

Changes of Body Weight and Hematological Parameters in a Fluctuating Population of *Apodemus flavicollis*

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Yellow-necked mice were collected at Białowieża Primeval Forest in spring and autumn of each year beginning from autumn 1981 to 1985. Body weight and hematological parameters of both red and white blood cells were determined. The population density varied, particularly in autumn, ranging from 7 to 63 inds ha⁻¹. In two years there was intense migration of individuals. From year to year, there were annual variations in the condition of animals reflected in their body weight (up to 30% differences between average values within the same age and sex groups) and in the ability of blood to carry oxygen (up to 40%) as well as in the immunity reflected in white blood cells parameters. The differences were greater when the corresponding age and sex groups were compared between years than those obtained for various sex and age groups within a particular year. It implied hematological changes associated with density fluctuations. The relationship between changes in rodent condition and the population processes at various stages of density fluctuations are also discussed.

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1. INTRODUCTION

Cyclic changes in population density in some rodent species have always been a puzzling and yet not completely explained phenomenon despite intensive research (*e.g.* Gipps *et al.*, 1986, Lidicker, 1988). Apart from purely demographic research in cyclic populations, genetic changes (*e.g.* Gaines & Krebs, 1971) and alterations in behaviour depending on the stage of population cycle (*e.g.* Krebs, 1985) were also studied. To our knowledge, no long-term studies on variability of hematological parameters in free living rodents have yet been carried out. The investigations of changes in hematological parameters in various seasons of the year have usually been limited to 1-2 years. The hematological parameters can be suitable indicators of the physiological status, condition and the state of immunological resistance of animals. Red blood cells (RBC) parameters reflect the ability of blood to carry oxygen *i.e.* the general metabolic capability of organism whereas

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the white blood cells (WBC) parameters reflect the level of immunological resistance, with their extreme values indicating pathological conditions. Hence, it seemed reasonable to study such parameters during various stages of annual variations in population numbers even though a single attempt of correlating hemoglobin level, growth and survival in a population of *Microtus agrestis* (Linnaeus 1761) once undertaken by Newson and Chitty (1962) was considered a failure.

In this study, the changes in population density were studied along with hematological parameters in various age and sex groups during four and a half year period in a population of the yellow-necked mouse, *Apodemus flavicollis* (Melchior, 1834).

2. MATERIAL AND METHODS

2.1. Collection of Mice and Age Determination

During five-year period (1981—1985) yellow-necked mice were trapped within a homogenous patch of natural oak-hornbeam old forest stand in forest compartment No. 370 of Białowieża National Park (NE Poland). Animals were caught in live traps in two sessions each year: in spring (May) and autumn (October), in 1981 only in autumn. The trapping sessions lasted 5 days (7 days in autumn of 1982) after three-day pre-baiting by oat grain put in open live traps. The traps were set on a 5.76 hectare area in a 12×12 grid (288 traps in 144 double stations) with 20 m distances separating stations. The animals were transported alive to a laboratory 3 kilometres away and put into individual cages with moss and hay. The mice were fed oat grain and given tap water *ad libitum*.

After 2—3 days in captivity the animals were anaesthetized with chloroform. Blood for hematological studies was collected from the heart; sex, reproductive activity, and body weight were then determined by dissection. The skulls were removed and age of animals determined on the basis of advancement of teeth growth and their wear (Adamczewska-Andrzejewska, 1967) to allocate mice to three age classes: up to four weeks, henceforth referred to as juveniles (class I according to Adamczewska-Andrzejewska, 1967), from four weeks to five months, called here young adults (classes II and III in the cited work), and the animals older than five months referred to as old adults (classes IV and V).

In population density assessment of yellow-necked mouse population all the animals collected (alive or those found dead alike) were taken into consideration. In total, 742 animals were caught (Table 1). The population density was calculated according to Zipin's formula based on maximum likelihood method (Southwood, 1978). In autumn of 1982 and 1985 no decrease in number of trapped animals occurred thus making the population density assessment impossible. In autumn 1982 even extending trapping session by two more days did not produced decrease in daily numbers of mice caught.

2.2. Hematological and Statistical Methods

Hematological studies involved only those animals that were found alive. Juvenile animals were also excluded since this first month of life is regarded in rodents as period of development of RBC and WBC picture of blood (see Wolk, 1985).

In years with high numbers of animals trapped (autumn of 1983 and 1985) the hematological studies were limited to randomly chosen samples. In all, 300 individuals of *A. flavicollis* were examined (Table 1).

The hematological tests were carried out immediately after blood collection without any anticoagulants added, and on fixed dry blood smears. Hemoglobin contents (Hb) were obtained by using the standard procedure for cyanmethemoglobin determination on the Ljungberg hemometer. Hematocrit determinations (Hct) were made by the micro-hematocrit method. The red blood cells (RBC count) were counted in a Thoma chamber. The diameter of erythrocytes (RBC diam.) was measured with a Zeiss micrometric eyepiece on smears stained by Pappenheim's method. Fifty RBCs were measured on each smear. On the basis of data obtained by the method given above, mean corpuscular hemoglobin (MCH) and mean corpuscular hemoglobin concentration (MCHC) were calculated. White blood cells (WBC) were counted in a Bürker chamber and differential counts were made from Pappenheim stained blood smears under oil immersion, using standard counting techniques. Basophils and monocytes occurring only sporadically were omitted.

An index (F) correlated with the capability to transport oxygen by unit volume of blood was calculated according to the formula of Kostelecka-Myrcha (1973):

$$F = \text{Hb} \times \text{RBC count} \times 4 (\text{RBC diam}/2)^2$$

The statistical significance of differences between hematological indices in animals of the same sex and age groups collected in various years were tested by one-way ANOVA and the Duncan tests. WBC parameters were transformed logarithmically because of considerable skewness of their distributions. The same methods were used to test the significance of differences among hematological indices in animals of different sex and age groups collected in a particular year.

As the material collected in spring seasons was scarce, all the data regarding blood parameters in animals collected in spring were pooled in one group.

Correlation coefficients were calculated for correlations between body weight and hematological parameters, and between RBC parameters and logarithms of WBC parameters. The coefficients of correlation were also determined between Hb and RBC diam. and between RBC count and RBC diam. Remaining correlations between RBC parameters were omitted because of their obviousness.

3. RESULTS

3.1. Population Density and Composition

The absolute numbers of mice caught in consecutive sessions varied widely, from 3 individuals in spring 1982 to 304 individuals in autumn 1983 (Table 1, Fig. 1A). The density of population ranged from 0.6 ± 0.3 to 62.8 ± 4.7 inds ha^{-1} (Table 1). In spring, the fluctuations in population density were much smaller than in autumn. Only in spring 1982 the number of mice was exceptionally low. Particularly high variation in population numbers appeared in the sequence of autumn seasons. The numbers were low in 1981, 1982, and 1984, high in 1983 and again in 1985. In autumn 1983, the number of mice caught decreased rapidly during first three days of trapping to stabilize in the next three days. Such pattern might indicate certain migration and/or filling the gap by animals living in adjacent areas — which would be no surprise in

Table 1
Number of trapped *A. flavicollis*, estimated population density, and number of hematological samples taken.

	1981	1982		1983		1984		1985	
	autumn	spring	autumn	spring	autumn	spring	autumn	spring	autumn
Number of trapped mice	48	3	54 ¹ 68 ²	23	304	25	42	15	214
Relative ⁵ density (per ha)	8.7±0.7	0.6±0.3	n.e. ³	4.9±1.3	62.8±4.7 49.7±3.2 ⁴	4.7±0.4	7.3±0.3	2.9±1.1	n.e. ³
Hematological samples (N animals)	43	2	68	21	50	16	33	14	53

¹ In first 5 days of trapping, ² In 7 days of trapping, ³ Not estimated; no successful removal, ⁴ Estimation based on the first 3 trapping days with high removal rate, ⁵ ±95% confidence limit.

Table 2
Body weight and hematological parameters in *Apodemus flavicollis* in springs. Averages (first column) and S.D. (second column) are given for each sex and age group.

Parameter	Males				Females			
	Young (n=11)		Old (n=17)		Young (n=12)		Old (n=13)	
Body weight (g)	25.77	3.37	41.32	5.40	25.38	7.8	38.9	5.18
Hb (g/dl)	15.97	1.67	15.22	1.33	14.79	1.20	14.51	1.76
RBC (x10 ⁶ /mm ³)	8.83	1.66	9.31	1.46	7.45	1.96	8.16	1.04
Hct (%)	48.23	5.12	45.30	12.16	41.67	5.59	41.81	8.35
RBC diam. (µm)	5.85	0.04	5.85	0.06	5.82	0.10	5.82	0.08
MCH (pg)	18.73	4.53	16.63	2.45	20.97	5.03	17.85	1.47
MCHC (%)	33.28	3.32	32.20	3.61	35.94	4.52	35.48	5.00
F	48.12	10.05	48.90	10.70	37.77	11.80	40.45	9.15
WBC (per mm ³)	4655	3394	3897	2386	3577	1716	4290	3347
Lymphocytes "	4234	3106	3046	1880	3020	1629	3657	2552
Neutrophils "	321.6	398.6	756.5	612.8	495.5	506.0	829.0	867.1
Eosinophils "	72.0	102.5	71.2	100.7	38.5	43.8	74.9	89.8

high population densities. The population density estimated from three initial days of trapping session in autumn 1983 was 49.7 inds ha⁻¹. In 1986 (not covered by this study), the population density of *A. flavicollis* in the study area was low (A. Wójcik, pers. comm.).

The age and sex composition of *A. flavicollis* population changed with time (Fig. 1A). In spring 1983, *i.e.* in the year of peak population density reached in autumn, there were no juvenile animals (age class I). It is also worth noting that young adult males were lacking completely in spring 1984 trapping session. In autumn sessions, no juveniles were caught in 1981, 1982, and 1983 while this class was represented in autumn of 1984 and 1985. The remaining age classes were represented more less uniformly in autumn of 1981 and 1983 while in 1982, 1984, and 1985 young males and young females dominated over old adult individuals (*e.g.* in 1982 only one old adult male was caught along with 28 young adult males).

3.2. Body Weight

The body weight of yellow-necked mice collected varied depending on season, age, and sex of individuals (Tables 2 and 3; Fig 1B; for sig-

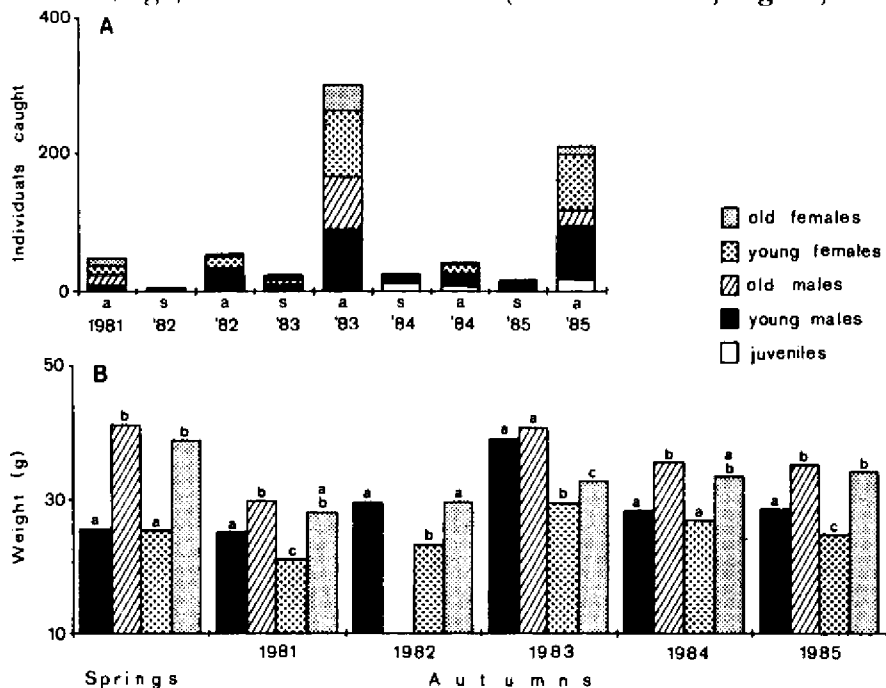


Fig. 1. Number of yellow-necked mice trapped (A), and an average body weight (B). In B — groups from the same year marked with the same letter do not differ significantly ($p > 0.05$). a — autumn, s — spring.

Table 3
Body weight and hematological parameters in *Apodemus flavicollis* in autumn.

Parameter	Males				Females			
	Young		Old		Young		Old	
	\bar{x}	S.D.	\bar{x}	S.D.	\bar{x}	S.D.	\bar{x}	S.D.
1981								
	n=6		n=15		n=10		n=12	
Body weight (g)	25.33	2.11	30.06	4.14	21.07	1.52	28.18	4.14
Hb (g/dl)	13.82	2.07	14.81	1.29	16.25	1.08	14.91	1.05
RBC ($\times 10^6/\text{mm}^3$)	7.81	1.31	8.31	1.17	8.56	0.66	8.38	1.68
Hct (%)	35.25	8.12	42.09	5.78	43.85	3.60	39.75	4.62
RBC diam. (μm)	5.67	0.07	5.61	0.15	5.65	0.14	5.62	0.07
MCH (pg)	17.77	1.13	18.06	2.22	19.03	1.02	18.28	3.08
MCHC (%)	40.17	5.34	35.62	4.34	37.14	2.05	37.81	3.47
F	35.35	9.92	38.92	7.42	44.67	7.17	39.70	9.42
WBC (per mm^3)	5025	3111	5367	3794	4075	1791	4592	2931
Lymphocytes "	4536	3172	4547	3295	3662	1698	3851	2561
Neutrophils "	487.1	525.1	669.8	585.3	335.6	206.1	576.8	548.1
Eosinophils "	35.2	38.3	101.9	185.5	23.4	33.2	103.6	143.8
1982								
	n=38		n=1		n=24		n=5	
Body weight (g)	29.68	5.61	32.30		23.36	5.29	29.72	2.16
Hb (g/dl)	15.03	1.16	15.30		15.20	1.40	14.92	1.00
RBC ($\times 10^6/\text{mm}^3$)	8.96	1.24	10.52		8.66	1.40	9.25	1.28
Hct (%)	46.73	4.73	54.00		45.17	6.93	49.00	3.24
RBC diam. (μm)	5.85	0.11	5.94		5.88	0.09	5.86	0.14
MCH (pg)	17.10	2.83	14.54		17.90	2.60	16.31	1.82
MCHC (%)	32.36	2.97	28.33		34.21	4.63	30.47	1.31
F	46.30	8.92	56.80		45.90	10.25	47.77	10.12
WBC (per mm^3)	4440	2826	4800		3630	2600	4450	913
Lymphocytes "	3828	2465	4656		3190	2173	3655	796
Neutrophils "	529.3	384.6	96.0		322.2	351.0	636.2	239.0
Eosinophils "	91.6	153.1	48.0		78.8	129.3	66.1	42.4

Table 3 cont.

Parameter	Males				Females			
	Young		Old		Young		Old	
1983								
	n=9		n=15		n=15		n=11	
Body weight (g)	39.22	3.37	40.83	4.67	29.58	3.72	33.02	3.10
Hb (g/dl)	14.91	0.70	14.64	1.19	14.88	1.12	14.82	0.72
RBC (x10 ⁶ /mm ³)	9.15	0.62	9.06	1.46	8.98	1.11	8.98	0.99
Hct (%)	45.39	5.41	43.97	7.17	45.30	6.72	46.41	7.27
RBC diam. (µm)	5.87	0.06	5.86	0.05	5.86	0.05	5.88	0.04
MCH (pg)	16.36	1.34	16.45	2.32	16.74	1.81	16.70	2.15
MCHC (%)	33.30	4.58	34.46	8.53	33.74	7.14	33.01	7.77
F	47.00	4.27	46.00	9.60	46.02	7.47	45.95	5.32
WBC (per mm ³)	5617	2527	5190	2572	5337	2029	5323	1904
Lymphocytes "	4470	2045	4439	2418	4681	1863	4666	1753
Neutrophils "	987.6	571.2	686.1	453.1	609.0	351.0	577.0	508.9
Eosinophils "	128.0	182.3	54.1	62.6	15.6	38.5	35.5	40.8
1984								
	n=16		n=4		n=10		n=2	
Body weight (g)	28.46	4.70	35.70	3.79	27.01	5.68	33.65	2.62
Hb (g/dl)	14.34	0.99	13.93	0.86	14.78	1.14	14.20	0.53
RBC (x10 ⁶ /mm ³)	9.52	1.35	9.91	0.98	9.38	1.74	9.54	1.01
Hct (%)	45.84	4.52	45.75	4.79	45.90	3.67	38.33	9.50
RBC diam. (µm)	5.94	0.07	5.94	0.06	5.90	0.06	5.90	0.12
MCH (pg)	15.31	2.04	14.10	0.66	16.25	3.19	14.96	1.11
MCHC (%)	31.49	2.97	30.58	2.04	32.32	2.85	33.89	3.01
F	48.25	8.87	49.00	6.95	48.52	10.90	47.27	6.65
WBC (per mm ³)	5206	2788	4200	2772	5130	1759	4133	1514
Lymphocytes "	4376	2379	3591	1935	4590	1617	3804	1381
Neutrophils "	730.2	772.8	577.5	722.6	459.6	387.5	255.0	182.6
Eosinophils "	43.2	46.0	76.0	116.1	54.9	53.7	46.7	42.3

Table 3 concluded.

	1985							
	n=19		n=7		n=23		n=4	
Body weight (g)	28.65	6.20	35.40	7.62	24.90	4.36	34.35	2.99
Hb (g/dl)	15.09	1.26	15.64	1.62	14.97	1.42	14.73	1.29
RBC ($\times 10^6/\text{mm}^3$)	9.95	1.11	9.52	1.14	8.92	1.22	7.67	0.67
Hct (%)	48.95	4.25	47.57	5.67	48.43	3.82	47.00	3.16
RBC diam. (μm)	5.88	0.04	5.85	0.03	5.88	0.04	5.90	0.07
MCH (pg)	15.28	1.63	16.62	2.50	16.94	1.60	19.34	2.66
MCHC (%)	31.06	4.10	32.37	4.24	30.96	2.41	31.33	1.64
F	52.12	8.10	51.05	8.17	46.47	9.90	39.10	2.67
WBC (per mm^3)	7028	4262	9936	2867	5889	3394	7263	2365
Lymphocytes "	6328	3826	9113	2770	5353	3061	6520	2422
Neutrophils "	597.2	576.4	484.6	206.8	456.7	366.7	557.9	215.8
Eosinophils "	62.2	73.8	110.9	118.7	66.3	87.4	97.5	86.6

nificance of differences see Figs 1B, 5). Old adults of both sexes were significantly heavier than corresponding young adults ($p < .05$) in spring and autumn sessions (except for autumn 1983). Young adult males from spring trapping sessions weighed significantly less than young males collected in autumn 1983 while old adult males collected in spring season were significantly heavier than old adult males on 1981, 1983, and 1984 autumn seasons ($p < .05$). Young adult females in spring were again significantly lighter than young adult females in autumn 1983. The body weight of old adult females in spring trapping sessions was significantly greater than that in autumn sessions throughout the study period.

3.3. Red Blood Cell Parameters

Hemoglobin value in mice collected in consecutive seasons did not differ significantly among various sex and age groups, except for young adult females in autumn 1981 which had significantly higher Hb level

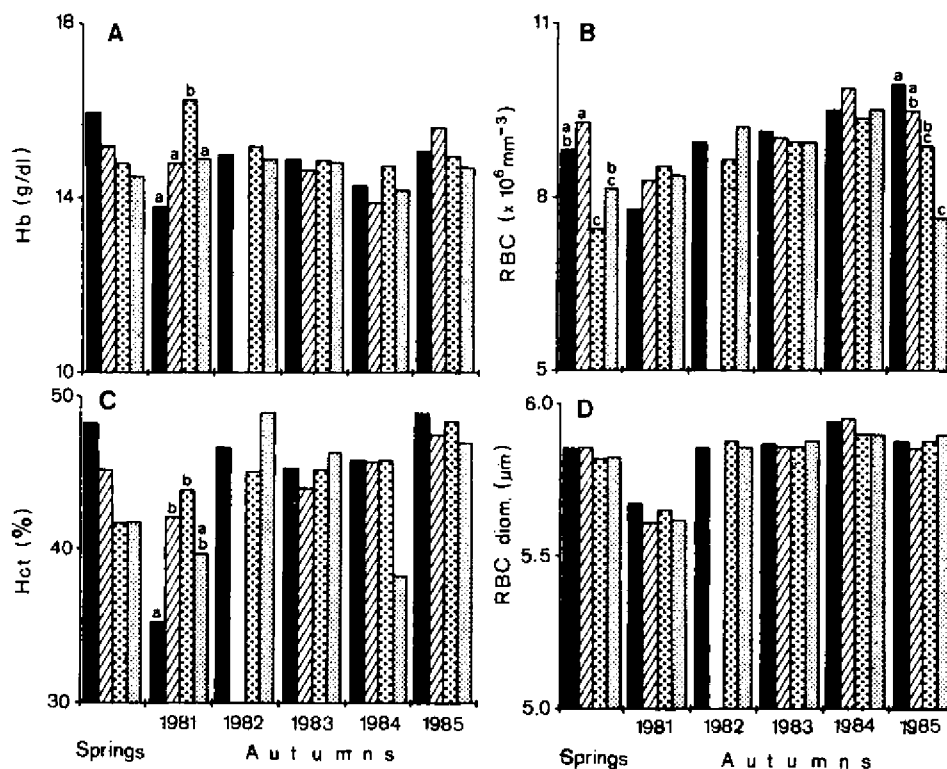


Fig. 2. A — Hemoglobin value (Hb), B — number of red blood cells (RBC count), C — hematocrit value (Hct), and D — the diameter of red blood cells (RBC diam.). For explanations see Fig. 1.

than other groups of animals caught at the same time (Fig. 2A; Tables 2, 3; $p < .05$). In females, there were no significant differences in Hb levels between years and seasons. The Hb level in young adult males collected in spring was, however, significantly higher than that in young adult males caught in autumn 1981 and 1984 — having the lowest values noted in the study period (Tables 2 and 3; Figs 2A, 5).

The largest differences in RBC counts among various sex and age groups occurred in mice collected in spring sessions, and in autumn 1985 (Tables 2 and 3; Fig. 2B). In old adult males in spring, RBC count was significantly higher than in both young and old adult females ($p < .05$). RBC count in both young and old adult males in autumn 1985 was significantly higher than in young and old adult females in this period ($p < .05$). A significantly lower RBC count was found in young adult females from all spring sessions compared with young adult females caught in every autumn except in 1981 ($p < .05$; Figs 2B, 5).

Hct values compared among sex and age groups varied significantly in autumn 1981: in young adult males the value of this parameter was significantly lower compared with old adult males and young adult females ($p < .05$; Tables 2 and 3; Fig 2C). There were the following differences in Hct values compared in consecutive years: Hct was significantly lower in young adult males in autumn 1981 than in young adult males caught in spring ($p < .05$; Figs 2C, 5A), Hct in old adult females in autumn 1982 was higher than that in old adult females in autumn seasons of 1981, 1983, and 1984 ($p < .05$; Figs 2C, 5B).

Even such a relatively stable parameter as the diameter of erythrocytes also showed considerable variation during the study period although it remained generally stable within particular seasons (Tables 2, 3; Fig. 2D). In autumn 1981, in all the sex and age groups the erythrocyte diameter was significantly lower than in corresponding groups of mice collected in spring seasons and those collected in the remaining autumn sessions ($p < .05$; Figs 2D, 5).

The mean corpuscular hemoglobin (MCH) was in spring significantly higher in young adult females than in old adult females and old adult males, a fact that stemmed from low value of RBC count in young females. In contrast, in autumn 1985, old adult females having significantly lower RBC count than other mice caught at the same time, and with hemoglobin level only slightly depressed, showed significantly higher MCH index (Tables 2, 3; Fig. 3A). In four and a half years covered by this study, MCH index was quite variable (Fig. 3A) but with relatively few of the differences significant. In the old adult males group the value of this index was significantly higher in autumn 1981 compared with autumn 1984 ($p < .05$). Among old adult females the index

was not variable (Fig. 5). More variability was found in groups of young adult males and females. The MCH values were significantly lower in autumn of 1984 and 1985 compared with spring series (when it reached highest value) and with autumn of 1981 ($p < .05$; Figs. 3A, 5).

The mean corpuscular hemoglobin concentration (MCHC), which belongs to the most stable hematological indices, did not varied much among particular sex and age groups (Tables 2, 3; Fig. 3B). MCHC index in old adult males and females did not vary significantly in the study period while in young adult males the value of this index was significantly higher in autumn 1981 than in all remaining autumn and spring trapping sessions ($p < .05$). In autumn 1985 MCHC in young adult females was significantly lower than in autumn 1981 and 1982 ($p < .05$; Figs 3B, 5).

The oxygen carrying capacity of unit blood volume (F) differed significantly among sex and age groups only in mice caught in spring trapping sessions and in autumn 1985. This capacity was decisively lower (even by 25%) in females than in males (Fig. 3C; Tables 2 and 3). In autumn 1981, F index was low in all sex and age groups, particular-

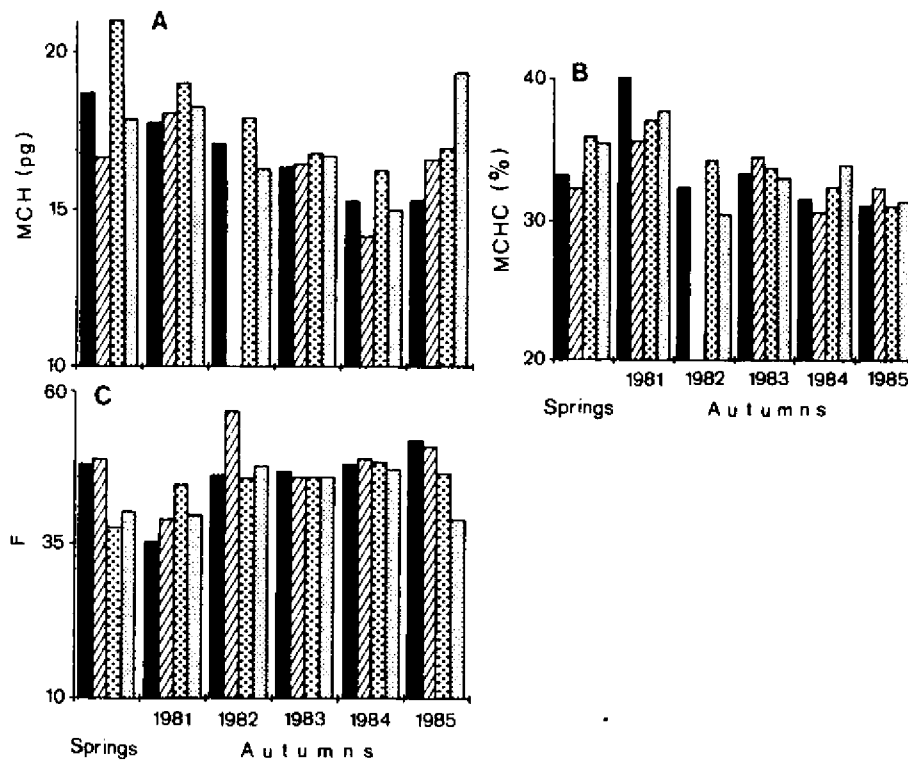


Fig. 3. A — Mean corpuscular hemoglobin (MCH), B — mean corpuscular hemoglobin concentration (MCHC), and C — the index F . For explanations see Fig. 1.

ly in males and old adult females. In addition, in autumn 1981, males showed much lower F index than in remaining years. In autumn sessions of 1982, 1983 and 1984 this index was relatively high and practically identical in all sex and age groups (Fig. 3C; Table 3).

3.4 White Blood Cell Parameters

Very high variability of both total leukocyte count and counts of separate WBC forms resulted in non-significant differences between them (*e.g.* in case of WBC and lymphocytes count) or only slight differences (Tables 2, 3; Figs 4A-D). Number of neutrophils in spring was significantly lower in young adult males than in old adult males and old adult females ($p < .05$; Fig. 4C). In autumn 1982, the neutrophil count in young adult females was significantly lower than in young adult males and old adult females ($p < .05$; Fig. 4C).

Eosinophil count in young adult females in autumn 1985 was significantly lower than in both young and old adult males ($p < .05$; Fig. 4D).

During several years of study WBC values in old adult males noted

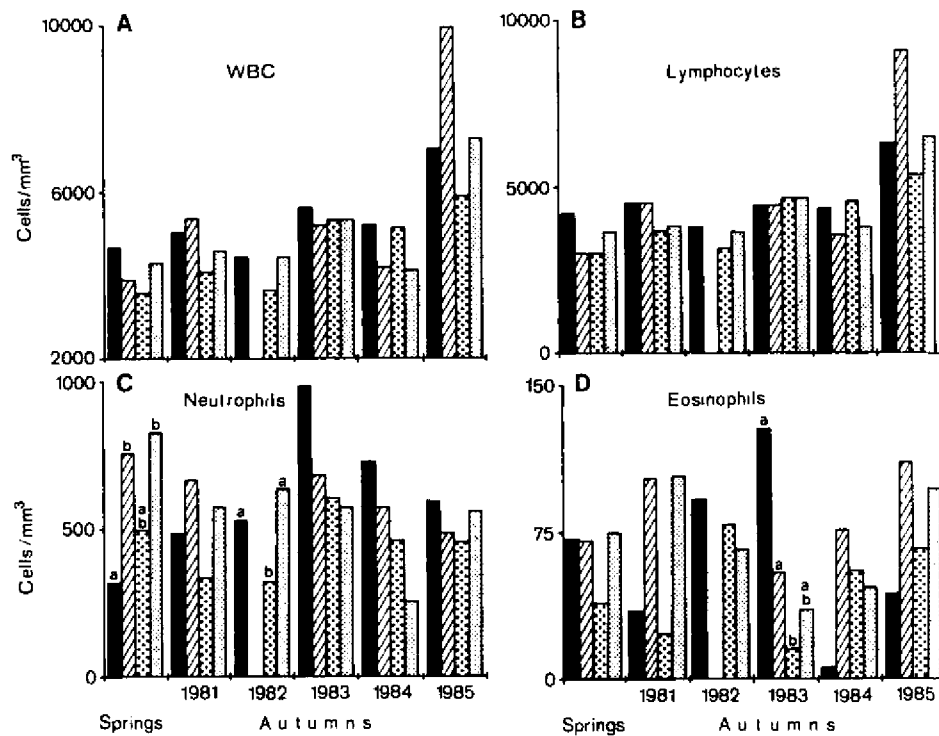


Fig. 4. A — Number of leukocytes (WBC), B — lymphocytes, C — neutrophils, and D — eosinophils. For explanations see Fig. 1.

in autumn 1985 was significantly higher than found in the same group of animals in spring trapping sessions and in other autumn sessions ($p < .05$; Figs 4A, 5A). There were no differences, however, in WBC values among young adult males. Among females, the situation was reversed, without significant differences among old adults and with WBC values in young adult females in autumn 1982 significantly higher than the values found in the same group in autumn 1983 and 1985 (Figs 4A, 5B).

In the period of this study, lymphocyte count in old adult males in autumn 1985 was the highest and significantly different compared with any remaining trapping sessions ($p < .05$; Figs 4B, 5A). In young adult males, however, there were no significant differences among young adult males. On the contrary, in old adult females there were no significant differences between years, and in young females in autumn 1982 this parameter was significantly lower than found in the same group in autumn of 1983, 1984, and 1985 ($p < .05$; Figs 4B, 5B).

The neutrophil count in old adult males taken in subsequent years did not change significantly whereas in young adult males collected in autumn 1983 it was significantly higher than in autumn 1981, 1982, and 1985 ($p < .05$; Figs 4C, 5A). Among adult females, both young and old, there were no significant differences in neutrophil count throughout the study period (Figs 4C, 5B).

The eosinophil count changed significantly neither in males nor in old adult females (Figs 4D, 5). In young adult females, however, it was significantly lower in autumn 1983 than the values found in autumn 1982, 1984, and 1985 ($p < 0.05$; Figs 4D, 5B).

The frequency distribution in various leukocyte forms were strongly skewed to the right, thus in the statistical analysis a logarithmic transformation was applied (Figs 6—8).

In spring, the modal value of lymphocyte count was very low *i.e.* it was only a few individuals with moderate lymphocyte count and no individuals with high counts. The frequency distribution for lymphocyte count in autumn 1983 (high population density year) showed a marked shift of the modal value toward higher counts, with few individuals having very high counts (Fig. 6). In autumn 1985, the distribution of lymphocyte counts had moderate modal value, but with a large number of individuals having high and very high lymphocyte counts (Fig. 6).

In spring, the modal value of neutrophil count did not differ much from autumn averages although in spring some individuals had neutrophil counts markedly higher than the maximum values found in autumn (except in autumn of 1984 and 1985; Fig. 7). In autumn 1983, the modal value of neutrophil count was markedly shifted towards higher

	Spring	Autumn 1981	Autumn 1982	Autumn 1983	Autumn 1984	Autumn 1985	
Spring	XXXXXX XXXXXX XXXXXX XXXXXX	Weight RBC d.	RBC c. MCH RBC d.	Weight RBC c. MCH	RBC c. MCH RBC d.	RBC c. MCH Hct MCHC Lymph	Young adult females
Autumn 1981	Weight RBC d.	XXXXXX XXXXXX XXXXXX	RBC d.	Weight RBC d.	Weight MCH RBC d.	Weight RBC d. MCHC	
Autumn 1982	Weight	Hct RBC d.	XXXXXX XXXXXX XXXXXX	Weight WBC Lymph Eosin	WBC Lymph	MCHC WBC Lymph	
Autumn 1983	Weight	Hct RBC d.		XXXXXX XXXXXX XXXXXX XXXXXX	Eosin	Weight Eosin	
Autumn 1984	Weight	RBC d.	Hct		XXXXXX XXXXXX XXXXXX XXXXXX		
Autumn 1985	Weight	Weight RBC d.				XXXXXX XXXXXX XXXXXX XXXXXX	
Old adult females							

Fig. 5. Statistical significance of differences between the same age and sex groups in different years and seasons. $p < .05$ for the parameters listed. A — males, B — females. Dash filled spaces — data too scarce for comparison. Symbols: Weight — body weight, Hb — hemoglobin value, RBC c. — the number of red blood cells, RBC d. — the diameter of red blood cells, MCH — mean corpuscular hemoglobin, MCHC — mean corpuscular hemoglobin concentration, Hct — hematocrit value, WBC — the number of leukocytes, Neutr — the number of neutrophils, Lymph — the number of lymphocytes, Eosin — the number of eosinophils.

values although as far as high counts of these cells are concerned that year did not differ from other years (Fig. 7). In autumn 1985, the neutrophil count was lower than in other years and the relevant modal value shifted left (Fig. 7).

Eosinophil counts were rather uniform throughout the study period (Fig. 8).

	Spring	Autumn 1981	Autumn 1982	Autumn 1983	Autumn 1984	Autumn 1985
Spring	XXXXXX XXXXXX XXXXXX XXXXXX XXXXXX	Hb Hct RBC d. MCHC F	Neutr	Weight Neutr	Hb MCH RBC d.	RBC c. MCH Neutr
Autumn 1981	Weight RBC d. F	XXXXXX XXXXXX XXXXXX XXXXXX XXXXXX	Hb RBC d. MCHC Neutr F	Weight RBC d. MCHC Neutr F	RBC d. MCHC F	Hb MCH RBC d. MCHC Neutr F
Autumn 1982	----- ----- ----- -----	----- ----- ----- -----	XXXXXX XXXXXX XXXXXX XXXXXX	Weight		
Autumn 1983		Weight RBC d. F	----- ----- ----- -----	XXXXXX XXXXXX XXXXXX XXXXXX	Weight Neutr	Weight
Autumn 1984	Weight	Weight MCH RBC d.	----- ----- ----- -----	Weight	XXXXXX XXXXXX XXXXXX XXXXXX	
Autumn 1985	Weight WBC Lymph	Weight RBC d. WBC Lymph F	----- ----- ----- -----	Weight WBC Lymph	WBC Lymph	XXXXXX XXXXXX XXXXXX XXXXXX

Young adult males

Old adult males

3.5. Correlations between Hematological Parameters

It was found that for all animals pooled there were many statistically significant correlations although of low values. In the course of dividing material into seasonal groups, particular years, sex and age groups the number of statistically significant correlations dropped (purely statistical effect - lower number of degrees of freedom) but they acquired ever increasing values in more progressively specified divisions (Table 4). Thus it seems, that the correlations between particular hematological parameters (and also between the body weight and these parameters) should be considered between season and age groups of the same sex. Among such groups, many strong correlations were found, even in the range of 0.7 of coefficient, between some RBC and WBC parameters (Table 4).

Table 4
Correlation coefficients (r) between body weight and hematological parameters, and between hemological parameters in *A. flavicollis*.

Group	Pair	n	r	p
Autumn 1981 Young males	data too scarce			
Autumn 1981 Old males	RBC — Neutrophils	15	0.56	<0.030
	MCH — WBC	15	-0.76	<0.001
	MCH — Neutrophils	15	-0.72	<0.002
	MCH — Lymphocytes	15	-0.73	<0.002
	Hct — WBC	15	0.52	<0.045
	Hct — Neutrophils	15	0.52	<0.045
	Hct — Lymphocytes	15	0.52	<0.048
	MCHC — WBC	15	-0.73	<0.002
	MCHC — Neutrophils	15	-0.62	<0.014
	MCHC — Lymphocytes	15	-0.73	<0.002
Autumn 1981 Young females	weight — WBC	9	0.72	<0.028
	weight — Lymphocytes	9	0.77	<0.016
Autumn 1981 Old females	no significant correlations ($n=12$)			
Autumn 1982 Young males	weight — MCH	38	-0.36	<0.025
	RBC count — WBC	38	0.41	<0.011
	RBC count — Lymphocytes	37	0.39	<0.018
	MCH — WBC	38	-0.34	<0.036
	Hct — WBC	37	0.49	<0.003
	Hct — Neutrophils	36	0.35	<0.039
	Hct — Lymphocytes	36	0.47	<0.004
	RBC diam. — Neutrophils	36	0.34	<0.039
	MCHC — WBC	37	-0.49	<0.003
	MCHC — Lymphocytes	36	-0.48	<0.004
	F — WBC	38	0.38	<0.019
	F — Neutrophils	37	0.34	<0.042
	F — Lymphocytes	37	0.36	<0.027
Autumn 1982 Old males & females	data too scarce			
Autumn 1982 Young females	weight — Neutrophils	24	0.44	<0.033
	RBC count — Lymphocytes	24	0.41	<0.049
	MCH — Lymphocytes	24	-0.41	<0.049
	F — WBC	24	0.41	<0.049
	F — Lymphocytes	24	0.42	<0.039
Autumn 1983 Young males	data too scarce			
Autumn 1983 Old males	weight — RBC diam	15	0.54	<0.038
	MCH — Eosinophils	15	0.65	<0.010
Autumn 1983 Young females	MCH — Neutrophils	15	0.64	<0.011
Autumn 1983 Old females	Hct — Neutrophils	11	0.61	<0.044
	MCHC — Neutrophils	11	-0.68	<0.022
	weight — F	11	0.71	<0.016
	F — Eosinophils	11	-0.64	<0.032

continued on p. 455

Table 4 concluded.

Autumn 1984 Young males	weight — Hb MCH — Eosinophils weight — F	16 16 16	-0.55 0.54 -0.57	<0.026 <0.031 <0.022
Autumn 1984 Old males & females	data too scarce			
Autumn 1984 Young females	MCH — WBC MCH — Lymphocytes	10 10	-0.72 -0.67	<0.019 <0.035
Autumn 1985 Young males	weight — RBC weight — F	19 19	-0.52 -0.49	<0.023 <0.032
Autumn 1985 Old males & females	data too scarce			
Autumn 1985 Young females	no significant correlations (n=23)			

In many groups strong positive correlations were found between erythrocyte count (RBC count) and the total numbers of leukocytes (WBC) as well as their various forms (Table 4). At the same time, however, there was strong negative correlation between both mean corpuscular hemoglobin (MCH), and the mean corpuscular hemoglobin concentration (MCHC), and the leukocyte number.

In several groups there were positive correlations between body weight and leukocyte count. In other groups there were positive correlations between body weight and RBC parameters (Table 4).

4. DISCUSSION

4.1. Fluctuations in Population Density in *A. flavicollis* at Białowieża Primeval Forest

In five-year study period, the minimum population density in subsequent autumn trapping sessions was 7.3 inds ha⁻¹, while the maximum density exceeded that nine times reaching 62.8 inds ha⁻¹. A mass occurrence of this rodent species was previously observed in 1977 *i.e.* six years before 1983 peak (Wołk & Wołk, 1982). In 1978 the density was exceptionally low, and in 1979 - moderate (E. Wołk, unpubl. data). Unfortunately, there is no data for 1980. The changes in population density, although remarkable, were not as drastic as those observed in lemmings or voles (*e.g.* Finerty, 1980). As sufficient long-term research is lacking, it cannot be stated with certainty if there are multi-annual population cycles in *A. flavicollis*. Jensen (1982) found in Easterr. Jutland (Denmark) in years 1970—79 much smaller density fluctuations in *A. flavicollis*— about 10 to 15 inds ha⁻¹. In the years of high density of the yellow-necked mice in deciduous forests they also appear in greater numbers in mixed coniferous forest where they normally constitute only a minor fraction among rodents caught in such

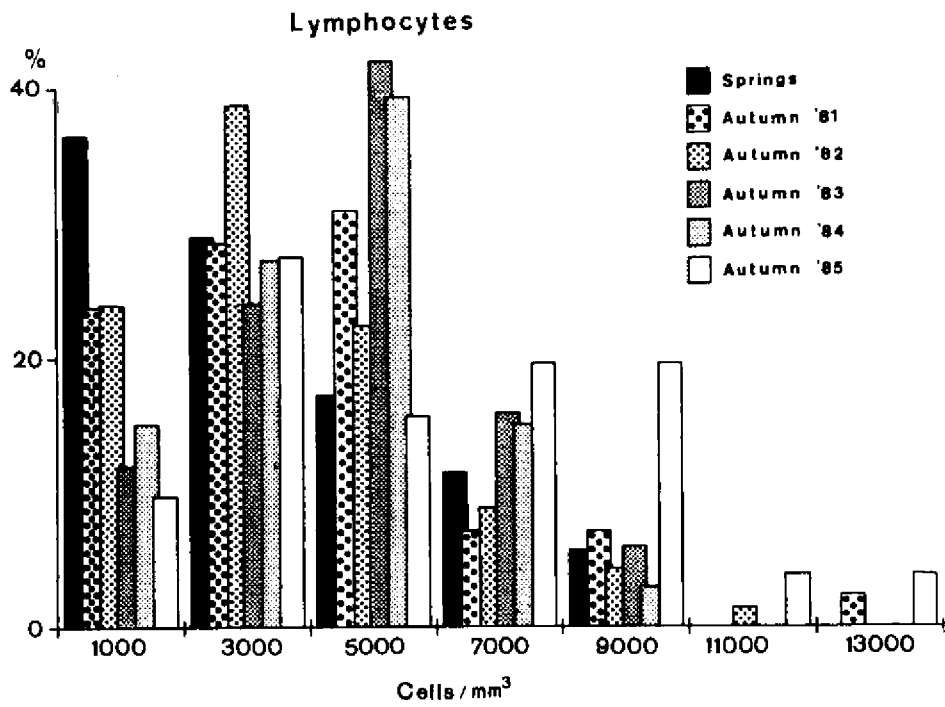


Fig. 6. Frequency distribution of lymphocyte number.

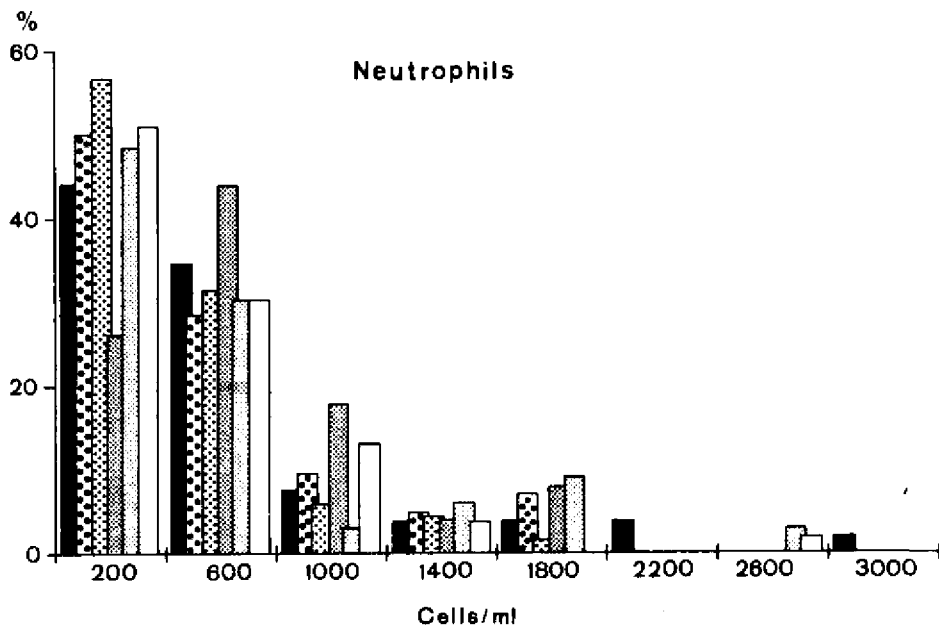


Fig. 7. Frequency distribution of neutrophil number. For explanations see Fig. 6.

habitats. For example, in 1977 which was a peak year of *A. flavicollis* in deciduous forest at Białowieża (E. Wołk, unpubl. data), the species constituted no less than 36% of all small mammals collected in mixed coniferous forest (Wołk & Wołk, 1982). In the next year there was no *A. flavicollis* in mixed coniferous forest and in the following years this species was represented by few individuals. Out of 86 yellow-necked mice caught in four-year period in a mixed coniferous habitat in Białowieża Primeval Forest as many as 77 were collected in 1977 alone (Wołk & Wołk, 1982).

A. flavicollis feeds mainly on seeds (Drożdż, 1968). In the deciduous forest habitats of the Białowieża Primeval Forest the production of seeds by trees is always considerable, in the range of 150 kg per hectare increasing to 2000 kg per hectare in hornbeam seed years (Falińska, 1971). The seed production in herbaceous forest layer in hornbeam-oak forest is much less - below 2 kg per hectare (Falińska, 1971). Seed production in mixed coniferous forests is considerably lower than in deciduous ones, also variable, and quite often it can be drastically low (unpublished data from National Forest Administration). It also seems that a poor herbaceous layer in mixed coniferous forests yield much less seeds and fails to provide safe hiding places from pred-

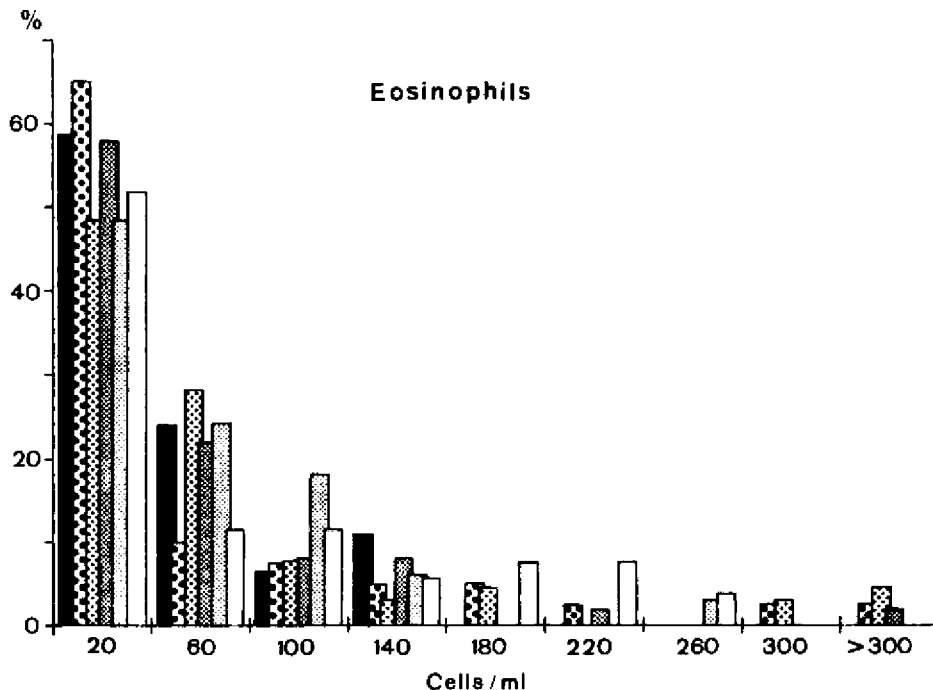


Fig. 8. Frequency distribution of eosinophil number. For explanations see Fig. 6.

ators. By this, the mixed coniferous forest sites may constitute dispersal sink (Lidicker, 1975) for *A. flavicollis* because both the insufficient food supply and predatory pressure do not encourage permanent settling of this species. It may be supposed that after the emergence of large migrating population the existing seed reserves are quickly depleted and take many years to be replenished while mice are being rapidly removed by predators which are numerous in Białowieża Primeval Forest.

A strong tendency to migrate in *A. flavicollis* was also directly found in autumn of 1982 and 1985. Although in some other species of genus *Apodemus* (notably *A. sylvaticus* and *A. agrarius*) spring and autumn migrations occur in connection with shifts from summer habitats to reproductive sites (Flowerdew, 1985; Viitala & Hoffmeyer, 1985) it is, however, highly unlikely in *A. flavicollis* at least at Białowieża National Park which is a huge and solid forest complex. The migration from the cultivated fields can be effectively excluded. It should also be noted that, in a marked contrast to *A. agrarius*, *A. flavicollis* is not a synanthropic species. There is also no doubt that this species inhabits deciduous forest habitats throughout the year and that it reproduces there. It is inconceivable to assume that the animals regularly give up the richest forest habitats to move on to poorer areas, especially if we remember that apart from peak years the species is hardly present in mixed coniferous forest of Białowieża Primeval Forest. It is very likely that the continuity of forest cover and lack of condition for seasonal migrations are the decisive factors in absence of *A. sylvaticus* in the entire Białowieża National Park. This species has been noted just once and only in the part of forest remaining under commercial management (Wołk & Wołk, 1979).

When immediate relationships between population dynamics and food supply are considered, the population peak usually occurs in the year following a seed year (Flowerdew, 1985). There is no such phenomenon in population dynamics of the population of *A. flavicollis* studied. The maximum density occurred in the year of abundant seed production by trees. Jensen (1982) did not find such population increases in *A. flavicollis* after seed years. The population peak is usually preceded by very early reproduction (even under the snow cover) that ended early. All this led to earlier occurrence of maximum numbers in the peak year (e.g. Bobek, 1973). Any winter reproduction in *A. flavicollis* has never been observed in Białowieża Primeval Forest. It seemed likely that the maximum density in 1983 was associated not only with the abundant food supply in autumn of that year but it was also linked to population processes taking place on in 1982 which led to intensive

migration. Exceptionally abundant food supply in 1983 might help mice to stay in good shape for long time without strong migratory tendencies that appeared in 1985 peak density.

4.2 Characteristics of *A. flavicollis* Population in Five-year Study Period Based on Changes in Body Weight and Hematological Parameters

(1) In autumn 1981, the population was in a bad condition as manifested by the lowest (in many years) average body weight in all the age groups. Low basic RBC parameters (RBC count, Hct), high MHC index and low capacity of unit volume of blood to carry oxygen also indicate the poor conditions for oxygen delivery transport. In young adult males and females, a low number of eosinophils (eosinopenia) may indicate their stress condition. According to Christian's hypothesis (1950, 1963) which sees the physiological processes as regulating cycling population numbers, the increase in pituitary-adrenocortical activity brought about by stress may cause a reduction in eosinophil number in circulating blood mainly by their destruction as effect of corticosterone action. Christian (1963) suggests that immunological processes play a significant role in regulation of population numbers and, most of all, in mortality among individuals in population. In young adult males and females of *A. flavicollis* caught in autumn of 1981, the leukocyte numbers were low which might be indicative of low immunological resistance. Indeed, the survivability of mice was low and in spring of 1982 the population density was extremely low (Table 1).

(2) In autumn 1982, young adults made up almost all the sample collected and moreover, there was intensive migration of mice. The body weight was low, and the mice had rather low leukocyte numbers.

(3) In spite of poor condition of population in autumn 1982 and low numbers of animals caught, in spring 1983 the population had a good start - as many as 23 mice were caught. It might be linked to immigration found in the preceding autumn - most probably from the areas where the population density was higher, and the condition of animals was better. The absence of juvenile individuals in spring 1983 trapping session might suggest that reproduction in this year started a bit earlier (the juveniles managed to the next age group). The density in spring, however, was not sufficiently high to suggest reproduction taking place in the preceding winter. In autumn 1983 the density reached exceptionally high figures (63 inds ha⁻¹).

The condition of animals caught in autumn 1983 was good, as indicated by high body weight in old and young adult males and young adult females. The body weight in young adult males from autumn

1983 trapping session exceeded significantly the corresponding values for the same group in other spring and autumn seasons while the body weight in old adult males in autumn 1983 significantly exceeded the relevant values in old adult males caught in other autumn trapping sessions. Hence both old and young males in year of peak density were heavier than in other years (the phenomenon called Chitty effect, see Lidicker, 1988). It might be associated with delaying maturity in young males because of extremely low chances of survival in very high population densities. The optimality of such delaying has been envisaged in Łomnicki's model (1978). A model put forward by Kozłowski and Wiegert (1987) predicts that putting off the reproduction should cause increase in body size, something actually found in our study. Newson & Chitty (1962) showed that the average body weight in *Microtus agrestis* was evidently lower in the year of low population numbers of these vole species. Larger body sizes were also found in *Clethrionomys glareolus* in peak year by Wiger (1979).

In the peak year that occur in the study period, RBC parameters in mice were moderate. In young adult males, however, extremely high numbers of neutrophils and eosinophils were found which might be indicative of bacterial infections and parasite invasion of animals in this age group. It seems contradictory of large body weight, but the adverse effect of parasites might have been offset by very good food conditions. Eosinopenia occurred in young adult females in particular, but also in old adult females. They probably were more susceptible to overcrowded conditions than males that ended reproduction earlier — hence the onset of stress-related eosinopenia. In fact, the survivability of animals was poor as indicated by their low population numbers in spring 1984.

(4) In spite of moderate population numbers in spring 1984, the mice were not numerous in autumn that year. It could be so because of low number of young adult males in spring (absent from spring collection). The mice caught in autumn were of moderate body weight and had relatively high capability of unit blood volume to carry oxygen.

(5) In spring 1985 the population number of yellow-necked mice was very low, probably because of low population number in the preceding autumn. In autumn 1985 many mice were caught but because the population was intensively migrating it prevented us from assessing the population number. A presumption that most of that year population migrated from outside cannot be discarded. Young adults of medium body weight dominated among animals collected. In young adults, high erythrocyte count and high hematocrit seems to indicate good conditions for oxygen exchange - the assumption supported by highest

value of *F* index noted throughout the study period. The highest leukocyte count, including also the highest lymphocyte count found at the same time, are indicative of high immunological resistance of the population and, possibly, its high survivability. Dobrowolska (1980) found in *Microtus arvalis* (Pallas, 1779) that the increased population numbers were accompanied by increase in survivability with simultaneous elevation of the serum levels of immunoglobulins, and lymphocytes are responsible for their production.

4.3. Hematological Characteristics of the Yellow-necked Mouse

As it has been described earlier both RBC and WBC parameters show many statistically significant differences when the corresponding sex and age groups are compared between years and seasons. It should also be noted that lack of significant differences does not signify absence of such differences but might often reflect merely the scarcity of the material. Having analyzed Figs 1-5 one may suspect that the number of statistically significant differences could have been much larger had the material been ampler. Less differences, however, appeared between various sex and age groups within particular seasons. Furthermore, in many cases, the values were rather uniform, that is why the increase in the number of data would probably not result in statistical significance of differences. The fact that the variability among various groups of mice collected various years is larger than between animals belonging to the various sex and age groups within the same season is astonishing. It casts a shadow on the validity of the concept of hematological norm of a species. It gives also ground for assuming that there is a relationship between numerical fluctuations and physiological changes reflected in the hematological parameters. A textbook concept maintaining that nature is only populated with strong and healthy individuals because those weaker would be quickly eliminated does not seem to hold any longer.

The hematological parameters of *A. flavicollis* in spring show many differences when compared with that in autumn. It is understandable, because in spring almost all individuals are sexually active, and this entails physiological changes. In young adult females, and even more, in old adult females, there were strikingly low levels of RBC parameters (Hb value, RBC count, Hct value). It might be associated with pregnancy-related anemia since most of the mature females are pregnant in spring.

In many species of free living mammals the RBC count and hematocrit, and often the hemoglobin value, increase while the diameter of red blood cells decreases - and it all happens in the period preceding enhanced thermoregulatory effort in winter (*e.g.* Sealander, 1962; Ko-

stelecka-Myrcha, 1967; Wołk, 1974; Morton & Lewis, 1980). The small value of WBC count in old adult males of *A. flavicollis* in spring, very low modal value of lymphocyte count, the presence of few individuals with moderate lymphocyte counts, and the emergence of mice with lymphocyte count elevated much in comparison to the maximum values observed in autumn (probably animals that were ailing) — all these facts indicated low level of immunological resistance in this group. It may be presumed that a high proportion old adult males present in spring do not survive till autumn.

It was surprising to see variability of such generally stable parameter as red blood cell diameter. Within particular seasons this parameter changed only a little (coefficient of variation in the order of 2%) while the maximum difference between the averages for several years of study reached 4%. The RBC diameter was particularly low in autumn 1981 when the mice were small and had, on average, very low RBC count. It cannot be excluded that here we face some changes in genetic composition of population.

Some interesting bits of information were also provided by the correlations between particular hematological parameters. Simultaneous presence of positive correlations between RBC count and total WBC count and the counts of lymphocytes and neutrophils, as well as strong negative correlations between MCH and MCHC indices and the number of leukocytes looks superficially paradoxical. It may be, however, that it represents an outcome of faster rate of erythrocyte production which has overtaken the rate of saturating them with hemoglobin. It may be associated with the urgent need to enhance oxygen carrying capacity *i.e.* intensifying use of hemoglobin as vehicle for oxygen transport. Such presumption may be further supported by the fact of positive correlation between the capability of unit blood to carry oxygen (F) with WBC count and the numbers of lymphocytes and neutrophils in many groups. Quite often, the body weight and RBC parameters were also correlated, indicating overall good condition of animals. The positive correlations found in several groups between the body weight and leukocyte count seem to indicate that high numbers of these cells reflect high levels of immunological resistance and not a pathological condition (perhaps with exception of extremely high values found in some old adult males in spring). Thus, the individuals with large body weight, both RBC and WBC counts high, and with high F index value may be regarded as animals in good condition having high capability of blood to carry oxygen and high resistance. Such groups should have high survival rate.

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ZMIANY MASY CIAŁA I PARAMETRÓW HEMATOLOGICZNYCH WE FLUKTUUJĄCEJ POPULACJI *APODEMUS FLAVICOLLIS*

Streszczenie

W okresie 1981—1985 odławiano myszy wielkookie leśne, *Apodemus flavicollis* (Melchior, 1834) wiosną i jesienią w grądzie Białowieskiego Parku Narodowego, określano wiek i masę ciała zwierząt, a także badano ich parametry hematologiczne, zarówno czerwonekrwinkowe jak i białokrwinkowe. Zagęszczenie zwierząt było zmienne, zwłaszcza jesienią, kiedy wahało się w granicach od 7,3 do 62,8 osobników/ha (Tabela 1, Ryc. 1A). W dwóch latach występowała intensywna migracja. Kondycja zwierząt, mierzona masą ciała (różnice średnich rzędu 30% w obrębie tych samych grup płci i wieku) i zdolnością krwi do transportu tlenu (różnice rzędu 40%), zmieniała się z roku na rok; zmieniała się też odporność zwierząt mierzona parametrami białokrwinkowymi (Tabele 2 i 3, Ryc. 1B-4, 6-8). Stwierdzono więcej różnic parametrów hematologicznych, gdy porównywano te same grupy płci i wieku między latami, niż gdy porównywano różne grupy płci i wieku w obrębie tego samego roku, co sugeruje, że zmiany hematologiczne towarzyszą zmianom liczebności (Ryc. 5).