UDC 004.9:612.822 **https://doi.org/10.15407/biotech18.01.016**

ADAPTATION IN EXTREME STRESSFUL CONDITIONS: SOME TECHNOLOGIES OF STUDYING

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Received 2024/04/30
Revised 2025/02/11
Accepted 2025/02/28

Adaptation is a fundamental phenomenon ensuring biological organisms' survival in changing environmental conditions.

Studying this and related phenomena is critically necessary for people not only in conditions of peaceful life but also in conditions of war.

Aim. Description of some research technologies and results of their application to study the adaptation of various organisms to stressful extreme mountain conditions.

Methods. Comparative analysis of a large number of the data from experiments and observations of phylogenetically different organisms under the changed stressful conditions of hypoxia and other factors of the highlands. Standard methods of laboratory analysis of some vital indicators of biological organisms. Day and night collection methods using a light trap were used to collect insects. In some cases, pheromones were used. Mathematical and program modeling.

Results. Modern concepts of physiological adaptation based on Ukrainian and foreign classical studies were observed. The evolutionary aspects of adaptation studies were observed, taking into account two main strategies of biological organisms adaptation, as well as evolutionary aspects of adaptation to hypoxia were considered using the examples of insects and mammals (gophers). The research technologies and obtained results were described in detail — both the results of field observations and those registered in laboratory conditions. The primary attention was focused on the results of contemporary works of Ukrainian scientists. In this way, various directions of research were characterized in detail for insects and mammals (gophers). Special attention was paid to the problems of human adaptation to stressful conditions. The effects were registered on volunteers from special groups (rescuers, pilots, others).

Conclusions. The results of numerous long-term studies of adaptation on examples of vertebrates and invertebrates were described. A comprehensive analysis of the obtained results was made. A number of general theoretical conclusions that were made on the basis of presented results were given as well. Functional adaptation was put in the base of hypoxytherapy methods.

Key words: adaptation, extreme conditions, stressful conditions, numerical indices of physiological functions, mathematical modeling.

Citation: Biloshitsky, P. V., Klyuchko, O. M., Onopchuk, Yu. M., Lyman, K. S., Lizunova, A. G. Adaptation in extreme stressful conditions: some technologies of studying. *Biotechnologia Acta*, 18(1), 16–31. https://doi.org/10.15407/biotech18.01.016

The ability to adaptation is an essential characteristic and property of biological organisms. Human tries to penetrate areas that are initially beyond their habitation, where the environment around them becomes “conditionally suitable” for life — highlands, sea depths, or completely unsuitable - space. To realize such aspirations, knowledge of the phenomenon of adaptation becomes especially important. Adaptation is a fundamental phenomenon that ensures biological organisms’ survival in changing environmental conditions.

Environmental extreme stressful conditions cause the adaptation; they and related effects are in focus of interest of contemporary researchers in the theoretical and practical aspects [1, 2]. Numerous investigations are devoted to studies of organisms’ adaptation to adverse environmental conditions and stressful influences on organisms. Studying modern sources of scientific literature, one can distinguish several areas in which researchers of the adaptation phenomenon of living organisms are currently publishing their results. Let us consider just a few of these areas.

Phenomenon of biological adaptation in extreme conditions: some areas of current researchs

Adaptation for the conditions of space flights [3–8]. Many such studies were carried out linked with space exploration: manned space flights and the problems of biological organisms survival and functioning on board spacecraft during space exploration missions.

Adaptation for the polar conditions of the Earth [9–11]. Biological organisms’ adaptability to the polar and sub-polar conditions form another great group of studies linked with the missions of Antarctic and Arctic exploring, human work, and other activities in these geographical regions.

Adaptation for the conditions of high mountain altitudes [12–29]. Adaptation to the conditions of the high mountain altitudes was characterized by higher levels of ionized radiation (solar, galactic, etc.) and oxygen deficiency (causing hypoxia) [17–19]. Life in these conditions initiates the processes of adaptation in biological organisms, too. Reliable, long-term physiological adaptation (PhA) is a necessary factor in expanding spheres of human activity. In extreme environmental conditions, it increases humans’ stability and efficiency of their work [24–26]. Numerous researches were done for the solutions of some of the above mentioned problems being modeled previously at the Earth highlands conditions [23–26]. In the process of performing work within the framework of such projects, the authors developed the latest information systems [19–21] and applied specific mathematical methods [22, 23].

Adaptation of biological organisms in water basins [30–32]. The literature most often considers the issue of adaptation at great depths [30]. Much attention is paid to the study of the mechanisms of adaptation of organisms under the influence of pollution of water basins with chemicals, with research carried out on the examples of fishes and microorganisms [31, 32].

Adaptation of biological organisms to extreme stress conditions caused by chemical pollution of the environment [33–36]. These studies of adaptation to stressful conditions are linked with environmental pollution in industrial centers and territories with chemical or radioactive pollution (including heavy metals pollution) as the result of accidents, armed conflicts, etc. [33–35]. During long years, the authors carried out the investigations in these directions [17, 18, 20, 36]. In the framework of these projects, some novel devices for biotechnology, and information systems were developed [20, 36]. Below, some results of the author’s works will be represented. Special attention such works attract in war conditions when significant numbers of people suddenly find themselves in stressful extreme conditions [19], and primarily theoretical knowledge becomes essential to preserve the health and sometimes even the life of the people.

Adaptation and changes of genome [37–52].

Extreme factors of chemical pollution often cause changes in the genome of biological organisms, and these studies are widely represented in scientific publications [37–52]. The most significant number of such studies were carried out with microorganisms [38, 39, 41, 42, 46, 49] and fishes [44, 45].

Adaptation of various biological organisms [53–70]. A) The most significant number of such studies were carried out with microorganisms of different types [53–70].

B) Some publications were devoted to studies of adaptation to unfavorable conditions of other biological organisms — rodents [61, 62], birds [63], marine organisms [64], and others.

C) A significant number of publications is devoted to studying those animals whom people use in their economic activities — guanaco lamas, and camelids [65–70]. Sure, the results of genetic studies of these animals are presented in publications, too. In the result of such studies appears the possibility of carrying out comparative analysis of results of various organism investigations.

Such work attracts particular attention in wartime, when a significant number of people suddenly find themselves in stressful extreme conditions [19]. To preserve the health and sometimes the lives of people, such theoretical and practical knowledge is essential.

In Ukraine, significant contributions to the study of PhA were made by such great scientists as I. Mechnikov, V. Vernadskyi, D. Grodzinskyi, and M. Syrotynin, who developed the concept of gradual step-by-step active PhA to hypoxia to increase endurance, work capacity, sports results, as well as medical treatment, prophylaxis of disorders and rehabilitation [17–19]. The tasks of the present paper were to represent the results of some studies of the problems of PhA, which were carried out by Ukrainian scientists in mountain conditions — Carpathian Mountains (areas in regions of Lviv, Ivano-Frankivsk. and Transcarpathian). Besides these results, there were analyzed ones obtained at the scientific base of the National Academy of Sciences of Ukraine — Elbrus Medical and Biological station (EMBS, located at Elbrus slopes, vil. Terskol, RF) until 2013, the mechanisms of hypoxia influence [17, 19], and high levels of radiation [17, 18] there where studied profoundly, forming the base for future understanding of mechanisms of adaptation. Such studies were carried out with phylogenetically different organisms using various methods. Also, we would like to demonstrate the contribution of Ukrainian members of the M. M. Syrotynin scientific school and their contribution to adaptation medicine and the theory of adaptation for further continuing of these critical studies.

Methods used. Comparative analysis of a large number of the data from experiments and observations of phylogenetically different organisms under the changed stressful conditions of hypoxia and other factors of the highlands. Some standard methods of laboratory analysis of some vital indicators of biological organisms. Day and night collection methods using a light trap were used to collect insects; in some cases, pheromones were used. Mathematical and program modeling.

The purposes of the present study were the description of some research technologies and the results of their application to study the adaptation of various organisms to stressful extreme mountain conditions.

Contemporary understanding of the notion and concept of adaptation

Modern knowledge of physiological adaptation (PhA) is primarily based on many years of research in many countries of the world, which is a complex, multifaceted concept that united a broad spectrum of phenomena. Below, there are some formulations of the concept and notions of adaptation, which the scientists did, classifications of some adaptation phenomena regularities, etc.

The notion of adaptation. Physiological adaptation is the process of adaptation of animal or plant organisms to changed environmental conditions.

Each factor that influences an organism causes a response of adequate quality and force of irritation. However, each of such protective reactions includes a non-specific component of the organism's reactivity, which characterizes the general state of the stress and the degree of activation of homeostasis preservation systems. Exactly this non-specific response component can be described as general adaptation syndrome (stress). Physiological adaptation to extreme factors can be realized in the form of an "activation" or "training" reaction. Below are some conclusions of known pathophysiologists who studied adaptation phenomena in stressful extreme conditions.

Adverse environmental effects on organisms can be compensated by appropriate behavior or technological inventions (f.e., using sealed cabins for experiments).

Dr. Kaznacheev V. distinguishes between "sprinters" and "stayers" according to their responses to stress. "Sprinters" have powerful physiological reactions to stress, but they are able to maintain them only for a short time. "Stayers" can maintain homeostasis for a long time but under medium physical loadings [19]. Physiological adaptation can be active (due to the hyperfunction of biological systems) as well as passive (due to their hypofunction), for example, in winter hibernation. A distinction can also be made between the immediate (urgent) and long-term PhA. The latter occurs gradually as a result of prolonged or repeated exposure to certain irritants.

The PhA concept unites the process and its result (the state to which the adaptation leads).

Dr. F. Meyerson [17–19] subdivided the genotypic adaptation (the organism's acquisition of resistance to the external environment in the process of long-term evolution, which is fixed genetically and inherited) as well as phenotypic adaptation (the process of acquisition of resistance to certain environmental factors that develops during individual's life).

Dr. Mirrakhimov M. proposed to distinguish the initial, transitional and stable stages of adaptation [19]. Adaptability is characterized by a set of structural and physiological features, quantitative and qualitative changes, reactions, properties, and indicators that are manifested at all levels of an organism's functioning: submolecular, molecular, biochemical, membrane, cellular, tissue, organ, systemic, and the whole organism, as well as at the level populations, species, biogeocenoses, ecosystems.

There are several degrees of adaptability can be distinguished:

– insufficient degree, when the level of functioning of an organism decreases in new conditions;

– satisfactory degree, when an average, usual level of functioning is ensured by uneconomical energy consumption;

– optimal degree when the required level of functioning is ensured by minimal energy consumption.

Intermediate qualitative states between them can also characterize adaptability. Intermediate qualitative states between them can also characterize adaptability. Therefore, mountain climbing, space flights, Antarctic and sea expeditions, desert crossings, sports competitions, and other extreme practices attracted significant attention from researchers.

Functional adaptation was put in the base of hypoxytherapy methods [19].

Evolutionary aspects of adaptation phenomena

These aspects had already focused on investigators' attention in the early 20th century [19]. Further multifaceted, long-term studies of PhA problems in comparative-physiological, evolutionary elements at all levels of an organism with the use of adequate modern methods [19–21], mathematical modeling [23–26], other mathematical methods [22, 23] became a broad general biological approach to the disclosure of adaptation mechanisms, changes of functions, development of mountain sickness, reliability of organism functioning in extreme conditions.

The widespread use of phylogenetic and ontogenetic approaches to the study of resistance and reactivity in animals of many species allowed to establish a familiar regularity. With the complication of organization in the process of phylogenesis, resistance to a sharp decrease of the partial pressure of oxygen decreases too. At the same time, reactivity increases, which provides highly organized animals and humans with more fantastic opportunities to compensate for an oxygen deficiency and maintain an average level of vital activity along with a moderate decrease in the partial pressure of oxygen in inhaled air. Due to these studies of scientists of M. M. Syrotynin school [19], the doctrine of reactivity as property of changes in the vital activity of a whole organism as a result of the influence of various factors of the external environment was formed in its finished form. The concept of changes in reactivity and resistance in phylogeny and ontogeny was substantiated. This concept, consequently, contributed to the development of the hypoxia doctrine. Concerning mammals, such studies helped to formulate the central imaginations about the adaptation to hypoxybaria as a process of establishing a new steady state that ensures the reliability of the organism's functioning in changed environmental conditions.

Comparative and evolutionary aspects of adaptation to hypoxia — insects studies. Two strategies of adaptation

The study of insects has attracted attention throughout the history of the development of natural sciences. One of the most important reasons for this is the large number of insects of various species in extreme conditions, for example, in the mountains. Another side of this phenomena — there two main types of adaptation strategies were discovered for multiple biological organisms. The higher organisms are more inclined to adapt by maintaining their homeostasis at a constant level (f.e., mammals, including humans). Contrary, insects demonstrate an explosive increase in their numbers under stressful extreme conditions, and at the same time, a number of their external characteristics change (colors of wings, bodies, etc.).

However, studying the mechanisms of insect adaptation to mountain conditions is not only of theoretical interest in the case of modeling the situations of living organisms transferring in conditions of space flights or conditions on other planets. The insects are significant objects as organisms with high levels of protection and survival in extreme conditions.

Below are the results of studies of changes in the adaptive characteristics of insects carried out by Klyuchko E.M. and Klyuchko Z.F. in the Caucasus Mountains in 2003–2007. The night insects — *Noctuidae (Lepidoptera*), or moths, became the objects of the study. Along with them, there was also such insect group as zygens (*Zygaenidae*) at mountain altitudes 2100 m a.s.l. and higher. Other insect species were collected as well. It is necessary to mention that all these listed insect groups were small in numbers of their representatives at mountain heights, and these numbers decreased dramatically up to 3100 m a.s.l. Day and night collection methods using a light trap were used to collect insects. In some cases, pheromones were used.

The collections were carried out at three altitudes: 2100 m a.s.l. (Baksan Gorge in the area ofmountain Cheget, a zone of mountain forests), 2800 m a.s.l. (Cheget, subalpine meadows), 3100 m a.s.l. (Terskol peak, the upper part of the subalpine meadows, where the snow line was in summer 2004). For each height, the species composition, total number of collected insects, behavioral differences, and differences in color and pattern were analyzed.

Forest species of *Noctuidae* that were common in the Caucasus were also expected to the most regions of the Palearctic: *Apamea illyria, Euchalcia variabilis, Xestia ohreago, Diachrysia chrysitis, Syngrapha interrogationis*, and many others. Some species were registered only in the Caucasus: *Cucullia propingua, Autographa aemula*. There were representatives of the steppe species, although in small numbers — some species of Cucullia, Acronicta euphorbiae. At the same altitude, some species of Zygaenidae were well represented *Z. lonicerae, Z. filipendulae*, and others).

Above 2800 m a.s.l., the single specimens of *Macrolepidoptera* were found. Primarily, representatives of *Microlepidoptera* were recorded there; the number of them also noticeably decreased. At the altitude of 3100 m a.s.l., it was possible to collect only representatives of *Muscidae* (including *M. domestica*) and several specimens of *Microlepidoptera*.

Analyzing the total number of insects collected at different altitudes, we can make a preliminary conclusion that the number of *Noctuidae*, which varies depending on the altitude, can be described by a curve with a maximum at the altitude of about 2100 m a.s.l. Above this mark, the number of *Noctuidae* decreased gradually to zero at the altitude of 3100 m a.s.l. The curves of number decrease for *Microlepidoptera* and *Muscidae* to the right side of this maximum (for higher altitudes) were flatter than for *Noctuidae*, i.e., representatives of these groups of insects were registered at such altitudes, where *Noctuidae* was no longer present. These data are in good agreement with the data of other authors obtained for different regions of the Earth [17, 18].

According to the theory [27–29], the organism reacts to unfavorable conditions, for example, high altitudes. These reactions can cause changes in insects' behavior and/or hormonal changes (changes in color shades of insect bodies, wings, and tissues).

For today, only behavioral differences in insects (*Noctuidae*, to a lesser degree *Muscidae*) with changes in altitudes in studied locations of the Caucasus Mountains have been reliably registered.

Individual insects, which demonstrated highly active behavior at 2100 m a.s.l., were passive at 2800 m a.s.l. Most often, they either "froze" motionless on plants or crawled sluggishly on them. Such behavior was also characteristic of a sunny, warm summer afternoon. Therefore, it can be assumed that the lack of oxygen can cause such behavior.

Flying insects, in the case of trying to catch them or unexpected gusts of wind, the most often "simulated death": they "frozen" suddenly, fall, and get lost among the plant's vegetation. Such a reaction was shown by the vast majority of insects at altitudes above 2800 m a.s.l., while only a few individuals showed it when it decreased to 2100 m a.s.l.

Adaptive capabilities of gophers

Studies of animals in states of natural winter hibernation were carried out at the scientific base of the National Academy of Sciences of Ukraine — EMBS (Elbrus Medical and Biological Station, before 2007). The aim was — including them in closed ecological systems during space exploration. The obtained results demonstrated that such organisms functioned in a balanced way, and their tissues were sufficiently supplied with oxygen. It was established that adequate oxybiotic relations in conditions of natural winter hibernation were ensured. Such a situation happened against the background of a significant decrease in oxygen demand of organism tissues, an increase in the number of erythrocytes and hemoglobin in the blood, oxygen content in arterial blood, and especially carbon dioxide (up to 49.2±1.7 vol.% against 29.4±1.4 vol.% in active individuals), maintaining of oxygen tension in the muscles equal to 14±1 mm Hg (18±1 hPa), a uniform decrease in the intensity of oxygen consumption in various tissues — the same for the brain, heart, and muscle tissues ($Q_{10} = 1.37$), etc.

Fulfilled research made it possible to identify some specificities of heterothermic animals in comparison with homoothermic ones. Therefore, the question arose of studying the mechanisms of adaptation to hypoxic environmental conditions in animals capable of minimizing vital activity.

Observations with further analysis were done with the spotted gophers of the Ukrainian steppes that were moved to the Caucasus Mountains and settled at different heights. It was found that in the process of gradual (staged) adaptation, as well as after an extended stay in the mountains at the altitude of 3000 m a.s.l. under the conditions of natural stay, the power of the systems responsible not only for supply but also for oxygen consumption increases.

When comparing the functional indicators of gophers brought to the heights of the Caucasus and gophers aboriginal of the highlands, significant differences were also noticeable. These facts evidenced the differences in the mechanisms of adaptation of these two groups of animals. In steppe gophers, in the process of adaptation to conditions of mountain heights, the number of erythrocytes increased, the hemoglobin content increased and remained at a high level for a long time.

In aboriginal gophers of the highlands, these values are relatively low despite the increased erythropoietic activity of the bone marrow, which is probably associated with an increase in the volume of circulating blood.

In aboriginal gophers, high-altitude adaptation was characterized by an increase in the volume of circulating blood with a slight increase in the hemoglobin content per unit of blood volume. Obviously, this type of adaptation was fixed genetically in the process of long evolution; it is optimal in terms of energy consumption. But with the increase in the volume of circulating blood and the need to maintain the speed of blood flow at a constant level, the increased work of the heart is required, and indeed - in such gophers, the ratio of heart weight to body weight is more significant than in those living on the plain.

In gophers adapted to the conditions of mountain heights, the intensity of oxygen consumption is high, with a tendency to decrease in the case of an increase in the duration of stay in the mountains. In mountain gophers, it is relatively low (a tendency to decrease with increasing altitude).

A decrease in the intensity of oxygen consumption, which ensures the preservation of the mountain population, is associated with a specific reduction in the general level of functioning of the organism's systems. However, the registered fact of low intensity of oxygen consumption in mountain gophers cannot be explained by the reduced oxygen demand of vitally important organs. The state of adaptation of hibernating animals to the conditions of a hypoxic environment is favorable for winter hibernation since its period is more extended in mountain animals than in plains ones.

Therefore, the genotypic adaptation of heterothermic animals to the conditions of the hypoxic environment, in contrast to phenotypic adaptation, is characterized by relatively low levels of hemoglobin content, the number of erythrocytes (with an increase in the volume of circulating blood), and the intensity of oxygen consumption by the organism.

The mechanism of development of phenotypic adaptation to hypoxybaria in homeothermic animals does not differ from that in active heterothermic animals [19, 62, 65-70]. Therefore, adaptation processes can be considered not only at the level of the whole organism of insects and gophers but also at the level of organism systems. Thus, a lot of attention to EMBS was paid to the study of the adaptation of the respiratory system in mammals and humans.

Mathematical model of short-term adaptation to hypoxia in mammals

As mentioned at the beginning of this article, the primary strategy of adaptation for humans (and mammals as a whole) differs from one for insects. The primary strategy for these evolutionary high organisms is to maintain metabolism levels for their organs and tissues. Physical, mathematical, and program modeling are potent techniques for a theoretical understanding of adaptation phenomena; the authors use them all [23–26].

Natural characteristics of living organism functioning measured in laboratory conditions on the plain (control) and the conditions of the mountains (EMBS) were put in base of developed mathematic models. This Table presents the data on changes in some physiological indicators that occur in the human body (men) during the process of adaptation to mountain conditions (2100 m a.s.l.); the recorded changes evidenced that the phenomenon of physiological adaptation

Table. **Organism regulatory reaction and tension of oxygen and carbon dioxide under the various types of perturbations (short-term adaptation)**

Type of perturbation	Parameter	Tissues					
		Brain	Heart	Liver	Kidney	Skeletal muscles	Other tissues
Physical load 600 kgf-m/min	${P_{TJ}}^{(1)}$	26.2	15.7	43.8	60.5	13.0	37.2
	${P_{TJ}}^{(2)}$	51.1	57.2	50.2	45.0	54.0	47.8
	Q_{cj}	23.5	29.5	42.6	16.0	298.8	11.4
Hypoxybaria	${P_{TJ}}^{(1)}$	32.2	20.8	38.1	44.0	26.0	36.1
(${P_A}^{(1)} = 70$, ${P_A}^{(2)} = 30$)	${P_{TJ}}^{(2)}$	30.0	33.5	30.4	28.2	40.5	44.1
	Q_{cj}	14.5	5.6	24.5	21.5	21.0	10.5
Hyperoxia	${P_{TJ}}^{(1)}$	43.0	27.5	46.0	62.1	29.5	38.0
(${P_A}^{(1)} = 205$, ${P_A}^{(2)} = 42$)	${P_{TJ}}^{(2)}$	47.0	38.0	47.0	45.0	50.0	48.0
	Q_{cj}	13.6	4.0	20.5	14.5	17.5	8.5

Note. The values ${P_{Tj}}^{(1)}$, ${P_{Tj}}^{(2)}$, ${P_A}^{(1)}$, ${P_A}^{(2)}$, are given in millimeters of Hg, Q_{Cj} in milliliters per second.

occurs during the observation period. Therefore, the process of breathing, during which transportation and mass exchange of respiratory gases takes place, was supposed to be a controlled dynamic system, and it was described using a system of differential equations and algebraic relations.

Control (self-regulation) parameters are: $\dot{V}, Q, Q_{Cj}, j = \overline{1, m}.$

They are given in the mathematical model of the functioning of the respiratory system [23–26]. Thus, it is supposed that the executive organs of breathing process regulation are the respiratory muscles, heart muscles, and smooth muscles of blood vessels in the tissues.

Perturbations that influence the functional respiratory system are divided into external perturbations (changes in the composition of the respiratory mixture, barometric pressure of environment) and internal ones (changes in the intensity of metabolic processes in organs and tissues); the indicators of them are utilization rates of oxygen $\left(q_{Tj}^{(1)}, j = \overline{1, m}\right)$ and release of carbon dioxide $\left(q_{Tj}^{(2)}, j = \overline{1, m}\right)$.

The role of short-term adaptation of the respiratory system to hypoxia is to transform the disturbed dynamic system of transport and mass exchange of respiratory gases to a specific stationary state, which will be stable for the formed conditions of the organism's vital activity.

For formal recording and solution of this problem, it is essential to set:

– the initial state of the system that is characterized by phase variables:

$$P_{RP}^{(1)}, P_{RP}^{(2)}, P_{AL}^{(1)}, P_{AL}^{(2)}, P_{LC}^{(1)}, P_{LC}^{(2)}, P_{A}^{(1)}, P_{A}^{(2)}, P_{Cj}^{(1)},$$

$$P_{Cj}^{(2)}, P_{Tj}^{(1)}, P_{Tj}^{(2)}, j = \overline{1, m}, P_{V}^{(1)}, P_{V}^{(2)},$$

at the time τ_0 of the start of disturbing factors;

– the area of changes of control parameters:

$$\left.\begin{aligned} &\dot{V}_{\min} \le \dot{V} \le \dot{V}_{\max}, \\ &Q_{\min} \le Q \le Q_{\max}, \\ &Q_{Cj,\min} \le Q_{Cj} \le Q_{Cj,\max}, \ j = \overline{1, m}, \\ &\sum_{j=1}^{m} Q_{Cj} \le Q; \end{aligned}\right\} \quad (1)$$

– the terminal set of states determined by the relations:

$$\left.\begin{aligned} &\left|G_{Tj}^{(1)} - q_{Tj}^{(1)}\right| \le \varepsilon_{Tj}^{(1)}, \ j = \overline{1, m}, \\ &\left|G_{Tj}^{(2)} - q_{Tj}^{(2)}\right| \le \mathring{a}_{Tj}^{(2)}, \ j = \overline{1, m}, \end{aligned}\right\} \quad (2)$$

Where $\varepsilon_{Tj}^{(1)}, \varepsilon_{Tj}^{(2)}, j = \overline{1,m}$ are enough small positive values.

The solution to the problem of short-term adaptation formulated in this way is any set of values of the control parameters from equation (1) because, after some time, it transfers the disturbed system to the state, which is characterized by conditions (2). At the same time, the level of hypoxia and degree of carbon dioxide accumulation in organisms will be more or less significant.

In this regard, the problem of short-term adaptation is represented as a problem of optimal self-regulation. It is supposed that the following set of control parameters from equation (1) is optimal, which ensures the minimum functional on the trajectories of the disturbed dynamic system:

$$I = \int_{\tau_0}^{\tau_0+T} \left[p^{(1)} \sum_{l=1}^{m} \lambda_{Tj} (G_{Tj}^{(1)} - q_{Tj}^{(1)})^2 + + p^{(2)} \sum_{l=1}^{m} \lambda_{Tj} (G_{Tj}^{(2)} - q_{Tj}^{(2)})^2 \right] d\tau,$$

where $p^{(1)}$, $p^{(2)}$ — are coefficients of the organism's sensitivity to hypoxia and hypercapnia, respectively;
$\lambda_{Tj)}$ — coefficients that characterize morpho-functional characteristics of each organ or tissue region and their "vital significance".

During the calculations, it was assumed that:

$$\lambda_{Tj} = \varphi\left(\frac{V_{Cj}}{V_{Tj}}\right), j = \overline{1,m}.$$

Usually, the quadratic function φ of the given in relation (3) characterizes the blood filling of a unit volume of the tissue reservoir. A series of computational experiments were carried out with the model of short-term adaptation, the results of which are given in the Table. Self-regulation of the respiratory system is going too at the stages of medium-term and long-term adaptation, when disturbances that affect the system are repeated constantly or periodically for a long time (weeks, months). Described phenomena cause the development of additional adaptive mechanisms; they allow more efficient organization of metabolic functions in tissues in response to disturbances.

Thus, adaptation is based on a significant number of complicated phenomena, and studies of them are essential for people not only in peacetime but also in even more in conditions of contemporary war in Ukraine. In the present review, numerous investigations of adaptation phenomena done by Ukrainian scientists were described for various species of living organisms. In the modern world, problems of adaptation have begun to cause great interest, too, in connection with global climate change. The results described in the article are in agreement with the results obtained by other authors, both for invertebrates [30, 32, 53–60] and vertebrates [61–70].

Conclusions

1. The first studies of the adaptation mechanisms of insects and their ecological and faunal analysis in the high mountain regions of the Ukrainian Carpathians and Caucasus Mountains revealed certain regularities. The most characteristic species of *Noctuidae (Lepidoptera)* from their list for the fauna of the Elbrus region were suggested; in it both forest and steppe species were determined. Preliminary data on the differences in species compositions for *Noctuidae (Lepidoptera)* and *Microlepidoptera* depending on altitude were obtained, which reflects the realization of adaptation mechanisms of these organisms at different altitudes. The distribution of insects' number' with height can reflect their adaptive properties, too, as it is the realization of one of the classic adaptation strategies for this group of organisms. The distribution curve of insects' numbers with height (supposed by the authors), coincides in main features with similar results of other authors obtained for other regions of the world. Such distribution curves can reflect the most general regularities of insects' adaptation at different heights and the influence of mountain factors regardless of their geographical location.

2. Registered differences in the mechanisms of gophers' adaptation to the conditions of mountain heights can be explained as follows. Oxygen supply to the tissues is determined by the partial pressure of oxygen in the inhaled air, the volume of pulmonary ventilation, the total diffusion surface of the lungs, the oxygen capacity of the blood, the volumetric velocity of blood flow in the lungs, and tissues, the gradient of oxygen tension at all stages of its transport to the tissues, the rate of oxygenation and deoxygenation, the contact time of erythrocytes with oxygen in the lungs, the volume of capillary blood flow to the volume of tissues, and other parameters. These parameters and ratios are not constant. They

can be changed depending on the functional needs and environmental conditions. Some of them (pulmonary ventilation volume, blood flow rate) increase even during short-term oxygen insufficiency, while others (oxygen capacity of blood) - during long-term one. However, the increase of these parameters has limits determined by functional capabilities, the "cost" of adaptation, inverse interdependencies (when an increase in one indicator leads to a decrease in another), etc. Therefore, it is not surprising that species and individual characteristics of the organism, interdependence of functional indicators, degree of hypoxia, and duration of adaptation determine the colorful picture of functional changes during adaptation to the highlands.

3. It was confirmed that, unlike the adaptation of organisms of higher mammals, the adaptations of insects were realized by another strategy, which differs from mammals'. The primary strategy for humans (and mammals in general) is in maintaining of metabolism level for their organs and tissues. Reproduction increasing for invertebrates was not studied. According to the theory, it was registered more often for the first way of adaptation (for organisms at lower levels of evolution). Still, some noticed phenomena for mammals (and humans) evidence that such effects are more complicated and need more detailed investigation.

4. As a result of analyses of obtained data mathematical model was developed – a model of short-term adaptation of the respiratory system in mammals; this model was described in the present article.

5. Adaptation of human organisms to hypoxybaria, taking into account the age-related changes in organism's reactivity, increases their work capacity and stability, protects against premature aging, and contributes to longevity. With age, the organism's ability to adapt to hypoxia decreases, but it is not entirely lost — older adults can adapt to mountain heights up to 5000 m a.s.l.

6. Functional adaptation was put in the base of hypoxytherapy methods.

7. Investigations of mechanisms of adaptation for extreme stressful conditions are essential in wartime when numerous people suddenly find themselves in stressful extreme conditions — theoretical and practical knowledge as well. Such knowledge has to preserve the health, sometimes the lives of the people.

Acknowledgments

The authors express their gratitude to Ukrainian invertebrate zoologist Prof. Zoya F. Klyuchko for her help in collecting insects (mainly *Noctuidae, Lepidoptera*), identification of insect species, and her advice on the taxonomy of insects.

Author Contributions

P. Beloshitsky — general supervision, planning the work, funding, analysis of results, contributed to the article's conception and writing of some fragments of article; O. Klyuchko — data analysis, carrying of some observations, manuscript article writing, editing, translation and paper preparation, provided the new literature data for review; Yu.M. Onopchuk — head of the works in mathematic modeling; G. Lizunov — some data curation, analysis; K. Lyman — mathematic modeling, algorithms construction; A. Lizunova — computer simulation, algorithms construction. All authors contributed to the manuscript's revision and read and approved the submitted version.

Funding

The study was funded under the themes according to the State registration 0107U002666 and No. 177-X04 (1.06.2004).

The authors declare no conflict of interests.

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АДАПТАЦІЯ В ЕКСТРЕМАЛЬНИХ СТРЕСОВИХ УМОВАХ: ДЕЯКІ ТЕХНОЛОГІЇ ДОСЛІДЖЕНЬ

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Адаптація є фундаментальним явищем, що забезпечує виживання біологічних організмів у мінливих умовах середовища; вивчення цього і пов'язаних з ним явищ критично необхідне людям не тільки за умов мирного життя, але й війни.

Мета. Опис деяких технологій досліджень та результати їх застосування для вивчення адаптації різних організмів до стресових екстремальних гірських умов.

Методи. Порівняльний аналіз великої кількості даних експериментів і спостережень філогенетично різних організмів у змінених стресових умовах гіпоксії, інших факторів високогір'я. Стандартні методи лабораторних аналізів деяких показників життєдіяльності біологічних організмів. Для збору комах застосовували денний і нічний методи збору з використанням світлової пастки; в деяких випадках використовувалися феромони. Математичне та програмне моделювання.

Результати. Розглянуті сучасні уявлення про фізіологічну адаптацію на основі українських та зарубіжних класичних та сучасних досліджень. Було розглянуто еволюційні аспекти досліджень адаптації з урахуванням двох основних стратегій адаптації біологічних організмів, а також розглянуті еволюційні аспекти адаптації до гіпоксії на прикладі комах і ссавців (ховрахів). Детально описані використані технології досліджень та отримані результати — як результати польових спостережень, так і зареєстровані в лабораторних умовах. Основну увагу було сконцентровано на результатах сучасних робіт українських вчених. Таким чином детально охарактеризовано різні напрямки досліджень — для комах і для ссавців (ховрахів). Особливу увагу було приділено проблемам адаптації людини до стресових умов; ефекти були зареєстровані на волонтерах зі спеціальних груп (рятувальників, льотчиків тощо). Продемонстровано математичну модель короткочасної адаптації людини до гіпоксії.

Висновки. Наведено результати багаторічних досліджень адаптації на прикладах хребетних та безхребетних організмів. Проведено комплексний аналіз отриманих результатів. Запропоновано також ряд загальнотеоретичних висновків, зроблених на основі представлених результатів. Функціональну адаптацію було покладено в основу методів гіпокситерапії.

Ключові слова: адаптація, екстремальні умови, стресові умови, числові показники фізіологічних функцій, математичне моделювання.