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Biological Solutions to Problems Arising from the Use of Modern Insecticides in the Field of Public Health.[1]

By MARSHALL LAIRD.

Insect control was revolutionized by the highly successful debut of DDT during World War II. The combination of lethality and enduring residual properties shared by this and other new synthetic insecticides enabled hitherto unattainable levels of control to be reached. Initial victories in the field of public health, notably against mosquitoes, flies and lice, coupled with the first enthusiastic reports from economic entomologists, fostered premature assertions that man had turned the final corner in the fight against his insect enemies.

Older insecticides such as paris green, NCI powder and borax became as outmoded in the armoury of the public health man as tanglefoot flypapers and the beer-baited traps formerly advocated for use against cockroaches. Few continued to interest themselves in naturalistic control, which had made headway in both medical and economic entomology in the years between the wars, and exciting avenues for research opened up among the chlorinated hydrocarbons and organophosphorus compounds. Many of the entomologists of the new generation viewed their work through the eyes of chemists rather than biologists. Their writings too often reveal that preoccupation with empirical formulae and mathematical niceties has clouded their appreciation of the fundamental fluidity and bewildering interdependence of living things. This is doubly unfortunate in that today, after some 15 years' use of the synthetic insecticides, we are confronted by most critical problems the solution of which must be delayed pending a general reawakening of interest in insect natural history.

These problems are insecticide resistance, and the upsetting of the balance of nature through the use of insufficiently selective toxic compounds against pest species. It became evident at an early stage that DDT may endanger wildlife (COTTAM and HIGGINS, 1946) and this aspect of pesticide toxicity was recently

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[1] Read before the 125th meeting of the American Association for the Advancement of Science, Washington, D. C., December 26th-31st, 1958. Abstract published in The Anatomical Record, *132,* 466.

reviewed by RUDD and GENELLY (1956). Birds and other animals may suffer through decimation of insects upon which they customarily feed, as well as by ingesting large numbers of poisoned arthropods (WEBSTER, 1948) or other organisms, both plant and animal, which have accumulated dangerously high concentrations of insecticides (RUDD, 1958). BROWN (1951) concludes from a detailed survey of the literature that the "aerial application of 1lb/acre of DDT, the favoured dosage for forest insect control, is definitely hazardous to fish; but the game fishes are less susceptible than the inhabitants of stagnant and exposed pools, and the hazard is less the denser the forest cover." However, only half this dosage has since proved highly dangerous to salmon in heavily forested watersheds of northern New Brunswick, subjected to aerial spraying to control a serious outbreak of spruce budworm (IDE, 1956).

It is probable that little lasting harm would be caused by a single application of this nature—after all, streams regularly recover from catastrophic losses of bottom insects due to flooding (HOFFMANN & SURBER, 1946). The real danger lies in the prospect of future aerial sprayings in closely succeeding years, felt necessary for the preservation of the trees (KERSWILL, 1958). It is estimated that by 1961 fish poisoning and food denial will have reduced adult salmon stocks in affected New Brunswick river systems to about 25% of their pre-DDT level (KERSWILL, 1958). This is disastrous enough in itself in an area where commercial and game fishing closely follow lumbering in importance; but when spraying finally ceases a further consequence, this time of public health importance, must be anticipated.

Blackflies (Simuliidae) are among the first aquatic insects to reappear after DDT-spraying, as has already been noticed in New Brunswick (KERSWILL, 1958). They then thrive in the interval before arthropod predators having a relatively longer life-cycle are able to restore the natural balance. Thus DAVIES (1950) recorded that the application of 6 lbs/acre to an Ontario stream in 1944 was followed by short-lived control of simuliids. These insects then showed a dramatic population increase before their natural enemies had reappeared in numbers, and by 1947 the average emergence rate was about 17 times that of the pre-control years.

Such a situation is sufficiently serious where only a biting pest is to be contended with, but more dangerous possibilities arise where the insects concerned are vectors of disease organisms. In 1945 it was observed that after wartime DDT-spraying ceased on Nissan Island, Territory of New Guinea, the malaria vector, *Anopheles farauti,* rapidly reinvaded the former controlled area and became extremely abundant in the absence of balanced populations of predacious Odonata, Hemiptera and Coleoptera (LAIRD, 1952). Once having set foot upon the treadmill of chemical control, sudden cessation is likely to be fraught with risk. It is obvious what could follow were a major control campaign based upon the use of synthetic insecticides in a populous area suddenly terminated by an economic or military catastrophe—the ensuing flourishing of vectors in the absence of normal biological checks would take place at one of those times of human want and disorganization that history shows most likely to favour epidemics.

Today's successful control of a pest by non-selective chemicals may thus set off chain reactions which terminate in new problems we must face tomorrow. To quote BROWN (1951), insecticidal chemistry is a weapon to "be used as a stiletto rather than a scythe".

This applies to other synthetic insecticides as well as DDT. A recent instance of scythe action concerns dieldrin, used in pellet form against larval *Culicoides* (Heleidae) in a Florida salt marsh (HARRINGTON & BIDLINGMAYER, 1957). At least 30 species of fish were eradicated in addition to the insects, as were crabs and crustaceans generally. Alone among the macrofauna molluscs appeared unharmed, and in the absence of other scavengers these thrived upon the remains of the insecticide's victims. Highly undesirable results might follow the application of this technique to mosquito control in areas where aquatic snails are intermediate hosts for human schistosomes.

To what extent, then, may chemicals be used selectively against insects? Kerosene and Paris green, among once-favoured insecticides, have little direct effect upon freshwater ecology beyond destroying mosquito larvae (BISHOP, 1940). RIPPER (1944) showed that when 95% nicotine is vapourized at a dosage of 3¼ lbs/acre, at temperatures above 60°F and with an exposure time of 1 minute, cabbage aphids suffer heavy mortality while their parasites and predators remain unharmed. Agricultural entomologists soon found, however, that DDT, unlike these once-favoured substances which lack any residual effect, often does more harm than good by killing parasitic and predacious arthropods at the same rate as insects under chemical attack to the ultimate advantage of the latter (VOLTERRA, 1928). They discovered a partial solution, effective against lepidopterous pests chiefly affected by ingesting DDT, whereby the crystals were pre-coated with a protective layer of degraded cellulose (RIPPER et al., 1948). This procedure, being designed to destroy the contact residual effect that adds so much to the value of DDT and related compounds from the public health standpoint, is obviously of limited value to medical entomologists.

The greater the care paid to the formulation and concentration of DDT-based insecticides, the greater the selectivity that will follow. Successful control of blackflies (PREVOST, 1946; COPE et al., 1949) and mosquitoes (TWINN et al., 1950) has been achieved with relatively little harm to other aquatic animals by strict regulation and supervision of these factors. Unfortunately, though, it is one thing to theorize from experiments conducted under nicely controlled conditions, but quite another to achieve the necessary precision in the field; especially in the face of the urgency so often underlying insect control measures.

In large-scale control programmes the plan of action is seldom put into effect by the entomologist who drew it up. The operative is sometimes the pilot of an aircraft equipped for spraying, sometimes a man on the ground working on his own or as part of a team either from a vehicle or on foot. Uniformity of dosage may be sadly influenced by the harassments inseparable from low-altitude flying. In the case of the worker on the ground it is affected by a multitude of factors ranging from the proximity of the lunch hour to bribery. Tropical paddy farmers and smallholders, fearing that mosquito larvicides will damage their crops, have been known to adopt the latter recourse, which results in the leaving of unsprayed pockets in the midst of overdosed areas. Failure of the human element is of course minimized by adequate training and supervision, but an emergency is likely to force these requirements to the wall. It is true that parathion and other organophosphorus compounds may be employed with greater selectivity than most chlorinated hydrocarbons through their volatility and because their high toxicity to man dictates painstaking supervision of their field use. Nevertheless, it must be conceded that over the last 15 years the insecticidal scythe has seen considerably more use than the stiletto.

Whatever the biological, physiological or genetical basis of a particular instance of insecticide resistance, the population concerned is comprised of the descendants of relatively few initially resistant examples which have replaced the susceptible majority through natural selection. The first report of a resistant insect of public health importance came in 1946, and concerned the cosmopolitan housefly in Italy. Within 10 years the number of species of such insects was placed at from 18 to 37, the former figure being given by BUSVINE (1957) who counted only instances verified with absolute certainty, the latter by QUARTERMAN and SCHOOF (1958) who included all reports. *Simulium, Phlebotomus* and *Glossina* are the only genera of major medical importance for which resistance has not yet been recorded (BROWN, 1958). Most published data concern DDT and other chlorinated hydrocarbons, but information on resistance to organophosphorus compounds is accumulating. As this is being written the first account of mosquito resistance to parathion has appeared (LEWALLEN and BRAWLEY, 1958). Resistance may involve one or more of the chlorinated hydrocarbons, one or more of the organophosphorus compounds, or insecticides of both groups. The problem is further complicated by the fact that exposure to one insecticide, whether resistance appears or not, may bring about a decided tolerance to other compounds. Again, strains of individual species exhibiting a certain pattern of resistance to a particular insecticide may appear in many parts of the world, in a few localities or in a single locality only. After all, the units we term "species" vary not only geographically but also in time within a single locality. It follows that their biological and physiological attributes vary from area to area at the same time as well as within a given area at different times (BUGHER, 1955).

The attention which this subject is receiving is shown by the fact that about 750 relevant papers had appeared by 1957. This literature has been very fully reviewed by BROWN (1958), to whose comprehensive and stimulating work those interested in a detailed account of insecticide resistance are recommended. For the present let it suffice to recall the decision of the Eighth World Health Assembly to request governments "to intensify plans of nationwide malaria control so that malaria eradication may be achieved and the regular insecticide-spraying campaigns safely terminated before the potential danger of a development of resistance to insecticides in anopheline vector species materializes" (WHO, 1955); and the continuing opinion of the WHO Expert Committee on Insecticides "that resistance is at present the most important single problem facing vector-control programmes" (WHO, 1958).

Suggested solutions include the mixing of two insecticides of independent action (HEWLETT and PLACKETT, 1950), the alternation of insecticides without waiting for resistance to appear (COYNE, 1951) and the use of basically different chemical compounds against larvae and adults of individual pest species (SIMMONS, 1954). When the first one was tested by exposing houseflies to DDT-malathion, it proved that resistance to each of the insecticides in the mixture developed at the same rate as when that compound alone was employed (USDA, 1957). The second holds some promise of better results, provided that the action of the chemicals used shows negative correlation (BROWN, 1958). If it does not, relief is temporary at best. Resistance to DDT, for example, may be perpetuated in the absence of this insecticide by others, including dieldrin and organophosphorus compounds. A return to DDT even after an interval of several years has been followed by the rapid reappearance of full resistance (Brown, 1958). Even where there is negative correlation, continued use of a compound to which resistance does not appear may predispose to resistance to other insecticides (Meltzer, 1956). Much remains to be learned before fully satisfactory rotation procedures are developed. An important contribution towards this end is the worldwide check on the onset of resistance made possible through the development of standard test methods and the distribution of appropriate test kits by the World Health Organization (WHO, 1958). Meanwhile, everything possible must be done to slow down the development of resistance. Perhaps the use of fundamentally different insecticides against adults and larvae offers a means of achieving this. However, as in the other solutions so far advocated, there would be disadvantages in increased costs and complexity of insecticidal control. Alternative remedies include the withholding of larvicides altogether so long as residual spraying against adults remains effective and economically practical (WHO, 1957), and control measures which do not involve insecticides at all.

Practical measures of the latter kind depend upon sound understanding of the bionomics of the species to be dealt with. It is to be noticed in this connection that at its most recent meeting the Expert Committee on Insecticides of the World Health Organization stressed the need for wide and urgent attention to currently neglected ecological aspects of insect control problems (WHO, 1958).

Some ingenious control procedures not involving the use of chemicals have been tested in recent years. One of these seeks to upset mosquito population balances by luring a high proportion of males to traps "baited" with amplified recordings of the humming of females. It should be noted that the congregation of male mosquitoes about a humming dynamo was observed at Saratoga Springs, New York, eighty years ago (Maxim, 1901), while the refinement of adding an electrocution device to a sound trap had already been tested by the turn of the century (Weaver, *in* Howard, 1901). More mundane traps have long been employed against many medically important insects. Further and more detailed studies of attractive baits are highly desirable. Relevant projects might follow the lines of Buxton and Hopkins' (1927) classic investigations of larval habitat selection in *Aëdes polynesiensis,* for our understanding of this whole subject is still far from complete. Ultrasonics offer a further field for research into the control of animals of public health significance. LAGRANGE (1951) has noted that ultrasonic waves kill miracidia, cercariae and adult snails, and Mr. G. WISHART is investigating possible mosquito control applications of ultrasonics at the Canada Department of Agriculture's Entomology Laboratory at Belleville, Ontario. Another technique entails the introduction of mass-reared males, sterilized by radioactivity, into wild populations of their species. The normal females with which they mate produce only sterile eggs. In the first field experiment using this method, screw-worms were eradicated from Curaçao in a matter of months (BAUMHOVER et al., 1955). An attempt to exterminate the same insect under continental conditions is now under way in Florida following promising field trials (LINDQUIST, 1955), and a pilot experiment involving the sheep blowfly has been commenced at Holy Island, Northumberland, England (ANON., 1957). KNIPLING (1955) has outlined other possible applications in both economic and public health spheres, and the technique may prove adaptable to tsetse control (SIMPSON, 1958).

HUFF (1929, 1931) demonstrated the hereditary nature of the inability of a strain of *Culex pipiens* to become infective for avian plasmodia. JONES (1957), recalling this, suggested isolating strains of vector species having inability to become infective as a dominant characteristic, for introduction into areas where vector strains had been reduced in numbers by standard control measures. Related suggestions include the selection and propagation of zoophilic strains of vectors. In this connection, agricultural entomologists are well aware that phytophagous insects may be diverted from economically desirable plants to weeds by the experimental selection of mutants hereditarily fixed in their preference for the new host (PAINTER, 1951).

Surely these avenues merit further exploration in view of present difficulties with modern insecticides. A variety of other such projects readily come to mind. Anti-mosquito measures imply the control of larvae and adult females; little is heard of the need for the destruction of pupae or males. And yet probably the most critical interval in the life of the mosquito is the emergence of the adult, an act requiring a high degree of stability of the air/water interface (BRUMPT, 1941). Chloroform breaks up the surface film, allowing surface-dwelling insects to drop through it and drown (LAIRD, 1956). Would it not be worthwhile to search for a reagent of equivalent volatility but more general acceptability, which could be dispensed from drip-tanks, the interval between drops being adjusted to anticipate the time required for the reformation of the surface film? Or to follow the suggestion of

MANZELLI (1941) and employ wetting agents to lower the surface tension, causing pupae to ride so high in the water that they lose equilibrium, topple over and suffocate—even if, in their helplessness, they are not taken by predators? Research into these questions is doubly desirable in that the susceptibility of pupae to insecticides is much less than that of larvae.

Considering the interest that has been taken in the Culicidae since the turn of the century, remarkably little has been published on the bionomics of males. Perhaps the fact that they do not feed on blood accounts for the lack of attention they have received, for available data cover little more than swarming and mating behaviour. New techniques opening up possibilities for research on such topics as ranging activity and resting places include tagging with radioisotopes (JENKINS, 1949), and the use of paints with reflecting properties (RENNISON et al., 1958) or which fluoresce in ultra-violet light (JEWELL, 1958). The first technique has already shown its worth in mosquito investigations, and the other two have been used successfully in tsetse research.

Insofar as is known, the food of male mosquitoes comprises nectar and other plant juices. This is the case for females as well in the non-biting culicids, and in certain species normally considered aggressive. The latter include some subarctic mosquitoes, for which food plant data have been obtained by treating vegetation with radioisotopes (WEST and JENKINS, 1951). Here is a means of establishing whether or not selective feeding takes place among the males of vector mosquitoes. If it should prove to do so in species where mating still takes place after the males have fed, extra means of control would become available. Systemic insecticides, already employed by economic entomologists (BENNETT, 1949), would have a place here, although they must be used with discretion because of possible danger to wildlife (RUDD, 1958).

In our preoccupation with synthetic insecticides we are apt to forget that some problems are best solved by time-honoured sanitary measures. For example, the control of such domestic mosquitoes as *Culex pipiens fatigans,* against which appropriate naturalistic practices afford an effective counter to resistance (LAIRD, 1958a). All kinds of environmental measures not requiring the use of chemicals were devised against mosquitoes in particular in the interval between the two World Wars. Various authors (e.g. EJERCITO, 1935) have noted the absence of larvae from stagnating waters having a bacterial scum at the surface. Such a scum serves as a biological indicator of the level of pollution, which as it proceeds renders water unsuited to the requirements of all but a few mosquitoes having broad tolerances. As food becomes steadily scarcer, the proportion of deleterious aquatic bacteria increases, and protozoan and other epibionts find their optimum conditions and most hamper the movements of larvae at a time when these are sickly and faced with severe food competition (LAIRD, 1958b). Deliberate pollution of the larval habitat, as advocated by WATSON (1911), has given good results against certain anophelines. *Anopheles minimus* was successfully controlled in Assam borrow pits by polluting these with cut jungle growth (RAMSAY and SAVAGE, 1932) or cow dung (RICE and SAVAGE, 1932). HARGREAVES (1933) eliminated *A. gambiae* and *A. funestus* from similar habits in Uganda by using rotting elephant grass as a filling; and MARTIAL (1937) and MACKAY (1938) used variations of the technique in Indo-China and Tanganyika respectively.

Salinification has controlled the breeding of *Anopheles albimanus* in Jamaica (WASHBURN, 1933) and *A. elutus* in Albania (HACKETT, 1937). Desalinification by freshwater irrigation was employed by SWELLENGREBEL and DE BUCK (1938) and MISSIROLI (1939) to force the replacement of a halophilic malaria-carrying subspecies of *A. maculipennis* by non-vector subspecies, and tide gates have been used in Malaya (BARROWMAN, 1936) and elsewhere to alter the salt balance of coastal waters to displace brackish water anophelines. These and many other such measures were dealt with in detail by WILLIAMSON (1949), who also drew attention to the possibility of larval control through iron impregnation suggested by the rarity of mosquitoes in naturally ferrugineous waters.

A renewal of interest in this approach to control could lead to practical anti-larval measures suited to a variety of problems and having the advantages of cheapness and delaying the onset of resistance by favouring the restriction of synthetic insecticides to peri-domestic use. As much and more may be expected from an intensive study of applied biological control through predators and parasites.

Arthropods and snails of public health importance have many natural enemies, knowledge of which is fragmentary and for the most part made up of chance observations by investigators primarily concerned with other problems. Nevertheless, the relevant literature is voluminous. How much bulkier might it have been had not so many parasitized and distorted specimens, briefly glanced at and rejected as imperfect, gone down unnumbered plugholes as unworthy of mounting!

A number of limited reviews of the subject are available, but none of them approaches completion. They include synopses of the natural enemies of mosquitoes (HOWARD et al., 1912; SPEER, 1927; HINMAN, 1934a, 1934b; CHRISTOPHERS, 1952; HORSFALL, 1955), houseflies (WEST, 1951), tsetse flies (BUXTON, 1955), blackflies (GRENIER, 1943; TWINN, 1939), cockroaches (SEMANS, 1943), and freshwater snails (MICHELSEN, 1957). The valuable account of insect pathology by STEINHAUS (1949) must not be overlooked. There is a real need for an annotated bibliography of the large and widely scattered literature on parasites and predators of all arthropods and molluscs of medical interest. Such a synopsis is prerequisite to a general evaluation of the biological control potentialities of these organisms.

The best known and most successful efforts to apply biological control methods to medical entomology, concern the larvivorous fish *Gambusia affinis* and *Lebistes reticulatus.* Numerous other fish have been tried as well, and the extent of the literature this research has produced is shown by the fact that GERBERICH (1946) was able to publish 298 relevant abstracts. The selection of fish as mosquito predators, like all biological control work, must be based on sound ecological planning, and disappointment has often been caused because this principle was overlooked. Thus the less permanent types of surface waters are unsuited to the requirements of *Lebistes* or *Gambusia.* As such waters are the source of a large proportion of the anophelines of the malarious islands of the Southwest Pacific, it would be advisable to restrict larvivorous fish introductions there to such species as the Fijian *Lairdina hopletupus* Fowler, an eleotrid which thrives in marshy places and readily throws itself over short stretches of waterlogged ground to invade fresh pools (LAIRD, 1956).

Interest in mosquito predation by animals other than fish was aroused well over half a century ago by the Lamborn Prize Essays on dragonflies (LAMBORN, 1890). Much has since been written on the larva-destroying potentialities of a variety of aquatic invertebrates ranging from *Hydra* and rotifers through crustaceans and insects of many kinds to molluscs, and on the imagocidal activities of animals from wasps and other insects to birds and bats. Authors have laid particular stress upon the importance of certain water beetles (notably various species of the Dytiscidae) and hemipterans (especially sub-surface feeders of the families Nepidae, Belostomatidae, Notonectidae and Corixidae) as larval predators.

These predators too readily become the subject of extravagant claims following laboratory experiments in which mosquito larvae comprise the only food offered them and under conditions of close confinement at that. Although field observations of the scarcity of developing mosquitoes in permanent ponds having a well developed macrofauna, by contrast with their abundance in nearby transient pools which lack predators (LAIRD, 1946a, 1956) provide convincing evidence of the importance of this balancing force in nature, more quantitative data are badly needed.

Some locally valuable predators are rare in nature—the Malayan *Cercometus* sp., a wingless and sluggish water scorpion (Nepidae) which feeds almost exclusively on mosquito larvae (WILLIAMSON, 1949) serves as an example—and their usefulness is thereby restricted. This by no means rules out the possibility that they might flourish when far removed from their own natural checks, and thus prove useful in mosquito control in other parts of the world. Predacious invertebrates are hardly likely to prove valuable in this respect if introduced into countries where their particular ecological niches are already fully utilized by close relatives. Thus although belostomatid bugs such as *Sphaeroderma* spp., and water scorpions (Nepidae) are redoubtable mosquito enemies (TOUMANOFF, 1941, WILLIAMSON, 1949), little could be expected from deliberate introduction into countries where representatives of these families have already established a balance with other aquatic animals. However, neither *Sphaeroderma* nor water scorpions occur in the Solomon Islands or the New Hebrides, where these insects are thus potentially useful. Suitable species could be brought there from tropical Australia, Indonesia or Southeast Asia, not forgetting Williamson's *Cercometus*.

In the South Pacific the choice of larvivorous animals which could be used in this fashion becomes ever wider as remoteness from Australasia becomes more pronounced. While complex associations of mosquito larval enemies occur in the lands at the western margins of the Pacific, their significance is reduced by competition among themselves and by the shelter afforded the Culicidae by a rich aquatic flora (LAIRD, 1956). But as distance eastwards increases, each island marks the furthest limit for some groups and the aquatic flora and fauna become progressively simpler. To instance but one order of importance in predation, the Hemiptera, the families Naucoridae and Nepidae are not known east of Queensland, the Belostomatidae extend no further than New Caledonia, the Corixidae and Hydrometridae are not represented east of the Loyalty Islands, the Pleidae stop short in the New Hebrides, the Mesoveliidae have not been reported east of Samoa, and only three families, the Gerridae, Notonectidae and Veliidae, occur as far afield as the Society Islands. Many other larvivorous invertebrates inhabiting a wider range of surface waters than the more commonly utilized fishes, could be considered for introduction into this region. For example, the niches normally occupied by larval *Cloëon* spp. (Plectoptera) and the families Dytiscidae and Gyrinidae (Coleoptera) are vacant in such groups as the Gilbert, Ellice, Tokelau and Cook Islands. The paucity of aquatic plants in these isolated islands would favour the chances of introduced mosquito enemies gaining the fullest possible access to larvae.

Unhappily, though, transient pools unsuited to most of these insects or to fishes form a major source of mosquitoes in the South Pacific. The voracious larvae of species of the subgenus *Lutzia* of *Culex* help control the breeding of other mosquitoes in such pools as far east as the Solomons, but as the adults sometimes bite man these insects are generally unsuitable for introduction experiments. A search for a suitable predator exhibiting a decided preference for transient pools would be a highly worthwhile undertaking. Non-biting mosquitoes of the subfamily Chaoborinae come to mind. KNAB observed larvae of *Chaoborus punctipennis* preying upon those of *Culex pipiens* in a temporary pool (HOWARD et al., 1912), and little-known tropical chaoborines occur in the Oriental and Neotropical Regions. Relevant data are accumulating on predation by species of *Eucorethra, Chaoborus* and *Mochlonyx* in subarctic North America (JENKINS, 1948; JENKINS and KNIGHT, 1950, 1952).

Radioisotopes now offer a means of studying mosquito predation in the field (JENKINS and KNIGHT, 1950; JENKINS and HASSETT, 1951; BALDWIN et al., 1955), even to the extent of allowing the number of larvae devoured by an enemy to be determined (PENDLETON, 1952). Other applicable techniques include parallel observations of normal larval habitats and adjacent ones from which part or all of the predatory fauna has been removed by sieving (CHRISTIE, 1958). The results of such studies in areas where predators are native, interpreted against a clear ecological understanding of habitats lacking them in the South Pacific, would provide a basis for reasoned introductions into the latter area. It might also prove practicable, in some cases at least, to follow larviciding by introducing mass-reared predators into the treated habitats.

Remarks made thus far apply to mosquitoes breeding in surface waters. The only serious attempts yet made to exploit predacious invertebrates as mosquito control agents concern container-breeding species of *Aëdes (Stegomyia)* against which exotic species of *Toxorhynchites* (non-biting Culicidae noted for their voracious larvae) have been imported into Fiji (PAINE, 1943), Hawaii (BONNET and HU, 1951; NAKAGAWA and MIKUNI, 1958), the Society

Islands (**Bonnet** and **Chapman**, 1956) and American Samoa (**Peterson**, 1956). It cannot be too strongly stated that if these introductions are to contribute to our knowledge of biological control mechanisms, they must remain the subject of close and continued population studies.

Biological control by means of an invertebrate predator has also been used against muscid flies in the South Pacific. Noting that the prevalence of these insects in cattle districts of Fiji contrasted with their relative scarcity in Malay and Indonesia, **Simmonds** arranged introductions of a Javanese predator to this group and neighbouring ones in 1938. The insect, a dung-dwelling histerid beetle, *Platylister chinensis,* has since helped to bring about considerable improvement in the fly problems of the areas concerned (**Simmonds**, 1958). A similar solution to another Pacific muscid problem, the breeding of huge numbers of flies in rotting coconuts and breadfruit on the atolls, would be most welcome.

Shortly before his death, Professor P. A. **Buxton** (1955) was of the opinion that remedies applicable to particularly difficult local tsetse problems might well result from the study of *Glossina* and its enemies in places where the fly is not common, reasoning that clues to the parasite/predator complex are best sought under such conditions. A similar argument may be advanced in favour of an intensive study of "oases" in generally malarious areas where anophelines are very rare or absent, as in the Bamgi-Ia region of Mappi Province, Netherlands New Guinea (**van Dijk**, 1958). Predation and interspecific competition are closely linked in the displacement of *Australorbis glabratus,* the snail intermediate host of *Schistosoma mansoni* in Puerto Rico, by *Marisa cornuarietis,* an ampullarid (**Ferguson** and **Palmer**, 1958; **Ferguson** et al., 1958). Many other instances of predation holding some promise of practical application cover the whole range of medical entomology.

Hemiptera/Heteroptera of the closely related families Reduviidae (assassin bugs) and Ploiariidae (emesine bugs, or thread bugs) deserve special mention here. At least three emesines feed selectively upon adult mosquitoes. Two of these, the North American *(Emesa longipes)* = *Ploiariola errabunda* (**Howard** et al., 1912) and the Mediterranean *Ploiaria domestica* (**Balard**, 1921; **Roubaud** and **Weiss**, 1927) are commonly found inside houses. The third, *Bagauda gilletti,* occurs on tree trunks in Uganda (**Gillett**, 1957). Assassin bugs have been seen attacking dangerous ticks (**Wellmann**, 1906), and the medically important members of the family (*Triatoma* spp.) are themselves preyed upon by other reduviids (**Wood**, 1954).

Predation is not altogether an animal prerogative, either. LLOYD (1942) gives a full account of the carnivorous aquatic plants, and WILLIAMSON (1936, 1949) records original observations and quotes relevant literature on the larvivorous attributes of bladderworts (Utriculariaceae). It is worth considering introducing species of *Utricularia* or *Aldrovanda,* an underwater sundew which also captures mosquitoes (HOWARD et al., 1912), into areas offering suitable conditions but as yet lacking these plants. According to LLOYD (1942) the former genus is unknown on any of the oceanic islands. Care should be exercised, though, to avoid establishing bladderworts in the presence of mosquitoes of the genus *Taeniorhynchus* (= *Mansonia*), developmental stages of which may include *Utricularia* among their host plants (VAN DEN ASSEM and METSELAAR, 1958).

Nothing has yet been said of parasites, which probably offer the brightest possibilities of all. SWEETMAN (1958) lists 76 parasites (compared with only 39 predators) which have been employed with good effect against economic pests. Medical entomologists, who can boast of no such achievement, were urged by BUXTON (1955) "to take a lesson from Canada and the United States . . . at the present moment Canada, more than any other country, is disposed to undertake long-range research on infections (by bacteria, fungi, viruses, protozoa) in all types of forest insects."

Adult Diptera often carry arthropod passengers or ectoparasites. Pseudoscorpions frequently cling to muscoid flies (KEW, 1901), the dispersal of larval water mites is aided by mosquitoes, and as unlikely a parasite as a sarcoptid occurs on Pupipara (SERGENT and TROUESSART, 1907). Certain midges (Heleidae) which suck engorged blood from mosquitoes (EDWARDS, 1923; LAIRD, 1946b) stand near the borderline between predators and parasites. There are also a number of records of purely chance associations, to which the recent report of a *Planidium*-type hymenopterous larva from an adult *Phlebotomus* (LARIVIÈRE and ABONNENC, 1958) is perhaps referable. However, insect endoparasites, chiefly Hymenoptera, comprise the bulk of SWEETMAN's records. Medically important arthropods are also subject to the attention of such insects.

Thus numerous species of Hymenoptera and bombyliid and sarcophagid Diptera parasitize tsetse flies (c.f. THOMPSON, 1943; BUXTON, 1955). Other representatives of the former order are known from tabanids and non-biting flies (c.f. THOMPSON, 1943). Chalcid wasps parasitize several hard ticks (c.f. NEVEU-LEMAIRE, 1938), another attacks fleas (c.f. NEVEU-LEMAIRE, 1938) and a scelionid has been described from reduviid eggs (DA COSTA LIMA, 1927). Braconid wasps of the genera *Ademon* and *Grypocampa* have been reared from pupae of the blackfly *Simulium aureum* in Europe (ENDERLEIN, 1921), but medically important Nematocera otherwise seem remarkably free from Hymenoptera. This holds for dipterous parasites as well, although some of the harmless Tipulidae are hosts for tachinid flies (c.f. THOMPSON, 1943). Other entomophagous insects of interest to us include beetles of the peculiar genus *Rhipidius* (Coleoptera: Rhipiphoridae), for which it seems that cockroaches are the sole hosts (CLAUSEN, 1940).

While some of these insects hold undoubted promise as biological control agents in special situations, and additional ones almost certainly await discovery, most suggestions thus far made for control by parasites in the public health field concern bacteria, fungi, protozoa or nematodes. Many of the species concerned are discussed by STEINHAUS (1949), and although the number of chance records far exceeds that of well documented accounts of life histories and experimentation, all these groups include organisms with which economic entomologists are at present obtaining promising results. In the realm of snail control, too, the possibility of utilizing viruses, bacteria and fungi has been recognized (MICHELSEN, 1957).

Protozoa of the order Microsporidia and fungi of the genus *Coelomomyces* (Blastocladiales) offer fruitful research material. WEISER (1946) listed 15 species of microsporidians from mosquitoes, and more have since become known. Further species have other medically important hosts including non-biting flies, blackflies, midges, cockroaches and fleas. WEISER (1958) reports high mortalities among caterpillars against which a microsporidian was tested under field conditions. Promising results from one-season experiments lead him to believe that this approach to insect control has practical application.

At least 21 species of *Coelomomyces* are recognizable (LAIRD, in press). Only two members of the genus (reported from a notonectid and a simuliid respectively) are known from insects other than mosquitoes. MUSPRATT (1946) kept a Rhodesian study area under observation between 1941 and 1945, and throughout this period the infection of *Anopheles gambiae* larvae by *Coelomomyces* spp. was responsible for a host mortality of 95⁰/₀.

Coelomomyces stegomyiae, a parasite of *Aëdes (Stegomyia) albopictus* in Malaya, is probably the first pathogen to be field-tested against an insect of public health significance. As part of a project sponsored by the World Health Organization with the active co-operation of the New Zealand Government, concentrates of sporangia of this fungus were taken from Singapore to the

Tokelau Islands[2] in an attempt to infect a parasite-free population of the *Wuchereria* vector *Aëdes (Stegomyia) polynesiensis*. This group consists of three widely separated atolls (the two closest, Fakaofo and Nukunono, lie 42 miles apart from one another) 270-350 miles north of Samoa. Larval, pupal and adult abundance were estimated at Nukunono, where 761 larval habitats (mostly tree holes, the site most often yielding parasitized larvae at Singapore) were seeded with material containing sporangia. Further population estimates were made at the other atolls of the group, Fakaofo and Atafu. Fakaofo was otherwise left untouched for control purposes, but a parallel larviciding operation with dieldrin-cement briquettes was undertaken at Atafu. The experiment is still proceeding and in due course further introductions of biological control agents may take place under the ideal conditions offering there. Rat control experiments are also called for, rat-gnawed coconuts being much utilized by *Stegomyia* there as elsewhere in the Pacific; but as these and other temporary larval habitats cease to harbour mosquitoes during adverse weather conditions, following which reinvasion takes place from tree holes and other "mother foci" (BONNET and CHAPMAN, 1958), mosquito larval enemies suited to the latter should be sought.

Predators which might be considered for introduction range from copepods to insects. Microcrustaceans known to feed upon mosquito eggs and larvae include *Microcyclops varicans* (HURLBUT, 1938), *Megacyclops viridis* (LINDBERG, 1949) and *Mesocyclops obsoletus* (BONNET and MUKAIDA, 1957). While these primarily occur in surface waters in nature, they are easily maintained in small containers in the laboratory. Although they are all widely distributed, extensive collecting in the Tokelau Islands has so far failed to reveal their presence. Their introduction might, however, prove antagonistic to that of insects having voracious larvae (BONNET and MUKAIDA, 1957) likely to be of greater value in mosquito control. Container-breeding insects which could be expected to adapt themselves to local conditions include non-biting mosquitoes of the genera *Toxorhynchites* and *Corethrella*, and the Brazilian cranefly *Sigmatomera shannoniana*. ALEXANDER (1929) noted that only 20 larvae of this cranefly, which was discovered in tree holes during a *Stegomyia* survey, destroyed no less than 2,500 *Aëdes aegypti* larvae in the laboratory. Climatic conditions would not be expected to favour the European anthomyiid fly *Phaonia mirabilis*, the larvae of which prey on mosquito larvae in tree holes (TATE, 1935), but perhaps tropical relatives of this

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[2] By the author and Dr. D. H. COLLESS of the University of Malaya, during August-October, 1958.

insect might prove of use. The tree-trunk-haunting Uganda emesine *Bagauda gilletti* is of potential value against adult *Aëdes polynesiensis,* but as the bug's early instars capture very small mosquitoes (GILLETT, 1957), and these are absent from the Tokelaus, it would first be necessary to determine whether heleids and other small insects already occurring there would ensure a satisfactory nymphal food supply.

Nothing approaching eradication of any medically important insect is likely to result from control procedures based upon the use of these parasites or predators. What is hoped is that measures along these lines may contribute towards the economical reduction of susceptible populations of dangerous insects below the level necessary for the continued transmission of human pathogens. As economic entomologists realize, the ideal control plan calls for a well considered integration of biological and chemical control procedures (RIPPER, 1944; ENGLISH, 1955; WEISER, 1958). A real contribution towards the alleviation of the resistance problem would be made by the ensueing restriction of insecticidal measures to situations most requiring them. Such an approach has particular point in underdeveloped Pacific atolls and other islands east of the New Hebrides, where filariasis is the chief insect-borne disease. There is the possibility, too, that intensified worldwide research in this field might reveal as yet unknown parasites of greater potentiality than those now available. I have viral and bacterial pathogens particularly in mind.

PEPPER (1955) states that "without a knowledge of the true relationships of both the host and the enemy to their environment as well as an understanding of the interrelationships between the two populations, there is no basis for postulating any effects, either beneficial or detrimental, of parasites or predators on the host populations". Insufficient saturation of the biotope with infective material, selective predation on diseased insects and removal of spores by scavengers and predators proved detrimental to field experiments with *Thelohania hyphantriae* against fruit tree Lepidoptera in Central Europe (WEISER and VEBER, 1957). Atolls like those of the Tokelau Group afford ideal conditions for studying these matters. Their isolation and limited fauna, flora, habitats and area, all favour advances in our understanding of such factors in planned introductions of natural enemies as the necessary degree of saturation of the biotope and the influence of predators in aiding or arresting the dispersal of pathogens. Added point is given to these recommendations by the fact that most instances of successful biological control concern oceanic or ecological islands (SWEETMAN, 1958). Pacific atolls can serve as outdoor laboratories for the development of measures ultimately applicable to larger islands and the continents.

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Résumé.

Pendant et directement après la deuxième guerre mondiale, des progrès spectaculaires ont été réalisés dans le domaine du contrôle chimique des dommages causés par les insectes. Malgré de premières performances, le contrôle biologique a perdu beaucoup de son importance en face des derniers succès remportés par le DDT et ceux plus tardifs dus aux chlorures de carbures hydrogènes et aux combinaisons organiques phosphorées. Aujourd'hui, cependant, la résistance aux insecticides porte préjudice au contrôle de divers insectes importants en matière de santé publique. L'action non sélective du DDT et d'autres composés synthétiques trouble parfois l'écologie d'un biotope à tel point que les insectes et autres vecteurs de maladies vont jusqu'à profiter de l'emploi de ces mêmes insecticides.

Ces problèmes demandent de nouvelles études écologiques. Une entière connaissance de la biologie des insectes d'importance médicale ferait ressortir les aspects négligés du contrôle. Notre échec dans le développement des moyens de destruction des nymphes et des moustiques mâles en est un exemple. Le fait qu'on est parfaitement au courant de l'existence d'un grand nombre d'agents

pathogènes et de prédateurs contraste singulièrement avec nos connaissances défectueuses du rôle qu'ils jouent dans la régulation naturelle des populations d'insectes. Des expériences faites dans le domaine de l'agriculture et de la culture forestière suggèrent que l'on pourrait tirer parti des ennemis naturels et des agents pathogènes dans le contrôle d'insectes et de mollusques d'importance médicale. Une bibliographie annotée de la littérature relative à ce sujet serait nécessaire pour servir de référence et de point de départ à un programme de recherche collective.

Des introductions expérimentales d'insectes devraient être effectuées aux endroits où des niches, par ailleurs remplies de parasites et de prédateurs, sont jusqu'ici inoccupées. Ainsi, différents Hémiptères aquatiques et Chaoborinae (Diptères) pourraient être incorporés à la faune des gîtes larvaires d'Anophèles sur quelques îles de Mélanésie. Ces insectes, ainsi que d'autres larves ennemies, sans oublier les Utriculariacées insectivores, pourraient être utilisés efficacement contre les moustiques vivant à la surface de l'eau en Polynésie.

Les noix de coco favorisent considérablement le développement de mouches et de moustiques sur les atolls de Polynésie, de Micronésie et de Mélanésie. Ces noix, rongées très fréquemment par des rats, deviennent des gîtes pour ces insectes et le contrôle des rats y est donc étroitement lié à celui des insectes nuisibles. Le champignon du moustique *Coelomomyces stegomyiae* a été introduit récemment aux îles Tokelau où l'on projette de nouvelles expériences avec des ennemis naturels de Culicides. Les insectes entrant en considération comprennent les moustiques non-piqueurs des genres *Toxorhynchites* et *Corethrella,* la mouche brésilienne *Sigmatomera shannoniana* et l'Hémiptère de l'Ouganda *Bagauda gilletti.*

L'introduction de prédateurs et de parasites soigneusement choisis pour occuper des niches jusqu'ici vides, combinée avec des mesures efficaces dans le contrôle des rats, aideront à résoudre les problèmes posés par le contrôle du vecteur de *Wuchereria,* non seulement aux îles Tokelau, mais également dans d'autres territoires du Pacifique. Des expériences pilotes effectuées dans des conditions favorables d'isolation et de limitation de la faune, de la flore et des différents gîtes, tels que le permettent ces atolls, sont prévues comme prélude au développement du contrôle biologique étendu à des îles plus grandes et aux continents dans le domaine de la santé publique.

Zusammenfassung.

Während des zweiten Weltkrieges und in den unmittelbar darauf folgenden Jahren wurden in der chemischen Schädlingsbekämpfung außerordentliche Fortschritte erzielt. Trotz früheren Errungenschaften verlor die biologische Bekämpfung viel an Impuls angesichts der anfänglich mit DDT und in der Folge mit neueren chlorierten Kohlenwasserstoffen und organischen Phosphor-Verbindungen erzielten Erfolge. Heute jedoch wirkt sich die zunehmende Resistenz diesen Mitteln gegenüber für die Bekämpfung zahlreicher gesundheitschädigender Insekten nachteilig aus, und die nichtselektive Wirkung des DDT und anderer synthetischer Verbindungen stört oft die Oekologie eines Biotops in solchem Maße, daß Schädlinge und Krankheitsüberträger sogar von deren Anwendung profitieren.

Diese Probleme erfordern neue oekologische Untersuchungen. Eine gründlichere Kenntnis der Lebensgewohnheiten der medizinisch wichtigen Insekten würde einige bisher vernachlässigte Seiten der Bekämpfung in den Vordergrund rücken. Als Beispiel diene die Tatsache, daß bisher keine Methode zum Vertilgen von männlichen Mücken und Puppenstadien gefunden werden konnte.

Unser Wissen um das häufige Vorkommen von Krankheitserregern und Prädatoren steht in scharfem Gegensatz zur geringen Kenntnis der Rolle, welche diese Organismen in der natürlichen Regulierung von Insektenpopulationen spielen. Erfahrungen in der Land- und Forstwirtschaft lassen vermuten, daß natürliche Feinde und Krankheitserreger mit Erfolg in der Bekämpfung der medizinisch wichtigen Insekten und Mollusken eingesetzt werden könnten. Eine ausführliche Bibliographie der ganzen einschlägigen Literatur als Nachschlagewerk und als Basis für gemeinsame Forschungen wäre dringend erwünscht.

Versuchsweise sollten Insekten in Gebiete gebracht werden, wo Schlupfwinkel, anderswo durch Parasiten und Prädatoren besiedelt, bisher noch unbewohnt sind. So könnten verschiedene Wasser-Hemipteren und Chaoborinen (Diptera) auf einigen melanesischen Inseln der Fauna von Anopheles-Larvenfundorten beigesellt werden. Diese und andere Larvenfeinde sowie insektenfressende Utriculariaceen könnten mit Erfolg gegen auf der Wasseroberfläche lebende Mücken in Polynesien eingesetzt werden.

Kokusnüsse fördern auf polynesischen, mikronesischen und melanesischen Atollen ganz wesentlich die Vermehrung von Fliegen und Mücken. Viele Kokosnüsse werden durch Rattenfraß ausgehöhlt und dadurch zu Brutplätzen von Insekten. Die Vertilgung der Ratten steht somit in engem Zusammenhang mit der Fliegen- und Mückenbekämpfung auf diesen Inseln. Der die Culiciden befallende Pilz *Coelomomyces stegomyiae* wurde kürzlich auf die Tokelau-Inseln gebracht, und es ist zu hoffen, daß dort weitere Experimente mit natürlichen Feinden von Culiciden gemacht werden können. Insekten, welche für die Bekämpfung in Frage kommen, umfassen nicht stechende Mücken der Arten *Toxorhynchites* und *Corethrella,* die brasilianische Fliege *Sigmatomera shannoniana* und die Hemiptere *Bagauda gilleti* aus Uganda.

Das Aussetzen sorgfältig ausgewählter Prädatoren und Parasiten an noch unbesiedelten Plätzen, verbunden mit wirksamen Rattenbekämpfungsmethoden, kann dazu beitragen, das Problem der *Wuchereria*-Übertragung nicht nur auf Tokelau, sondern auch in anderen Gebieten des Pazifik zu lösen.

Unter günstigen Bedingungen durchzuführende Kontrollversuche an der Fauna und Flora, in Brutplätzen und Gegenden, wie sie auf den Atollen vorkommen, werden ins Auge gefaßt als Vorbereitung für eine weitere Ausarbeitung biologischer Bekämpfungsmethoden im Hinblick auf Probleme des öffentlichen Gesundheitswesens größerer Inseln und ganzer Kontinente.