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Ethological defence mechanisms in insects. II. Active defence

Etologiczne mechanizmy obronne owadów. II. Obrona czynna

SUMMARY

Based on literature data, the current article presents active defence strategies employed in the world of insects. Examples of escape increasing the probability of survival of potential prey that has not only been localized but also already attacked are described here. Also, the modes of warding off predators adopted by threatened individuals as well as effectiveness of immobility have been discussed. We have described threatening behaviour of potential victims and use of more than one defence strategies. Construction of shelters by some species larvae has been regarded in the article as a form of active defence.

STRESZCZENIE

W niniejszym artykule na podstawie danych z piśmiennictwa przedstawiono aktywne strategie obrony stosowane w świecie owadów. Opisano przykłady ucieczki, zwiększającej prawdopodobieństwo przeżycia nie tylko zlokalizowanej potencjalnej ofiary, ale nawet już zaatakowanej. Omówiono także sposoby straszenia drapieżcy, skuteczność znieruchomienia zagrożonych osobników. Przedstawiono zachowania grożące ewentualnych ofiar i stosowanie przez nie więcej niż jednej strategii obrony. Jako formę aktywnej obrony uznano i przedstawiono tworzenie budowli przez larwy wybranych gatunków owadów.

K e y w o r d s: insects, active defence, escape, threatening behaviour, immobility, stratagems, building mechanism

Słowa kluczowe: owady, aktywne strategie obrony, ucieczka, sposoby straszenia drapiecy, znieruchomienie, strategie obrony, mechanizm tworzenia budowli.

Due to large number of species, their inhabitation of various ecological niches and a relatively small body size, insects live under high predation pressure exerted by animals belonging to many taxonomic groups and exhibiting different modes of hunting. This requires that the insects – potential prey – should readily recognize the threat. They have to detect an approaching enemy as early as possible and anticipate its attack (32, 30).

The most common way of active defence is to escape or jump in a direction opposite to that of the approaching danger. This type of behaviour also includes motionlessness, adoption of a threatening posture, exposure or even use of defence organs, various stratagems, and group life. In individual cases, animals interact with representatives of other species that provide security for them. Larvae of many insect species build shelters, which serve as a refuge also for pupae, adults and eggs that they lay. Once a defence mode strategy proves effective even in only a few percent, it fulfils an essential role in species life and, being a positive trait, is subject to natural selection (26, 10).

Escape

It has already been mentioned that escape, if it proves to be effective, is one of the active defence strategies (10). It increases the probability of survival when the prey has been localised or even attacked. The quicker the prey moves in comparison to the attacker, the higher its chances for survival are; the escape reaction depends on the predator's tactics and the living environment. Although escape seems to be the simplest defence strategy, it requires substantial energy input (26, 30).

While larvae of some mayfly species from the family *Baetidae* living in the lake littoral zone can cover a distance of several centimetres with one swift leap and evade its pursuer – a fish (30), others, when in emergency, are carried away by the water current (29). At the sight of their relatives floating on water, the larvae of these mayflies rapidly leave their feeding sites as well. Water striders, e.g. the common water strider (*Gerris lacustris*) (*Gerridae*), the residents of the surface of stagnant waters – puddles and ponds, and of slow-flowing waters, stay and run on the surface using two mechanisms: thanks to their long, thin legs, their body weight is evenly distributed over a large area and the air bubbles trapped among the dense setae on the second and third pair of legs allow them to slide on the water. During the escape, the second pair of legs serves as oars – they hit the water surface and push the animal forward at a distance of approximately a dozen or even 100 cm, while the third pair of legs controls the direction of the motion (4, 5, 31, 34). Water striders evade the risk of cannibalistic attacks launched by larger individuals by jumping sideways and then circling around the attacker. This is a very effective method of defence, as a hunting water strider cannot change the direction of motion, hence the tracks of the prey and the attacker diverge (30). Individuals of some water strider species aggregate during the day and form a big collective body for safety. It they are threatened, they rapidly scatter in various directions. This method is effective, as the hunting predator must approach and focus its eyes on the prey. When the possible victim disappears from its sight, the pursuer now has to attack another individual. A repeated change of the target "muddles and confuses" the predator and makes it impossible to select the prey precisely and effectively (13). A similar strategy of defence is employed by beetles (*Gyrinidae*), e.g. the whirligig beetle (*Gyrinus natator*). A group of individuals float on the surface of stagnant water with the use of oar-like hind legs, thereby constantly generating waves around them. When disturbed, they scatter rapidly in all directions and confuse the predator. When the danger disappears, they aggregate again. Safety rather than preying or reproduction is the only benefit of aggregation behaviour in these beetles (18, 31).

This type of defence is well illustrated by an experiment in which a few table tennis balls of the same colour are tossed simultaneously. While scattering in different directions, the balls distract attention of the person who wants to catch one of them but fails.

The human flea (*Pulex irritans*) (*Pulicidae*) escapes successfully by jumping from a standstill to reach a 120–130 up to 200-fold greater height than the length of its body, with the rate of 500 times within an hour. This is possible thanks to exceptionally elastic muscles in the hind legs and arches of body segments containing an elastic protein called resilin (3). During a leap, resilin expands and, thanks to the energy accumulated in it, the thoracic segments spread apart while the strong hind legs with long coxae stretch out and throw the flea rapidly up into the air within 0.7–1.2 µsec (5, 19, 34).

Springtails (*Collembola*) also effectively escape from their predators. Lack of wings is compensated by a special jumping apparatus consisting of the so-called furcula and hinge. The furcula – modified abdominal legs – is a forked, tail-like appendage folded forward underneath the body. When in danger, the insect bends the abdomen; then, the furcula is released from the hinge, springs against ground and within 4 µsec forces the insect to leap forward through the air at the height of approximately 20 cm away from the predator. While in the air, the animal performs one or a few somersaults and rapidly disappears from the attacker's sight. During the jump, the apparatus returns to the initial position (4, 31, 19, 34).

A unique escape mode is used by the *Boreus westwoodi* (*Boreidae*), which is active throughout the year. The wing stumps in the male and quite rudimentary wings clinging to the body in the female do not provide the ability to fly. However, the threatened insect evades predators by making a mighty jump, thanks to the structure of the legs. The joints contain microscopic pads, at rest tightly blocked by muscles. In danger, the insect releases the pads, which rapidly expand and ensure an instantly jump increasing the chance to evade predators (11, 31).

The desert cricket *Schizodactylus monstrosus* (*Schizodactylidae*) hides in the sand in the case of emergency. Legs with propeller-shaped tarsi enable the insect to dig a hole instantly, and wings rolled in the form of springs at this time are secured and do not offer resistance (25).

Threat and escape

Many species of moths and butterflies ensure themselves enough time by using shock tactics against the attacker. The most common is the image of an eye on the wings; in some butterflies it is composed of dark spots only – the pupils, whereas in others concentrically arranged spots form a more accurate eye image, in which a "pupil" and an "iris" can be distinguished.

The moth *Reucanelle leucane*, for instance, has an image of a pair of eyes on the underside of the wings. The black "pupil" is surrounded by orange, brown, and black circles. They are not visible when the moth is safe; when disturbed, however, it suddenly spreads its wings and demonstrates these "scary eyes". The view of the colourful patches deters the attacking bird, which is probably deceived to see a big, dangerous animal, as the whole body of the moth resembles the head of the bird's predator – the cat. The moth takes advantage of the element of surprise and flies away (23, 34). Many studies confirm the hypothesis of the "surprise effect" exerted mainly by the eye-like pattern (21).

A similar tactic is employed by the eyed hawk-moth (*Smerinthus ocellata*) (*Sphingidae*). When sitting on an apple tree trunk with the forewings covering the hindwings, it reminds of a drooping withered leaf. If this sort of camouflage fails, the butterfly moves its forewings rhythmically and the hindwings, which are usually attacked by the predator, show the eyespots. The defensive position confuses the predator, which allows the butterfly to fly away (6). Similarly to butterflies, bugs resort to the tactics of displaying the scary, false eyes as well. The eyes of *Fulgora laternaria* (*Fulgoridae*) startle the predator when the disturbed insect begins to move.

When motionless, the European grasshopper (*Oedipoda miniata*) (*Arcididae*) merges into the background and looks like a mottled stone. In danger, it suddenly shows its pink hindwings flashing against the predator; before the attacker recovers from the shock, the victim is already far away (34). Similarly, the mantis *Pseudocreobotra wahlbergi* (*Mantidae*) also startles its enemies. When an insectivorous mammal approaches, the insect adopts a defensive position: it spreads the forelegs and bright wings, which are usually hidden under the elytra. The mantis flutters the wings, and the terrifying effect is enhanced by the eye-shaped spots. The defensive behaviour of the mantis distracts the predator, which allows it to escape (4). The mantis is occasionally provided with security while devouring a hornet. As long as the praying mantis feeds on it, the warning colour of the hornet deters even such an effective predator as the chameleon; however, after the feast, the mantis usually becomes its victim.

Immobility – thanatosis

While preying, many predatory insectivorous animals are attracted not by the appearance of a possible victim, but its mobility, which draws attention and incites the attack. Even the slightest movement is a valuable clue for the preying animal to launch an attack; therefore, immobility of the victim is an extremely effective form of defence applied by insects. When the prey ceases to move, it is difficult to be spotted in the surroundings. In a dangerous situation, caterpillars of many insects curl up into a ring shape and inertly fall off the leaf or twig to which they have been strongly attached. After a longer time, they resume locomotion in the new environment, provided the predator has lost track of them. Such behaviour is not a “trick” but an instinctive response to disturbance (22). The immobility tactics are employed in emergency by dragonfly larvae to deter fish and by mosquito larvae for protection against the common backswimmer (*Notonecta glauca*) (*Notonectidae*) (30).

Females of the horntail from the order *Hymenoptera*, equipped with a long and strong ovipositor, lay eggs into the wood of coniferous trees at a depth of several centimetres. The larvae of these horntail drill large, irregular tunnels up to 40 cm long. These may seem to be absolutely safe refuges. Unfortunately (or fortunately from the point of the human economy) the larvae are threatened by some hymenoptera from the family *Ichneumonidae*, which ensure the development of its larvae by depositing eggs in the body of horntail larvae. The female of *Megarhyssa macrura* runs along the tree trunk to find the feeding site of the horntail larvae. This is possible thanks to two senses: smell and hearing. With the use of receptors located on the antennae, it detects volatile substances emitted by a fungus growing on the faeces of horntail larvae; the “eavesdropping apparatus” made up of sensory cells arranged on all legs is employed for localisation of vibrations induced by the larval feeding activity. When the female discovers the exact feeding site of the pest larvae, it pauses, bends the abdomen upward and firmly introduces the ovipositor into the wood for several minutes until it reaches the larval body and lays an egg on it (5, 31, 22). However, horntail larvae have developed a defence mechanism; namely, they cease their activity and simply become motionless on receiving the sound of the drilling ovipositor. As a result, the *Megarhyssa macrura* female often fails to reach the larval body and lays its egg next to it, thus causing destruction of the egg (11).

Threatening behaviour

A common form of insect threatening behaviour is increasing the body size and use of sounds. In emergency, the Madagascar hissing cockroach (*Gromphadorhina portenosa*) (*Blattidae*) inhales as much air into the respiratory system as possible. This phenomenon has a double significance: the animal body size increases and makes it look more dangerous and it produces a hissing sound when the air is exhaled. When the whole colony of cockroaches makes the sounds, even a very hungry predator gives up.

The cricket *Hemideina thoracica* (*Stenopelmatoidae*) takes a threatening position when alarmed: it lifts the massive hind legs armed with spines, with which it may even injure the predator. Furthermore, the spines on the legs produce unpleasant sounds when the insect starts to move (25).

The larvae of the carpet beetle (*Anthrenus scrophulariae*) (*Dermestidae*) have tufts of short setae on the body, and larger tufts on the last abdominal segment which they can ruffle. When touched, the insects raise the setae and thus seem to be bigger and similar to a little hedgehog (6).

The openings of bumblebee nests are protected by guard workers. Until midnight, the guard emits short buzzing sounds at irregular intervals. When it spots the danger, it raises the alarm. Other individuals leave the nest, take the supine position, put forward their stings and hold them upwards. A certain group of termites exhibits highly advanced threatening behaviour. When the colony is attacked, some soldiers inhale air and increase the size of the body so enormously (in many cases they explode) that they block the lumen of the tunnel along which attackers could get inside the nest and threaten the queen and young individuals.

The African weaver ants, e.g. *Oecophylla longinoda* (*Formicidae*), living on grapefruit tree branches in Kenya, do not retreat when in danger, but assume a threatening posture: they raise the antennae for better detection of air currents caused by the enemy, lift their abdomens and open their mandibles widely. They demonstrate self-confidence and decisiveness in aggression, and instantly attack the predatory animal. Their colonies in Kenya are so large that one of them can inhabit the branches and trunks of up to 17 large trees (19).

The caterpillar of the privet hawk moth (*Sphinx lingustri*) (*Sphingidae*), is pale green with white and purple slanting stripes along the body and is equipped with a pointed spine protecting the rear part of the body. In danger, it takes a threatening position, lifting the anterior part of the body as high as possible (6, 31).

Having exhausted its reproductive capacity, the bee *Halictus zebrus (Halictidae)* assumes the role of a "doorman" in its nest: it continuously stands on guard with its head in the nest entrance and, by retreating, opens it only to the colony members, while strangers are kept at a distance (ants, flies). A nest intruder wishing to enter the nest is deterred by body movements; if the attacker does not resign, the doorman leaves its stand, runs up and pounces on it, tugs and forces it back; next it returns to the nest and continues fulfilling the function of a doorman until death (14).

The caterpillar of the swallowtail butterfly (*Papilio machaon*) from the family *Papilioninae* is equipped with a special weapon. When touched, it exhibits a bifurcated, threatening structure behind the head, simultaneously emitting a distinctive odour (6, 31).

Stratagems

This part of the paper presents the behaviour of insects which use more than one strategy or its particular type to evade the enemy.

Most moths are prey for insectivorous bat species. They use several kinds of strategies against the bat's sonar and their flying tactics. The first weapon that moths use is "masking of sound". A special arrangement of scales on the whole body and fringes of a length of 2 mm and a diameter of 0.007 mm in the wings reduce air turbulence to a minimum. These structures not only prevent reflection of sounds, but also absorb them. In this way, the moths are quite elusive for the predator's sonar at a distance of more than 6 meters (11, 12).

In turn, bear moths have a special hearing apparatus: specific ears to "monitor" the ultrasounds emitted by the enemy at a distance of up to 30 meters. The moth ear consists of the tympanic membrane, behind which there is an air cavity and a band of connective tissue with two nerve cells. The nerve fibres extend from these cells to the tympanic membrane at one end and the brain at the other. At the distance below 30 metres, the moth rapidly changes the course of flight and moves away from the echolocation range of the enemy. The bat has not yet tracked down the prey from this distance. Moths do not perceive differences in the sound pitch but can sense subtle differences in sound intensity. Loud sounds trigger more signals in the nerve fibres and stimulate a more prompt response of the ear neurons. Both signals together exclude errors. The bat uses a zigzag-shaped flight path, which allows him to attack its victim by surprise; by flying only in a straight line, it would probably not find any insect (11). When the bat approaches the prey at a distance below 6 meters, it can "see" it on its sonar. At that time, moths still try to defend themselves: some fold their wings and nose-dive, while others sharply rise up in the air to regain the lost altitude; some other species perform "barrel rolls" or "loops" during the flight. Four out of ten individuals save their life in this way. Some representatives of this group of insects apply all these manoeuvres, and the flying pursuers often fail to catch them. In addition to the acrobatic figures, in the case of the highest emergency, bear moths resort to emitting ultrasounds – "shrieks" of at the same frequency as their persecutors, which deters bats from preying and makes them fly away (12, 24). The butterfly's transmitter is a flexible, toothed, chitinous plate located on both sides of the base of legs III and a "resonance box" underneath – an air container. The plate vibrates when the moth tightens and relaxes its leg muscles. The moth makes sounds when the bat approaches it only at a distance ± 0.5 m (34). It has not been fully explained yet how moth's ultrasounds affect the bat – whether they disturb the echolocation tracking the prey or inform and persuade the predator that "I am an inedible animal" (11).

The rove beetle (*Stenus bimaculatus*) (*Staphylinidae*), known in America as the Jesus beetle, inhabiting the coastal zone of our lakes, escapes to water when attacked by ants in order to take advantage of the water's surface tension. It moves along the surface thanks to the layer of tarsal setae on all the legs, which trap small air bubbles. The beetle glides on water thanks to these bubbles, which act as floats (12). When attacked in water by predatory striders or spiders, the rove beetle uses a different "secret weapon" – it sprays the surface of water with a camphor-like substance secreted by two abdominal glands, which acts as a detergent. It reduces molecular attraction of water, thus the predators drown. The beetle itself is not only outside the zone of the released substances, but is also pushed forward by a tiny, breaking wave which is generated where the water surface tension vanishes. Thus, as if it was motor-driven, the insect moves along the surface at a three-fold greater speed than when it is undisturbed. Additionally, bending of the abdomen allows it to change the direction of the movement quickly and get on the shore out of reach of aquatic predators (2, 31, 12). An interesting defence mechanism is employed by a tropical long-legged mosquito species. When in danger, it spins the legs so fast that it disappears from sight and becomes invisible even for the human eye, in a similar manner as the spinning aircraft propeller does. Nevertheless, the mosquito often fails to deceive the predator.

A peculiar defence tactic is used by the larva of the tortoise beetle (*Cassida nebulosa*) *(Cassidinae)*: it collects its own faeces, mounts them on the bifurcated abdomen, and offers it to ants trying to bite it (12).

A relative of the green tortoise beetle – the beetle *Hemisphaerota cyanea* (*Chrysomelidae*), inhabiting Florida, is a real athlete. It can adhere to the ground for two minutes tightly enough to withstand predator's attempts to detach it with power that is 60–300 times higher than its body weight. This is possible thanks to special adhesive pads on the legs, covered with fine setae (10,000 on each tarsus). The bifurcated setae release a drop of oily substance, which enhances their adhesion and thus allows the whole animal body to adhere tightly to the ground. This prevents ants from gaining access to the soft ventral parts of the body (34). A similar defence tactic is applied by the European beetle *Amphotis marginata* (*Nitidulidae*), which resembles a turtle. Lurking at the trails of the ant *Lasius fuliginosus* (*Formicidae*) at night, it mimics ants' begging behaviour – by striking the workers on the head or lower mandible with its antennae, the beetle urges the ants to donate a drop of food. However, when the ants realise they have been deceived, they mount an attack on the intruder; the beetle then hides its legs and antennae under the crust and adheres to the ground with the use of special setae on the legs. Ants are not able either to overturn it or carry it to the anthill. The beetle waits till the threat is over and looks for next prey (19).

Japanese bees (*Apis cerana japonica*) (*Apidae*) defend their hive against hornets in a sophisticated way. They wait until the hornet scout enters the hive and then an army of about 500 soldiers surrounds it tightly, forming a "live ball". The movement of the wings increases the temperature to 47°C, which does not harm the bees but quickly kills the intruder; one could say that the aggressor is roasted alive, since the lethal temperature for the hornet is already above 44°C. This prevents the hornet scout from passing the chemical information to its relatives about the location of the bees' nest; thus a collective attack of Japanese hornets is prevented. The defence exhibited by the Japanese honeybee is possible, because the temperature that is lethal for this species ranges from 48° to 50° C. The European bees, however, do not have such an ability to defend themselves (27).

Hatched larvae of *Ascaloptynx furcifer* (*Ascalaphidae*), a species from the order of net-winged insects (*Neuroptera*), form a collective body as an emergency defence reaction. They aggregate tightly pointing their heads toward the oppressor and threaten it by raising and lowering the heads, and alternately clenching and opening their long and sharp jaws (33).

The larva of the puss moth (*Cerura vinula*) (*Notodontidae*) "grazes" on leaves. The colour of its body is exactly the same as the colour of the leaves of the plant, i.e. it is usually bright green. When an intruder shakes the twig and disturbs the caterpillar, its inconspicuous body changes rapidly. It pulls its head into the abdominal segments and reveals a scarlet mask – a red outline of a head with sharply marked black spots looking like eyes; this makes the mask resemble the snout of a vertebrate animal. Additionally, it runs away lifting up the distal bifurcated segment of the body. If, however, the attacker does not give up and still approaches the prey, the larva uses long blood-red flagellae to whip the air around it. Extremely unrelenting enemies are attacked by a stream of formic acid squirted from a gland located near the mouth (1, 22).

An interesting strategy of defence was found in *Umbonia crassocornis* (Corsica), a representative of *Membracidae*. The nymphs of this species are often attacked by wasps while feeding on the sap from acacia branches wounded by the female. At first, the larvae become motionless. When the predator tries to remove one of them from the branch, all the larvae begin to stamp. Only rhythmic stamping is interpreted by the protective mother, which at that time is staying at the resting position at the bottom of the branch, as a signal for maternal response. The female approaches and attacks the predator by kicking it with the hind legs. The wasp gives up the prey, but it still circles around. The nymphs continue to stamp, while the mother threatens the predator until it flies away. Now the female sends out reassuring signals to the larvae, which become calm and begin to move: these at the edge of the group take the central position, and larvae occupying the centre of the aggregation move to the edge (27).

Very interesting and effective defence mechanisms are employed by worker ants from the hot climate zone. *Odontomachus bauri,* a representative of the subfamily *Ponerinae*, defends its nests by attacking the enemy with thin, long, serrated jaws that can open 180°; when it only threatens the predator, it snaps the mandibles in the air with an accompanying metallic sound. The closing of the mandibles lasts only one millisecond. Such a quick response is possible thanks to the sensory setae at the base of the mandibles, large nerve cells placed in the air spaces, and thick fibres conducting action potentials to the brain. A mechanism that increases the effectiveness of nest defence is the ants' ability to catapult themselves. When the workers bend their heads and hit the mandibles against a hard surface, they are thrown up in the air to a height of about 40 cm. While falling, they attack the enemy on unexpected places of the body. Another defence organ in *Odontomachus bauri* is a sting, used simultaneously with the mandibles. The ants insert it into the predator's body, which is accompanied by bending the abdomen and injecting formic acid (19).

In contrast to other species, *Basiceros manni* (*Formicidae*) ants do not scatter when their nest is discovered, but remain motionless for several minutes without even moving their antennae. This behaviour ensures safety from predators that use the sense of sight in preying, e.g. birds and lizards. Additionally, safety is enhanced by ground particles deposited on ants' bodies. These are held by long, bifurcate setae covering the dorsum. The older the workers are, the more "dirt" they wear on themselves. Compared to other species, these ants devote very little time to body care, which makes them particularly well camouflaged against mouldering soil and litter (19).

Construction of bags

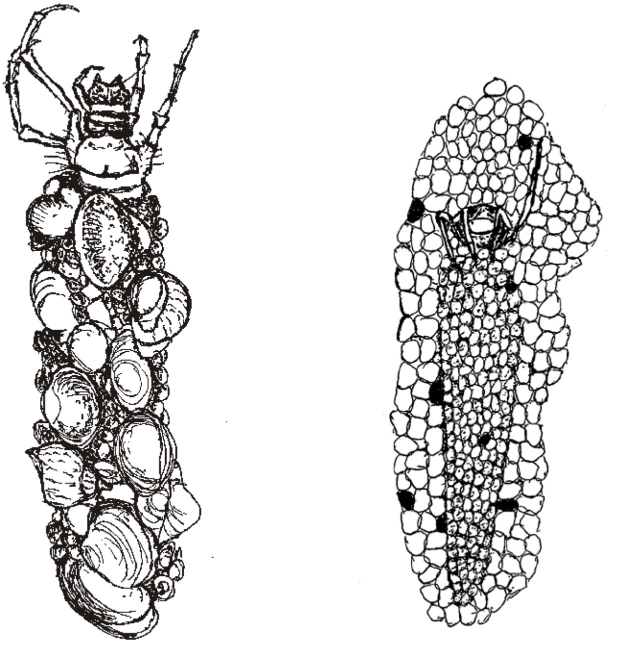
Construction of various types of hide-away shelters from materials collected in the environment is regarded as a special kind of defence acquired through evolution.

The woolly apple aphid (*Eriosoma lanigerim*) (*Erisomatidae*) appearing en masse on apple trees secretes white waxy strands. The entire insect colony (as well as tree branches) is covered with it and thus protected from enemies.

The leaf beetle larva (*Clytra quadripunctata*)(*Chrysomelidae*) is a pest of ant nests, as it feeds on their eggs. In the anthill, it remains hidden in its own shelter – a case, from which it shows the anterior part of the body. The larva builds the case using its own excrements and expands it when necessary. When attacked by ants, the larva quickly hides in its shelter and thus remains safe.

Larvae of many species of caddis flies (*Phryganeidae*), inhabiting streams, shores of large lakes and ponds, are masters in building shelters. The first step of the construction of a portable case is building a tubular structure made of silky secretion of the salivary glands, to which the larvae then attach various elements that constitute the final form of the shelter, e.g. sand, gravel, stones, water-soaked pieces of wood, and snail shells, sometimes still housing their residents. The choice of material depends on the environment and on the genetically conditioned behaviour. Obviously, the front part of the shelter expands as the larva grows. The proper length of the shelter is established by the larva with the use of sensory setae located at the distal part of the body (11). The method of construction, the composition of the materials used for the structure, and the shape of the shelter are usually quite distinctive and allow unmistakable identification of the particular species from this group of insects (15) (Fig. 1). An important function of the portable, tubular case of the caddis fly larvae is primarily to provide camouflage against predators, e.g. larvae of other insects, fish and birds. This is achieved by adjusting the colour and shape of the case to the background (9). Additionally, the shelter offers mechanical protection to the soft larval body. When the larva moves, its head and the anterior part of the body is outside the case, and in emergencies, the larva retreats inside. The structure is attached to the first segment of the abdomen by a dorsal appendage and to the posterior segment by two bifurcated appendages. In addition to the tubular, portable cases, the caddis_fly larvae build stationary refuges.

Yet another defence strategy has been described in caddis flies inhabiting lakes. Faced with pressure from large predators such as fish and birds, caddis flies prefer the strategy of "dispersal of the population mass" i.e., the individuals are small but numerous, which reduces the intensity of optical and mechanical signals sent by them. However, an opposite strategy of "aggregation of the population biomass", in other words, "size refuge" (7) i.e., where there are only a few but large individuals, is employed by the victims in the case of small invertebrate predators, i.e. larvae of aquatic insects: beetles, some runners, bugs, and dragonflies. Hence, large *Limnephilus politus*, *L. flavicornis* (*Limnephilidae*), *Phryganea grandis,* and *Phryganea bipunctata* (*Phryganeidae*) larvae were found in the absence of pressure from large predatory fish. In the case of these caddis flies, their size is increased by the bags, which prevents predatory invertebrates and small fish from attack (9). Victims from other groups, such as *Ephemerellidae* mayflies and some *Plecoptera* stoneflies, increase the size of the body through forming different additional structures, which impede capture and consumption by the predator (20). The presented strategy of dispersal and aggregation of the



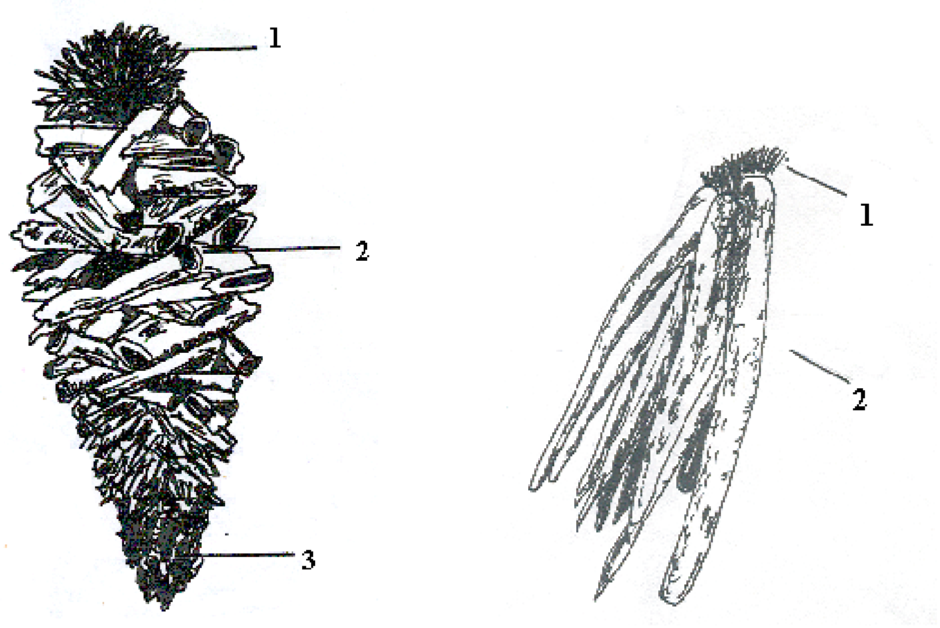
A B

Fig. 1. Bags of the larvae: A – *Limnephillus flavicornis* Fabr.,
B – *Molanna angustata* Curtis

population biomass is a common regularity observed in a variety of environmental groups and ecosystems (8, 9).

Cases are also built by caterpillars of many species of moths, with bagworm moths (*Psychidae*) to be distinguished in this respect. Their bags exhibit a complex structure and protective usability reaching far beyond the larval life. For example, in the species *Psyche viciella* and *Fumea casta*, the wingless female resides in the case and lays eggs there; it is also a building supply base for the newly hatched caterpillars, which leave their egg shells there. The larvae come out and immediately start to build the foundations of their own shelters, using the material from the mother's bag. They build their cases in stages. In the first phase of construction, the shelter consists of a chain of small plant parts linked with glandular secretion. In the second phase, the larvae build a case along their bodies; initially, they carefully line up the interior, and next they decorate the case with previously measured, bigger plant parts gathered outside the female's shelter. The central part of the case is the largest; external building materials from herbaceous plants and shrubs are piled on its top in a way characteristic of the butterfly species (Fig. 2). The shelter has two openings – at the front and at the back; they are framed with collars that are easy to be drawn inside. The case is enlarged gradually throughout the lifetime of the larva. Species living on thick tree trunks have smooth-surfaced shelters. Their grey colour and robust structure also provide larvae with security (16, 17).

Caterpillars of the *Cataclysta lemnata* moth (*Crambidae*) build shelters as well. The first one is built 5 days after hatching; the building material includes duckweed leaves and fragments of bulrush stems. At this stage, the shelters only play a protective role. Ten days after hatching, the colour of



A B

Fig. 2. Bags of caterpillars: A – *Psyche viciella* Schiff., B – *Fumea casta* Pall.
1 – front collar, 2 – shaft of the bag 3 – back collar (acc. to Gromysz-Kałkowska, 1967)

the larvae changes into dark brown after moulting II and they become hydrophobic; although they are still under water, they start breathing oxygen from the air contained in the shelter. Therefore, the shelters have a dual role: to provide security and store the air (28).

The above-presented defence strategies used by insects do not always yield the expected results. The predator often turns out to be an effective hunter. While preying, however, it makes a selection, allowing only the strongest and best individuals to survive. There is close, mutual interdependence of the persecutors and their prey. In natural conditions, there is coexistence of victims and their predators. The competition between prey and predators facilitates maintenance of natural balance in wildlife.

REFERENCES

1. Attenborough D. 1979. Życie na ziemi. Historia naturalna, Wydawnictwo Wilga, Warszawa.
2. Attenborough D. 1984. Żyjąca planeta, Wydawnictwo Wilga, Warszawa.
3. Attenborough D. 1993. Na ścieżkach życia. Historia naturalna zachowań zwierzęcych, Wydawnictwo Wilga, Warszawa.
4. Birkhead T., Dunbar R., Evans P., Gatti A., Helton D., Jameson C., O'Connell S. 1999. Na tropach sekretów przyrody. Zdumiewający świat zwierząt, Reader's Digest Przegląd Sp. z o.o., Warszawa.
5. Boczek J. 1990. Owady i ludzie, PWN, Warszawa.
6. Brehm A. 1968. Życie zwierząt. Bezkręgowce. PWN, Warszawa.

7. Brodacki M. 2003. Sposoby i koszty obrony przed drapieżnikami wśród bezkręgowców dennych. Wiad. Ekol. 49, 27–47.
8. Czachorowski S. 1994. Chruściki jezior lobeliowych – wyniki wstępnych badań. [In:] Jeziora lobeliowe, charakterystyka, funkcjonowanie i ochrona. Cz. II. M. Kraska (ed.), Idee Ekologiczne, t. 7, ser. Szkice, 59–73.
9. Czachorowski S. 1998. Chruściki jezior Polski. Charakterystyka rozmieszczenia larw. Wydawnictwo WSP Olsztyn.
10. Demel K. 1969. Zwierzę i jego środowisko. PWN, Warszawa.
11. Dröscher V. B. 1966. Świat zmysłów. Wiedza Powszechna, Warszawa.
12. Dröscher V. B. 1999. Ludzkie oblicze zwierząt. PIN, Warszawa.
13. Eibl Eibesfeldt I. 1987. Miłość i nienawiść. PWN, Warszawa.
14. Fabre J. H. 1925. Z życia owadów, Książnica – Atlas, Lwów–Warszawa.
15. Griffin D. R. 2004. Umysły zwierząt. Czy zwierzęta mają świadomość. Gdańskie Wydawnictwo Psychologiczne, Gdańsk.
16. Gromysz K. 1960. Experimental investigations on innate behaviour when building its bag, of the caterpillar *Psyche viciella* Schiff. in its ontogenetic development. Folia Biologica, 8 (3), 199–268.
17. Gromysz-Kałkowska K. 1967. The building mechanisms of the caterpillars of *Fumea casta* Pall. (*Lepidoptera*, *Psychidae*). Folia Biologica, 15 (2), 145–176.
18. Heinrich B., Vogt F.D. 1980. Aggregation and foraging behaviour of whirligig beetles (*Gyrinidae*). Behav. Ecol. Sociobiol. 7, 179–186.
19. Hölldobler B., Wilson E.O. 1998. Podróż w krainie mrówek. Prószyński i S–ka, Warszawa.
20. Kalinowska A., Pijanowska J. 1987. Jak się nie dać zjeść? „Żywy pokarm" w kontrataku. Wiad. Ekol. 33, 1–20.
21. Krebs J. R., Davies N. B. 2001. Wprowadzenie do ekologii behawioralnej. PWN, Warszawa.
22. Łuczyńska H., Wojtusiak R. J. 2007. Z życia i obyczajów zwierząt. Agencja Wydawnicza Ad Oculos, Warszawa–Rzeszów.
23. McGowan Ch. 2000. Drapieżca i ofiara, Wydawnictwo Rebis, Poznań.
24. Meckelburg E. 2004. Sekretne życie zwierząt, ich niewiarygodne zdolności, osiągnięcia, inteligencja i magiczne siły. Wydawnictwo Amber, Warszawa.
25. Mound L. 1991. Owady. Arkady, Warszawa.
26. Naumow N. P. 1961. Ekologia zwierząt. PWRiL, Warszawa.
27. Nowakowska M. 2004. Dzikość serca. Wielka Księga Zachowań Zwierząt. Ipressa, Warszawa.
28. Pabis K., Grabowski M. 2008. Biologia wodnego motyla *Cataclysta lemnata*. Wszechświat, 109 (10–12), 303–305.
29. Peckarsky B. L. 1996. Alternative predator avoidance syndromes of stream-dwelling mayfly larvae. Ecology, 77, 1888–1905.
30. Rutkowski D. 1999. Mechanizmy obrony przed drapieżnictwem u bezkręgowców litoralnych. Kosmos, 48 (4), 509–518.
31. Sandner H. 1990. Owady zwierzęta świata, PWN, Warszawa.
32. Ulrich W. 1973. Zoopsychologia. Biblioteka Problemów PWN, Warszawa.
33. Wilson E. O. 2000. Socjobiologia. Wydawnictwo Zysk i S-ka, Poznań.
34. 1000 Cudów Przyrody. 2003. Reader's Digest, Warszawa.