BERESINA, V. M., Die Veränderungen der Entomofauna von Böden beim Übergang aus Steppenverhältnissen zu Waldverhältnissen. Rev. Ent. URSS, **27**, 77—112, 1937 (Russ.).

GEBERSTEIN, S., Schriften über Moskovia. S.-Petersburg, 1866 (Russ.).

GHILAROV, M. S., The influence of soil conditions on the soil vermin fauna. Pochvovedenie (Pedology), Nr. 9, pp. 121—137, 1939 (Russ. m. engl. Zusammenf.).

—, Die Rolle der Steppennagetiere in der Herkunft der Feldbodenfauna und der Feldunkräuter. Doklady Akad. Nauk SSSR, **79**, 669—671, 1951 (Russ.).

—, Bodenfauna in Schluchtwäldern. Zool. Thurn., **32**, 328—347, 1953 (Russ.).

—, Bodenfauna der Gehölze und der Steppe. Trudy Inst. lesa Akad. Nauk SSSR, **30**, 235—278, 1956 (Russ.).

—, Millipeds (*Juloidea*) of the steppe zone of the eastern part of the Ukrainian SSR and their role in the soil-forming processes. Pochvovedenie (Pedology), Nr. 6, pp. 74—80, 1957 (Russ. m. engl. Zusammenf.).

—, FOLKMANOVA, B., Chilopoden der Steppenzone des Süd-Ostens des europäischen Teils der UdSSR als Indikatoren der Bodenbedingungen in Gehölzen. Izvestija Akademii Nauk SSSR, Ser. biol., Nr. 2, p. 211—219, 1957 (Russ.).

GOLGOFSKAYA, K. J., Typen der Schluchtwälder in der Umgebung der Derkul-Versuchsstation (Feld-Waldschutzdienst). Trudy Inst. lesa Akad. Nauk SSR, **39**, 5—82, 1958 (Russ.).

DOKUTSCHAJEW, W., Unsere Steppen früher und heute. S.-Petersburg (Russ.).

MAKSIMOV, A. A., Über die historischen Verbreitungsänderungen von Microtus arvalis Pall. Compt. rend. (Doklady) Akad. Sci. URSS, **60**, 677—680, 1948 (Russ.).

MELNITSCHENKO, A. N., Feldwaldstreifen und Vermehrung der Tiere. Moskau, 1949 (Russ.).

PEREL, T. S., Dependence of the population density and specific composition of the earthworms on the specific composition of forest stands. Zool. Zhurn., **37**, 1307—1315, 1958 (Russ. m. engl. Zusammenf.).

SEMENOVA-TIAN-SHANSKAYA, A. M., Veränderungen der Pflanzendecke der Waldsteppenzone der Russischen Ebene im XVI.—XVIII. Jh. unter dem Einfluß der Menschentätigkeit. Botan. Zhurn., **42**, 1398—1407, 1957 (Russ.).

WYSSOTSKY, G. N., Über die hydrologischen und meteorologischen Einfluß der Wälder. 2. Aufl., Moskau, 1950 (Russ.).

An Experimental Study of Thanatosis in Insects

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Thanatosis or death-feigning is well developed in many animals and particularly in beetles. When feigning death an insect assumes an immobile posture by pressing its legs and antennae to the body. Most workers have been concerned with the posture of the animal and with the induction and termination of thanatosis (SEVERIN & SEVERIN, 1911; WEISS, 1947; HOLMES, 1903, 1906). Some have also made a preliminary study on the effect of light and temperature on thanatosis (HOLMES, 1906; SEVERIN & SEVERIN, 1911;

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Kozanshikov, 1931). A few authors report on the part of the nervous system responsible for death-feigning (Robertson, 1904; Kozanshikov, 1931; Holmes 1906). In the present paper a detailed study of thanatosis, including the factors affecting it, has been made.

Material and Method

Different species of insect having a duration of thanatosis as low as a few seconds and as high as a few hours were selected for the present work. The insects used were:

Calandra granaria (L.); *Calandra oryzae* (L.); *Coccinella septempunctata* (L.); *Adalia bipunctata* (L.); and *Carausius morosus* (Br.).

Handling excites insects so that experimental insects, individually, were allowed to remain undisturbed for a responable time before thanatosis was induced. Food was supplied to the insects during this period. Because of differential sensitivity of different parts of the body of animals to mechanical and other stimuli the method of evoking thanatosis was varied. In *C. granaria* and *C. oryzae* a touch on almost any part of the body induces thanatosis. The best way to induce thanatosis in coccinellios is to press the body lightly with a hard blunt rod. Thanatosis was induced by applying the stimuli, which vary with the insects, to the thorax; a pressure on the thorax by a needle was used for *Calandra*, on the ventral side of the insect by the finger for coccinellids and on the sides of the thorax, exercised by thumb and fore finger for *C. morosus*. In all the insects except *Carausius morosus* the termination time was recorded when the antennae moved. On account of the long duration of thanatosis, as much as 5—6 hours, in *C. morosus*, the insects were observed every 10 minutes instead of continually, as for the other species. In most cases the approximate time of termination was calculated by averaging the time of the last inspection before termination, and the first after termination.

Experiments to study the effect of light were conducted in a dark constant temperature and humidity room, and a special box was used in which the heat of the bulb was prevented from reaching the animals by keeping a trough filled with cold water between the source of light (Tungsten lamp) and the experimental insects which were confined under glass funnels. The experimental insects were conditioned for 24 hours in the dark.

Experiments were performed with batches of adults of about the same age. The low illumination, under which the observations were made, had previously been proved not to stimulate them. The square root transformation was applied to the data to help to normalise the distribution of data and to make the variance in any group of observations more nearly independent of the mean.

Results and Discussion

Thanatosis is very widely distributed among insects specially the beetles. Studies on thanatosis have been made by several authors in various insects such as *Belostoma flumineum*, *Nepa apiculata Geotropes stercorarius*. *Lochmea capreae*, *Bruchus obtechus*, *Alobates barbata*, *Boletotherus bifurcus*, *Diplotaxus liberta*, *Alobates pennsylvanica*, *Idiobates castaneus*, *Gyrinus natator*, *Dixippus morosus*, *Forficula* and *Neides*.

In agreement with Darwin, quoted by Holmes (1908), who observed 17 species of arthropods, the postures assumed by insects while in the state of thanatosis were found to be different from those assumed by dead specimens. Termination may be instantaneous as in some coccinellids, or gradual as in granary weevils. In some of the coccinellids the termination is preceded by trembling of the antennae and the tarsi. Generaly it begins with the movement of the antennae followed by that of legs.

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Thanatosis in response to different stimuli

Different durations of thanatosis were obtained as a result of the application of various grades of mechanical stimuli to *C. granaria* (Table 1). Short periods were obtained by subjecting the insects to a weak stimulus such as moving air or touching them with a piece of cotton. These results were supported by similar observations on the other three beetles. *C. oryzae*,

Table 1. Thanatosis response of insects to different stimuli

Insects	Transformed response in seconds						
	Air	Cotton	Brush	Glued thread	Glass rod	Needle	Finger
	Mean values of 20 insects						
C. granaria	0.31	0.53	1.35	2.1	—	2.38	—
C. oryzae	0.6	1.4	2.1	3.9	—	5.5	—
	Mean values of 10 insects						
C. septempunctata	0	0	1.53	3.4	5.25	—	9.88
A. bipunctata	0	0	0.84	1.66	4.02	—	7.93

C. septempunctata and *A. bipunctata* and suggest an association between the length of the period of thanatosis and the intensity of stimulus. WEISS (1947) has also pointed out the possibility of some correlation between the strength of the stimulus and the duration of death-feigning: the variation in the number and frequency of nerve impulses transmitted from the receptors, when stimuli of different intensities are applied, may be the cause of the different responses obtained on subjecting the specimens to such stimuli.

Response to repeated application of the stimulus

It has been observed (KOZANSHIKOV, 1931), that the frequently repeated application of the same stimulus to an insect exhibiting thanatosis causes a

Table 2.
Thanatosis response of insects to repeated application of stimulus

Insects	Transformed response in seconds on each application										
	1st	2nd	3rd	4th	5th	6th	7th	8th	9th	10th	11th
	Mean values of 20 insects										
C. granaria	2.2	1.71	1.23	1.03	.85	.5	.3	.28	.21	.05	0
C. oryzae	2.06	1.29	.86	.56	.24	.12	0	—	—	—	—
	Mean values of 10 insects										
C. septempunctata	9.21	4.25	1.07	0	—	—	—	—	—	—	—
A. bipunctata	7.8	2.2	.47	0	—	—	—	—	—	—	—

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decline in the magnitude of response until finally a stage is reached when the animal ceases to respond. The present series of experiments confirms this finding (Table 2). The successive stimuli were applied after the termination of thanatosis induced by the preceding stimulus. As the stimuli were presented in succession relatively slowly, the failure to respond to a stimulus does not appear to be as a result of adaption of the sense organs but may be due to synaptic fatique. Different numbers of applications of the same stimulus are required by the different insects before fatigue is exhibited: fewer repeatedly applied stimuli are required by the species of coccinellids than are required by *C. granaria.*

Thanatosis as influenced by age and sex

In newly emerged beetles the duration of thanatosis is shorter than matured ones (Table 3). As the individual ages, a gradual approach to the

Table 3. Thanatosis response of insects at different ages

Insects	Transformed periods in seconds prior to emergence from grain berry		Transformed periods in seconds after emergence				
	with white elytra	with brown elytra	1st day of emergence	5 days old	10 days old	15 days old	20 days old
	Mean values of 20 insects						
C. granaria	.074	.22	1.39	2.19	2.25	2.48	2.3
C. oryzae	—	.21	1.21	2.0	2.23	2.22	—
	Mean values of 10 insects						
C. septempunctata	—	—	2.47	4.56	7.94	9.43	9.3
A. bipunctata	—	—	3.23	7.8	8.41	8.23	—
	About 15 days old		2—3 months old		7—8 months old		
C. morosus	4.39		9.47		17.33		

normal value is observed and this value is retained throughout the rest of the adult life. It is interesting to note that the period required to complete pigmentation in granary weevils and rice weevils and coccinellids is nearly the same as the period taken for the attainment of the normal duration of thanatosis. Perhaps there is some relation between thanatosis and the development associated with pigmentation. It might be that as the hardness of suticle increases and pigmentation develops the sensitivity of cuticular sense organs to touch may be increasing with hardness of cuticle.

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The durations of thanatosis were determined separately for the sexes of the beetles *C. granaria* and *C. oryzae* and the difference between the means is significantly smaller than the residual variance would predict. Sexing of adults was done according to RICHARDS (1947).

Effect of amputations on thanatosis

Attemps were made, by mutilating different organs of the body, to locate the parts played by different divisions of the nervous system responsible for thanatosis. Decapitated insects failed to feign death whereas in insects whose abdomen had been removed, it was possible to induce thanatosis for a time shorter than the normal. The maximum duration of thanatosis is obtained by applying the stimulus to the thorax (Table 4). No shange in

Table 4. Thanatosis response of insects to amputations

Insects	Transformed response in seconds after mutilating					
	Head	Antennae	Abdomen	Fore-legs	Mid-legs	Hind-legs
	Mean values of 20 insects					
C. granaria	0	2.16	1.95	2.06	2.30	2.10
C. oryzae	0	2.16	1.68	2.16	2.23	2.07
	Mean values of 10 insects					
C. morosus	0	17.28	10.59	17.56	18.02	18.49

the duration of thanatosis was recorded after cutting off either the legs or the antennae. In the light of the results of the present experiments and the findings of the previous authors (HOLMES, 1906; ROBERTSON, 1904; REISINGER, 1928), it appears that besides the functioning of the head ganglia, the co-operation of other ganglia is necessary, to bring about thanatosis.

Table 5. Thanatosis response of *C. granaria* to the application of the stimulus to the different parts of the body

	Thanatosis response of the insects on the application of the stimulus to:											
	Dorsal side					Ventral side						
	Antennae		Head	Thorax	Elytra	Fore-legs		Mid-legs		Hind-legs		
	Right	Left				Right	Left	Right	Left	Right	Left	
	Mean values of 20 insects											
Mean transformed periods of insects in seconds	.25	.26	1.2	2.2	1.3	.7	.7	1.32	1.34	.5	.52	2.3
Percentage of insects showing thanatosis	21.7	21.7	70	86.7	60	50	50	61.7	61.7	31.7	31.7	91.7

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Rabaud (1919) pointed out that most arthropods possess regions of the body which seem to be loci of tactile reflexes causing the animal to pass into a state of immobility, characterised by heightened tonicity of the skeletal musculature. Experiments were performed to locate the regions of the body most sensitive to mechanical stimuli in *C. granaria.* The results of table 5 show that the maximum duration of thanatosis and the maximum percentage of insects responding were obtained when the stimulus was applied to the thorax. The same results were obtained whether the stimulus was applied to the dorsal or ventral surface of the thorax. These results are in accordance with those of Rabaud (1919) who suggested that the antennae, thorax and wing bases are in general the regions which, when stimulated, induce immobilisation. The mid-legs are more sensitive than the fore or hind legs.

Influence of starvation on thanatosis

The effect of starvation was studied in senescent as well as in newly emerged insects (Table 6). A steady increase in the duration of thanatosis

Table 6. Thanatosis response of insects to starvation

Insects	Transformed response in seconds													
	after being starved for								of 4 days starved insects after being fed for					
	24 hours		48 hours		72 hours		92 hours		2 hours		4 hours		6 hours	
	A	B	A	B	A	B	A	B	A_1	B_1	A_1	B_1	A_1	B_1
Mean values of 20 insects														
C. granaria	2.6	2.0	3.4	2.3	4.1	2.2	4.5	2.1	3.3	2.1	2.6	2.1	2.1	2.3
C. oryzae	2.2	1.9	2.7	2.1	3.3	2.1	3.7	2.1	2.9	2.1	2.2	2.0	—	—
Mean values of 10 insects														
C. septempunctata	11.8	9.5	13.9	9.9	17.3	9.8	—	—	—	—	—	—	—	—
	6 hours		12 hours		24 hours		48 hours							
	A	B	A	B	A	B	A	B						
A. bipunctata	9.5	8.3	10.3	8.0	11.3	8.8	12.8	8.8						

A = Starved, B = Control, A_1 = With wheat, B_1 = Control

of the insects was associated with an increase in the duration of starvation. The duration of thanatosis falls to normal in a few hours if the starved insects are fed. Newly emerged insects are more affected than senescent ones (Table 7). *C. oryzae* is more resistent to starvation and recovers more quickly than *C. granaria.*

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Table 7. Thanatosis response of newly emerged insects to starvation

Insects	Transformed duration of thanatosis of							
	Starved insects				Fed insects			
	Day of emergence	Starvation period 24 hr.	48 hr.	72 hr.	Day of emergence	Feeding period 24 hr.	48. hr	72 hr.
	Mean values of 20 insects							
C. granaria	1.2	3.4	3.8	—	1.1	1.2	1.5	—
C. oryzae	1.1	2.2	2.7	3.0	1.0	1.4	1.6	1.7

	Day of emergence	After 3 days of starvation	Day of emergence	After 3 days of feeding
	Mean values of 10 insects			
C. septempunctata	2.5	14.9	2.5	3.9

Effect of illumination on the duration of thanatosis

(I) Response to different illuminations

Exposure of insects to light also affects thanatosis, the duration of which decreases with the increase in illumination. Holmes (1906) found that the duration of death feint in *Ranatra* is deminished, as a rule, by exposure to bright light. In the present work the experiments were performed with a number of species by exposing them to light of different intensities. A gradual fall in the duration of thanatosis is observed in *C. granaria*, *C. oryzae*, and *A. bipunctata* until a certain level of illumination is reached (Table 8). On further increasing the light intensity, the duration of thanatosis decreases rapidly. On exposure to light of still higher intensity, great nervous exci-

Table 8. Thanatosis response of insects to different illumination

Insects	Transformed duration in seconds to different illuminations (in Log. Foot Lamberts).							
	.3	.9	1.0	1.1	1.5	1.55	1.8	2.0
	Mean values of 20 insects							
C. granaria	2.63	2.28	1.45	1.40	0.72	0.63	0.28	0.08
	.6	1.0	1.4	1.5				
C. oryzae	2.07	1.81	1.50	0.98				
	.2	.5	.8	1.1	1.3			
	Mean values of 10 insects							
C.septempunctata	9.79	7.2	5.84	3.89	2.05			
	.5	1.2	1.4	1.5				
A. bipunctata	8.33	7.29	5.06	1.82				

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tability was shown. Irradiation of insects, which were in the state of thanatosis, brought them out of this state sooner than they would otherwise have emerged from it.

(II) Response to increased duration of exposure to light

The stimulation effect of light led to an investigation of the effect of different durations of exposure to the same level of illumination. A steady fall in the duration of thanatosis was observed on increasing the duration of exposure to light of the same intensity (Table 9). Long exposures to light

Table 9. Thanatosis response of insects to increased period of exposure to light

Insects	Transformed response in seconds on different exposures of				
	1 hour	2 hour	4 hour	6 hour	8 hour
Mean values of 20 insects					
C. granaria	—	1.8	1.1	0.9	0.3
C. oryzae	1.8	1.51	1.04	—	—
Mean values of 10 insects					
C. septempunctata	8.7	6.4	3.0	—	—
A. bipunctata	7.3	4.5	1.7	—	—

caused nervous excitability. *C. morosus* responded in a different fashion. This insect remains inactive in daylight and it remained in a state of thanatosis as long as it was exposed to the artificial light. It came out of thanatosis soon after the light was switched off.

(III) Colour vision in *Calandra granaria*

Colour vision in *Calandra granaria* was studied by exposing the insects to different coloured lights. The different periods of thanatosis, obtained on subjecting the insects to different coloured lights (Table 10), suggest that colour perception exists in *C. granaria*. Violet, blue, green, orange and red lights of illuminations .015, .05, .012, 1.99 and .063 ft lamberts respectively measured by a commercial "Lumeter" photometer, were used. As in pre-

Table 10. Thanatosis response of *C. granaria* to different coloured lights

	Transformed duration of thanatosis in seconds to different coloured lights				
	Violet-.015 ft. lambert.	Blue-.05 ft. lambert.	Green-.01 ft. lambert.	Orange-1.99 ft. lambert.	Red-.063 ft. lambert.
Mean values of 20 insects	1.38	1.44	2.20	1.97	2,37

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vious experiments, no change in the duration of thanatosis of *C. granaria* has been found on exposing them to artificial white light of similar low illuminations, exposures to these coloured lights of low illuminations might not have been expected to affect the duration of thanatosis. However, a decrease in the period of thanatosis does occur on exposing the insects to violet, and blue lights, although no change occurs on exposure to green, orange and red lights. To decide what part is played by sensitivity of perception and what by brightness of light of different wave lengths, it would be necessary to compare the energies associated with irradiation by the lights actually used, but the low illuminations by violet and blue lights (as noted from photometric measurements) strongly suggest that the weevils are particularly sensitive to light of these wavelengths.

(IV) Stimulation by ultraviolet light

Calandra granaria and *Calandra oryzae* apear to perceive ultraviolet light. The insects were subjected to ultraviolet irradiation for different periods and a gradual fall in the duration of thanatosis was noticed on increasing the exposure periods (Table 11). Sensitivity of insects to ultraviolet irradiation

Table 11. Thanatosis response of insects to different exposures to ultra-violet light

Insects	Mean transformed durations of 20 insects on exposures of			
	$^1/_2$ hour	1 hour	2 hours	4 hours
C. granaria	1.9	—	1.56	1.13
C. oryzae	—	2.05	1.75	1.09

has been reported by several entomologists mentioned by Weiss (1943) in his review on 'Colour perception in insects'. Weiss (1943) has also mentioned that Hess (1920b) demonstrated that bees and some other arthropods are more sensitive to ultraviolet irradiation from a mercury vapour lamp than to ordinary light. *Carausius morosus* behaved in the same way when exposed either to ultraviolet or to visible light.

Effect of temperature and heat radiation on the duration of thanatosis

The duration of thanatosis diminishes with increase in temperature (Table 12). This finding agrees with the results obtained by Holmes (1906). Nervous excitability was shown by the insects at high temperatures whereas they were found inactive at low temperatures. If the nervous system is in a more excited condition and it is then put into a condition associated with the state of thanatosis, reversion occurs quicker than if the nervous system is in a less excited condition. The effect of heat radiation on thanatosis

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Table 12. Thanatosis response of insects at different temperatures

Insects	Transformed response in seconds to different temperatures		
	11 °C	26 °C	36 °C
Mean values of 20 insects			
C. granaria	4.4	2.3	1.7
	14 °C	20 °C	25 °C
C. oryzae	4.0	3.0	22.2
	11 °C	24 °C	35 °C
Mean values of 10 insects			
C. septempunctata	13.7	9.6	1.0
	22 °C	26.8 °C	34 °C
A. bipunctata	10.6	9.4	4.7

response of coccinellids was also studied. For transmitting the heat radia tions to the insects, a needle, heated in a flame for 30 seconds, was brought about ½ cm. away from the right antenna of the insects, which were lying in the state of thanatosis. An earlier termination of thanatosis was recorded on subjecting the coccinellids, while in a state of thanatosis, to heat radiations (Table 13). Such coccinellids were found moving about excitedly after the termination of thanatosis.

Table 13. Thanatosis response of coccinellids to heat radiations

Insects	Mean transformed response of 10 insects in seconds	
	Before subjecting to heat radiations	After subjecting to heat radiations
C. septempunctata	9.8	2.7
A. bipunctata	7.8	1.6

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Summary

In general an insect assumes a compact form by tightly pressing its legs and antennae to the body, while in a state of thanatosis. This posture is quite different from that assumed by dead insects. Generally at the termination of thanatosis the antennae are

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moved first and then the legs. Frequently repeated applications of the same stimulus lead to progressively shorter periods of thanatosis until insects no longer respond.

Newly emerged beetles show a shorter duration of thanatosis in response to standard stimuli than the normal value attained when the individual ages. This result suggest some relations between tactile sensitivity and the development associated with the hardening and darjening of the cuticle. No differential sexual response was recorded. The duration of thanatosis increases with an increase in the duration of starvation. Newly emerged insects are more affected than senescent ones. It appears that besides the functioning of the head ganglia, the cooperation of other ganglia is necessary to bring about thanatosis. The thorax in *Calandra granaria* (L.) appears to be the part most sensitive to mechanical stimuli. The mid-legs are more sensitive than the fore and hind legs.

On increasing the intensity of illumination the duration of thanatosis falls. On exposure to high intensity nervous excitability is induced: the duration of thanatosis also falls with increase in the period of irradiation by light.

Calandra granaria (L.) appears to be most sensitive to blue and violet light: *C. granaria* and *C. oryzae* (L.) appear to perceive ultraviolet light. The duration of thanatosis diminishes with increase in temperature. At high temperatures insects show nervous excitability. An earlier termination of thanatosis takes place on subjecting coccinellids, while in a state of thanatosis, to radiant heat.

Zusammenfassung

Während der Thanatose nimmt ein Insekt gewöhnlich eine kompakte Form an, indem es die Beine und die Fühler eng an den Körper preßt. Diese Stellung ist durchaus verschieden von der, die tote Insekten einnehmen. Gegen Ende der Thanatose werden im allgemeinen zuerst die Antennen und dann die Beine wieder bewegt. Häufig wiederholte Anwendung derselben Reize führt zu immer kürzeren Thanatose-Perioden, bis das Insekt nicht mehr darauf reagiert. Frisch geschlüpfte Käfer zeigen kürzere Dauer der Thanatose auf standardisierte Reize als die normalen Werte, die man erhöht, wenn die Individuen älter werden. Dieses Ergebnis deutet auf Beziehungen zwischen der Empfindlichkeit gegen Berührungsreize und der Entwicklung in Zusammenhang mit der Härtung und Ausfärbung der Cuticula. Sexuelle Unterschiede in der Reaktion wurden nicht festgestellt. Die Dauer der Thanatose erhöht sich mit zunehmender Dauer der Hungerperioden. Frisch geschlüpfte Insekten werden stärker beeinflußt als alte. Es entsteht der Eindruck, daß außer der Funktion der Kopfganglien das Zusammenwirken anderer Ganglien für das Zustandekommen der Thanatose erforderlich ist. Bei *Calandra granaria* (L.) ist wahrscheinlich der Thorax für mechanische Reize am stärksten empfänglich Die Mittelbeine sind empfindlicher als die Vorder- und Hinterbeine. Bei Erhöhung der Beleuchtungsintensität sinkt die Dauer der Thanatose. Durch den Einfluß hoher Intensität wird nervöse Erregbarkeit verursacht: Die Dauer der Thanatose nimmt auch ab durch Erhöhung der Intensität während der Bestrahlungsperiode. *Calandra granaria* (L.) scheint am meisten empfindlich gegen blaues und violettes Licht: *C. granaria* (L.) und *C. oryzae* (L.) können offenbar ultraviolettes Licht wahrnehmen. Die Thanatose-Dauer verringert sich mit zunehmender Temperatur. Bei hohen Temperaturen zeigen Insekten nervöse Erregbarkeit. Ein früheres Ende der Thanatose tritt bei Coccinelliden ein, wenn man sie während der Thanatose Wärmestrahlen aussetzt.

Резюме

Во время танатоза насекомое обычно принимает компактную форму, тесно прижимая ноги и щупальца к туловищу. Это положение весьма различно от положения, занимаемого мертвыми насекомыми. К концу танатоза насекомое сперва шевелит щупальцами, а затем и ногами. Частое применение одних и

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тех же раздражений приводит ко все болэе коротким периодам танатоза, пока насекомое вовсе не реагирует на такое раздражение. Свежевылупившиеся жуки проявляют более короткий период танатоза на стандартизированные раздражения, по сравнению с нормальными величинами, которые получаются, когда насекомые становятся старше. Этот результат указывает на существующие связи между чувствительностью против раздражения от соприкосновения и развитием в связи с уплотнением и выкрашиванием кутикулы. Половых разниц в реакции не было установлено. Длительность танатоза возрастает с удлинением периодов голодания. Свежевылупившиеся насекомые сильнее подвергаются влиянию, чем старые. Получается впечатление, что за исключением функции головных ганглиев, необходимо совместное действие других ганглиев для осуществления танатоза. У *Calandra granaria* (L.) вероятно грудная клетка чувствительнее всего против механических раздражений. Средние ноги чувствительнее передних и задних. При увеличении интенсивности освещения длительность танатоза уменьшается. Под влиянием сильной интенсивности освещения вызывается нервная возбудительность. Продолжительность танатоза сокращается при повышении интенсивности облучения. *Calandra granaria* (L.) повидимому боллее всего чувствительна против синего и фиолетового света: *C. granaria* (L.) и *C. oryzae* (L.) повидимому в состоянии воспринимать ультрафиолетовый свет. Длительность танатоза уменьшается с возрастающей температурой. При высоких температурах насекомые проявляют нервную возбудимость. Скорый конец танатоза наступает у Coccinellidae, если они подвергаются во время танатоза облучению тепловыми лучами.

References

Holmes, S. J., Death feigning in *Ranatra*. Journ. comp. Neurol. Physiol., **16**, 200—216, 1906.

—, Death-feigning in terrestrial amphipods. Biol. Bull., **4**, 191—196, 1903.

—, Instinct of feigning death., Pop. Science Month., **22**, 179—85, 1908.

Kozanshikov, I., Interrelations between the thanatosis and the central nervous functions in *Lochmaea capreae* L. Bull. Plant., Protect. Leningrad, **3**, 233—240, 1931.

Rabaud, E., L'immobilisation reflexe et l'activité normale des Arthropodes. Bull. biol. France Belg., **53**, 1—149, 1919.

Reisinger, L., Katalepsie der indischen Stabheuschrecke (*Dixippus morosus*). Biol. Zentralbl., **48**, 162—167. 1928.

Richards, O. W., Observations on grain weevils, *Calandra* (*Col.*, *Curculonidae*). I. General biology and oviposition. Proc. Zool. Soc. Lond., **117**, 1—43, 1947.

Robertson, F. B., On the sham death reflex in spiders. Journ. Physiol., **31**, 410, 1904.

Severin, H. H. P. & Severin, H. C., An experimental study on the death-feigning of *Belostoma flumineum* Say and *Nepa apiculata* Uhler. Behav. Monogr., **1**, 44pp., 1911.

Weiss, H. B., The death feints in *Idiobates castaneus* Koch and *Belototherus bifurcus* fab. Journ. New York ent. Soc., **55**, 275—279, 1947.

—, Colour perception in insects. J. econ. Ent., **36**, 11—15, 1143.

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