making and social conflict in the control of gypsy moth in west-coast cities. *Bull. Entomol. Soc. Am.* 32:36–41
15. Dahlsten DL, Garcia R, eds. 1989. *Eradication of Exotic Pests: Analysis with Case Histories*. New Haven, CT: Yale Univ. Press. 296 pp.
16. Dahlsten DL, Garcia R, Lorraine H. 1989. Eradication as a pest management tool: concepts and contexts. See Ref. 15, pp. 3–15
17. Davidson NA, Stone ND. 1989. Imported fire ants. See Ref. 15, pp. 196–217
18. Dennill GB, Moran VC. 1989. On insect-plant associations in agriculture and the selection of agents for weed biocontrol. *Ann. Appl. Biol.* 114:157–66
19. Dowell RV, Penrose R. 1995. Mediterranean fruit fly eradication in California 1994–1995. In *The Medfly in California: Defining Critical Research*, ed. JG Morse, RL Metcalf, JR Carey, RV Dowell, pp.

- 161–85. Riverside: Univ. Calif. Coll. Nat. Agric. Sci.
20. Driestadt SH. 1983. An assessment of gypsy moth eradication attempts in Michigan (Lepidoptera: Lymantriidae). *Great Lakes Entomol.* 19:143–48
21. Driestadt SH, Weber DC. 1989. Gypsy moth in the Northeast and Great Lakes states. See Ref. 15, pp. 229–56
22. Duffy PA, Wetzstein ME, Cain DL, Young GY. 1994. Boll weevil eradication program benefits Alabama cotton farmers. *Highlights Agric. Res.* 41:3
23. Eden WG. 1978. Eradication of plant pests - pro. *Bull. Entomol. Soc. Am.* 24:52–54
24. Fischhoff B. 1977. Cost benefit analysis and the art of motorcycle maintenance. *Policy Sci.* 8:177–202
25. Galvin TJ, Wyss JH. 1996. Screwworm eradication program in Central America. *Ann. NY Acad. Sci.* 791:233–40
26. Getz CW. 1989. Legal implications of eradication programs. See Ref. 15, pp. 66–73
27. Hagen KS, Allen WW, Tassan RL. 1981. Mediterranean fruit fly: The worst may yet be to come. *Calif. Agric.* 35(Mar.–Apr.):5–7
28. Hanna M. 1982. Gypsy moth (Lepidoptera:Lymantriidae): history of eradication efforts in Michigan. *Great Lakes Entomol.* 15:193–98
- 28a. Jaques RP, Hardman JM, Laing JE, Smith RF, Bent E. 1994. Orchard trials in Canada on control of *Cydia pomonella* (Lepidoptera: Tortricidae) by granulosis virus. *Entomophaga* 39:281–92
29. Jemal A, Hugh-Jones M. 1993. A review of the red imported fire ant (*Solenopsis invicta* Buren) and its impacts on plant, animal, and human health. *Prevent. Vet. Med.* 17:19–32
30. Jewell D, Grodhaus G. 1984. An introduction of *Aedes aegypti* into California and its apparent failure to become established. In *Commerce and the Spread of Pests and Disease Vectors*, ed. M Laird. New York: Praeger
31. Kaneshiro K. 1993. Introduction, colonization, and establishment of exotic insect populations: fruit flies in Hawaii and California. *Am. Entomol.* 39:23–29
32. Kazmierczak RF, Smith BC. 1996. Role of knowledge and opinion in promoting boll weevil (Coleoptera, Curculionidae) eradication. *J. Econ. Entomol.* 89:1166–74
33. King EG, Phillips JR, eds. 1993. *Cotton Insects and Mites: Characterization and Management*. Cotton Found. Ref. Book Ser. No. 3. Memphis: Natl. Cotton Counc.
34. Klassen W. 1989. Eradication of introduced arthropod pests: theory and historical practice. *Misc. Publ. Entomol. Soc. Am.* 73:1–29
35. Knipling EF. 1976. Report of the technical guidance committee for the pilot boll weevil eradication experiment. Washington, DC: US Dep. Agric.
36. Knipling EF. 1978. Eradication of plant pests - pro. *Bull. Entomol. Soc. Am.* 24:44–52
37. Knipling EF. 1983. Analysis of technology available for eradication of the boll weevil. In *Cotton Insect Management with Special Reference to the Boll Weevil*, ed. EP Lloyd, WH Cross, pp. 401–486. Washington, DC: US Dep. Agric.
38. Knipling EF. 1985. Sterile insect technique as a screwworm control measure: the concept and its development. In *Symposium on Eradication of the Screwworm from the United States and Mexico*, ed. OH Graham, *Misc. Publ. Entomol. Soc. Am.*, 62:4–7. Entomol. Soc. Am.
39. Knipling EF. 1992. *Principles of Insect Parasitism Analyzed from New Perspectives*. U.S. Dept. Agric. USDA Agric. Handb. 693. 337pp.
40. Koyama J, Tanaka K. 1984. Eradication of the oriental fruit fly (Diptera: Tephritidae) from the Okinawa Islands by a male annihilation method. *J. Econ. Entomol.* 77:468–72
41. Krawfur ES, Lindquist DA. 1996. Did the sterile insect technique or weather eradicate screwworms (Diptera, Calliporidae) from Libya? *J. Med. Entomol.* 33:877–87
42. LeVeen EP. 1989. Economic evaluation of eradication programs. See Ref. 15, pp. 41–56
43. Lofgren CS. 1986. The economic importance and control of imported fire ants in the United States. In *Economic Impact and Control of Social Insects*, ed. SB Vinson, pp. 227–56. New York: Praeger Sci.
44. Lorraine H, Chambers DL. 1989. Eradication of exotic species: recent experiences in California. In *Fruitflies: Their Biology, Natural Enemies and Control*, ed. AS Robinson, G Hooper, pp. 399–410. Amsterdam: Elsevier
45. Luttrell RG. 1994. Cotton pest management, part 2: a US perspective. *Annu. Rev. Entomol.* 39:527–42
46. Marshall E. 1981. Man versus medfly: some tactical blunders. *Science* 213:417–18
47. McCullough DG. 1994. In Michigan, gypsy moth management means education. *J. For.* 92:17–21

48. Merrill LD. 1989. Citrus canker. See Ref. 15, pp. 184–95
49. Miller JD, Lindsay BE. 1993. Willingness to pay for a state gypsy moth control program in New Hampshire: a contingent valuation case study. *J. Econ. Entomol.* 86:828–37
50. Morse JG, Simmons GA. 1978. Alternatives to the gypsy moth eradication program in Michigan. *Great Lakes Entomol.* 11:243–48
51. Morse JG, Simmons GA. 1979. Simulation model of gypsy moth *Lymantria dispar* introduced into Michigan forests. *Environ. Entomol.* 8:293–99
52. Myers JH, Iyer R. 1981. Phenotypic and genetic characteristics of the European crane fly following its introduction and spread in western North America. *J. Anim. Ecol.* 50:519–31
- 52a. Myers JH, Rothman L. 1995. Field experiments to study regulation of fluctuating populations. In *Population Dynamics: New Approaches and Synthesis*, ed. N Cappuccino, PW Price, pp. 229–50. San Diego: Academic
53. Newsom LD. 1978. Eradication of plant pests - con. *Bull. Entomol. Soc. Am.* 24:35–40
54. Oladunmade MA, Dengwat L, Feldmann HU. 1986. The eradication of *Glossina palpalis palpalis* (Robineau Desvoidy) (Diptera: Glossinidae) using traps, insecticide impregnated targets and the sterile insect technique in central Nigeria. *Bull. Entomol. Res.* 76:2775–86
55. Oliver A. 1993. Gypsy moth in the lower mainland. Vancouver: Univ. BC
56. Perkins JH. 1980. Boll weevil eradication. *Science* 207:1044–50
57. Perkins JH. 1982. *Insects, Experts, and the Insecticide Crisis: The Quest for New Pest Management Strategies*. New York: Plenum. 304 pp.
58. Proverbs MD, Newton JR, Campbell CJ. 1982. Codling moth: a pilot program of control by sterile insect release in British Columbia. *Can. Entomol.* 114:363–76
59. Proverbs MD, Newton JR, Logan DM, Brinton FE. 1975. Codling moth control by sterile insect release of radiation sterilized moths in a pome fruit orchard and observations of other pests. *J. Econ. Entomol.* 68:555–60
60. Rabb RL. 1978. Eradication of plant pests—con. *Bull. Entomol. Soc. Am.* 24: 40–44
61. Reichard RE, Vargas-Teran M, Abu Sowa M. 1992. Myiasis: The battle continues against screwworm infestation. *World Health Forum* 13:130–38
- 61a. Richardson RH, ed. 1979. *The Screw-worm Problem*. Austin, TX: Univ. Texas Press. 151 pp.
62. Roland J, Embree DG. 1995. Biological control of winter moth. *Annu. Rev. Entomol.* 40:475–92
63. Rowen H. 1975. The role of cost-benefit analysis in policy making. In *Cost-Benefit Analysis and Water Pollution Policy*, ed. HM Peskin, EP Seskin, pp. 361–69. Washington, DC: Urban Inst.
64. Shores EF. 1994. The red imported fire ant: mythology and public policy, 1957–1992. *Ark. Hist. Q.* 53:320–39
65. Siebert JB, Cooper T. 1995. Embargo on California produce would cause revenue, job loss. *Calif. Agric.* 54(July–Aug.):7–12
66. Simberloff D. 1976. Species turnover and equilibrium island biogeography. *Science* 195:572–78
67. Sun M. 1984. The mystery of Florida's citrus canker. *Science* 226:322–23
68. USDA. 1985. *Insects of Eastern Forests*. Washington, DC: US Dep. Agric. For. Serv.
69. Vinson SB. 1997. Invasion of the red imported fire ant: spread, biology and impact. *Am. Entomol.* 43:23–39
70. Vinson SB, Greenberg L. 1986. The biology, physiology and ecology of imported fire ants. In *Economic Impact and Control of Social Insects*, ed. SB Vinson, pp. 193–226. New York: Praeger Sci.
71. Walker JC. 1969. *Plant Pathology*. New York: McGraw Hill



CONTENTS

Golden Age of Insecticide Research: Past, Present, or Future? <i>John E. Casida, Gary B. Quistad</i>	1
Nutritional Interactions in Insect-Microbial Symbioses: Aphids and Their Symbiotic Bacteria <i>Buchnera</i> , <i>A. E. Douglas</i>	17
Chemical Ecology of Phytophagous Scarab Beetles, <i>Walter Soares Leal</i>	39
Plasticity in Life-History Traits, <i>S. Nylin, K. Gotthard</i>	63
Life on the Edge: Insect Ecology in Arctic Environments, <i>A. T. Strathdee, J. S. Bale</i>	85
Fire and Insects in Northern and Boreal Forest Ecosystems of North America, <i>Deborah G. McCullough, Richard A. Werner, David Neumann</i>	107
Phylogeny and Evolution of Host-Parasitoid Interactions in Hymenoptera, <i>J. B. Whitfield</i>	129
Indirect Sperm Transfer in Arthropods: Behavioral and Evolutionary Trends, <i>H. C. Proctor</i>	153
Biology of the Mantispidae, <i>Kurt E. Redborg</i>	175
Insect Performance on Experimentally Stressed Woody Plants: A Meta-Analysis, <i>Julia Koricheva, Stig Larsson, Erkki Haukioja</i>	195
The Biology of Nonfrugivorous Tephritid Fruit Flies, <i>D. H. Headrick, R. D. Goeden</i>	217
Integrated Pest Management: Historical Perspectives and Contemporary Developments, <i>Marcos Kogan</i>	243
Biodiversity of Stream Insects: Variation at Local, Basin, and Regional Scales, <i>Mark R. Vinson, Charles P. Hawkins</i>	271
Predaceous Coccinellidae in Biological Control, <i>John J. Obrycki, Timothy J. Kring</i>	295
Reproductive Caste Determination in Eusocial Wasps (Hymenoptera: Vespidae), <i>Sean O'Donnell</i>	323
Manipulating Natural Enemies by Plant Variety Selection and Modification: A Realistic Strategy? <i>Dale G. Bottrell, Pedro Barbosa, Fred Gould</i>	347
Biological Control of Weeds, <i>Rachel E. Cruttwell McFadyen</i>	369
Ecology and Management of Hazelnut Pests, <i>M. T. AliNiazee</i>	395
Higher-Order Predators and the Regulation of Insect Herbivore Populations, <i>Jay A. Rosenheim</i>	421

Parasites and Pathogens of Mites, <i>G. Poinar Jr., R. Poinar</i>	449
Eradication and Pest Management, <i>Judith H. Myers, Anne Savoie, Ed van Randen</i>	471
Ecological Considerations for the Environmental Impact Evaluation of Recombinant Baculovirus Insecticides, <i>Andrew Richards, Marcus Matthews, Peter Christian</i>	493
Malaria Parasite Development in Mosquitoes, <i>John C. Beier</i>	519
New Insecticides with Ecdysteroidal and Juvenile Hormone Activity, <i>Tarlochan S. Dhadialla, Glenn R. Carlson, Dat P. Le</i>	545
Spatial Heterogeneity and Insect Adaptation to Toxins, <i>Casey W. Hoy, Graham P. Head, Franklin R. Hall</i>	571
The Ecology and Behavior of Burying Beetles, <i>Michelle Pellissier Scott</i>	595
Evolution and Ecology of Spider Coloration, <i>G. S. Oxford, R. G. Gillespie</i>	619
Biology and Use of the Whitefly Parasitoid <i>Encarsia formosa</i> , <i>M. S. Hoddle, R. G. Van Driesche, J. P. Sanderson</i>	645
Differential Gene Expression in Insects: Transcriptional Control, <i>Lawrence G. Harshman, Anthony A. James</i>	671
Sustainability of Transgenic Insecticidal Cultivars: Integrating Pest Genetics and Ecology, <i>Fred Gould</i>	701