SOME ADAPTATIONS OF MYRMELEONTID (NEUROPTERA) AND RHAGIONID (DIPTERA) LARVAE TO LIFE IN HOT DRY SAND

PART I. TEXT

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1. INTRODUCTION

Larvae of the families Myrmeleontidae, Neuroptera, (ant-lions) and Rhagionidae, Diptera, (worm-lions) all live in hot dry sand. Many of the ant-lion larvae and all the worm-lion larvae, construct small conical pits in the sand which are used for the capture of prey (Haub, 1942; Youthed and Moran, 1969a). Those ant-lion larvae which do not construct pits lie in wait for their prey just below the surface of the sand.

Observations of ant-lion species, commonly occurring around Grahamstown, showed that the larvae were often found in regions where the sand temperatures exceeded 60°C. These temperatures are considerably higher than the upper lethal temperature limits recorded for the majority of insects (Bursell, 1964; Cloudsley-Thompson, 1964b) which raises questions about the adaptations of ant-lion and worm-lion larvae enabling them to survive in such inhospitable habitats.

In this study the temperature and water relations of four species of ant-lions and one species of worm-lion have been investigated. The species studied were: (a) three pit building ant-lion species namely; *Myrmeleon medialis* Banks, *Myrmeleon obscurus* Ramb., and *Cueta lanceolatus* Navas, (b) a pit building worm-lion, Lampromyia intermedia Stuckenberg, and (c) a non-pit-building ant-lion, Syngenes longicornis Ramb. Five different species were chosen for this study because their habitats range from warm sand in shady caves to exposed rocky habitats where the sand becomes extremely hot. Also, ant-lions and worm-lions are morphologically very different and come from widely divergent orders of insects. This poses questions about their convergence with respect to adaptations to life in dry sand. The adaptations of pit building ant-lions compared with those of non-pit-building ant-lions, are also of interest.

Preliminary studies were made on overall distributions of these species in South Africa in order to establish any correlation between distribution and gross climatic factors. Also, the conditions in the microhabitat of the larvae of each species were investigated, bearing in mind that these animals live in small isolated deserts. Exposure of the habitats to sunlight, and the temperature conditions prevailing in the pits and in the sand were the main aspects studied. Using these data, the temperature relations of the larvae were investigated. This included their tolerance to high temperatures and their behavioural responses to light, shade and temperature. The present investigation has been confined to an appraisal of the responses of whole organisms and no attempt has been made to investigate any of the phenomena at the cellular level.

2. MATERIAL AND METHODS

All the myrmeleontid and rhagionid larvae used in the present investigation were collected in the Grahamstown district, except for the larvae of S.longicornis which were collected along the coastal sand dunes from Port Alfred to Jeffrey's Bay. In the laboratory the larvae were maintained at 18 ± 3°C under normal daylight conditions and each larva was fed one ant, Plagiolepis custodiens Santschi, per day.

The experiments which were performed in this investigation were very varied and this has necessitated a description of many of the methods used at intervals through the text. Some general methods are, however, described below.

(i) Measurement of sand and pit temperatures

A major part of this investigation involved the recording of sand temperatures. In the field, sand temperatures were studied using a set of six thermistors connected to a multichannel graphic recorder. The thermistors were placed in the following positions: 1 cm. above the sand surface, on the surface of the sand, and 1 cm., 3 cm., 5 cm.and 7 cm. below the surface. Thermistors were also used to measure sand temperatures in the laboratory and were placed at the following depths: 0 cm., 0,5 cm., 1,5 cm., 2,5 cm., 3,5 cm., 4,5 cm., 5,5 cm., 6,5 cm. and 7,5 cm. In the laboratory, thermistors could only be used during the period 6 a.m. to 8 p.m.

when the temperature of the sand was relatively high. At night the temperature of the sand fell below the recording range of the thermistors and then mercury thermometers had to be used. The thermometers, because of their larger size, gave less accurate readings but this error was not considered to be important since at night all the sand was at about the same temperature.

The temperatures prevailing in the pits of ant-lion and worm-lion larvae, both in the field and in the laboratory, were also recorded with thermistors. These temperature readings were taken on the surface of the sand half way up the sides of the pit in the north, south, east and west quadrants. The temperatures of the pit base, that of the general sand surface, and of the air 1 cm. above the sand surface were also recorded.

(ii) The measurement of internal temperatures

Thermocouples were used to determine the internal temperatures of the larvae in this investigation. The method used was based on that of Edney (1969). The thermocouples were made from 47 S.W.G. (0,051 mm.) silver soldered copper and "Contra" wire and were connected to a galvanometer. The circuit also included a switch so that six thermocouples could be used at the same time. Sensitivity was controlled by a 10K potentiometer. This apparatus had various shortcomings. Firstly, it was found that, while the galvanometer reading always increased linearly with temperature, the absolute value varied slightly from experiment to experiment. This was probably due to a slight thermocouple effect in regions where other circuit wires were soldered together, such as the junction between the copper wires and the switch. The effect of this factor was minimised as far as possible by enclosing the switch and potentiometer in an insulated box. It was also overcome by using one of the six thermocouples as a "calibration" junction in each experiment. This calibration junction was taped to the bulb of a standard thermometer and placed in a water bath, thus providing a calibration curve for each experiment.

The second major shortcoming was the difference between the various thermocouples. The different junctions sometimes varied by as much as 0,3°C. This variation was probably due mainly to the amount of silver solder used in the making of each junction. The effect of individual thermocouple variation was minimised by ensuring that, in each replicate of an experiment, the temperature of any particular species of larva was measured on all available thermocouples. In this way it was hoped to "standardise" any errors so that valid comparisons could be made between the various species. This method did not always work satisfactorily since the thermocouples were extremely fragile and had to be replaced fairly frequently.

The final problem inherent in the circuit was that of conduction of heat, from external sources such as the water bath, along the wires of the thermocouples. Edney and Barrass (1962) calculated this error to be in the order of 5% (about 0,1°C). Digby (1955), however, states that the transfer of heat along the wires of very thin thermocouples is negligible. In the present investigation conduction of heat along the wires was eliminated as far as possible by coating each wire with several layers of clear varnish. The total error inherent in the circuit was about 0,3°C.

The main problem encountered with the use of these thermocouples was that of inserting them into the insects. The conventional position for the insertion of thermocouples is the thorax (Gunn, 1942) but in ant-lion and worm-lion larvae this was not possible. These larvae have a relatively soft cuticle and bleed profusely when cut. It was therefore necessary to insert the thermocouples into a part of the body which could be conveniently ligatured. The posterior end of the abdomen was found to be the most convenient site in these animals. Due to the difficulty of ligaturing, only large final instar larvae were used in these experiments. Ligatures of human hair were found to be the most suitable and the thermocouples could then be inserted through the dorsal surface of the abdomen. Each thermocouple was gently pushed through the centre of the ligature so that it came to lie in the layer of fat just above the gut. The incision was then sealed with wax, which not only prevented blood loss, but also helped to hold the thermocouple in position. In initial experiments the ligature was removed but, since it was found to have no effect on the temperatures recorded, it was left intact in later experiments.

After each experiment the larvae were dissected to ensure that the thermocouples were in the correct position and that the gut had not been punctured since Digby (1955) has shown that the internal temperature of an insect may vary by as much as 2,9°C depending on the position of the thermocouple. It should be noted that insertion of thermocouples in this way did not appear to cause serious harm to the insects since it was found that they could survive for at least a week with the thermocouples in position, although they were unable to burrow or to construct pits because all ant-lions use the posterior end of the abdomen to dig their way into the sand.

(iii) Light experiments and the establishment of temperature gradients in sand

In experiments designed to test the responses of the larvae to light, incandescent lights of the following intensities were used: 200 lux (25W), 600 lux (60W) and 1200 lux (100W). In addition a tungsten-halogen lamp of about 14000 lux (500W) was used to provide high illumination. The illumination of the sand in the experimental trays was measured with a photographic light meter. When the 100W and 500W lights were used it was necessary to use a heat filter in order to prevent undue heating of the experimental sand. The heat filter used in conjunction with the 100W light bulb consisted of a glass tray filled with water to a depth of 2 cm. which was supported 60 cm. above the surface of the sand. This type of filter was not adequate for use with the 500W tungsten-halogen lamp, which produced much heat, and the problem was overcome by reflecting the light off a mirror onto the experimental trays, using the mirror as a heat sink. The angle of incidence of the above lights varied and is dealt with in the relevant sections of the text. In all cases the direction from which the light was shining was regarded as north.

The establishment of temperature gradients in the laboratory was achieved by the use of infra-red lights (250W). This infra-red light was assumed to be "invisible" to the ant-lion and worm-lion larvae since Youthed and Moran (1969b) have shown that red light does not affect the activity or pit construction of M.obscurus.

In experiments designed to test the responses of larvae to pit temperatures the infra-red lights were placed at angles of incidence of 90°, 60° and 40°. The height of the lamps above the experimental sand was also varied from 60 cm. to 40 cm. In this way the larvae were not only subjected to different surface sand temperatures, depending on the distance of the lights above the containers, but were also subjected to various temperature gradients within the pits, depending on the angle of incidence of the infra-red lights. As the lights were lowered from 60 cm. to 40 cm. the general sand surface temperature increased from about 33°C to about 53°C and as the angle of incidence was altered from 90° to 40° the temperature gradients within the pits increased. As in the experiments using visible light, the direction from which the light was shining was regarded as north.

The establishment of vertical temperature gradients in sand was achieved by suspending infra-red lights above cylindrical plastic dishes (depth 10 cm., diameter 10,5 cm.). The temperature conditions in the laboratory sand were manipulated to simulate the sand temperature conditions found in the field. The dishes were placed in a constant environment room which maintained a temperature of 16°C from 8 p.m. to 6 a.m. After 6 a.m. the temperature rose to 25°C and remained so until 5 p.m. when it once again fell to 16°C. The infra-red lights, and flourescent lights of about 1500 lux, were switched on from 9 a.m. to 5 p.m. each day. By varying the height at which the infra-red lights were suspended above the experimental dishes, the surface sand temperature was varied from about 36°C to about 63°C. The lights were placed at 10 different heights so that each time they were lowered by one level the temperature of the surface sand rose by about 3°C. Preliminary observations showed that the lights could not be lowered by a constant distance each time. When the lights were high above the sand a small change in height had little or no effect on the temperature of the sand, whereas when the lights were close to the sand a small alteration in height made a large difference to the sand temperature. Furthermore, the heat produced by individual infra-red lights differed. The height at which each lamp was suspended had therefore to be determined empirically prior to each experiment.

The responses of ant-lion and worm-lion larvae to these vertical temperature gradients were determined by placing each individual in a cylindrical plastic container with a diameter of 10,5 cm. which was filled with sea sand to a depth of 10 cm. These containers had slots at one centimeter intervals into which thin metal plates could be pushed, thus dividing the column of sand vertically. The depth of each larva could thus be determined. In the case of large ant-lion larvae intervals of two centimeters were used to avoid slicing the larvae in half with the metal plates.

3. DISTRIBUTION AND HABITAT CHARACTERISTICS

Numerous species of ant-lions and worm-lions occur in South Africa and many patches of fine dry sand are inhabited by the larvae of one or more species. Fig. 1 shows the general distribution of the five species included in this study. This information was obtained from museum collections and supplemented by records of larvae collected in the field. It is probable that Fig. 1 does not include the full range of these species because they have seldom been extensively collected. Nevertheless some general comments may be made about their distribution.

(i) The worm-lion, L.intermedia, has only been recorded from a very limited area in the south eastern coastal region. There are no records of this species from the warm, dry interior of the country. Large numbers of larvae of this species have been observed in isolated groups throughout its range.

(ii) The ant-lion, M.medialis, also appears to be very limited in its distribution and has only been recorded from the southern and south eastern coastal region. The larvae of this species are seldom found in large numbers.

(iii) The ant-lion, M.obscurus, has a wider area of distribution and has been recorded in the south western, southern and eastern coastal regions as well as in the north eastern and north western parts of the country. The larvae of this species occur in large numbers throughout its range.

(iv) The ant-lion, S.longicornis, is an almost exclusively coastal species, although in the northern part of its range it may extend a short distance up river valleys, where suitable sand is available. Large numbers of larvae have been recorded throughout its range.

(v) The ant-lion, C.lanceolatus, is an exclusively inland species which has never been found less than about 64 kilometers from the coast. Small numbers of larvae occur in isolated groups.

Since the distribution of the various species is so limited it may be suspected that their distribution is correlated with broad climatic factors such as temperature and/or rainfall. The distribution of the various species with respect to temperature, rainfall and the annual duration of sunshine has therefore been considered.

In a study of the influence of temperature on distribution several different factors might be important. Firstly, the distribution might be correlated with the mean annual temperature. Secondly, the maximum temperatures might be a limiting factor and thirdly, the minimum temperatures might be the most important limiting factor. The distribution of the various species with respect to these three factors is shown in Figs. 2, 3 and 4.

Fig. 2 shows that L.intermedia and M.medialis were only found in regions with a mean annual temperature of between 60-65°F (15,5-18,3°C). The temperature range in which M.obscurus, S.longicornis and C.lanceolatus were found was slightly greater and included areas with mean annual temperatures of 70°F (20,9°C) or above. When maximum summer temperatures are considered, however, a slightly different picture is obtained. From Fig. 3 it can be seen that, while the almost exclusively coastal species S.longicornis is never found above 100°F (37,4°C), L.intermedia, M.medialis and C.lanceolatus are found in regions with maximum summer temperatures of up to 105°F (40,2°C). The highest summer temperatures were found in the habitat of M.obscurus where maximum temperatures of up to 110°F (42,9°C) have been recorded.

A consideration of the minimum winter temperatures shown in Fig. 4 indicates that, as might be expected, the coastal species S.longicornis was not found in very cold regions, the minimum temperatures being about 35-40°F (1,6-4,4°C). Species which occurred further inland experienced lower temperatures ranging from 30-35°F (1,1-1,6°C) for L.intermedia, 20-25°F (-6,6 to -3,9°C) for M.medialis and M.obscurus, to less than 20°F (-6,6°C) in parts of the range of C.lanceolatus.

To summarise the distribution of the various species with respect to overall temperature regimes, it can be said that S.longicornis inhabits the area with the narrowest, most moderate, temperature range (35-100°F) and this would be expected as it is a coastal species. L.intermedia and M.medialis are found in areas which experience slightly higher temperatures during summer of

105°F (40,2°C) and slightly lower temperatures during winter of 20-30°F (-6,6 to -1,1°C). The highest summer temperatures were recorded in the areas inhabited by M.obscurus where the temperature rose to 110°F (42,9°C), and the lowest winter temperatures were recorded in the habitat of C.lanceolatus where the temperature fell to less than 20°F (-6,6°C).

The influence of rainfall on the distribution of the various species was also considered and included both the mean annual rainfall and the rainfall frequency. Rainfall frequency was considered to be important since all the species under consideration rely on the presence of soft dry sand for prey capture and regions in which rain was very frequent might not provide suitable habitats for these insects.

The distribution of the various species with respect to the mean annual rainfall is shown in Fig. 5 and from this it can be seen that all species were found in areas with an average rainfall of 15-25 ins. (381-635 mm.) per annum. M.medialis, M.obscurus, S.longicornis and C.lanceolatus were also found in wetter areas with an average rainfall of over 25 ins (635 mm.) but only C.lanceolatus and M.obscurus were found in very dry regions with an average rainfall of less than 10 ins. (254 mm.). It would thus appear that in South Africa rainfall is not a limiting factor in the distribution of ant-lions and worm-lions, although low rainfall may limit the distribution of some species. Systematic collection of the various species throughout the country would have to be undertaken in order to establish fully the effect of rainfall on distribution.

The distribution of the insects with respect to rainfall frequency is shown in Fig. 6. Apart from the fact that only C.lanceolatus and M.obscurus were found in areas with less than 40 days of rain per annum, there did not appear to be any correlation between rainfall frequency and distribution.

A similar result was obtained when considering the distribution of the various species with respect to the annual duration of sunshine, as shown in Fig. 7. Only C.lanceolatus and M.obscurus were found in areas which were sunny for 80% of the time.

To summarise the overall distribution of the four myrmeleontid and one rhagionid species in the Republic of South Africa it may be said that low temperature is probably not an important limiting factor since all species, except the exclusively coastal species S.longicornis and the worm-lion L.intermedia, were found in regions where the air temperature fell to below 0°C in winter. High temperatures might limit the distribution of L.intermedia, M.medialis, S.longicornis and C.lanceolatus since these species have only been recorded from regions with a maximum air temperature of less than 40,2°C. Low rainfall might also limit distribution since only C.lanceolatus and M.obscurus were found in regions with an annual rainfall of less than 254 mm. No other obvious correlation between distribution and broad climatic factors was evident and it is probable that these factors do not give an accurate indication of the conditions to which the sand dwelling larvae are exposed. Since the larvae live far longer (1-2 years) than the adults (1-2 weeks) it is likely that distribution is determined more by the conditions within the larval microhabitats than by overall climatic factors. It is therefore necessary to consider in more detail the microhabitats of the larvae.

Preliminary observations indicated that the larvae of the pit building worm-lion, L.intermedia, inhabited the coolest microhabitat. These larvae were only found in very sheltered areas such as in caves, garages and the shelter of very dense bush or hedges. A typical habitat in the shelter of a dense hedge is illustrated in Fig. 8. The pits of this species were found to be relatively small (about 2 cm. in diameter) and close together, as shown in Fig. 9. The larvae occurred in groups containing about 20-50 individuals. These colonies were widely scattered.

The larvae of the pit building ant-lions M.medialis and M.obscurus occurred sympatrically and the pits of both species were often found side by side. Both species appeared to prefer a moderately sheltered habitat and were frequently found in gardens and in the shelter of hedges. A typical habitat of the larvae of M. medialis is shown in Fig. 10, while Fig. 11 shows a more detailed picture of the pits which, in this species, were generally large (about 7 cm. in diameter) and at least 5 cm. apart. A typical habitat of M.obscurus larvae is illustrated in Fig. 12 and the pits are illustrated in Fig. 13. The pits of this species were generally smaller in size (about 3 cm. in diameter) than those of M.medialis and were separated from one another by a distance of at least 4 cm.

The larvae of the non-pit-building ant-lion, S. longicornis were found to be confined entirely to the coastal sand dunes. The larvae were only found on the sunny northern slopes of the dunes, closely associated with the sparse dune vegetation in which the Port Jackson Willow, Acacia saligna, predominated. The larvae were always found in close proximity to this vegetation although never actually in its shade, or in the region of sand beneath the bush which contained large quantities of leaves and other organic matter. A typical habitat of the larvae of this species is shown in Fig. 14, while Fig. 15 shows a larva about to burrow into the sand.

The larvae of the pit building ant-lion C.lanceolatus occupied a very distinct microhabitat. They were only found in very exposed rocky areas. Many larvae were found in the middle of disused gravel roads and in old stone quarries. The pit themselves were constructed in areas which were almost completely devoid of vegetation. A typical habitat in a disused quarry is shown in Fig. 16. A more detailed view of the pits in Fig. 17 shows the rocky nature of the ground in which the pits were found. It is interesting to note that the larvae of this species possess hard sclerotised plates on the posterior end of the abdomen to facilitate pit construction in hard stony soil. The pits themselves were generally small (about 2 cm. in diameter) and very shallow. These observations on the habits and habitats of the five species under consideration are summarised in Table 1.

These microhabitats were then studied in more detail with special reference to;(a) exposure of the habitats to sunlight, (b) general sand temperatures, (c) pit temperatures, and (d) depth of sand. The responses of the larvae to these parameters were also studied.

3,1 EXPOSURE TO SUNLIGHT

The most obvious difference between the microhabitats of the various species of ant-lion and worm-lion larvae was the length of time for which they were exposed to direct sunlight. This was investigated in the field by direct observation during the period 20th October to 18th November, 1969. Two different types of observation were made. Firstly, in the habitat of the non-pit-building ant-lion larvae, S.longicornis, the average time for which 10 different sand dune slopes were exposed to the sun was calculated. These observations included only those slopes of the dunes known to be inhabited by larvae, and did not take into account the odd shadows cast by vegetation, since larvae were seldom found in such patches of shade. Secondly, in the habitats of pit building ant-lions and worm-lions the exposure of individual pits to sunlight was timed. A total of 60 pits of each species was examined. Continuous observations were taken and in this way the effect of passing shadows was taken into consideration. Some difficulty was experienced in habitats which were exposed to the rising or setting sun, since in these cases it was very difficult to determine exactly when the weak rays of the sun reached or left the habitat. In these instances the times of sunrise and sunset were determined from The Astronomical Ephemeris for 1969 (1967). This led to a slight overestimate of exposure times since the rays of the rising and setting sun were horizontal and often did not reach the pits due to irregularities in the ground. From these observations the mean exposure time for each group of 60 pits was calculated and the results are shown in Fig. 18.

Fig. 18 shows that there was considerable variation in the length of exposure to sunlight in the different habitats. The pits of *L.intermedia* were exposed to an average of one hour of direct sunlight a day, while *C.lanceolatus* habitats were exposed to more than 10 hours of direct sunlight. The habitats of *M.medialis*, *M. obscurus* and *S.longicornis* fell between these two extremes. Statistical analysis revealed that the habitat of *S. longicornis* was exposed to significantly more sunlight than the habitat of *M.obscurus* ('t'= 3,9, $p < 0,001$) and that the habitat of *M.obscurus* was exposed to significantly more direct sunlight than the habitat of *M.medialis* ('t'= 6,5, $p < 0,001$). The latter result is surprising in view of the fact that the pits of M. obscurus and M.medialis are often found very close together. One would therefore expect these two species to be exposed to similar conditions. Fruther investigation revealed, however, that some parts of the microhabitat were shaded by overhanging vegetation for considerable periods of time. These shaded areas were inhabited mainly by the larvae of M.medialis. They were found particularly in areas which were shaded during the hottest period of the day. This is illustrated in Fig. 19 where the positions of M.medialis and M.obscurus pits at 12 noon, in one particular habitat, are indicated together with the pattern of shade cast by the surrounding vegetation. Thus it is clear that, although these two species of larvae may construct pits within a few centimeters of each other, the larvae of M.medialis occupy a distinctly shadier microhabitat than the larvae of M.obscurus.

3,2 GENERAL SAND TEMPERATURES

It has been shown that the habitats of different species of myrmeleontid and rhagionid larvae were exposed to direct sunlight for varying lengths of time (Fig. 18) and it would be expected that the temperature of the surface sand would differ greatly in the different habitats. The sand temperature would also vary with depth below the surface and such temperature gradients are well known (Buxton, 1923; Cloudsley-Thompson, 1962a and b, 1964a; Haub, 1942). The temperature of the surface sand and the temperature gradients below the surface in ant-lion and worm-lion habitats were studied in the field as described in Material and Methods. Continuous recordings were taken for a week in each of the habitats during summer (October to January, 1969) and the mean temperatures calculated. Recordings taken during the winter months (June to July, 1969) showed that at this time only very slight temperature gradients were present in the sand and these data have therefore not been dealt with in any detail.

It was found, from the recordings taken during summer that the daily temperature changes in all the habitats followed a similar pattern, and it is necessary to understand these general changes before a more detailed comparison can be made between the various habitats. Fig. 20 shows the temperature changes of the air, surface sand and sand at a depth of 7 cm. in the habitat of M.medialis as an example. The results for the remaining depths have been ommitted for the sake of clarity and will be dealt with in the more detailed discussion. It should be stressed that, while this figure is representative of the type of temperature changes which took place daily in all ant-lion and worm-lion habitats, it is not representative of the absolute values or the exact times at which the changes occurred.

Shortly after 6 a.m. each day the air and the surface sand began to warm up (Fig. 20). The temperature of the air initially rose more rapidly than that of the surface sand, until approximately 8 a.m. at which time the surface sand began to increase in temperature more rapidly than the air above it. This point corresponded to the time at which the sun reached the habitat. During this time the temperature of the deeper layers of sand increased steadily although more gradually. When the sun left the habitat, at about noon, all temperatures started to drop. The temperature of the deeper layers of sand, however, fell more gradually than that of the upper layers, with the result that by about 4 p.m. the sand at 7 cm. was warmer than the surface sand. Apart from minor fluctuations in the temperature of the surface sand due to air movements, this situation was maintained throughout the night. Similar relationships between temperature, time and depth were recorded in all the other habitats investigated.

The differences between the habitat of M.medialis and those of L.intermedia, M.obscurus, S.longicornis and C.lanceolatus may be illustrated by comparing the surface sand temperatures (Fig. 21). It can be seen from this figure that the temperature in the habitat of L.intermedia rose very little during the day. Maximum temperatures were recorded between about 9 a.m. and 2 p.m. and these temperatures were considerably lower than those recorded in the habitat of M.medialis. In the habitat of M.obscurus, on the other hand, the temperatures reached were higher than those recorded in the habitat of M.medialis and remained high for a longer period of time. This difference between the habitats of these two species which apparently live in the same habitat was due to the fact that the pits of M.obscurus were exposed to direct sunlight for a longer period of time than the pits of M.medialis. Even higher temperatures were recorded in the habitat of S.longicornis and here the maximum temperatures did not occur until 1-2 p.m. Finally, in the habitat of C.lanceolatus very high temperatures were recorded and the sand surface was above 40°C from 9 a.m. until 3 p.m. and above 45°C from 10 a.m. to 2 p.m.

In this investigation the fluctuations in temperature during the day (6 a.m. to 6 p.m.), and the resulting temperature gradients in the sand, were of particular interest since it is during this period that near lethal sand temperatures might be encountered by the larvae. In order to compare the different habitats directly all results were expressed as hour degrees centigrade (above ambient) per day. Ambient temperature was, for convenience, defined as the temperature at any particular depth at 6 a.m. At 6 a.m. the sand temperature at all depths was very low and was similar to the temperatures recorded throughout the night. This temperature also remained nearly constant on successive days. Conversion of all temperatures to hour degrees centigrade above ambient (Fig. 22) expresses the amount of temperature change in the various habitats rather than absolute values.

Fig. 22 shows that in the habitat of L.intermedia the temperature of the air (1 cm. above the surface) and the temperature of the sand itself varied from ambient very little during the day. The temperature change was relatively constant at all depths and no steep temperature gradients were present in the sand. This very stable condition was correlated with the low exposure to direct sunlight (one hour/day) in this habitat (Fig. 23).

In the habitat of M.medialis the air and upper layers of sand showed a marked increase in temperature of about 80 hour^{o}C/day due to the heating effect of direct sunlight. With increasing depth there was a decrease in temperature rise, till at a depth of 7 cm. the temperature rise was only about 37 hour^{o}C/day. The lower layers of sand were therefore far more stable with respect to temperature than the upper layers. Steep temperature gradients were present during the day from the upper to lower sand layers.

Similar temperature gradients were present in the habitats of M.obscurus, S.longicornis and C.lanceolatus, except that in these habitats the surface layer of sand was at a lower temperature than either the air or the sand at a depth of 1 cm. This temperature difference between the air and surface sand was probably caused by evaporative cooling from the surface of the sand. Greater cooling thus took place in those habitats which were exposed to wind. The amount of cooling of the surface sand layer varied from day to day in the different habitats and the temperatures prevailing at a depth of

1 cm. were therefore used for all further habitat comparisons. The temperature changes (hour^{o}C) at a depth of 1 cm. in the various habitats were analysed statistically by means of "Students' t" test. This analysis revealed that all the habitats differed significantly from one another. The probability 'p' was in all cases less than 0,001.

During the winter months (June-July) the temperature of the sand in all the habitats was similar and only very slight temperature gradients were present. These results are expressed in Tables 2a and b, where the mean temperature of the air and the sand at various depths, over a period of seven days, is given. Since the lowest sand temperatures occur at night, the mean sand temperatures for both day and night are given. The night-time temperatures from 6 p.m. to 6 a.m. are presented in Table 2a, and these results show that the sand in all habitats was above 8^{o}C. Youthed and Moran (1969a) have shown that the larvae of M.obscurus will build pits at a temperature of 10^{o}C and will continue to survive at considerably lower temperatures. Green (1955) has also shown that the larvae of Myrmeleon immaculatus are active at 2^{o}C. Low temperatures are therefore not considered to be an important limiting factor in the lives of ant-lion and worm-lion larvae. In all the habitats the lower layers of sand were slightly warmer than the upper layers during the night but this difference never exceeded 3^{o}C. The temperatures in the various habitats differed slightly, the habitat of

L.intermedia, for example, being about 4°C cooler than the habitat of S.longicornis. It seemed unlikely, however, that such small temperature differences would affect the distribution of the various species.

The mean day-time winter temperatures from 7 a.m. to 5 p.m. are given in Table 2b. From these results it can be seen that only very slight temperature gradients were present in the sand. The largest gradients were recorded in the very exposed habitat of C.lanceolatus where there was a difference of just over 5°C between the surface sand and sand at a depth of 7 cm. The temperature of the surface sand ranged from 14°C to 24°C and, since Green (1955) has shown that the optimal temperature for M.immaculatus is 16-34°C, it is unlikely that winter temperatures would be a limiting factor for local ant-lion species.

To summarise, it can be seen that the habitat of L.intermedia showed the least diurnal fluctuation in temperature and the smallest temperature gradients, while the habitat of C.lanceolatus showed the greatest diurnal temperature fluctuations and the steepest gradients. The habitats of M.medialis, M.obscurus and S.longicornis fell between these two extremes but approximated more closely the condition of the habitat of C.lanceolatus.

3.3 PIT TEMPERATURES

The general sand temperatures in the various myrmeleontid and rhagionid habitats have been shown to vary considerably depending mainly on their exposure to direct sunlight. General measurements of sand temperature may adequately define the conditions under which non-pit-building species of ant-lion, such as S.longicornis, live. In the case of pit building larvae, however, these general sand temperatures are further modified by the pit itself.

The effect of pits on general sand temperatures has been investigated by Green (1955). He studied the pits of M.immaculatus and showed that the various sides of a pit, which were exposed to the sun, differed widely in their temperatures. For example, he found that the temperature of the pit base was from 3-5°C lower than the temperature of the surrounding surface sand, while the pit slopes facing the sun were 0-10°C above the temperature of the pit base. It seemed likely that similar temperature differences would exist in the pits of L.intermedia, M.medialis, M.obscurus and C.lanceolatus and pit temperatures were therefore investigated in the field. These measurements were taken in ten pits of each species at 10 a.m., 12 noon and 2 p.m., except in the case of M.obscurus where 20 pits were examined at each of these times (Fig. 24). These times were chosen since it was only during the warmer parts of the day that the pit temperatures differed markedly from the temperature of the surrounding sand. At each of these times the direction of the sun's rays was determined by noting the position of the shadow cast by a vertical stick, while the angle of incidence was calculated from tables in The Astronomical Ephemeris for 1969 (1967).

Before considering the results of this investigation it should be noted that 99% of the pits of L.intermedia and 75% of the pits of M.medialis were in the shade at noon, and all the pits of both species were shaded at 2 p.m. The direction and angle of incidence of the sun's rays could therefore not be calculated at these times. In the case of M.obscurus some pits were exposed to sunlight continuously throughout the experimental period, others were shaded for part of the time and a small percentage were shaded throughout. The percentage of pits in the sun at 9 a.m. was 94%, at noon, 42% and at 2 p.m., 36%.

The results presented in Fig. 24 show that three distinct categories of pit may be distinguished. Firstly, those pits which were shaded throughout the experimental period (M.obscurus, shade). The temperatures recorded within these pits never differed by more than 2°C from the air temperature or the general surface sand temperature. No marked temperature differences were obvious between the various quadrants of the pits.

The second category included pits which were in sunlight at 10 a.m., partially or completely shaded at noon, and in complete shade at 2 p.m. (L.intermedia and M.medialis). In these pits at 10 a.m. the western quadrants were the warmest, having a temperature 5-7°C higher than the temperature of the air and 3-5°C higher than the temperature of the surrounding sand. The temperature of the north, south and east quadrants did not differ from the air temperature by more than 4°C, or from the surface sand by more than 2°C. At noon, when the pits were partially shaded the pit temperatures were generally slightly lower than the temperature of the air and surrounding sand, except for the southern quadrant which still retained some heat. This was particularly noticeable in the pits of M.medialis which were exposed to full sunlight for a longer period of time than the pits of L.intermedia. By 2 p.m. all temperatures recorded within the pits agreed to within 3°C with the temperature of the air and the surface sand.

The final category of pits included those which were exposed to sunlight throughout the experimental period. This category included the pits of M.obscurus (sun) and C.lanceolatus. Throughout the experimental period the southern quadrants of these pits were considerably hotter than the other quadrants, while the northern quadrants were the coolest. The greatest temperature differences were recorded in the pits of M.obscurus where there was a difference of 11°C between the warm southern quadrant and the cool northern quadrant at 2 p.m.

This work indicates that ant-lion and worm-lion pits in the shade have temperatures very close to those of the surrounding air and surface sand, while negligible temperature variations are present in the pits themselves. Pits in direct sunlight, on the other hand, show marked temperature variations and differ considerably from the temperature of the air and surrounding sand. In all pits exposed to direct sunlight the base of the pit was at a higher temperature than the air. At 10 a.m. the temperature of the pit base and the surrounding surface sand always agreed to within 2°C, while at noon and 2 p.m. the pit base was always slightly cooler than the surrounding sand. The difference in temperature between the pit base and the air ranged from 1°C to 4°C, while the difference between the pit base and the surrounding surface sand ranged from 0°C to 3°C. In general the smallest temperature variations within the pits were recorded at 10 a.m. and the greatest at noon and 2 p.m.

The responses of ant-lion and worm-lion larvae to these temperature variations were complex and are discussed in a later section of this work.

3,4 DEPTH OF SAND

Preliminary observations indicated that the depth of fine surface sand in the various ant-lion and worm-lion habitats differed considerably. The depth of loose surface sand was studied in the field by taking 25 readings of sand depth in the habitat of each species.

Since the larvae of all species, except the non-pit-building ant-lion *S.longicornis*, are found in scattered groups each set of 25 readings was obtained from at least five different colonies of larvae. In the case of *S.longicornis* habitats, the readings of sand depth were obtained from five different sand dunes. All readings were taken on the same day, approximately one week after the last fall of rain. The depth of the sand was determined using a graduated metal probe 3 mm. in diameter which was pushed as far as possible into the sand with the palm of the hand.

It was found that, not only were there considerable differences in the depth of soft sand in the various habitats, but the depth of sand in different parts of the same habitat also varied. In general the habitats could be divided into three types on the basis of sand depth. Firstly, there was the very deep sand (31,1 ± 5,7 cm.) recorded in the sand dune habitat of *S. longicornis*. The sand depth in this habitat varied enormously but was never less than 10 cm. The soft dry sand was generally deeper near the top of the dunes than it was at the base of the dunes. In the second type of habitat the fine sand ranged in depth from 1,5 cm. to about 10,0 cm. This sand was found in the habitat of *L.intermedia* (4,2 ± 0,4 cm.), *M.medialis* (4,8 ± 0,3 cm.) and *M.obscurus* (3,7 ± 0,8 cm.). Of these habitats that of *M.obscurus* showed the greatest variability. Finally, in the third type of habitat the sand was always extremely shallow. This was found in the habitat of C.lanceolatus in which the depth of soft surface sand was 1,3 ± 0,3 cm. In many instances the probe would not penetrate the general sand surface at all. In these regions the soft sand was limited to the ant-lion pits themselves, the sides of which were covered with a layer of soft sand about 1 cm. thick. This sand was obviously loosened by the hard sclerotosed plates on the posterior end of the abdomen of the larvae during the process of pit construction.

When the above results were compared statistically, using "Students' t", it was found that there was no significant difference between the depth of soft surface sand in the habitats of L.intermedia, M.medialis and M.obscurus (p in all cases $> 0,1$). The habitat of S.longicornis was significantly different from all the other habitats (p in all cases $< 0,001$). The habitat of C.lanceolatus also differed significantly from the other habitats ($p < 0,001$, except when compared with the habitat of M.obscurus where $p < 0,01 > 0,001$).

3,5 SUMMARY OF HABITAT CHARACTERISTICS

The various myrmeleontid and rhagionid habitats have been shown to differ in a number of ways and the main temperature characteristics and depths of sand from each habitat are summarised in Table 3 (from Figs. 18, 21, 22 and 24).

The habitat of the worm-lion L.intermedia was found to be very sheltered and was exposed to an average of one hour of direct sunlight per day. The sand temperatures were therefore very stable and no marked temperature gradients were present either in the sand or in the pits. Sand depth in this habitat was variable and could not be distinguished from that found in the habitats of M.medialis and M.obscurus.

Exposure to sunlight was somewhat greater in the habitat of the ant-lion M.medialis, where it was approximately four and a half hours per day. The habitat was exposed to sunlight mainly in the morning and during this time temperature gradients were present in the sand and in the pits. The habitat of M.obscurus was exposed to about six hours of direct sunlight per day and marked temperature gradients were present in the pits and surrounding sand. Marked temperature gradients were also recorded in the habitat of S.longicornis, the non-pit-building ant-lion. This habitat was exposed to approximately seven hours of direct sunlight per day and the sand was significantly deeper than that recorded in any other habitat.

Finally, in the habitat of C.lanceolatus the exposure time to sunlight was about 11 hours. Very marked temperature gradients were present in the pits and surrounding sand. The sand in this habitat was also significantly shallower than that recorded in any other habitat.

It may be argued that the substrate particle size in the various habitats should have been taken into consideration since Youthed and Moran (1969a) have shown that particle size affects the size of pits constructed by *M.obscurus*. It was observed, however, that all the species under consideration were able to construct normal pits in both fine and coarse sand and this factor was therefore not investigated further.

The characteristics of myrmeleontid and rhagionid habitats outlined above formed a basis for the subsequent experiments on temperature relations.

4. TEMPERATURE RELATIONS

The hot dry sandy habitats in which myrmeleontid and rhagionid larvae live may, at least in some respects, be considered as desert regions. While many desert dwelling animals have obvious morphological and behavioural adaptations which enable them to survive in hot sand, no such obvious adaptations are present in ant-lions and worm-lions. These larvae are unique in that they do not appear to burrow to any depth into the sand, but lead an almost sedentary existance near the surface of the sand. The question of how these animals are able to survive high sand temperatures is therefore of particular interest. Three aspects of the temperature relations of these ant-lion and worm-lion species were considered; (i) the upper lethal temperature limits, (ii) diurnal variations in temperature sensitivity, and (iii) the internal temperature of the larvae.

4,1 THE UPPER LETHAL LIMITS

The temperature of the sand in different ant-lion and worm-lion habitats has been shown to differ greatly and it would therefore be expected that the upper lethal temperatures of the different species would vary accordingly. This aspect was investigated in the laboratory.

The first problem in this work was to define the criteria of death for ant-lion and worm-lion larvae. It was observed that, when subjected to high temperatures, all the larvae first showed a period of very vigorous movement, followed by a period during which they lay completely still but could be stimulated to move by prodding with a pair of forceps. In ant-lions such prodding generally produced vigorous movements of the legs and mandibles, while in worm-lions it produced violent flexion and extension of the body. Finally, the larvae became completely immobile and showed no response to prodding. Later work indicated that a lack of response to prodding was not really an indication of death but of heat coma. In these experiments, however, coma was used as the criterion of heat death since coma was always followed in a very short time by death, if the insects remained at high temperatures. If the insects were removed from high temperatures during heat coma they recovered and were able to construct pits, but death generally followed after a period of 1-6 weeks, and none of these insects ever again managed to moult or pupate successfully. Heat coma may thus be regarded as the first stage of death and cannot be superficially distinguished from death.

All the larvae used in lethal limit determinations were subjected to a standard pretreatment. They were maintained at a constant temperature of 25 ± 1°C for a period of at least seven days prior to the experiment and during this time they were each fed one ant a day. This period of pretreatment was used since it has been shown by Youthed and Moran (1969a) that the influence of the previous thermal history of the larvae of M. obscurus is eliminated by seven days under constant conditions.

The upper lethal temperature limit of each species was initially determined by subjecting the larvae to high temperatures for a period of 24 hours. In these preliminary experiments 24 hours was chosen as the exposure period since this is the period which has been used in determinations of the lethal temperatures of many desert arthropods (Cloudsley-Thompson, 1962a; El Rayah, 1970a). The experiments were performed on groups of 10 individuals of each species which were drawn at random from the stock population. To prevent the larvae killing each other during the experiments each individual was placed in a separate glass test tube. The glass tubes contained a small amount of fine damp sea sand to prevent them floating. The relative humidity in the tubes was tested with cobalt thiocyanate paper and found to be about 90%. The tubes were lightly corked with cotton wool and the humidity did not change by more than 3% during the course of the experiments. Damp sand was used since, in the words of Edney (1957), "The highest temperature an insect can withstand at 90% RH is close to its true death point". The test tubes were placed in a water bath at various temperatures and the number of dead larvae determined after a period of 24 hours. The percentage mortality at each temperature was then calculated.

The results presented in Fig. 25 show that in all species the percentage mortality increased very sharply over a narrow range of temperature. The larvae of L.intermedia died between 38-42°C, while 50% mortality occurred at about 40,5°C. The temperature range causing death was even narrower for M.medialis and M.obscurus where it was 46-48°C and 47-48°C respectively with 50% mortality occurring at 47,2°C and 47,6°C. The larvae of S.longicornis and C.lanceolatus showed higher temperature tolerances. For S.longicornis the temperature range causing death was 50-52°C with 50% mortality occurring at 50,8°C, while the larvae of C.lanceolatus died at 49-53°C with 50% mortality at 51,9°C.

In general, from this experiment it was clear that the upper lethal temperature of ant-lions from warm habitats (e.g. S.longicornis and C.lanceolatus) was higher than the upper lethal temperature of larvae from cooler habitats (L.intermedia, M.medialis and M.obscurus). The experimental technique used in this investigation may, however, be criticised. Although the lethal limit of many different species of animals has in the past been assessed as the highest temperature survived by 50% of the population over a fixed period of time, Orr (1955) has indicated that the survival of any animal at high temperatures is dependent on the time of exposure. In order to define the conditions of heat death accurately a curve in which both time and temperature are represented should be obtained. Furthermore larvae in the field would never be exposed to a constant high temperature over a period of 24 hours. Experiments in which both the variables of time and temperature were taken into account were therefore performed.

In these time/temperature experiments, groups containing 10 individuals of each species were subjected to a range of different temperatures. The exact temperature range used depended on the species involved. The lowest temperatures used were those (to the nearest 2°C) which have been shown to produce a 50% mortality over a period of 24 hours. These temperatures were chosen as a starting point since the larvae in the field would never be exposed to high temperatures for as long as 24 hours and the lethal limits of the larvae during shorter exposures to high temperatures were therefore of greater interest. The temperature tolerances of the larvae were then tested at intervals of 2°C.

The groups of larvae used in this experiment were drawn at random from stock populations which had been maintained in a constant environment room at 25 ± 1°C for seven days. The larvae were placed in individual test tubes and the onset of heat coma was recorded. The relative humidity within the test tubes was tested with cobalt thiocyanate paper and found to be about 40%. This low relative humidity was chosen since, in the field, high temperatures are usually associated with low relative humidities. All the experiments in this series were started between 9-10 a.m. and the importance of this timing will be discussed in a later section of the work.

Each group of larvae contained individuals of various sizes and they entered heat coma at a wide range of different times. Fig. 26 shows the mean time at which heat coma occurred for each species. It is obvious that the survival time of all species increased markedly over a very small temperature range. For M.obscurus, for example, a decrease in temperature from 50°C to 48°C increased the mean survival time from 35 mins. to just over six hours (372 mins.). This fact may be of great importance in the field since if the larvae are able to move into areas of sand with a temperature only a few degrees below their lethal limits they would be able to survive for far longer periods of time.

The temperature tolerances of the various species in this experiment differed greatly. If the temperatures giving a mean survival time of five hours are compared the following results are obtained: L.intermedia, 41,4°C; M.medialis, 47,3°C; M.obscurus, 48,2°C; S.longicornis, 51,2°C and C.lanceolatus, 53,4°C. The survival time of five hours was chosen as a basis of comparison since this is the approximate length of time for which maximum sand temperatures prevail in the field (see Fig. 21).

All the larvae used in these experiments were kept at 25 ± 1°C for seven days prior to the start of the experiments. Higher temperature tolerances would undoubtedly have been recorded if the larvae had been acclimated at higher temperatures and such acclimation effects have been described for a number of different insects (for example: Mellanby, 1954; Mynard Smith, 1957; Dingley and Mynard Smith, 1968; Cloudsley-Thompson, 1969; Levins, 1969 and Davison, 1971). Seasonal acclimation in response to the increasing temperatures of early summer may affect the lethal limits of ant-lions and worm-lions but it seems unlikely that acclimation to the very rapid daily temperature changes would have any marked effect on the survival of larvae in the field. Also, it will be shown in a later section of this work that the behaviour of the larvae normally ensures that they do not encounter temperatures near their lethal limits.

The larvae in the present investigation were not standardised with respect to age, although the importance of this factor in lethal limit determinations has been shown by Baldwin (1954) and Heeg (1967). In the present experiments there was no evidence of any age effect and random samples were therefore used.

Finally, it should be noted that the present experiments were all performed at a relative humidity of 40%. It is well known (Chapman, 1969; Wigglesworth, 1965) that relative humidity has a marked effect on the lethal limit of some insects; low relative humidities are more favourable during short exposures to high temperatures, since the insects are then able to cool themselves by the evaporation of water. However, the problem of evaporative cooling of ant-lion and worm-lion larvae is dealt with in a later section of this work and indicates that evaporative cooling is not important in the majority of these species.

As stated earlier, all the above experiments were started between 9 a.m. and 10 a.m. In preliminary experiments, ant-lion and worm-lion larvae appeared to die more rapidly when the experiments were performed in the late afternoon and evening than they did if the experiments were performed in the morning. Investigations were therefor initiated to establish whether the temperature sensitivity of the larvae varied at different times of the day.

4.2 DIURNAL CHANGES IN TEMPERATURE SENSITIVITY

The diurnal changes in the temperature sensitivity of myrmeleontid and rhagionid larvae were investigated using three groups containing 10 individuals of each species. Each group of larvae was exposed to high temperatures at either 9 a.m., 5 p.m. or 7 p.m. and the mean time to death determined. Additional experiments were performed at 2 p.m., 3 p.m. and 4 p.m. using the larvae of M.obscurus only. The temperatures used were chosen so that all the larvae died within an hour. This was done because it seemed likely that the temperature sensitivity might change during a longer exposure period.

All experiments were performed at a relative humidity of approximately 40%.

The results of these experiments are presented in Tables 4a and b. All the larvae, except those of L.intermedia, were more sensitive to high temperatures at 5 p.m. and 7 p.m. than they were at 9 a.m. Statistical analysis of the results (applying Bessell's correction for small numbers) showed that, apart from the larvae of L.intermedia, there was a highly significant difference between the survival times at 9 a.m. compared with those at 5 p.m., whereas there was no significant difference between the results obtained at 5 p.m. compared to 7 p.m. The increase in temperature sensitivity must therefore have occurred before 5 p.m. and this is illustrated in the experiments performed on the larvae of M.obscurus. From Tables 4a and b it can be seen that, in the case of M.obscurus, there was no significant difference between the survival time at 9 a.m. compared to 2 p.m.; there was a slight difference at 2 p.m. compared to 3 p.m. and marked differences between the results for 3 p.m. compared to those at 4 p.m. and for 4 p.m. compared to 5 p.m. This suggests that the temperature sensitivity of the larvae of M.obscurus began to increase at about 3 p.m. and that the larvae became progressively more sensitive until about 5 p.m. Sensitivity remained at a high level until at least 7 p.m. The decline in temperature sensitivity between 7 p.m. and 9 a.m. was not investigated due to a shortage of material and because in the field the temperature is low at night and would not approach the lethal limit of the larvae. The peak of minimum temperature sensitivity in these larvae coincided with the hottest part of the day.

The peak of maximum temperature sensitivity recorded in these experiments occurred at the time at which maximum pit building activity was observed in the larvae of M.obscurus by Youthed and Moran (1969b). A similar correlation between peak sensitivity and an activity rhythm was noted by Nowosielski et al (1964) for Gryllus domesticus. These workers found that the sensitivity of G.domesticus to various narcotics was greatest during the early part of the night, at which time these animals showed their maximum activity. Also, more recent work by Haverty and Ware (1970) has shown that Pectinophora gossypiella was more sensitive to X-rays during the period of activity. No direct relationship between activity and sensitivity to narcotics or X-rays was, however, demonstrated by these workers. It seemed possible that in ant-lion and worm-lion larvae some direct connection might exist between the activity rhythm and temperature sensitivity and this question was investigated further. This problem was of particular interest in this study since, if pit construction and temperature sensitivity are closely linked, then the behavioural responses of the larvae to temperature might be markedly affected. In order to study this problem in myrmeleontid and rhagionid larvae it was first necessary to demonstrate the existence of a circadian activity rhythm in all the species under consideration.

The activity of five individuals of each species was investigated using the actograph described by Grobbellaar et al (1967). The daily activity of each individual was recorded for two days under normal laboratory light-dark conditions. Each individual was fed one ant per day at random times between 6 a.m. and 11.30 p.m. The results obtained are shown in Fig. 27, and from this it is evident that the larvae of M.obscurus, M.medialis and C.lanceolatus possessed very well defined circadian activity rhythms with the peak at about dusk. It is interesting to note that all three species live in hot habitats where such circadian rhythms may be of great survival value and this aspect will be discussed later.

The larvae of L.intermedia showed considerable activity at dusk but they were also active at other times of the day, particularly after feeding. It would thus appear that these larvae do possess a circadian activity rhythm, but this rhythm is not as sharply defined as in the ant-lion larvae. L.intermedia larvae live in very shady areas where a circadian activity rhythm may not be of great survival value.

The larvae of the non-pit-building ant-lion, S. longicornis, showed a very low level of activity, but with a definite indication of a peak at dusk. The very low level of activity recorded was probably due to the fact that these larvae do not build pits and the actograph used was more sensitive to vigorous movements on the surface of the sand than to movements below the surface.

It can therefore be said that not only were the larvae of all species (except L.intermedia) more sensitive to temperature at about dusk but that they also showed their maximum activity at this time. The larvae of L.intermedia which did not show a marked daily activity rhythm also lacked any indication of a peak of temperature sensitivity. This suggested the possibility of a link between temperature sensitivity and the rhythm of locomotor (or pit building) activity. It is well known (Aschoff, 1965; Harker, 1961) that the circadian activity rhythm of insects can be altered by a change in the light-dark cycle. This also applies to M.obscurus, as shown by Youthed and Moran (1969b). If the light-dark cycle was altered so that the dark period fell during the day, the activity rhythm immediately altered so that the activity still occurred just before "dusk". Such a change in the daily activity rhythm should therefore produce a change in the time of peak temperature sensitivity if these two factors are linked. This was investigated in the laboratory using mainly the larvae of M.obscurus. Only a few experiments were performed on the remaining species due to a shortage of material.

A number of larvae of each species were placed in a reversed light-dark cycle in which the lights (about 1500 lux) were switched on at 8 p.m. and off at 10 a.m. After 14 days the activity rhythm of each species was recorded. These activity recordings were obtained from five larvae of M.obscurus and a single larva of each of the remaining species. The activity of each individual was recorded over a period of 48 hours. The results, which are shown in Fig. 28, indicate that, with the exception of the larva of L.intermedia, all the larvae showed a marked peak of activity at about 10 a.m. That is, the daily activity rhythm had altered so that peak activity was recorded just before "dusk". The activity rhythm of all the ant-lion species therefore responded to reversed light-dark cycles in the same way as that of M.obscurus.

Having shown that the daily activity rhythm was altered by a reversed light cycle it was then necessary to investigate possible changes in the time of maximum temperature sensitivity. Groups of 10 individuals of M.obscurus were therefore drawn at random from the experimental population, which had been exposed to a reversed light-dark regime for 14 days, and the temperature sensitivity of each group tested. The experiments were carried out at 10 a.m., which was the new activity time, and at 5 p.m. and 7 p.m., which was the old activity time and time of maximum temperature sensitivity. At each of these times 10 larvae of M.obscurus were exposed to a temperature of 50°C and the time at which each individual died was noted. Similar experiments were conducted on from three to five individuals of each of the remaining species at 10 a.m. and 5 p.m. The temperatures used in these experiments varied from species to species and are indicated, together with the results, in Table 5. It should be noted that only the results obtained from the larvae of M.obscurus could be analysed statistically since only very small numbers of individuals of the other species were obtainable.

Table 5 shows that the larvae of M. obscurus, after exposure to a reversed light-dark cycle, were now significantly more sensitive to temperature at 10 a.m. than they were at 5 p.m. There was, however, no statistical difference between the results at 5 p.m. compared to those at 7 p.m. It thus appeared that the peak of temperature sensitivity of these larvae had altered in the same way as the rhythm of daily activity in response to the reversed light-dark regime. Similar changes in temperature sensitivity were indicated by the results obtained from the larvae of M. medialis, S. longicornis and C. lanceolatus. In all cases the larvae died considerably more rapidly at 10 a.m. than they did at 5 p.m. The larvae of the worm-lion L. intermedia, on the other hand, showed no difference in the survival times recorded at 10 a.m. and 5 p.m.

The above results therefore support the suggestion that temperature sensitivity and the daily activity rhythm are interdependent. Furthermore, these results suggest that the diurnal changes in temperature sensitivity are not due to an independent endogenous circadian rhythm since, although it is possible for two independent rhythms to be reset to approximately the same time by a reversed light regime, it is unlikely that they would correspond so closely. In order to investigate this problem further both temperature sensitivity and the daily activity rhythm were investigated under conditions of constant light. This was done since it is well known (Harker, 1961) that the circadian rhythms of insects have an intrinsic oscillation which only approximates 24 hours. During periods of constant light or dark when the "clock" can not be reset each day the rhythms tend to "drift". It is, therefore, probable that if there is an independent circadian rhythm of temperature sensitivity in ant-lion larvae it would "drift" at a different rate from the circadian activity rhythm. That is, it is unlikely that two independent rhythms would possess the same free-running period.

It has been shown by Youthed and Moran (1969b) that when larvae of M.obscurus are exposed to constant light their activity rhythm occurs slightly earlier each day, so that after two weeks the period of maximum activity occurs at about 4 p.m. instead of at 7 p.m. This was confirmed in the present investigation using a single individual of M.obscurus. The activity of this larva was recorded for four days under normal laboratory daylight conditions and for two weeks in constant light of about 1500 lux. The larva was fed one ant a day at times which were randomly determined. The results are illustrated in Fig. 29 and it can be seen that there was a gradual shift in the time of activity under conditions of constant light. The activity occurred slightly earlier each day and after a period of two weeks in constant light the activity peak had shifted from about 8 p.m. to about 3.30 p.m. If the diurnal changes in the temperature sensitivity of M.obscurus larvae are due to an endogenous circadian rhythm then the amount of "drift" in the period of peak sensitivity would be expected to differ from the rate of "drift" recorded for the peak of daily activity. In order to test this a large number of *M.obscurus* larvae were exposed to constant light for a period of two weeks. Groups of 10 individuals were then withdrawn from this population at random, and their temperature sensitivity tested at various times of the day. The tests were performed at 9 a.m. during the period of inactivity, at 4 p.m., the new "induced" activity time, and at 7 p.m., the time at which the original daily activity and peak of temperature sensitivity occurred. The larvae were exposed to a temperature of 50°C at each of these times and the mean survival times determined.

The mean survival times recorded in this experiment are indicated in Table 6. Statistical analysis of the results showed that there was no difference between the survival times recorded at 9 a.m. compared to those at 7 p.m. The results obtained at 9 a.m. compared to those at 4 p.m., however, were significantly different, as were the results obtained at 4 p.m. compared to 7 p.m. The period of peak temperature sensitivity had therefore shifted from about 7 p.m. to about 4 p.m. during a two week period in constant light. This corresponded with the change in the activity rhythm recorded under similar conditions. Although the free-running period of two independent circadian rhythms may only differ by a few minutes, and smaller time intervals should therefore be used in determining the temperature sensitivity, such experiments were not possible here as it was very difficult to determine the time of death accurately over very short exposure periods. The results of this experiment, however, supported in some measure the suggestion that the diurnal changes in temperature sensitivity were not due to a distinct endogenous circadian rhythm but were linked to the endogenous activity rhythm.

4,3 THE INTERNAL TEMPERATURE OF THE LARVAE

It has been shown experimentally that the upper lethal temperature limit of ant-lion and worm-lion larvae varied from species to species. The lethal limit also varied at different times of the day. Only ambient temperatures were recorded in these experiments and the internal temperatures of the larvae might have differed considerably from ambient at the time of death. Most of the previous experiments were carried out at low relative humidities of about 40% and the internal temperatures of the larvae might have been considerably lower than ambient due to evaporative cooling. Such evaporative cooling has been noted in a number of different insects such as tsetse flies (Edney and Barrass, 1962) and honey bees (Free and Spencer-Booth, 1962). Experiments were therefore conducted to determine the internal temperatures of ant-lions and worm-lions at various ambient temperatures and at various relative humidities.

Thermocouples were inserted into ant-lion and worm-lion larvae as described in material and methods. Each larva was then placed in a large glass test tube which was partly filled with sea sand. A round of filter paper was placed on top of the sand to prevent the insects from attempting to burrow and thus dislodging the thermocouples. The humidity of the sand was controlled by drying the sand thoroughly in a crucible and then adding a known quantity of water. In this way relative humidities of almost 0% and about 100% could be obtained. Saturated salt solutions were not used to control the humidity in these experiments because it was found that they had a marked effect on the behaviour of the animals. They generally induced a state of hyperactivity. The humidity within the test tubes in each experiment was tested with cobalt thiocyanate paper. The tubes were corked with cotton wool and placed in a water bath, the temperature of which was raised from 22°C to 56°C at a rate of 2°C per 10 mins. This approximates the rate of temperature rise found in the field (see section 3,2).

Only five thermocouples were available for use in measuring the internal temperatures of larvae (the sixth one being used for calibration) and in each replicate of the experiment one individual of each species was used. The experiment was repeated so that the internal temperatures of a total of five individuals of each species was recorded at both 0% and 100% RH.

The results of these experiments, which are shown in Tables 7 and 8, have been expressed as the mean differences between the internal and external temperatures for each group of larvae. It should be noted that, for convenience, the external temperatures have been expressed to the nearest whole number since it was not always possible to raise the temperature of the water bath by exactly the same amount. It should also be noted that, while slight individual variations in temperature were recorded, the temperatures of all the larvae within any group followed similar trends and thus only the mean values need be considered.

The most obvious feature of the data in Table 7 (100% RH) is the very slight differences which were recorded between ambient and internal temperatures. Nearly all the readings fell within the 0,3°C error inherent in the circuit, and it is therefore obvious that the internal temperature of all the larvae was very close to ambient under these conditions. This is, in fact, the result one might expect since at 100% RH the larvae would not be able to cool themselves by the evaporation of water. The larvae of S.longicornis and C.lanceolatus had internal temperatures which were consistently slightly higher than ambient. The fact that these results were so consistent makes it unlikely that these results were due entirely to errors in the circuit (although most of the results fell within the 0,3°C error inherent in the circuit). It is possible that these increases in internal temperature were due to the production of metabolic heat, since the larvae of S.longicornis were very active during the experiment. The larvae of C.lanceolatus, however, did not show much activity and the increase in internal temperature above ambient cannot be explained at this stage. In general, from this experiment it was concluded that at 100% relative humidity the internal temperature of the larvae followed the changes in external temperature. These results agree with those obtained by Edney (1951a) for woodlice. He found that in saturated air the internal and external temperatures agreed to within 0,1°C.

The internal temperature of the ant-lion and worm-lion larvae at 0% RH was also very close to ambient at all temperatures, as shown in Table 8. This was particularly noticeable in experiments using the larvae of L.intermedia, where no consistent differences between internal and external temperatures could be distinguished. It would therefore appear that this species does not cool itself by the evaporation of water. In the remaining species the internal temperature was consistently lower than ambient. The fact that these results were so consistent indicated that the results were not due entirely to errors in the circuit, and it was concluded that these larvae were able to cool themselves slightly by the evaporation of water. Table 8, however, indicated some differences between the various species in this respect. The internal temperature of the larvae of C.lanceolatus, for example, was never more than

0,6°C below ambient and remained almost constant at a value of 0,3°C below ambient during most of the experimental period. In the larvae of M.medialis, M.obscurus and S.longicornis, on the other hand, the internal temperature showed maximum depression at ambient temperatures ranging from about 30°C to about 50°C. At ambient temperatures above and below these values the internal temperature followed the changes in ambient temperature more closely. This may be explained by the fact that at temperatures below 30°C the larvae were not very active and their spiracles would thus not have been fully open. Also, since the temperature was low they would not need to evaporate water to cool themselves. Above 50°C the majority of the larvae showed little or no activity and a number of them appeared to be dead. At ambient temperatures between 30°C and 50°C, however, the larvae of all three species were very active.

In general from these experiments it was concluded that some slight evaporative cooling may be possible in ant-lion larvae. These results agree with those obtained by other workers such as Edney (1951a) who found that the internal temperature of the cockroach Blatta was 0,7°C lower than ambient at 20°C and 2,4°C lower than ambient at 37°C. Church (1960) also recorded evaporative cooling in the order of 0,5-1,2°C in various insects.

The temperature differences recorded in the above experiments were very slight but, since it has been shown in Fig. 26 that a very small temperature decrease may produce a marked increase in the survival time of the larvae, this cooling might be of some importance. In order to determine whether the evaporative cooling actually enabled the larvae to survive significantly higher temperatures their lethal temperatures were determined at both 0% and 100% relative humidity. As in the previous experiments only large final instar larvae were used and the temperature was raised at a rate of 2°C per 10 minutes. Groups of 10 individuals of each species were used and the number of deaths recorded after each 0,5°C rise in temperature. The mean temperature at which death occurred in each species is shown in Table 9, where it can be seen that only the larvae of M.medialis and M.obscurus showed a significant difference between the lethal temperatures at 0% and 100% RH. The remaining species of larvae appeared to die at the same temperature regardless of the relative humidity used. In these experiments, however, the number of deaths was only determined at 0,5°C intervals and it is possible that differences in the lethal temperatures might become obvious if more sensitive methods were used.

The above experiments were conducted in still air and greater evaporative cooling would be expected in moving air. No experiments of this nature were done, however, since in the field the larvae are always below the surface of the sand during the heat of the day and would therefore be in areas of stationary air and relatively high humidity. It is therefore probable that evaporative cooling plays only a minor part, or no part at all, in the survival of larvae in the field.

5. BEHAVIOURAL ADAPTATIONS

The present studies have given some indication of the upper lethal temperature limits of the various ant-lion and worm-lion species and have also indicated the average temperatures of the surface sand in which these larvae live. The maximum temperatures recorded in ant-lion and worm-lion habitats were considerably higher than the mean values and it is these extreme temperatures which would determine whether or not the larvae were able to survive. The highest mean surface sand temperatures (Fig. 21), the maximum observed surface sand temperatures and the lethal temperatures of the larvae over an exposure period of five hours (Fig. 26) are shown in Table 10. The exposure period of five hours was chosen since this is the approximate length of time during which high temperatures would normally prevail in the field. The maximum recorded temperatures (apart from those in the habitat of S. longicornis) were all taken between 1 p.m. and 2.30 p.m. on 14th November, 1969. The recording from the habitat of S.longicornis was taken on 3rd December, 1969. All the values represent a mean of 10 readings.

As shown in Table 10 the average temperature of the surface sand in the various habitats was considerably lower than the lethal limits of the larvae. The maximum recorded sand temperatures, on the other hand, exceeded the upper lethal temperature in all species except

L.intermedia. Since these maximum temperatures were recorded during early summer it is probable that even higher temperatures would occur in these habitats later in the season. It is thus likely that the larvae have behavioural responses which enable them to avoid these high temperatures and the following aspects of the behaviour of these animals was therefore investigated: (i) responses of the larvae to light, shade and temperature; (ii) orientation of the larvae within their pits; (iii) movement of the larvae in vertical temperature gradients, and (iv) responses of the larvae to sand depth.

5,1 RESPONSES OF THE LARVAE TO LIGHT, SHADE AND TEMPERATURE

In the natural habitats of myrmeleontid and rhagionid larvae, light and shade differences lead to considerable differences in sand temperature. For example, on 12th December, 1970 the mean temperature of the sand in the sun outside the laboratory was 46°C, while the mean temperature of sand in the shade was 24°C. In selecting their microhabitat the larvae might therefore be responding to either light or temperature differences, or to a combination of these two factors. A further possibility is that the microhabitat might not be selected by the larvae at all, but by the adults. Adult habitat selection seemed unlikely since the adults of all myrmeleontid species appeared to be nocturnal and were very seldom observed on the wing during the day. Adults of the worm-lion, L.intermedia, were occasionally seen to be active during the day, but were never observed ovipositing. Thus, although little is known about the behaviour of myrmeleontid and rhagionid adults, it seems that the larvae play the major part in the selection of the microhabitat.

Four series of experiments were designed to test the responses of the various larvae to light, shade and temperature. Throughout these experiments metal containers (36 cm. by 24 cm.) filled with sifted sea sand to a depth of 3 cm. were used. The inner sides of the containers were painted black to eliminate the reflection of light. The sand in each container was marked off into six squares (12 cm. by 12 cm.) and a wooden framework supported 12 cm. above the sand allowed squares of blackened card to be placed over any of the sand blocks, thus shading them. In each replicate of an experiment six individuals of a particular species were used, one individual being placed in the centre of each square of sand at the start of the experiment. The positions of the larvae at the end of the experiment were recorded either by noting the positions of the pits or (in the case of the non-pit-building larvae of S. longicornis) by dividing the sand into blocks by means of card and then examining each block for the presence of larvae. A total of 60 larvae of each species was used under each set of conditions and their positions noted after a period of two days.

Initially, control experiments were designed to determine whether or not larvae, placed in evenly lighted and heated sand, distributed themselves evenly in the container. This was done since it seemed possible that the larvae might select particular parts of the container, such as the area adjacent to the walls, for pit construction, or that they might tend to aggregate. In these experiments the sand trays were maintained in a constant environment room at a temperature of 30 ± 1°C and evenly lighted from above by flourescent tubes (approximately 1500 lux). The lights were switched on at 8 a.m. and off at 5 p.m. each day. The results of these control experiments are shown in Table 11. Statistical analysis of the results indicated that none of the larvae showed a preference for any particular square of sand. Observations taken during these experiments indicated that the larvae generally moved around the container for some time before constructing a pit. These movements were not confined to any particular part of the container and the larvae showed no tendency to aggregate or to select the sand adjacent to the walls of the container. Experiments were then designed to test the following: (i) the responses of the larvae to visible light of various intensities, (ii) the responses of the larvae to light when subjected to uniform high sand temperatures, (iii) the responses of the larvae to surface sand temperatures, and (iv) the responses of the larvae to a combination of light and temperature gradients. Details of the experimental procedures for each series of experiments are listed below and the results of all the experiments are recorded in Tables 12-16. These results are then discussed as a whole.

(i) Responses of the larvae to visible light of various intensities

In this series of experiments the responses of the larvae to visible light of various intensities was tested while the sand was maintained at a constant temperature of $30 \pm 1^{o}C$. The lights, which have been described in Material and Methods, were switched on during the hours 8 a.m. to 5 p.m. each day. The sand in these experiments was maintained at a constant temperature by placing the trays in a water bath so that, despite the heating effect of the lights, there was never more than a $1^{o}C$ difference between the lighted and shaded areas of sand. In each replicate of these, and all further experiments, 50% of the sand was shaded and the shaded blocks were varied randomly. The experiments were replicated until the responses of 60 larvae of each species had been investigated at each light intensity.

(ii) The responses of the larvae to light when subjected to uniform high sand temperatures

These experiments were performed to test the responses of the larvae to light under differing general sand temperatures. Larvae which selected lighted areas of sand at low sand temperatures might select shady areas if the general sand temperature was high.

The sand in these experiments was heated to 35°C or 45°C in a water bath. It should be stressed that the sand was evenly heated and no temperature gradients were present in the sand. As in the previous experiments the sand was lighted from 8 a.m. to 5 p.m. with lights of various intensities.

(iii) Responses of the larvae to surface sand temperatures

This series of experiments was designed to investigate the responses of the larvae to differences in sand temperatures in the absence of visible light. The container of sand was maintained in the dark and the sand heated from above by a 250W infra-red light, suspended at 40 cm., 50 cm. or 60 cm.above the sand. In this way the difference in temperature between the lighted and shaded areas of sand could be varied. As with experiments using visible light the infra-red lights were only switched on between 8 a.m. and 5 p.m. each day, since no pits could be constructed by the larvae during periods of high surface sand temperature.

(iv) Responses of the larvae to a combination of light and temperature gradients

In the final series of experiments the responses of the larvae to a combination of light and temperature gradients were investigated. The sand was illuminated with light of various intensities and heated by infrared lights suspended 50 cm. above the surface of the sand.

The results of all the above experiments are recorded in Tables 12-16. The responses of the various species of larva differed considerably and each species will therefore have to be considered separately.

The larvae of the rhagionid L.intermedia (Table 12a) showed no response to light of low intensity (200 lux) at sand temperatures of either 30°C or 35°C. At light intensities of 600, 1200 and 14000 lux they responded by moving to the shade at both sand temperatures. No results could be obtained for this species at a sand temperature of 45°C since this temperature lay above the lethal limit for these larvae. In the absence of visible light, but in the presence of temperature gradients, the responses of the larvae depended on the temperatures used (Table 12b). When the temperatures were low (column A) no responses were observed. When the temperatures were increased to 38°C (light) and 29°C (shade) the larvae moved to the shaded areas (column B). At still higher temperatures of 53°C (light) and 34°C (shade) 55% of the larvae died (column C).

This was due to the fact that a temperature of 53°C is above the lethal limit for these larvae and they did not appear to be able to move rapidly enough to escape the rising temperatures in the lighted areas of sand. When visible light and temperature gradients were presented simultaneously it was found that the larvae moved into the shade at all light intensities (columns D to G). Thus it appears that the larvae of L.intermedia will respond to both light and temperature gradients in the sand when these factors are above a critical level. Light and temperature act together to increase the responses of the larvae.

The responses of the larvae of the ant-lion M. medialis are shown in Tables 13a and b. These larvae showed a general tendency to select shaded pit building sites but, at low sand temperatures of 30°C and 35°C, this response was only obvious when the light intensity reached 14000 lux (Table 13a). At a higher sand temperature of 45°C the responses of the larvae were increased and they responded to light of lower intensity (1200 lux). In the absence of visible light, but in the presence of temperature gradients (Table 13b), the larvae moved into the shade when the temperature of the infra-red lighted areas of sand was 38°C and 53°C (columns B and C) but did not respond when the temperature was 33°C (column A). When light and temperature gradients were presented simultaneously the larvae moved into the shade at all light intensities (columns D to G).

The larvae of M.obscurus showed somewhat different responses to light and shade, as shown in Tables 14a and b. They showed no response to light of any intensity when the sand temperature was 30°C (Table 14a). At 35°C they moved into the <u>lighted</u> areas when the light intensity was 14000 lux. This response was reversed at 45°C, when the larvae moved into the <u>shade</u> at a light intensity of 14000 lux. Thus, when the temperature of the sand was low, the insects moved to the lighted areas, which in the natural habitat would also be warmer. When, however, the sand temperature was high and approached the upper lethal limit, then the response to light was reversed and the larvae moved into the shade. In the absence of visible light (Table 14b) the larvae only showed a response when the temperature of the infra-red lighted areas of sand was very high (53°C) (column C). Under these conditions the larvae moved into the shade. Light, at all intensities, combined with temperature gradients caused the larvae to move into the light (colums D to G). Thus a combination of light and temperature gradients was more effective in evoking a response than either of these factors presented individually.

The larvae of the non-pit-building ant-lion, <u>S. longicornis</u>, did not respond to light of 200 lux at any sand temperature, as shown in Table 15a. They did, however, respond to light of higher intensities. At sand temperatures of 30°C and 35°C they moved towards the lighted areas of sand, whereas at 45°C they moved towards the shade. The responses of these larvae to light were therefore similar to the responses observed in the larvae of M.obscurus in that the response to light reversed at high sand temperatures. Table 15b shows that, when the larvae were exposed to temperature gradients in the absence of visible light, they moved into the infra-red lighted areas of sand when the temperature of these areas was 38°C (column B). When the temperature in the lighted areas was raised to 53°C the larvae moved to the shade (column C). Temperature gradients combined with light, at all intensities, caused the larvae to move towards the light (columns D to G).

Finally, the responses of the larvae of the ant-lion C.lanceolatus are indicated in Tables 16a and b. As shown in Table 16a these larvae only responded significantly to a light intensity of 14000 lux at a sand temperature of 35°C. Under these conditions the larvae moved towards the light. Apart from this the larvae showed no significant response to visible light. The larvae of this species also showed variable responses to temperature gradients in the absence of visible light (Table 16b). The larvae only moved towards the infra-red lighted areas of sand when the temperature of these areas was 38°C (column B). When the temperature of the lighted areas was 33°C or 53°C (columns A and C) no significant movement of the larvae was recorded. This may be explained by the fact that at 33°C the temperature gradient between the lighted and shaded areas was not great and may be below the threshold for the response, whereas at 53°C the temperature of the lighted areas was still below the upper lethal limit for this species. At these high temperatures the movement of the larvae to the lighted areas may have been inhibited, although the response to temperature gradients was not actually reversed as it was in the larvae of M.obscurus and S.longicornis. A reversal of the response would probably have been recorded if temperatures above 53°C had been used. As might be expected, significant movement towards the light was recorded at all light intensities in the presence of moderate temperature gradients (columns D to G). It should be stressed, however, that this did not necessarily indicate that these larvae were sensitive to light since they responded to temperature gradients even in the absence of visible light.

In general from these experiments it may be seen that the larvae of both ant-lions and worm-lions were able to select either shaded or lighted areas of sand in which to construct their pits or lie in wait for their prey. The responses of the larvae to light, shade and temperature can be correlated with the habitats in which the five species are found. Thus the larvae of L.intermedia and M.medialis, which inhabit the coolest, shadiest microhabitats, moved to the cool, shady areas of sand. The larvae of M.obscurus, which are found in more exposed habitats, moved to warm, lighted sand at low temperatures and to cool, shady sand at higher temperatures. The responses of the larvae of

S.longicornis, from the coastal sand dunes, were similar to those recorded for the larvae of M.obscurus. Finally, the larvae of C.lanceolatus, which live in very hot exposed habitats, selected warm, lighted sand at low temperatures but did not move to cooler areas even when the surface temperature of the lighted sand reached 53°C, which was near the upper lethal limit for this species.

The larvae of all species, except C.lanceolatus, responded to both light and temperature when selecting a pit building site. A combination of light and temperature gradients was more effective in evoking a response than either of these factors presented individually.

5,2 ORIENTATION OF THE LARVAE WITHIN THEIR PITS

It has been shown in section 3,3 that the temperatures in different quadrants of the pits of ant-lion and worm-lion larvae may vary enormously and may rise above the upper lethal limit for the various species. The daily movements and orientation of larvae in their pits were therefore investigated to determine if these insects possess the appropriate behavioural responses to cope with these high temperatures.

The orientation of local myrmeleontid larvae within their pits was investigated both in the field and in the laboratory. In the field the orientation of larvae was determined by visual observation. Generally the mandibles of the larvae were visible at the base of the pit, but if they were not visible a slight disturbance of the pit base with a probe caused the insect to move, revealing its position. The larvae were then recorded as being either in the north, south, east or west quadrant. The orientation of the larvae and the pit temperatures were recorded in 50 pits of each species at 10 a.m., 12 noon and 2 p.m. In some of the pits examined no larvae could be found. This absence of larvae was particularly noticeable in observations of M.obscurus and C.lanceolatus larvae during the warmer part of the day (12 noon and 2 p.m.). Table 17 shows the percentage of larvae apparently absent from their pits at various times of the day, together with the mean temperature of the warmest side of the pit. From Table 17 it can be seen that, when the temperature of the warmest side of the pit was below 40°C, the majority of the larvae of all species were present in their pits. When the temperature rose above 40°C in the pits of M.obscurus and C.lanceolatus a large percentage of the larvae were "absent" from their pits and it is suggested that the larvae had moved deeper into the sand to avoid the high surface temperatures. This situation would correspond to that described by Green (1955) for M.immaculatus in which the larvae were absent from the pit base at temperatures above 48°C.

It should be noted that in these observations on the orientation of larvae within their pits no results are given for the worm-lion, L.intermedia, since these larvae normally lie with their bodies stretched across the base of the pit and can therefore not be said to lie in any particular quadrant. Similarly no results are given for S.longicornis since these larvae do not construct pits. Two sets of results are, however, given for the larvae of M.obscurus because at each observation some of the pits were in direct sunlight while other pits were in the shade.

The orientation of the larvae within their pits is illustrated in Fig. 30, together with the mean temperatures recorded in the various quadrants of the pits of each species. Each temperature represents the mean of 50 readings and is given to the nearest 1°C. In addition, Fig. 30 shows the direction of the sun's rays for those pits which were exposed to direct sunlight.

The pits illustrated in Fig. 30 may be divided into three categories on the basis of their exposure to direct sunlight. The first category included those pits which were completely shaded throughout the period of observation (M.obscurus, shade). In these pits the temperatures of the various quadrants never varied by more than 3°C, although the temperature of the pits as a whole rose from about 23°C at 10 a.m. to about 32°C at 2 p.m. The larvae were nearly evenly distributed in all quadrants, except for a slight concentration (37%) of larvae in the southern quadrant at 2 p.m. The second category of pits included those which were exposed to direct sunlight for a limited period of time (M.medialis). In these pits the sun warmed the western quadrant at 10 a.m. and resulted in a large concentration of larvae (45%) in this area. At noon the pits were no longer exposed to the sun and, although all the quadrants were at about the same temperature, the majority of the larvae (41%) remained in the western quadrant. By 2 p.m., however, the larvae were almost evenly distributed in all quadrants. The third category of pits included those which were exposed to sunlight throughout the experimental period (M.obscurus, sun and C.lanceolatus). In these pits at 10 a.m. the highest temperatures (35-41°C) were recorded in the western and southern quadrants and a total of 63% (C.lanceolatus) and 70% (M.obscurus) of the larvae were found in these regions. This contrasted markedly with the results obtained at noon and 2 p.m. At noon the temperatures of the southern and western quadrants had risen to 46-52°C and only 13% of the M.obscurus larvae and 20% of the C.lanceolatus larvae were present in these quadrants. At 2 p.m. the eastern and southern quadrants were the warmest (49-55°C) and only 16% of the M.obscurus larvae and 10% of the C.lanceolatus larvae were present there.

The results of these observations may be summarised as follows. Early in the day, if temperature gradients were present in the pits, the larvae of all species were able to orientate themselves so that they lay in the warmest regions. If the pits were then shaded the larvae gradually shifted their positions until they were evenly distributed in all quadrants. If, however, the pits continued to be exposed to direct sunlight, so that the temperature of the warmest quadrant rose above about 46°C, then the majority of the larvae moved into cooler quadrants or withdrew entirely into the sand away from their pits. Ant-lion larvae in the field are therefore able to orientate themselves within their pits with respect to temperature.

More detailed experiments on pit temperatures and larval orientation were conducted in the laboratory. In these experiments individual larvae were allowed to construct pits in plastic containers with a surface area of 20 cm^2. and a depth of 8 cm. The containers were heated from above with infra-red lights at various heights and angles of incidence, as described in Material and Methods. The lights were switched on for a period of three hours, after which time the temperatures of the various parts of each pit were taken. It should be noted that, with the infra-red lights at 90° no temperature gradients were present in the pits and, under these circumstances, this experiment acted as a control. At angles of incidence of 60° and 40°, however, the southern sides of the pits were exposed to the infra-red light and became warm, whereas the northern sides were in shadow and remained cool. The position of 20 individuals of each species was determined under each set of conditions. The results of these experiments are shown in Tables 18a and b.

The temperature gradients recorded in the pits in this experiment were considerably more pronounced than the temperature gradients recorded in the field (see Fig. 30). This was due to the fact that in the field the general air temperature rose considerably during the day, thus warming the shaded sides of the pits, whereas in the laboratory the air temperature remained almost constant at 18 ± 3°C. A number of larvae died during these experiments and these mortalities have been indicated in parentheses in the tables.

The responses of the larvae of L.intermedia differed considerably from those of the remaining species. When the lights were at a height of 60 cm. (Table 18a) and temperature gradients were present in the pits (angles of incidence of 60° and 40°) the larvae showed a preference for the cooler eastern and western quadrants. Very few larvae were found lying in a north-south direction since, although the northern quadrant was cool (27°C), the southern quadrant was relatively warm (34°C). When the lights were lowered to a height of 40 cm. (Table 18b) 90% of the worm-lions died due to the fact that the lowest temperatures recorded in the pits (36,9 - 42,3°C) were close to the upper lethal limit for this species. Apart from one individual, the few surviving larvae had all withdrawn completely into the sand away from their pits.

The responses of the larvae of M.medialis, M. obscurus and C.lanceolatus were all very similar. None of these species showed any preference for a particular quadrant in the absence of temperature gradients (angle of incidence 90°). In the presence of temperature gradients and low sand temperatures all species showed a marked preference for the warmer southern quadrant.

Very few larvae were found in the cool northern quadrant. In the presence of temperature gradients and high sand temperatures (Table 18b) 23 M.medialis larvae and 10 M.obscurus larvae had withdrawn entirely from their pits and buried themselves in the sand below their pits. The remaining larvae of these species were concentrated in the cooler northern quadrant. The larvae of C. lanceolatus, on the other hand, were all present in their pits and were found mainly in the eastern and western quadrants where the temperature was in the region of 44-50°C. It is probable that the larvae of this species would also have withdrawn into the sand away from their pits if the infra-red lights had been switched on for a longer period of time.

These results therefore confirmed the field observations and showed that when the sand temperature was low, as it would be in the early morning, all the ant-lion larvae selected the warmest side of the pit, while the larvae of the worm-lion, L.intermedia, selected slightly cooler areas. When the temperature was high the larvae of M.medialis and M.obscurus either selected the coolest quadrant or withdrew entirely into the sand, while the larvae of C.lanceolatus tended to select temperatures in the region of 44-50°C. The experiments thus indicated quite clearly that ant-lion larvae have the appropriate behavioural responses to avoid fatally high temperatures within their pits. They do not, however, withdraw into the sand away from their pits until the temperature of the coolest quadrant of the pit becomes too high. This may be explained by the fact that these insects can only catch prey when they are in their pits and they therefore remain in their pits for as long as possible.

In the field, temperature gradients within the pits are always combined with differences in light intensity. It has also been shown (in the previous section of this work) that the larvae can respond to light when selecting a pit building site. It therefore seemed probable that the larvae would orientate themselves within their pits with respect to light as well as temperature. This was investigated in the laboratory by exposing ant-lion larvae to lights of various intensities at two different angles of incidence. Angles of incidence of 90^{o} and 40^{o} were chosen for these experiments since it seemed possible that the larvae might be induced to burrow into the sand away from their pits when the light was directly overhead, as it would be in the field at midday, while lights at an angle of 40^{o} gave rise to marked shadows in the pits. In order to test the responses of the larvae to light at both high and low sand temperatures the sand was maintained at a temperature of either $18 \pm 3^{o}C$ or $35 \pm 1^{o}C$.

Groups of 20 larvae of M.medialis, M.obscurus and C.lanceolatus were used in each replicate of these experiments. The larvae were allowed 24 hours of normal laboratory daylight conditions in which to construct their pits, after which they were exposed to the experimental lighting conditions for a period of three hours. The position of each individual within its pit was then determined. As in the previous experiments the direction from which the light was shining when at an angle of 40° was regarded as the northern quadrant.

The results of these experiments are shown in Tables 19a-d. Table 19a shows that when the light was directly overhead and the sand temperature was low (18°C) the larvae of all species were evenly distributed in all quadrants. A similar result was obtained when the sand temperature was raised to 35°C, as shown in Table 19b. None of the larvae burrowed into the sand away from their pits and it would appear that this behaviour only occurs in response to high temperatures and not in response to light.

When the larvae were subjected to light at an angle of 40° and a low sand temperature of 18°C (Table 19c) only the larvae of _M.obscurus_ showed a significant response. The larvae of this species orientated themselves in the lighted southern quadrants of the pits when the light intensity was 14000 lux. They did not respond to light of lower intensities. When the temperature of the sand was raised to 35°C (Table 19d) the larvae of _M.medialis_ moved into the shaded northern quadrants at light intensities of 1200 lux and 14000 lux. No response was obtained from the larvae of _C.lanceolatus_ at any light intensity. The larvae of _M.obscurus_ showed some indication of movement to the light southern quadrants, but these results were not statistically significant.

In general from these experiments it can be concluded, firstly, that the burrowing of ant-lion larvae into the sand away from their pits is only elicited in response to high temperatures and not in response to light. Secondly, the orientation of the larvae within their pits is primarily dependent on temperature gradients within the pits. Larvae of M.medialis and M.obscurus, however, did orientate themselves to some extent in response to light, but only at high light intensities.

5,3 MOVEMENT OF THE LARVAE IN VERTICAL TEMPERATURE GRADIENTS

It has been shown that, when the temperature of the sand was relatively low (below about 46°C), ant-lion and worm-lion larvae were able to orientate themselves within their pits with respect to temperature. Above this temperature the larvae withdrew entirely into the sand away from their pits. It has also been shown that considerable vertical temperature gradients were present in the sand in the natural habitat (section 3,2) and it was observed that, at high surface sand temperatures, the larvae migrated downwards away from their pits. In order to investigate this further, the vertical movement of myrmeleontid and rhagionid larvae in sand was studied in the laboratory. It was not possible to study the vertical movement of larvae in the field since no practical method could be found for determining the depth of the larvae without disturbing them.

5,31 The establishment of vertical temperature gradients in sand columns

In the laboratory, vertical temperature gradients were established in sand as described in Material and Methods. Two different types of sand were used in these experiments, white sea sand from the habitat of S. longicornis and fine black sand from the habitats of M.medialis, M.obscurus and L.intermedia. The temperature of each type of sand was recorded at three hourly intervals, starting at 1 a.m. An extra reading was taken at 5 p.m. since the sand temperature changed rapidly at this time. A total of 10 readings of sand temperature, at various depths, was taken at each time of day.

The temperature changes observed in the sand during these experiments can be divided into four distinct phases. Firstly, the night phase from 8 p.m. to 6 a.m. when the environment room was at 16°C and no external source of heat was supplied to the sand. This was similar to the conditions found in the field at night. Secondly, the early morning phase from 6 a.m. to 9 a.m. when the temperature of the environment room rose to 25°C, but the infra-red lights had not yet been switched on. This corresponded to the situation in the field where the sun had risen but was not yet shining directly on the pits. Thirdly, the day-time phase from 9 a.m. to 5 p.m. when the sand was heated by the infra-red lights. Finally, the evening phase from 5 p.m. to 8 p.m. when the infra-red lights and flourescent lights were switched off but the temperature of the environment room had not yet begun to drop from 25°C to 16°C. This corresponded to the field situation where the rays of the sun no longer reached the habitat but the sun had not yet set. It should be noted that the angle of incidence of the infra-red lights did not change during the day in the same way as the sun's rays.

The difference between the laboratory and field temperature gradients is illustrated in Fig. 31, where the laboratory results are compared with those obtained from the habitats of M.obscurus and S.longicornis (see Fig. 21, section 3,2). The sand temperatures recorded in the laboratory during the "night" showed that both the sea sand and the black sand were at the same temperature as the air. That is, at a temperature of 16°C. There were no temperature gradients in the sand. This differed from the situation found in the natural habitat where the deeper layers of sand were always slightly warmer than the upper layers during the night. This difference between the laboratory and field results was due to the fact that, in the laboratory, the lower layers of sand could not be insulated sufficiently to retain their heat for any length of time. This difference was, however, not considered to be of any great importance since in the field the maximum temperature gradients recorded in the sand at this time were only about 2°C.

During the early morning phase the sand in the laboratory rose to a temperature of 25°C, following the rise in temperature of the constant environment room. In the field the deeper layers of sand did not respond quite so rapidly to the increase in ambient temperature. Very definite temperature gradients were present in both black and white sand in the laboratory during the daytime phase. It was found, however, that the fine black sand reached slightly higher temperatures and retained its heat for slightly longer than the coarser sea sand. This difference was very slight and in all further experiments only sea sand was used. When these laboratory results were compared with the temperature changes recorded in the natural habitat the most important difference was that, in the natural habitat the highest temperatures were recorded at about 1 p.m., after which time the temperature dropped sharply, while in the laboratory maximum temperatures were recorded at 3-5 p.m. and the temperature decrease was more gradual, particularly in the deeper layers of sand. This difference may be explained by the fact that in the laboratory the infrared lights remained directly over the dishes of sand, whereas in the field the sun's rays became more and more oblique during the afternoon and the habitat was also shaded to some extent by the surrounding vegetation.

The surface temperature of the sand in these experiments and the steepness of the gradients could be altered by lowering the infra-red lights. The effect of altering the height of the lights is shown in Fig. 32, where the sand temperatures at noon are given. The noon results were used because marked temperature gradients were present at this time. Fig. 32 shows very clearly that, as the infra-red lights were lowered, both the temperature of the surface sand and the temperature gradients within the sand increased. These data are used later in dealing with the upper temperature tolerance limits.

5,32 Responses of the larvae to vertical temperature gradients

Preliminary observations had indicated that large and small larvae might react differently to temperature gradients, and in these experiments the insects were divided into two size groups, using the length of the body from the end of the abdomen to the base of the mandibles as the criterion of size. Small larvae were those which had a body length of less than 15 mm. for L.intermedia, 12 mm. for M.medialis, 9 mm. for M.obscurus, 14 mm. for S.longicornis and 9 mm. for C.lanceolatus. Large larvae were those which had body lengths longer than the above. 20 large and 20 small individuals of each species were used. Each individual was subjected to a whole range of surface temperatures from about 36°C to about 63°C over a period of 10 days, as described in Material and Methods. In addition to the infra-red lights, light of about 14000 lux was provided between 6 a.m. and 8 p.m. each day so that a normal activity cycle could take place. The depth of an individual larva of each species, the depth of its pit and the surface temperature of the sand was determined at three hourly intervals starting at 3 a.m. The position of each individual was only determined once each day since every time a reading was taken the larva was disturbed and its pit destroyed. The experiment was then repeated so that a total of 40 readings was obtained for each size group at each time of day.

These experiments showed clearly that both ant-lion and worm-lion larvae moved downwards through the sand if the surface temperature was high. This is illustrated in Fig. 33, where the depth of the larvae at noon is shown. The noon results were chosen since at this time marked temperature gradients were present in the sand. It should be noted that these noon results included 40 larvae of each species at 10 different heights of the infra-red lights (i.e. 400 readings for each size group).

Fig. 33 shows that the higher the surface temperature the deeper the larvae were found. Large larvae generally moved deeper into the sand than small larvae. There was, however, considerable individual variation in the depth at which larvae were found at any particular surface temperature. For example, large larvae of C.lanceolatus, at a surface temperature of about 56°C, were found at depths varying from 2 cm. to 5 cm. At low temperatures of less than 40° the majority of the larvae were within 2 cm. of the surface. The exact depth at which they were found depended on the depth of the pits constructed by the larvae. Large larvae therefore remained in their pits at higher temperatures than small larvae because their pits were deeper and the rise in surface temperature did not affect them so rapidly.

These results indicated that the larvae remained in their pits until the surface temperature of the sand rose above a critical level, between 40-50°C depending on the species. This is further illustrated in Figs. 34a and b where the depth of the larvae at various times of the day is shown. These results were obtained with the infra-red lights at a height of about 30 cm. Under these conditions the surface sand reached a maximum temperature of about 63°C during the day, and marked temperature gradients were present.

Figs. 34a and b indicate that, until 9 a.m., all the larvae were near the surface of the sand. As the temperature rose the larvae moved downwards. The larvae returned to the surface as the temperature dropped. None of the larvae started migrating downwards until the temperature began to rise and this indicates that the larvae were not moving downwards in response to a circadian rhythm.

Figs. 34a and b do not show the exact temperature at which movement of the larvae began since the readings were only taken at three hourly intervals, and no results were obtained during the period of sharp temperature rise (9 a.m. to noon) and sharp temperature drop (6 p.m.

to 9 p.m.). A further experiment was therefore performed using the larvae of M.obscurus only. The responses of these larvae to vertical temperature gradients in sand were investigated in the same way as in the previous experiment. Twenty large and twenty small individuals were used and the experiment repeated to give a total of 40 readings for each size group. The position of the larvae was recorded once each day during the period 8 a.m. to 9 p.m., the recording time being 30 minutes later on each successive day. The results of this experiment are shown in Fig. 35, together with the temperature of the sand at various depths. The sand temperatures at a depth of 5,5 cm. are not shown since these temperatures were very similar to those recorded at a depth of 4,5 cm.

Fig. 35 shows that both large and small larvae of M.obscurus began migrating downwards through the sand when the temperature of the surface sand reached about 44°C and when the temperature at a depth of 1,5 cm. reached 39°C. The small larvae continued to migrate downwards until they reached a depth of 3-4 cm., where they remained until 5 p.m. During the period for which the larvae remained below the surface the temperature at a depth of 3,5 cm. was about 42°C. At 5 p.m. the small larvae began to move back towards the surface although the temperature at a depth of 3,5 cm. remained high until nearly 7 p.m. The large larvae of M.obscurus also migrated downwards, reaching a depth of 5,5 cm. at about noon. They remained at this depth, at a temperature of about $39^{o}C$, until 5 p.m. The larvae then began to move towards the surface of the sand, although the temperature at a depth of 5,5 cm. was still high. Between 7 p.m. and 8 p.m. all the larvae were very close to the surface and many were observed to be in the process of pit construction. After 8 p.m., when pit construction was completed, the depth at which the larvae were found increased slightly.

The above results suggest that the downward migration of the M.obscurus larvae was triggered solely by temperature. The return of the larvae to the surface of the sand, on the other hand, was not cued by temperature but occurred at a particular time of day. The larvae returned to the surface at about 5 p.m., although the temperature of the surface sand at that time was as high as the temperature which had caused the downward migration of the larvae earlier in the day. It should be noted that in the field the temperature of the surface sand would have been considerably lower at 5 p.m. than it was in the laboratory. Pit building activity, once the insects have returned to the surface of the sand, is controlled by an endogenous circadian rhythm in the larvae of M.obscurus and it seemed likely that the daily migration through the sand might be controlled by the same daily endogenous rhythm. Several experiments were performed in an attempt to verify this suggestion. These experiments involved mainly the larvae of M.obscurus but supplementary experiments were performed on other species where possible.

The first experiment in this series was based on the fact that if the *downward* migration of ant-lion larvae were endogenous it whould continue even when the temperature was sufficiently low to make such migration unnecessary. The depths of larvae of *L.intermedia*, *M.medialis*, *M.obscurus*, *S.longicornis* and *C.lanceolatus* were therefore determined at various times throughout the day at low temperatures and in the absence of temperature gradients. The experiments were performed in a constant environment room at a temperature of 25 ± 1°C. The depths of 10 large and 10 small individuals of each species were recorded once each day, the recording time being three hours later on each successive day. The results of this experiment showed no evidence of downward migration in any species. This confirmed that movement of the larvae away from the surface of the sand only took place in response to high temperatures.

The second experiment in this series was designed to investigate the factors controlling the *upward* movement of ant-lion larvae through the sand. Since previous work had shown that large and small larvae differed only in the depth to which they migrated, and not in the times at which migration occurred, only large larvae of *M.obscurus* were used in these experiments. A group of 20 larvae was exposed to high sand temperatures from 9 a.m. to noon. During this period the sand was heated with infra-red lights. The depth of one larva was determined every hour between 8 a.m. and 1 p.m. and every 30 minutes between 1.30 p.m. and 8 p.m. The experiment was then repeated until 10 sets of results had been obtained. The results are recorded in Fig. 36, together with the temperature of the surface sand and sand at a depth of 5,5 cm.

Fig. 36 shows that the ant-lion larvae moved downwards through the sand as the surface temperature increased. It was noted that they continued to move downwards after noon although the surface of the sand was no longer being heated. The temperature of the sand at a depth of 5,5 cm. was, however, still rising slightly. This was probably due to the conduction of heat from the warmer upper layers of sand. The larvae remained at a depth of 5,5 cm. until 5 p.m., although by 4 p.m. the temperature at this depth had fallen to 25°C. These results therefore show that the upward movement of the ant-lion larvae was independent of sand temperature.

These results were confirmed in an experiment in which the heating of the sand was continued until 8 p.m. Under these conditions, if the larvae were responding purely to sand temperatures, one might expect their return to the surface to be delayed until after 8 p.m. As in the previous experiment 20 large M. obscurus larvae were used, the position of one individual being determined at hourly intervals between 9 a.m. and 4 p.m. and at 30 minute intervals between 4 p.m. and 10 p.m. The experiment was then repeated until 10 sets of results had been obtained. The results are shown in Fig. 37, together with the temperature of the sand at various depths.

The larvae, as shown in Fig. 37, migrated downwards through the sand as the temperature increased until they reached a depth of about 5,5 cm. They remained at this depth until about 5 p.m. when they showed slight upward movement. During the period 6 p.m. to 8 p.m. the larvae were found mainly at a depth of 3-4 cm., although some larvae were found at 1-2 cm. and others at 6-7 cm. This indicated that considerable movement of the larvae was taking place in both an upward and a downward direction. This suggested that the larvae were highly active after 5 p.m. but were prevented from reaching the surface of the sand by the very high temperatures. After 9 p.m., when the temperature of the surface sand had dropped considerably, all the larvae moved to the surface where they were observed to construct pits.

These experiments all showed that the upward movement of M.obscurus larvae to the surface of the sand was controlled by the normal circadian activity rhythm. Changes in the time of this activity rhythm would therefore produce changes in the time at which the larvae returned to the surface. This was confirmed experimentally. 25 large larvae of M.obscurus were maintained for two weeks in a light-dark regime in which the light of 1500 lux was switched on from 10 p.m. to 2 p.m. the following day. Activity thus occurred just at the start of the dark phase at 2 p.m. These larvae were then placed in sand which was heated from 9 a.m. to noon and the depth of one individual was determined every 30 minutes between

8 a.m. and 9 p.m. over a period of 10 days. The results are shown in Fig. 38 and it can be seen that the larvae migrated downwards in the usual way between 10 a.m. and 1 p.m. At 2 p.m., however, the larvae began to move upwards through the sand at a time corresponding to their new induced activity period. All the larvae had reached the surface before 5 p.m. Thus it can be seen that a change in the daily activity rhythm of the larvae of M.obscurus produced a corresponding change in the time at which these larvae moved upwards through the sand.

The daily responses of M.obscurus to temperature may thus be summarised as follows. In the morning all the larvae were at the base of their pits near the surface of the sand. If the temperature of the sand remained low the larvae remained in their pits throughout the day where they were able to catch prey. Under these conditions the larvae orientated themselves within their pits so that they were in the warmest regions of the pit early in the day, and in the cooler regions of the pit later in the day. If the temperature of the surface sand rose above about 46°C the larvae migrated downwards away from their pits into cooler areas of sand. They remained below the surface until about 5 p.m. when a general increase in activity due to the endogenous circadian activity rhythm caused them to move back towards the surface, where they reconstructed their pits.

These generalities apply to all the other ant-lion larvae investigated but do not apply to the larvae of the worm-lion L.intermedia. Worm-lion larvae move downwards into the sand away from their pits at very much lower temperatures and, since these larvae do not possess a marked daily activity rhythm, their return to the surface is probably a direct response to temperature. Not enough worm-lion larvae were available to investigate this suggestion experimentally.

5,33 Upper temperature tolerance limits

Although no specific experiments were performed to determine the upper temperature tolerances of the various species this information can be deduced from data presented above. The data which are relevant to a determination of temperature tolerances are;(a) those from noon to 3 p.m. when distinct temperature gradients were present in the sand, (b) those in which the surface sand temperature rose above 40°C. At surface temperatures of less than 40°C the larvae of all species remained within their pits or on the surface of the sand. Thus the data used to determine temperature tolerances was obtained from Figs. 32 and 33 and included 40 large and 40 small individuals of each species at noon and at 3 p.m. The infra-red lights in these experiments were at six different heights between about 44 cm. and 30 cm. This gave a total of 480 readings for each size group. The results are shown in Fig. 39.

It can be seen from Fig. 39 that small ant-lion and worm-lion larvae had a slightly higher temperature tolerance than larger individuals. This was probably due to the fact that smaller individuals were not able to move to as great a depth as large individuals. The lowest temperature tolerance was shown by the larvae of the worm-lion L.intermedia, which were found mainly in the range 34-38°C. No individuals of this species were ever found at temperatures above 42°C. A slightly higher temperature tolerance of 38-40°C was shown by the larvae of M.medialis, while the larvae of M.obscurus and C.lanceolatus were both found mainly in the range 36-42°C. Finally, the larvae of S.longicornis were found mainly in the range 38-42°C. Apart from the larvae of L.intermedia, therefore, the upper temperature tolerances of the various species were very similar. This result is suprising in view of the considerable differences in the upper lethal temperatures of the various species (Fig. 26, section 4,1). The larvae would, however, seldom be subjected to temperatures near their upper lethal limit provided that the sand was deep enough to enable them to migrate downwards away from their pits.

5,4 RESPONSES OF THE LARVAE TO SAND DEPTH

The larvae of myrmeleontids and rhagionids have been shown to move down through the sand in response to temperature gradients. This response is obviously very important in ensuring their survival in the field where the temperature of the surface sand may well rise above their upper lethal temperature limits. It was therefore decided to determine whether or not the larvae were able to select sand which was deep enough to enable them to make use of their vertical migration behaviour. A number of experiments were performed in the laboratory to determine whether or not the various species of ant-lions and worm-lions showed a preference for any particular depth of sand in which to build their pits or lie in wait for their prey.

In preliminary experiments a choice chamber was used in which the depth of the sand varied from 1 cm. at the "shallow" end to 15 cm. at the "deep" end. This increase in depth took place over a horizontal distance of 50 cm. The sand in this choice chamber was marked off into five blocks in which the depth ranged from 1-3 cm., 4-6 cm., 7-9 cm., 10-12 cm. and 13-15 cm. respectively. One individual was placed in the centre of each sand block at the start of the experiment. The larvae were allowed 48 hours in which to construct their pits under normal laboratory daylight conditions and a temperature of 18 ± 3°C. After this time the position of each pit was noted and the depth at which it was constructed was measured. In experiments involving the non-pit-building ant-lion S. longicornis the choice chamber was divided into 10 cm. intervals with pieces of stiff card before location of the larvae took place. The experiment was replicated until a total of 16 larvae of each species had been used.

It was found, in this experiment, that the majority of the larvae remained in the positions in which they had been placed. Occasionally a larva moved from its original position but these movements did not follow any particular pattern. At times the movement was from the "shallow" end to the "deep" end, while in other cases it took place in the reverse direction. These experiments therefore indicated that at low sand temperatures the larvae did not select any particular sand depth in which to construct their pits. Under these conditions, however, the larvae did not show any downward migration through the sand and it seemed possible that high sand temperatures might be required to stimulate the larvae to move away from shallow pit building sites. The effect of temperature on sand depth selection was therefore investigated.

In these experiments the sand in the choice chamber was heated from above by infra-red lights which were switched on from 9 a.m. to 5 p.m. each day. This allowed pit construction to take place at dusk in the normal manner. The temperature of the surface sand, at noon, under these conditions was $52 \pm 2^{\circ}C$. 16 individuals of each species were allowed to construct their pits over a period of 48 hours, after which time the depth of the sand in which each larva was found was determined.

The results of this experiment showed no evidence of movement of the larvae to any particular depth of sand and appeared to indicate that myrmeleontid and rhagionid larvae were not able to select sand of any particular depth. In an attempt to confirm these results a second choice chamber was constructed. The floor of this chamber was stepped so that, when the container was filled with sand, the depth of the sand in one half of the choice chamber was 20 cm., while the depth of the sand in the other half was only 1 cm. The total surface area of the chamber was 70 cm^2. Three individuals were placed at each depth and allowed to construct pits under normal laboratory daylight conditions and a temperature of 18 ± 3°C. After four days the position of each pit was noted. In the case of the non-pit-building larvae a cardboard division was placed in the sand on the edge of the step before the positions of the larvae were determined. The experiment was repeated until 12 individuals of each species had been used. The responses of a further 12 individuals of each species were then tested under conditions of high sand temperature. The choice chamber was heated from above with infra-red lights between 9 a.m. and 5 p.m. so that the temperature of the surface sand at noon was about 52°C. The results of these experiments are shown in Table 20.

Table 20 shows that very little movement of the larvae took place. No significant movement of the larvae took place when the temperature of the sand was 18°C. When the sand temperature was 52°C only the larvae of M.medialis showed a significant movement from the shallow to the deeper sand. The larvae of L.intermedia, M.obscurus and S.longicornis showed some tendency to move to deeper sand but these results were not statistically significant. The results of these experiments were not conclusive due to the small number of larvae involved. No further larvae were available for this work and it is possible that the larvae may be stimulated by high temperatures to construct their pits in deeper sand. It seems unlikely, however, that this factor would be of any great importance in the field especially as the larvae of all species, except *S. longicornis* which lives in the coastal sand dunes, inhabit isolated pockets of sand in which only slight variations in sand depth would be available.

6. WATER RELATIONS

Ant-lion and worm-lion larvae are only able to construct pits in dry sand and it is probable that during the warmer months of the year, when the sand in which they live gets very hot, desiccation might be a serious problem. It should, however, be borne in mind that all species live below the surface of the sand where the humidity would be considerably higher than in the surface layers of sand. Edney (1958), for example, showed that in the Algerian desert the humidity in a woodlouse hole never fell below 80% relative humidity at a depth of two inches, while the air immediately outside the hole fell to below 20%RH. Although the conditions recorded in a woodlouse hole would not be the same as living directly in the sand these results do give some indication of the differences in humidity which could occur over relatively short distances in the sand. Cloudsley-Thompson (1962b and 1967a) has also indicated that, in temperate regions, the humidity below the surface of sand is generally high. No actual measurements of sand humidity were taken during the present investigation due to the lack of a suitable method, although attempts were made to measure the relative humidity using weighing methods. These methods were, however, unsuccessful.

A number of experiments on the water relations of myrmeleontid and rhagionid larvae were performed in the laboratory in an attempt to determine whether these larvae obtain sufficient water from their prey, or whether they are reliant on free water or high atmospheric humidity for their survival. Experiments were also performed to determine whether the interaction between temperature and humidity is of importance in the biology of these animals.

Initially, experiments were performed to determine the rate of water loss and the resistance to desiccation of the various ant-lion and worm-lion species. All the larvae used in this work were subjected to a standard pretreatment. They were kept in the laboratory for seven days at a temperature of $18 \pm 3^{\circ}C$, and each fed one ant a day during the first six days. The one day period of starvation before the start of the experiments was necessary because, although ant-lion larvae are unable to defaecate due to the fact that the midgut and hind gut are not continuous (Imms, 1957; Bushinger and Bongers, 1969), they have been observed to excrete considerable quantities of urine immediately after a meal. Such excretion during the course of an experiment would lead to inaccurate estimates of weight loss. All the larvae were starved during the course of the experiments.

After the period of pretreatment, 30 large, final instar, larvae of each species were placed in a desiccator containing silica gel. Each individual was placed in a small dry plastic container covered with plastic gauze, both the container and the gauze having been found to be non-hygroscopic. The desiccator was then placed in an incubator at a temperature of 32 $\pm$ 1°C and the containers with their enclosed larvae were weighed at noon each day until three days after the death of the last larva. Weighings were only performed once a day since the rate of water loss from these animals was extremely low and because frequent opening of the desiccator caused large variations of the humidity within it. It was found that about 15 minutes were required for the humidity to stabilize after the desiccator had been opened for three minutes.

The results of this experiment, which are shown in Tables 21a and b, indicate that the mean survival time for all species was at least 24 days. Death after this time was not due to starvation as it was found that the larvae would survive without food for at least 50 days under normal laboratory conditions. During the experiment the larvae lost between 21-33% of their original body weight.

Table 21b shows that there was no significant difference between the survival times of the larvae of *L.intermedia* and *M.medialis*. Both these species, which live in relatively cool sheltered habitats, survived for significantly less time than the larvae of *M.obscurus* and *C.lanceolatus*, which live in more exposed habitats. There was no significant difference between the survival times of *M.obscurus* and *C.lanceolatus*. The larvae of *S.longicornis*, from the coastal sand dunes, survived for significantly less time than the larvae of M.obscurus and C.lanceolatus but did not survive for significantly longer than the larvae of L.intermedia and M.medialis.

With respect to weight loss, Tables 21a and b show that the larvae of L.intermedia, which live in the coolest habitats, had lost an average of 21% of their body weight at the time of death. This was significantly less than the weight loss recorded in any other species. (It should be noted that the percentage weight loss for these species was normally distributed which justified the use of a conventional "Student's t" test). The larvae of M.medialis lost 23,3% of their body weight and this value was significantly different from the loss recorded in any other species. A statistically significant result was also obtained for the larvae of S.longicornis which lost 28,3% of their body weight. Finally, the larvae of M.obscurus and C.lanceolatus lost 33,2% and 31,9% of their body weight respectively. These results did not differ significantly from one another. From these results it is clear that larvae which inhabit cool shady places tolerate a smaller loss of body weight than larvae from warmer habitats.

The results of the above experiment are shown in more detail in Fig. 40, where the mean daily weight loss for each species is shown. The most obvious feature of Fig. 40 is that all species lost weight most rapidly during the first 4-6 days of the experiment. This was probably due to the fact that the larvae were more active at the start of the experiment than they were later on.

After the first 4-6 days the rate of water loss generally remained fairly constant until just before the death of the larvae, when a slight decrease in weight loss was noted. This decrease in weight loss was probably due to the fact that the larvae were less active before they died and some of the larvae appeared to be in a state of coma. After the time of death the rate of water loss rose noticeably. Although the water loss of all species followed similar trends the actual amount of weight lost per day varied greatly from species to species. These differences in actual weight loss can, however, not be compared directly due to the different sizes of the various species. For example, the larvae of *S.longicornis* lost considerably more weight per day than the larvae of *M.obscurus* but, when their relative sizes are taken into account, it is found that the larvae of *M.obscurus* actually lost a greater percentage of their body weight than the larvae of *S.longicornis* (see Tables 21a and b). This is also illustrated graphically in Fig. 41 where the mean daily weight loss is expressed as a percentage of the body weight. In all species the percentage loss of body weight increased rapidly after the death of the animals, suggesting an active control of water loss in the living animals. Furthermore, the percentage of body weight lost before death did not increase as the weight of the larvae decreased. It seems possible that this control of water loss in the living animals was due largely to closure of the spiracles, since it has been shown that shortly before death, when the larvae were inactive or comatose, the weight loss was low.

The methods used in the above experiments have a number of shortcomings. Firstly, all weight losses were recorded as a loss in the fresh weight of the animals and, since the larvae were starved during the experiment, the loss in weight certainally included a loss of dry weight due to the metabolism of the animals. Meats (1967), however, has shown that in Tipula oleracea the dry weight loss was only about 4% of the original fresh weight. He therefore concluded that dry weight loss was an insignificant component of fresh weight loss. The survival time of T.oleracea was, however, extremely short and in the present investigation where the larvae survived for a prolonged period of time a greater loss of dry weight would be expected. For comparisons between the various species, however, total weight loss may be regarded as a measure of water loss.

A further criticism which might be levelled at this work is the use of a still air desiccator, since it has been pointed out by Ramsay (1935) that such a system is both vapour and membrane limited. The animals used in this study were, however, very small in comparison with the size of the desiccators and lost water very slowly so that the effect of the vapour limited system may be regarded as negligible.

Finally, it has been shown by many workers such as Heeg (1967) that the size of the animals and the stage within an instar may greatly affect the rate of water loss from insects. In this study all the larvae used were in the final instar but their stage within the instar could not readily be determined and this factor may have given rise to some of the variability recorded, but the large sample number (30) was probably sufficient to minimise this effect.

The experiments on water loss were carried out at a relatively low temperature which was well within the normal tolerance limits of the various species. At such low temperatures the larvae would not need to evaporate water in order to cool themselves. At higher temperatures, near the lethal limit for each species, however, the larvae might lose more water. This question is of particular importance since, in the natural habitat, dry periods are generally associated with high day-time temperatures. The effect of high temperature on water loss was therefore investigated in the laboratory.

The temperatures used in these experiments depended on the species and were such as to allow the larvae to survive for a period of at least 20 days. The mean weight of 30 individuals of each species was recorded over a period of 10 days during which time the larvae were maintained in desiccators at 0% RH. The rates of water loss were then compared with the rates of water loss recorded at low temperatures. The results are shown in Table 22.

From Table 22 it can be seen that there was no significant difference between the weight lost at low temperature or at high temperature in any species. It was therefore concluded that rhagionid and myrmeleontid larvae lose very little water by evaporation, even at temperatures close to their upper lethal limit. This confirms the suggestion (see section 4,3) that the larvae make very little use of evaporative cooling at high temperatures.

A further aspect of the problem of desiccation which must be considered is that of water uptake. Both ant-lion and worm-lion larvae ingest their food in liquid form, since both groups employ extra-intestinal digestion. Thus, provided that food is plentiful, sufficient water would be obtained in this way. In times of food shortage, however, other methods of water uptake might be used. It is, for example, well known that many insects are able to take up atmospheric water if placed in high relative humidities. The uptake of water at high relative humidities has been reported by many authors including Mellanby (1932), Edney (1966) and Noble-Nesbitt (1970a and b). It seems possible that a similar mechanism might be used by ant-lions and worm-lions since there is no evidence of these insects drinking free water.

The larvae used in these experiments were all subjected to a standard pretreatment. Each larva was fed one ant a day for seven days, after which time they were starved for a further seven days. During the period of starvation all the larvae were kept in a desiccator at a temperature of 32 ± 1°C. 20 individuals of each species were then weighed and placed in atmospheres with relative humidities of 96% or 98% at a temperature of 25 ± 1°C. These humidities were obtained using salt solutions described by Winston and Bates (1960). Saturated atmospheres were not used due to the difficulty of eliminating free liquid water. Relative humidities of 96% and 98% should be amply high to allow for water uptake since Edney (1966) has shown that for Arenivaga the lower limit for water absorption is 82% RH, while Noble-Nesbitt (1970b) has shown that Thermobia domestica can absorb water down to 50% RH. The humidities used in these experiments were measured by means of cobalt thiocyanate paper. After 24 hours at high humidity all the larvae were reweighed and their change in weight calculated. A period of 24 hours for the animals to take up water is more than adequate since in the field the larvae are only subjected to high humidities for less than 12 hour periods at night.

The results of this experiment indicated that there was no significant change in weight in any species and this is illustrated in Table 23, where the results for 98% relative humidity are given. The larvae do, therefore, not absorb atmospheric water over a period of 24 hours and it seems unlikely that they would do so if left for longer periods of time. The larvae of L.intermedia, M.medialis, S.longicornis and C.lanceolatus showed a slight increase in weight which was probably due to the adsorption of water onto the cuticle of these insects. The larvae of M.obscurus, on the other hand, showed a slight decrease in weight. This weight loss was probably due to sand grains falling off larvae which had been insufficiently cleaned prior to the experiment or to general metabolic weight loss. A number of other arthropods have also been shown to lack the ability to absorb atmospheric water, and these include the cockroaches Periplaneta and Blatta (Edney, 1967b), the desert dwelling beetles Eleodes armata and Cryptoglossa verrucosa (Ahearn and Hadley, 1969), and the desert scorpion Hadrurus arizonensis (Hadley, 1970).

To summarise, the work on the water relations of myrmeleontid and rhagionid larvae shows that all the species investigated were extremely resistant to desiccation and could live for prolonged periods of time in completely dry air. Water loss did not increase at temperatures near the upper lethal limit. Finally, water was not absorbed directly from the atmosphere, even at high relative humidities. The main source of water gain must therefore be the food which has been shown by Youthed and Moran (1969b) to be extremely plentiful in ant-lion habitats, although the possibility of the larvae drinking free water during rainy periods cannot be excluded.

7. DISCUSSION AND CONCLUSIONS

The present investigation of the larval microhabitats of four species of Myrmeleontidae and one species of Rhagionidae showed that these species were confined exclusively to areas of dry sand. The microhabitats of the different species varied considerably with respect to temperature. They ranged from relatively sheltered, thermally stable, habitats to those which were exposed and therefore experienced more extreme temperatures. The habitats may be arranged in order of severity as follows: L.intermedia, M.medialis, M.obscurus, S.longicornis and C.lanceolatus. These habitats may be compared in some respects with deserts. Although, at present, there does not appear to be any standard definition of exactly what constitutes a desert, it is generally agreed (Buxton, 1923; Williams, 1954; Kirmiz, 1962) that one of the main characteristics of a desert climate is the existence of great diurnal fluctuations in temperature. For example, Buxton (1923) states that in the Algerian Sahara the daily range in air temperature during summer is of the order of 29°C. This may be compared with the ranges of about 13°C recorded in the habitat of L.intermedia, 24°C for M.medialis, 33°C for M.obscurus, 36°C for S.longicornis and 38°C for C.lanceolatus. The higher ranges recorded in this study might be due to the fact that these readings were taken just above the surface of the sand (at a height of 1 cm.)

whereas the temperatures recorded in the Sahara were obtained from a standard meteorological screen. With respect to surface sand temperatures, Buxton (1924) states that during summer in Palestine the surface temperature is about 55-62°C. These temperatures are similar to the maximum temperatures recorded in ant-lion habitats, which ranged from 50°C to 65°C. The maximum surface temperature recorded in the habitat of the worm-lion L. intermedia, on the other hand, was only 35°C.

During the course of this work it was observed that neither ant-lion nor worm-lion larvae were able to construct pits, or capture prey, unless the surface sand was dry and desiccation would, therefore, be expected to pose a serious problem in the survival of these animals. It was found, however, that all species had an exceptionally low rate of water loss and could survive desiccation for prolonged periods of time. The ability of ant-lion and worm-lion larvae to withstand desiccation may be compared with desert insects. Although there is a considerable amount of literature available on the water relations of desert arthropods, including the works of Edney (1967a, 1971a), Cloudsley-Thompson (1967b), Ahearn and Hadley (1969), Ahearn (1970) and Hadley (1970), there is little on the total length of time for which desert dwelling insects can survive under conditions of low relative humidity, or on their total water loss at the time of death. The few references which are available have been summarised in Table 24, together with the results recorded from the present investigation.

Table 24 shows clearly that the mean survival time of all the ant-lion and worm-lion species investigated equalled or exceeded that of desert insects. Although only the mean survival times are quoted in the literature and no references are available on the maximum recorded survival times, the maximum values of 33 to 46 days recorded in this investigation appear remarkable. In Table 24 the mean survival times of 9-24 days and 15-24 days recorded by El Rayah (1970b) for Adesmia antiqua and Pimelia grandis were dependent on the size of the insects. He found that larger individuals survived for longer periods of time than smaller individuals. It is probable that this effect was due to the larger surface to volume ratio, and hence greater rate of water loss, of the smaller individuals. A number of other workers, such as Edney (1971a), have stressed the effect of size on water loss. Although only large individuals were used in the present investigation it is likely that a similar size effect would be found if the different sizes were taken into account.

Table 24 also shows that, despite their longer survival time, ant-lion and worm-lion larvae did not lose a greater percentage of their body weight than desert insects. This is a clear indication that the larvae of ant-lions and worm-lions have an exceptionally efficient water conserving mechanism. This is borne out by the very low rates of water loss which were recorded in this study. From the literature, the rate at which water is lost by various insects has been expressed in a number of different ways, which leads to difficulty in making comparisons between various species. In the present investigation all results were expressed as the percentage loss of fresh body weight because this is the form in which the water loss of many desert insects has been expressed. In Table 25 the rates of water loss of ant-lions and worm-lions are compared with the rates recorded for a number of desert insects. Since all these animals lose weight very slowly the mean loss per day has been used as a basis for comparison rather than the mean loss per hour.

Table 25 shows that the ant-lion and worm-lion larvae lost less weight per day than any of the other species. These results may, however, be slightly misleading since the majority of other workers only recorded weight loss over a relatively short period of time and the present investigation has shown that, due to increased activity, the rate of water loss may be at its highest during the first few days of an experiment. A similar result has been recorded by Edney (1971a) who showed a decrease in weight loss on successive days in Onymacris plana. Edney found that these insects lost 1,2% of their original body weight on the first day and only 0,8% on the fifth day.

One problem which should be considered in relation to the rate of water loss is that of abrasion by dust. It is well known (Beament, 1945) that dust abrades the waterproofing layer on the cuticle of many insects giving rise to a great increase in transpiration. This phenomenon has also been reported in a number of other arthropods. Davies and Edney (1952), for example, recorded a six fold increase in evaporation from spiders when abraded by dust, while Hafez et al (1970) recorded a marked increase in the transpiration of abraded desert ticks. It would therefore be expected that ant-lions and worm-lions which live below the surface of the sand would be constantly abraded. Such abrasion may be prevented by the large number of hairs covering the bodies of ant-lion larvae, but this seems unlikely since considerable amounts of dust are always present at the base of these hairs. Worm-lions possess very few hairs which could protect them in this way. A further possibility is that the wax layer of the cuticle is very rapidly repaired as has been shown by Edney (1966) for Arenivaga. Hafez et al (1970) have also shown that the ticks Hyalomma dromedarii and Ornithodoros savignyi could re-establish most of their cuticular impermeability to water on the first day after abrasion if kept at 96% RH. The cuticular impermeability was, however, never completely restored in either species. These workers also showed that the greater the cuticular abrasion the less the ability of the ticks to recover their initial impermeability. Such a regenerative process seems unlikely to occur in ant-lion and worm-lion larvae as an almost continuous secretion of water-proofing material would then be required. A more likely explanation of the very efficient water conserving mechanism of these sand dwelling insects is that their epicuticular wax layer is protected by a layer of very resistant cement. The presence of epicuticular cement layers is well known in insects (Wigglesworth, 1965) and it seems likely that these layers may in some cases be resistant to abrasion. For example, Hafez et al (1970) have shown that the ticks H.dromedarii and O. savignyi were not abraded when merely shaken up in a tube with dust. It was necessary to rub the animals with dust before abrasion of the cuticle occurred.

In relation to the possibility of ant-lion and worm-lion larvae possessing a very hard, resistant, waterproofing layer it is interesting to note that, even at temperatures near the upper lethal limits for the various species there was no evidence of a "transition temperature". This is the temperature at which the cuticular waxes of a large number of insects have been shown to melt, giving rise to a great increase in transpiration. This phenomenon has been well documented by a large number of workers including Beament (1945, 1958, 1959), Wigglesworth (1945), Mead-Briggs (1956) and Ahearn (1970). These transition temperatures may, however, be very high and lie above the lethal limits for the animals concerned. For example, Hafez et al (1970) demonstrated that the transition temperatures for the desert ticks H.dromedarii and O.savignyi were 52°C and 63°C respectively. The upper lethal temperatures of both ticks were found to be a few degrees below the temperature at which destruction of the waterproofing layer took place. It seems probable that a similar situation could apply to ant-lion and worm-lion larvae and that their transition temperatures lie above their upper lethal limits. This transition temperature would therefore not be of importance in the lives of these insects.

In general, from the present investigation, water loss should not be considered as an ecological problem in these cases, since all the ant-lion and worm-lion larvae studied were able to survive for at least 24 days at a relative humidity of 0%. It would be impossible for them to be stressed as much as this under natural conditions since all the species live below the surface of the sand where the humidity would be considerably higher than on the surface. It is also highly unlikely that ant-lion and worm-lion larvae would have to survive for as long as 24 days without food, except during very rainy periods when pit construction, and hence prey capture, would not be possible. Humidity and water loss may therefore be disregarded as an important parameter in the lives of ant-lions and worm-lions. The water relations of ant-lion and worm-lion larvae, however, remains an interesting physiological problem worthy of further investigation. In particular the questions as to how these larvae are able to tolerate desiccation for such prolonged periods of time and how they overcome the problem of abrasion are of great interest.

High temperature appears to be the major factor affecting the survival of ant-lions and worm-lions. There is a vast amount of literature available on various aspects of the temperature relations of different insects, including the works of Green (1955), Edney (1952), Clarke (1967), Phelps and Burrows (1969), Heath and Wilkin (1970), El Rayah (1970a) and Blumberg (1971). It is generally agreed, however, (Bursell, 1964) that, over short exposure periods of about an hour, the upper lethal temperature limit of most insects lies in the range 40-50°C. Some species of insects and other arthropods are, however, capable of survival at considerably higher temperatures. From the few references which are available on the lethal limits of desert arthropods over a 24 hour period it is obvious that most of them are very resistant to high temperatures. The upper lethal temperatures of some desert arthropods are summarised in Table 26 and compared with the lethal limits of ant-lion and worm-lion larvae recorded in this study. From Table 26 it can be seen that, while the mean lethal temperature of worm-lion larvae was below that recorded for desert arthropods, the lethal temperatures of the ant-lion species equalled or exceeded that of the desert arthropods over a 24 hour exposure period. Although the results quoted in the literature were obtained at low relative humidities it is unlikely that significantly lower lethal temperatures would have been recorded at higher humidities since well water-proofed desert arthropods generally show very little evaporative cooling. The upper lethal temperatures of a number of other desert insects have been recorded over shorter periods of time and in general range from 48-51°C (Edney, 1971b) for exposure periods of about 30 minutes.

Of great interest in a discussion of lethal temperatures is the daily variation in temperature sensitivity which has been noted in ant-lion larvae. Maximum temperature sensitivity in these larvae occurred at the same time as the circadian activity rhythm. Although other authors, such as Nowosielski et al (1964), Rensing (1969), Haverty and Ware (1970) and Fondacaro and Butz (1970), have recorded daily variations in the sensitivity of insects to such factors as narcotics, insecticides and X-rays there does not appear to be any experimental evidence in the literature linking such sensitivity cycles directly with circadian activity rhythms. It is generally accepted (Harker, 1956, 1960, 1961; Fingerman, Lago and Lowe, 1958; Rensing, 1964 and Roberts, 1966) that circadian activity rhythms are controlled by an hormonal system. It is possibly this hormonal system which is very sensitive to temperature. The causes of variations in temperature sensitivity and the general mechanism of heat death in insects are not understood.

A number of different suggestions have been made about the causes of heat death in arthropods and include general protein coagulation, asphyxiation, accumulation of metabolic waste products and the breakdown of cellular lipids (Fraenkel and Hopf, 1940; Larsen, 1943; and

Cloudsley-Thompson, 1962a). However, it is generally agreed that none of the above theories alone can account for heat death. Of relevance in the present discussion is the work of Larsen (1943) on Musca domestica. Larsen showed that the pupae of this species were more sensitive to temperature during periods of increased metabolic activity. These were periods of profuse hormonal secretion and extensive mitosis. Rensing (1969) has also correlated peak sensitivity of Drosophila to X-rays with periods of increased nucleolus volume and hormone synthesis. There is thus evidence which suggests that the synthetic processes within cells are particularly vulnerable to such factors as heat.

The existence of daily variations in temperature sensitivity may prove to be of considerable importance in a study of the lethal limits of insects generally. Previous workers in this field have not mentioned the time of day at which their experiments were undertaken. Also, the lethal temperatures of many insects have been determined over a period of several hours and might well have included periods of maximum temperature sensitivity. The results obtained under these conditions would therefore not provide an accurate estimate of the temperatures which insects could survive during the rest of the day.

The correlation of maximum temperature sensitivity and circadian activity poses the question as to the situation in diurnal insects in which such a correlation would lead to maximum temperature sensitivity during the heat of the day. This suggests that the coincidence of maximum temperature sensitivity and activity may not be a general phenomenon in insects.

In this study, all the ant-lion species were shown to possess a daily rhythm of activity with peak activity occurring at about dusk. Some suggestions have been made by Youthed and Moran (1969b) about the functional significance of the activity and pit building rhythm in Myrmeleon obscurus. They suggested that, since ant-lion pits are easily damaged by wind and the struggling of prey, it is necessary for the larvae to reconstruct their pits daily. This pit construction necessitates movement of the larvae on the surface of the sand and the larvae can therefore only construct their pits when the temperature of the surface sand is relatively low. This would apply particularly if the activity period is also a period of increased temperature sensitivity. The ant-lions thus construct their pits at dusk to enable them to make use of the whole night for prey capture. This poses the question as to why the larvae of S. longicornis, which do not construct pits, also possess an activity cycle with the peak at dusk. The larvae of S.longicornis have been shown to migrate downwards into the sand during the day in response to high surface sand temperatures and it seems probable that the function of the daily activity rhythm in these insects is to ensure that they return to the surface at dusk. The larvae would then be able to catch prey throughout the night. Prey catching at night may be particularly important in this species for two reasons. Firstly, these larvae have been observed to pursue their prey across the surface of the sand if they do not manage to grip the prey sufficiently firmly at first. The S.longicornis larvae would therefore be exposed to predators during the process of prey capturing and would be less vulnerable during the hours of darkness. It should be noted that ant-lion larvae are blind as they do not possess compound eyes. Prey capturing appears to take place in response to vibrations caused by movement of the prey and ant-lions are therefore able to pursue their prey in total darkness. Secondly, the larvae of S.longicornis would have to migrate downwards into the sand far earlier in the day than pit building species. This is due to the fact that the temperatures within the pits of ant-lions may differ considerably from the temperature of the surrounding sand. For example, it has been shown that, in the habitat of M.obscurus at 2 p.m., the temperature of the surface sand was 47,3°C, whereas the temperature of the cool northern sides of the pits was only 40,0°C. Under these conditions the larvae would still be able to remain in their pits and catch prey, whereas non-pit-building larvae would already have had to migrate downwards into the sand in response to the high surface temperature. The construction of pits may, therefore, not only increase prey capturing efficiency but also allow the larvae to capture prey for a longer period of time each day. The construction of pits would thus be of considerable survival value in hot dry sand.

The pit making habit in the Myrmeleontidae is undoubtedly a comparatively recent one since the Archimyrmeleontidae and other more primitive Neomyrmeleontidae do not construct pits (Withycombe, 1925). The majority of the more morphologically primitive Myrmeleontidae merely conceal themselves under the surface of sand and debris. Such non-pit-building species do, however, have the advantage of being able to survive in windy areas in which the construction of pits would not be feasible. Thus the pit building ant-lion species are never found on the very exposed coastal sand dunes which are inhabited by the larvae of *S.longicornis*. The pit building species do, however, occur in areas sheltered by dense dune vegetation.

Although ant-lion and worm-lion larvae do not possess any obvious morphological adaptations (such as those which are well known in desert Tenebrionidae) to enable them to survive in hot dry sand, they do have a number of physiological and behavioural adaptations. Their very high temperature tolerances and remarkable resistance to desiccation suggests an ancient association of these insects with sand. The larvae of the rhagionid *L.intermedia*, which inhabit the coolest microhabitat, are physiologically less well adapted to life in sand than the myrmeleontid species and could therefore not inhabit the very exposed habitats in which myrmeleontid larvae are found. Ant-lion larvae would, however, be able to exist in the more temperate areas inhabited by worm-lions and this raises questions as to why ant-lions are never found in these apparently favourable habitats.

A probable explanation is that prey is not as plentiful in very sheltered habitats as it is in those which are more exposed.

Possibly the most important adaptations of ant-lion and worm-lion larvae to their life in sand are their behavioural responses to temperature. These responses ensure that the larvae are normally not subjected to temperatures close to their upper lethal limit. It has been shown that all species were able to orientate themselves within their pits in response to temperature gradients. All species were also able to migrate deeper into the sand when subjected to high surface sand temperatures. This phenomenon of burrowing into sand in order to escape high surface temperatures is well known in arthropods. For example, Bursell (1960) showed that the larvae of _Glossina pallidipes_ burrow into the soil in response to high surface temperatures, while Edney (1958) showed that the woodlouse _Hemilepistus reaumuri_, living on the fringes of the Sahara desert, retreated into holes in the ground in response to rising temperatures. The burrowing of desert arthropods has also been recorded by Cloudsley-Thompson (1964b, 1968) and Chapman _et al_ (1926). This burrowing behaviour is undoubtedly of great survival value to ant-lion and worm-lion larvae, even in habitats such as that of _C. lanceolatus_ in which the sand is very shallow.

In general, the behavioural responses of the various ant-lion and worm-lion larvae to temperature correlates well with the habitats in which the larvae are found.

Larvae from the coolest habitats have lower temperature tolerances and select cooler shadier pit building sites than larvae from warmer habitats.

In conclusion it may be said that myrmeleontid and rhagionid larvae not only show convergent evolution as far as habitat and pit construction are concerned, but also show convergent evolution in their adaptations to life in sand. The major differences between the adaptations of ant-lions and worm-lions lies in the degree of adaptation rather than in the adaptations themselves.

8. SUMMARY

1) Some adaptations of myrmeleontid and rhagionid larvae to life in hot dry sand were investigated in the field and in the laboratory. The species studied were: (a) three species of pit building ant-lions (Myrmeleontidae, Neuroptera) namely; Myrmeleon medialis, Myrmeleon obscurus and Cueta lanceolatus, (b) one species of non-pit-building ant-lion (Myrmeleontidae, Neuroptera) Syngenes longicornis and (c) one species of worm-lion (Rhagionidae, Diptera) Lampromyia intermedia.

2) An attempt was made to correlate the known distribution of the various species in the Republic of South Africa with overall climatic factors such as rainfall and temperature. No striking correlation was found between distribution and gross climatic factors.

3) The larval microhabitats of the various species were investigated and found to differ in a number of respects. The most important difference between the various habitats was the length of time for which they were exposed to direct sunlight each day. The following approximate exposure times were recorded: L.intermedia, 1 hour; M.medialis, 4,5 hours; M.obscurus, 6 hours; S.longicornis, 7,5 hours and

C.lanceolatus, 11 hours.

4) The general sand surface temperatures in the field were correlated with the exposure of the habitats to direct sunlight. In all habitats, temperature gradients were present in the sand during the day. The upper layers of sand were warmer than the deeper layers. The daily rise in sand temperature (above ambient at 6 a.m.) at a depth of 1 cm. was about 20 hr°C/day in the habitat of L.intermedia, 80 hr°C/day for M.medialis, 100 hr°C/day for M. obscurus, 115 hr°C/day for S.longicornis and 130 hr°C/day for C.lanceolatus.

5) In pits which were exposed to direct sunlight the pit walls facing the sun were always warmer, whereas the pit bases were always cooler, than the surrounding surface sand.

6) The depth of soft surface sand differed in the different habitats. The larvae of S.longicornis were found in the deepest sand, while the larvae of C.lanceolatus were found in the shallowest sand. The habitats of the remaining species fell between these two extremes.

7) The upper lethal temperature limits of all species were investigated. Various exposure periods and relative humidities were used. The larvae survived

the following temperatures for a period of five hours at a relative humidity of 40%: L.intermedia, 41,4°C; M.medialis, 47,3°C; M.obscurus, 48,2°C; S.longicornis, 51,2°C and C.lanceolatus, 53,4°C. These lethal temperatures are correlated with the known habitats of the various species.

8) The upper lethal temperatures of ant-lion larvae differed at various times of the day. Maximum sensitivity to temperature was recorded at about dusk. The larvae of L.intermedia, however, did not exhibit this peak of temperature sensitivity.

9) All the ant-lion larvae were shown to possess a circadian activity rhythm with the peak of activity occurring at about dusk. The larvae of L.intermedia did not possess a marked circadian activity rhythm. The period of peak temperature sensitivity was shown to be closely linked to the normal circadian activity rhythm. Alterations in the activity rhythm brought about by a reversed light-dark regime or by constant light produced corresponding changes in the period of maximum temperature sensitivity.

10) The internal temperatures of the various species were measured with thermocouples which were inserted into the posterior end of the abdomen. At a relative humidity of 100% the internal temperature of all species was within 0,3°C of the ambient temperature.

At a relative humidity of 0% very slight evaporative cooling was observed in ant-lion larvae but no evaporative cooling was observed in the larvae of L.intermedia.

11) Evaporative cooling at low humidities did not enable the larvae of ant-lions and worm-lions to survive significantly higher temperatures, except for the larvae of M.medialis where it raised the lethal temperature by about 2°C.

12) The larvae of ant-lions and worm-lions showed a number of behavioural responses to temperature. The larvae of L.intermedia and M.medialis selected cool shady pit building sites, while the larvae of C.lanceolatus moved towards warm lighted areas. The larvae of M.obscurus and S.longicornis selected warm lighted areas at low sand temperatures and cool shaded areas at high sand temperatures.

13) Field and laboratory studies showed that the larvae were capable of orientating themselves within their pits in response to temperature gradients. At low sand temperatures the larvae selected the warmest sides of the pits, whereas at high sand temperatures they either moved to the cooler parts of the pits or withdrew entirely into the sand below their pits.

14) Downward movement of the larvae into the sand below their pits only took place in response to high surface sand temperatures. Large larvae migrated deeper into the sand than small larvae. The return of the larvae to the surface was found to be controlled by the circadian activity rhythm in the larvae of *M.obscurus*. Changes in the circadian activity rhythm produced corresponding changes in the time at which the larvae returned to the surface of the sand.

15) A study of the responses of the larvae to sand depth indicated that none of the species possessed the ability to select any particular depth of sand in which to construct their pits or lie in wait for their prey.

16) The upper temperature tolerances of the various species were found to range from about 34°C to about 42°C.

17) The water relations of the various species were investigated and all species were found to be extremely resistant to desiccation. The mean survival times at 0% relative humidity were as follows: *L.intermedia*, 24,5 days; *M.medialis*, 26,1 days; *M.obscurus*, 31,8 days; *S.longicornis*, 27,2 days and *C.lanceolatus*, 33,1 days.

18) Decreases in the original fresh weight of the larvae were used as a criterion of water loss. The larvae lost from 21% to 33% of their original weight at the time of death. The rate of water loss was found to be greatest during the first four to six days of the experiment when the larvae were very active. Water loss decreased shortly before death and increased again after the death of the larvae.

19) There was no evidence of evaporative cooling when the rates of water loss were compared at high and low temperatures.

20) There was no evidence of water uptake at high relative humidities.

21) Some aspects of the temperature and water relations of myrmeleontid and rhagionid larvae are discussed and compared with what is known about the temperature and water relations of desert dwelling arthropods.

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