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2.1.7 Indirect methods of estimating field metabolism of mammals

The importance of different species within a biocoenosis is determined in the end by their function in the cycling of matter, and in promoting energy flow; which in turn depend on many factors. The most important of these are: the amount of energy fixed in the total biomass of a population; the amount of energy necessary for the synthesis of biomass; the turnover rate; the amount of energy necessary to maintain normal life activity of the species (including the amount of energy necessary to maintain biomass cycling under normal environmental conditions); and the change in the environment caused by the life activity of the species. By extreme simplification of the real state of things in nature we can say that if the metabolism of an elephant is ten times less intensive than that of a shrew, then a population of shrews equal in biomass to a population of elephants, will play a much more important part than elephants in the total energy flow of the biocoenosis. This example emphasizes the importance of the problem taken as a whole. A large animal exercises a very conspicuous influence on the life of a coenosis whilst the actual role of small animals, the biomass of which is dispersed in millions of individuals, can only be discovered when we encounter distinct disturbances in the life of the coenosis. This affords a clear explanation of the paradoxical fact that the importance of small birds in destroying insect pests, or the importance of voles in the life of forest, has yet to be proved. It is therefore not accidental that, although many species of forest rodents are the main factor in the renewal of the most valuable sorts of trees, the regulation of their abundance does not come into the obligatory work programme of any forestry scheme in the world. Consequently we can say without fear of

exaggeration that the determination of the importance of individual species in the cycling of matter, and in the promotion of energy flow, in biocoenoses of different types is the most important prerequisite of any scientific management of production in nature.

However, investigations of this problem may come up against exceptional difficulties, the most important of which are outlined below.

In order to determine the role of the species in the energy metabolism of the ecosystem we must, first of all, determine with the necessary reliability the following parameters of the population: the absolute numbers of animals; their biomass; the structure of the population (because the intensity of the matter and energy metabolism of animals of different weight, sex, age, physiological condition differ); the turnover rate of the population, and the intensity of metabolism of different groups of animals. A direct determination of any of these major parameters for a population is very laborious and in many cases impossible in practice. For example, we can count deer or wolves from an aeroplane and, with the help of a dog, — squirrels and sables (to say nothing of the difficulties and expenses of such works) but a direct calculation of mosquitoes in tundra, or cod-fish in the ocean, is practically unachievable. Determination of the level of energy metabolism of individual specimens is even more complex. Whilst it is not difficult to estimate the intensity of metabolism of certain species in a calorimetric chamber, it is practically impossible to estimate the loss of energy by a bat, a mole or a dolphin in the process of their natural life activity (taking into account daily and seasonal dynamics). The application of new techniques (the utilization of tritium and deuterium, etc.) will enable us to carry out many of the physiological experiments in nature. However, for the period surveyed, and for the majority of species, this outline of the present state of affairs should not be regarded as deliberately pessimistic. Along with the perfection of direct methods of biomass determination and population energetics it is also necessary to try and use more widely indirect methods based on the application of sufficiently well-proved ecological and eco-physiological regularities (the method of morpho-physiological indicators; S c h w a r z 1958). Let us consider the possibilities of these methods as applied to individual problems.

1. ABSOLUTE NUMBERS OF ANIMALS

The perfection of methods of estimating animal numbers is acknowledged by all zoologists as one of the most important problems of theoretical and applied ecology. Many investigations have been devoted to this problem therefore I shall not dwell upon it but only mention that the best prospect, in my opinion, lies in the use of indirect methods of calculation based on

changes in the population structure of species. The theoretical prerequisites of these methods may be summarized as follows: Any influence on the population changes its structure, this follows from one of the most fundamental laws of modern biology: the law of biological heterogeneity of populations. Therefore any influence (hunting, exploitation of forest, sharp changes of weather, etc.); individuals, differing biologically (irrespective of the reasons which account for these differences — genetic, physiological, connected with age), will act differently and spark off changes in the structure of a population. It is an inevitable change and the stronger the influence on the population the more sharply will it reduce numbers, and hence the more effective will the change be. Besides depending on the initial number of animals this inevitable change of the structure of a population may manifest itself in differing degrees. To find out the dependence between the initial number of animals and the changes in population structure when the population is influenced by a known factor (e. g. hunting with definite efficiency) — requires an indirect method of determining the number of animals. Some concrete ways of solving this problem have been described in a series of works by V. S. Smirnov and some American and Japanese zoologists. However, it seemed important to emphasize here the general theoretical bases of this very important problem.

2. DETERMINATION OF BIOMASS OF ANIMALS AND ITS DYNAMICS

When the numbers of animals and the average weight of individuals belonging to a population are known it is not difficult to calculate the total biomass of the population. If we know the population dynamics and changes of the weight of animals then the dynamics of biomass is thereby known as well. There is no need to demonstrate that it is most desirable not only to determine the weight but also the chemical composition of the body of animals. However, it is necessary to draw attention to the fact that biomass alone only indicates the value of the energy content of body tissues and does not give any indication of the role of the given species population in the energy flow in the ecosystem. When extreme cases are taken into consideration the situation becomes self-evident: the biomass of animals during hibernation remains unchanged whereas the role of sleeping animals in the energetics of a population falls to zero. When differences in the activity of animals are less sharply manifest then the dynamics of the energetical role of a population not connected with a change of biomass are frequently not taken into consideration and may lead to some major errors. The data which show that the energy used for the synthesis of biomass forms only an insignificant part of the total energy flow passing through the population of a given species indicate above all the scale of such mistakes. A significant part of energy

is used to maintain the normal life activity of animals (insectes — from 85 to 99 per cent, mammals — 98 to 99 per cent). Hence it is evident that mistakes in determining the energy of life activity (the energy of respiration) of animals may lead to as important errors in determining the role of a population in the total energetics of the ecosystem as those made in determining the abundance of animals (determination of biomass). In practice such mistakes may be even more important as it is more difficult to determine changes in the level of respiration energy (especially non-periodic) than changes in the abundance of animals. However, it must be noted that the energetic role of a population is not solely the sum of the levels of energy metabolism of single individuals but is also connected with the influence of the animals on the habitat.

3. INDIRECT INFLUENCE OF ANIMALS ON THE ENERGY FLOW IN THE ECOSYSTEM

In the process of its life activity an animal affects the course of energy metabolism in the ecosystem not only by using some quantity of biomass, transforming it into biomass of its own body and waste-products of metabolic processes, which in their turn undergo biological and abiological transformation (moreover some part of energy is lost for the ecosystem as a whole), but also by changing the structure of the ecosystem. The beaver gathering building materials for a dam not only substantially changes the correlation between living and non living biomass in the biogeocenosis but frequently changes markedly the structure of the coenosis. However this influence on the life of the system is only indirect and is not connected with the nutrition of the beaver, that is the transformation of materials and energy carried out by the population of beavers. Many analogous examples could be given here, however, in an immeasurably greater number of cases similar animal activity is not so striking and remains unestimated. Thus in this way sometimes a larger, sometimes a smaller, but always a significant part of the influence on the energetics of the coenosis escapes from our field of vision. Therefore it is necessary to define that part and, if possible, to define it in quantitative expressions.

Moreover, it is not enough to be guided by direct observations as they are not always possible and do not always supply material for corresponding prognoses. Indirect data may lead to more important and more interesting conclusions. Let me illustrate this reflection by an example.

It is known that young field-voles chiefly eat green, young (rich in vitamins) parts of plants. In identical conditions adult (i. e. which have finished growing) animals consume the energy rich underground parts of plants to a considerably greater degree. These distinctions in the types of

nutrition of juveniles and adult animals besides having a direct influence on the energetics of the coenosis, play also a considerably more important indirect role. E.g. *Ondatra* eating the green, upper parts of a young reed does not destroy the plant; on the other hand the same *Ondatra* eating a rhizome destroys the plants and in this way uses up only an insignificant part of the biomass which is being withdrawn from its ecosystem. These are evident and important distinctions. When we know not only the general spectrum of the nourishment of an animal but also its details we shall be able to predict the change in the role of the species in the ecosystem after the environment, or the structure of a population has been altered.

A deficiency of microelements in the grassy cover will force deer to use twigs as forage: a deficiency of manganese will make deer choose forest edges as their main feeding sites; a disturbance of the optimum correlation of phosphorus and calcium in the grass and twigs of grown trees will force the deer to switch over to feeding on young trees and/or shrubs.

There are many such similar regularities already known. At best they enable us, without any additional investigations, to determine more precisely the role of single populations (of species) in the life of a well defined biocenosis. At worst they lend a necessary direction to these investigations. It is advisable therefore to indicate how different these landmarks, which show us ways of determining more exactly the role of single populations of different species in various conditions of the environment, may be.

The enriching of natural resources with fats reduces the need for thiamin by animals; a lowering of the environmental temperature raises the need for ascorbic acid; the need for thiamin and choline increase together with raised temperature; when the atmospheric pressure falls a carbo-hydrate diet is especially favourable for animals; a diet enriched with animal protein increases the need for calcium and creates favourable conditions for accumulation of vitamin A in the liver; peculiarities of the chemical composition of plants, especially the predominance of various carbohydrates (lactose, arabinose, galactose) increases or reduces the assimilability of calcium by animals; an increased content of dextrine in the food may assist in a better assimilation of proteins; when there are no manganese salts the ability of animals to synthesize vitamin C falls sharply.

These and analogous physiological regularities determine the actual behaviour of animals in biogeocoenoses because in the end all animal behaviour is determined by one general cause — the striving to maintain the balance of energy in the processes of carrying out the seasonal and daily cycles of their life-activity.

When we know the conditions of the existence of animals we can, without additional investigations and experiments, determine peculiarities of their diet and in this way determine their role in the life of the ecosystem. I could supply a great number of examples showing

that conclusions substantiated in this way and concerned with the energetics of a population in a system of various coenoses frequently proves to be more precise than those which could be drawn on the basis of direct observations. On the other hand as was shown above, the direct approach to the problem enables us to orientate correctly the programme of indirect observations and thus assists in increasing its effectiveness.

An obstacle to the more widespread acceptance of the ideas put forward in this part of my lecture consists, very likely, in the lack of confidence of biologists in biological laws. The sooner this distrust is overcome — the more fully the whole arsenal of the facts accumulated by biology will be put to a good use to solve many problems, especially — problems of the determination of the indirect influence of animals on their habitat.

4. ENERGY METABOLISM OF ANIMALS

A direct determination of the level of energy metabolism of animals in natural conditions is, in a majority of cases, connected with considerable and frequently insurmountable difficulties. The importance of indirect methods is only increased by this fact. Their essence relies on the fact that the level of metabolism is determined on the basis of studying those features of animals which are most closely correlated with the intensity of metabolism.

4.1 DIMENSIONS OF THE BODY

It is well-known that in the same conditions small animals have a much more intensive metabolism, than large animals. Therefore when we know the dimensional structure of a population it has an independent importance (and not only as an index of its age structure or conditions of existence) which enables us to determine the peculiarities of energetics of a population. On the other hand small dimensions of the body may also have an independent adaptive importance (the possibility of using disseminated food). On the whole the problem of the importance of dimensions of animals has been well analyzed in numerous special papers and for this reason I shall not go deeply into its examination.

4.2 THE GROWTH OF ANIMALS

The growth period of animals is a period of intensification of metabolism. The higher the energy of growth, the more significant are the energy needs of an organism. This is governed by the fact that energy is necessary for

the process of growth itself, that is the transforming of food materials into its own living tissues. As far as a growing organism is concerned a large part of the energy of food is transformed into potential energy with a relatively smaller part played by the energy of metabolism (with adult animals the contrary is true). The correlation between dimensions of different organs and tissues changes with age. As far as a young organism is concerned, the internal organs with a higher metabolism are relatively better developed. This increases the intensity of metabolism and gives an opportunity to evaluate it without having recourse to direct methods of determination. Hence it is evident that the determination of the rate of growth of animals in nature is a most important prerequisite for the correct determination of the level of energy metabolism of populations.

Naturally in many cases (when the investigations are continuous) the rate of growth can be determined only indirectly, e. g. by way of periodic sampling of the population. In this way we can determinè the begining of the period of spring growth of rodents and thereafter determine the rate of growth. On the other hand the growth of animals may be also determined by way of making use of information concerning correlations between physiological indices of animals and their rate of growth. This connection may be specific, and the following observations indicate this. It is known that in middle and northern latitudes in autumn the growth of rodents ceases completely. However, young animals having attained maturity earlier (for some reason or other) and correspondingly taken part in reproduction sooner, stop growing earlier than other animals of the same age which did not take any part in reproduction. Consequently it may be maintained, that other parameters being equal (age ratio, numbers), the need of energy by young rodents in autumn will be much larger in the case when they have still not participated in reproduction. It is not difficult to express quantitatively this dependence for well investigated species. (We are not concerned here with the problem of the importance of reproduction of young rodents in the dynamics of abundance.) Even this one example proves that information on the growth of animals may also be obtained without carrying out direct observations. However approaches similar to the one described above cannot be treated as universally applicable.

The second method is characterized by a greater degree of universality based on the fact that a change in rate of growth may lead to changes in the proportions of the body of animals. The theory of this problem was subjected to analysis in my special paper from 1962 and so I shall restrict myself to one example and try to show what importance this regularity may have as applied to the determination of the energetics of populations.

The rate of growth of the cranium of rodents is exposed to much less significant fluctuations than the rate of growth of the body. Therefore the higher the rate of growth, the smaller the relative length of the cranium. This dependence is so evident that by analysing a series of captured rodents

we can determine with absolute precision the rate of growth of the animals. It must be stressed that the exactness of this proposition will be immeasurably higher for a well investigated species than for one which may be achieved by way of direct observations in nature. It is only necessary to draw up beforehand tables of corresponding calculations based on experimental data and make use, as far as possible, on not one but several mutually not correlate indices (as the latter, for example, dimensions of some internal organs may be used).

The advantage of indirect methods of estimating the growth of animals consists in the fact that with their help we can determine differences between the rate of growth of physiologically different intrapopulation groups (males with a different degree of sexual activity, females in a different phase of oestrus cycle, young animals born in different periods of time, etc.). These alone enable us to make considerably more precise the determination of the level of metabolism of a population as a whole.

4.3 SPECIFICITY OF THE LEVEL OF METABOLISM OF POPULATIONS

Hereditary features of individual populations of animals, concerned with peculiarities of their metabolism, may be determined in a laboratory in an experimental way (examples may be found in any compendium on ecological physiology). However, this method is very laborious, and above all, it does not remove the truly sacramental question about the possibility of the extrapolation of conclusions drawn from laboratory experiments to natural populations of animals. Therefore indirect methods, based in this case on the correlation of constitutional feature of animals with the level of metabolism, may again prove useful.

The dimensions of the kidney and the adrenal gland may be used as the simplest indices. An increase in the weight of these organs serves, in a great majority of cases, as a direct indication of metabolic activity (quantitative expression of this relation should in each individual case be determined experimentally).

In some cases constitutional characteristics of populations, reflecting the specific character of the intensity of their metabolism, are hereditary features. And so, for example, it was stated in our laboratory that many subarctic populations are characterized by a lowered energy metabolism (a consequence of perfecting physical thermoregulation). Accordingly, in equal conditions of the environment, northern populations are characterized by a low kidney weight. (For northern tundra voles, bred for many generations in captivity, the relative weight of the kidney may be expressed by the allometric dependence $y = 10.66x^{0.747}$, and for southern field-voles $y = 6.13x^{0.939}$).

The content of vitamin A and C in tissues, the dimensions of the heart

and some hematologic indices, etc. may serve, within the limits of species (besides the kidney and adrenal), as indicators of specificity in the intensity of metabolism of different populations. Those features of a population, which are directly connected with the level of metabolism may have a particular importance. Most of all we may treat as such features differences in the rate of growth and intensity of reproduction.

It was shown by extensive investigations that northern populations of a majority of species of rodents are notable for an increased fertility. For northern field-voles the average number of embryos is approximately one and a half times larger than for southern representatives of this species. It is only natural that the period of lactation and pregnancy of northern populations is connected with larger losses of energy than in the south. There is also a change in the required quality of food. Let me repeat that in a given case this conclusion may be adequately proved, even without special observations and experiments. Is the observed difference between populations from the energy point of view significant? Some numbers which help to answer this question will be given below as they are connected with solving another problem and I shall try here to analyse them on the evolutionary level.

As an example I shall take the northern populations of rodents best investigated by us. When different species are compared, their degree of adaptability to the conditions of subarctics being various, it turns out that an increased fertility is mainly characteristic of a northern population of a widely-distributed species which has not yet acquired the ability for a full mastering of vast subarctic territories. Typically arctic animals (lemmings, Middendorf's voles) have relatively low fertility. This suggests that a sharp increase in fertility forms a preliminary adaptation of the species to the conditions of the arctic regions. This type of adaptation proved to be energetically unsuitable and in the process of evolution was substituted by another one, which increased the ability of the animals to survive and in consequence enabled them to do without a sharp increase of fertility, thus reducing tenseness in the balance of energy. It may also be revealed that when we analyzed the quality of food needed, special observations showed that females of the species which were characterized by an increased fertility, were not able in the period of pregnancy and lactation, to accumulate vitamin A (everything went to the embryos). Species with a lower fertility in the equal conditions of the environment accumulated a large quantity of vitamin A both in the period of pregnancy and during lactation.

These observations show that an increase in losses of energy, connected with a increase in fertility, have a real importance to animals and is so significant that in the process of evolutionary transformations of populations it is more advantageous to shorten fertility in order to reduce tenseness in the balance of energy. This means that an increase in energy needs, even

if it seems to be an insignificant one, sets new problems for animals and changes the role of the species in the ecosystem. And this is frequently not taken into account. General observations of the way of life of animals in nature produce an impression that energy reserves are abundant (only the tenseness in obtaining additional nutritional substances is fixed — vitamins, microelements, etc.) this notion is incorrect.

In each case it is necessary to consider the reserves of energy and the losses of energy in acquiring food. The higher the energy needs the larger (other conditions being equal) is the area from which the animal gets its food. Therefore in nature frequently (and more often than is usually admitted) the situation arises when food is abundant (e.g. grass) but its disposition is such that the energy loss in acquiring it surpasses its potential energy — the animal starves in spite of the abundance of food! The role of such a species in the energetics of the system is thus sharply reduced — the animal is not able to make use of the available food. In many cases the situation may arise when a sharp reduction in numbers and cessation of population reproduction start long before reserves of energy of the ecosystem are used up. As far as dominant species are concerned (*Microtus* on pastures and old fields, lemmings in tundra, etc.) this may lead to a cardinal change in the flow of energy in the biocenosis: the phase of intense energetic metabolism is substituted by the phase of the accumulation of potential energy in primary producers. It is impossible to distinguish the initial phase of this process, which is undoubtedly a significant event in the life of an ecosystem, by means of direct observations. Indirect methods may yield in such cases exceptionally valuable results, for a first, even negligible disturbance of the normal feeding of animals is reflected in their physiology and may be fixed. In accordance with our aim we do not enumerate all those features of the physiology of animals, which are signals of the beginning of a change in the balance of inflow and outflow of energy. Only for the sake of illustration shall I show that the initial stage of this process may be distinguished by means of changes of liver weight of animals from different intrapopulation groups. In such cases, for example, when the weight of liver of young and middle aged pregnant females is normal, and when the weight of liver of older females is below the norm we may state with full certainty that we have encountered the first stage of an increase the tenseness of the balance of energy (we are not concerned here with any consideration of a purely physiological aspect of this phenomenon) which affects their position in the ecosystem as a whole.

The most general conclusion which may be drawn from this part of my lecture consists in the fact that any change in the degree of losses of energy by each individual may exert no less an influence on the energetics of the ecosystem as a whole than does a change in the number of animals. Therefore maximum attention should be devoted to the study of the specific characters of various populations of the species.

The above comments stress the necessity of determining the level of metabolism in different stages of the life-cycle of the population. It is only natural that, first of all, we should take into consideration the cyclic recurrence of the physiological condition of animals, connected with such processes as shedding of hair, reproduction, hibernation, etc. As was shown, the level of energy metabolism of mammals during pregnancy per unit of weight increases by 8—10 per cent. This is connected with an increase of energy losses of the female and a higher level of metabolism of the foetus. An increase in the level of metabolism of embryos roughly corresponds to their total surface. This accounts for the fact that before parturition the metabolism of embryos may be twice that of the female herself. Besides, the intensity of metabolism of pregnant females at the end of pregnancy also increases sharply when it is evaluated per unit of weight (50—100 per cent). It is especially important to note that when the litter is very large the increase of the level of metabolism grows disproportionately fast. The need for energy increases considerably in the period of lactation (up to 300 per cent). When a litter of small predatory mammals or rodents is increased by one young it intensifies the need for food by 30—50 per cent (of the energy requirements of sterile females).

Data of this kind may be obtained with the help of physiological experiments. If we know the relationship between the physiological condition of the animal and its energy needs it is not difficult to determine also the change of the role of the given population (of the same species) in the total energetics of the ecosystem.

However, it is no less important to determine whether the energy needs of the animal are fully met in certain given conditions. Indirect data are of decisive importance when we want to solve this problem. It is well known that some discrepancy between environmental conditions and the physiological state of the animal causes some tension in the organism and gives rise to a stress-state. There exists a series of excellently investigated indices with which not only the existence of stress-reaction can be established but its degree as well. In many cases we may obtain a satisfactory answer in this way to the above stated problem. However, more precise methods can also be used.

Let us consider, for the sake of illustration, the case of pregnant females. In the period of pregnancy the ability of females to accumulate glycogen in the liver increases, and thus the weight of the liver of pregnant females is almost always high. For this reason the variability in the weight of the liver during pregnancy is lowered. An increase in the coefficient of variation of the weight of the liver of pregnant females is an undoubted index of tenseness in the balance of energy of a population. A decrease in the coefficient of variation gives evidence to the contrary. It is possible to make even more

precise our notion of the energy balance of a population. In such cases when the population is able to completely satisfy all of its energy needs (this case occurs much more rarely than it is usually considered), not only pregnant females but also males completely realize their ability to accumulate glycogen in the liver and differences in the size of this organ between males and pregnant females disappear; as does the difference in the degree of variation of the liver weights. In such populations energy needs of pregnant females are fully realized. We can state with certainty that the real energetics of females closely corresponds to the theoretical one.

An analogous method may also be applied to determine the degree of realization of the increased need for food in animals during periods of lactation, shedding of hair, growth, seasonal changes in the type of metabolism, etc. It is not difficult to understand how important such an approach may be, not only to determine the general state of a population but also to estimate its role in the life of an ecological complex.

As has been shown a change in the size of organs is one of the causes of changes in the level of metabolism of animals in various stages of their life-cycle. This change may be determined because we know the intensity of tissue metabolism of the various organs. A correction which takes into account constitutional peculiarities of animals may in itself be considerable and thus introduce significantly more precision into the calculation of the energetics of a population. The more significant this correction the more fully the correlation for the development of various organs and their systems have been taken into account. It was shown, for example, that there exists a clear-cut relation between the weight of the heart and the weight of the skeletal muscles (from this point of view several dozens of animal species have been analyzed in our laboratory). Therefore solely on the grounds of a change in heart weight we can, with considerable precision, indicate a general change in the level of metabolism of the animal.

However, it is even more significant that within a single population an increase in the weight of the heart (or other internal features) signalizes certain changes of conditions, or way of life of the animal, connected with changes in energy loss. From this point of view only in our laboratory have such indicators as relative weight of the kidney heart, brain, several endocrine glands, content of vitamins in tissues, hematological indicators, etc. been studied. We have already dwelt on their importance in the determination of the biological specificity of various populations. Let us turn now to their importance in the determination of temporal changes in energy losses by animals. We shall take in this case the simplest of all indicators — the weight of the heart. It is well known that in a period of increased activity (e. g. during migration) animals in nature display a reverse change in the weight of the heart. Are we entitled to make use of these data in order to determine quantitatively an increase in energy losses of animals? In order to answer this question we should once again compare investigations in nature with

experiments in the laboratory. The latter showed that an increase in the weight of the heart by 5—6 per cent occurs when the relative physical load is insignificant. When the load is significantly higher — causing a twofold (!) increased need for food — the heart enlarges by 20 — 30 per cent. Similar changes are by no means rare in natural populations. This means that taking into account only one parameter — the heart index — we may avoid a significant error in determining the energy needs of the investigated population. By taking into account other indices, which supply information about the degree of satisfying the needs of animals, we make our calculations more precise and in individual cases we may also determine in detail the use of the energy by animals. For example, in our laboratory we have accumulated considerable material, obtained from many species and have demonstrated that if the hypertrophy of the heart muscle is accompanied by an enlargement of the dimensions of the kidney it is evidence of a systematic increase in the level of metabolism. A reverse case indicates a short-term increase in motor activity accompanying a change in metabolism. The number of similar examples could be easily increased but those listed above are sufficient to illustrate the possibilities of indirect methods in estimating the energetics of populations.

5. CONDITIONS FOR SUCCESSFUL APPLICATION OF INDIRECT ESTIMATIONS OF THE ENERGETICS OF POPULATIONS

In order to determine the perspectives of any development of indirect methods of estimating the role of populations of any species in the total energetics of a biocenosis we have proceeded from the following basic assumption. Any successful working out of the problem first of all depends on answering the two co-ordinative questions: determining the number of animals and determining the level of metabolism of the individuals making up a population. Determination of the number is an independent problem and we have only touched upon it in passing. Much attention has been given to the principles of determining the intensity of metabolism of animals which in total make up a population. Difficulties in solving this problem are caused by the heterogeneity of populations and constant, both periodical and aperiodical, changes in metabolism of animals even within the limits of physiologically homogeneous intrapopulation groups. Therefore it is not only impossible to proceed from average indices to the species but also to well defined populations. It is necessary to know the structure of the population and be able to determine the specificity of metabolism within the limits of physiologically and ecologically homogeneous groups of animals. This specificity in its concrete quantitative expression can not be determined directly for each investigated population. However, it is relatively simple

to establish a correlation between the intensity of metabolism and some morpho-physiologic indices which may be easily determined in nature. This is only the first stage of a programme in which the leading role is given to long term experimental investigations in laboratory conditions at well-equipped field stations. As a result of this work we may establish a dependence between the intensity of metabolism and several morpho-physiological indices (quite a number of them are already established). These dependences can not be very precise because their concrete expression is influenced by many secondary factors. And so, for example, the dimensions of the heart are extremely accurately correlated with the intensity of metabolism but depending on the physiological condition of animals (including here psychological factors) a quantitative expression of this correlation varies. The same may be said about — dependence between the level of metabolism and the rate of accumulation and utilization of nutritive substances, the dimensions of the kidney, the amount of oxygen in blood, etc. In the conditions of the experiment we may take into consideration many factors which alter the experimental results, but obviously not all of them. And consequently it is practically unattainable to avoid errors altogether when the calculation tables "The intensity of metabolism — morpho-physiological indicator" are drawn up. But these errors in the true sense of the word are insignificant when compared with those errors which may be made when an investigator tries to determine energy metabolism of the population by taking into account average data which characterize metabolism of the species in the standard laboratory conditions.

The second stage — studying morpho-physiological indices of animals in natural populations — is even simpler. An experienced laboratory assistant during one day of field work investigates more than 50 individuals according to the complex of various indices (the dimensions of the organs, hematological indicators, content of vitamins in tissues, proportions of the body, etc.). The simplicity of these investigations enables to take the precision up to almost any level with the help of a simple increase in the material gathered and improving its biometric treatment. This stage, in principle, does not introduce any error into the solution of the whole problem.

The main source of error lies somewhere else. As we have tried to show, the differences in the intensity of metabolism are discovered not only between such physiologically different groups of animals as juveniles and mature animals, or males and females, but also between animals apparently belonging to one physiological group. Let us mention the differences between females in different phases of pregnancy, pregnant females of different age, animals of the same age but with different times of birth (the influence of the different age of females is not excluded), animals having different positions in the intrapopulation scale of ranks, settled animals, migratory animals, polygmic and monogamic males, etc. The more precisely the structure of a population is determined, the more precisely its energetics will be estimated. Let me

repeat that the method of morpho-physiological indices enables us to determine the specificity of metabolism of any of the given groups of animals. The main point of the problem is to distinguish these groups.

In this way the first condition for a successful application of indirect methods of determining the energetics of populations is correct determination of its structure. It follows from this that the advantages of indirect methods consist of the possibility of taking into account differences between various intraspecific and intrapopulation groups. If this advantage is not turned to account then the method as a whole loses its force.

The second circumstance is the dynamics of the metabolic processes of animals. This situation is so well-known that we have considered it unnecessary to argue in detail. It is important, however, that the variability in the level of metabolism of the above mentioned groups is various. The coming of autumn colds causes different changes in the metabolism of males and females, males sexually mature or not, etc. The same conclusion is valid when we compare changes in metabolism with changes in the number of a population. An increase in the numbers causes different reactions in reproducing and non-reproducing females, juvenile and mature animals, or dominants and subdominants. The method of morpho-physiological indicators may easily cope with such difficulties, but its successful application is determined by the precision of our data about the dynamics of metabolic processes of physiologically diverse intrapopulation groups. This is the second prerequisite of applying indirect methods to the determination of energetics of a population.

It is easy to see that the above mentioned difficulties may be easily overcome. This clears the way for a wide introduction of the recommended methods which will enable us to increase the precision of investigations concerned with the energetics of biological macro-systems.

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