An Examination of the Value of Ecological Research in the Control of Bilharziasis

WITH SPECIAL REFERENCE TO THE INTERMEDIATE HOSTS IN SOUTHERN AFRICA

BY

B. R. ALLANSON
Rhodes University, Grahamstown.

In this paper I would like to ask three questions and try to provide answers to them. They are:

(1) What is meant by ecological research and what is contained within its ambit as regards the intermediate hosts?

(2) What results have been obtained and what do they tell us?

(3) Are we correctly orientated? If the answer is a direct no, in what way can we change our orientation to meet more effectively the control of bilharziasis?

I could not hope, in the time available, to review the ecological research throughout the world into the transmission of the disease. I have therefore restricted my appraisal of the literature to that from Southern Africa and, in particular, south of the Zambesi river.

The Meaning of Ecology

In a recent examination of the meaning of the term "ecology" by Lambert and Goodman[15] there is every indication that many biologists are, to say the least, unhappy about what the subject is all about. Indeed, to some there seems to be no clear definition of the sort of work that is being done in the field of the animal and its environment.

At the root of this misunderstanding lies a poor appreciation by many of us of exactly what we are trying to achieve by our work. I am of the opinion that until we can spell out in simple terms the questions we want to ask in investigations of animal-environment interaction, I cannot see the rôle of the ecologist in bilharziasis research improving. We must expect our colleagues in the field of medical parasitology—the epidemiologist—to look somewhat askance at our scattered efforts to understand the ecology of fresh water snails. Indeed, an examination of the literature from Southern Africa, while containing important work, gives the impression that we seem to be working on the basis of immediate personal interest rather than developing research along well-defined "question and answer" paths in the important field of control.

It is generally recognised (but little seems to be done about it) that our efforts so far have been too directed at specific topics within the bilharziasis problem without really appreciating —or perhaps because of it—the complexity of this biological problem. Mostofi[16] has called for a holistic approach in bilharzial research. But these calls go very largely unheeded.

There are three main lines of attack:

(1) The ecology of the intermediate hosts.

(2) The biology of the parasitics organisms, schistosomes.

(3) The ecology of the primary host, Man.

The first two have been the subject of serious work for a great number of years; the third, largely because of the pioneering work of Pitchford and his colleagues, is only now beginning to receive the attention it justly deserves.

Results Obtained

Taxonomy

In 1955 the C.S.I.R. in South Africa established a snail research unit at the University of Potchefstroom. This unit became the repository of the national snail collection and a source of taxonomic information which has led to a clearer understanding of what snail species exist in the Republic's fresh water.

Professor J. A. van Eeden, his colleagues and students[3, 4, 25, 26, 27] have been at great pains to establish the distribution of a number of helminthologically important snail species. In this work they have been assisted by Dr. D. S. Brown, of the Medical Research Council, U.K., and Dr. David Davies, of the Medical Ecology Group, State Health Department. As a result of this co-operative effort the pattern of snail distribution in South Africa is clear (*vide* van Eeden's results given in the previous paper).

Taxonomic tangles do, however, exist in the Southern African snail fauna and are an important field of continuing research. Brown *et al*.[6] for example, have suggested a correlation between infestation by miracidia and a polyploid condition in the *Bulinus* (*Bulinus*) group such that *B*. (*Bulinus*) *tropicus* with a chromosomal complement of 18 is not infected by human schistosomes. *B*. (*Bulinus*) *truncatus* with a chromosome number of 36 is infected and is the important intermediate host of bilharziasis schistosomes in North Africa. Such a separation is distinct, but unfortunately chromosome counts cannot always be expected to yield such clear systematic aid, as in the case of *B*. (*Physopsis*) *globosus* and *B*. (*P*.) *africanus*. Brown[3] has provided evidence on the basis of morphological observations which indicates that *B*. (*P*.) *globosus* is a tropical species with the northern part of Natal as its southerly limit. *B*. (*P*.) *africanus*, on the other hand, is widespread in the waters of the eastern parts of South Africa.

I suggest that the literature to which I have referred records three intermediate hosts in Southern Africa:

(1) *Bulinus* (*Physopsis*) *africanus*.

(2) *Bulinus* (*Physopsis*) *globosus*.

(3) *Biomphalaria pfeifferi*.

However, the recent work of Brown and his colleagues[5] and that of Pitchford[19] suggests that the picture may not be so simple. Within the Bulinids, important in bilharziasis transmission, two distinct groups have been defined—

(1) the tropicus-truncatus group; and

(2) the africanus-globosus group.

Brown *et al*.[6] have shown that the specification of the first group needs further study. This is of particular urgency since Pitchford[19] has presented evidence that snails belonging to the "truncatus" group and established from South African material have been found susceptible in his laboratory to *S. haematobium* (*S. capense*) and *S. mattheei*. He found, furthermore, that these snails were no less susceptible to both of these schistosomes than the *Bulinus* (*Physopsis*) sp. of the "africanus" group.

Superimposed upon this taxonomic confusion is the existence of three, if not four, schistosome species.

(1) *S. haematobium;* (2) *S. capense* (?); 3, *S. matheei;* (4) *S. mansoni*.

Of particular significance is the relation between *S. haematobium* and *S. capense*. Wright[28] in reporting on the work of Pitchford and his colleagues makes out a case for the existence of these two species in Southern Africa. *S. capense* becomes specifically associated with *B*. (*P*.) *africanus* complex, while *S. haematobium* develops only in snails of the *B*. (*P*.) *truncatus* complex, so making *S. haematobium* a North African species.

Unfortunately Wright did not refer to a later paper by Pitchford,[19] in which evidence is given to support the view that *S. capense* should be regarded as a synonym of *S. haematobium*. In view of this omission it is difficult to know what Wright's views would be on this synonymy. Nevertheless, Wright's paper exposes or underlines the close host-parasite relationship between larval trematodes to their snail hosts. Arising from this specific association is that a population of schistosomes is usually better adapted to its local race of snail than to other races of the same species. This can lead to the segregation of parasite populations and consequent reduction in genetic interchange between one group and another. We can expect from this segregation a close parallel evolution of worm and snail host, and as a result races of parasite may become differentiated. Implicit, as I see it, in these considerations of Wright's is the stability of the populations of the definitive host, Man. Emigration and migration within human populations would play havoc with the integrity of any local schistosome gene pool and would result in the production of viable hybrids with possibly less restrictive requirements as regards races or isolates of intermediate hosts. Pitchford[18] has shown the existence of hybrids between *S. haematobium* and *S. mattheei* in Man and successfully established such hybrids in rodent stocks kept in his laboratory. Indeed, Fig. 1, p. 108 of Pitchford's paper[19] shows on the basis of egg measurements a very remarkable size gradation between *S. mansoni*, *S. mattheei*/*S. haematobium* hybrids and *S. haematobium*.

In the light of these findings and the lack of specificity by the schistosomes as regards their definite hosts, we must conclude that where gene flow is as unrestricted as it may be in Africa, there appears to be no valid reason as yet for accepting unequivocally Wright's suggestion that local races of snails play a really significant rôle in schistosome population dynamics.

Intermediate host-environment interaction

There are a number of Rubicons which the hatchling parasite-miracidia and primordal worm-cercariae have to cross in the transmission from one stage in the life cycle to another. Obviously the availability of intermediate and definite hosts is essential.

But first, what do we know about the ecology in qualitative terms of the snail species I have mentioned. Van Eeden and Combrink[26] have reported on the association between *Lymnaea natalensis* and *B.* (*P.*) *africanus*. A similar correlation was observed by a number of earlier workers, namely, van Someren[2] and Azoredo,[2] who found that *L. natalensis* was strongly correlated with *Biomphalaria pfeifferei;* and Brown[2] working in Ethiopia records the same type of correlation between *Biomphalaria pfeifferi* and *B. truncatus sericinus*. How has this information been used in the development of our understanding of snail ecology? Van Eeden[26] has suggested that where *L. natalensis* is abundant and *B. tropicus* rare or absent — the area may be regarded as potentially suitable for the South African *Physopsis* species — and vice-versa. Presumably this type of observation will lead on to an examination of causal properties of these differences. Should a careful analysis of the ecologic requirements of these three species be available, how would we use this information in the control of the disease?

Perhaps the most important work in answer to these questions to come from Southern Africa is that of Shiff ([20, 21, 22, 23]) upon the quantitative ecology of the snail *B.* (*Physopsis*) *globosus*. These four papers report the results of studies on the effect of temperature on the mean generation time and "r" the intrinsic rate of natural increase. In *B.* (*P.*) *globosus* "r" is maximal at 25° C. and the population expands until other factors become restrictive. This is followed by the effect of sub-optimal temperature upon "r." Under these conditions Ro (mean generation time) becomes considerably longer than under optimal conditions and the species becomes vulnerable to changes in the environment. From this it follows that a high value for "r" is advantageous to species in an environment in which favourable and unfavourable conditions alternate relatively rapidly. To be successful a species, for example *B.* (*P*) *globosus* has to recover rapidly from frequent catastrophes. The pond habitat in the highveld of Rhodesia is such a place where seasonal droughts followed by rain, become the environmental variations which required rapid response if the snails are to be successful. The high value of "r" in *B.* (*P.*) *globosus* at temperatures of 25° C is a perfect adaptation to the temporary nature of the habitat in which it is normally found.

Pitchford & Visser[19] have given us clear evidence of the pattern of schistosome (cercarial) transmission in the lowveld of the Transvaal — for *S. mansoni* and *S. mattheei*. Their field study was supported by a carefully designed laboratory study of infection and transmission from the intermediate host under conditions of ambient temperature variations. Transmission patterns of *S. mansoni, S. mattheei* and *S. haematobium* cercariae as judged by infectivity success in rodents showed a marked seasonal trend. There is a greatly protracted winter incubation which is clearly dependent upon water temperature. This is particularly marked in *S. haematobium* where incubation times as great as 29-30 weeks have been recorded. To Pitchford & Visser this indicated that cercarial transmission may not take place every year, but only during exceptionally hot years would transmission to Man be possible. This could account for the low to moderate incidences of *S. haematobium* in numerous areas. The authors, while acknowledging the rôle of temperature on incubation periods as a well established fact, consider that their contribution has shown the cyclical nature of transmission, and emphasizes the need to be careful of short term investigations in the laboratory and field. Although their "control experiments in the laboratory showed that this cyclical nature of transmission was not due to seasonal variation in intermediate host numbers, it cannot be ruled out such variations in host density may also be a component in transmission cycles. Cridland[8] has shown that *Biomphalaria sudanica tanganicensis* does undergo cyclical changes in number which are not the effect of parasitism by the flukes. *Lymnaea exserta* on the other hand were almost obliterated at times through infection.

Frank[9] has provided experimental evidence, albeit over short term periods of the effect of temperature on the *rate* of development and emergence of schistosome cercariae. His evidence suggests that the schistosome species depend to varying degrees on a diurnal temperature fluctuation to synchronise the release of cercariae.

Harrison and his colleagues have provided evidence which supports the view that snail population studies should be continued without delay, particularly at the genetic or physiological race level. I know of no work that is current in this field in Southern Africa at present, certainly not so far published. These authors have spoken — or hinted at genetic barriers, chemical or physical which may prevent or restrict gene flow, and implicit in these suggestions is that these barriers (albeit ill defined) may be sufficient to isolate populations and begin the separation into distinct races. We are aware of this within schistosomes differentiated on the basis of their intermediate host requirements: *vide* the four main geographical races of *S. japonicum* (Wright [28] and Pesigan et al. [17]). Kendall [14] in a review of literature on *Fasciola* and the molluscan hosts, produces evidence of races in both flukes and snails, but once again on a geographical scale. Nonetheless he suggests that minor differences may be found in restricted geographical areas. I have pointed out to the possible unlikelihood of this in Southern Africa as far as schistosomes are concerned, but small differences in snail populations, particularly as regards their response to specific environmental conditions may be important in deciding the effectiveness of molluscicìding programmes.

Harrison et al.[13] have shown that the streams of the Umvukwes hills to the north of Salisbury in Rhodesia are free of aquatic pulmonate snails due very largely to the high magnesium-to-calcium ratio which is characteristic of these waters. This ionic condition seriously inhibits egg laying in laboratory populations of *Biomphalaria pfeifferi*. Williams (in press), working in Harrison's laboratory at the University College of Rhodesia, showed further that egg-laying rate in the small snail species was also influenced by the concentration of calcium ions. He obtained maximum egg-laying rates at concentrations of 10-36 mgm/litre of Ca^{++}. Armed with this sort of research information Harrison investigated [10, 11] the effect of "Bayluscid" on the gastropod and other aquatic fauna in two streams near Salisbury. These streams were chosen because of their widely differing water qualities. One had soft water, bicarbonates 15-40 mg./1 as $CaCO_3$ and the other moderately hard water, bicarbonates 114-163 mg./1 as $CaCO_3$. The subsequent effect of the molluscicide application was that recolonisation of *Bulinus* (*Physopsis*) spp. and *Biomphalaria* was slow. In the hard water stream they began to reappear 10 months after treatment, while in the soft water none was found after 22 months following treatment.

I believe that these sort of studies reveal with far more impact, the response of animals to environmental situations, than does the descriptive anecdotal approach. I know from our own work in hydrobiology that, as soon as we got away from the purely descriptive and designed our research around specific problems requiring careful observation in the field and rigorous experimental treatment in quasi-laboratory or field laboratory designs, only then did meaningful results emerge which rapidly increased our understanding of the specific problems.

The orientation of research

In a recent review on the measurement of schistosome populations Bradley [1] has emphasized that the study of bilharziasis has now reached a stage where some attempt to be systematic is essential. A great deal is known about the major aspects of the disease, its transmission, but different parts have been studied in different places and under different environmental circumstances. While this fragmentation is often the only way in which information arises about a particular disease problem, its direct implementation in one or other endemic area is well nigh impossible.

It seems to me that the ecologists' rôle in any future national control programme of bilharziasis is to assemble the facts about animal-environmental interaction into a reasoned whole and design the control programme to interrupt transmission at the parasite's most vulnerable stage. I have in mind two programmes currently running in South Africa and Rhodesia, as examples of what is being attempted at present.

A number of us may not be familiar with the human ecology approach developed by Pitchford and his colleagues in the lowveld of the Republic. Pitchford, in a penetrating, yet very simple analysis of human behaviour patterns in the African communities of a number of large subtropical fruit growing companies, saw that transmission could be effectively interrupted if access to irrigation canals or semi-natural water bodies was made difficult. It was, however, necessary to provide alternative and artificial facilities near the compounds which had the same ecological impact, e.g. the presence of flowing water, concrete slabs to replace beating stones for washing and shallow paddling pools for "piccanin" amusement while mother was either washing or talking! Simple but effective swimming pools at strategic sites in the compounds replaces the natural pool or reservoir. Furthermore, molluscicides become a realistic control tool in these quasi-artificial situations.

The second programme has been developed by the Blair Laboratory of the Health Department, Rhodesia. This involves the use of molluscicides on a greater scale than envisaged by Pitchford and his group at Nelspruit.

Molluscicides constitute a catastrophe (vide Shiff *op cit*) and few snails will survive but if mollusciciding operations are performed at times of optimal or near optimal temperature, the species will recover rapidly. In Rhodesia some notice of this has been taken, but while the Rhodesian workers may be reasonably satisfied with the programme of blanket spraying with molluscicides and subsequent surveillance, I as a reviewer of what they have reported would strongly urge a more clearly defined programme related specifically to Shiff's findings on *B. (P.) globosus*. For example, Clarke et al [7] and Shiff and Clarke [24] have reported their results of snail surveillance in natural waterways in Rhodesia, and although use is made of Shiff's findings — indeed they go as far as to say that that system was "evolved from a study of snail behaviour and population dynamics both in the laboratory and in the field" — this is insufficient evidence upon which to judge the effectiveness of the mollusciciding programme. Shiff [20, 22] was perfectly clear about the possible relationship between molluscicides and the rate of natural increase in *B. (P.) globosus*. Subsequent work by Harrison and his colleagues (*op cit*) and the Blair laboratory in Rhodesia has shown that a slow recovery of planorbid snails following specific molluscicide treatment may be expected. In a way these results support Shiff's original conclusions, but regrettably no clearly defined programme including the refinements of Shiff's earlier techniques has been applied to natural populations. Surely the questions to be asked are (1) why does recovery in stream populations of snails take up to 22 months? (2) What are the interactions between rate of natural increase "r," the chemical composition of natural waters and the molluscicides applied. I submit that until we know this, our results from surveillance studies remain anecdotal and that effective manipulation of the snails' environment remains as uncertain as before. I believe that the Rhodesian workers have provided distinct clues towards our eventual understanding of these complex snail-environment interactions, but they must be taken up and developed.

From this review of some of the significant work in Southern Africa on bilharzial biology I do not consider our work poorly orientated, but we should, in addition, arrange the facts of the ecology of the disease in Southern Africa and use them as a springboard to develop effective control measures. To do this I see a concentrated attack on three fronts.

1. The species status of closely related schistosome species and their intermediate hosts.
2. The refinement of the surveillance techniques developed here in Rhodesia. This will require a close scrutiny of existing infection patterns relative to water type and their influence upon snail populations and fecundity.
3. The development of the human ecological approach advocated by Pitchford and his colleagues for restricted communities.

REFERENCES

1. BRADLEY, D. J. (1967). *Bilharziasis*, Ed. F. K. Mostofi. 301-327. Springer Verlag., Berlin.
2. BROWN, D. S. (1964). *Observations on the distribution and ecology of freshwater gastropod mollusca in Ethiopia*. Contribution from the Faculty of Science Series C (Zoology) **40**, 5.
3. BROWN, D. S. (1966). *Ann. Natal Mus.* **18**, 401.
4. BROWN, D. S. (1967). *Ann. Natal Mus.* **18**, 477.
5. BROWN, D. S. & BURUN, J. B. (1967). *Malacologia*, **6**, 189.
6. BROWN, D. S., SCHUTTE, C. H. J., BUREN, J. B. & NATAVAJAN, R. (1967). *Malacologia*, **6**, 175.
7. CLARKE, V. DE V., SHIFF, C. J. & BLAIR, D. M. (1961). *Bull. Wld. Hlth. Org.*, **25**, 549.
8. CRIDLAND, C. C. (1968). *J. trop. Med. & Hyg.*, **61** (1), 16-20.
9. FRANK, G. H. (1966). *Zoologica Africana*, **2**, 211.
10. HARRISON, A. D. & FARINA, T. D. W. (1965). *Ann. trop Med. & Parasit.*, **59**, 327.
11. HARRISON, A. D. (1966). *Hydrobiologia*, **28**, 371.
12. HARRISON., A. D. (1966). *Cent. Afr. J. Med.*, **12**, 124.
13. HARRISON, A. D., NDUKU, W. & HOOPER, A. S. C. (1966). *Ann. trop. Med. & Parasit.*, **60**, 212.
14. KENDALL, S. B. (1965). *Advances in Parasitology*, Vol. 3., Ed. Ben Darves.
15. LAMBERT, J. M. & GOODMAN, G. T. (1967). *The Teaching of Ecology*, Ed. by J. M. Lambert. Blackwell Scientific Publications, Oxford.
16. MOSTOFI, F. K. (1967). *Bilharziasis*, Ed. F. K. Mostofi, 330-340. Springer Verlag, Berlin.
17. PESIGAN, T. P., HAIRSTON, N. G., JAUREGUI, J. J., GARCIA, E. G., SANTOS, A. T., SANTOS, B. C. & BESA, A. A. (1958). *Bull Wld Health Org.*, **18**, 481.
18. PITCHFORD, R. J. (1961). *Trans. roy. Soc. trop. Med. Hyg.*, **55**, 44.
19. PITCHFORD, R. J. & VISSER, P. S. (1965). *Bull Wld Hlth Org.*, **32**, 83.
20. SHIFF, C. J. (1964). *Ann. trop. Med. & Parasit.*, **58**, 94.
21. SHIFF, C. J. (1964). *Ann. trop. Med. & Parasit.*, **58**, 106.
22. SHIFF, C. J. (1964). *Ann. Trop. Med. & Parasit.*, **58**, 240.
23. SHIFF, C. J. & HUSTING, E. L. (1966). *Rhodesia Scientific Association*, **51**, 2.
24. SHIFF, C. J. & CLARKE, V. DE V. (1967). *Cent. Afr. J. Med.*, **13**, 133.
25. VAN EEDEN, J. A. (1966). *Nature*, **210**, 1172.
26. VAN EEDEN, J. A. (1965). *Tydskr. Natuurw.*, **5**, 152.
27. VAN EEDEN, J. A. & COMBRINK, C. (1966). *Zoologica Africana*, **2**, 95.
28. WRIGHT, C. A. (1967). *Bilharziasis*, ed. F. K. Mostofi. Springer Verlag, Berlin.

No discussion was recorded.