Biological Control: Implications of the Analogy Between the Trophic Interactions of Insect Pest–Parasitoid and Snail–Trematode Systems

ARMAND M. KURIS [1]

G. W. Hooper Foundation, University of California, San Francisco, California 94122

KURIS, A. M., 1973. Biological control: implications of the analogy between the trophic interactions of insect pest–parasitoid and snail–trematode systems. *Experimental Parasitology* 33, 365–379. An analogy between the tropic interactions of insect pest–hymenopterous parasitoid and snail–larval trematode systems is proposed. The goal of most agricultural pest management programs is increase in production of a plant crop, the deleterious agent is an herbivorous insect pest, the controlling agent, a parasitoid. Other parasitoid species may or may not have a significant effect on the control of the host by the key mortality factor.

In snail–schistosome systems the goal is reduction of worm burdens in human populations, removed in space and time from the snail–sporocyst interaction; the deleterious agent is the schistosome, trophically equivalent to the hymenopterous parasitoid. Therefore, control may be achieved through competitive displacement of the schistosomes by other larval trematodes having superior intrinsic competitive abilities and better searching efficiencies at low host densities.

Hyperparasites, sciomyzid Diptera and *Daubaylia* may also play a role in this view of schistosomiasis control. The Hassell–Varley parasite quest theory is applied to larval trematodes. The inversely proportional relationship between the area of discovery and miracidial density when logarithmically transformed is further evidence for the dynamic similarity of snail–trematode and insect–parasitoid systems.

Other applications of the generally accepted principles of insect pest biological control to a medically important trematode indicate that (1) schistosome population control, not eradication, is the appropriate goal of public health programs, (2) the criteria for implementation and success of such programs must be in terms of the relationship between medical injury and the frequency distribution of worms in humans, and (3) a good biological control agent is likely to have a high searching efficiency at low host densities, kill more than one snail host, be highly host specific, be scarce when successful, reside in regions were schistosomiasis is negligible as a medical problem.

INDEX DESCRIPTORS: *Anagrus epos; Aphytis maculicornis;* "Area of Discovery"; Biological control; *Biomphalaria glabrata; Coccophagoides utilis;* Competitive displacement; *Coragyps atratus foetens; Cryptochaetum ceryae; Daubaylia; Echinostoma liei; Echinostoma lindoense; Echinostoma malayanum;* Hyperparasite; *Hypoderaeum dingeri;* Life cycles; Mortality factor key; *Marisa cornuarietis;* Microsporida; Miracida; Model parasite quest; Castration, parasitic; Parasitoid; *Paryphostomum segregatum; Perezia helminthorum;* Pest control; Redia; *Schistosoma japonicum; Schistosoma mansoni; Schistosoma spindale;* Schistosomiasis; Sciomyzidae; Snail; Sporocyst; Antagonism, trematode; Trophic interaction.

[1] Present address: Department of Zoology, University of Michigan, Ann Arbor, MI 48104.

Successful biological control of an economically important insect pest was first achieved in the late 1880's (Doutt 1958), in which the cottony cushion scale was all but eliminated by the vedalia beetle and the parasitoid, *Cryptochaetum ceryae*. The possibility of biological control of a helminthic parasite was first seriously discussed a scant 15 yr ago (Chernin, Michelson, and Augustine 1956; Michelson 1957; Chernin 1962; Berg 1964). Limited successes in field trials were reported by Chock, Davis, and Chong (1961), Heyneman and Umathevy (1967), and Lie, Kwo, and Owyang (1970, 1971). What research strategy will be most productive to help reduce the 80-yr lag time for biological control of human and veterinary parasites? Insect pest control is a system analogous to the schistosome–snail–human interaction and can provide a theoretical model and a background within which to assess efforts and order priorities in developing the nascent science of biological control of parasitic disease. This comparative methodologic approach is a familiar one to biologists in general and to parasitologists in particular. Discoveries in plant genetics foreshadowed similar relationships in animal genetics, which, in turn, repeatedly led to discoveries in human ge-

netics. Significant features of the biology and life cycle of the agents of human malaria were first discovered in the study of avian malarias.

RELATIONSHIPS BETWEEN INSECT PEST CONTROL AND SCHISTOSOMIASIS

A general model for the operation of most successful insect pest control strategies is presented in Fig. 1. Perusal of any recent compendium on insect pest management (DeBach 1964a; Rabb and Guthrie 1970; Huffaker 1971) shows that most successful programs employed hymenopterous and dipterous parasitoids. Genetic manipulation, use of general predators, and other techniques of more limited application will not be discussed here. Many interesting deviations from the scheme outlined in Fig. 1 could be presented, but this is representative of the basic approach to insect pest control.

Briefly, an economically disadvantageous system involving an insect pest and a valuable plant species is brought under control by the introduction and successful maintenance of a primary parasitoid. Successful control means that the pest population density is reduced to a level such that the damage inflicted is economically permissible.
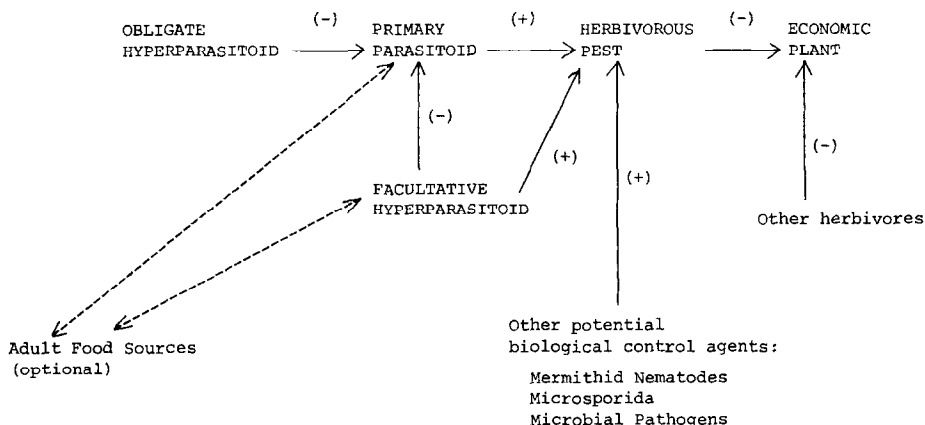

FIG. 1. Generalized model of insect pest biological control systems using parasitoid insects. Solid arrows indicate trophic interactions in the food web of the agroecosystem. Positive (+) and negative (−) signs refer to the beneficial or deleterious aspects of the adjacent trophic interaction in terms of biological control. Double-headed dashed arrows refer to interactions separated in space and time from the agro-ecosystem.

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                            castration
                            and mortality
MICROSPORIDA   (+?)  SCHISTOSOME      (+)        HERBIVOROUS   (+)  AQUATIC
          ──────────> SPOROCYSTS ──────────────>  SNAIL     ─────> PLANT

                         (+)            castr. and/or mort.   (+)       (+?)

                                              (+)        (+)

                      TREMATODE                                  Other herbivores
Human & Reservoir     ANTAGONISTS
Hosts (Pathogenic)                      Other potential snail
                                        biological control agents:

                                            Sciomyzid Diptera
              Second Intermediate           Daubaylia
              and/or Definitive Hosts       Microsporida
              (Little or No Pathogenicity)
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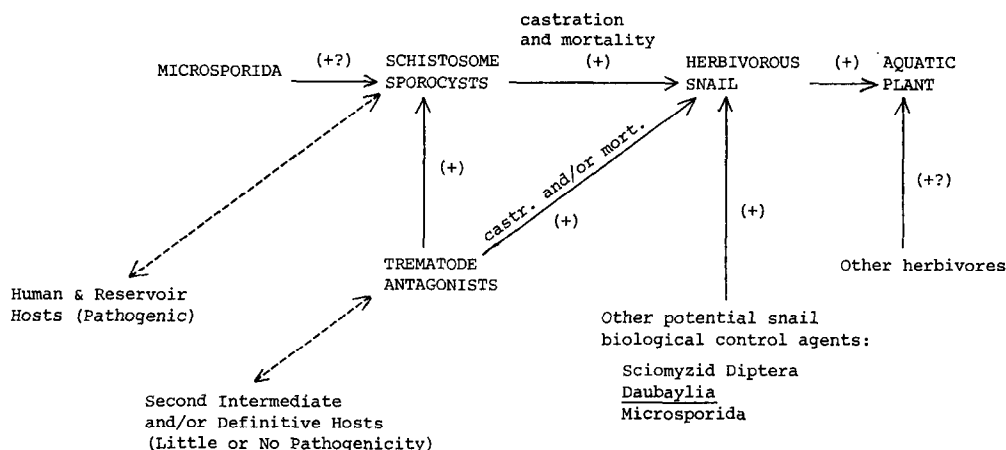
FIG. 2. Generalized theoretical model of the trophic interactions of a schistosome–snail system. Solid arrows indicate trophic interactions in the food web of this aquatic ecosystem. Positive (+) and negative (−) signs refer to the beneficial or deleterious aspects of the adjacent trophic interaction in terms of proposed biological control programs. Double-headed dashed arrows refer to interactions separated in space and time from the aquatic ecosystem.

Successful control by the primary parasitoid may be disrupted or reduced by the actions of obligate hyperparasitoids and facultative hyperparasitoids. Obligate means that these organisms are never primary parasitoids; facultative hyperparasitoids may act as primary parasitoids whenever development occurs in an unparasitized host. Negative facultative interactions include suppression of first-instar parasitoids by previously established interspecific infections. The primary parasitoid in Fig. 1 is often the key mortality factor (Flanders 1971). Should environmental circumstances change, another species (shown here as a facultative hyperparasitoid) might assume the principal regulatory role. The former primary parasitoid would then be considered with the facultative hyperparasitoids. These facultative hyperparasitoids may or may not have a significant effect on the control of pest populations, depending in part on whether their action as parasitoid or hyperparasitoid is of greater significance. The superbly documented control of the olive scale by *Aphytis maculicornis* and *Coccophagoides utilis* is a system in which control is enhanced by the secondary species, *C. utilis*

(see Huffaker and Kennett 1966; 1969; Huffaker, Messenger, and DeBach 1971).

Other potentially significant biotic factors in the control of insect pests include parasitic nematodes, whose trophic interaction is actually that of a parasitoid, protozoal and microbial pathogens. If a key pest is brought under control, other herbivorous pests may become ascendent, as with citrus scale insects (DeBach, Rosen, and Kennett 1971), or difficulties in the control of the key pest (needing heavy applications of insecticides) may preclude the use of successfully developed biological control practices for other economically significant pests (Harpaz and Rosen 1971).

Aquatic weeds or other vegetation provide the principal food source for the herbivorous snail intermediate hosts and constitute the base of the trophic interactions involving larval schistosomes (Fig. 2). I believe that larval trematodes (including schistosomes) have the potential to serve as important factors in the control of snail host populations. Many trematodes (Wright 1966; Køie, 1969), castrate their snail hosts. Some species may also cause differential mortality of infected hosts (Sturrock and Webbe 1971). I recognize

that, in many active foci of schistosomal transmission, the various trematodes present are not controlling snail populations, which may be exceedingly dense. In some cases, environmental manipulations, such as reservoir construction and irrigation networks, may provide such an unstable habitat with very low species diversity that snail populations can no longer be controlled by their restricted trematode populations, as appears to be the case in typical agroecosystems. However, in many situations small snail populations still maintain epidemiologically significant schistosome populations. These host populations may be regulated by larval schistosomes.

Obligate hyperparasites (hyperparasitoids?) such as the microsporidan of trematode larvae *Nosema eurytremae* (= *Perezia helminthorum*) may possibly become agents of schistosome population control (see Lie and Basch 1970). Probably of greater significance, however, are other trematodes that can serve as antagonists, whether through direct predation by rediae (Lie 1967), or by indirect suppression by rediae or sporocysts (Basch, Lie, and Heyneman 1969). Of the echinostome species studied experimentally (*cf.* Lie, Basch, Heyneman, Beck, and Audy 1968) and one cathaemasiid species (Basch, Lie, and Heyneman 1970) all but one (*Hypoderaeum dingeri*) were able to eliminate the schistosome with which it was paired and prevent establishment of subsequent schistosome infections. Field trials using inundative (blanket) releases of *Echinostoma malayanum* eggs from lab-infected rats against the bovine schistosome *S. spindale* (Heyneman and Umathevy 1967; Lie, Kwo, and Owyang 1970; 1971), suggest that the combination of antagonism between the trematode species, coupled with decline of the snail host's population under experimentally induced high rates of parasitism may lead to very reduced populations or elimination of the schistosome. Competitive exclusion of the target schistosome by a trematode

species of negligible medical or veterinary importance is the goal of currently expanding control studies involving trematode antagonism.

Other suggested control agents having some promise are sciomyzid Diptera (Berg 1964; Bratt, Knutson, Foote, and Berg 1969), which are parasitoids or highly specialized snail predators, as reviewed here by Doctors Eckblad and Berg; the nematode *Daubaylia* (Chernin 1962), which also functions as a parasitoid, and Microsporida parasitizing snails (Michelson 1963; Barrow 1965; Lie, Kwo, and Owyang 1970).

Herbivores (such as *Marisa cornuarietis*) that compete with snail hosts of schistosomes (*Biomphalaria glabrata*) and feed on their eggs have been employed in Puerto Rican schistosome control programs with limited success (Jobin, Ferguson, and Palmer 1970). *Marisa*, however, may cause problems with rice cultivation (Ortiz-Torres 1962) and may be an intermediate host for other parasites. Generally the danger of introducing a large, unspecialized snail species such as *Marisa* limits the usefulness of these competitor species.

The series of trophic interactions possible for both insect pest and larval schistosome populations are strikingly similar (compare Figs. 1 and 2). A key to their similarity lies in the proven means of insect pest population control by parasitoid insects and the suggested role of larval trematodes in the control of snail host populations. A single insect parasitoid larva ultimately consumes one and only one host. Infection by a single miracidium ultimately causes the castration (reproductive death) and/or premature mortality of one and only one host. Several other life history and trophic interaction similarities between parasitic castrators and parasitoids will be given elsewhere (Kuris, in preparation).

Demonstrating the fundamental similarity of the parasitoid–insect pest and the trematode–snail relationships, permits the

important differences between these systems to be logically and critically compared. This comparison may lead to some overlooked but necessary features in the development of a biological control program for trematodes.

The first such difference is that in an agricultural situation, the population to be protected is the plant crop at the base of the tropic web. The aquatic weed at the base of the schistosome food web is of no direct interest from the standpoint of protection and has received little attention in discussions of schistosome control. The *Marisa* competition work in Puerto Rico is the chief exception (Ferguson 1968). There is almost no information on the role of the snail hosts of *Schistosoma* spp. in limiting their plant food sources. Nor is there adequate information on the effects of food availability on the snail host populations. A valuable study in this respect is that of Eisenberg (1966), who studied the trophic relations of a lymnaeid species.

Secondly, while the web of trophic interactions involved in insect pest and larval schistosome dynamics is basically similar, the position of the target species for proposed control efforts is not. In the insect model, the pest is an herbivore, controlled by a primary parasitoid. The herbivorous snail population is not the pest. Rather, it is the schistosome, the trophic equivalent of the parasitoid.

The difference in trophic positions of the target species has important theoretical considerations. To control an herbivorous pest, the agent of choice must act in a density-dependent manner and have a good searching ability at low host densities. Control of nonherbivores is less clearly understood, at least in terms of translation of theory to practical control. Although insect pest control studies have rarely been interested in the control of a parasitoid species, several studies show instances in which flourishing populations of parasitoids have been eradicated, reduced to permanent low levels, or to restricted geographic ranges. This happened on several occasions after introduction of a new parasitoid species into an existing parasitoid complex (DeBach and Sundby 1963; Flanders 1965).

Flanders (1966) found two basic mechanisms for competitive exclusion of populations: intrinsic and extrinsic. In the former, the interaction is between individuals, the superior species being capable of mutilation, starvation, suffocation, ingestion, or production of toxic substances which kill, inhibit development, or prevent infection of the inferior species. Such replacement, Flanders argued, can take place regardless of host abundance. It is obvious that the categories of interspecific trematode antagonisms described by Lie and co-workers (Lie, Basch, Heyneman, Beck, and Audy 1968; Basch, Lie, and Heyneman 1969; Lie, Kwo, and Owyang 1971) and reviewed by Lim and Heyneman (1972) are remarkably similar phenomena.

Extrinsic competition resulting in competitive replacement is a population interaction. The superior species has better host-habitat finding, host-finding, and host-acceptance attributes (Flanders 1966). Hassell and Varley (1969) have mathematically described some of the parasitoid searching characteristics determining species replacement. Data for schistosomes in combination with various echinostome species indicate that the species replacement predictions of these authors may also apply here. An important feature of these systems is that the replacement species usually is a more effective host population control agent (Flanders and Badgley 1963; Huffaker and Kennett 1966; van den Bosch 1968; Hassell and Varley 1969).

If a species is both a superior intrinsic and extrinsic competitor, then replacement of the inferior species would seem to be a necessary result of the introduction of the superior species (Flanders 1966). If this conclusion is valid, and the parasitoid–larval trematode analogy developed herein

is tenable, then the methods successfully employed by pest control entomologists are of vital interest to the control of trematode diseases.

A third significant difference is that the obligate hyperparasitoid, a component insect biological control workers attempt to exclude from their systems, may be of considerable importance in the control of larval schistosome populations. The only hyperparasites of larval schistosomes noted are Microsporida. Their interactions with *S. spindale* in field experiments are complex, but they did not appear to reduce the trematode populations without involvement of larval echinostomes (Lie, Kwo, and Owyang 1970). Perhaps the most serious defect of microbial agents of biological control is that they are inefficient at low host densities (Huffaker, Messenger, and DeBach 1971). Thus, although their actions are density dependent and they can be shown to drastically reduce high-density host populations, they are poor candidates for permanent biological control (for some notable exceptions see Falcon 1971).

Fourthly, the most glaring difference between the insect pest and schistosome problems in relation to the model analogy is that both schistosomes and their potential trematode antagonists have complex life cycles; involving other hosts (Fig. 2). Thus, a considerable portion of the trematode population is spatially and temporarily separated from the trophic interactions presumed necessary for the operation of a classical biological control program. The theoretical significance of the complex life cycle in biological control programs has received little attention. Consideration of this aspect should result in a substantial broadening of the basic theory of biological control.

The two-way interactions of trematodes with their second intermediate and/or definitive hosts symbolized by the double-headed arrows of Fig. 2 may be visualized as a temporal third dimension in the control system model. This additional dimension challenges the insect parasitoid–larval trematode analogy, questions both the goals of schistosome control programs, and the possibility that schistosome population control can occur principally via the snail-related larval stages (miracidia, sporocysts, cercariae).

Although the relationship is more tenuous than are the trophic interaction analogies, I think that the requirements of many hymenopterous parasitoids for adult-stage food supplements from other than insect pest populations (Doutt 1964; Askew 1971) is comparable to the two-host life cycle of some trematodes. The occasional need for some parasitoid populations to pass certain seasons of the year in noneconomic hosts, while controlling pest populations at other times, is perhaps even more comparable. The mymarid, *Anagrus epos* controls populations of the grape leaf hopper in the San Joaquin Valley of California only when it can overwinter in the eggs of another species of leaf hopper that feeds on wild blackberries (Doutt and Nakata 1965). Thus, some parasitoid generations are both spatially and temporally separated.

An interesting feature of the efficacy of those parasitoids requiring supplementary food sources or hosts is that the parasitoid's ability to regulate the pest population is not very sensitive to changes in the availability of the additional nutritional or host sources. *A. epos* controls grape leaf hoppers up to 2 miles from the blackberry patches (Doutt and Nakata 1965). This flexibility in the quantitative need for supplemental food and food sources is consistent with the disturbing reports that chemotherapy of the human populations in endemic schistosomiasis foci does not necessarily lead to a sharp drop in the percentage of snails infected nor to reduced cercarial output from these snails (Jordan 1965). The extreme conclusions of Macdonald (1965) with regard to the unimportance of good sanitation in the control

of schistosomiasis are not accepted in this context (see Hairston 1971).

The supplementary needs of adult parasitoids are usually supplied by a brief interaction with the nonpest source, whereas the complex life cycles of schistosomes and their possible trematode antagonists involve long, intimate parasitic contact with their vertebrate hosts. While this difference in degree of intimacy weakens the model analogy, I do not think that it weakens the possibility of competitive replacement of the schistosome by other trematodes. Replacement could occur as long as the potential replacement species does not have a significantly longer numerical response time because of its complex life cycle, than does the schistosome. In practice, this probably means that a species having a three- or four-host life cycle, with concomitant lengthy generation times, may not be able to exert a successful extrinsic competition pressure.

Another interesting difference between the insect pest and schistosome control model is that the goal of the former, to maximize the economic value of the plant crop, is a direct outcome of the reduction of the pest population to a noneconomic level by the parasitoid; while the goal of schistosome control through actions on larval stages within snail hosts is the indirect elimination of medical injury to the human host.

Can the population of adult schistosomes in human hosts be reduced below the level of medical injury chiefly through manipulation of the snail-inhabiting larval populations? If the population dynamics of snails, schistosomes, and their potentially important interactants, trematode antagonists and sciomyzid Diptera, are as intimately coupled as insect–parasitoid insect pest systems, then I think that such a means of control is not only possible, it may be necessary for long-term regulation of schistosome populations at a subinjurious equilibrium level.

APPLICATION OF THE PARASITE QUEST THEORY TO SCHISTOSOMIASIS

Hassell and Varley (1969) reviewed the relationship of a, the Nicholsonian area of discovery, to host and parasitoid density. They show how the assumption that the searching efficiency of the parasitoid (measured by a) is a constant leads to population oscillations, rather than to an equilibrium density as predicted by Nicholson and Bailey (1935).

The term "area of discovery" is a misnomer in that a is rarely calculated as an area, but rather in terms of host and parasitoid densities such that

$$a = \ln(u_1/u)/P, \qquad (1)$$

with P being the density of searching parasitoids, u_1 initial host density, and u the final host density (the density of unparasitized hosts). Generally, a decreases with increasing parasite density (Huffaker and Kennett 1969; Hassell and Huffaker 1969; Hassell and Varley 1969) so that log a is inversely proportional to log P. Thus,

$$\log a = \log Q - m \log P \qquad (2)$$

Here, Q, the quest constant, is the area of discovery for an individual parasitoid (the value of a when $P = 1$), and m, the mutual interference constant, is the slope of the regression of log a on log P (a measure of the degree of interference between parasitoids as their density increases).

Substituting the density–dependent relationship for a of Eq. (2) into the Nicholsonian Eq. (1), Hassell and Varley (1969) produced a model for parasitoid searching with a direct density-dependent attribute. They showed how this model can yield stable host and parasitoid densities. Using their parasite quest relationship, Hassell and Varley showed the possible interference relationships when a third parasitoid is introduced into situations where two parasitoids coexist. Their model predicts that in all instances involving in-

troductions of a less efficient parasitoid, it will fail to become established. In most instances involving a parasitoid with searching abilities similar to or better than the coexisting parasitoid pair, the biological control of the host will be improved, although the previous parasites' densities will decline. Only when a is nearly constant over the range of parasitoid densities will unfavorable population oscillations be induced. As discussed above, such oscillations are rarely reported. The important biological control implication of the parasite quest theory is that multiple introductions of control agents are likely to have either a beneficial effect or fail to show an effect. Only in unusual circumstances (capable of prediction from laboratory data?) will the previous level of biological control be impaired (Hassell and Varley 1969).

For trematode–snail systems, the relationship between the area of discovery, a, and miracidial density, P, may be calculated in much the same manner. This hypothesis was tested by the following experimental procedure.

All exposures were to 5 ± 1 mm individual *Biomphalaria glabrata* of the NIH albino strain in 5 ml distilled water in small vials. Known numbers of miracidia of *S. mansoni* or the echinostomes *Paryphostomum segregatum, Echinostoma lindoense,* and *E. liei* were placed with the snails for 2–3 hr. Positive infections by schistosome

daughter sporocysts or echinostome redia were recorded through the transparent shell 1–2 wk postexposure. Early examination reduced the confounding effects of snail mortality and snail recovery in the investigation of infection dynamics.

All systems tested showed an inversely proportional relationship between log a and log P, much as in insect parasitoid systems. This is further evidence for the dynamic similarity of these systems. Regression lines for the four trematodes species are shown in Fig. 3, regression constants being provided in Table I. Interestingly, these few species show two of the four theoretically possible curves discussed by Hassell and Varley (1969). *E. lindoense* and *E. liei* are predicted to coexist with *S. mansoni* because their values of m and Q are similar. Each successive introduction should cause the snail schistosome densities to decrease. *P. segregatum*, on the basis of its searching ability, is predicted to replace the other species because at all miracidial densities the searching efficiency of this echinostome is substantially higher than its competitors. Line I would describe a parasite with poor searching ability. Such an inefficient species should fail to become established. Only a parasite having a high quest constant, Q, and little mutual interference (low m) could lead to a possibly unfavorable outcome (line II). Such a parasite, of course, best fits the original assumption of an area of discovery that is not density dependent (Nicholson and Bailey 1935). Introduction of a parasite with these characteristics might result in violent population fluctuations and the release of the host from natural control. However, parasite II should replace its competitors and thus still have a favorable outcome for schistosomiasis control since it is the elimination of the schistosome competition not the reduction of snail density that is our ultimate concern. Thus, the outlook for biological control of ecologically homologous parasites by larval trematodes is even more promis-

TABLE I

Regression Constants for the Equation
$$log\ a\ =\ log\ Q\ +\ m\ log\ P$$

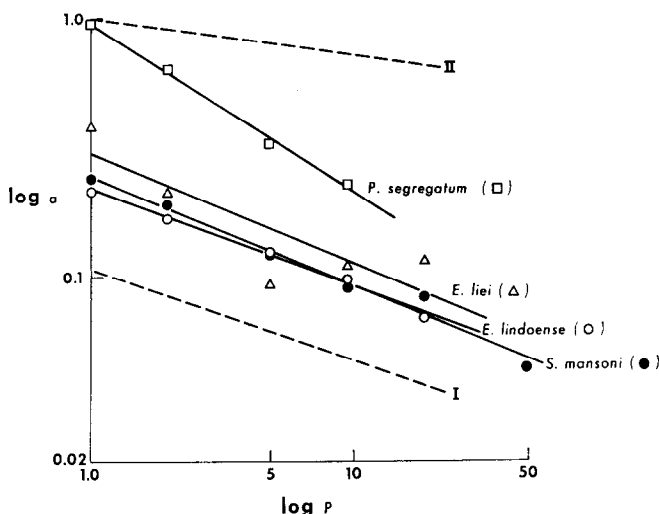| Trematode	Quest constant (Q)	Mutual interference constant (m)
Schistosoma mansoni	0.245	−0.416
Echinostoma lindoense	0.219	−0.370
Echinostoma liei	0.300	−0.418
Paryphostomum segregatum	0.955	−0.641

Fig. 3. The relationship between the searching efficiency of a trematode miracidium and miracidial density expressed as a regression of the area of discovery, a, on parasite density, P, after logarithmic transformation. Lines I and II are hypothetical relationships. See text for further explanation.

ing from this point of view than is the control of insect pests as discussed by Hassell and Varley (1969). According to this application of the parasite quest theory, all introduced trematodes will either reduce the density of larval schistosomes or have no effect. No such introduction will increase schistosome density.

These theoretical considerations do not call for unbounded optimism. Violent fluctuations of the snail population caused by a type II parasite would present a continual hazard for the epidemic reintroduction of schistosomes into the aquatic ecosystem. Such reintroductions would certainly be expected in view of the longevity of the worm in the vertebrate host and the migratory human populations over the geographic range of schistosomiasis. Of greater concern, the four interference relationships (Fig. 3) do not provide sufficient conditions for the theoretical control of schistosome populations. Unlike the insect parasitoids considered by Hassell and Varley (1969), trematodes require permanent populations of second intermediate and definitive hosts, each with access to the primary snail-host

habitat. Without input of trematode eggs from the definitive host the relative searching abilities of the rival parasites are of no consequence. Prospective control using *P. segregatum*, the competitor species with the best laboratory performance both intrinsically (Lim and Heyneman 1972) and extrinsically (herein), is particularly ironic since to date this species has been maintained only in Brazilian urubu vultures (*Coragyps atratus foetens*). Until an ecologically significant definitive host is found, *P. segregatum* offers little hope of becoming a control agent.

GOALS AND SUCCESS CRITERIA OF SCHISTOSOMIASIS CONTROL PROGRAMS

Whether one accepts the validity of the insect parasitoid–larval trematode analogy outlined here, some of the well-established biological control principles are at odds with certain viewpoints about goals and success criteria of schistosomiasis control programs frequently expressed by parasitologists and public health workers. Eighty years of applied pest control experience have forged these evaluations. Programs

using all means of natural control, para- sitoids, predators, and microbial pathogens, share certain basic considerations. In light of the long history of their success it would seem that the burden of proof must rest on those promulgating untested alternatives.

Berg (1964) admirably stated the case for the desirability of biological control as opposed to chemical control (mollusci- cides). His considerations with regard to the need for selective toxicity, short-term chemical stability, and snail resistance studies are heartily endorsed. Regrettably, development of molluscicides with these desirable attributes still lags.

Control vs Eradication

One of the most uniformly accepted tenets of insect pest biological control pro- grams is that the ultimate goal is regulation of the pest population at an equilibrium density that is below the level causing economic damage (Flanders 1966; 1971; Clark 1970; Watt 1970; DeBach 1964; Huf- faker, Messenger, and DeBach 1971). Eradication has rarely been successfully sought (Southwood and Way 1970). Rabb (1970) summarized this attitude succinctly:

"The philosophy of biological control is to manage the pest population rather than to eradicate it. Obviously this philosophy is incompatible with the public's poorly conceived notion of a pest-free environ- ment."

The significance of this goal is that the solution is long term and general. As neither the pest nor its control will have been eliminated, the system is buffered from the effects of reintroduction that often lead to explosive outbreaks. This outlook regards the pest as a necessary and persist- ent component of a stable ecosystem. Stressing the practical importance of this philosophy, Huffaker and Kennett (1956) demonstrated that a low-level stability of strawberry mite populations was attained more rapidly when both pest and predator were simultaneously introduced than when

predators were introduced after the pest had been recognized as a problem. Another important consideration in the choice of strategies of control versus eradication is that the economic cost of pushing the schistosome population to the elimination point is likely to rise drastically as eradica- tion nears (see Chiarappa, Chiang, and Smith 1972). In other words, destruction of the few remaining schistosome or snail populations will tend to cost more than the program responsible for the great reduc- tions in population density. With the ex- tremely limited funds available for schis- tosome control programs in underdeveloped countries, costs and benefits must be care- fully weighed. In light of these considera- tions, it is discouraging to note that eradica- tion of schistosomes or their snail hosts is the goal, stated or implicit, of most schis- tosome control programs and of most med- ical, parasitologic, and public health work- ers engaged in this difficult field.

Implementation and Success Criteria

If population regulation rather than eradication is the goal of schistosome con- trol campaigns, what are the criteria for implementation and success of such pro- grams? For insect pest control programs the establishment of implementation cri- teria necessitates the recognition of levels of allowable economic injury (Smith 1970; Clark 1970; Watt, 1970; Headley 1972; Chiarappa, Chiang, and Smith 1972). Clark (1970) stressed the need for investigation of the economics of injury as an essential prerequisite to the selection of control options. Watt (1970) found "the thresh- old density at which we decide to apply control as one of the most important fac- tors determining the cost-benefit ratio of different strategies." The lower the ulti- mately acceptable threshold, the more fre- quent and costly the treatment. Addition- ally, the higher the density of the pest population termed an outbreak, the greater the proportion of the susceptible popula-

tion that must be protected in order to contain the pest. Way (1953; 1954) described the relationship between outbreak density of the coconut bug and the percentage of the crop protected.

Watt (1970) stressed that it is absolutely necessary to set up a rigorous criterion for the effectiveness of control. Along with a favorable cost-benefit ratio, such a policy should have long-term effects and minimal need of future measures. Biological control agents best meet these criteria.

In a similar vein rational schistosome control schemes necessitate the estimation of an allowable medical injury level of schistosomiasis. To do this, the relationship of pest (schistosome) density to morbidity and mortality of the human populations must be clarified. Unfortunately, there is a paucity of information regarding this crucial question. Cheever (1968) provided the only data bearing on this relationship in an admirable autopsy study in Brazil. His data implicated a worm burden of 100+ female S. mansoni as a serious mortality factor. Much more information of this sort is needed in order to determine regional differences and mild and severe nonfatal worm densities. Cheever's (1968) worm burden data give a good fit to the negative binomial distribution (Kuris, unpublished; Hairston, in press). Such a fit is not unexpected as the negative binomial arises from several realistic models of parasite infection dynamics (Crofton 1971). Negative binomial distributions are strongly clumped, including many more uninfected and heavily infected cases than expected from a random (Poisson) distribution. The aim of schistosomiasis control programs becomes a task of reducing the worms' population equilibrium so that the frequency distribution shifts well to the left. If such a rise in the frequency of low-level infections does occur, the few who are ill with schistosomiasis may be more readily identified and treated individually with the relatively expensive techniques available.

Costly massive treatment programs, economically impossible in many places, will no longer be necessary.

In addition to allowing us to establish and evaluate success criteria, establishment of a worm burden–pathology frequency distribution may permit an indirect estimation of schistosomiasis-related mortality, using the truncated distribution analysis of Crofton (1971). These data should be drawn from as random a segment of the host population as possible.

Further work is also needed on the relationship between egg production and worm density, host age, and time of infection. This will facilitate use of egg counts, the most easily obtained quantitative data, in the determination of threshold levels for schistosomiasis management.

CHOOSING A GOOD BIOLOGICAL CONTROL AGENT

Rational selection of insect pest control agents remains perplexing. Review of past successes is not completely illuminating. Only a few characteristics of biological control agents have been consistently evident (see DeBach 1965).

1. "Ability to find hosts at low population densities is a prerequisite for successful biological control and of course, a great advantage in competition with other species which parasitize the same host species" (DeBach and Sundby 1963). That the ability to search effectively at low host densities is a crucial characteristic of a successful biological control agent seems definitional. If the host–parasite system "uncouples" at low densities then the host population would be likely to rebound. Fluctuating epidemics and/or possible extinction of the biological control agent may result. The views of Wright (1968) and Webbe (1968) regarding density dependence as an unsuitable feature of control programs are directly counter to the overwhelming evidence from successful insect pest management studies. Cyclical patterns

are rarely in evidence in insect host parasitoid field studies (Hassell and Varley 1969). Rapid restoration of pest population levels has been noted after pesticide usage (Watt 1970), not following biological control practices. Density-independent mortality does not lead to unbalanced age structures. These, in turn, will not necessarily lead to an ultimate eradication of the population.

The competitional advantage afforded by greater success in searching ability at low host densities seems less obvious. However, it seems valuable provisionally to regard searching ability as an important factor, as this is one comparative feature that can be tested in the lab.

If so, this suggests the following additional data needs: searching ability of schistosomes versus trematode antagonists over a wide range of snail densities conducted in realistic volumes of water (not 5 ml as above).

2. An organism is likely to be a better biological control agent if it kills more than one host (implied by DeBach and Sundby 1963). This seems to apply only to control of the primary host, the snail. Sciomyzid larvae seem promising here.

3. Good biological control agents are usually highly specific to the host (DeBach 1965). Thus, the suggested use of trophic generalists as biological control predators (Wright 1968), is not supported by the experience of insect pest management. Nonspecialists switch their food (or host) preference before the pest population has been adequately reduced. After switching they tend to leave the pest population undisturbed, promoting its rapid recovery. These aspects of predator switching are documented by Murdoch (1969). Only trophic specialists are adapted to cope with very low host densities. How else could they survive?

4. " 'A good parasite is a scarce parasite.' It is well to bear this in mind in searching for new parasites to import for biological control projects" (DeBach and Sundby 1963).

I think this is a very important clue for detecting a potentially successful schistosome biological control agent. As Hassell and Varley (1969) and DeBach and Sundby (1963) showed from different lines of evidence, after the elimination of its competitor, a successful displacing agent is quite capable of reducing a host population to such a low level that its own numbers are reduced. A new low-level equilibrium is established.

5. If DeBach and Sundby's (1963) elegant example of competitive displacement is at all typical of this phenomenon, then the good schistosome biological control agent probably resides in regions (local or widespread) where schistosomiasis is a negligible or unimportant disease.

"Relative success in the country of origin may furnish the best predictive leads" (DeBach 1965). This suggests the following research need: careful mapping at several scale levels (continental, national, provincial, and local) of schistosomes and their potential homologs; Angola (Berrie 1970) and some more restricted localities have been identified as regions with *Biomphalaria* and little or no schistosomiasis.

Homologs capable of competitive exclusion must necessarily have mutually exclusive geographic ranges. A conceivable use of this principle might involve introduction of the zoophilic Taiwanese form of *S. japonicum* to mainland China or the Philippines. "Biological control workers should never consider, *a priori*, that two similarly appearing populations in different geographical areas represent the same species, . . . such lack of knowledge . . . precluded the importation of the most important parasites of the red scale into California . . ." (DeBach 1969).

CONCLUDING REMARKS

The fledgling discipline, biological control of human and veterinary diseases, will

gain much from critical appraisals of the theory and methodology of its vigorous fraternal science, biological control of insect pests. If the trophic analogy of schistosomes and other "pestiferous" helminths to primary parasitods is valid, then certain research areas demand prompt attention: the relative searching ability of schistosome miracidia and their presumptive ecological homologs, measurement of the allowable human morbidity levels and the frequency of such cases in populations, and the further geographic mapping of schistosomes and their intermediate hosts to enable rational searches for potential natural control agents to be conducted.

The remarks of Rabb (1970) are considered to be equally applicable to schistosomiasis:

"Pest management deals primarily with populations, communities, and ecosystems. Thus, the basic biological discipline involved is unequivocally ecology, and there should be no fuzzy thinking on this fact. Other disciplines have provided and will continue to provide valuable information relative to specific control methods and agents; however, final decisions regarding the use of any method or combination of methods must be made by persons firmly grounded in ecological principles and thoroughly familiar with the population dynamics of the pest to be controlled."

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