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R. L. Davidson; J. R. Wiseman; V. J. Wolfe

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ENVIRONMENTAL STRESS IN THE PASTURE SCARAB *SERICESTHIS NIGROLINEATA* BOISD.

I. MORTALITY IN LARVAE CAUSED BY HIGH TEMPERATURE

By R. L. DAVIDSON, J. R. WISEMAN and V. J. WOLFE

CSIRO, Division of Animal Physiology, Armidale, 2350, *Australia*

INTRODUCTION

Pasture soils on the Northern Tablelands of New South Wales almost always carry populations of several species of melolonthine, ruteline or dynastine scarabs. The abundance of larvae under pasture varies greatly from year to year, and their distribution is discontinuous. A study of environmental stress has been undertaken to determine how far this spatial and temporal variation is caused by microclimate. Most of the work so far has been done with *Sericesthis nigrolineata* Boisd. (Melolonthinae: Scarabaeidae).

This investigation measured the responses of each metamorphic stage of the species (egg, larval instar, etc.) to the range of environmental factors (temperature and soil moisture in the first instance) that would be experienced in the field. From these data a simulation model is being developed, by means of which survival of *S. nigrolineata* larvae should be predictable under a range of environmental conditions. To test the simulation model, captive populations of *S. nigrolineata* larvae are exposed to four semi-controlled environments in the field (factorial combinations of shaded/unshaded and irrigated/not irrigated). Profiles of soil moisture and temperature are recorded in each of the four microclimates at half-hourly intervals, and used with the simulation model on each occasion when survival of the captive scarab populations is measured. The agreement between actual and predicted survival on four occasions in each of the past two years has been reasonably good.

The long life cycle in these pasture scarabs makes it feasible to develop a simulation module for each metamorphic stage separately (Davidson, Wiseman & Wolfe 1970). Each module can be tested in the field by assessing mortality over 2–8 week periods. A complete set of modules for a species can be tested against past records of abundance, and then used to predict future populations of the species.

The first two papers in this series deal with laboratory studies of environmental stress, and the third will present the results of the field experiments.

Life cycle of Sericesthis nigrolineata

Adults feed on the leaves of *Eucalyptus* spp. mainly in December and January, though smaller numbers are sometimes active a few weeks before and after these two months. Eggs are laid during December/January about 5 cm deep in a loose cluster after the female has burrowed into the soil under pasture. The eggs hatch after about a month, and the larvae remain more or less active in the soil for 10 or 20 months, feeding underground on roots and other organic matter. The three larval instars last for respectively 4–8 weeks, 16–24 weeks and 25 or 50 weeks (depending on whether metamorphosis is completed in 1 or 2 years). In *Sericesthis nigrolineata* some individuals complete the life

cycle in 1 year, but a varying proportion take 2 years, remaining active third-instar larvae through two winters and a summer. The larvae pass through a short prepupal stage, followed by a pupal stage lasting about a month in an earthen cell 2–5 cm deep in the ground. Adults remain in the soil until weather conditions are favourable for emergence.

LABORATORY EXPERIMENTS

In 1968 and 1970 a series of experiments was done on first- and second-instar *Sericesthis nigrolineata* larvae reared from eggs laid by adult beetles maintained at 20° C. The aim was to define precisely the mortality caused by heat stress and soil-moisture stress in wet and dry soil, in order to predict survival of larvae under summer and autumn field conditions. The experiments were designed to simulate these conditions. Before exposure to stress, the larvae were kept at 16–20° C in soil at 12–15% moisture content. In each experiment five larvae were placed in 80 g soil of the required moisture content in 100-ml conical flasks closed with cotton wool. These were kept in incubators or waterbaths at fixed temperatures for the specified time, and then returned to 16–20° C. The soil in these flasks took about 3/4 h to attain the stress temperature, and about the same time to cool. The larvae were examined 1–2 days after exposure to stress, then placed in soil at 12–15% moisture content and examined 7–15 days later. In some experiments larvae were transferred to 800 g soil in open glass jars planted with ryegrass and examined after the next moult.

After examination larvae were classed as active, moribund or dead; only the active larvae are included in the survival data, because it was found that larvae which were moribund after 1 or 2 days did not recover.

The soil used in early experiments was a grey silt loam from native pasture, but in all later experiments a black silt excavated from a river bank was used. This was also used in the field experiments to be described later. Soils were not sterilized. Moribund larvae from the first experiments were examined for pathogens by Dr R. H. Goodwin, but none was diseased.

All the experiments were factorials with various combinations of temperatures, moistures, durations of exposure, number of exposures and periods of recovery between exposures. The longer durations were not included in the higher temperatures, and the shorter durations were not included in the lower temperatures.

First-instar larvae

Experiment 1

In February 1968 five replicates each with five larvae in grey silt loam at 12% moisture were exposed for 3, 6, 12, 24 or 48 h to temperatures of 25, 30, 35, 40 or 45° C. Fifteen replicates were maintained at 16° C as controls. Treated larvae were returned to 16° C and counted two days later (Fig. 1).

Experiment 2

In March 1968 late first-instar larvae in grey silt loam at 12% moisture were exposed once, twice or four times to temperatures of 30, 32·5, 35 or 37·5° C for durations of 1·5, 3 or 6 h with rest periods between the double and quadruple exposures of either 1, 2 or 4 days ($3^3 \times 1^4$ factorial). Only two batches of larvae were available as controls at 16° C.

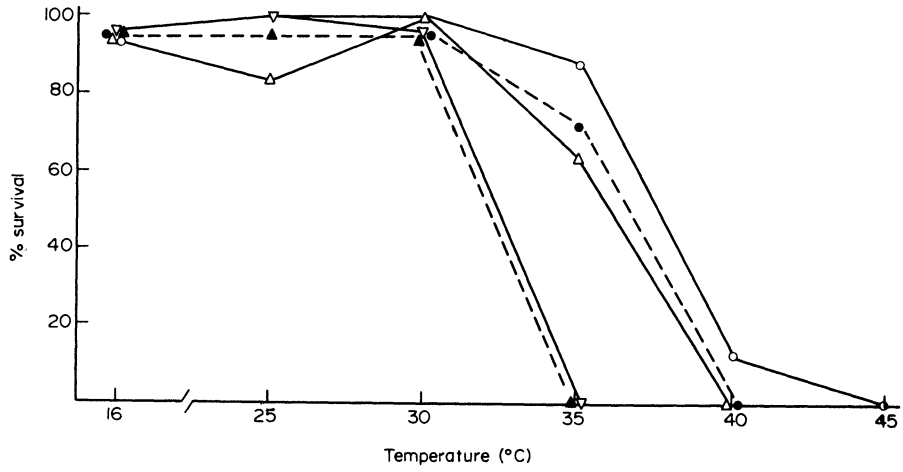

FIG. 1. Percentage survival of first-instar larvae reared at 20° C after a single exposure to temperatures 25–45° C followed by two days at 16° C. Data not adjusted for mortality in controls (4% at 16° C). Duration of exposure (h): ○, 3; ●, 6; △, 12; ▲, 24; ▽, 48.

Before and after each exposure the larvae were maintained at 16° C, and examined after 7 days (Table 1 and Fig. 2).

Experiment 3

In February 1970 groups of five newly hatched larvae were placed in black silt in 100-ml flasks at either 9% or 15% moisture content, and exposed to 30, 32·5, 35, 37·5, 40 or 42·5° C for 0·75, 1·5, 3 or 6 h on 1, 2, 4 or 8 consecutive days in a $1^2 \times 2^4 \times 1^6$ factorial. Before and after exposure to these temperatures, the larvae were maintained at 20° C in soil planted with ryegrass seed. Seven control batches at each moisture content were

Table 1. *Percentage survival of first-instar larvae 7 days after one, two or four exposures for* 1·5, 3 *or* 6 *h with* 1, 2 *or* 4 *days rest between exposures to four temperatures*

	Temperature (° C)				
	30	32·5	35	37·5	Mean
Durations** (h)					
1·5	76	71	82	67	74
3	84	78	78	56	74
6	76	84	29	11	50
Exposures^{NS}					
1	80	87	62	44	68
2	82	71	62	47	66
4	73	76	64	42	64
Rest periods^{NS} (for two and four exposures only) (days)					
1	73	87	73	27	65
2	83	63	57	53	64
4	77	70	60	53	65
Temperature means**	79	78	63	44	

Significant temperature × duration interaction*

*, $P<0·05$; **, $P<0·01$; ^{NS}, not significant.

maintained throughout at 20° C. Three days after the last treatment first- and second-instar larvae in each flask were counted, and the 9% and 15% moisture treatments were put together in 800 g fresh soil with 12% moisture content and seeded with ryegrass.

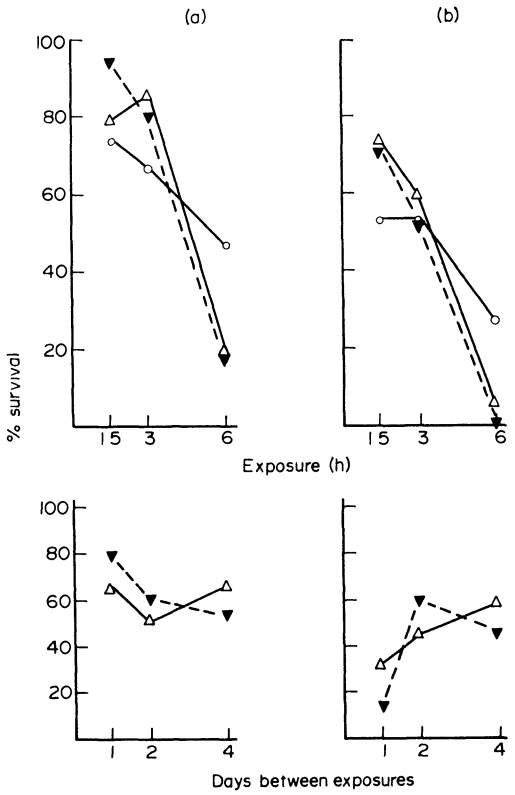

FIG. 2. Survival of first-instar larvae after 1 (○), 2 (△) or 4 (▼) exposures to 35 (a) and 37·5° C (b) for 1·5, 3 or 6 hours, with 1, 2 or 4 days between exposures, after 7 days at 16° C, not adjusted for control mortality (50% at 16° C).

These were examined a month later to determine whether the temperature stress had affected ecdysis (Table 2 and Figs. 3, 4 and 5).

Second-instar larvae

Experiment 4

Second-instar larvae which had been reared at 20° C in grey silt loam with ryegrass seedlings were used in a temperature stress experiment in June 1968; the larvae were close to ecdysis. Batches of five larvae were placed in 80 g grey silt loam at 12% moisture content and exposed once, twice or four times, with rest periods of 1, 2 or 4 days between exposures. The durations of exposure were 1·5, 3 or 6 h, to temperatures of 30, 32·5, 35 or 37·5° C. After treatment the larvae were maintained at 16° C, and ryegrass plants were placed in the flasks. The numbers of second- and third-instar larvae were counted 8 days and 25 days after the last treatment (Table 3 and Fig. 6).

Table 2. *Survival of first-instar larvae exposed to various temperatures for 0·75, 1·5, 3 or 6 h on 1, 2, 4 or 8 consecutive days at 9 or 15% soil moisture*

(a) *Percentage survival after 3 days*

Temperature (°C)	9% moisture				15% moisture			
	Duration (h)							
	0·75	1·5	3	6	0·75	1·5	3	6
30	100	100	80	90	80	100	100	100
32·5	60	80	95	85	100	100	95	75
35	90	85	90	80	90	100	75	60
37·5	95	50	5	0	85	45	0	0
40	0	0	0	0	0	0	0	0
42·5	0	0	0	0	0	0	0	0
Means	53	45	46	42	53	49	44	39
Moisture means		46·5%				46%		
Control means		91%				91%		

Exposures	Temperature (°C) 30	32·5	35	37·5	40	42·5	Mean
1	–	85	98	50	0	0	93
2	–	95	85	30	0	0	84
4	98	90	83	35	0	0	83
8	90	80	75	25	0	0	72
Means	94	90	85	35	0	0	

(b) *Survival after 33 days*

Temperature (°C)	Exposures 1	2	4	8	1	2	4	8
	Number of larvae				% still first instar			
30	–	–	35	29	–	–	9	10
32·5	–	–	31	27	–	–	3	7
35	35	33	31	22	3	0	0	18
37·5	17	10	12	8	0	0	0	0
Means					1·5	0	3	9
Controls			60			5%		

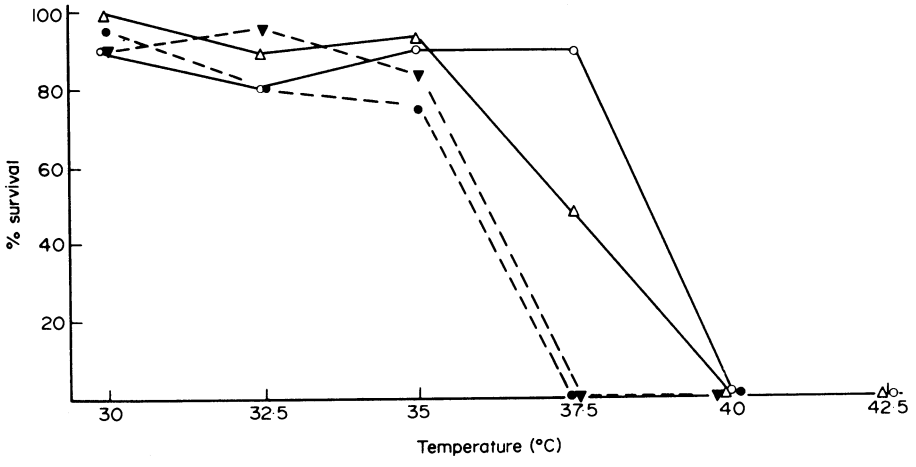

FIG. 3. Percentage survival of first-instar larvae after short exposures to high temperatures (means of 9% and 15% moisture, and one, two, four and eight exposures of each duration) after 3 days at 20° C. Not adjusted for control mortality (8·6% at 20° C). Duration of exposure (h): ○, 0·75; △, 1·5; ▼, 3; ●, 6.

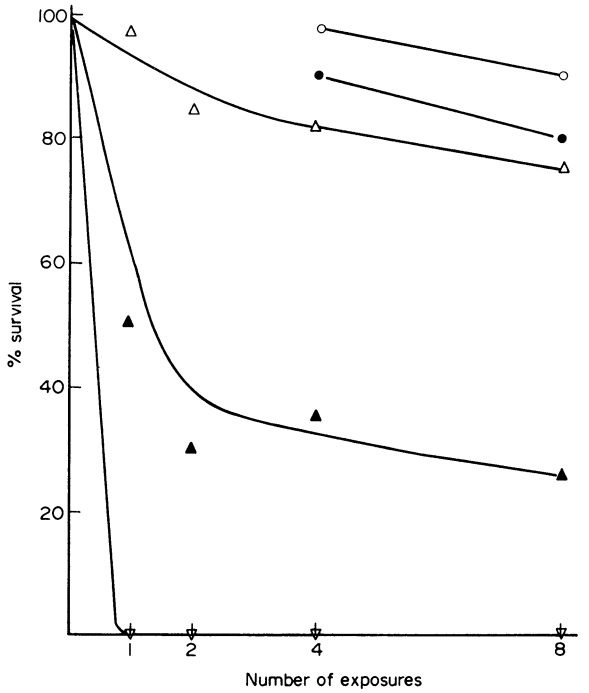

FIG. 4. Effect of repeated short exposures to various temperatures (○, 30; ●, 32·5; △, 35; ▲, 37·5; ▽, 40° C) on survival of first-instar larvae (means of 9 and 15% moisture, and all durations) after 3 days at 20° C, not adjusted for control mortality (8·6%).

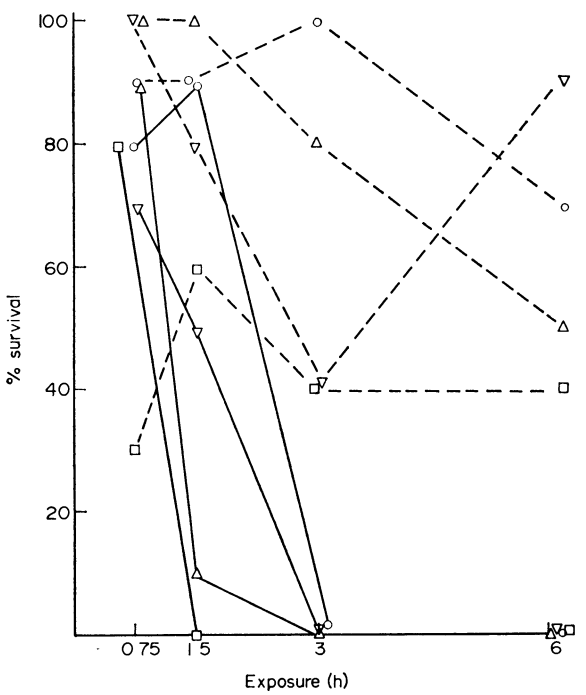

FIG. 5. Relationship between repeated exposures (○, 1; △, 2; ▽, 4; □, 8) and durations of exposure to 35 (– – –) and 37·5° C (——) and survival after 33 days at 20° C (means of 9 and 15% moisture), not adjusted for control mortality (14·3%).

Table 3. *Survival of second-instar larvae after one, two or four exposures for 1·5, 3 or 6 h with 1, 2 or 4 days rest between exposures to various temperatures*

(a) *Percentage survival after 8 days*

	Temperature (° C)				
	30	32·5	35	37·5	Mean
Durations** (h)					
1·5	82	93	89	89	88
3	82	100	84	87	88
6	84	93	44	40	66
Temperatures***	83	95	72	72	
Controls (16° C)			100%		
Significant temperature × duration interaction*					
Exposures^{NS}					
1	89	98	80	80	87
2	77	93	73	73	79
4	82	96	64	62	76
Rest periods^{NS} (for two and four exposures only) (days)					
1	70	93	63	60	72
2	80	100	73	63	79
4	90	90	70	80	82

(b) *Survival after 25 days*

	Duration (h)						
	1·5	3	6	1·5	3	6	Mean
Temperature (°C)	Number of larvae			% still second instar			
30	33	33	31	70	73	68	67
32·5	38	36	39	74	75	79	76
35	30	32	18	70	84	72	76
37·5	34	36	17	73	83	65	74
Mean	34	34	26	72	79	69	

**, $P<0·01$; ***, $P<0·001$; ^{NS}, not significant.

RESULTS

Detailed tables of results of the four experiments are available from CSIRO records through the authors. The data, summarized in the tables and diagrams referred to in the descriptions above, have been used to define the effect of soil temperature on survival of first- and second-instar larvae. Survival data were not adjusted for mortality in the controls except in Figs. 7–10, which generalize the data and draw comparisons between experiments. Abbott's correction was applied only in these four figures.

After exposure to stress, larvae were maintained at optimum temperature and moisture long enough to determine any long-term effect on survival. Mortality occurred mainly in the first few days after the stress was terminated (Fig. 8 and Table 2). In Experiment 3 the additional mortality between the third and thirty-third day after exposure was 6% in the controls, 14% at 30° C, 10% at 32·5° C, 9% at 35° C and 6% at 37·5° C. The comparatively slight change in the controls after 33 days (when 95% of the larvae had moulted) gave an overall survival of 86% in the controls. In several experiments the larvae were maintained under optimum conditions until after ecdysis, and the percentage of survivors which moulted was no less in the severely stressed than in the unstressed larvae (Tables 2 and 3).

Temperature stress

In soil with a moisture tension between pF 2·4 (field capacity) and pF 3·0 (half field

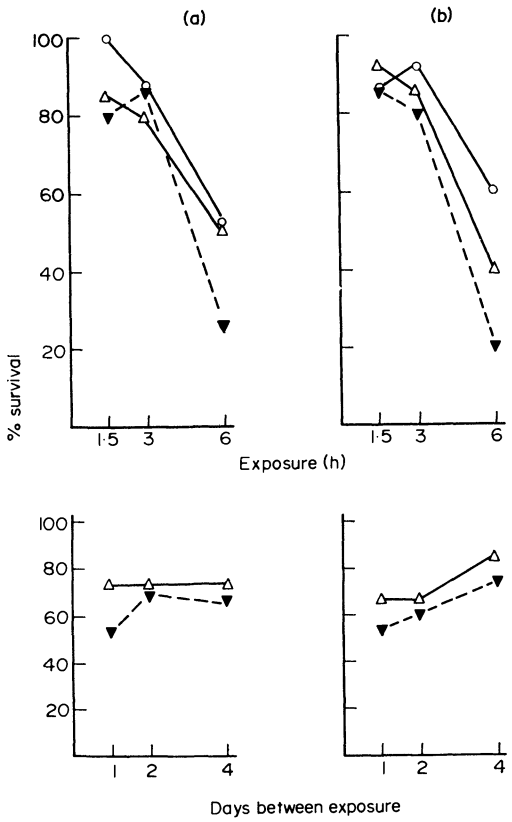

FIG. 6. Survival of second-instar larvae after 1 (○), 2 (△) or 4 (▽) exposures to 35 (a) and 37·5° C (b) for 1·5, 3 or 6 h, with 1, 2 or 4 days rest between exposures, after 8 days at 16° C. No mortality in controls.

capacity) first- and second-instar larvae reared at 16–20° C were not adversely affected by a single exposure to temperatures up to 30° C. In these experiments larvae were exposed up to 48 h without any increase in mortality compared with the controls (Figs. 1 and 3). At 35° C a single exposure for 24 h killed all first-instar larvae but 62% survived 12 h, 70% survived 6 h, and 85% survived 3 h. A single exposure to 37·5° C killed 73% of first-instar larvae and 40% of second-instar larvae in 6 h (Figs. 2 and 6). Recently hatched larvae did not survive 3 h at 37·5, but 90% of these survived 1·5 h at this temperature in Expt 3. A few larvae survived 3 h at 40° C, but all died later. In Expt 3 newly hatched larvae did not recover after 0·75 or 1·5 h at 40° C. The marked effect on survival of duration of exposure to any one temperature is shown in Fig. 5, and similarly the large difference in survival between high temperatures, only 2·5° C apart, for any one duration of exposure, is shown in Fig. 3.

High temperature stress in larvae of *Sericesthis nigrolineata* having been demonstrated between 30–40° C, it was necessary to define over this temperature range the effect of (a) the duration of each exposure, (b) the number of exposures, and (c) the rest period between exposures on survival of larvae.

Analysis of variance of the results from Expt 2 (first instars) and Expt 4 (second instars), with combinations of three durations, three exposures, and three rest periods between exposures to temperatures between 30 and 37·5° C, showed no interaction

between components except a temperature × duration interaction ($P<0{\cdot}05$). The main effects of temperature and duration were highly significant in both instars, but neither the number of exposures, nor the rest between exposures, significantly affected survival over all temperatures. These effects can be best defined at temperatures of 35 and 37·5° C, where mortality is neither too low nor too high.

An analysis of the data from both instars showed that mortality from temperature stress was greater in first that in second-instar larvae ($P<0{\cdot}001$), especially at the higher temperatures (significant temperature × instar interaction, $P<0{\cdot}05$). Over all durations, exposures and recovery periods the survival of first-instar larvae at 37·5° C was 44%, and of second-instar larvae 71%. The difference in survival at 35° C was less, respectively 63 and 70% in first- and second-instar larvae.

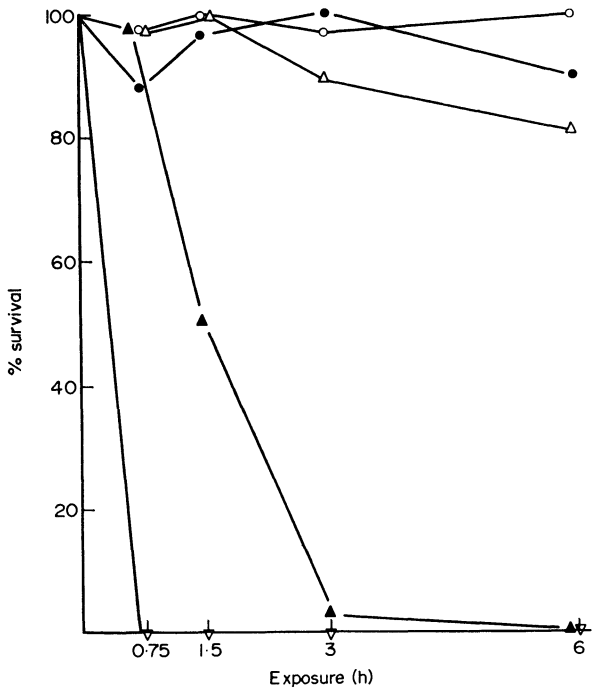

FIG. 7. Change in the relationship between survival and duration of exposure to different temperatures (○, 30; ●, 32·5; △, 35; ▲, 37·5; ▽, 40° C) (means of 9 and 15% moisture and one, two, four and eight exposures), adjusted for 8·6% mortality in controls after 3 days at 20° C.

Duration of exposure

At any one temperature, the mortality increased as the duration was extended. The relationship between survival and duration appears to be linear (Figs. 5 and 7), though it is difficult to define at low and very high mortalities. The slope of the regression of survival × time increased with increasing temperature (Fig. 7). At 37·5° C survival fell from 90% at 0·75 h to 3% at 3 h, whereas at 35° C survival fell from 90% at 0·75 h to 75% at 6 h.

Repeated exposure

In the analysis of variance over all temperatures, the difference in survival of first- and second-instar larvae was not influenced significantly (P slightly $>0{\cdot}05$) by the number of

exposures (one, two or four). It is evident from Figs. 2 and 6, however, that there is some additive effect from two and four exposures to 35 and 37·5° C. The effect of repeated exposure on consecutive days was examined further in Expt 3, with up to eight exposures (Fig. 4). While these figures demonstrate that repeated exposure to any stress temperature caused additional mortality, the percentage mortality was considerably less than that calculated from the percentage mortality after the first exposure applied to the surviving larvae (Fig. 8). There was no delayed effect, and the discrepancy between actual and predicted survival was as marked after 33 days as after 3 days.

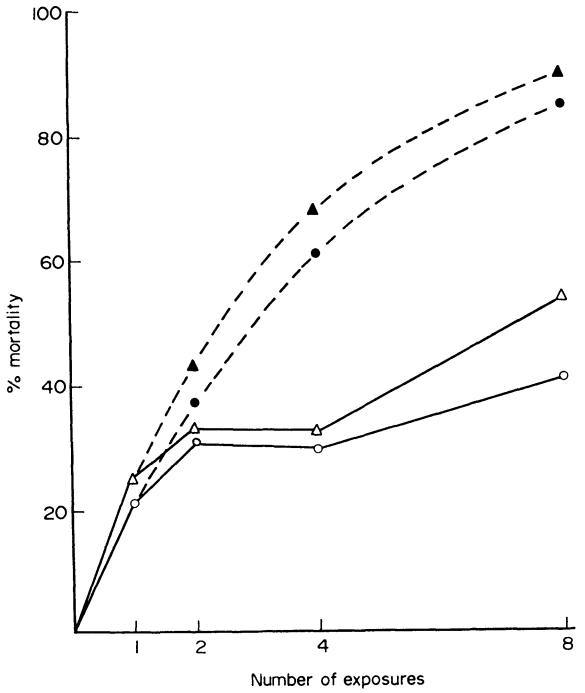

FIG. 8. Actual mortality (adjusted for mortality in controls) (——) and mortality calculated from the mortality after the first exposure (– – –), means of 32·5, 35 and 37·5° C at two moisture levels and four durations of exposure of first-instar larvae. ○, 3 days after exposure; △, 33 days after exposure.

Recovery between exposures

In two experiments in which larvae were exposed twice and four times to temperatures between 30 and 37·5° C, the period between exposures to temperature stress was either 1, 2 or 4 days. The effect of this recovery period on the mortality after subsequent exposure to stress was not apparent when mortality was low, and in analyses of variance of first- and second-instar data the main effect of rest is insignificant. At 37·5° C, the ameliorating effect of rest prior to subsequent exposures was more marked (Figs. 2 and 6). Over all treatments at 37·5° C the mean survival of both instars with recovery periods of 1, 2 or 4 days was 43%, 58% and 67% respectively. Further work is needed to define the difference between repeated exposures to stress on consecutive days and with various periods of recovery. So far the mortality from repeated exposure seems to be 15% higher on consecutive days than with 2 days between exposures; 3- and 4-day rests between exposure seem to reduce mortality less than this.

Soil moisture × temperature interaction

In Expt 3 combinations of two soil moistures, 9% (pF 2·4) and 15% (pF 2·2), with all temperature treatments were used. Survival at these two moistures was identical, and no moisture × temperature interaction was evident. Work reported later in this series will show that mortality at high temperatures is only slightly affected by soil moisture, at the wet extreme more than at the dry extreme of soil moisture.

DISCUSSION

Pasture scarabs lay eggs in summer, and these eggs and the first- and second-instar larvae (which are mostly in the upper 5 cm of soil) may be exposed to excessively high temperatures for short periods on a number of days during the summer and early autumn (Table 4). This study of high temperature stress in one of the scarab species was designed to provide the quantitative data necessary to predict the mortality of *Sericesthis nigrolineata* larvae from these sporadic exposures to heat stress. The physiological data will be used in a collaborative study of scarab ecology, including detailed microclimate recording by means of a specially-designed telemetering data acquisition system (Wiseman 1967). It is intended that the physiological response data be as precise as the microclimate data, so that the mortality following each exposure to stress may be predicted.

Table 4. *Number of days and mean daily duration of soil temperatures exceeding* 30, 32·5, 35 *and* 37·5° *C under perennial ryegrass pasture at Pastoral Research Laboratory, Armidale, July* 1967 *to June* 1968

	Temperature (° C) exceeding							
	30		32·5		35		37·5	
	Days	Hours	Days	Hours	Days	Hours	Days	Hours
3·75 cm depth								
November	18	3·2	4	3·0	2	2·0		
December	25	5·7	19	4·8	15	3·7	8	1·5
January	7	2·3	0	0				
February	18	2·5	2	3·0				
March	4	2·8						
7·5 cm depth								
November	1	5·0						
December	16	3·8	2	0·5				
January	0	0						
February	1	1·0						

Little is known about the effects on insects of temperatures above the fairly well-defined range of temperatures within which poikilothermic organisms remain viable. Exactly what causes death at the higher temperatures is still in doubt (Bursell 1964; Clarke 1967). A logarithmic relationship between survival time and temperature has been shown in several insect species (Baldwin 1954; Maynard Smith 1957; Platt, Collins & Witherspoon 1957). A sigmoid relationship exists between mortality and temperatures between 39·6 and 42° C after a 40-min exposure of *Calliphora erythrocephala* (Davison 1969). Probit analysis has been used to calculate the temperature causing 50% mortality for any duration of exposure (Davison 1969), and also to calculate the duration of exposure necessary to cause 50% mortality (Riordan 1957; House, Riordan & Barlow 1958). From these LD_{50} values differences in high temperature tolerance between insect species and between stages of development in *Calliphora* have been demonstrated. The

lethal temperature for a species may be varied by acclimation, either by rearing the insects at a higher temperature (long lasting *developmental* acclimation) or by a short exposure to sublethal temperatures (transitory *physiological* acclimation), a distinction proposed by Maynard Smith (1957).

No work has been reported yet which attempts to analyse the effect of intermittent exposures to high temperatures on mortality of scarabaeid larvae. Elaterid larvae appear to tolerate temperatures up to 47° C for about 20 min, and higher temperatures for shorter periods (Fulton 1929). No other data on heat resistance of subterranean insects have been reported. In the study of *Sericesthis nigrolineata* so far the shortest exposure to

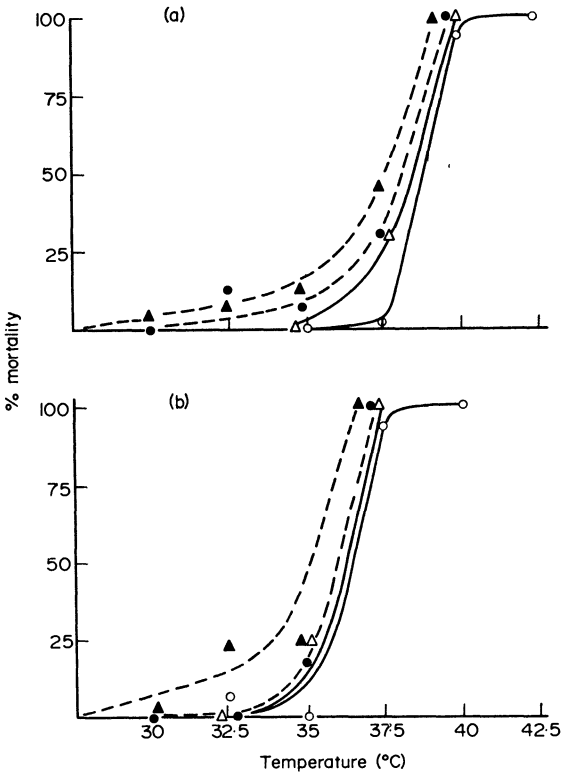

FIG. 9. Percentage mortality (adjusted for 8·6% mortality in controls) one week after exposure to temperatures between 30–42·5° C for (a) 0·75 and 1·5 h and (b) 3 and 6 h. Number of exposures: ○, 1; △, 2; ●, 4; ▲, 8.

40° C (45 min) was lethal, and the longest exposure to 30° C (192 h) was apparently harmless. Within this range there was an exponential relationship between mortality and temperature, for any one duration of exposure (Fig. 9). There was no indication of a sigmoid response to temperature (cf. Davison 1969), except as an artefact when the 100% mortality at high temperatures is plotted. In these experiments temperature intervals of 2·5° C were used, because these are the categories within which field data on soil temperature are being collated. In view of the steep mortality/temperature gradients above 37·5° C it may be necessary to collate data for higher temperatures within narrower intervals.

At any one temperature the relationship between mortality and duration of exposure

may be regarded as linear for the purpose of predicting the survival of field populations. At temperatures of 35 and 37·5° C the temperature quotients are so high that no departure from linearity can be detected (Figs. 5 and 10). Mortality from a single exposure to 37·5° C changes by about 80% between 0·75 and 1·5 h. The regressions of mortality on duration do not pass through the zero origin, because short exposures to sublethal temperatures are harmless, even after the next moult. There is therefore a change with temperature of both the slope and intercept of these regressions.

In all experiments in which larvae were exposed more than once to sublethal temperatures, the percentage mortality after the first exposure was greater than after the subsequent exposures (Fig. 8). There are two possible explanations: (i) that short-term physiological acclimation occurs at the first exposure, or (ii) that the more temperature sensitive individuals are killed at the first exposure, leaving a batch which is more resistant to later exposures to the same temperature. The latter explanation is more likely, because the response to repeated exposures was nearly linear at the lower stress temperatures (Fig. 4).

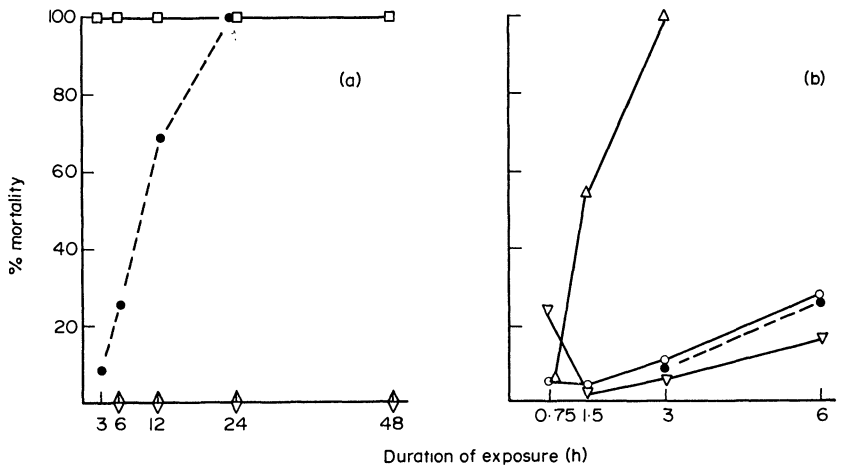

FIG. 10. Percentage mortality (adjusted for mortality in controls) of first-instar larvae exposed once for various times (a) in Expt 1 after 18 h and (b) in Expt 3 after 33 days. In diagram (b) the 3-h and 6-h mortalities at 35° C in Expt 1 are superimposed in solid symbols. Temperatures (° C): ◇, 30; ▽, 32·5; ○, 35; △, 37·5; □, 40.

Furthermore, at the higher temperatures, repeated exposures with 2 and 4 days rest between exposures gave better survival than the same number of exposures on consecutive days (Figs. 2 and 6), which is consistent with a slow recovery from stress, extending beyond 24 h (Baldwin 1954). It is unlikely that physiological acclimation will improve during periods of rest at 16–20° C, since the resistance conferred by sublethal temperatures is thought to be associated with partial dehydration (Baldwin & House 1954; Baldwin & Riordan 1956).

In all the work described here the larvae were continuously in a saturated atmosphere in soil, because at soil moisture tensions less than pF 4·2 (wilting point) the soil air is saturated. In the next paper in this series the interaction between temperature and a wider range of soil moistures will be discussed.

From the work presented here, for a range of moderate soil moistures, it appears feasible to identify from weather records the separate occasions when *S. nigrolineata* larvae are stressed by sublethal temperatures in the field (Davidson *et al.* 1970). The

laboratory data are consistent enough to provide a basis for a prediction of survival over several weeks, although it would be advisable to test the tentative model with irregular patterns of temperature in the laboratory, or with captive batches of larvae in the field.

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SUMMARY

First- and second-instar larvae of *Sericesthis nigrolineata* Boisd. (Scarabaeidae; Coleoptera) have been exposed for short periods to temperatures between 30–45° C, to define empirically the effects of duration, number of exposures and recovery periods on mortality. The data are needed to collate field microclimate measurements to predict larval survival in the field. At moderate soil moistures the longest exposure to 30° C (192 h) was harmless, and the shortest exposure to 40° C (45 min) was lethal. Above 30° C, the effect of temperature for any one duration of exposure was exponential. At any one temperature the relationship between duration of exposure and mortality appeared to be linear, but the gradients between the 2·5° C temperature intervals were too steep to be clearly defined. Repeated exposures to sublethal temperatures caused a slightly lower percentage mortality than at the previous exposure to the same temperature. When the interval between repeated exposures was extended from 1 day to 2 or 4 days, the mortality was slightly less than that after the same number of exposures on consecutive days, but the difference was not statistically significant over all temperatures.

All these exposures to temperature stress were in soil with moisture contents above wilting point. No temperature × moisture interaction occurred.

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