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**Geographical distribution of the dark phase of the squirrel
(*Sciurus vulgaris fuscoater* Altum) in Poland**

**Rozmieszczenie geograficzne ciemnej formy wiewiórki
(*Sciurus vulgaris fuscoater* Altum) w Polsce**

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I. INTRODUCTION

In this work I have dealt with the question of the occurrence of the dark phase of the squirrel, subspecies *S. vulgaris fuscoater* Alt., and have endeavoured to explain this phenomenon.

The fact of the occurrence of the squirrel in two colour phases is given in literature (Miller, 1912; Shorten-Vizoso, 1954). We encounter this phenomenon in the following subspecies: *S. vulgaris fuscoater* Altum, *S. vulgaris italicus* Bonaparte,

S. vulgaris lilaeus Miller, *S. vulgaris alpinus* Desmarest, *S. vulgaris numantius* Miller and *S. vulgaris infuscatus* Cabrera.

Various research workers have examined the question of the two colour phases of the squirrel, and have endeavoured to explain this phenomenon. Amongst the more important works on this subject, we may include the work of Lühri g (1928) who interpreted the appearance of the dark phase as due to the influence of the geographical environment (height above sea level) and that of Spärc k (1936), who considered this phenomenon due to the quality of the food eaten by the squirrel (fruit of the spruce).

A full discussion of the works referred to above is given in the section of this work devoted to the analysis of the geographical range of the dark phase.

The first description of the black squirrel in Polish zoological literature is given by Pietruski (1853), who created a new species for it, *S. carpathicus* Pietruski, and wrote as follows: „Back dark brown or completely black, white belly. Front teeth far yellower, beautiful tail, bushier and wider, head more rounded, tufts on ears $\frac{1}{4}$ as long again as those of the red squirrel, and body sturdy, shorter and fatter. It lives in our mountains, and in certain years, but very seldom, descends to the plains, likes fir and spruce forests”¹⁾.

Mention is made of the occurrence of the black squirrel in various works on the fauna of our mountains and hills. Nowicki (1866) observed black, grey and red specimens in the Tatra Mountains, and Schaiter (1867) states that a black variety is occasionally found in the Rzeszów district. According to Jachno (1867) this phase occurs fairly seldom in the Sandomierz forest area. Kocy an (1868) in his work on the mammals of the Tatras, states „*S. vulgaris* more grey than red, lives in the „regle” (mountainous woodland areas — E. Z.) and Podhale, wherever fir cones are to be found. Black squirrels are only encountered near villages”.

Lubicz - Niezabitowski (1903) found this variety in the Rytro district. He writes: „Chiefly the dark-coloured variety occurs here. The most common are the grey and almost black, and the scarcest the red”.

¹⁾ All quotations in English translation.

This author, in his key to the identification of the vertebrates of Poland, edited by Hoyer (1910) writes „The red squirrel in the plains, usually in pine forests. The dark brown or dark gray (*S. vulgaris* var. *carpathicus* Pietruski) in the spruce or fir forests of the Carpathians”.

Udziela (1924) in his work on the geographical varieties of squirrels in Poland, gives a review of practically the entire zoological bibliography concerning this question. He quotes the German zoologists Gloger and Henzel, who reported the occurrence of numerous dark-coloured and black squirrels in Silesia.

The distribution of black squirrels is presented as follows by Udziela „*S. vulgaris carpathicus* occurs in Poland in the Carpathians and their foothills, going from the southeast frontier towards the west and northwest, in a belt lengthways, which extends vertically to the upper limit of the forests. The squirrel occurs in the Beskid and Gorce Mts. (Sitowski), and descending from Podhale towards Cracow, reaches as far as Mogilany. Further to the north it confines itself to the Cracow — Wieluń Jura. This variety is encountered in the Kielce and Sandomierz mountains (Poliński)”.

The author then gives the places where the black squirrel is found in the Wilno district, in Lithuania, Esthonia and Latvia. These data would, however, appear to be of very problematical correctness, since no later authors have confirmed the information given in his work. In addition I am of the opinion that the environment conditions with which this phase is generally associated, do not exist there.

Sokołowski (1947) states that the black squirrel occurs in the Świętokrzyskie Mountains. Skuratowicz (1948) did not find the black squirrel during his investigation of the mammalian fauna in the forests of the Zamość district. Grodziński (1957) in his work devoted to the vertebrate fauna of the Bieszczady Mountains, reported the presence of this phase, which, similarly to Lubicz - Niezabitowski (1933) he identified as *S. vulgaris carpathicus*. As is clear from the above data from literature on the subject, the black squirrel has hitherto been observed in Poland only in the mountainous and foothill regions. The range of the dark phase has not so far been exactly established. Udziela's data on the range of their occurrence would appear to be of pro-

blematical correctness and require detailed checking. This was in fact one of the reasons for the present work.

As far as the systematic position of the black squirrel is concerned, this has not so far been established, since it has either been considered as a separate species (Pietruski) or a subspecies (Udziela, Sokołowski). Sidorowicz (1958) however, on the basis of craniometric material from the whole of Poland, confirmed that the black squirrel is identical with the subspecies *S. vulgaris fuscoater* Altum.

On these grounds I shall refer in the present work to the „dark phase” as the colour phase of the above subspecies.

I wish to express my hearty thanks to my Director, Professor Dr August Dehnel for his valuable help in preparing this work.

II. DESCRIPTION OF AREA AND METHODS

The area investigated included the following provinces of southern Poland: Zielona Góra, Wrocław, Opole, Katowice, Kraków, Kielce, Rzeszów and Lublin. From the point of view of physical geography this area includes the following regions: Carpathians and the whole of the Carpathian foothills, the Cracow — Wieluń Jura, Silesian plateau, Sudety foothills, Sudety Mountains, Świętokrzyskie Mountains, part of the Małopolska plateau, the Silesian depression and the Lubusk region (Jarosz, 1954).

The Carpathians have an average height of about 1400 m while the highest chain, the Tatras, reach over 2000 m and are covered with forest up to a height of about 1500 m. Mountain forests are divided into two levels: the extensive woods of the lower „regiel” and the forests of the upper „regiel”. In the Carpathians the woods of the lower „regiel” occur between heights of 400 and 1100 m msl. and consist chiefly of fir and beech, with the addition of spruce. In the lower sections pine and plane trees are present as well. Annual rain and snowfall over 800 mm, average annual temperature 7° C.

The forests of the upper „regiel” begin at a height of over 1100 m msl. and reach the upper level of the forest belt. They consist of dense spruce forests. The annual rain and snowfall here is over 1200 mm and average temperature 4,7° C.

The Carpathian foothill area from the point of view of distribution of forests forms the transitory stage between the lowland and mountain forests. The trees here are pine, fir, beech and spruce. Average annual temperature about 8° C, rain and snowfall from 712—870 mm per annum, height above sea level 200—400 m.

The Cracow — Wieluń Jura is from 300—600 m above sea level. The forests are chiefly composed of: fir, beech, spruce and larch, with the addition of some pine and oak. Annual rain and snowfall 557—718 mm, average temperature per annum 7,6° C.

The Silesian plateau is situated at 200—400 m above sea level, and here there are large areas of pine forest, although spruce, fir, beech and oak also occur. Annual rain and snowfall 605—709 mm. Average annual temperature 8,1° C.

The Silesian depression is situated in the valley of the river Odra. There are moorland-type woods here, although the area is on the whole scantily wooded. Pine and spruce are encountered, and deciduous forests of oak, lime and plane trees. The area is from 100—200 m above sea level.

The Sudety foothills are covered with mixed forests composed of various species, including beech, oak, spruce and fir. Wide variations in height are encountered ranging from 150—600 m. The true Sudetens, the lower „regiel” of which lies at heights between 400—900 m, have an annual rain and snowfall over 600 mm, average annual temperature 5,5° C. In addition to spruce, beech and fir, we find larch, plane and pine trees, the latter not however growing at heights over 600 m. At heights from 900—1250 m the forests are of the upper „regiel” type. Average rain and snowfall is over 1100 mm and average yearly temperature 2,4° C.

The Lubusk region lies at a height of 100—200 m above sea level. Large stretches of pine forest are encountered, in addition to oak, yoke-elm and beech. Fir and spruce are found further to the south. Average annual rain and snowfall 505—593 mm, average annual temperature 7,6° C.

The Małopolska plateau, within the limits of which lies the belt of the Świętokrzyskie Mountains, is situated at heights ranging from 200—600 m above sea level. The forests here are fir and beech, spruce, pine and oak. Average rain and snowfall 558—718 mm, average yearly temperature 7,6° C.

The Lublin highlands vary in height from 200—400 m above sea level, and form a sparsely-forested area. The limits of the range of mountain-type spruce, beech, and fir run through this area. The chief components of the forest stands in this region are pine and oak, with the addition of yoke-elm, beech, fir, spruce and Polish larch. In the north-east section there are mixed forests, with pine forests predominating.

As the total area to be included in my research was so great, I decided to make use of the questionnaire method. This method, which was adopted by *Surdacki* (1956), in his investigation of the occurrence of the ground squirrel in the Lublin region, gave very good results.

In my case the questionnaires were completed by forest intendants and foresters, i. e. persons possessing at least secondary education. In addition, since the foresters spend a great part of their time in the forests, they are as a rule well acquainted with the

numbers of the forest animals, especially as the squirrel is an animal both noticeable and frequently encountered.

Great help was given me in this work by the Ministry of Forestry ¹⁾, which sent out a communication to the respective State Forests Boards asking for their support in the area covered by the questionnaire, which was circulated by the Mammals Research Institute of the Polish Academy of Sciences in Białowieża.

The questionnaire was drawn up in a simple way and was therefore easy to complete. A total of 2500 questionnaires was sent out, in packets of 5, accounting that each forest intendancy had at least 5 forest regions coming under its administration. 465 forest intendancies received these packets, which in turn were to be transmitted by them to their respective forest regions. In certain cases, where the number of forest regions exceeded 5, they made extra copies as required. Some forest intendancies returned collective forms, completed by the forest intendants.

Many of those who supplied information, in addition to the questions contained in our form, added several valuable remarks supplementing the required data.

I received 1927 replies from 414 forest intendancies, i. e. 89,03% of the forest intendancies concerned.

The table given below gives the number of forest intendancies which replied (divided according to province).

Table No. 1.
Number of forest intendancy in all investigated provinces.

No	Province	Number of forest intendancy in every province	Number of forest intendancy which answered for a questionnaire			Per cent of answers
			Total	With black phase	Without black phase	
1.	ZIELONA GÓRA	88	78	—	78	88,63%
2.	WROCLAW	76	67	39	28	88,16%
3.	OPOLE	36	35	32	3	97,30%
4.	KATOWICE	44	41	33	8	93,18%
5.	KRAKÓW	48	42	39	3	87,50%
6.	KIELCE	62	58	19	39	93,55%
7.	RZESZÓW	63	63	43	10	84,13%
8.	LUBLIN.	48	40	—	40	83,33%
Total		465	414	205	209	89,03%

¹⁾ I would like to take this opportunity of expressing my thanks to the Director of the Hunting Department, of the Ministry of Forestry and Timber Industry, Mr. Tatarski, for all the help so kindly given by him.

The material obtained from these questionnaires is included in the collection of the Mammals Research Institute of the Polish Academy of Sciences in Białowieża. As I did not wish to base my conclusions on the results of the questionnaires only, the replies, where appropriate, e. g. stations on the boundaries of the squirrel's range — were checked on the site.

The results of the observations carried out on the various sites in the main coincided with the replies returned on the forms. The heights above sea level of the various stations, which were required when working out results of the enquiry, were taken from a map to scale 1:100.000, and the replies from the forest intendancies were entered on a state forest administration map scale 1:1.000.000.

The black squirrel was noted as occurring in 205 of the 414 forest intendancies returning replies.

In 57 forest intendancies the black squirrel was found to predominate over the red. These forest intendancies are situated in the mountains (over 400 m). As will be seen, a query was included in the questionnaire regarding occurrence of hybrids of black and red stock. In areas where the black squirrel occurs, the reply to this was usually in the affirmative. The purpose of this question was to establish the occurrence of the transitory phases in the colour of the coat. We know from other sources that both colour phases, black and red, interbreed freely (Shorten - Vizoso, Sokółowski).

An undoubted confirmation of the existence of red and black hybrids may be obtained from examination of the squirrel skins in the collection of the Mammals Research Institute of the Polish Academy of Sciences, which come from the Bielsko-Biała district. A red line of hair is visible in these skins along the edge of the black fur of the back and sides, and the white fur of the belly. In the light of the material obtained from the enquiry, and observations made on the various sites, it should be stated that there is wide individual variation in colour. There are specimens with dark tails, dark brown specimens etc. This material is also to be found in the collection of the above Institute. Data given in literature also confirm these observations (Sidorowicz). Naturally the question as to whether in our case we are concerned with hybrids,

or whether they are phases indirectly created by the influence of environment factors, would require special investigation.

The material obtained from our enquiry, and the observations made on the sites, indicate that both colour phases, black and red, live together, feed not only on the same species of trees, but even occasionally feed on the same tree-top, and thus do not exhibit any antagonism to each other.

In order to establish the possible connection of the dark phase of the squirrel with one definite type of forest, a question was included in the form concerning the character of the forests of the given forest intendancy. As will be seen from the form (included above), the following types of forest were given: coniferous-pine, coniferous-spruce, coniferous-mixed, mixed forest, and deciduous forest. This provided a guarantee that no difficulty would be experienced in reply to this question, and that the reply would be objective in character. If I had used the phyto-sociological terminology (Matuszkiewicz and Polakowska, 1955; Matuszkiewicz and Borowik, 1957; Kornaś - Medwecka, 1955) it might have proved difficult for the foresters to answer this question, as they do not make use of this terminology.

Under the definition of each of the above types, I gave the following explanations:

As per instructions No. 4, Min. of Forestry.

1. Coniferous forest-pine — Dry forest and green forest.
2. Coniferous forest-fir — Upper „regiel” forest.
2. Coniferous forest-mixed — Lower „regiel” forest.
4. Mixed forest — Forest containing pine, spruce, with addition of deciduous trees.
5. Deciduous forest — Forest consisting chiefly of deciduous trees such as: oak, beech, yoke-elm with small addition of coniferous trees.

In addition the information supplied contained in certain cases more exact particulars of the forest stand.

The data obtained by our enquiry enabled us to obtain a qualitative picture only of the forests concerned (Fig. 1).

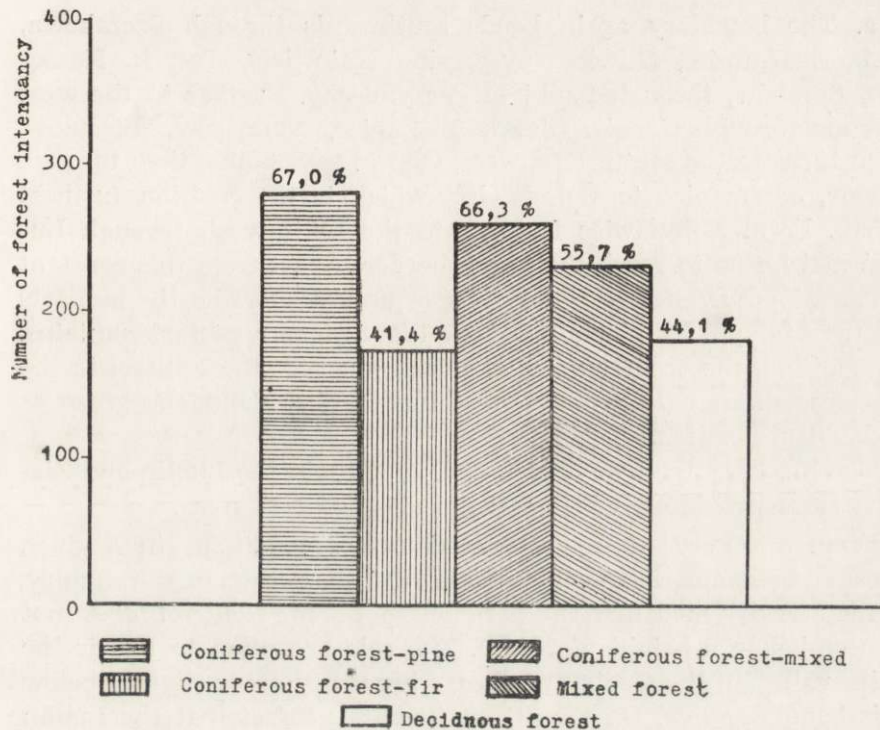


Fig. 1. The character of the forests on the investigated area.

I obtained information as to the quantitative composition of the forests from the phyto-sociological monographs (Kornaś - Medwecka, Matuszkiewicz) and from the instructions of the Ministry of Forestry — Technical and cultivation principles.

III. ANALYSIS OF THE GEOGRAPHICAL RANGE OF OCCURRENCE OF THE DARK PHASE OF THE SQUIRREL

The following picture of the distribution of the dark phase of the squirrel is obtained after entering its positions on the map. The range of occurrence of the dark phase embraces the southern part of our country. The northern boundary of this area runs from the east along the river San to Rozwadów, through the Sandomierz Forest area, Mielec, Dąbrowa Tarnowska, Wierzchosławice, Niepolomice Forest area, whence, skirting Cracow, it runs downwards to the south as far as Kalwaria Zebrzydowska. It then rises again towards the north, passes through Alwernia, Ojców, Olkusz to Pi-

lica. The boundary again bends southwards through Szczakowa, Kobiór, Knurów, Gliwice (by-passing Katowice), Toszek, Koszęcin, Boronów, through Panki to Parzymiechy. Further to the west it runs through Gorzów Śląski, Biskupice, Namysłów, Bierutów, then turns to the south (Bystrzyca, Olawa) to Sobótka, then through Jawor, Jerzmanice to Bolesławiec, which is the position furthest north. From Bolesławiec it turns to the south-west, through Lubań and Leśna to reach the Czech border. Apart from this constant range of occurrence, the dark phase occurs sporadically in parts of the Małopolska plateau and in the Świętokrzyskie Mountains. In addition, the occurrence of the dark phase of the squirrel in the Roztocze district (Horyniec Forest Intendancy) should be given as a doubtful position.

The black squirrel was not found to occur in the Lublin and Zielenka Góra provinces, which were used as control areas.

From a survey of the characteristics of conditions in a given area, and a comparison of these data with the results of the enquiry, it may be assumed that the dark phase of the squirrel does not appear below a height of 200 m. The sole exception to this is the Odra valley in the Opole province, where they occur slightly below this boundary line. On the other hand it is a fact that the Lublin highlands, which are suitable as regards height, and where the black squirrel might be expected to occur, is not included in the range of its occurrence. In the entire remaining territory, however, the boundary line of its range corresponds to a line defining a height of 200 m.

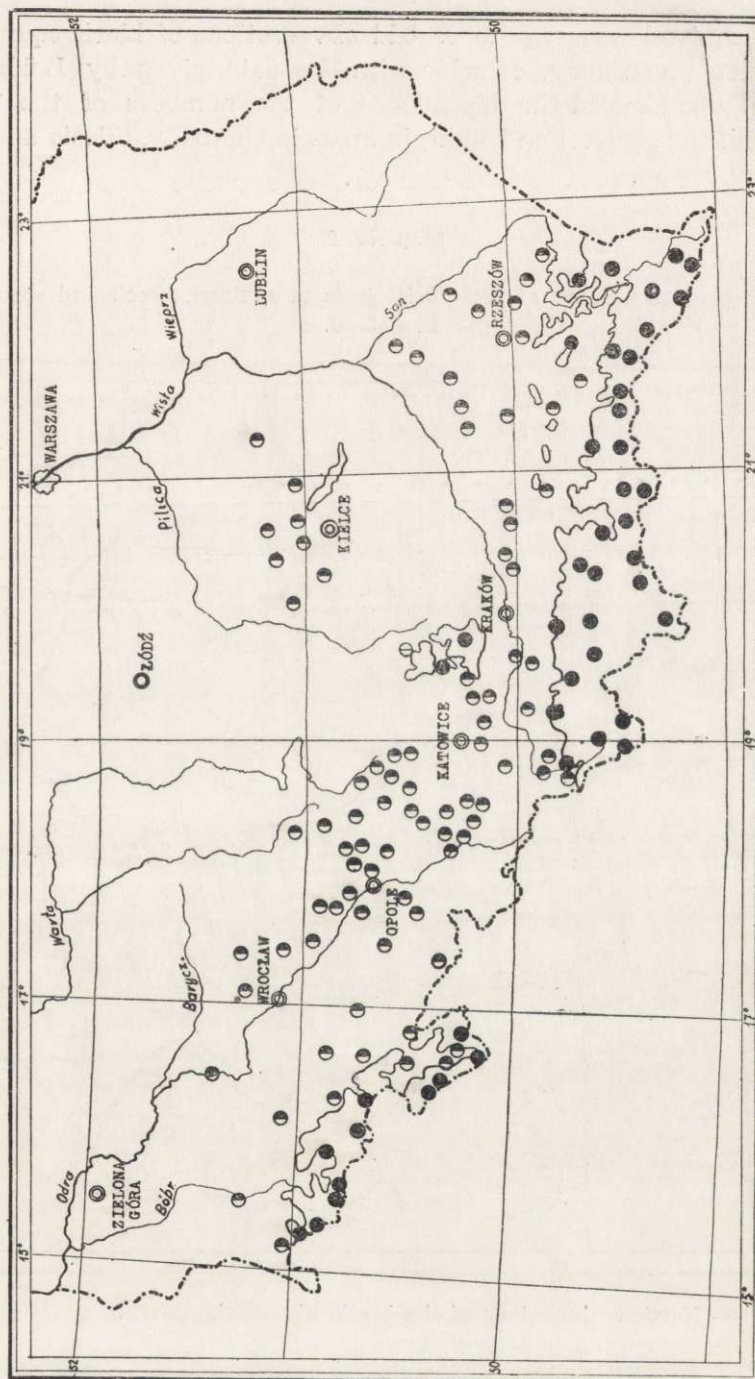
The absence of occurrence of the black squirrel in the Cracow and Katowice districts may be explained by the small amount of forest areas in this region, and the existence of the dense industrial concentration here.

A clear proof of the connection between the occurrence of the black squirrel and a definite height is the fact that over 400 m this squirrel markedly predominates over the red phase (Map No. 2).

The above is born out both by the replies given in the questionnaire and by observations made on the spot. In 57 replies from the forest intendancies in which the dark phase predominates over the red, none of the intendancies lies below 400 m above sea level.

Observations made in Bielsko-Biała show a ratio of 1:10 against the red squirrel, and in Polanica, which is situated even higher, only

Map No. 1.
Distribution of the black phase of squirrel in South Poland.



● red phase in predomination. ● black phase in predomination.

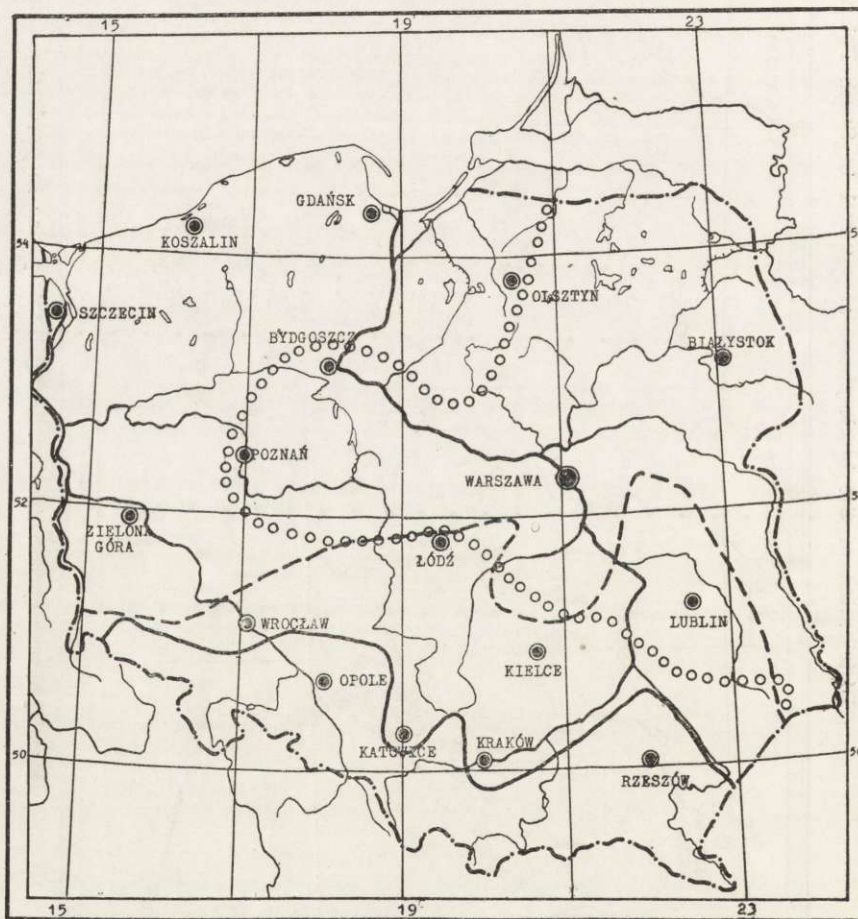
● red phase in predomination. ● black phase in predomination.

CW 31984.

1 red squirrel was seen to 60 odd observations of black squirrels. The facts given above coincide with the data given by Lühri \ddot{g} (1928), who showed the dependence of the numbers of the dark phase of the squirrel on height, in areas in Germany, Silesia and the Mazury region.

Map No. 2.

Range of occurrence of the black phase of squirrel, beech and spruce in Poland.



- Northern boundary of the black phase of squirrel.
 - - - - Northern boundary of spruce.
 oooooo Eastern boundary of beech.

CW 31984.

The diagrams in his work, show that with the increase in height above sea level, the number of black and dark specimens increases. This author divided specimens of the subspecies *S. vulgaris fuscoater* into 6 classes of colour, of which the first 3 were „light” and the other 3 „dark”. He included completely black individuals in the 6th class. The diagrams obtained by this method are very similar for all mountain territories, but differ significantly from diagrams from lowland areas.

Udziała (1924) attempted to link the distribution of the subspecies of squirrel which he distinguishes in Poland with the annual rain and snowfall over this area. He further stated that the amount of atmospheric rain and snow fall has a certain connection with the colour of the coat i. e. that a higher rain and snowfall causes darkening of the fur.

There are no grounds for indicating several „subspecies” of squirrel in Poland (Sidorowicz), but it is a fact that there is a mutual dependence of occurrence and distribution of the black squirrel on the amount of snow and rainfall and the height of the area concerned. On this basis it may be indirectly concluded, that the dark phase of the squirrel does not occur in areas where the amount of annual snow and rainfall, is less than 600 mm.

As far as the connection between the black squirrel and the forests in which it lives is concerned, it may be concluded, on the basis of the results of the enquiry and observations on the spot, that it does not occur in purely pine or purely deciduous forest stands. As proof of this we may take the fact that in forest areas where only the above types of forest are found, we have no data on the occurrence of the dark phase of the squirrel, although neither the height at which the area is situated nor the annual snow and rainfall would form an obstacle to this. In areas where the dark phase occurs, that is, in hilly or mountainous areas, the forest stands differ greatly as to the species composing them, from the lowland forests. Amongst the most characteristic differences we should mention the large percentage of coniferous trees in mountain forests, such as fir or spruce (90%), and also beech (up to 50%). In higher parts (approx. 1000 m) the forest consists almost entirely of spruce, whereas the pine, which forms the chief component of lowlands forests, is only sparsely represented (about 20%). In lowland forests, of the coniferous trees, the pine is predominant (about 50%) and of deciduous trees, oak, beech, lime, yoke-elm, ash and others.

From the above data it appears probable that the range of the black squirrel is in some way connected with the occurrence of the beech, fir and spruce trees as a group, and it would seem that the fruits of these trees are the main food of the squirrel in these areas. These data agree with data from literature (Spärc k, 1936), who states in his work that the chief factor causing the occurrence of the dark colour in the squirrel's coat is the type of food.

An interesting fact is that there is a certain coincidence between the occurrence of the black squirrel and the range of occurrence of the beech and spruce in Poland. Map No. 2 given above will serve to illustrate this fact.

In the light of the data I have collected, the range of the black squirrel coincides with information given in Polish faunistic literature (Schaiter, 1867; Jachno, 1867; Kocyan, 1867; Lubicz - Niezabitowski, 1903, 1910; Udziela, 1924; Kuntze and Szynal, 1933; Sokołowski, 1947; Grodziński, 1957).

It should also be emphasised that the range of occurrence of the black squirrel has not changed during the last 100 years.

The dark phase of the squirrel was undoubtedly formed as a geographical phase of the subspecies *S. vulgaris fuscoater* Altum. Of course the formation of such a phase must have been due to a whole series of environment factors, such as height above sea level, climate, type of food etc., and it has not yet been established which of these factors is the decisive one. It may be concluded from my data that the basic factor is height, although this problem requires further investigation.

IV. CONCLUSIONS

1. On the basis of replies to the questionnaire despatched to 8 provinces of southern Poland, the authoress has established that the dark phase of the squirrel of subspecies *S. vulgaris fuscoater* Altum occurs in Poland in hilly and mountainous districts.

2. The northern boundary of the range of this phase is as a rule formed by areas not less than 200 m in height above sea level.

3. At heights over 400 m this phase markedly predominates over the red phase.

4. The black squirrel does not occur in forest stands composed only of pine or of deciduous trees, but would appear to be connected with the occurrence of beech and spruce.

5. The black squirrel occurs in areas where the annual snow and rainfall is relatively high: over 600 mm, which may have some connection with the colour of the coat.

6. It should be added, that no one of these environmental factors is the decisive one, but all factors complex.

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STRESZCZENIE

Na podstawie odpowiedzi na rozesłaną do ośmiu województw południowej Polski ankietę oraz badań własnych, autorka ustaliła, że czarna faza wiewiórki podgatunku *Sciurus vulgaris fuscoater* Altum występuje u nas na terenach podgórskich i w górach. Granicą północnego zasięgu czarnej wiewiórki jest zasadniczo wysokość 200 m n. p. m. Od wysokości 400 m n. p. m. występuje ciemna faza w znacznej przewadze liczebnej nad rudą (Mapa Nr. 1 i 2). Czarna wiewiórka nie występuje w czystych drzewostanach sosnowych lub liściastych, natomiast wydaje się być związana z występowaniem buka i jodły. Na terenach jej występowania jest stosunkowo duża roczna ilość opadów (ponad 600 mm), co może mieć pewien związek z ubarwieniem. Należy jednak dodać, że o występowaniu czarnej formy wiewiórki nie decyduje żaden czynnik środowiskowy oddzielnie, ale cały kompleks czynników.