1972 – ACTA UNIVERSITATIS PALACKIANAE OLOMUCENSIS
FACULTAS RERUM NATURALIUM – TOM 39

Katedra zoologie a antropologie přírodovědecké fakulty University Palackého v Olomouci
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THE EMERGENCE OF BURYING BEETLES FROM THE SOIL AFTER THEIR METAMORPHOSIS AND ITS DEPENDENCE ON DAY LIGHT *(COL. SILPHIDAE)*

VÝSTUP HROBAŘÍKŮ Z PŮDY PO PROMĚNĚ A JEHO VAZBA NA DENNÍ SVĚTLO *(COL. SILPHIDAE)*

NADĚŽDA ŠPICAROVÁ

(Předloženo dne 15. srpna 1971)

INTRODUCTION

We find many works in literature which deal with the study of rhythms in the last phases of the metamorphosis of holometabolous insects and the dependence of the emergence of imagoes from pupae upon a certain time of the day. These papers predominantly summarize the results of laboratory experiments and the separate orders of insects are not proportionately represented. It is understandable, because every author chooses for such experiments such species of insects, which have a short life cycle without diapausing generations and can be propagated in large numbers under laboratory conditions, or species, in which we can without difficulties obtain a great number of larvae in a more progressed larval state of development under natural conditions. From the following enumeration of papers it follows that these requirements of the experimentator are best met by the *Diptera* or *Lepidoptera.* So e. g. Barnes (1930), Kalmus (1935, 1940), Phillipp (1938), Lewis and Bletchly (1943), Mori (1949), Pittendrigh (1954, 1966), and Remmert chose *Diptera* for their experiments, Scott (1936), Götz (1950, 1951), Moriarty (1959) experimented with *Lepidoptera* and Paarmann and Thiele (1968) focused their attention on *Coleoptera.* It is also remarkable that three of the quoted authors experimented with some species of the genus *Drosophila Fallén.*

Beetles can usually be bred only with difficulties or the breeding of separate species has not yet been methodically worked out. As the author of the present paper had obtained good experiences with the breeding of the species *Necrophorus vespillo (L.)* — Špicarová (1969), she applied them also to the study of diurnal activity, which she investigated in adults leaving the soil medium after their metamorphosis.

MATERIAL AND METHODS

The experimental material was gained by the breeding of burying beetles of the species *Necrophorus vespillo* in isolators under natural conditions. The author started the breeding at the end of May 1970. Each of the isolated parental couple got 80 gr of meat. When the larvae became pupae and the pupae were sufficiently ripe the author brought them with the isolators into the laboratory and started with the experiments.

The pupae for the second series of experiments were obtained in a similar way. After they had been brought into the laboratory on September 18th 1970 the author prepared the conditions for further experiments.

The methods applied in both experimental blocks were somewhat different and therefore the results obtained were somewhat different too.

In the first series of experiments the author hung the isolators containing the soil and pupae of the burying beetles in earth cradles into a transparent polyethylene foil on a stand in such a way that the burying beetles could creep over the edge of the glass part of the isolator from where they fell into a spacious funnel made of glass and through its lower narrowed part into an automatic trap. In it a clockwork was driving a carrying tub with 13 tanks in such a way that each of them remained for 2 hours under the entrance hole (the 13th tank is used in case the trap has run down and is not in use anymore). A more detailed description of the automatic trap is to be found in the paper of B. Novák (1971); At the same time the author refers to the joined photograph (Fig. 1) which presents the proceedings in the second series of experiments in which the author has put the isolators with the pupae into a bigger cylinder made of wire-netting, so that the lower part of the isolator (also of wire-netting) and almost its whole upper part of glass could be covered with a layer of soil about 2.5 cm thick. Thus a quick drying out of the isolator was prevented. Water permeated through the soil up to the cradles with pupae. From time to time the author moistened the soil from above, around the protruding glass part of the isolator. Fig. 1 shows how the burying beetles crept from the isolator into the automatic trap, the content of which has been taken out in the photograph. Fixed to the lid of the trap on its bottom under the entrance hole there was a funnel made of metal which directed the falling beetles to the corresponding collecting tank. On the bottom of the collecting tank the author put moistened cotton-wool.

In the first series of experiments from July 13th to 24th there were on the whole 5 isolators and in each of them the offsprings of one parental couple; i. e. also 5 automatic traps. The parental couples consisted of individuals of the same agegroup. The traps were checked and set every day at 10 o'clock in the morning. The room-temperature was daily measured in periodical intervals.

The second series of experiments from September 24th to October 7th included only 4 isolators with further filial generations of burying beetles, i. e. only 4 automatic traps were used. The author recorded the changes and set the traps at 10 o'clock every day.

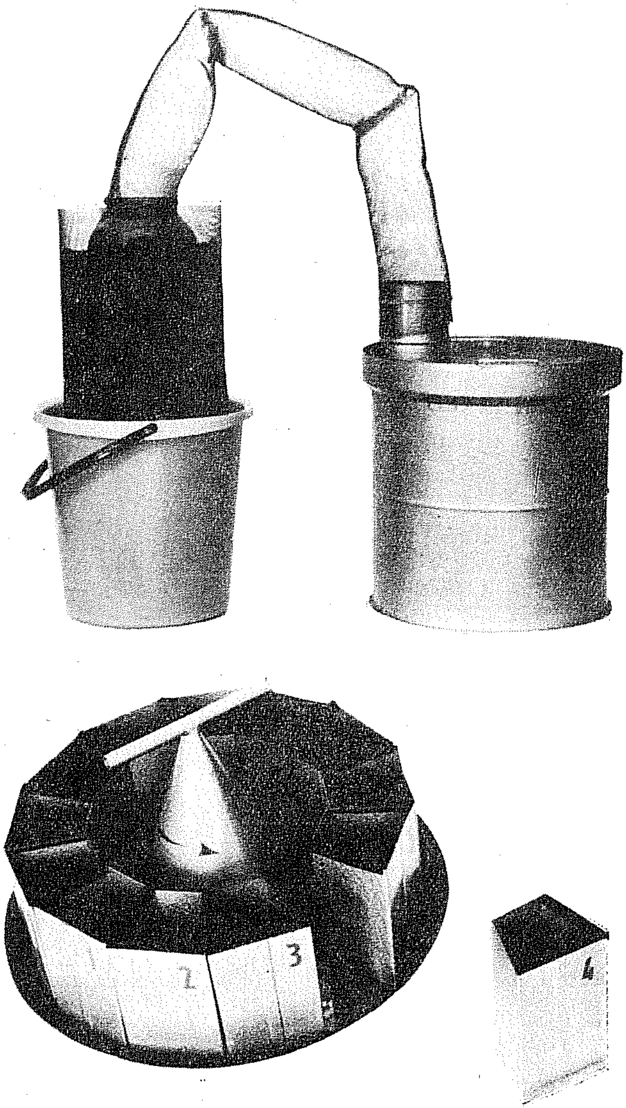

Fig. 1 — Isolator with pupae of burying beetles connected with the automatic trap by a corridor of wire-netting. Below the inside of the automatic trap (the carrying tub with collecting tanks; in the middle of the tub the driving clockwork).

RESULTS

In the first series of experiments the total number of 107 imagoes (52 males and 55 females) crept over from the isolator into the automatic trap. The data in Table

Table 1 — Results of the first series of experiments

N. vespillo	10 — 12	12 — 14	14 — 16	16 — 18	18 — 20	20 — 22	22 — 24	24 — 02	02 — 04	04 — 06	06 — 08	08 — 10	On the whole
1970	♂♂ ♀♀	♂♂ ♀♀	♂♂ ♀♀	♂♂ ♀♀	♂♂ ♀♀	♂♂ ♀♀	♂♂ ♀♀	♂♂ ♀♀	♂♂ ♀♀	♂♂ ♀♀	♂♂ ♀♀	♂♂ ♀♀	♂♂ ♀♀
13. VII.	– – –	– – –	– – –	– – –	1 1 –	– – –	– – –	– – –	– – –	– – –	– – –	– – –	1 1 –
14.	2 1 1	2 2 –	– – –	– – –	– – –	– – –	– – –	– – –	– – –	– – –	– – –	– – –	4 3 1
15.	– – –	– – –	– – –	6 3 3	3 1 2	1 1 –	3 2 1	– – –	1 1 –	2 2 –	5 2 3	6 2 4	27 14 13
16.	3 1 2	1 – 1	4 1 3	4 1 3	2 – 2	1 – 1	– – –	– – –	1 1 –	2 2 –	1 1 –	2 – 2	21 7 14
17.	1 1 –	1 1 –	2 1 1	1 – 1	3 3 –	– – –	– – –	2 – 2	1 – 1	2 1 1	2 1 1	3 1 2	18 9 9
18.	1 1 –	3 3 –	2 – 2	1 1 –	1 – 1	1 – 1	– – –	– – –	– – –	– – –	– – –	– – –	9 5 4
19.	– – –	2 2 –	– – –	– – –	1 1 –	2 1 1	– – –	1 – 1	– – –	1 – 1	– – –	– – –	7 4 3
20.	1 – 1	1 – 1	1 1 –	3 2 1	1 – 1	– – –	1 1 –	– – –	– – –	1 1 –	– – –	– – –	9 5 4

21.	– 1 1	– – –	2 2 –	1 1 –	– – –	1 1 –	– – –	– – –	– – –	– – –	– – –	– – –	4 5 1
22.	– – –	– – –	– – –	– – –	– 3 3	– – –	– – –	– – –	– – –	– 1 1	– – –	– – –	– 4 4
23.	– – –	– – –	– – –	– – –	– – –	– – –	– – –	– – –	– 1 1	– – –	– – –	– – –	– 1 1
24. VII.	– – –	– – –	– – –	– – –	– 1 1	– – –	– – –	– – –	– – –	– – –	– – –	– – –	– 1 1
On the whole	4 9 5	8 10 2	5 11 6	8 16 8	6 16 10	3 6 3	3 4 1	– 3 3	2 4 2	6 9 3	4 8 4	3 11 8	52 107 55

Table 2 — Results of the second series of experiments

N. vespillo 1970	10 — 12 ♂♂ ♀♀	12 — 14 ♂♂ ♀♀	14 — 16 ♂♂ ♀♀	16 — 18 ♂♂ ♀♀	18 — 20 ♂♂ ♀♀	20 — 22 ♂♂ ♀♀	22 — 24 ♂♂ ♀♀	24 — 02 ♂♂ ♀♀	02 — 04 ♂♂ ♀♀	04 — 06 ♂♂ ♀♀	06 — 08 ♂♂ ♀♀	08 — 10 ♂♂ ♀♀	On the whole ♂♂ ♀♀
24. IX.	– – –	1 1 –	– – –	– – –	– – –	– – –	– – –	– – –	– – –	– – –	– – –	– – –	1 1 –
25.	– – –	– – –	– – –	– – –	– – –	– – –	– – –	– – –	– – –	– – –	– – –	– – –	– – –
26.	1 1 –	1 1 –	– – –	1 1 –	– – –	– – –	– – –	– – –	– – –	– – –	– – –	– – –	3 3 –
27.	– – –	3 3 –	1 1 –	1 – 1	– – –	– – –	– – –	– – –	– – –	– – –	– – –	– – –	5 4 1
28.	1 1 –	5 2 3	4 3 1	– – –	– – –	– – –	– – –	– – –	– – –	– – –	3 2 1	8 5 3	21 13 8
29.	13 7 6	15 6 9	5 3 2	7 3 4	1 1 –	– – –	– – –	– – –	– – –	– – –	1 – 1	– – –	42 20 22
30. IX.	10 5 5	1 1 –	2 – 2	2 1 1	1 – 1	– – –	– – –	– – –	– – –	1 – 1	– – –	1 1 –	18 8 10
1. X.	1 – 1	1 1 –	4 1 3	1 1 –	– – –	– – –	– – –	– – –	– – –	– – –	– – –	2 – 2	9 3 6

2.	2 4 2	7 9 2	1 1 –	– – –	– – –	– – –	– – –	– – –	– – –	– – –	– – –	– – –	10 14 4
3.	– – –	1 1 –	– – –	– – –	– – –	– – –	– – –	– – –	– – –	– – –	– – –	– – –	1 1 –
4.	– – –	– – –	– – –	– – –	– – –	– – –	– – –	– – –	– – –	– – –	– – –	– – –	– – –
5.	– – –	1 1 –	– – –	– – –	– – –	– – –	– – –	– – –	– – –	– – –	– – –	– – –	1 1 –
6.	1 1 –	– – –	– – –	– – –	– – –	– – –	– – –	– – –	– – –	– – –	– – –	– – –	1 1 –
7. X.	– – –	– – –	– – –	– – –	– – –	– – –	– – –	– – –	– – –	– – –	– – –	– – –	– – –
On the whole	17 31 14	24 38 14	9 17 8	6 12 6	1 2 1	– – –	– – –	– – –	– – –	– 1 1	2 4 2	6 11 5	65 116 51

1 and the graph in Fig. 2 show a considerable interfilial dispersion in the emergence of burying beetles from the soil; a dispersion seen within 24 hours, as well as a dispersion in the interval from July 13th when the first individual left the isolator to July 24th when the last adult fell into the trap. In spite of that it is obvious both from the Table and the graph that the majority of burying beetles emerged from

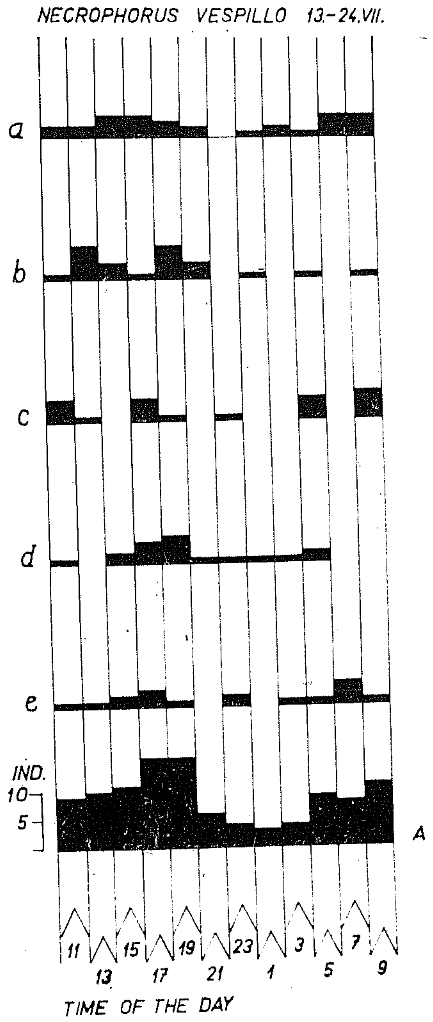

Fig. 2 — Graphical illustration of the emergence of burying beetles from the separate isolators in dependence upon a certain time of the day; a, b, c, d, e = the offsprings of the separate parental couples; A = set of ♂♂ and ♀♀ from all isolators. Below the two hours'time intervals.

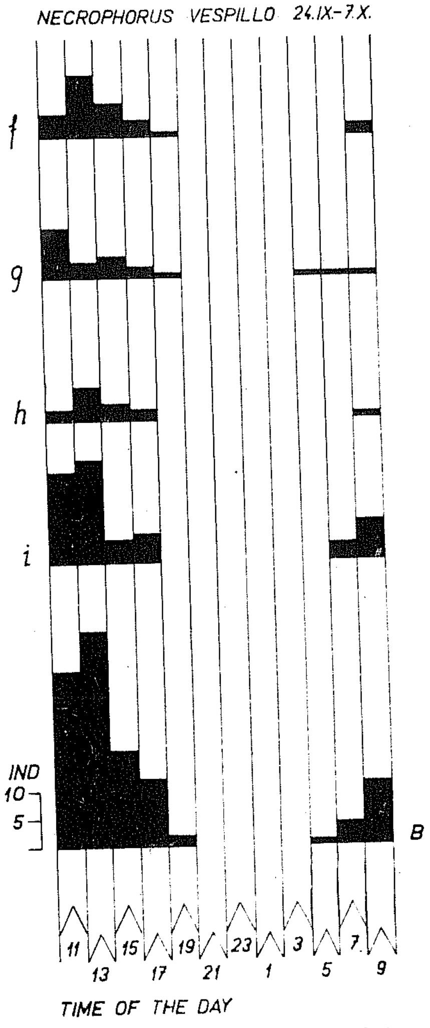

Fig. 3 — Graphical illustration of the emergence from the separate isolators in dependence upon a certain time of the day; f, g, h, i = the offsprings of the separate parental couples; B = the set of ♂♂ and ♀♀ from all isolators. Below the two hours' time intervals.

the soil by daylight and only a small number by night, and that there was an escape in masses from the soil on July 15th which continued to be very intensive during the next two days.

The results of the second series of experiments are unambiguous. The relation between the emergence of burying beetles from the soil and daylight is much more remarkable. On the whole 116 individuals (65 males and 51 females) crept through the corridors into the automatic traps. Table 2 and the graph in Fig. 3 did not record a single adult in the collecting tanks which would have fallen into the trap between 8 p.m. and 4 a.m. The greatest number of imagoes had left the soil of the isolators between noon and 2 p. m. and only one single adult in the interval from 4 a.m. to 6 a.m., and only 2 individuals from 6 p.m. to 8 p.m.. If we follow the time dispersion in the emergence of burying beetles from the first imago on September 24th to the last imago on October 6th, we get a similar picture as in the first experimental series. The summit was reached on September the 29th and also on the day before and on the next day the activity of burying beetles was relatively high if we evaluate it according to the number of individuals which emerged during the other days of the experiments.

If we consider only the offsprings of separate parental couples, the variation range of dispersion (intrafilial dispersion) from the first to the last individual is smaller. It is evident from Tables 3 and 4, in which the isolators with the offsprings of separate parental couples are denoted with small letters of the alphabet. In the Tables are also given the maximal temperatures of the day.

Table 3 – The time dispersion in the emergence of imagoes of *Necrophorus vespillo* from the soil in the first series of experiments.

Isolator	July												On the whole
	13.	14.	15.	16.	17.	18.	19.	20.	21.	22.	23.	24.	
a	–	2	13	12	2	–	–	–	–	–	–	–	29
b	–	–	–	1	7	8	5	2	–	–	–	–	23
c	–	2	8	6	3	–	–	1	–	–	–	–	20
d	–	–	–	–	–	1	1	6	4	4	1	1	18
e	1	–	6	2	6	–	1	–	1	–	–	–	17
On the whole	1	4	27	21	18	9	7	9	5	4	1	1	107
Temperature °C	28	28	25.5	25	23.5	22.5	21	21	20.5	21	22.5	23.5	

In the first series of experiments (Table 3) the room temperature was at the beginning higher. Therefore with greatest probability the majority of individuals leaves the soil on the second or third day if reckoned from the moment when the first adult appeared in the trap. This is demonstrated by the values obtained in the separate isolators if we follow them every day. In the following experiments (Table 4) the burying beetles left the soil in greater number at lower room temperature, generally on the fourth or fifth day. In those days the room with isolators was heated up a little and the temperature reached the maximum of 24.5° C.

Table 4 – The time dispersion in the emergence of imagoes of *Necrophorus vespillo* from the soil in the second series of experiments.

Isolator	September							October							On the whole
	24.	25.	26.	27.	28.	29.	30.	1.	2.	3.	4.	5.	6.	7.	
f	–	–	–	–	–	1	6	7	11	1	–	1	–	–	27
g	–	–	–	2	–	7	7	2	3	–	–	–	1	–	22
h	1	–	1	1	5	5	1	–	–	–	–	–	–	–	14
i	–	–	2	2	16	29	4	–	–	–	–	–	–	–	53
On the whole	1	–	3	5	21	42	18	9	14	1	–	1	1	–	116
Temperature °C	22.5	19	18	17	24.5	23	22	22	22.5	19.5	18	22	23.5	24	

DISCUSSION

From the literature given above and to which the author is going to refer again in the present discussion it is evident that the final phases of the metamorphosis of holometabolous insects are very often dependent on the diurnal photoperiod and less upon the daily variability of temperature or even on other conditions of the environment.

So e.g. Barnes (1930) examined several species of the *Cecidomyidae* family and found that the separate species emerged from their pupae at a different time of the day, the males usually with a small start before the females, further that there were also seasonal differences with regard to the day rhythm of emergence, that the photoperiod worked as a synchronizing factor and that females were more sensitive to the effects of exogenic factors as males. Kalmus (1935) found in the species *Drosophila melanogaster (Meigen)* a dependence of the emerging of individuals from the pupae upon the photoperiod and introduced the terms »autochronic« and

»allochronic« functions (the former proceed in their own speed which is independent on the conditions of the environment, the latter on the contrary depend upon the environmental conditions). The same author (1940) has shown that the majority of fruit-flies emerged from their pupae under normal light conditions in the hours preceding the sunrise, that they kept this time of day even in the dark and were not substantially influenced by temperature. In individuals which have been bred in the dark the mentioned diurnal rhythm of emerging from pupae can even be called forth by a photoperiod of one single day. The dependence of the emergence from the pupae in fruit-flies on the alternation of light and dark is thus according to Kalmus obvious. Phillipp (1938) found that *Chironomus thummi Kieffer* emerge exclusively during daylight, mostly between noon and 4 p.m. (in some cases the daily curve had two summits one before noon and one in the afternoon). According to this author the emerging of *Chironomus thummi* depends upon the alternation of light and dark and not upon the oscillations of temperature or on the changing contents of oxygen in water. The diurnal rhythm of the emergence from the pupae of the dung-fly-*Scatophaga (L.)* was studied by Lewis and Bletchly (1943). They also found a dependence of the emergence upon the photoperiod. The dung-flies get in greatest numbers out from the pupae between 9 a. m. and 2 p. m. The suggested protogynia has no reference to the diurnal rhythm of the emergence from the pupae which is inherited and is not influenced by temperature; the warmth factor plays a greater rôle only seasonally. Mori (1949) has hinted at the differences between the diurnal rhythms in mutants of the fruit-fly. Pittendrigh (1954) experimented with fruit-flies of the species *Drosophila pseudoobscura Sturtevant* and found an endogenic biological rhythm of emergence (»clock system«) which did not depend upon the diurnal changes of temperature. The author criticizes the conclusions of Kalmus quoted above. In another paper Pittendrigh (1966) has shown that the dispersion of emergence differed in imagoes of the same species in different photoperiods; it was greater during an extremely long or short light phase than at the more natural photoperiod. We constantly observe two summits of the curve separated from each other by an interval in which the emergence from pupae did not take place. Remmert (1955) experimented with the midge of the species *Pseudosmittia arenaria*. He suggests not to use the term »diurnal rhythm of emergence«, but to denote it more accurately »the emergence dependent upon a certain part of the day«. The dependence of the emergence of adults from the pupae upon the light phase was thus also observed by this author in the quoted species of midge. The greatest number of individuals get out of the pupae 6—8 hours since the beginning of the light cycle of the day. In continuous dark the midges do not emerge, in continuous light the emergence is dispersed all over the cycle of 24 hours. The relation of the maximum to the initiation of the light phase is obvious. Temperature alone or only the trophic factor without light does not influence the diurnal dependence of emergence quoted above.

In the experiments of Scott (1936) the imagoes of the flour-moth *Ephestia* *kühniella (Scott)* - emerged from the pupae in the afternoon with the maximum between 5 p.m. and 6 p.m. The summit depended upon the diurnal cycle of temperature in such a way that it set in after the drop of temperature. The experiments have shown that the relation between the emergence and the determined day time was hereditary; the light of a certain intensity inhibited the flour-moth. Götz (1950) found that the vine-moth - *Sparganothis pilleriana (Schiff.)* emerges from the pupae especially between 8 a.m. and 9 a.m., much less during the day and then again in a greater number between 8 p.m. and 9.p.m., i.e. his metamorphosis into an imago is characterized by a curve with two summits. Moriarty (1959) experimented with the flour-moth similarly as Scott. At different photoperiods - (even extreme ones) his imagoes emerged in greatest numbers in about 8 hours since the beginning of the light phase.

Paarmann and Thiele (1968) emphasized that the *Carabidae* become pupae in the soil and that the freshly emerged bugs stay for several days in earth cradles. That is why daylight cannot influence the pupae in the soil. Any kind of rhythm in the emerging from the pupae would thus hardly be of any adaptation importance. Only with the change of the endogeic way of life into the epigeic one, i. e. as soon as the imago emerges to the surface of the earth, light gains in importance as the inducer of diurnal rhythmical phenomena even in the *Carabidae*.

The same could be said about burying beetles. Yet their emergence from the soil remarkably depends upon the light phase and simultaneously upon the temperature cycle, the influence of which is considerable in the uppermost layers of the soil.

As the author has stressed in the previous chapter the imagoes of the species *Necrophorus vespillo* come out of the soil by daylight shortly after having left their pupae and they are most active in the first hours of the afternoon, when the temperature of the day reaches its maximum. This fact shows that even their feeding activity is probably bound to light and that we should denote this species as a day species and not as a dusk or even night species. Captures of imagoes in automatic traps under outdoor conditions support this opinion as well. At the same time it must be stressed that the higher temperatures are more favourable for the leaving of the soil in masses than lower ones.

As their is a certain diurnal rhythm according to which the burying beetles *Necrophorus vespillo (L.)* leave the soil shortly after having emerged from the pupae, we must also reckon with a time inducer of this rhythm (»Zeitgeber«) as described by Aschoff (1954). The circumstances given above suggest that the daily cycle of soil temperature probably synchronizes even the rhythm of the emerging of imagoes that is even the final phase of the metamorphosis accompanied by the emerging of imagoes to the surface of the soil. If it is not the case, the daily fluctuations of temperature and the photoperiod may operate as synchronizers as soon as the individuals approach the soil surface after their cuticle has become fully developed. If the emergence of burying beetles from the soil depends upon daylight and is most intensive in the first hours after noon, when the temperature of the air and soil reaches its maximum, there are hardly any other abiotic factors and their daily cyclic changes which could be of greater importance for the synchronization of the periodic emergence of burying beetles from the soil after their metamorphosis.

The imagoes usually leave in the isolator a system of corridors which enables an easy vertical movement. It may be that the imagoes having left the cradles of the pupae gather for a certain time in these corridors and leave them only by daylight at raising temperatures. These hypotheses will have to be proved by further experiments.

Among the burying beetles which live in our biotopes we find species which hibernate in the stage of imagoes and species which spend the winter in larval stage. They become pupae and emerge later in spring. *Necrophorus vespillo* belongs to the first group. Contrary to e.g. the species of *Necrophorus germanicus L.* the former develops in our territorial conditions in two generations - the individuals of the second generation emerge from the soil at the end of September and at the beginning of October - B. Novák (1961). Similarly as in *Carabidae* the species *Necrophorus vespillo* could be with regard to its development cycle classified as a spring species - see Larson (1939). For the spring species of *Carabidae* the activity by daylight is characteristic - see Thiele (1969). If *Necrophorus vespillo* also belongs to the species which are active by daylight, we find a congruence between the daily activity rhythm and the development cycle similarly as in many members of the *Carabidae* family.

CONCLUSIONS

1. Using automatic earth traps the author has found in metamorphosed imagoes of *Necrophorus vespillo* a remarkable dependence of the emergence from soil upon the light phase of the day.
2. The greatest number of individuals left the ground within the first hours after noon when the soil temperature reached its maximum.
3. The temperature factor influences the intra- and interfilial dispersion of imagoes during the emergence from soil, if we follow the offsprings of separate parental couples or the individuals from a greater number of isolators in general on successive days.
4. The leaving of earth cradles by imagoes is with greatest probability synchronized by the temperature cycle of the day. The final phase of emergence from soil can also be regulated by the photoperiod.

VÝSTUP HROBAŘÍKŮ Z PŮDY PO PROMĚNĚ A JEHO VAZBA NA DENNÍ SVĚTLO (COL. SILPHIDAE)

ZÁVĚRY

NADĚŽDA ŠPICAROVÁ

1. Nasazením automatických zemních pastí zjistila autorka u metamorfovaných imag druhu *Necrophorus vespillo* za výstupu z půdy výraznou vazbu na světelnou fázi dne.

2. Největší počet jedinců opouštěl půdu v prvních hodinách po poledni, kdy obyčejně vrcholí i půdní teplota.

3. Tepelný faktor působí i na intra- a interfiliální rozptyl imag za výstupu z půdy, sledujeme-li potomky jednotlivých rodičovských párů nebo jedince z většího počtu isolátorů v sohrnu v posloupných dnech.

4. Opouštění půdních kolébek imagy je se vší pravděpodobností synchronisováno denním teplotním cyklem. Konečnou fázi výstupu z půdy může usměrňovat i fotoperioda.

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