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Mechanical Aspect of Recreational Load and Defensive Behavioral Strategies in Grass-Dwelling Insects

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Abstract—The “mechanical” aspect of recreational load, i.e., the effects of anthropogenic physical contacts on the biota is discussed. The influence of the mechanical aspect of the disturbance factor upon the defensive behavior of hortobiont insects was studied by the example of two coccinellid species with different ecologies. Species-specific strategies of defensive behavior were revealed: predatory species resort to the active strategy (easy falling and immediate resumption of activity), while mycetophagous species resort to the inert strategy (“reluctant” falling and slow resumption of activity, frequently involving thanatosis). In response to mechanical impact those reactions may be considered adaptive which minimize the time and energy spent to maintain the acceptable level of safety. Under recreational load, the rational energy and time budget becomes a priority.

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The anthropogenic impact on natural ecosystems is rather variable and therefore it is quite logical to consider its different aspects (Gashev, 2000), including recreational load. The meaning of the “recreation” concept varies in different branches of knowledge depending on the aspect of consideration. Following the working definition of Sionova (2005), we will consider recreational load as the impact on the environment related to man’s rest and relaxation activities. Recreational load may be manifested in trampling down grass, damaging trees and shrubs, disturbing nesting places and shelters, noise pollution, input and output of matter and energy, etc. The effect of recreation on animals may be both direct (destruction, pursuit, disturbance) and indirect, acting through changes in the environment (vegetation, soil, hydrologic regime, trophic resources) (Cole and Landres, 1995). In our opinion, of principal importance is interpretation of recreation as kind of activity, implying physical activities of man in landscape: “Recreation is first of all the subject’s activity” (Sarancha, 2009). Recreation as such may serve as the object and purpose of research, but it may also serve as a convenient model for studying the general theoretical problems and more specific questions.

The field of study of anthropogenic impact is dominated by works on toxicology (Nesterkov, 2009), whereas the so-called “mechanical” aspect remains one of the least studied. By this term we understand the physical action of anthropogenic nature exerted on the components of wildlife. This definition mainly includes the direct action of man and machinery, and, in a broader sense, any human activity which influences the biota mechanically.

The mechanical aspect of sublethal anthropogenic action may be interpreted as “disturbance factor.” The types of disturbance may be classified in various ways: by its nature it may be mechanical, chemical, acoustic, optical, etc.; on the subjective basis a variety of agents, or elementary stimuli, can be distinguished: man, domestic animals, cars and other machinery; by the duration of action, the disturbance factors may be subdivided into constant, temporary, and short-term ones (Davygora, 2000). A more specific definition proposed by Vladyshevskii (2004) appears to be quite useful: “The disturbance factor is the action of external stimuli on animals which they perceive as a danger signal.” In our opinion, the well-known “stimulus-response” formula of behaviorism (Gorokhovskaya, 2001) is quite applicable to invertebrates, in particular free-living insects: they respond not to the disturbance factor (stressor) on the whole but to concrete stimuli conditioned by this stressor, in which case there are no principal differences between natural and anthropogenic stimuli.

The impact of recreational load on the biota is usually assessed by the example of vertebrates (Zakharov, 1998; Zhigarev, 2005, etc.), while invertebrates are less studied in this respect. The problems of mechanical impact of herbivorous mammals, as well as humans and mechanisms, on hortobionts remain unstudied.

It is the grass layer and the hortobiont and hortophilous animals (in the terminology of Lagunov, 2008) inhabiting it that are considered the first to be affected by recreational load. The leading direct factor of disturbance is the mechanical impact exerted upon hortobionts by vacationers.

Owing to their behavioral mechanisms, animals have three principal ways of responding to the external action of stressors (*Bioindication*…, 1988): avoiding the stressor in space and/or time; using the specific features of their organisms, including specific motor activity; changing the properties of the environment. The first and especially the third way are uncommon for invertebrates; below we will consider the second way, namely the motor activity.

In this communication we will consider the influence of the mechanical aspect of the disturbance factor on defensive behavior of hortobiont insects.

Our first task was to reveal elements (tactical methods) of defensive behavior demonstrated by insects under the action of the mechanical stressor. The second task was to test whether different species have different tactical methods (in other words, whether the strategies of defensive behavior vary between species). The third task was to estimate the efficiency of the behavioral strategies observed under the conditions of mechanical recreational load.

MATERIALS AND METHODS

The material was collected on July 19–20, 2009 in the territory of one of the recreation centers in the South Cis-Ural Region (the Bashkortostan Republic), near Zirgan, on the left bank of the river Belaya (53°16' N, 55°19' E).

The study objects were two species of beetles of the family Coccinellidae: the twenty-two-spot ladybird *Psyllobora vigintiduopunctata* (L., 1758) and the fourteen-spot ladybird *Coccinula quatuordecimpustulata* (L., 1758). Below, the two species will be designated by their generic names for brevity. Both ladybirds are typical hortobionts, common in the study region, of average size (3.5–4 mm); they do not actively fly in search of food and are quite conspicuous. The differences lie in their trophic specialization: the former species is a mycetophage, feeding on powdery mildew, while the latter is an entomophage, feeding on aphids. The predaceous *Coccinula* are much more agile and move actively in search of food, whereas the mycetophagous *Psyllobora* are quite sedentary. Our material comprised 22 ind. of *Coccinula* and 54 ind. of *Psyllobora*.

The work was carried out at the edge of a deciduous light forest, within an area of about 100 m^2 of forb vegetation (the better lighted part with grass patches being the habitat of *Coccinula*, the less lighted part with some shaded spots, the habitat of *Psyllobora*). The air temperature during our work was 22–25°C, the weather was partly cloudy with weak wind.

As a mechanical source of disturbance, we considered a man who exerts a physical (mechanical) action on hortobiont insects by walking on grass. This action was imitated in the experiments in the following way: a patch of grass with an insect was smoothed with a hand (as a man would accidentally do while walking at a normal speed). Whether the beetle itself was touched was left to chance; it depended on the position of the insect on the plant. If the beetle did not fall after the first mechanical impact, the hand movement was repeated until it did (this allowed us to estimate how fast it was clinging to the plant). To estimate the risk of mechanical damage to the fallen beetles, we stepped on 15 randomly chosen specimens, both in the state of thanatosis and motile (our previous observations gave us ground to assume that such action did no harm to the beetles in the grass).

The following responses of beetles to mechanical disturbance were recorded during the experiments:

(1) Whether the ladybirds notice the approaching man and fly away at his approach;

(2) Whether the beetle remains on the plant on mechanical impact;

(3) Whether, when falling, the beetle tries to spread its wings and fly away or to cling to the plant;

(4) Whether the beetle enters the state of thanatosis, and how soon it resumes activity after falling.

The time from the moment of falling to the moment of resuming activity was measured to 1 s. Every beetle was tested in this way only once (if not stated otherwise). The pairs in copula were tested together with single individuals.

The presence or absence of thanatosis was recorded. According to Reimers (1988), thanatosis is a defensive behavioral response of animals in which they take on the appearance of being dead. Brief immobilization, i.e., a short lag between falling and resumption of normal activity, was described as “freezing.” We could not find in the literature a clear criterion to distinguish between freezing and thanatosis; therefore we established an arbitrary threshold value of 5 s: the immobile state lasting 5 s or less was regarded as freezing, and that exceeding 5 s, as thanatosis.

The data were statistically processed using MS Excel 2003 and Statistica 5.1 software packages. The significance of differences was estimated using nonparametric criteria: χ^2 and the Mann-Whitney U-criterion.

RESULTS AND DISCUSSION

Insects exist under specific conditions and respond to stressors within a relatively small range of perception of visual, acoustic, chemical, vibratory, mechanical, and other stimuli. To understand whether ladybirds respond to the approaching man we will first consider which stimuli they can perceive at a distance and which main behavioral responses they have.

Optical stimuli. The members of Coccinellidae are known to have three types of visual receptors (Lin, 1993): those sensitive to blue (420 nm), green (520 nm), and ultraviolet (360 nm) light with the total range of 350–700 nm and a maximum at 500–600 nm. It is essential that the food objects are detected within a small radius: 0.7 cm for larvae and about 1 cm for adults (Stubbs, 1979). Ladybirds can discern the outlines of big objects at a distance: they are attracted by the shape of a tree (Hattingh and Samways, 1995). Based on our observations, we can conclude that larger species of Coccinellidae, such as the eyed ladybird *Anatis ocellata* (L., 1758) which is over 4 mm long, can notice a man and respond to his approach at a distance of 0.4–0.6 m; whereas the medium-sized and small species of the genera *Stethorus*, *Scymnus* s. lato, *Coccinula*, *Psyllobora*, and *Tytthaspis* (up to 4 mm long) do not visually respond to man at a distance of 0.25–0.4 m.

Olfactory (chemical) stimuli. The aphidophagous ladybirds were experimentally shown to respond to the scent of the food plant of the aphids (the food objects of ladybirds), which appears to release some attractants (Schmidt, 1972). The response to the extract of food plants, and also to the scent of the aphids themselves was also revealed (Schalter and Nentwig, 2000).

No data on perception of acoustic stimuli by coccinellid beetles could be found in the available literature. According to our observations, ladybirds did not respond to the background noises related to human activity, such as speech or laughter. In the absence of strong odors of perfume, the chemical impact of man may be also neglected. For example, all the development stages of the ten-spotted ladybird *Adalia decempunctata* L., 1758 and the two-spotted ladybird *A. bipunctata* L., 1758 were present in large numbers on a Scots pine growing in front of the main gate of the campsite where material was collected (see *Material and methods*). Pronounced anthropogenic impact during the night: crying of children, music, noise, whistling, artificial lighting, smoking, did not reduce the abundance of ladybirds.

Mechanical stimuli. As a rule, under the action of weak tactile stimuli the ladybirds assume a passive-defensive posture, tucking in their legs and clinging close to the substrate. Under the action of strong tactile stimuli, they enter the state of torpor or thanatosis.

Based on observations of beetles affected by the simulated mechanical impact, we distinguished the following defensive tactics (alternative variants of behavior):

(1) If the approaching stressor can be revealed at a distance, the insect has a choice: to fly away or to stay.

(2) In case of immediate mechanical impact (the moment of contact), the insect has a choice: to cling to the plant or to let go and drop to the ground.

(3) During the fall, there is a choice: to spread the wings and fly away or to continue falling to the ground.

(4) After falling to the ground, there is a choice: to freeze / enter thanatosis or to resume active movement immediately.

Let us discuss the tactical methods used by the model species.

Tactics no. 1. In the model species this tactics was not revealed: not a single attempt to fly away was observed at the approach of man, which is not surprising, taking into account the “short-sightedness” of lady-

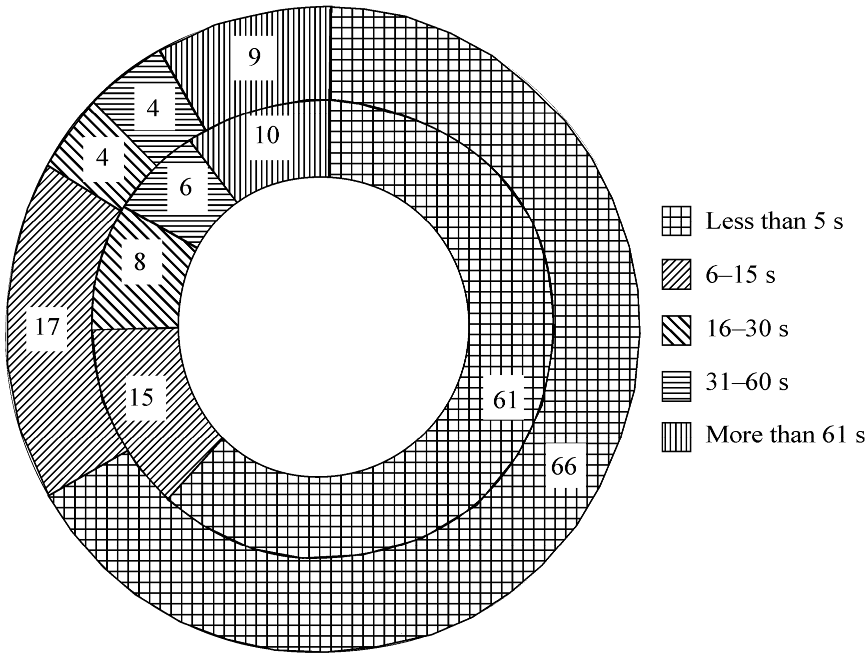

Fig. 1. Distribution (%) of ladybirds by the duration of freezing. Inner circle: *Psyllobora vigintiduopunctata*; outer circle: *Coccinula quatuordecimpustulata*.

birds (see above). This tactics is mainly characteristic of desert species (Savoiskaya, 1983).

Tactics no. 2. Most ladybirds (97.4% for both species, including 100% of *Coccinula* and 90.9% of *Psyllobora*; the difference is significant at $p < 0.05$) fell after the first mechanical impact. Two ind. of *Psyllobora* held fast to the plant and fell only after the fourth and fifth impact.

Tactics no. 3. Start of flight during the fall was recorded only twice (in both cases these were *Psyllobora* which were not taken into account in subsequent calculations). Yet it should be noted that both times this happened on isolated and sufficiently high plants (more than 30 cm, the average height of the grass stand in the study area being 12–20 cm). It was impossible in our situation to test the whole sample of beetles by placing them on high plants. It should be noted that this tactical method is regularly used by small ladybirds of the genus *Scymnus* s. lato: they start flying during the fall.

Tactics no. 4. *Psyllobora* fell into the state of thanatosis somewhat more frequently than *Coccinula* (38.5% and 31.8% of cases, respectively; the difference is statistically non-significant).

The rates of activity resumption after falling were as follows (Fig. 1). In *Psyllobora* ($n = 52$), the mean time of activity resumption was 15.5 s after falling (range: 0–121 s); in *Coccinula* ($n = 22$) it was 11.2 s (range: 0–103 s) (the differences were non-significant). If we compare only the individuals which did not enter the state of thanatosis (i.e., those which resumed activity within the first 5 s after falling to the ground), it becomes clear that *Coccinula* resumed their activity faster: on average, in 0.8 s against 1.8 s (the differences were statistically significant at $p < 0.05$). At the same time, the fraction of *Coccinula* which resumed their activity immediately after falling (with the time lag of 0 seconds) was significantly larger than that of *Psyllobora* (11 ind., or 50%, against 8 ind., or 15.4%; $p < 0.01$).

None of the copulating pairs tested (1 couple of *Coccinula* and 8 couples of *Psyllobora*) separated at the mechanical impact. After falling the female of *Coccinula* resumed its activity in 2 s, the females of *Psyllobora*, in 40 s on average (range: 0–102 s). The males in copula stay motionless; only in one case a *Psyllobora* male began to display activity starting to move its fore legs before the female (in 62 s, as compared to 102 s in the female).

Any behavioral strategy, including the defensive one is realized by means of a set of specific tactical methods and actions. The defensive mechanisms of insects are diverse (see, for example, *Coleoptera and Coleopterists*…, 1999). One of the best known mechanisms is aposematic coloration. However, Defensive strategies of hortobiont ladybirds under mechanical impact

Strategy	Advantages	Drawbacks
Active	Lower risk of falling victim to a predator or "insurmountable force" Possibility of supplementing this tactics by freezing or thanatosis Additional feeding on the ground	Greater time and energy expenditures
Inert	Saving of time and energy	Higher risk of falling victim to a predator or "insurmountable force"

aposematic coloration does not protect insects from mechanical impact: both natural agents (big wild animals passing by, wind, and rain) and anthropogenic agents (domestic animals, cars, mechanisms, and people) affect insects regardless of the presence or absence of warning coloration. The behavioral mechanisms play an important role in this case.

Based on the interpretation of the obtained data on tactical methods, we distinguished two different defensive strategies in the model ladybird species:

In the first (conditionally passive) strategy, the behavior of insects is characterized by the following features:

—they hold to the plant faster at the mechanical impact,

—they spend more time in the state of torpor (i.e., they resume their activity slower),

—they fall into the state of thanatosis more often.

In the second (conditionally active) strategy, the behavior of insects is characterized by the following features:

—the insects do not keep a fast hold of the plant, falling to the ground even at a slight mechanical impact,

—the insects stay less time in the state of torpor (i.e., they resume their activity practically immediately after falling),

—they fall into the state of thanatosis not so often.

Some difficulties arose when naming the above strategies, since the terms "active" and "passive" are too common and their meaning is too vague. Therefore we suggest that the term "busy" should be used for the conditionally active and the term "inert" for the conditionally passive strategies.

The strategy of defensive behavior in response to the stressor is formed under the influence of two opposite motives: on the one hand, the need to ensure safety, on the other hand, the need to minimize the time and energy expenditures for achieving this safety (see, e.g., Vladyshevskii, 2004). This contradiction can be interpreted as sets of advantages and drawbacks (table) inherent in strategies skewed towards maximum safety or minimum time and energy losses.

By clinging to the plant, insects do not have to spend energy on seeking another suitable plant after falling down, climbing it, and finding a suitable place on it. Since it is energetically disadvantageous for insects to fall to the ground at each gust of wind and then spend energy and time on climbing, selection seems to be in favor of fixing the ability to cling to the plant. On the other hand, by clinging to the plant insects increase the risk of suffering from mechanical action, for example, that of an entomophage (the risk of being eaten), big herbivores (the risk of being accidentally swallowed together with grass) or simply "insurmountable force" (the risk of being crushed or mutilated by a large, massive object: a vertebrate, a man, or a mechanism). At strong gusts of wind (exceeding some threshold value of the swinging intensity) as well as at direct physical contact it may be more adaptive not to continue clinging to the plant but fall to the ground.

By dropping to the ground the insect considerably decreases the risk of falling victim to a predator or "insurmountable force." In a number of cases (under the action of an insurmountable force) this is sufficient; however, in order to play it safe in case of a predator's attack this tactics can be supplemented by freezing or thanatosis. It is interesting that ladybirds gain other advantages by falling. Since the mechanical impact acts equally on all the hortobionts, some aphids also use the falling tactics and may become prey to

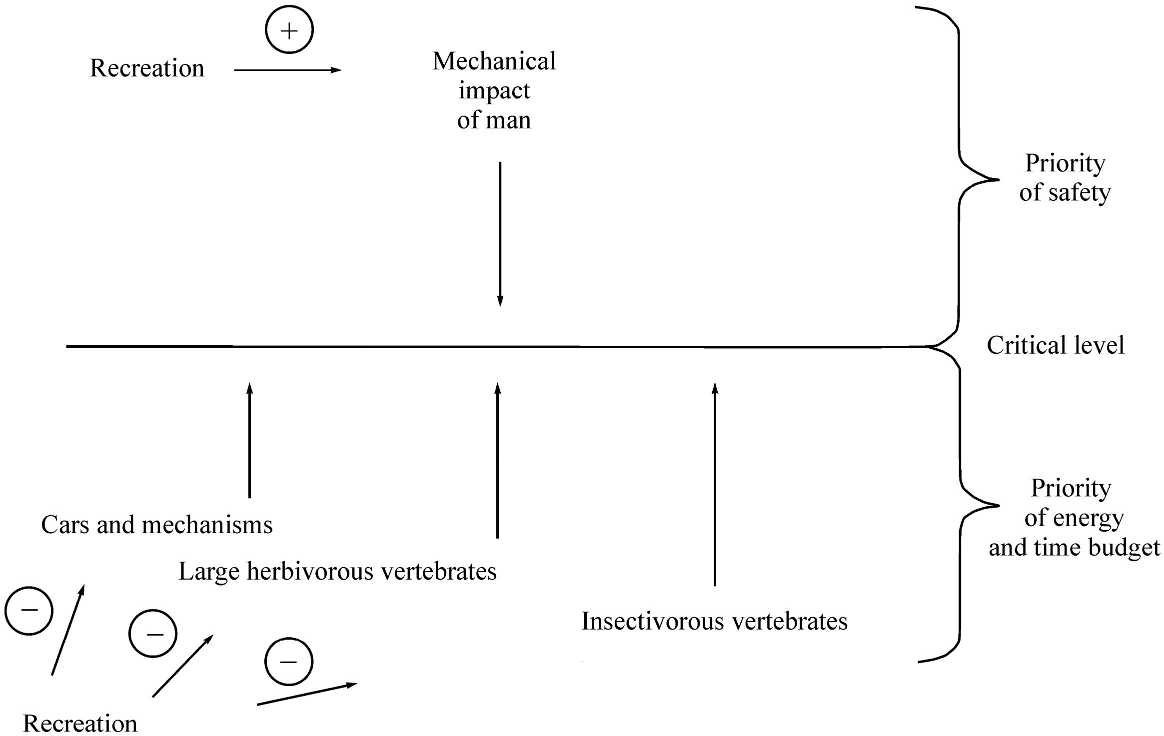

Fig. 2. The mechanically mediated modifying effect of recreational load upon the trade-off safety level. For explanations, see text.

aphidophages on the ground. For example, in wheat fields 30% of the victims of the seven-spotted ladybird are aphids moving on the ground (Ferran and Dixon, 1993).

In our opinion, the choice of strategy depends on the ecology of the species (first of all, its trophic ecology): *Coccinula*, as active predators, apply the busy strategy, whereas *Psyllobora*, as sedentary insects consuming immobile food objects, apply the inert strategy.

What is the specificity of mechanical action on hortobionts under the conditions of recreational load?

First, it is conditioned by the recreational load with all its attributes: disturbance, trampling, and littering. Disturbance is first of all manifested in mechanical action, while the influence of littering can be neglected in properly managed recreation areas; the intensity of trampling may be considered low, not leading to degradation of phytocenoses (we do not consider here the recreational impact on the fauna mediated by vegetation and soil). The physical influence of vacationers on hortobiont insects also seems exaggerated: the motile (jumping and flying) insects can actively avoid physical contact, whereas sedentary ones hide or find shelter in the litter. The direct pressure is also not a significant factor. According to different estimates, the static pressure of a standing man on the soil is 180–375 g/cm^2 (Liddle, 1997), this value decreasing on the grass. When studying the pressure exerted by the human body on the insects present on the ground in the grass, we did not find any external damage or changes in subsequent activity in any of the 15 ladybirds tested. Observations of beetles immediately after the experimental action did not reveal any visible negative consequences: all the ladybirds continued their routine activity. No changes in the ladybird population density in the model site before and after research were observed. The question of intensity of recreational load on the natural ecosystems is beyond the scope of this work and should be considered separately; here we can only note that in places of organized recreation with a network of roads and paths, the nominal indices of recreational load intensity (e.g., 40 men/ha) may be considerably (1.5–2.0 times) higher for the grass stand than the real ones.

Second, from the viewpoint of hortobiont safety the following factors conditioned by organized recreation are important:

—limited traffic and work of mechanisms;

—absence of large herbivores, both wild and domestic;

—reduced pressure of insectivorous vertebrates; a decrease in the diversity and abundance of vertebrates as a whole and insectivores in particular in such areas is usually observed (Sionova, 2005, etc.).

These limiting factors directly affect the safety and survival of hortobionts, the first two in a purely mechanical way. Recreational load reduces or completely levels the action of these factors, decreasing selection pressure in the direction of achieving maximal safety.

Besides modification of the existing factors, recreational load adds a specific "mechanical" factor affecting the efficiency of defensive behavioral strategies: a man walking on the grass exerts random physical impacts on all the hortobionts which happened to occur in his way, but does not purposefully pursue or kill them. This factor does not result in elimination of hortobionts but at the same time affects their time and energy budget.

The principal scheme is as follows (Fig. 2): there is a "critical level," a trade-off between maximization of the animal's safety and minimization of energy and time expenditure on safety, which is achieved and maintained by the defensive behavior of hortobionts. On the one hand, the recreational load weakens the pressure of the natural selection vectors (in our case cars and mechanisms, large herbivorous and insectivorous vertebrates), threatening the safety of hortobionts (marked with a "minus" sign in the scheme). On the other hand, the recreational load adds (the "plus" sign) a new selection vector: an indifferent mechanical impact of man which is not critical for safety but which affects the time and energy budget. By reducing the action of the natural factors it shifts the border of the trade-off level from the zone of safety priority to that of energy and time priority. Thus, the recreational load balances the defensive behavior of hortobionts in the range of some trade-off "critical level" indirectly, via counterbalance of the above vectors.

Thus, under the conditions of mechanical impact those behavioral reactions may be considered adaptive which make it possible to minimize time and energy expenditure while maintaining an acceptable level of safety. In our case, such responses are sticking to the plant (since falling means expenditure of both time and energy) and immediate resumption of activity in case of falling to the ground (minimization of time loss). The first response is characteristic of the inert strategy, the second, of the busy one.

The inert strategy seems somewhat more preferable, which under conditions in question is practically devoid of drawbacks indicated in the table, since the sources of risk are fewer: in organized recreation areas the pressure of insectivorous vertebrates is lower, there are no large herbivores, the movement of cars and mechanisms is restricted. On the contrary, the advantages of the busy strategy (table) run idle in this situation, due to a lower abundance of insectivores and a smaller probability of "insurmountable force" action. However, since the rate of "holding fast" to the plant is inconsiderable (3.7%) in the model species, its role cannot be important.

On the other hand, adaptations aimed at minimization of energy loss increase time loss or reduce safety (or vice versa). This conflict of interests or, in terms of the evolution theory, the counterbalance of the selection vectors (Severtsov, 1998) reflects the contradictory nature of some defensive behavioral reactions of hortobiont insects, which may be difficult to unite within a single strategy.

This scheme, based on general deductive reasoning, may be later verified and corrected by particular empirical experiments. In prospect, it may be possible to quantitatively assess the intensity of factors, for example, in the system of coordinates (x, y, z): (the safety level, the level of energy expenditure, time loss), assigning each measurement a certain relative weight.

CONCLUSIONS

(1) Hortobiont insects are characterized by tactical methods of defensive behavior the set and specificity of which depend on the species.

(2) Different defensive strategies have been revealed: the predaceous *Coccinula* use a busy strategy (easy falling and fast resumption of activity); the mycetophagous *Psyllobora* adhere to an inert strategy ("reluctant" falling and slow resumption of activity, often accompanied by thanatosis).

(3) Under the conditions of moderate recreational load, when the action of limiting factors is weakened, the energy and time budget is given preference over safety. The advantage of the busy strategy is the efficient use of time.

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