ARTICLES

BIOLOGICAL CONTROL OF MOSQUITOES—HAS IT A FUTURE?[1, 2]

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It was an unexpected honor to receive an invitation from AMCA to give this Memorial Lecture dedicated to the memory of Harry H. Stage. Although I have read many of Dr. Stage's papers, unfortunately I never had the privilege of meeting him. Nevertheless, I would like to think that he would have approved of the subject matter of this lecture—biological control of mosquitoes—and hopefully have agreed with some of the things I have to say.

INTRODUCTION

Some of us here today have seen the "rise and fall of DDT." Mosquito nuisances and mosquito-borne diseases are still with us, malaria will not go away, or if it does, it threatens to return with a vengence. We face other problems such as escalating pesticide costs, increasing spread of insecticide resistance and environmental pollution. I am not saying that insecticides have not brought enormous benefits; Tony Brown in his Memorial Lecture in 1980 aptly described their achievements, but they have often given short-term solutions. General disillusionment with chemical control methods has led to the resurrection of biological control from the pre-DDT era, and to it becoming prematurely regarded by some as *the* solution to control problems. Is such confidence justified, or has biological control feet of clay? In attempting to answer this question I want to begin by discussing some ecological considerations relevant to biological control.

Progress in biological control of vectors has been slow but the situation has improved during the past 10 years, due partly to research funding by the WHO-TDR program (Burges et al. 1981). We are still, however, trailing a long way behind the progress made in biological control of agricultural pests, but there are reasons for this. Uniformity and ecological stability of orchards, perennial crops and monocultures allow continuous interactions between pests and introduced enemies. In marked contrast mosquito larval habitats are very variable and unstable ecosystems. It is worth remembering that in agriculture successes have usually been against exotic pests or been achieved by importing exotic natural enemies to attack indigenous pests. In agriculture the aim is frequently to reduce pest populations below an economic level, in other words low populations are tolerated. This level of suppression is usually unacceptable with vectors because considerable disease transmission may still occur.

Mosquitoes generally have high fecundity, short generation time, high dispersal potential and are efficient colonizers. They also experience large natural mortalities, but are very resilient and can quickly recover from such population reductions. In consequence their populations are frequently booming and crashing. These life-history strategies are not very important in insecticidal control but they can create difficulties with biological control. Thus although natural, or introduced, enemies may cause large mortalities they may not produce the desired levels of control. Natural mortalities of immature mosquitoes can commonly be 95% or more, yet the numbers of emerging adults may still constitute a problem (Service 1977a, 1981a). The important question is, how are *adult* populations affected? For example, in certain situations adult female populations of *Anopheles gambiae*, probably the world's most efficient malaria vector, must be reduced 1000 fold to substantially reduce malaria transmission (Service 1982). Admittedly in many cases less drastic reductions will give acceptable control, but the point I am making is that in order to evaluate the effectiveness of biological control programs, it is essential to monitor adult populations. This, however, is very rarely done.

Now, it is generally believed that biological agents should be highly pathogenic, but theoretical considerations predict that maximum population reduction will be caused by parasites having low to moderate pathogenicity (Anderson 1979, 1982). With very pathogenic organisms repeated introduc-

[1] Fifth Annual AMCA Lecture delivered before the American Mosquito Control Association, Lake Buena Vista, Florida, February 28, 1983.

[2] Acknowledgments are made to the Lowndes Engineering Company, Inc. and the Zoecon Corporation for their participation in sponsoring the 1983 Memorial Lecture.

tions are probably essential for sustained suppression of vector populations; successful recycling is usually associated with low pathogenicity. High infection rates alone, or combined with high pathogenicity, may result in self destruction of the biological agent, but not of its host or prey. For example, the failure of *Romanomermis culicivorax* to recycle in some habitats may be due to high infection rates (84–97%) obtained when the nematodes are first introduced. This could cause such high mosquito mortality that the nematodes eventually die out (Petersen and Willis 1975). Similarly predators, especially monophagous ones, may kill so many prey that they drive themselves to extinction. Polyphagous predators, though unlikely to suffer this fate, will probably not give acceptable levels of control. Oligophagous predators, that is those that have preference for specific prey, but switch to alternative prey when populations become very low, are more likely to give sustained control. What is needed is a more stable association between natural enemies and their hosts or prey, neither driving the other to extinction. Density-dependent population processes are important in achieving equilibria between parasites and host densities.

A difficulty with mermithids and some other biological candidates, including *Toxorhynchites*, is that their life-cycles are considerably longer than those of their prey, so they can't respond quickly to changing mosquito densities. Such delays lead to instabilities—that is violent fluctuations in population size of the prey (May and Anderson 1978).

It is fashionable to recommend integrated control. For example, because certain biological control agents, such as *R. culicivorax*, can withstand normal larvicidal dosages, it is suggested that they be integrated with insecticides. Such a strategy, however, may be unwise if larvicides reduce mosquito larvae to such an extent that biological control agents cannot survive. Similarly, the integration of predators and parasites may be detrimental if, for example, mosquito predators feed directly on parasites or on their intermediate hosts (e.g. copepods infected with *Coelomomyces*). Furthermore, if diseased larvae are more sluggish than healthy ones they may be more readily caught, but nothing is gained by this because infected larvae are likely already destined to die. Predation on diseased larvae may also reduce the survival of parasitic infections.

The degree of spatial overlap between populations of mosquitoes and their parasites or predators is also important. Clearly there must be some overlap otherwise there would be no control, but the relationship is not simple. Mosquito larvae are usually highly aggregated, so it seems reasonable to expect that for maximum control parasites and predators should be similarly dispersed. But this can sometimes result in mutual interference, that is, competition amongst predators or parasites for a prey or host. This wastes the predators' time and energy, and may increase the chances of mosquito larvae escaping capture. The aggregation of predators may, however, allow some mosquito larvae to survive in refuges where initially there are few or no predators. But when few mosquito larvae remain it becomes advantageous for predators to disperse and seek out larvae hiding in the refuges.

The occurrence of aggregations and refuges can provide stabilizing mechanisms for predator-prey and parasite-host relationships. It gets rather complicated, and even speculative, but the point is—dispersion characteristics of natural enemies and mosquito larvae are important factors in population dynamics.

Population regulation in mosquitoes can be extremely complex and difficult to understand. It is not easy to predict, or even assess, the impact of adding exotic living organisms to an aquatic ecosystem. For these reasons alone biological control will prove much more difficult to achieve than insecticidal or environmental control measures. Consequently, there will be a continuing need for more and better trained vector ecologists. Unfortunately in the past biological control has quite wrongly been equated with "natural control" and the discipline has been discredited by those dabbling in a subject they know little about.

PARASITES AND PREDATORS

Let us now briefly inspect our armory of potential biological control agents.

Although viruses are sometimes used to control agricultural and forest pests, few have been marketed and there is little interest in their commercialization for vector control. One problem, though not unique to viruses, is that they are fairly host specific, which is decidedly unattractive commercially. Viruses also tend to be difficult and costly to produce in quantities needed for field applications.

There are three main groups of viruses in mosquitoes. One of the easiest to recognise is the iridescent viruses, but infection rates are very low (1–8%) (Chapman et al. 1966, Service, 1977b). Although Nuclear Polyhedrosis Viruses (NPV) have been proposed as control agents, only a few mosquito species are highly susceptible and natural infection rates are also usually low (Stiles 1980). A problem with a third group, the Cytoplasmic Polyhedrosis Viruses (CPV) is

that despite reports of relatively high infection rates (Clark and Fukuda 1971), infected larvae often pupate and give rise to apparently healthy adults (Clark et al. 1969). As yet there is little prospect of employing viruses in vector control.

The most famous biological control agents for mosquitoes are *Bacillus thuringiensis israelensis* (H-14) and *B. sphaericus* 1593. Four companies in North America and one in France are already producing commercial quantities of *Bti*. It is a microbial insecticide acting as a stomach poison, it does not persist in the environment and consequently has to be repeatedly applied. Ecologically *Bti* is not very interesting, but this should not detract from it being one of the better new insecticides, though it is not without its limitations. Suspended particulate matter, organic and inorganic pollutants and surface vegetation reduce its efficiency, and in deep waters it tends to settle down amongst bottom sediments so that little is ingested by mosquito larvae. There is also evidence that with high larval densities insufficient toxin may be ingested to kill the larvae (Mulla and Federici 1982). *Bti* is more effective against *Aedes* and *Culex* than *Anopheles* larvae, but even within a species different strains show variations in their susceptibilities. It has proved effective in small-scale field trials in Indonesia against *Aedes aegypti*, *Culex quinquefasciatus* and *Anopheles sundaicus* (Sudomo et al. 1981), and against a variety of species in North America, Europe, Asia and Australia. As far as I am aware, however, it has not yet been evaluated in large-scale trials against mosquitoes let alone to see whether disease reduction is feasible. However, I believe large-scale trials are now planned in different tropical environments and against a number of mosquito vectors (Dubitiskij 1982, WHO 1981).

We now come to *Bacillus sphaericus*—which I understand Lee County Mosquito Control District in Florida is routinely producing for local use. Of about 12 genetically distinct insecticidal strains, 1593 is the most potent. (Two new strains, 2013–4 and 2013–6 originating from Romania, appear to have comparable toxicities to mosquito larvae (Lacey and Singer 1982, Singer 1980)). The toxin is associated with the spore wall but its mode of action is not yet clear. Viable spores ingested by mosquito larvae germinate and when the larvae are killed many more spores than were ingested are released (Davidson 1982). Spores have remained viable in sewage tanks for up to 90 days (Hornby et al. 1981) and larvicidal activity in tree holes has persisted for 9 months (Singer 1980). But it is not enough that spores survive, they must be in a zone enabling them to be ingested by mosquito larvae if there is to be sustained larval mortality. Recycling does not always occur, but seems to be favored by organic pollution. Most *Culex* species, inculuding *Cx. quinquefasciatus*, are highly susceptible to *B. sphaericus*, but *Ae. albopictus*, *Ae. sierrensis* and *Ae. taeniorhynchus* are little affected, although other *Aedes* species such as *Ae. nigromaculis* and *Ae. stimulans* are susceptible (Mulligan et al. 1978, Wraight et al. 1982). In general, *Anopheles* are more susceptible to *B. sphaericus* than they are to *Bti* but this varies according to species and even strains of the same species (see Burges 1982 for summary of mosquito susceptibilities). Particulate matter, strong ultraviolet radiation, low temperatures and alkalinity decrease larvicidal activity (Mulligan et al. 1980, Wraight et al. 1982), and as with *Bti* rapid settling of toxic entities results in reduced larval mortality. Better formulations are needed, especially as toxicity tends to vary from batch to batch. Despite these limitations and the fact that as yet it has not been produced commercially in large quantities, *B. sphaericus* 1593 has good potential, and because it has the ability to recycle is ecologically more interesting than *Bti*.

Because *Bti* and *B. sphaericus* 1593 are both fairly easily produced, it has been suggested (Hertlein et al. 1980) that encouragement be given to cottage industry production in developing countries, as this would overcome high costs of importing insecticides. I fear, however, that lack of standardization and quality control during production will make it difficult to assess the results of field trials. Moreover, there may be problems of safety during manufacture and packaging, and the danger of contamination with microbial agents poisonous to man.

Microsporidians are common protozoans of natural mosquito populations, and have been recorded from about 116 mosquito species (Hazard and Chapman 1977, Castillo 1980). Typically they produce enzootic infections. Best known are *Vavraia culicis*, a parasite mainly of culicines, and *Nosema algerae* which is most effective against *Anopheles*. Despite promising laboratory studies neither has had a very good track record. *Vavraia culicis* was introduced onto the Pacific island of Nauru in 1967 in an attempt to control *Cx. quinquefasciatus*, but although the parasite was still present in some habitats 2 years later, infection rates were very low and mosquito population size appeared unaffected (Reynolds 1972). When *N. algerae* was used against *An. albimanus* in Panama it was found that infection rates were dose-dependent, ranging from 16% after a single treatment to 86% infection after 4 applications (Anthony et al. 1978b). Mortality decreased rapidly after treatments stopped. In Pakistan infection rates of 40–50% were recorded in *An. stephensi*, but no lasting control was achieved,

probably because the spores sedimented out and were not ingested (Undeen 1982). The high infection rates and persistence recorded in laboratory experiments is probably due to the use of clean, shallow water where settling is not a problem. In addition to sedimentation difficulties and lack of persistence, spores of *V. culicis* and *N. algerae* cannot withstand desiccation or tolerate strong ultraviolet radiation. A difficulty in evaluating their effectiveness is that there are commonly long delays between infection and larval mortality, and in light infections adverse effects may only become apparent in the adults, such as reduced longevity and fecundity (Anthony et al. 1972, Haq et al. 1981, Undeen and Alger 1975) and reduction of vectorial capacity for malaria (Anthony et al. 1972, 1978a, Gajanana et al. 1979, Savage et al. 1971). It might be pointed out, however, that reduction in reproductive potential of infected hosts—here mosquitoes—is a highly desirable attribute for population regulation (Anderson 1982).

For these reasons and difficulties in mass production, it must be concluded that the Microsporidia do not as yet offer much hope for biological control of mosquito larvae.

Let us now progress to the fungi. One immediately thinks of *Coelomomyces* of which there are about 40 species. Although they have been considered as potential biological agents since the 1930's, they are not particularly promising candidates. Most are basically host-specific, infection rates are unpredictable, their distribution can be very localized, and they have a complicated and incompletely understood life-cycle involving an obligatory sexual cycle in copepods or ostracods before they can infect mosquitoes (Whisler et al. 1974, 1975). Furthermore, cultures cannot be established on artificial media. To me these restrictions exclude them as biocontrol agents.

What of other fungi? I can only mention a few. Although some of the Imperfect Fungi can be relatively easily cultured on artificial media (Roberts and Sweeney 1982), and commercial preparations (including species of *Beauveria* and *Metarhizium*), are marketed for control of agricultural pests, they do not offer much hope as mosquito larvicides. Problems include poor recycling and the need for high dosage rates.

Among the better known fungi is *Culicinomyces clavosporus*, which is toxic to all mosquitoes so far tested. Although initially this excited considerable interest, it has not lived up to expectation. Larval mortalities in field trials in Australia have been both variable and unpredictable, possibly arising from differences in environmental conditions, such as degrees of oxygenation and pollution. Other problems are that large volumes (100–1000 liter ha^{-1}) are necessary because of low spore production in cultures, infected larvae sometimes appear to cast off infections when they molt (Sweeney 1981) and they are intolerant of high salinities (Sweeney 1978) and temperatures above 30°C.

Lagenidium giganteum is another fungus which can be grown in artificial media and was believed to have control potential (Jaronski and Axtell 1982). It has caused relatively high mortalities in some trials, especially against *Culex* and *Aedes* mosquitoes, but in others results have been disappointing (Fetter-Lasko and Washino 1977, Merriam and Axtell 1982b). Recycling can be quite good so long as water temperatures are not too low; infections have persisted for 8 years in California rice fields (Washino 1981) and for 3 years in Louisiana (Glen and Chapman 1978). *Lagenidium* can withstand drying out (Fetter-Lasko 1980, Washino 1981) but not, unfortunately, organic pollution or salinity (Fetter-Lasko and Washino 1977, Merriam and Axtell 1982a, b; Washino 1981) and it has a rather narrow temperature range. These limitations help prevent it being of interest commercially.

Nematodes are among the more common contenders for mosquito control, the best known being *Romanomermis culicivorax*, the only mermithid that has been mass produced. There was a commercial product known as "Skeeter Doom" but unhappily eggs exhibited reduced viability following transportation. Another company expressed interest in culturing *R. culicivorax* but lost it when a feasibility study indicated that there would be poor financial returns on developing biocontrol agents. *Romanomermis culicivorax* infects at least 16 mosquito species naturally and over 80 species can be experimentally infected (Petersen and Chapman 1969); *Anopheles* seem the most susceptible. Caution is needed, however, in interpreting laboratory results. For example, in the laboratory *R. culicivorax* readily infects *Ae. sierrensis* (Petersen et al. 1969), but as the nematode cannot tolerate tree hole water it is useless against natural populations of this mosquito (Petersen and Chapman 1969).

What then are the nematode's good points? Well, it can fairly easily be reared *in vivo* in the laboratory—as yet *in vitro* methods have failed to produce male worms (Chapman and Finney 1982). Water depth does not appear important because preparasites concentrate near the surface and thus have a high degree of contact with mosquito larvae. In El Salvador, however, wave action along Lake Apastepeque reduced its effectiveness against *An. albimanus* (Petersen et al.

1978). Moreover, a mean infection rate of 96% dropped to 74 and 89% when applications were made before heavy rain (Willis et al. 1980).

Romanomermis culicivorax tolerates normal larvicidal dosages of organophosphate insecticides and IGR's, in fact compounds such as methoprene, which extend larval life, may enhance the chances of postparasite emergences (Winner et al. 1978). This may allow good integration of *R. culicivorax* with IGR's. *Romanomermis culicivorax* has the potential to recycle (Petersen 1976, Petersen and Willis 1975, Washino 1981, Westerdahl et al. 1981) but recycling can be poor and unpredictable (Chapman et al. 1972, Dhillon and Mulla 1980, Mitchell et al. 1974).

So what are its limitations? *Romanomermis culicivorax* cannot tolerate even slightly saline water, polluted waters and low oxygen concentrations (Brown and Platzer 1978, Imbriani and Platzer 1981, Petersen and Willis 1970). Aquatic fauna including beetles, dragonfly nymphs, ostracods and copepods appear to be predators of the pre- and postparasitic stages (Platzer and MacKenzie-Graham 1978, 1980). High preparasitic to host densities need to be avoided as they may kill mosquito larvae before the nematodes have had time to complete their development (Kurihara 1979). High parasite burden also increases the proportion of male nematodes, and if there are as many as 7 parasites in a larva only male worms are produced. Timing of parasite applications also seems critical to its survival (Washino 1981).

Another concern is the evolution of resistance against infections. Melanization of the parasite and its partial or complete destruction has been recorded in *Mansonia uniformis* (Kerdpibule et al. 1974), *An. sinensis* (Mitchell et al. 1974), *Ae. triseriatus*, *Cx. territans* (Petersen 1975, Petersen et al. 1969), *Ae. canadensis* and *Ae. communis* (Galloway and Brust 1976). In a laboratory colony of *Cx. quinquefasciatus* subjected to parasite infections for some 300 generations, infection rates were 32–42% lower than in a wild population not having experienced selection pressure (Petersen 1978).

Finally, from theoretical considerations (Hominick and Tingley 1982) and field observations (Molloy and Jamnback 1977, Mondet 1981) it appears that mermithids are likely to cause only moderate reductions in vector populations. This is not to say they do not have a role in biological control, but their potential is probably not as great as sometimes believed. The best approach may be to apply them as periodic inundative releases to give immediate control (Hominick and Tingley 1982), with little effort devoted to getting them to recycle.

We now come to predators, of which fish are the most commonly used in mosquito control; the best known being *Gambusia affinis* and *Poecilia reticulata*. Both are viviparous, have high reproductive rates and are small—an important consideration if you do not want them to be caught for food. *Gambusia affinis* can tolerate relatively high salinities while guppies, though more sensitive to brackish water, can withstand higher organic pollution and so are better suited for controlling *Cx. quinquefasciatus* (Sasa and Kurihara 1981). They are, however, not so voracious as *Gambusia* and cannot survive such low temperatures. Neither *Gambusia* nor *Poecilia* can survive in temporary habitats that periodically dry out—this severely limits their usefulness. Because *G. affinis* tend to kill indigenous fish, they are not generally recommended for introductions by WHO (1982). It is fashionable currently to advocate the use of indigenous larvivorous fish, but detailed ecological studies will still be needed to monitor their ecological impact, as well as evaluate their potential. *Gambusia* also preys on various invertebrates and this may result in algal blooms, which may cause fish to die and thus allow mosquitoes to increase in numbers (Hulbert et al. 1972, Hulbert and Mulla 1981). It might be remembered that some insecticides such as chlorpyrifos can also result in large increases in phytoplankton (Hoy et al. 1972, Hulbert et al. 1972). This emphasizes that biological control agents, as well as insecticides, can generate undesirable ecological disturbances. This should not be surprising, since the introduction of exotic agents or increasing populations of indigenous enemies creates artificial situations, some of which may be detrimental.

V. N. Beklemishev and colleagues considered that during the 1930's *Gambusia* helped reduce malaria transmission in the Ukraine (Gerberich and Laird 1968), but as other mosquito control measures were used simultaneously, I doubt if there is any evidence for this. In the Indian subcontinent *Gambusia* and *Poecilia* are commonly put in wells in the belief that they control the urban malaria vector *An. stephensi*, and in Afghanistan and Iran they have been integrated into antimalarial campaigns. Despite a blind faith in fish based on their undoubted ability to reduce larval densities I am not convinced that fish have ever been shown to have reduced mosquito biting densities or malaria transmission. The very few claims that have been made are based almost entirely on circumstantial evidence.

Of the invertebrate predators considered for biological control, I must mention *Toxorhynchites* and the triclad *Dugesia*. *Toxorhynchites* mosquitoes can only be contemplated for control of

mosquitoes breeding in container habitats such as *Ae. aegypti*, *Ae. albopictus* and *Ae. polynesiensis*. There is no doubt that they can destroy large numbers of larvae, more than they can eat, nevertheless there are many reasons why I do not consider them serious contenders for biological control. For instance, their spatial and temporal distributions do not overlap well with those of their prey, their life-cycle is 2–3 times longer than their prey, their eggs cannot withstand desiccation and they disperse relatively little. In most cases any local successes will depend on repeated inundative releases (Focks et al. 1979, Gerberg and Visser 1978) and I just cannot imagine *Toxorhynchites* being mass produced, especially on a non-living diet, transported and released on any economic and worthwhile scale. In many instances environmental sanitation approaches are better suited than biological methods to control container breeding mosquitoes. Admittedly this has rarely succeeded, but I believe that biological control will be even more difficult.

A non-cannibalistic strain of *Dugesia dorotocephala* discovered on the University of California campus at Riverside (Legner and Medved 1972) has been shown to be an effective mosquito predator. It can be mass produced by asexual fission (2 transverse cuts yield three worms), and it produces semi-dormant eggs capable of surviving winter conditions, but I really cannot believe in a factory producing large numbers of planarians.

Finally, we come to genetic control. Fortunately there is not much time to discuss this approach, because I have little good to say about it. Mosquitoes, with their high fecundity, high population densities and r-type life history strategies are among the worst targets for population suppression by genetic control techniques (Service 1981b, 1983). Theory tells us that if populations are under strong density-dependent regulation even a ratio of sterile:fertile males of 40:1 can fail to result in population reduction (Berryman et al. 1973). That is theory, what about practice? Well, despite injections of high sterility levels into local *Ae. aegypti* populations in trials in Kenya there were no reductions in pupal production or adult biting rates due, it was thought, to density-dependent population regulation (McDonald et al. 1977, Petersen et al. 1977, Service, 1983). Apart from biological reasons, simple logistics will prevent genetic control becoming a realistic component of any but a very small and localized control program. Genetic methods are among the most elegant strategies, but their successful implementation must remain a pipe dream!

FINAL CONSIDERATIONS

An attraction of biological control agents is that their host-specificity allows survival of non-target organisms, but paradoxically specificity deters commercialization. The vector market is already small and manufacturing a parasite effective against only a few vectors is even more economically unattractive; I cannot imagine any company contemplating production of predators! Nevertheless, commercial production is essential if biological control is to be seriously contemplated. Another appeal of biological control was the belief that there would be no resistance. But past experience should have warned us that because of nature's enormous genetic variability the evolution of resistance was likely.

Ideally the objectives of biological control are not to eradicate pests, but to maintain their populations at low densities through the coexistence of introduced natural enemies. But this is much easier said than done partly because it is very difficult to understand the population dynamics of mosquito habitats—with chemical control this is not necessary. As an example of the complexities let us look at the role of copepods such as *Cyclops*. Because they can prey on mosquito eggs and larvae and are intermediate hosts of *Coelomomyces* they appear to be beneficial, but unfortunately they are also predators of *R. culicivorax*. Now, IGR's can drastically reduce *Cyclops* (Ali and Lord 1980), but at the same time by extending larval life of mosquitoes they favor the survival of *R. culicivorax*. This emphasizes the need for ecological and theoretical studies before rushing into biological control programs. But the problem with ecology is that it takes a long time and may give results applicable only to the local study area, while funding agencies want quick answers and results, as well as generalizations. There must be some compromise between theory and practice, but the difficulty is in deciding when theory should be replaced by practice and whether the mosquitoes and biocontrol agents have understood the theory of population dynamics and will behave as we believe they should! Many of us, including myself, have believed that recycling was a desirable feature of a biological control agent, but Anderson (1982) argues otherwise on theoretical grounds. He believes that in the absence of repeated introductions, recycling by pathogens can cause epizootics followed by periods of little host mortality. We need to test this and other recent hypotheses put forward by population modellers, by field experiments if we are to make progress. We cannot afford to become armchair ecologists.

At last we come to the question—has biological control a future? I believe the answer is yes, but only so long as we get our priorities right. I see little value in devoting large resources to approaches that will almost certainly not be practical, such as genetic control or use of predators like *Toxorhynchites*. This does not imply that such research should cease, but if the principal objective is the suppression of pest populations then we must concentrate on methods we believe can be developed for large-scale control.

I am forced to admit that *Bti* is the front runner and possibly the 'pathogen for all seasons,' although ecologically it is rather a dull creature. But I also believe that *B. sphaericus* eventually may prove to have better prospects. What about *R. culicivorax*? Well, because this is a more 'natural' enemy than the bacteria I believe it will be more difficult to use as a biological control agent, but I nevertheless think it, as well as a few other mermithids, has considerable potential.

Finally, one must be careful not to oversell new disciplines, but I believe bioengineering offers exciting possibilities. For example, it might be possible to improve toxin yield in commercial preparations of *Bti*, or to transfer the gene coding for the toxin to naturally occurring bacteria that persist longer in aquatic habitats. So while the future looks exciting, biological control at present offers little to alleviate suffering from mosquitoes.

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