TEMPERATURE AND ITS BEARING ON THE DISTRIBUTION AND CHEMICAL CONTROL OF FRESHWATER SNAILS

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Two of the many questions often asked in connection with bilharziasis in the Republic of South Africa refer to the possibility that the intermediate host snails may still be expanding their present range of distribution, and to the prospects of chemical control of these snails. These questions, however, cannot be answered without knowledge concerning the bionomics of the snails concerned, and the present investigation must be regarded as one of several possible approaches aimed at shedding more light on these issues.

From an analysis of their distributional data collected at this Institute over the past 13 years Van Eeden and Combrinck[1] concluded that a statistically significant correlation exists between the distribution patterns of *Lymnaea natalensis* (Krs.) and *Bulinus* (*Physopsis*) (Krs.) and they furthermore argued that this correlation might reflect a certain agreement between the ecological requirments of these snails. Since *L. natalensis* is much more common and more easily bred in the Potchefstroom area than *Bulinus* (*Physopsis*) sp. and on the strength of the argument cited above, it was decided to approach the problem concerning the distribution potential of *Bulinus* (*Physopsis*) sp. by investigating the bionomics of *L. natalensis*. *Bulinus* (*B.*) *tropicus* (Krs.) was included in the programme because, like *L. natalensis*, it is known to be a transmitter of trematodes of veterinary importance.

POPULATION STATISTICS

Experimental Procedure

Our experimental snail populations were started from eggs laid in the laboratory during the same 24-hour period. These eggs were hatched and reared in 6 aquaria kept at constant temperatures of 30°, 27°, 25°, 21°, 18° and 15°C, all ± 0·5°C, to which a continuous feed of water, matured in a large plastic tank, was maintained by recirculation. Each aquarium was partitioned in two by means of plastic gauze so that the eggs of the two species could be hatched and reared in separate halves of the same aquarium. For the rest the investigational procedure was the same as that described by Leslie and Park,[2] Howe,[3,4] Andrewartha and Birch,[5] Slobodkin[6] and Shiff.[7]

Incubation Period

Our findings, summarized in Table I, show that, depending on the temperature, *L. natalensis* hatched within 14 - 26 days from the date of egg laying and *B. tropicus* within 9 - 19 days. The latter species therefore had an advantage over the former of 5 days at 30°C and this increased with decreasing temperature to 7 days at 15°C.

TABLE I. INCUBATION PERIOD IN DAYS AND PERCENTAGE EGGS HATCHED AT DIFFERENT CONSTANT TEMPERATURES

Temperature °*C*	*L. natalensis*		*B. tropicus*	
	Days	*% hatched*	*Days*	*% hatched*
30	14	56·3	9	27·5
27	13	93·4	9	72·3
25	14	98·3	9	89·3
21	17	74·0	10	74·3
18	19	93·6	13	84·4
15	26	98·4	19	67·6

Life Tables

In order to save space, the life tables compiled for the different temperatures and which summarize our findings on survivorship and fecundity over a period of 30 weeks are omitted from this report. From these data, however, the following facts emerged.

The first 5 weeks after hatching seemed to be critical to both species, so much so that at 30°C all the snails died out within the first fortnight. This juvenile mortality was distinctly more noticeable in the case of *B. tropicus* for which, moreover, it was more marked at all temperatures from 21°C downwards, and particularly at 18°C.

In general the survivorship recorded for *L. natalensis* was superior to that for *B. tropicus*, although both species survived relatively well throughout the observation period (30 weeks) at all the temperatures below 25°C. At 27°C both species started dying in significant numbers from the 10th week onwards. *Bulinus tropicus* survived best at 15°C as against 18°C for *L. natalensis*.

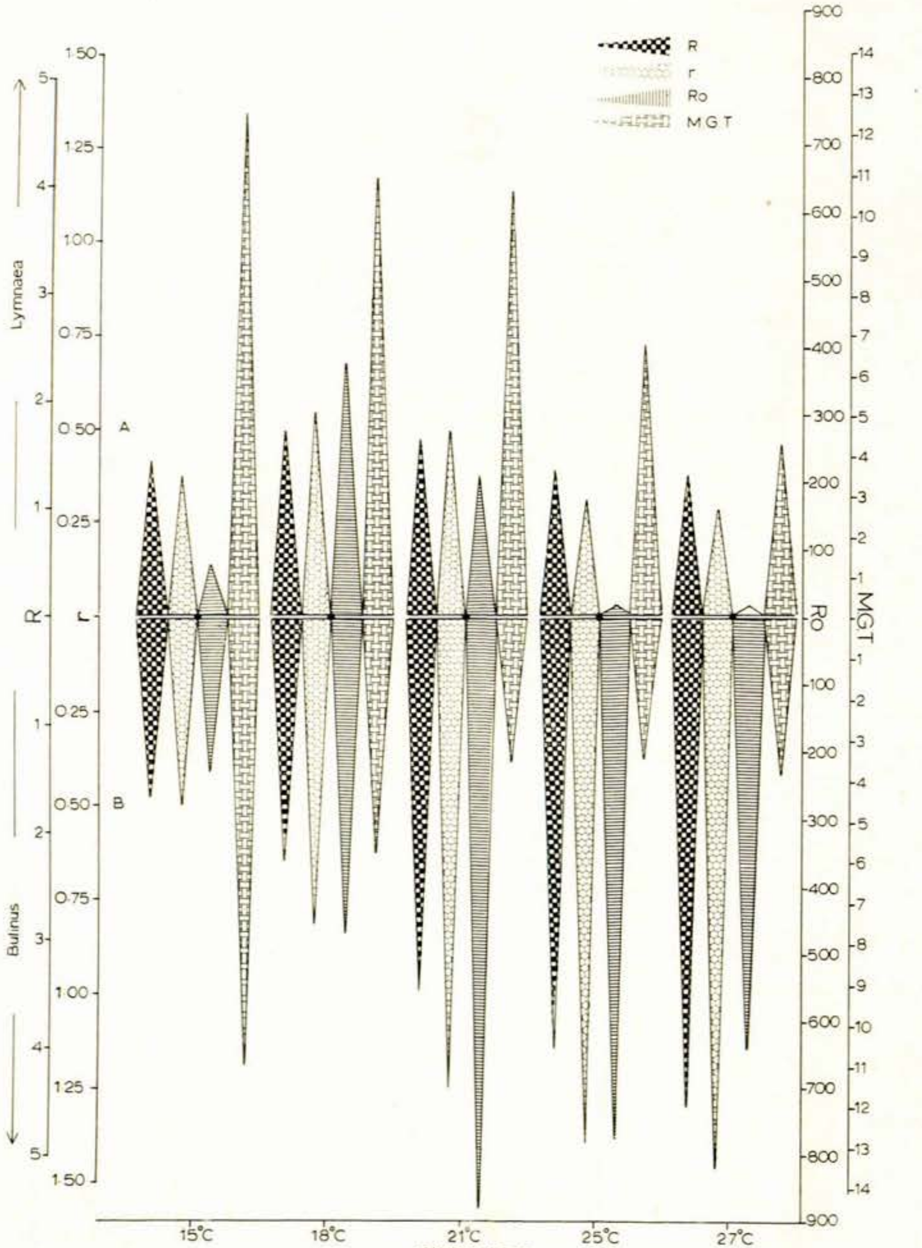

Fig. 1. Diagrammatic presentation of the population parameters of *L. natalensis* (A) and *B. tropicus* (B).

In both species the onset of egg laying was progressively delayed with decreasing temperature, although it was maintained up to the end of the observation period at all the temperatures below 25°C. For all practical purposes *L. natalensis* laid no eggs at 30°C. In fact, excluding 21°C and 18°C, where egg laying commenced at 10 and 14 weeks respectively after hatching, the fecundity of this species remained low throughout. At 25°C it produced a mere 5·9 eggs per snail per fortnight as against its over-all maximum of 75·4 eggs per snail per fortnight at 18°C. In contrast to this *B. tropicus* produced large numbers of eggs at all temperatures and its lowest number, recorded at 15°C, still exceeded the over-all maximum for *L. natalensis*. The over-all maximum for *B. tropicus* of 246 eggs per snail per fortnight was produced at 27°C. This species, furthermore, commenced laying eggs much sooner after hatching than *L. natalensis*. At 27°C it started laying eggs after only 5 weeks, and at 15°C after 13 weeks, compared with corresponding values of 7 and 19 weeks for *L. natalensis*. Added to the incubation period *B. tropicus* now had a gain over *L. natalensis* of 6 days at 27°C and 13 days at 15°C. Both species maintained egg laying longest at 21° and 18°C. For *L. natalensis* the periods were 19 and 15 weeks respectively and for *B. tropicus* 25 and 21 weeks. These differences are accounted for by the shorter maturation period required by the latter species. In general, egg laying by *L. natalensis* was not so profoundly influenced by temperature differences as it was for *B. tropicus*.

Other Population Parameters

The population parameters calculated from the data represented in the life tables are summarized in Table II and represented graphically in Fig. 1. In the present context two of these merit special comment.

TABLE II. POPULATION PARAMETERS FOR *L. natalensis* AND *B. tropicus* AS CALCULATED FROM THE LIFE TABLES (ALL VALUES BASED ON A TIME INTERVAL OF A FORTNIGHT)

Temperature °C	*Species*	*R*	*r*	*Ro*	*MGT*
27	*L. natalensis*	1·334	0·2905	3·58	4·39
	B. tropicus	4·285	1·7361	647·66	3·73
25	*L. natalensis*	1·365	0·3374	9·85	6·78
	B. tropicus	4·064	1·8622	757·07	3·56
21	*L. natalensis*	1·652	0·5023	210·81	10·75
	B. tropicus	3·475	1·9796	890·17	3·34
18	*L. natalensis*	1·710	0·5489	382·82	10·96
	B. tropicus	2·244	1·070	464·76	5·74
15	*L. natalensis*	1·403	0·3451	75·96	12·65
	B. tropicus	1·637	0·5074	236·23	10·83

R = finite rate of increase; r = intrinsic rate of natural increase; Ro = net reproductive rate; MGT = mean generation time in fortnights.

The intrinsic rate of natural increase (r) remained roughly constant and rather low for *L. natalensis* at all the temperatures tested, although it increased very slightly with decreasing temperature to a maximum at 18°C. For *B. tropicus* the values started off with a maximum at 27°C and decreased appreciably with decreasing temperature. As in the case of fecundity these values lead to the conclusion that *L. natalensis* was less affected, either positively or negatively, by temperature differences than *B. tropicus*.

The mean generation time (MGT) was shorter, throughout, for *B. tropicus* than for *L. natalensis*. While, in the case of the latter, it increased with decreasing temperature, from approximately 8½ weeks at 27°C to more than 25 weeks at 15°C, it remained more or less constant for *B. tropicus* on 6½ - 7½ weeks at 27° - 21°C. Beyond this temperature it rapidly increased with further temperature decrease to 21½ weeks at 15°C. These findings together with those on the incubation period and the time lapse between hatching and subsequent egg laying, in our opinion, must be taken into consideration when determining the spacing between successive applications of chemicals to the habitat.

DISCUSSION

In spite of its short MGT at 27° and 25°C, the *r* and *Ro* values for *L. natalensis* at these temperatures are so low that, theoretically, this species could hardly be expected to maintain itself in habitats subject to prolonged temperatures of this order of magnitude. If, in addition to this, the habitat was subject to intermittent drying up, the species would be further hampered by its low egg-laying capacity, particularly at these temperatures. This conclusion naturally militates against the occurrence of *L. natalensis* and *Bulinus* (*Physopsis*) sp. in Natal and the Transvaal lowveld.

Exactly the reverse of this could be expected to apply to *B. tropicus* whose phenomenal fecundity, high intrinsic rate of natural increase and short MGT, particularly in the higher temperature ranges, should enable a small number of survivors to very rapidly repopulate the habitat when summer rains replenish the water after drying up or after chemical treatment of the habitat. In addition to the foregoing, should survivorship be brought into consideration as well, then *B. tropicus*, whose egg production at 15°C is high compared with that of *L. natalensis*, could be expected to survive low temperatures better than does the latter species. On the basis of these arguments its wider range of temperature tolerance is in complete agreement with the fact that *B. tropicus* is more widespread in the Republic than either *L. natalensis* or *Bulinus* (*Physopsis*) sp. On the other hand its stronger reaction to temperature differences might produce greater periodic fluctuations in the population densities of *B. tropicus*, and at times great densities may be expected to build up.

Any speculation based on the findings of the present investigation and conclusions drawn from them are, unfortunately, subject to two important considerations. They would first of all not take into account that temperature stratification might simultaneously establish both favourable and unfavourable temperatures in the same habitat. In fact Shiff[7] established that, on a very hot day, water at a depth of 25 cm. will normally be 4 - 5°C cooler than water at the surface. Secondly, our findings, derived as they were from observations at constant temperatures, may be significantly affected by the day/night fluctuations in temperature. Both these phenomena might go a long way towards explaining the presence of *L. natalensis* in Natal and the Transvaal lowveld where, according to our results, this species should not occur.

Like *Bulinus* (*Physopsis*) sp.,[7] *L. natalensis* furthermore probably also performs best within a narrow temperature range, a finding which could be regarded as being in line with Van Eeden and Combrinck's conclusion.[1] This range, although apparently of a lower order than that obtained for *B.* (*P.*) *globosus* in Rhodesia, could very well be one of the factors governing the restricted distribution of *L. natalensis* and *Bulinus* (*Physopsis*) species in the Republic.

The differences between the bionomics of *L. natalensis* and *B. tropicus* indicate that any mollusciciding programme, if it is to be conducted economically, has to be adapted to the particular species it is required to control. Our present findings, however, necessarily have to be checked and supplemented by studies at naturally fluctuating temperatures before they can be put to practical application.

SUMMARY

The influence of temperature on certain aspects of the bionomics of *L. natalensis* and *B. tropicus* was studied at constant temperatures ranging from 15°C to 30°C. The two snail species were found to differ significantly in their performance at the same temperatures. It is concluded that any mollusciciding programme must be adapted to the particular species it is required to control.

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