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Temperature Tolerance and Predatory Strategy of Pit-Building Ant-Lion Larvae (Neuroptera: Myrmeleontidae)

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This study focuses on the nocturnal and diurnal temperature relations inside and around the pits of *Myrmeleon bore* pit-building ant-lion larvae living in unsheltered microhabitat and *Euroleon nostras* living in sheltered microhabitat. The larvae's potential hunting activity and prey handling phase of predation in relation to the temperature conditions were observed. Due to the structure of pitfalls and the thermal layers above and under the sand surface, the larvae must suffer less temperature fluctuation during the day than their environment. The role of the pitfall seems to be just as important in prey capturing as in temperature tolerance. This function of pits especially prevails in unsheltered microhabitats. In unsheltered microhabitats temperature influences the potential predator activity as well as the distribution of prey handling phase of predation in time. The potential hunting activity of larvae is not influenced by temperature in sheltered microhabitats, where their prey handling phase of predation depends mainly on the activity of prey species. It takes one year for both species to develop, but underdeveloped individuals of two-year life cycle can also be found. During the observation period, the chances of development for normally developed larvae living in unsheltered microhabitats proved far better than the chances for underdeveloped larvae due to the temperature. During their evolution, pit-building ant-lion larvae have strongly adapted themselves to extreme environmental factors physiologically and behaviourally as well.

Keywords: Pit-building ant-lion, predation, temperature tolerance.

Ant-lions are one of the most peculiar species of sandy areas. They are primarily known for their distinctive predatory strategy: the prey capturing pits they build on the loose surface. This unique predatory strategy was developed in adaptation to the special environmental conditions typical to sandy surfaces.

Sand is a formation consisting grains with a diameter of 0.2–2 mm, which directly allows precipitation to escape, so its surface dries up rapidly. The temperature of open sand surface exposed to direct solar radiation increases as rapidly as it cools down, so the fluctuates widely. These extremities of the precipitation and temperature prevailing on sand surfaces provide the living creatures with only limited life conditions, so the fauna of dry sandy stretches, physiologically and behaviourally adapted to those extreme environmental conditions (Wheeler, 1930).

On open sand surfaces extremely high temperature records were obtained: 84 °C in tropical zone, 78 °C in the Sahara, but surface temperature reached 74 °C even in temperate zone (Chapmann et al., 1926; Gepp and Hölzel, 1989). Since no living creature is able to endure such a high temperature, they usually dig themselves into the soil, run nocturnal life, or climb up on the plants to keep themselves far away from the hottest zone, the surface of the soil. According to several observations, insects leave the surface hotter than 50 °C so as to survive the very hot period, which is lethal to them (Cain, 1987; Kitching, 1984; Klein, 1982; Parker, 1930).

The ant-lion larvae appear to be exposed to the prevailing hot surface temperature. Ninety percentage of the species avoid open sand surfaces regarding their predatory strategy and build pitfalls on areas protected from direct sunshine, or do not build pits at all (Gepp and Hölzel, 1989). On the basis of predatory strategy, several types of species can be distinguished, as it can be seen the review of the subject by Wheeler (1930). The classification of the lifestyles of Central-European species was carried out by Gepp and Hölzel (1989) recently.

The relationship between the behaviour of ant-lions and the thermal conditions inside the pits was researched by several authors (Geiler, 1966; Green, 1955; Youthed, 1969). At the same time, the pit building location of the same species shows remarkable geographical variability. For example, *Myrmeleon formicarius* builds pits only in sheltered microhabitat in Hungary, while in Germany it thrives in unsheltered microhabitats (Yasseri and Parzefall, 1996).

The aim of this paper is to reveal the differences observed in the temperature tolerance and predatory strategies of pit-building ant-lion species living either in sheltered or unsheltered microhabitats.

Materials and Methods

The area of Duna-Dráva National Park (SW Hungary) contains the sandy stretches of Inner Somogy running alongside the River Dráva. Therefore, this observation was carried out within the framework of the nature protection survey of ant-lion fauna alongside the River Dráva, at Tótújfalu (UTM code: YL 08). Due to the annual precipitation of 600–700 mm (Marosi, 1990), this sandy area is naturally covered by woods, but owing to the landscape forming activity of man, on its surface juniper woodlands mixed with dry grasslands *(Festuco Corinepheretum – Juniperotosum)* have developed secondarily. Due to stock farming and sand mining certain parts of this grassland is continuously disturbed and it is in the early stage of succession. These areas, open sand stretches, abandoned opened sand mines provide excellent microhabitats for ant-lions.

During faunistical surveys (Ábrahám, 1995, 1998), seven ant-lion species were found in the national park. According to pit-making characteristics, the ant-lion larvae could be divided into four groups:

– Pit-building species in unsheltered microhabitat: *Myrmeleon inconspicuus**, *Myrmeleon bore**;
– Pit-building species in sheltered microhabitat: *Euroleon nostras**, *Myrmeleon formicarius;*
– Facultatively pit-building species in sheltered microhabitat: *Megistopus flavicornis**;
– Not pit-building species: *Creoleon plumbeus**, *Distoleon tetragrammicus.*

Since in the vicinity of Tótújfalu, only 5 ant-lion species were found (indicated by *), for the present investigation the two most abundant species were chosen. In unsheltered microhabitat the larvae of *Myrmeleon bore* (Tjeder, 1941) while in sheltered microhabitat the larvae of *Euroleon nostras* (Goeffroy in Fourcroy, 1785) occur in higher density. The pits of sheltered microhabitats were found in cavities of a sand-wall facing east.

During the sampling, the temperature was measured periodically, fifteen times throughout the day, using the electric TES 1310 digital thermometer [the heat sensitive bimetal part of the thermometer measured the temperature at the end (peak) of the detector other thermoelectrodes are able to read only the average temperature of an object consisting of several thermolayers by sensing the temperature of the whole surface of contact, therefore the type of the thermo-electrode is of high importance in correct data recording]. The temperatures were obtained at the surface and at heights of 5 and 200 cm above the sand surface, and at depths of 1, 2, 3, 4 and 5 cm below the surface, which equals the depth of the pits of ant-lion larvae. The temperature below the surface was measured 5 cm from the pit's edge. While measuring the temperature at the sand surface and below it, the temperature was simultaneously measured at the pit-base (pb), in the middle of the sunny side (fsp) and around the edge of the pit (pe) of the pit-building ant-lion larvae living in sheltered and unsheltered areas *(Fig. 1).* All the temperature records were repeated three times in each measuring places occasionally, and in the analysis the mean values of the data were used.

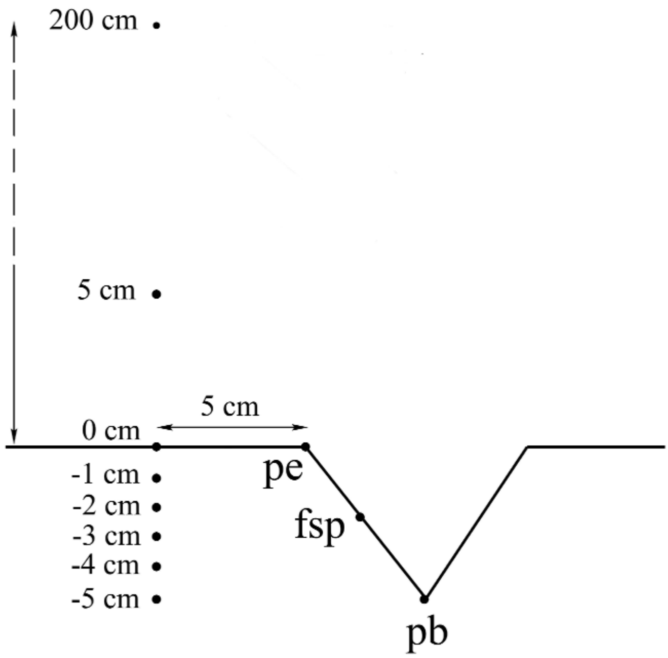

Fig. 1. Position of the measurement places in pit and its surrounding

In order to analyse the spatial relation of the temperature, infra photos were made by infrared camera about the temperature distribution in the pits of the pit-building ant-lion larvae. Besides the infrared photos can prove the accuracy of measurement made by thermometer.

During the temperature records, activity of the larvae was visually observed in 50 third instar pits in unsheltered microhabitats and 10 pits in sheltered microhabitats at every occasion of the observation. The percentile distribution of data demonstrates the typical correspondence between temperature and potential hunting activity.

The larval-stage was determined according to the pit diameter and body size. According to my previous observations and the relevant literature, the more developed larva builds bigger pit (Geiler, 1966; Griffiths, 1986; Kitching, 1984).

According to the daily rhythms of hunting activity three phases of predatory behaviour can be distinguished.

– The first is potential hunting activity phase of predation when larvae sit on the base of their pits waiting for the preys with open mandibles.
– The second phase of activity, if a larva it is sucking the captured prey. This will be referred as prey handling phase of predation ("handling time") (Griffiths, 1980; Matsura, 1986).
– The third phase is an inactive larva that draws back under the surface of the sand.

The sample series presented here was carried out on the 18–19th May 1997 from 6 h a.m. to 6 h a.m., when the sky was clear and the sand surface received direct rays of the sun throughout most of the day. The sun rose at 05.09 h and sat at 20.13 h.

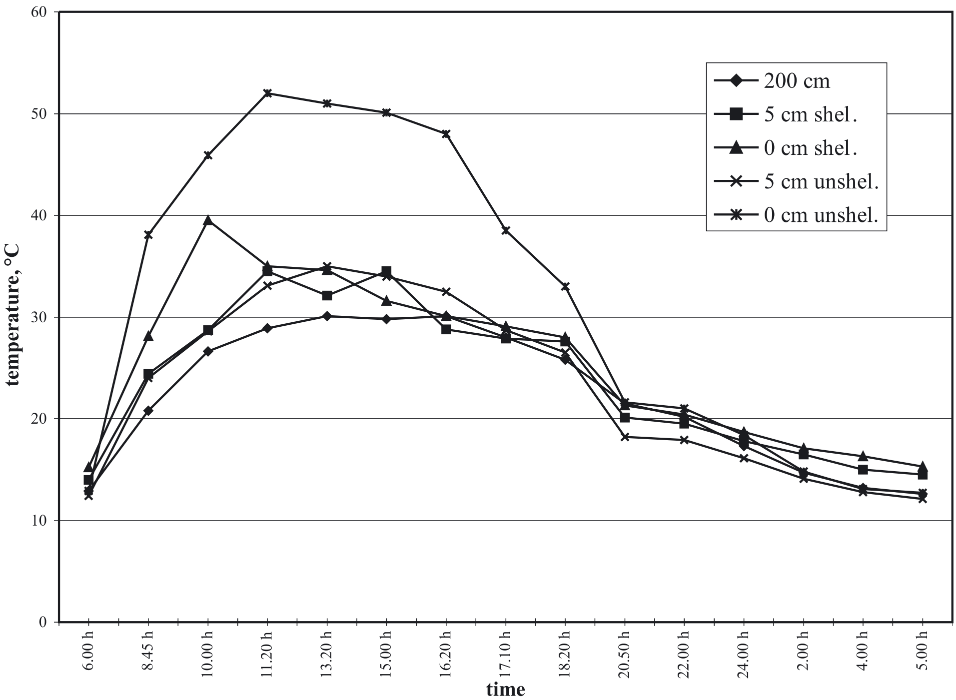

Fig. 2. Temperature distribution at heights of 200 cm, 5 cm and 0 cm in sheltered (shel.) and unsheltered (unshel.) microhabitats

It takes one year for both species to develop, but underdeveloped specimens of two-year life cycle can also be found (Ábrahám, 1995). The observed population in this study consisted of larvae of different age and development stage. The ant-lion larvae were in third instar stage with 85% of dominance.

However, the sample series were repeated for three times in each season (in April; at the end of May or early in June; in September) in order to record data from each development stages of the species.

Results

The result of the investigation is presented like a snapshot taken by a measurement series carried out on a typical day. During the observations, the minimum of the daily temperature was 12.9 °C at 06.00 a. m., the maximum was 30.1 °C at 13.20 p. m. *Figure 2* shows the daily variation of temperature relations. The thermal layers of the still air in the morning are clearly demonstrated by the figure: the air is cooler above the sand surface and at a height of 5 cm than at a height of 200 cm. The insolation after sunrise causes rapid increase in temperature above the surface of the soil and the temperature of the air equalises because of the air turbulence. During the diurnal period, until the decline of the radiation in the late afternoon, the temperature at a height of 5 cm above the surface is warmer than the temperature of the air at a height of 200 cm. During the night, the air temperature is gradually decreasing due to the back radiation of the ground. The temperature relations at a height of 200 cm are influenced by cold-warm wind and air turbulence above the surface although the temperature here also declines.

The regular daily temperature distribution in the air resulting from solar radiation can be modified by the shading effect of clouds. During this present examination, the Sun was covered by clouds for 30 min after 11.20 a. m. which had an impact on temperature distribution on the surface and sub-surface as well.

Due to excessive back radiation from the ground, the temperature relations in thermal layers formed under the sand surface are reversed after sunset *(Fig. 3):* at around 21.00 pm, the temperature measured at 5 cm below the surface proved to be the highest. The temperature variations between the surface and sub-surface gradually increased till dawn, when the surface heat radiation reversed the temperature distribution in depth.

In the vicinity of sheltered pits, the air temperature distribution shows a pattern rather different from that of open or unsheltered sand surfaces *(Fig. 2).*

At a height of 200 cm, the two microhabitats show no variations regarding temperature conditions. Since the distance between the two sampling sites was not exceeded 25 meters, the temperature readings with the same value are not shown separately in *Fig. 2.* At a height of 5 cm above the pits, the temperature fluctuation of sheltered microhabitats was influenced by site orientation, since there was no direct insolation after 11.20 a. m. due to the shading effect of the sand wall *(Fig. 2).* This effect was even more obvious in case of the surface temperature fluctuation. In sheltered microhabitats the highest daily temperature did not exceed 39.5 °C at the surface.

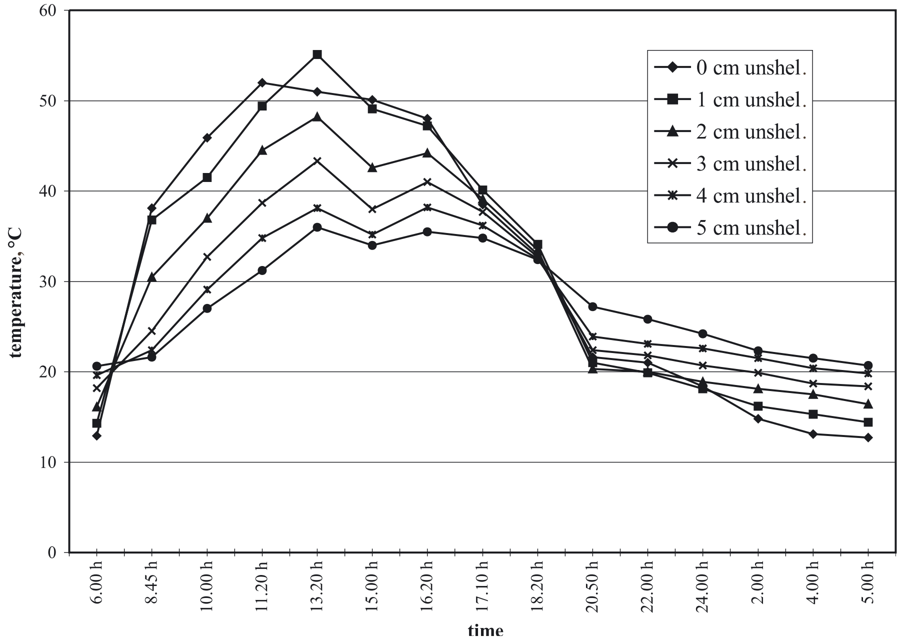

Fig. 3. Temperature distribution at depths between 0 and 5 cm in unsheltered (unshel.) microhabitats

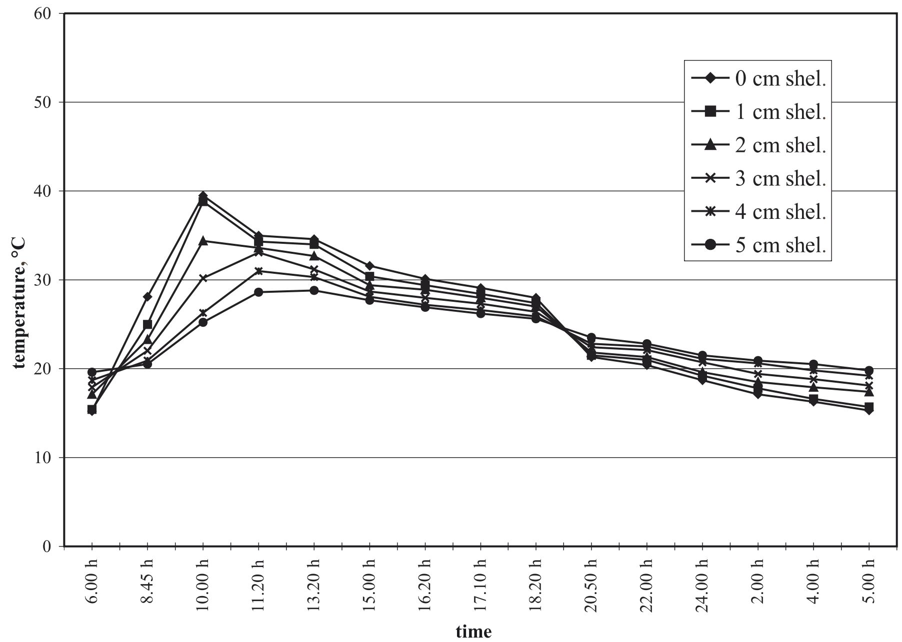

Fig. 4. Temperature distribution at depths between 0 and 5 cm in sheltered (shel.) microhabitats

The temperature distribution under the surface shows significant layer formation in sheltered microhabitat *(Fig. 4),* but its scale has never reached the differences measured in unsheltered microhabitats *(Fig. 3).* During the night, the inversion of sub-surface temperature distribution was also observed, though the decrease in temperature was more gradual than in unsheltered microhabitats, especially during the first half of the night. At 5:00 a. m., the temperature difference measured on the surface and at a depth of 5 cm was only 7.2 °C. As the sheltered pits were exposed to direct solar radiation, the temperature increased rapidly after sunrise on the sand surface.

Figure 5 shows the daily temperature fluctuation measured in pits of unsheltered microhabitats. The records obtained in pits slightly differ from the figures measured in sand-layers. The temperature of the pit's edges is slightly lower than that of the surface. In the morning, the temperature obtained at the slope of the pit directly facing the sun was lower than the surface temperature, but it became higher in the afternoon (max. 51.1 °C). Due to the angle of incident of the sun's rays and the shading effect of pit's edge, it was inexpedient to obtain more records after 17.00 p. m.

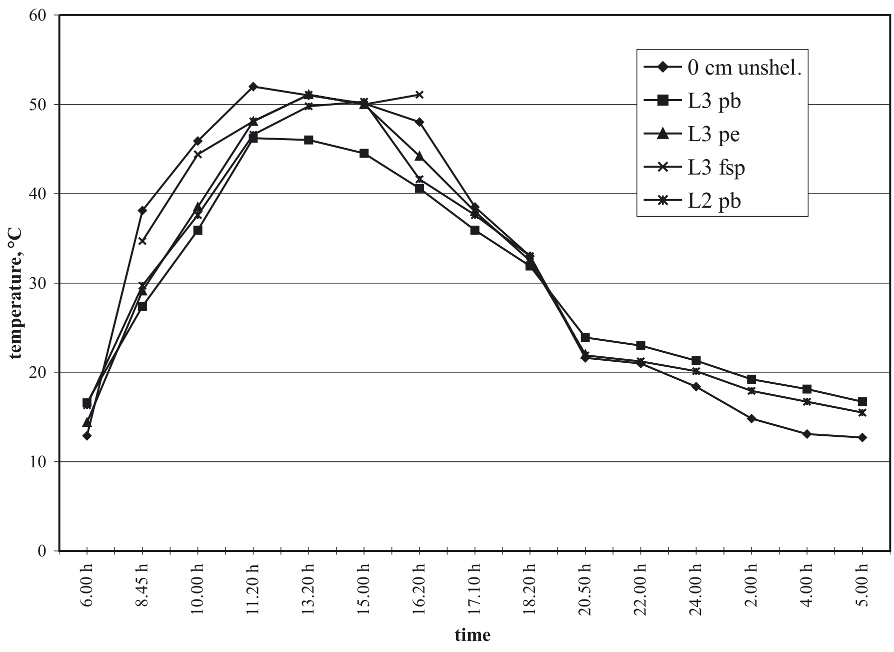

Fig. 5. Temperature distribution at the pit's edge (pe), on the slope facing the sun (fsp) and on the pit base of the second and third instar larvae (L3 pb, L2 pb) in unsheltered microhabitats

From the perspective of the observation, the temperature conditions of pit base proved to be the most interesting. The third instar larvae of *Myrmeleon bore* are situated at deeper layer than the second instar larvae, similar to those species which were studied previously, similarly larvae of other species (Griffiths, 1986; Kitching, 1984). The temperature at the pit base of third instar larvae proved to be lower than it was in the case of second instar larvae; the highest absolute difference was 5.8 °C at 15.00 p. m. Due to the back radiation from the ground at night, the temperature conditions of the base are similar to the surface temperature fluctuation, although it is considerably hotter at the base than on open surfaces. The smallest absolute difference between records was 4 °C measured at 5.00 a. m. On the other hand, the surface temperature was lower than the temperature obtained at the base before and after the insolation.

Figure 6 shows temperature measurements obtained in the case of third instar larvae of *Euroleon nostras.* Due to its eastern orientation, the pits of the sheltered microhabitat are exposed only to morning solar radiation, so we obtained only two measurements at the pit-slope facing the sun. Before the sunrise (6.00 a. m.) and following the afternoon decline of daily insolation (18.20 p. m.), the temperature at pit base is lower than on the surface.

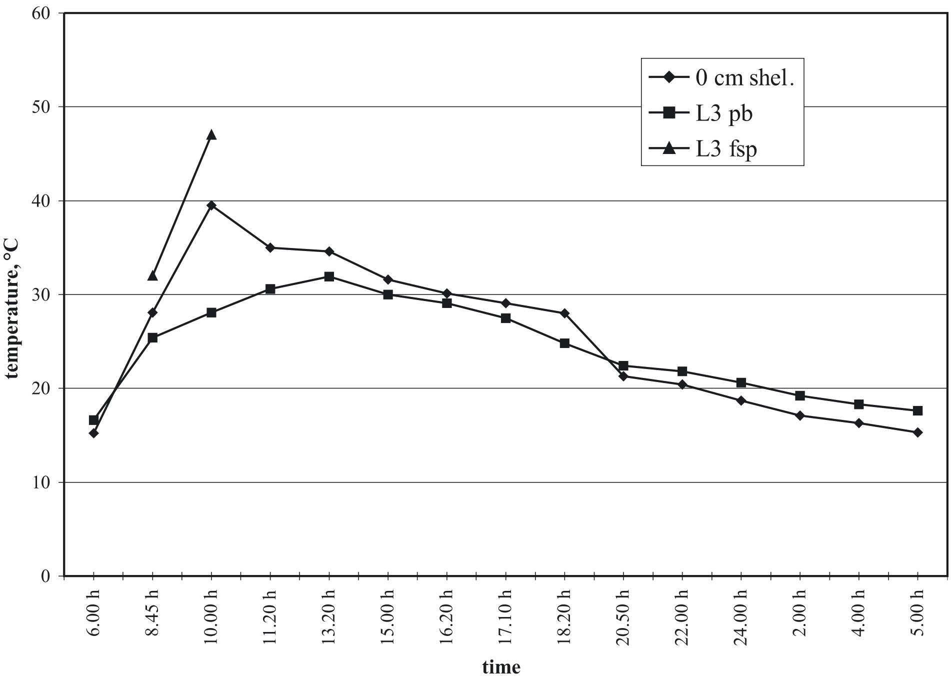

Fig. 6. Temperature distribution on the slope facing the sun (L3 fsp) and on the pit base of the third instar larvae (L3 pb) in sheltered microhabitats

According to the diagrams, there are two extreme temperature conditions regarding the daily fluctuation around the pits. The first case, when the temperature is considerably lower at the pit base than on the surface. This is demonstrated by the infrared photo *(Fig. 7),* which shows the close vicinity around a pit in unsheltered microhabitat. This kind of temperature distribution is typical during the daytime.

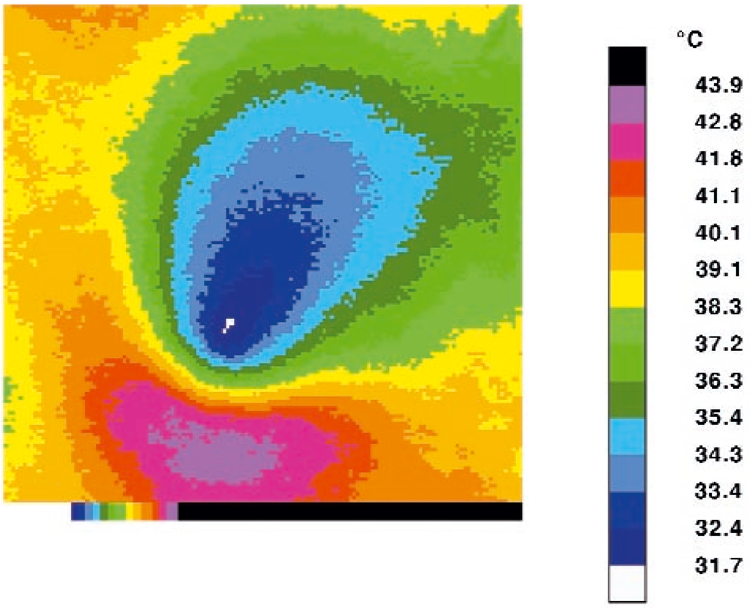

Fig. 7. Photo of temperature distribution in unsheltered microhabitat during diurnal period taken by infrared camera

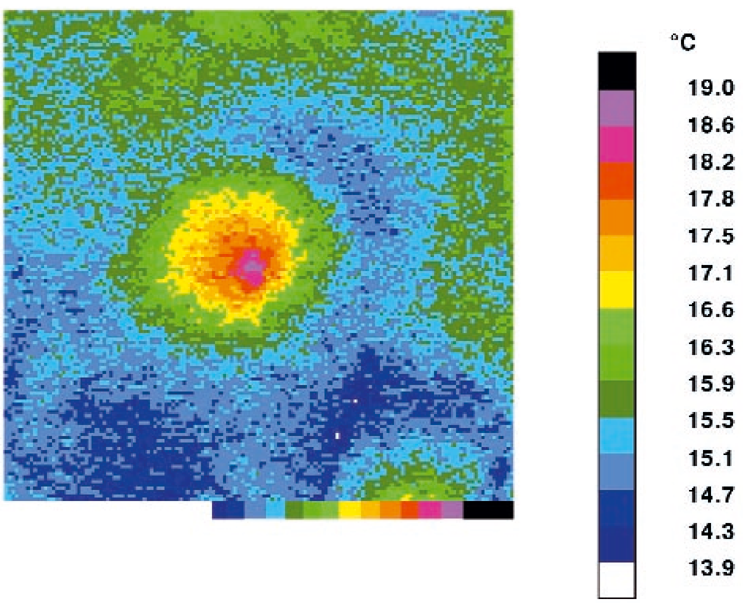

Fig. 8. Photo of temperature distribution in unsheltered microhabitat during nocturnal period taken by infrared camera

In the other case, the temperature patterns are the inverse of the previous ones. Therefore, from the evening hours until the beginning of insolation, the temperature is higher at the pit base than on the surface *(Fig. 8)*. An additional proof is provided by another observation: the dew precipitating on sand surface and plants, makes the sand surface wet except for the pits and their surroundings, since these locations emanates the heat of deeper sand layers which does not allow vapour to form precipitation.

The predatory behaviour was easily observed by eye.

The larvae of *Myrmeleon bore (Fig. 9)* were apparently inactive during the hottest period of the day (11.20–16.20), when they retreated underneath the sand surface. This tiny sand pile provides the inactive individuals with additional insolation. During the night, higher temperature in the deeper sand layers enables the ant-lions to maintain its potential hunting activity completely. The prey handling phase of predation, just like the potential hunting activity, culminates twice a day, following the daily temperature fluctuation in general. With the increase of insolation, the prey animals become active on the surface, then in the noon hours they either leave the overheated surface, or they hide. Ant-lions reach the daily peak of the prey consumption in the late afternoon, early evening hours, when the prey species become active again and, in most of the cases, are captured as well.

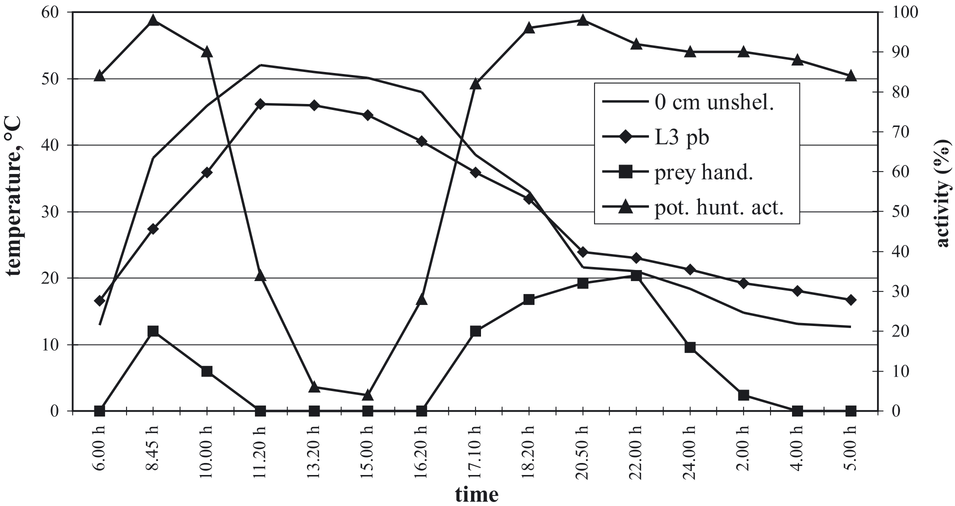

Fig. 9. Distribution of potential hunting activity (pot. hunt. act.) and prey handling phase of predation (prey hand.) relating to time in unsheltered microhabitats

In case of *Euroleon nostras,* the larvae sit on the base of their pits with open mandibles and wait for the prey to fall into the pit all day long. So they always maintain their potential hunting activity *(Fig. 10),* irrespective of the daily temperature fluctuation. However, their prey handling phase of predation also culminates twice a day: once during the morning hours, for the second time in the late afternoon and evening hours. The daily fluctuation of temperature does not seem to influence the potential hunting activity, therefore the daily prey consumption solely depends on the movement of the potential prey species (what makes them to fall a victim to ant-lion larvae). The temperature conditions and the environmental circumstances are more balanced for the development of the larvae of *Euroleon nostras* living in sheltered areas. On the other hand, the prey handling frequency is only one fourth of *Myrmeleon bore* living in unsheltered microhabitat.

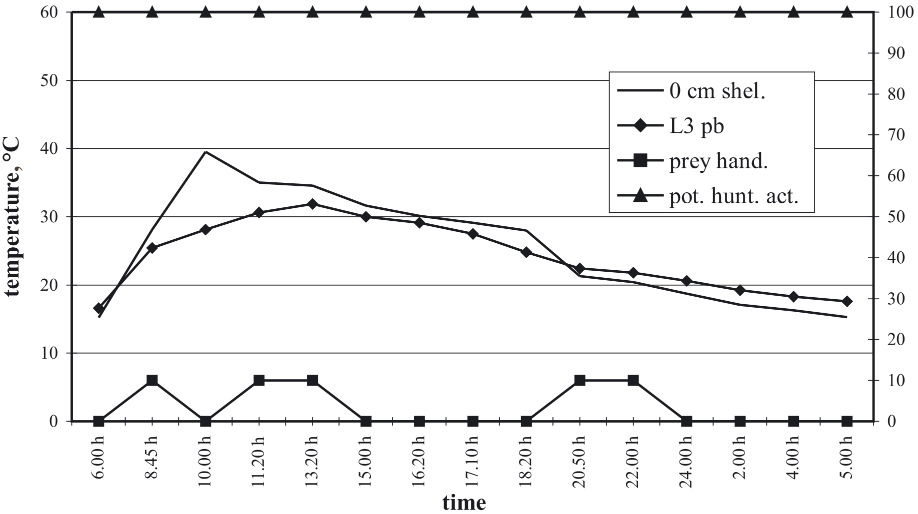

Fig. 10. Distribution of potential hunting activity (pot. hunt. act.) and prey handling phase of predation (prey hand.) relating to time in sheltered microhabitats

Discussion

Based on morphological and physiological investigations (Gepp and Hölzel, 1989), it can be said that ant-lions have several characteristics that help them cope with extreme temperature conditions. One of these characteristics is the temperature optimum of the digestive enzymes, lipase and esterase, of *Euroleon nostras* which is 59 °C (Bongers and Koch, 1981). The ant-lion larvae's metabolical rate is twice lower than the spiders' also low metabolical rate (Lucas, 1985), although both of them are sit and wait predators.

Since ant-lion larvae suck on the body fluid of their prey and they do not consume any solid food. They eliminate their faeces at the end of their larval life, during pupation (Gepp and Hölzel, 1989). This degeneration of a bodily organ is also one of those results of the evolution that helps the balance of water in the larvae.

During the day, the pitfalls in unsheltered microhabitats are significantly colder than the surface temperature. During nocturnal period, the pitfalls are warmer than the sand surface (Geiler, 1966; Green, 1955). This phenomenon enables the ant-lion larvae to live under less extreme temperature condition than their environment. Beside their prey capturing function, the pitfalls perhaps play an important role in the temprerature tolerance of the ant-lion larvae, as it was noted by Gepp and Hölzel (1989) as well. This function of unsheltered habitats is promoted by shading effect of the edge of the pit (Gepp and Hölzel, 1989) and the fact that there is a greater probability of the larvae staying on that side of the pit which is not exposed to direct sunrays (Geiler, 1966).

It was verified by several investigations and observations (Green, 1955; Griffiths, 1980; Kitching, 1984; Matsura, 1986) that ant-lion species living in different areas reduce their potencial hunting activity above 40 °C.

According to Geiler's observation (1966), on an overcast day, the temperature relations of an unsheltered microhabitat are similar to those of a sheltered area. The feeding behaviour of the ant-lion larvae living in unsheltered microhabitats is, therefore, determined by the daily rhythm of the activity of their prey animals.

After observing the relationship between the potential hunting activity and the temperature, it can be concluded, that the habitat characteristics of ant-lion larvae living in sheltered and unsheltered microhabitats are different in many respects.

The observation presented above suggests that *Euroleon nostras* along with other pit-building species living in sheltered microhabitats, prefer areas with more balanced temperature conditions (Lucas, 1989) but with less food supply. On the other hand, species living in unsheltered microhabitat, including *Myrmeleon bore,* can be found in areas of extreme temperature conditions but which is abundant in food. The advantages and disadvantages of the two kinds of predatory behaviour are complementary in time and they are influenced by several environmental factors and interactions.

During the year of observation, the sampling series carried out at different periods provided us with information especially on *Myrmeleon bore,* and thereby on the development of other species living in unsheltered microhabitats.

The one-year life cycle of *Myrmeleon bore* is also an advantage, since they are in pupation in June, the hottest period of the summer. The imagoes are emerging in July, and the first instar larvae appear in the middle of August, when the heat of the sand surface temperature is starting to decline. The chances of survival for the second instar larvae at the peak of the summer are low. Due to the temperature and precipitation distribution in autumn, when the ground surface is ideal for development, the chances of survival of the same larvae in their third instar stage are also low, as compared to the larvae in first and second instar stage which dig themselves lower than those. At the same time, this disadvantage of the third instar larvae is compensated by the bigger size of the capturing pitfall, since with a bigger pit the larvae are capable to capture more prey (Griffiths, 1986; Matsura, 1986).

In sheltered microhabitats the age of the larvae of different stages are distributed more evenly than in unsheltered microhabitats.

According to the results of anatomical and physiological observations mentioned above and because of the pitfall as a prey capturing tool and its temperature tolerance function, the ant-lions can be considered very specialised species in the evolution. From behavioural point of view, they adopted themselves to extreme environmental circumstances remarkably well.

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