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Some Morphological and Physiological Parameters of Mountain and Lowland Populations of the Bank Vole

[With 6 Tables]

Physiological and morphological comparative studies were made of mountain (1850 m above sea level) and lowland (170 m above sea level) populations of the bank vole *Clethrionomys glareolus* (Schreber, 1870) and also of lowland individuals acclimatized in mountains, and mountain individuals acclimatized in lowland areas. Examination was made of the morphological blood picture, blood volume, oxygen consumption value, weight of the heart, liver, lungs and spleen, weight and length of the alimentary tract and isolation value of the fur. No statistically significant differences were found between the mountain and lowland populations of the bank vole in respect of the values of morphological indices of the blood characterizing the hemoglobin function, in the total volume of blood or oxygen consumption rate. Mountain bank voles, on the other hand, have higher indices for the internal organs, the value of these indices decreasing considerably in animals acclimatized in lowland areas. The isolation value of the fur is greatest in mountain bank voles, but in animals acclimatized in lowland areas the reduction is statistically significant and approaches the level found in individuals originating from lowland areas.

I. INTRODUCTION

During the course of studies on the variations in blood indices characterizing the function of hemoglobin our attention was attracted by the fact that the mountain and lowland populations of the bank vole, *Clethrionomys glareolus* (Schreber, 1780) exhibit statistically uniform values of these indices (Kostelecka-Myrcha, 1967). This absence of differences would appear interesting in view of the data to be found in literature referring to the effect of altitude on the blood picture (Kalabukhov, 1937; Morrison, 1964; Morrison *et al.*, 1963a, 1963b; Folk, 1966). It was therefore decided to re-examine individuals from both types of population. The inclusion of other morphological and physiological indices, in addition to the blood picture,

should make it possible to reach conclusions as to the possible mechanism which enables the bank vole to settle in areas with low partial oxygen pressure, while retaining the same erythrocyte blood picture as found in lowland animals.

II. MATERIAL AND METHODS

The voles used for the study were caught in the Tatra Mountains near the Mor-skie Oko lake (20°04' E, 49°09' N), at an altitude of about 1850 m above sea level (group A), and at Białowieża (group B), where they were caught in the Białowieża National Park (23°48' E, 52°40' N), at an altitude of about 170 m above sea level. In addition we examined animals from Białowieża acclimatized in the Tatras (group C), keeping them in cages on a uniform diet for a period of three months. The fourth and final group (D) consisted of voles caught in the Tatras and acclimatized at Białowieża. In all we examined 170 individuals of *C. glareolus*.

The morphological blood picture was determined in 20 individuals of group A in June 1966, and in 27 individuals of group B in May 1965. In addition 20 voles belonging to group C and 20 to group D were examined in September 1966. The hemoglobin level was determined with a Zeiss-Ikon hemometer. The blood corpuscles were counted in a Thom chamber, and their diameter measured by means of a Zeiss measuring eye-piece on slides stained by the Pappenheim method. Hematocrite was determined by the micromethod. Total amount of blood was examined by the extraction method.

Oxygen consumption rate in voles belonging to groups A, B and C was measured in June 1966 in a total number of 64 individuals. Rodents belonging to group D were examined in September 1966. Measurements were made in a closed respirometer of the Kalabukhov type (Gębczyński, 1963), at a temperature of 20°C for 45–60 minutes. During this time the animals were kept singly in 1 l chambers, and their movements limited by placing them in a wire cage measuring 3 × 3 × 8 cm. During this time the voles were given neither food nor water. The oxygen consumption results obtained were converted into kcal for metabolic body size ($\text{kg}^{3/4}$), assuming that the caloric equivalent of 1 l of oxygen is equal to 4.8 kcal. Formulation of results in kcal/ $\text{kg}^{3/4}$ per hour made it possible to compare these values, irrespective of differences in body weight between the animals in the various groups.

Examination was also made in the same groups of voles for which the hemoglobin function was described of the weights of certain internal organs, and weight of the alimentary tract, including the weights of its various parts. The heart, spleen, liver, kidney and lung were weighed on a torsion balance with accuracy to 0.001 g. The weight of the stomach, small and large intestine and the caecum were determined in the same way after these organs had previously been thoroughly cleaned of their food contents. Calculation was next made of the relative weights (indices) of the organs examined, of the whole alimentary tract and its various parts. The length of the different parts of the alimentary tract were measured with accuracy to 0.1 cm on a glass plate in a normal saline solution medium and their linear indices calculated.

Additionally the isolation values of the fur were measured by means of a Hill catathermometer, according to the previously accepted method (Gębczyński & Olszewski, 1963). The results of these measurements were expressed in mcal per $\text{cm}^2 \times \text{sec}$.

A statistical analysis was made of the results obtained describing mountain and lowland populations of the bank vole, and also the two groups acclimatized at different altitudes. Each collection was described by a confidence interval based on variable $t(\pm \frac{ta}{\sqrt{n-1}})$ s). Comparison between the groups was made by means of the *t*-Student test for difference in the average values for the two independent groups.

III. RESULTS AND DISCUSSION

The mean values of blood indices defining the respiratory function of hemoglobin are given in Table 1. The data obtained at Białowieża in May 1965 were used for comparison of the blood picture in lowland and mountain voles (Kostelecka-Myrcha, 1967), since it was found that at this time of the year the temperature conditions in the Białowieża National Park and the vicinity of the Morskie Oko lake were very

Table 1.

Mean values (\pm confidence interval) of blood indices in the bank vole from a mountain population, a lowland population and acclimatized individuals. A — bank voles from Tatras, B — bank voles from Białowieża, C — lowland bank voles acclimatized in the mountains (1850 m above sea level), D — bank voles from mountains acclimatized in lowlands (170 m above sea level).

Index	Groups			
	A	B	C	D
n	20	27	20	20
Hb, g ^{0/0}	19.5 \pm 0.9	19.2 \pm 0.8	17.8 \pm 0.8	16.9 \pm 1.0
RBC, mln/ccm	12.00 \pm 0.75	12.36 \pm 0.65	12.55 \pm 0.81	11.89 \pm 0.72
MCH, $\gamma\gamma$	16.3 \pm 0.9	15.7 \pm 0.5	14.3 \pm 0.5	14.2 \pm 0.7
Hematocrit, $\%_0$	52.4 \pm 1.6	51.3 \pm 1.3	50.3 \pm 2.4	45.0 \pm 2.1
RBC, Diam., μ	5.49 \pm 0.07	5.37 \pm 0.07	0.08 \pm 0.07	5.13 \pm 0.14
RBC, Thickness, μ	1.87 \pm 0.05	1.86 \pm 0.06	2.00 \pm 0.09	1.84 \pm 0.08
RBC, Vol., μ^3	44.1 \pm 2.2	42.0 \pm 2.1	40.4 \pm 2.0	37.9 \pm 1.8
MCHC, $\%_0$	37.2 \pm 1.1	37.6 \pm 0.7	35.3 \pm 1.2	37.5 \pm 1.4
Vol. of blood ¹⁾ , ccm/100 g	7.57 \pm 1.37	8.82 \pm 1.35 ²⁾	7.34 \pm 0.59	8.22 \pm 1.6

¹⁾ n = 10; ²⁾ Data from July 1966.

similar. The blood indices of the two populations did not differ to a statistically significant extent ($P > 0.05$). The total volume of blood does not differ significantly in voles from groups A and B.

It would seem the results obtained for the two groups of acclimatized animals (groups C and D) should not be compared with the data characterizing the blood picture in lowland and mountain rodents, since the

acclimatized animals were kept in cages for three months. When the blood indices of lowland voles acclimatized at Białowieża are compared it is found that there are no significant differences in the blood picture of these two groups. Only hematocrite (*Hct*) is significantly lower in voles from group *D*, which after calculation gives a significant difference in the average thickness of blood cells and in mean cell hemoglobin concentration (*MCHC*). The number of erythrocytes is slightly greater in voles from group *C*, although these differences are not statistically significant ($P > 0.05$), neither does the diameter of their blood cells differ to a statistically significant extent. It would not appear that the cause of the difference in the *Hct* value could be the difference in the thickness of blood cells. As an index calculated on the basis of *Hct* and diameter of erythrocytes, their different thickness is more the mathematical consequence of a different hematocrite value. This difference in the *Hct* value is thus not physiologically justified and it should be treated as fortuitous.

Table 2.

Oxygen consumption rate in mountain, lowland and acclimatized bank voles. For explanation of symbols see Table 1.

Group	n	Body weight, g	ccm O ₂ /g/h	kcal/kg ^{3/4} /h
A	23	28.29±1.70	4.49±0.25	8.80±0.40
B	20	23.73±1.48	4.72±0.13	8.90±0.34
C	20	21.99±1.79	4.83±0.22	8.96±0.33
D	20	27.41±2.45	4.28±0.14	8.48±0.34

It may therefore be said that in general the morphological values of blood indices characterizing the respiratory function of hemoglobin, and also total blood volume, do not differ significantly in lowland and mountain bank voles. On this account a search was undertaken for some other physiological mechanism which permits the bank vole to occupy and settle in areas with low partial oxygen pressure.

It would seem that definition of metabolic level expressed by oxygen consumption is the best starting point in such a search. Table 2 gives the results characterizing the value of energy requirements expressed both in ccm O₂/g per hour, and in kcal/kg^{3/4} per hour. It was found that these indices do not differ significantly in comparisons between the groups examined.

Relatively little research has been carried out on the metabolism of mammals originating from mountains and lowlands. In other species of

rodents also these relations, although slightly different from those in the bank vole, are not unequivocal. Roberts, Hock & Smith (1966) measured oxygen consumption in deer mice (*Peromyscus maniculatus sonorensis*) living in the mountains of California. They found that in summer the metabolism of animals originating from an altitude of 3800 m above sea level is lower than in individuals from areas situated only just above sea level. These differences were, however, statistically significant only at temperatures of 20°C and above, but non-significant at lower temperatures. It must be mentioned that they did not exhibit significant differences between individuals from populations inhabiting areas at altitudes of 3800 and 1220 m above sea level.

Table 3.

Length of intestines (cm) and their indices (I) in relation to body length.

Experimental groups*)		A	B	C	D
No. of animals		20	20	20	13
Small	cm	47.9±2.0	28.8±1.3	32.2±1.3	30.2±2.7
	I	4.37±0.1	3.04±0.2	3.31±0.1	2.90±0.3
Large	cm	20.6±1.0	14.0±0.7	14.3±0.7	18.5±2.0
	I	1.87±0.1	1.48±0.1	1.47±0.1	1.78±0.2
Caecum	cm	10.0±0.8	5.7±0.6	6.0±0.6	7.0±0.6
	I	0.91±0.1	0.61±0.1	0.62±0.1	0.67±0.1
Total	cm	78.5±2.7	48.5±2.4	52.5±2.3	55.7±4.2
	I	7.15±0.2	5.13±0.3	5.40±0.2	5.35±0.4

*) Explanation of symbols are given in Table 1.

In autumn the differences between the groups examined completely disappear. In winter these relations are observed to be reversed in comparison with summer. Deer mice from an altitude of 3800 m have a significantly higher oxygen consumption at all temperatures in comparison with individuals from 1220 m and sea level. Therefore in summer and autumn oxygen consumption in deer mice is almost the same in individuals from all populations, since it differs only at certain temperatures and with extreme differences in altitude. Complete differentiation of this index did not take place until the winter.

Examination was also made of the indices of weight and length of the alimentary tract (Tables 3 and 4) in bank voles from all the groups. If the lowland and mountain animals had different energy requirements then their alimentary tract would have to digest qualitatively and

quantitatively differing food. The alimentary tract, as is known, is a very changeable system and its size depends to a very great extent on the current food conditions in the habitat. The mountain animals have higher weight index, and index of length of the different parts of the alimentary tract and of the tract itself as a whole. It would, however, seem that the cause of these differences does not lie in the greater energy requirements of the mountain bank voles, but the different kind of food available and eaten by *C. glareolus* in mountains and in lowlands. It is for instance known that northern bank voles, in the food of which the green parts of plants dominate, have a longer alimentary tract (Naumov, 1948; Koškina, 1957; Vorontsov, 1961), than the representatives of

Table 4.

Mean values of the weight (g) and of indices (%) of the different parts of the alimentary tract.

Experimental groups*		A	B	C	D
No. of animals		20	20	20	13
Stomach	g %	0.42±0.02 1.4±0.1	0.23±0.02 1.2±0.1	0.23±0.02 1.0±0.1	0.29±0.05 1.1±0.2
Small intestine	g %	0.75±0.15 2.5±0.2	0.39±0.04 2.0±0.2	0.45±0.04 2.1±0.2	0.59±0.06 2.3±0.3
Large intestine	g %	0.41±0.16 1.4±0.1	0.21±0.02 1.0±0.2	0.23±0.02 1.0±0.1	0.43±0.07 1.7±0.3
Caecum	g %	0.37±0.03 1.2±0.1	0.14±0.02 0.7±0.2	0.14±0.02 0.6±0.1	0.20±0.01 0.8±0.1
Total	g %	1.95±0.12 6.6±0.3	1.01±0.08 5.0±0.4	1.05±0.09 4.8±0.5	1.52±0.20 5.9±0.8

* Explanation of symbols is given in Table 1.

the southern population, which to a great extent feed on seeds (Naumov, 1948; O brazcov, 1951; Myrcha, 1964). Animals from groups C and D kept in cages on uniform diet have in fact very similar indices. This is convincing evidence that differences in the morphology of the alimentary tract in mountain and lowland voles should be connected only with the different food preferences of the two populations. In the light of data on the respiratory function of hemoglobin and of oxygen consumption it would seem that the amount of calories supplied from a different amount of different food is the same in bank voles from mountains and lowlands.

The indices of some of the internal organs are highest in rodents from group A (Table 5). No changes were observed in the values of the indices of heart, spleen, liver and lungs in bank voles from group C. In animals belonging to group D, however, all these indices change to a statistically significant degree, reaching even lower values than in the lowland population of *C. glareolus*.

The higher values of the indices of these organs in mountain voles would appear to be due to the need for supplying the same amount of oxygen as in lowland areas with a lower partial pressure of oxygen in the atmosphere. The respiration rate, heart rhythm and blood flow are therefore probably more rapid in mountain bank voles. The diffe-

Table 5.
Mean weights (g) and indices (I) of some internal organs.

Experimental groups*		A	B	C	D
No. of animals		20	20	20	13
Heart	g	0.20±0.01	0.12±0.01	0.13±0.03	0.12±0.01
	I	0.64±0.01	0.61±0.04	0.57±0.02	0.46±0.01
Spleen	g	0.09±0.02	0.06±0.02	0.05±0.01	0.04±0.01
	I	0.29±0.06	0.26±0.04	0.21±0.04	0.14±0.03
Liver	g	2.14±0.12	1.25±0.14	1.33±0.10	1.08±0.15
	I	7.20±0.36	6.26±0.48	5.98±0.33	4.09±0.03
Lung (left)	g	0.12±0.02	0.07±0.01	0.07±0.01	0.06±0.00
	I	0.40±0.04	0.35±0.04	0.32±0.05	0.24±0.02

* Explanation of symbols is given in Table 1.

rence between the lowland and mountain population of bank voles would therefore consist only in certain morphological adaptations serving to maintain physiological processes on the same level.

The isolation value of the fur (Table 6) is highest in voles from the mountain population. In Białowieża animals acclimatized in the Tatras the effect of the cage should undoubtedly be taken into consideration, yet tendencies are observed to increase in the isolation value of fur. In animals from mountains acclimatized in lowland areas, however, the isolation value of the fur decreases to a statistically significant degree and does not differ from the value characteristic of lowland voles.

Such differences in the isolation value of the fur, with simultaneous absence of differences in metabolism such as are found between the mountains and lowland population, have been described previously in comparisons of arctic and tropical species of birds and mammals (S c h o-

lander *et al.*, 1950). It is, however, difficult to say how great physiological importance can be attributed to the greater isolation value of the fur in mountain voles. In view of the fact that the temperature conditions at Białowieża in June were similar to analogical conditions in the Tatras in May it may however be assumed that mountain voles lose less heat than lowland animals. If the reasoning can be accepted as correct, then bank voles from mountainous areas would have a greater amount of energy at their disposal in metabolic processes than lowland voles. It would not, however, appear that this fact is of decisive importance in physiological differentiation of the two populations of the bank vole.

Table 6.

Isolation value of the fur in mountain, lowland and acclimatized bank voles.

Group	n	$\frac{\text{mcal}}{\text{cm}^2 \cdot \text{sec}}$
A	10	3.06±0.26
B	10	4.54±0.46
C	13	4.00±0.34
D	13	4.80±0.50

From the physiological aspect the two populations can thus surely be treated as identical. On these grounds it may be assumed that *C. glareolus* belongs to species which formed under mountain conditions during the process of evolution and gradually spread to and inhabited lower-lying areas.

The correctness of this assumption could be checked only by making comparative studies of the lowland and mountain populations of other species, the evolution of which is better known.

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NIEKTÓRE MORFO-FIZJOLOGICZNE WSKAŹNIKI GÓRSKIEJ I NIZINNEJ
POPULACJI NORNICY RUDEJ

Streszczenie

Przeprowadzono porównawcze, morfo-fizjologiczne badania górskiej (Tatry — 1850 m n.p.m.) i nizinnej (Białowieża — 170 m n.p.m.) populacji nornicy rudej, *Clethrionomys glareolus* (Schreber, 1780), a także osobników nizinnych aklimatyzowanych w górach i górskich aklimatyzowanych w Białowieży. Badano morfologiczny obraz krwi, objętość krwi, wielkość zużycia tlenu, ciężar serca, wątroby, śledziony i płuc, ciężar i długość przewodu pokarmowego oraz wartość izolacyjną skóry.

Nie stwierdzono różnic istotnych statystycznie pomiędzy górską i niziną populacją *C. glareolus* w wielkości wskaźników morfologicznych krwi, charakteryzujących funkcję hemoglobiny, w ogólnej objętości krwi i wielkości metabolizmu (Tabele 1, 2). Górskie nornice mają natomiast większe indeksy badanych narządów wewnętrznych, przy czym wartości tych indeksów obniżają się znacznie u zwierząt aklimatyzowanych na nizinach (Tabele 3—5). Wyższe wartości indeksów badanych narządów u górskich *C. glareolus* są prawdopodobnie wynikiem konieczności dostarczenia tej samej co na nizinach ilości tlenu przy jego mniejszym ciśnieniu parcjalnym. Stwierdzone różnice w ciężarze i długości przewodu pokarmowego porównywanych grup zwierząt spowodowane są natomiast różnym rodzajem dostępnego dla nornic pokarmu w Tatrach i w Białowieży.

Wartość izolacyjna skóry jest największa u górskich *C. glareolus*, a u zwierząt aklimatyzowanych w Białowieży obniża się istotnie statystycznie i zbliża się do poziomu jaki stwierdzono u zwierząt nizinnych (Tabela 6).

Opierając się na powyższych danych można wysnuć wniosek, że górską i niziną populacją *C. glareolus* są pod względem fizjologicznym jednakowe. Może to świadczyć o tym, że gatunek *C. glareolus* w procesie ewolucji ukształtował się w warunkach górskich i stopniowo zasiedlał tereny niżej położone.