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Znaczenie wzroku i pamięci w zdobywaniu pokarmu przez chrząszcze z gatunku *Cicindela hybrida* L. *(Coleoptera, Cicindelidae)*

The rôle of sight and memory in food capture by predatory beetles of the species *Cicindela hybrida* L. *(Coleoptera, Cicindelidae)*

napisał

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Problem

The question of how predatory insects capture their food is a very complicated problem, which may be considered from two different points of view: 1) as an ethological phenomenon including the behaviour of individuals of a given predatory species in its natural environment in the presence of species forming its natural nourishment, 2) as a psychological phenomenom including problems connected with visual perception, memory, ability to learn, etc.

With regard to the sense of sight, certain questions must be considered: the field of vision, the perception of differences in the quality light, perception of direction, shape, movement etc.

The aim of the work was to investigate and analyse some particular ethological and psychological phenomena in the behaviour of the sand-beetle *Cicindela hybrida* L. Among the many senses which probably play a part in the capture of food

by sand-beetles, sight was chosen. We also paid some attention to the phenomena of memory. The investigations on these questions include both observations in the natural enviroment and laboratory experiments.

Material and method

The experiments were carried out on the sand-beetle *Cicindela hybrida* L., a heliophile and polythermic species. It has well developed organs of locomotion. The eyes, which are large, convex and ovoidal, set on both sides of the head, are also especially well developed. *Cicindela* leads a very active life.

These beetles spend all their time running or flying over sand hills. As man approaches, they react from about 4 m. (c. 13 ft.) by quick flight. Their optimum of activity occurs in the hottest part of the day and ends in the late afternoon hours (about 4.5 p. m.). During rainy or cold days and during the night they remain buried in the sand, hidden under roots of plants, or under stones. Their food consists of small adult insects and their larvae [4]. The larvae of the sand beetles, like the adults, are predatory; the only difference is that they spend all their time underground in short tunnels dug perpendicularly to the surface. The field observations of the sand beetles were made in the vicinity of Kraków (Cracow), at Tyniec, on limestone hills partly overgrown with young pine forest and partly covered with sand. The experiments were performed in a laboratory lit by windows on the south and partly from above, through a glass ceiling. The live material was kept in terraria of different types. In 1948 two terraria made completely of glass [dimension: 25×16×18 cm and 40×25×25 cm] were used. In 1950 only one terrarium in which glass panes were fixed in iron frames [dim. 55×32×31 cm] was used. All terraria were set on window-sills and covered with glass and wire netting. In 1948 no arrangements were made for shelter; in 1950 paper screens were used which covered the whole side turned from the light and thus separated the interior from the observer: The floors of the terraria were sprinkled with sand brought from the places where the insects had been caught. Xerophilous plants were planted in the sand.

The method of experiment consisted in presenting the insects with food of various kinds. Food was thrown into the terrarium

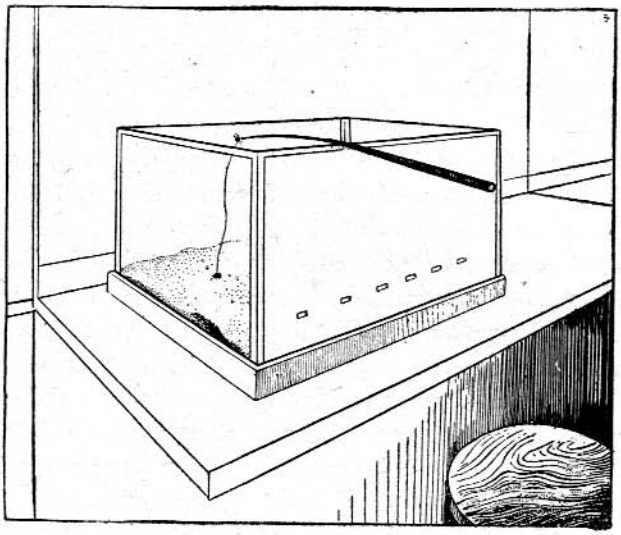


Fig. 1

from above, or let down by means of a „fishing rod", composed of wire and a long thread (fig. 1). The fishing rod was also used

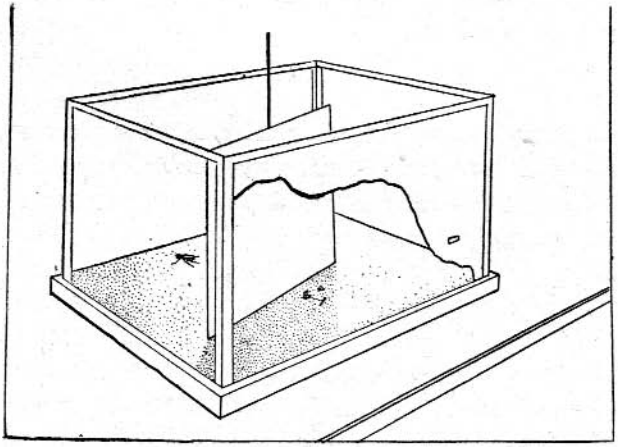


Fig. 2

when the sand beetles were fed with dead insects, in order to create the impression of living prey. Additional small paper screens, which were afterwards removed, were often placed in the terrarium before the experiment in order to conceal the location of the food from the insects (fig. 2). The experiments were performed at different times of day, both during direct insolation and also on cloudy days. The interior of the terraria was always kept dry, sprinkling the surface of the sand with water only once a day. This was necessary to keep the insects in good condition, for otherwise they soon died.

The aim of these experiments was to observe whether the behaviour of sand-beetles in the presence of food is always the same and therefore inborn, or if the reactions in particular cases vary and result from the adaptation of the insects to different situations. The second problem of our investigations was to determinate wheter the reactions of the beetles are based on the ability to see and recognize the movements or shape of the objects, or both combined.

As a criterion for recognizing the nature of the reactions was taken the movement of the bait or, conversely, the lack of it, and various kinds of movement were also taken into consideration. These were distinguished as follows: 1) Immobile bait. This include horse meat, the flesh of frogs and fishes and several invertebrate animals, e. g. molluscs (shellfish), insects, etc. 2) mobile bait, which may be divided into two equal subdivisions: a) live bait, actively, moving, b) dead bait passively moving (artificially moved).

Live bait might move in one place; this happened especially when we used living fragments of insects cut across: Movement of bait could also involve a change of place, as was the case when running or creeping insects were used. The movement of bait might also be characterized by continuity, or discontinuity.

In examining the behaviour of sand-beetles during particular experiments, in the presence of various kinds of bait, the influence of extraneous factors having their source in the environment of experiment (e. g. light, temperature, the presence of the observer etc.) were taken into account. By using several precautionary arrangements, such as paper screens isolating from exter-

nal influences, it was possible to avoid some of these. The only factor impossible to avoid notwithstanding all our efforts was the unidirectional lightning, which constantly caused photoactive reactions in the beetles.

Introductory observations in the laboratory

Conditions: 9^{30} a. m. No direct insolation. The side of the terrarium facing the room covered with paper screen in which several narrow holes were cut, so that the beetles might be observed. Temperature inside the terrarium 21°C.

The behaviour of the animals showed the strong influence of the unidirectional sunlight. All specimens were grouped near the glass lighted from the window side. Their movements were violent. Some of the insects ran to and fro along the frame or tried to climb up the glass, sometimes getting on another's backs. Several ran to the opposite of the box and hid under the leaves of the xerophilous plants.

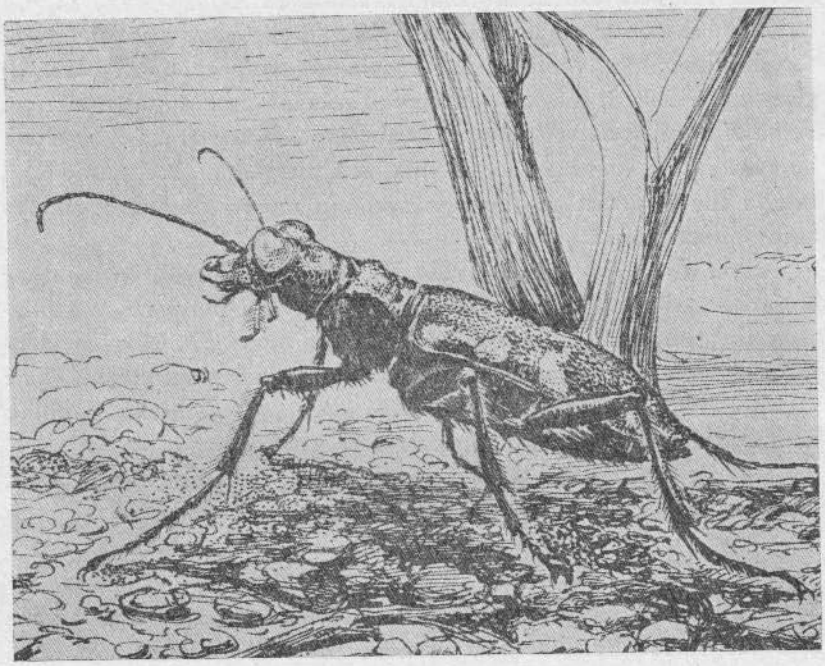
When some of the individuals were transferred to another terrarium, the remaining two changed their behaviour immediately; they began to search the ground thoroughly, seizing accidentally encountered small objects with their mandibulae. Their attention was attracted by such things as small sticks, pebbles, damp adherent grains of sand, etc.

The insects readily drank any kind of moisture they found, even sucking water out of the ground.

Reactions to immobile food

A shell-fish freshly killed and denuded of its shell was thrown into the terrarium. The place where the bait fell had not been screened, so that the presence of the food might be perceived by the insects. The reaction of the beetles appeared only after a considerable period. Only one specimen began to search for food, while the other was turned towards the light and did not pay any attention to the bait. The hunting insect ran in tortuous tracks, seizing with its mandibulae accidentally found objects, which were immediately thrown away. It was impossible to ascertain whether any of the tracks had a determined direction. The bait was found quite accidentally after 7 minutes. The beetle seized it

with its mandibulae and immediately began to devour the food. The action attracted the attention of the second specimen, which abandoned its attitude of complete indifference and changed over to violent attack. It assumed an alert position, turning its head towards the prey and raising itself high on its front legs (fig. 3). It approached its prey by running for short distances almost in a straight line. The act of devouring lasted comparatively long, about 16 minutes. The distance between the beetle and its prey was in this case 16 cm, the time of attack, 4 sec.



Flg. 3

The experiments in this series were repeated 8 times (nos. 2 to 9). In all cases a lack of orientation in the searching insects was observed, and a decided and rapid orientation towards food by attacking individuals. In 6 cases out of 8, the reaction of the second specimen appeared only after the food had been found by the first. The distances from which the food was attacked were in the individual cases: 15 cm, 17 cm, 23 cm, 10 cm, 20 cm.

Experiments were carried out in various conditions of light, between 9^{30} a. m. and 1^{00} p. m. and between 2 p. m. and 5 p. m.

Reactions to bait moving in one place

In this series of experiments insects of various kinds were used as bait; beetles, flies, or caterpillars. The insects were given to the sand-beetles either whole, or severely injured. Beetles belonging to the species *Tenebrio molitor* L., or *Geotrupes silvaticus* Panz. were cut into two, so that the head with the prothorax was separated from the rest of the body. In this manner two pieces were obtained of which the hind was immobile while the front one remained active. In order to prevent completely all movement in the hind part, the ganglia were destroyed with a needle. Both pieces, mobile and immobile, were given at the same time. Flies used in the experiments as mobile bait had their wings and feet cut off, and were also tied to small metal weights anchored in the sand. We also threw flies into the terrarium without fastening them to anything, and let them move freely. Such flies were only deprived of their feet (*tarsi*) so that they could not climb up the glass of the terrarium and had to remain on the ground. Anchored specimens were limited in their movements to a maximal space of 2 square cm. Insects used as immobile bait were killed mechanically and placed at some distance from the living bait.

The experiments belonging to this series may be divided into two series according to situation. In the first series only one (live) bait was used, in the second, two (mobile and immobile) were used at the same time.

Experiments with one bait only

Experiment No. 10

Conditions: 11 a. m. strong insolation. Temp. in the interior of the terrarium 37°C. One specimen only near the glass-pane exposed to the light.

A small additional screen was placed in the terrarium in order to hide the bait. As food was given a fly belonging to the species *Lucilia caesar* L. This had its wings and feet cut off, but in

spite of this it moved fairly quickly. When the screen was removed the sand beetle was in the opposite end of the terrarium. Its reactions appeared after some time, during which the insect ran along the glass and then hid in a tuft of pine. The bait was noticed from the distance of 7 cm. The beetle did not assume its habitual posture of attack (with the front part of the body raised), but threw itself directly on to the bait. The first blow of the mandibles missed its aim. At the second blow the beetle seized the victim's head. After a short fight the fly was divided into two parts, and then reduced to small pieces. The act of the devouring took a long time, about 15 minutes.

Experiment No. 11

Conditions: 10 a. m. Incomplete insolation, only a small part of the terrarium was directly lighted by the sun. Temp. 28°C. There were two specimens, hidden in clumps of plants.

A small caterpillar of the moth *Galleria mellonella* L. was thrown into the terrarium, at a distance of 25 cm. from the nearer sand-beetle.

The bait was perceived by the beetle from a distance of 12 cm. The attack was typical. The beetle, having assumed its habitual posture, approached the larva quickly but stopped at a distance of 15 cm. There was a moment's pause in the attack, and then insect began to bite various parts of the victim's body. Finally when the caterpillar was lying motionless on the ground, the beetle seized it in its mandibles, pulled it some pieces away slowly began to devour. The act of devouring took place in the open, and lasted about 20 minutes.

Experiment No. 12

Conditions: Slightly cloudy weather, incomplete insolation, temp. 28°C. two specimens.

A live larva, about 3 cm. long, of *Tenebrio molitor* L. was thrown into the terrarium. Only one specimen showed a reaction. The attack was carried out from a distance of 6 cm. and was directed at the front part of the larva, which showed no sign of resistance. All the efforts of the beetle to kill it were in vain, however for each thrust of the mandibles slid over the hard chi-

TABLE I

Species of bait	Number of sand-beetles	Behaviour of beetles	Distance from which bait perceived (in cm)	Result of reaction
Lucilia caesar L.	1	immediate attack single bite	7	devoured
Sarcophaga carnaea L. (large specimen)	2	preparatory posture, several attacks and bites	10	sand-beetle attracted by the bait, discontinued the attack.
Sarcophaga carnaea L. (small)	2	direct attack, bite on thorax	10	fight, victim torn into pieces, swallowed in about 15 mins.
Calliphora vomitoria L.	2	attack after 5 min.	20	rapid dissection of the victim into small pieces, devoured in about 15 mins.
" "	2	"	15	"
" "	2	"	22	"
Lucilla caesar L.	3	"	10	devoured; attack of the second specimen on the same victim.
Tenebrio molitor L. (injured)	2	typical attack with preparatory posture	10	devoured, transportation of the victim.
" "	2	"	25	devoured
" "	2	typical reaction without preparat. posture; bite	?	devoured
" "	3	reaction distinctly weakened, slow	?	3x no reaction
Tenebrio molitor L. (larva)	2	5 attacks	6-7	seizing without devouring

Species of bait	Number of sand-beetles	Behaviour of beetles	Distance from which bait perceived (in cm.)	Result of reaction
Galleria melonella L. (caterpillar)	2	many bites during attack	25	devoured
Calliphora vomitoria L.	2	violent attack seized near head	25	,,
,, ,,	2	violent attack seized by thorax	25	,,

tinous cover of the animal. After four successive blows, the sand-beetle turned back and did not renew its attacks.

The same larva served as a victim to the second specimen, which joined in the final attacks of the first. The second specimen, like its predecessor, attacked the bait several times, but after the fifth try turned back. All its bites were directed at the head or front part of the caterpillar's body.

Fifteen observations similar to these were carried out changing the kind of the bait, and the mode of presenting it to the beetles. In 11 instances the results were positive, and 4 negative. The results may be given in the form of the simple table.

Experiments with two kinds of bait, mobile and immobile

Experiment No. 25

Conditions: 4^{30} p. m. Strong insolation of the whole terrarium. Inside temp. 39°C. Activity very considerable. Two specimens running quickly on sand.

An additional paper screen was placed in the terrarium, to conceal the place where the bait had been laid from the insects. As bait two halves of a beetle belonging to the species *Tenebrio molitor* L., were used. The front piece, consisting of the head and the prothorax, continued to move the legs, palpi, and antennae, while the hind part was completely immobile. The bait had been laid on the ground in such a way that the two halves were about 5 cm. away from each other. The screen was removed.

The bait was noticed by one sand-beetle immediately after

the removal of the screen. The insect assumed its habitual posture of attack, raising its body on the anterior legs. The attack took place immediately afterwards and was directed decidedly towards the mobile bait. The action was observed by the second

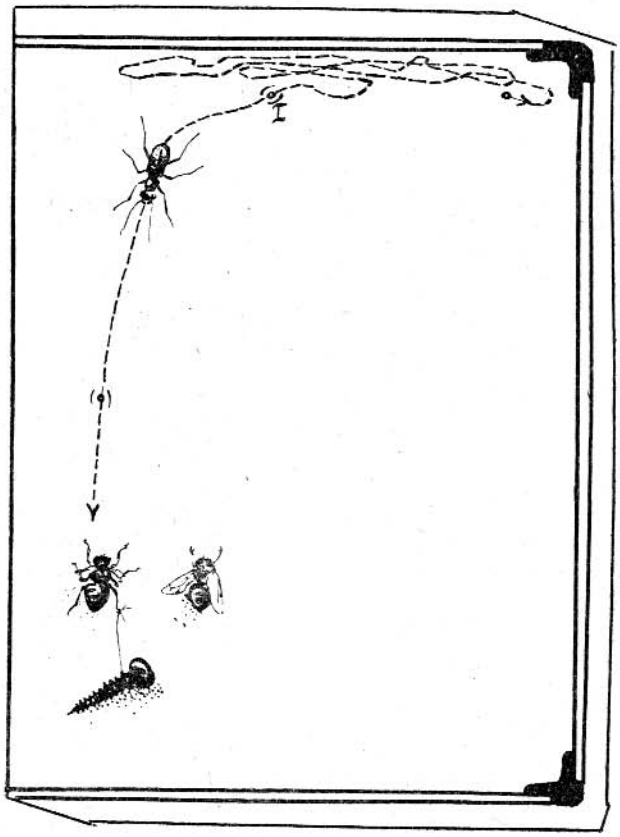


Fig. 4

specimen, which immediately passed from a state of repose to deliberate attack, omitting the preparatory habitual posture. The victim became the subject of battle between the two beetles. The weaker or less energetic one was thrust aside after several seconds of violent struggle. The stronger tore the food into pieces and began slowly to consume it. The distance from which the bait was seen was in both cases about 20 cm.

Experiment No. 26

Conditions: 11^{15} a. m. Strong insolation, temp. inside the vessel 30°C. Insects extremely active. Two specimens.

Two flies belonging to the species *Sarcophaga carnaea* L. were thrown behind a screen in the terrarium. One was alive, with its

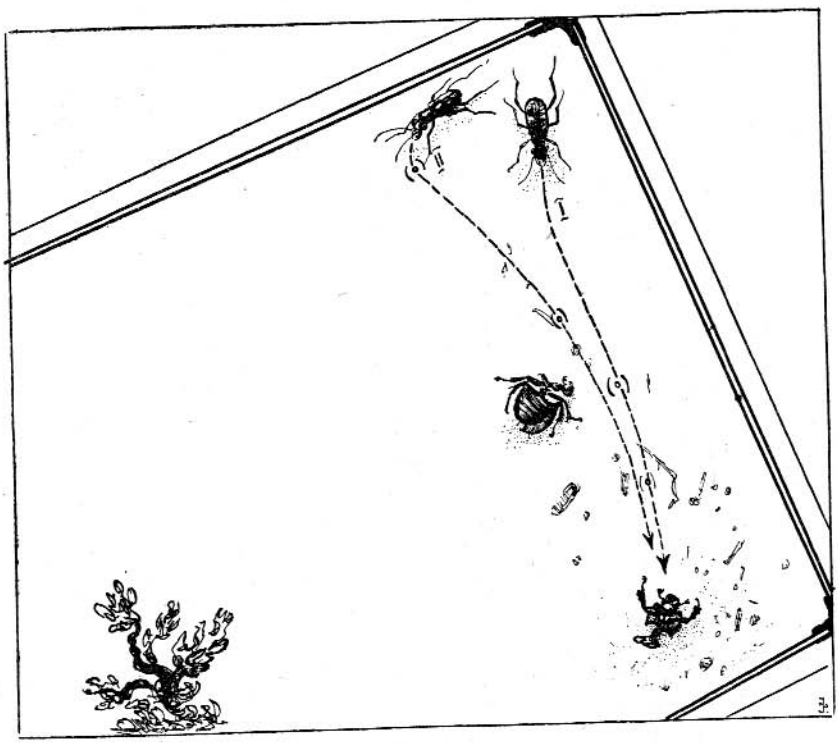


Fig. 5

wings cut off and also the feet on all three pairs of legs. It was tied to a short fine thread with a weight at the end. The second specimen was dead but not deformed and fresh (it had been killed just before the experiment). The distance between the two flies was 7 cm. The sand-beetle did not show any immediate reaction. The two insects ran about on the sand, searching the ground thoroughly. The bait was observed only after 3 minutes. The attack, carried out from a distance of 20 cm., was directed at the living bait. The fly was quickly torn into pieces and consumed (Fig. 4).

Experiment No. 41

Conditions: Terrarium of dimensions 30×40 cm. without anterior screen. Strong insolation. Time 5 p. m. Three specimens under the glass wall of the terrarium on the window side.

Two halves of a beetle (*Geotrupes silvaticus* Panz.) were thrown into the terrarium. They were placed at unequal distances from the front wall of the vessel. The immobile half was placed somewhat farther away in the opposite corner (Fig. 5), while the mobile half was near the front glass. The beettles reacted almost immediately after the food had been thrown into the terrarium. The specimen which attacked first assumed the habitual posture and run straight to the mobile half, which was about 20 cm. away, missing the immobile bait on the way. The second specimen made a similar attack, along a still shorter and straighter track than that of the first.

The experiments in the sub-group in which the beetles had to choose between mobile and immobile bait were carried out 17 times. The results are given below in tabular form.

Reactions to changes in the location of bait

Experiment No. 57

Conditions: Insolation incomplete, temperature 35°C. One specimen near the glass of the terrarium exposed to light.

A water beetle, *Acilius sulcatus* L., was thrown into the terrarium. The sudden appearence of the insect caused a rather quick reaction in the sand-beetle at that time near the glass lighted by the sun. The attack was typical, beginning by the taking up of the caracteristic „preparatory posture", after which the sand-beetle jumped towards the victim. In consequence of the rapid movement of the bait, which jumped in all directions, the pursuit took a very complicated course. Each turn of the pursuited water beetle caused a change of direction in the attack. The distance between the two insects was inconsiderable, from 2 to 3 cm. The sand-beetle tried to seize the constantly escaping victim in its mandibles. It succeeded only after a long and complicated chase. The victim was caught, torn to pieces and devoured. The duration of the whole reaction was extraordinarily short, about 20 sec. The distance from which the victim was perceived was 7-8 cm. (fig. 6).

Experiments of the above type were repeated 7 times (Nos. 58-64); the results obtained were each time almost identical. The distances from which the victims were perceived varied between 7 and 20 cm. The duration of the reaction was never more than 20 sec.

TABLE II

Species of bait	Type of bait	Distance from which bait perceived (in cm)	Result
Tenebrio molitor L. (transected into two parts)	mobile part (head+prothorax)	23	bait seized, devoured
	immobile part (meso- and metathorax with abdomen)	—	no reaction
	mobile part	?	bait seized, devoured
,,	immobile part	—	bait seized but relinquished
,,	mobile part	20	bait seized but relinquished
	immobile part	—	no reaction
	mobile part	16	typical choice, devoured
,,	immobile part	—	no reaction
	mobile part	25	typ. choice (hesitation) bait seized, devoured
	immobile part	—	no reaction
,,	mobile part	—	not noticed?
	immobile part	17	bait seized, devoured
,,	mobile part	22	decided choice, devoured
	immobile part	—	missed in choice
,,	mobile part (slight motion)	?	seized, devoured (second reaction)
,,	hind part (energetic movement of limbs)	18	bait seized and relinquished (first reaction) Possible memory of shape?
Calliphora vomitoria L.	dead contra living „anhored"	—	in 5 cases choice of the live bait. Result is seizing and devouring, or seizing and running away from the bait.

Reactions to changes in the activity of bait

The experiments described in the preceeding chapter referred only to cases in which the bait did not change the degree of their activity during the entire duration of the experiment, and moved steadily in the same way and without any pause in action.

The cycle of observations which is the subject of the present section includes cases in which the bait showed a variable type

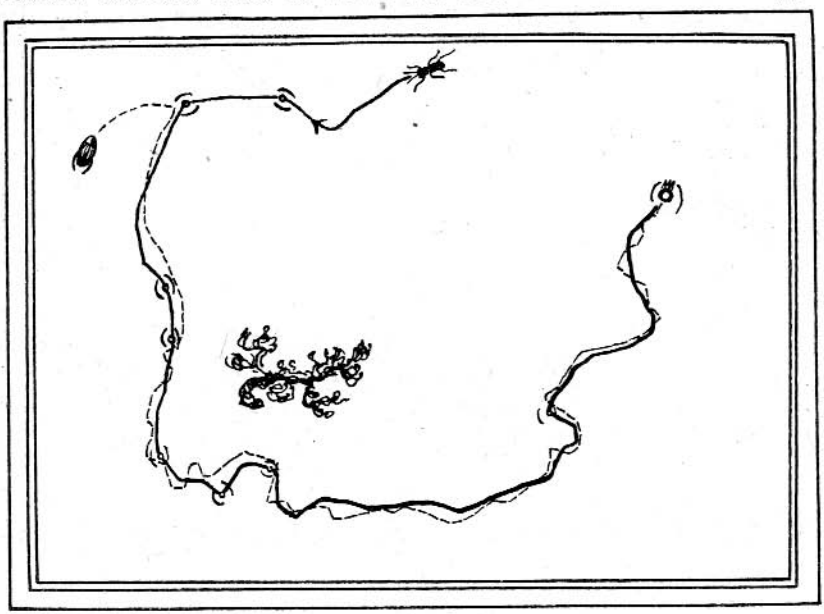


Fig. 6

of activity. Such changes might be the result of injury or the normal mode of defence of the pursued insects, consisting in a sudden transition from a state of full activity to one of complete immobility. The state of immobility might be permanent, as in those cases in which insects cut in half were used, or uninjured insects unable to live on dry land, e. g. larvae of dragon-flies. In these cases it usually meant death for the insect used as bait. Immobility of the bait might also be only temporary state, resulting from the insects assuming a posture of defence.

It was hoped that the reactions of the sand-beetle to changes in the activity of live bait would give an answer to the question of its ability to perceive and recognize food. Especially important

for our question were those reactions during which the bait passed into a state of immobility at the moment when the sand-beetle attacked or seized it.

Experiment No. 42

Conditions: 9^{30} a. m. Insolation as yet incomplete, lighting only a small strip of the terrarium. Two specimens hidden in plant clumps.

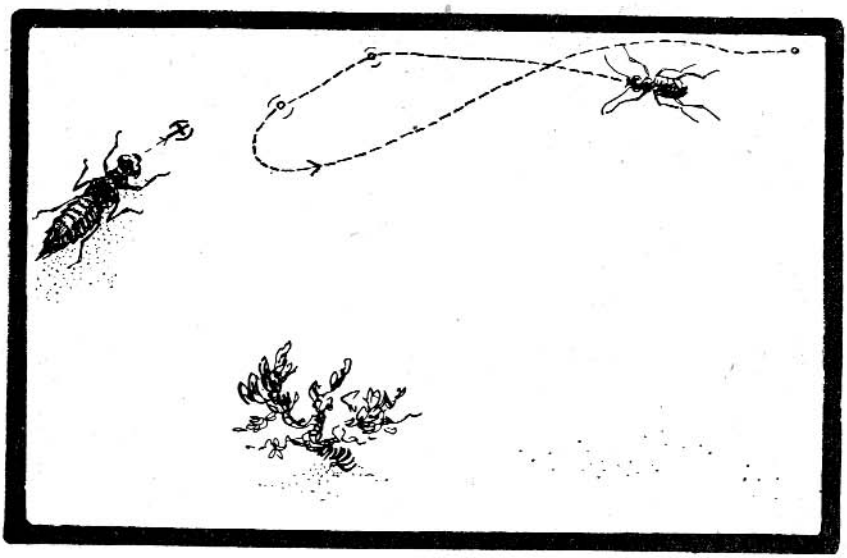


Fig. 7

After covering part of the experimental area with a paper screen, a larva of dragon-fly belonging to the genus *Aeschna* Leach. was placed on the floor of the terrarium (fig. 7). The insect crept very slowly over the sand, moving feebly. When the screen hiding it from view was removed, the bait was immediately attacked by one of the sand-beetles, which was about 10 cm away from it. The attack began typically with the characteristic posture of the insect. The moment in which the sand-beetle approached the victim to seize it, all movement in the larva ceased.

The beetle only ran a short way, did not reach its aim, turned, and exhibiting no interest whatsoever, went off towards the sunlit pane of the terrarium. The body of the larva remained in

its place for a whole hour and was never even touched by the beetles, which did not show any inclination to search for it during further experiments.

Experiment No. 43

Conditions: 2^{00} p. m. Strong insolation. Temperature inside the terrarium 40°C. Bait moving and changing place.

A beetle belonging to the specimen *Dermestes lardarius* L. was thrown into the terrarium on the sunlit side. The sudden appearence of an actively moving bait caused an immediate reaction in the sand-beetle, which attacked from a distance of 15 cm. The attack was extremely violent and was performed with great accuracy of direction. It did not succeed, however, since as soon as the aggressor drew near, the *Dermestes* fell into a state of complete immobility, drawing up all three pairs of legs. As result of this the sand-beetle passed the bait and ran beyond it. It aimed blows with its mandibles in a completely wrong direction, towards an assortment of various foreign objects such as sticks of wood, small stones, grains of sand caked by damp, but still missed its aim. After some abortive efforts the insect ran away towards the sunlit of the terrarium. But the battle was not ended; the resumption of the movement by the bait caused a new series of attacks on the part of the beetle, taking a course similar to that of the first.

The victim became for the time being immobile, the aggressor missed it and after unsuccessful trials turned away, losing interest in it, without getting food.

This was repeated twice more; afterwards the appearance of the bait produced no visible reaction in the sand-beetles and their sensitiveness to it ceased. The results are given in the table III.

Experiment No. 47

Conditions of the experiment: p. m. cloudy, temperature 35°C. Two specimens. A fly, *Lucilla caesar* L., as bait.

A dead fly was laid in the terrarium. The insect, absolutely immobile, did not cause any reaction in the sand-beetles, which were searching the whole area. Although the bait was left for

about 20 minutes, it was never perceived, or touched even by accident.

Another specimen of *Lucilla caesar* L. was placed at a distance of 7 cm. from the dead bait. This was done behind a screen, so that it could not be observed by the beetles. The new bait was living and fastened to short (2 cm.) thread ending in a weigth. The „anchored" specimen moved slowly; its feet and wings were cut off.

TABLE III

Bait	Reaction
Hister fimetarius Hrbst., actively moving.	Attack with greath accuracy of direction from distance 7 cm.
The same, but immobile	Bait seized and relinquished, abortive searching in its neighbourhood, running away.
Again immobile.	Aggressor turns and runs away.
Returning into action.	Immediate attack on the bait.

Hister fimetarius Hrbst., presented to the sand-beetle after 15 min. pause in the course of experiments. The bait moves quickly. Complete lack of reaction of the beetles. Only slight preparatory attitude, observed, without any consequences. The distances between the bait and the beetles varied from 20 to 7 cm.

After removing the screen, an immediate reaction was shown on the part of one beetle, which launched a decided attack against the mobile bait. The reaction was not concluded, because the bait became immobile too soon. The aggressor waited for a while in an attitude of attack, at a distance of about 3 cm. from its victim, and finally with drew and began to search in the near victim, and finally withdrew and began to search in the near caused a new attack, during which the insect nevertheless missed its aim, throwing itself toward the thread by which the bait was fastened to the weight and passing by the insect itself. When the bait again fell into a state of immobility, the beetle was completely bewildered. In its search, it seized many small objects in the neighbourhood, but even so did not find the food. The bait was seized only during the third attack.

In the next experiment (No. 48) the conduct of the beetle was somewhat different; confused by the lack of motion of the bait it turned immediately towards the dead specimen lying near by, at a distance of about 5 cm.

Another case (No. 49) greatly resembled the experiment with the *Aeschna* Leach larva. The beetle failing to make a choice, returned when only half-way and abandoned the bait.

The last two experiments (Nos. 50 and 51), using the species *Lucilla caesar* L. and *Calliphora vomitoria* L. gave no results, because the „anchored" flies elicited no reaction in the beetles.

Reactions to dead bait artificially moved

In order to analyse the essential differences between the reactions of beetles towards immobile and mobile bait, dead was moved artificially. The aim of these investigations was to decide whether the beetles react to any kind of movement by the bait, or only to a special type of movement.

Experiment No. 52

Conditions: 3^{30} p. m. Strong insolation. The specimens, running quickly over the sand, with a distinct tendency to make for the light.

A dried specimen of the water-beetle *Acilius sulcatus* L. was placed in the terrarium on a thread. It was possible to make the bait move, in imitation of the live insect, by light pulls on the thread. The motion of the dried bait did not cause any visible reaction in the beetles in the terrarium. During the whole course of the experiment the sand-beetles ran about indifferently in the vicinity of the bait, not even taking up the posture of attack. When the dead bait approched too close, the sand-beetles turned and ran to the other end of the terrarium.

In the next experiment (No. 53) a freshly killed but uninjured fly, *Sarcophaga carnaea* L. was used instead of a dry water beetle. Although flies belonging to the same species had been given to and eaten by the beetles the previous day, the bait caused no positive reaction; in the contrary it rather frightend the insects.

The next two experiments (Nos. 54 and 55) took a similar course; in these two species of flies *Calliphora vomitoria* L. and

Musca domestica L., and in four experiments (Nos. 54-59) *Sarcophaga carnaea* L. were used as a bait. An exception was experiment No. 60, in which the beetle seized an artificially moved dead fly, when the beetles favourite species *Calliphora vomitoria* L. was used. The attack was markedly „inhibited", and visibly carried out with apprehension and caution. The approach to the bait was rather slow, often interrupted with pauses. It was also observed that the beetle drew back and tried to attack from many sides. Once the bait was caught, the further reactions, i. e. the act of devouring followed a quite normal course.

The rôle of memory in the capture of food

Experiment No. 55

Conditions: 3^{20} p. m. Strong insolation. Near the lighted side were the remains of beetle, *Geotrupes silvaticus* Panz., left over from a former experiment performed 6 hours before with the same sand-beetles.

A water-bug, *Notonecta glauca* L., was thrown into the terrarium. The appearance of a quickly moving bait caused an immediate reaction in one sand-beetle, which carried out a lighting attack in its direction. As usual in such situations, a long chase began, ending in the capture of the bait.

At the moment when the victim was in the mandibles of the beetle, I interrupted the normal course of action by taking away the dead victim with a long forceps. The beetle, confused by its loss, looked around for the bait, running away and returning many times to the same place. In spite of repeated efforts, it did not find the food, and ran towards the *Geotrupes* remains left over from the previous experiment, in the opposite corner. The recognition of food was unhesitating. The insect made no mistake in its choice and seizure, although many inorganic objects were lying in the neighbourhood, which might have attracted its attention. It should be emphasised, as a characteristic fact, that an attack was made only on those pieces which had been used in the former experiment as mobile. Not once did the beetle turn to the immobile abdominal part, which had been untouched during the previous experiment, and lay near by.

During the experiments with flies it was observed that the beetles returned several times to the abandoned remains of *Tenebrio*, and also that they often returned with special stubborness to those places where they had been fed with mobile pieces of *Geotrupes*.

The question then arose, how would the beetle behave when the food taken from them was given back in another place?

In one experiment of this type (No. 67) a fly, *Calliphora vomitoria* L. was used as bait. After taking the bait from the grasp of the beetle's mandibles, and waiting some seconds during which the beetle searched intensively in the immediate neighbourhood, I put the same bait down, 10 cm. from the first place. The beetle immediately rushed in the new direction, seized the fly without mistake and at once began to devour it.

In an experiment with a water-bug, *Notonecta glauca* L., the beetle after the food was taken away, attacked an immobile dead bait, held in forceps about 5-6 cm. from the original place.

A characteristic illustration of the behaviour of the beetles at the moment of recovering lost food were those experiments in which a situation of choice was arranged. The beetles had to choose between dead, immobile bait which had just been taken from their mandibles and a new, quickly moving bait.

In six experiments performed at different periods, in the intervals between other experiments, the beetles always seized only that food which they had themselves first hunted. The attack was usually direct, unpreceded by preparatory phases, and the reaction particularly violent.

In these reactions, the insects showed a distinct ability to remember the shape and direction of the hunted bait.

Discussion

From the experiments we may state that sand-beetles obtain food in two ways: 1) by a continual search, in which case the victim is caught incidentally as the result of a direct meeting with it; 2) by a deliberate attack evoked by perception of the prey from a distance. A closer analysis of the two ways of getting food indicates that there are numerous differences between them.

In the first type, visual recognition does not play an important part, as the beetle literally catches at everything that happens to come its way, recognising the object only when in direct contact, presumably as a result of the action of chemo- or tango-receptors. The finding of food depends rather on accident, the prey as such never being recognized from a distance. The insects very often treat food as a neutral object, whereas in other cases inedible objects attract its attention. The search for food is chaotic, as is shown by the lack of decision as to the direction in which to run in order to get food. The duration of the reaction, taken from the moment of offering the prey to the time of its capture by the insects is comparatively very long, and may last in some extreme cases about 30 minutes. Beetles always search in this manner regardless of whether the prey is in the terrarium at the moment or not. This refers only to immobile bait.

Bait whose motion is caused by its organic life, evoked a different reaction, and is caught by deliberate attack. Bait whose motion is caused artificially does not cause any reaction, or else has a frightening effect.

The behaviour of the beetles towards live and mobile bait should be considered as a type of complex reaction. It consists of several successive stages, the number of which can be changed according to the reaction. In a typical reaction there are four stages. The first stage consists in the insect's taking up a preparatory attitude. By this we mean: a) a change in the position of the insect's body from the horizontal to a steeply inclined stance. In the majority of cases this appears distinctly, but may sometimes subside, or be barely noticeable: b) the turn of the long axis of the body towards the bait. The actual attack forms the second stage, consisting in a quick approach towards the prey by an interrupted run. The attack may be in one direction only, or may consist of short runs in different directions. The third stage is the capture, and the fourth, the devouring of the prey.

The typical picture of the reaction may be changed in many cases, as a result of the omission of certain stages. Depending on which of the four stages is missing, three kinds of reaction of a simplified character may be distinguished. These are: 1) Reactions limited to the assumption of a preparatory posture

by the beetle, the carrying out of the attack and capture, followed by the relinquishing of the prey (absence of stage 4). 2) Reactions in which the attack is only partial and therefore lacks both the remaining stages 3 and 4. 3) Reactions reduced to the first stage, i. e. the assumption of the preparatory attitude, followed a return to a state of quiescence.

Deviations from the typical reaction are chiefly caused by the behaviour of the bait, or because of its physical nature, for instance its hardeness or bad taste. The full course of the reaction can be observed in cases when the capture is characterized by continuous and longlasting movements. Simplified reactions (composed of 1 or 2 stages) appear when the bait at the moment of attack suddenly changes from a mobile to an immobile state. This change simultaneously evokes a change in the conduct of the sand-beetle, which begins to behave as it does in the presence of any immobile bait, i. e. it begins to search in a confused manner.

It may be concluded from this that the difference in the reaction depends exclusively on the kind of movement of the bait, not on its shape, which remains unchanged throughout the experiment. Further complications in the above reactions are constituted by phenomena in which the ability of the sand-beetle to remember appears as an additional factor. From the point of view of our problem these create special difficulties when inferring the possibility of distinguishing the shape of the bait, independently of its movement. Insects in which a lack of recognition of immobile objects has been many times confirmed, can in certain individual cases find their way with the help of sight to completely immobile food, thus showing a typical deliberate reaction. This takes place only when the food has previously been given to the insects as mobile bait. Sand-beetles also return to places in which bait has been formerly laid, but later removed.

The contradiction that occurs between the reactions of sand-beetles towards immobile and mobile baits on the one hand, and their reactions to immobile baits that were previously mobile on the other, can be solved if the ability of these insects to perceive the shape of objects is investigated.

The construction of the eye of the sand-beetle is not uniform, because the ommatidia are more dilated in some parts, while in others on the contrary they are set nearly parallel with each other. Moving from top to bottom, we first meet with a small

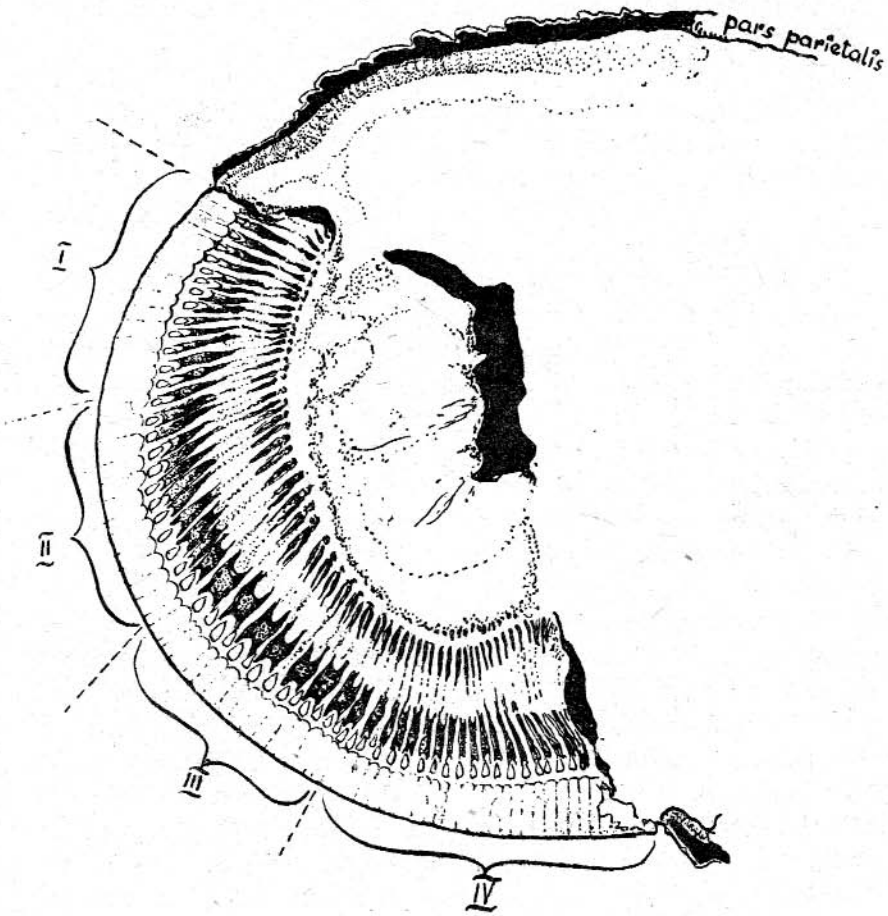


Fig. 8

group of short ommatidia placed very closely together and forming a widely spreading fan. (Group I. fig. 8). Directly below lies a group of ommatidia which are slightly longer and more widely separated (group II). This group as a whole indicates a certain definite direction of sight, more or less the same for all ommatidia. This direction is oblique and inclined downwards.

The next group (group III) differs from the former in the morphology of its ommatidia, which are distinctly broad here owing to a comparatively slight shortening in length. The lowest part of the eye is occupied by closely packed ommatidia of markedly slender construction. They are directed downward obliquely, some of them being completely perpendicular to the ground. Acuity of vision in these insects varies according to which part of the eye is used in the perception of objects. This may be calculated theoretically from the average value of the angle enclosed between the adjacent ommatidia (Baumgärtner [2]. On the basis of the calculations, according to Baumgärtner's geometrical formula, it may be ascertained that the optimum acuity of vision in *Cicindela hybrida* L. is found in the middle part of the eye (ommatidia groups II and III). It may be calculated that the eye of a sand-beetle, using the most acute of its parts, divides an object 1 cm. in length viewed from a distance of 20 cm. into 20 points of impression. In the case of two-dimensional objects, the number of points of impression is raised to the second power, so an object with an area of 1 cm^2. would be seen as a collection of 400 points about 0.5 cm. apart from each other.

Baumgärtner [2] carried out research on the structure of the field of vision and the accuracy of perception in bees. He used horizontal and vertical sections across the eye and head of these insects and also measured the angles enclosed between the axes of the ommatidia. His calculations shoved that the optimum vision in bees is found in the antero-medial section of the eye. This causes binocular vision to be found just in that part of the eye, whereas in other parts of the eye there only exists monocular vision and there is no special acuity of vision. Acuity diminishes towards the back of the head and is least in the superior and inferior parts of the eye. In bees only certain parts of the eye are designed to receive the picture of objects, and the remaining ommatidia serve as an apparatus for indicating the direction of objects.

Similar research was carried out on the larvae of the dragon-fly *Aeschna cyanaea* Müll. by Baldus [1], who obtained very similar results to those of Baumgärtner. The optimum acu-

ity of vision in the larvae of *Aeschna cyanaea* Müll. appears in the supero-anterior part of the eye. Calculations carried out on many species of insects (*Dytiscus* L., *Aeschna* F., *Simulium* Latr. show that the eyesight of sand-beetles is nearest to that of *Dytiscus marginalis* L., but differs very markedly from the acuity of vision in the dragon-fly larvae, in which the optimal acuity is found in the superior part of the eye. The visual acuity of the sand-beetle, compared with that of the human eye, is very interesting. Man is able to see an object whose size is not less than 1.68 mm. from a distance of 6 m. [8]. A sand-beetle can see an object 30 cm. in size from the same distance, using the average „sharp" part of the eye (ommatidia groups II and III). The superior part of the eye (Group 1) may be considered as the part adapted to seeing the movement of objects, i. e. the apparatus by which the insect can be directed towards certain objects which attract its attention by their movement, but cannot be recognized on account of their small size or the distance.

The physiological faculty of seeing objects from not too great a distance, however, does not mean that sand-beetles always distinguish the food-bait as such in a given shape. Inability to distinguisch occurs in the case of immobile bait. Situations where memory plays a part form an exception. This fact can be explained by the biological type of the sand-beetle, which is a predatory insect, feeding on living and actively moving food. From this point of view may be understood also the case of non-reaction to any type of movement differing from that which characterizes living organisms.

In the first place, sand-beetles react to movement of a definite type. This allows them to distinguish living food from other surrounding elements not constituting food, e. g. leaves moving in the wind. The sand-beetle's ability to see shapes is specially apparent in cases where memory cooperates. Beetles remember the places where the bait was put down, as well as the shape of the latter and possibly also its taste or smell and texture. The behaviour of sand-beetles towards food is typical of those animals whose chief sense of orientation is vision.

In other predatory insects, e. g. *Dytiscus marginalis* L., which feeds at night or at twilight, and also under water, the sense of

vision plays a subordinate part, although it possesses a relatively well-developed organ of vision, and in such cases the cybernetic sense is the chemical. The research of Schaller [7] shows that the sense of vision in *Dytiscus* L., never works alone, but only in cooperation with the chemical sense and also with that of touch. In coprophagic beetles which have a nocturnal life the only sense of orientation as to their food is the sense of smell. Wahrnke's research [10] on the life of two species of beetles, *Geotrupes silvaticus* Panz. and *Geotrupes vernalis* L., showed a „double" orientation in these animals: the so-called „wide-range orientation", of which the organs are the chemoreceptors found on the antennae, and „near orientation", less accurate, effected by the action of other chemoreceptors placed on the maxillary and labial palps. The rôle of the sense of sight in the two species is limited to the orientation of the animals towards the incidence of light.

Visual orientation, e. g. in the above-mentioned dragon-fly larvae, recalls the orientation of sand-beetles. The reactions of capture are caused only by living objects, well detached from the background. The distances from which these animals react to their food does not exceed a few centimetres, which is much less than in the sand-beetles. According to Baldus [1], the dragon-fly finds its way with the aid of a chemical sense, though the rôle of this is subsidiary.

As to the importance of the chemical sense in the space orientation of sand-beetles, we still lack knowledge and this question demands separate research.

STRESZCZENIE

Celem niniejszej pracy było zbadanie i zanalizowanie zachowania się chrząszczy z rodzaju *Cicindela* L. przy zdobywaniu pokarmu. Metodyka badań polegała na podawaniu owadom żywych lub martwych, a więc poruszających się lub nieruchomych, zwierząt bezkręgowych, np. mięczaków, chrząszczy, much, pluskwiaków. W doświadczeniach stwierdzono, że trzyszcze reagują jedynie na pokarm żywy i poruszający się w sposób naturalny, nie

reagują natomiast na podawane im zwierzęta martwe i nieruchome lub poruszane przy pomocy nici. Stwierdzono u trzyszczy również wybitne zdolności pamięciowe. Odnajdowały one miejsce, na którym niegdyś znajdowała się przynęta, jak również rozpoznawały samą przynętę.

PIŚMIENNICTWO — LITERATURE

[1] Baldus, K., Experimentelle Untersuchungen über Entfernungslokalisation der Libellen (*Aeschna cyanaea*), Zeitsch. vergl. Physiol., Berlin, 3, 1926, p. 475-506.
[2] Baumgärtner, H., Der Formensinn und die Sehschärfe der Bienen, Zeitsch. vergl. Physiol., Berlin, 7, 1928, p. 56-81.
[3] Hertz, M., Die Organisation des optischen Feldes der Biene, Zeitsch. vergl. Physiol., Berlin, 8, 1929, p. 693-749.
[4] Hesse, und Doflein, Tierbau und Tierleben, Leipzig 1914.
[5] Handlirsch, A., *Insecta* in Kükenthal, Handbuch der Zoologie, Bd. 4, Berlin 1933-1936.
[6] Reuther, O. M., Lebensgewohnheiten und Instinkte der Insekten, Berlin 1913.
[7] Schaller, A., Sinnespsychologie und psychologische Untersuchungen an Wasserkäfern (*Cybister*, *Dytiscus*), Zeitschr. vergl. Physiol., Berlin, 4, 1926, p. 370-465.
[8] Szabuniewicz, B., Zarys fizjologii człowieka, Kraków 1949.
[9] Uexküll, J. und Brock, Fr., Atlas zur Bestimmung der Orte in den Seheräumen der Tiere, Zeitsch. vergl. Physiol., Berlin, 5, 1926, p. 167-179.
[10] Wahrnke, G., Experimentelle Untersuchungen über den Geruchsinn von *Geotrupes silvaticus* Panz., Zeitsch. vergl. Physiol., Berlin, 14, 1931, p. 121-200.
[11] Weber, H., Lehrbuch der Entomologie (Sinnesorgane), Jena 1933.