Ann. Zool. Fennici 18: 1–36. 1981

Differences in spotting pattern between populations of Aphantopus hyperantus (Lepidoptera, Satyridae) in southern Finland

Raija Seppänen

Seppänen, R. 1981: Differences in spotting pattern between populations of Aphantopus hyperantus (Lepidoptera, Satyridae) in southern Finland. — Ann. Zool. Fennici 18: 1—36.

In the butterfly *Aphantopus hyperantus* (L.), frequencies of spotting patterns were recorded in altogether 21 populations in the districts of Mikkeli (1961, 1968—75), Porvoo (1961—64, 1971—73) and Tampere (1958) in southern Finland.

In the Mikkeli district, for comparison, six populations of *Erebia ligea* (L.) were investigated in 1970—74 and three populations of *Coenonympha glycerion* (Bkh) in 1971—73.

In *Aphantopus* some wing areas showed changes in spot number concomitantly with changes in the general climate. A climatic index characterizing temperature and humidity conditions was calculated for the summers of 1968—74. The changes in the frequencies of the 2-spot phenotypes on the upperside of the fore and hind wings of males paralleled changes in the climatic index. The parallelism between the curves for climate and for phenotype was close enough to suggest a causal connection between them.

In certain populations, occasional deviations from the afore-mentioned parallelism took place. Such deviations were most marked in populations living in habitats adversely affected by the activities of man.

It seems possible that these activities of man were indirectly responsible for such irregular variability in spot number. It is possible to state whether the effect was due mainly to changes in selection pressure or to random factors.

Spotting pattern frequencies in the *Erebia* and *Coenonympha* populations at the same sites varied somewhat similarly to those of *Aphantopus*, a situation lending some support to the conclusions drawn from the study of *Aphantopus*.

Raija Seppänen, Pellonpäänkuja 13 H, SF-45150 Kouvola 15, Finland.

1. Introduction

Many authors have shown that the study of isolated Lepidoptera populations can provide valuable data on a variety of biological problems. Particular interest attaches to studies continued from generation to generation, as in *Maniola jurtina* L. (see Ford 1971, 1976).

This paper describes a study of polymorphic variability in wing spotting in southern Finnish populations of the Ringlet, *Aphantopus hyperantus* (L.) (Satyridae), a species which has not earlier been investigated in this respect. The Ringlet is one of the commonest and most widespread butterflies in Europe, except in the extreme north and the Mediterranean region (Higgins & Riley 1970). Its distribution extends across Eurasia from the Atlantic to the Pacific coast.

Aphantopus is essentially a butterfly of meadows, grassy hillsides, open places in woods, and roadsides.

The butterfly affords interesting material for population studies because in the course of time many varieties of the Ringlet have been found and described (see Wahlgren 1930, Collier 1956, 1967, Lincome 1967, Baletto et al. 1975).

Studies made by Ford (1945) indicated that the eye-spots in the Ringlet are controlled on a multifactorial or polygenic basis. Besides, investigations have been made on the variation in the ground colour of the wings. Most of these studies have been made in the British Isles. There the coloration of the underside of the butterfly shows a slight cline. The underside of the Ringlet "is of rather an ashen tint in Scotland and the north of England . . ., but becomes of a rich chocolate shade in the south" (e.g. Kent; Ford 1945).

At least two counts have been made of the chromosomes of the Ringlet, with different results. Federley (1938) found n = 29, whereas Bigger reported n = 23 (Robinson 1971).

In this study, I have tried to find out whether there are differences in spotting pattern between *Aphantopus* populations in different localities and in different years, and if this is so, what the reason might be. For this purpose, I examined the spotting pattern in different years in relation to population size, population density and weather conditions.

2. Material and methods

2.1. Study areas

In Finland, stable local populations of *Aphantopus* are found almost continuously as far north as Vaasa (63°N). The main study area around the town of Mikkeli (see below) lies in the northern part of the area of continuous distribution of the species, and scattered stable populations are found as far north as about 65°N, for example at Haapavesi and at Ristivesi near Kajaani (Valle 1935, Nordström 1955). In Norway the butterfly reaches its northern limit south of Årdahlsner (61°N), and in Sweden south of Skellefteå (64°N).

In 1968—75 altogether 6034 individuals of *Aphantopus hyperantus* were examined with regard to sex and spotting phenotype in populations living in the south of Finland (Table 1, Fig. 1). The main material of the study was collected in 1961), and in 1968—75 from ten populations in and around the town of Mikkeli (= M) (61°40′ N) as follows: Mikkeli (populations M1, M4 and M9), Porrassalmi (M3), Otava (M10), Karikko (M5), Korpijärvi (M6), Tähkämäki (M2), Rahula (M7) and Kaihlanen (M8) (Fig. 2).

Later I will use the symbols M1, M2, M3 and so on both for the population of *Aphantopus hyperantus* and for the meadow where the population lives. The context will show whether the symbol refers to the population or the meadow.

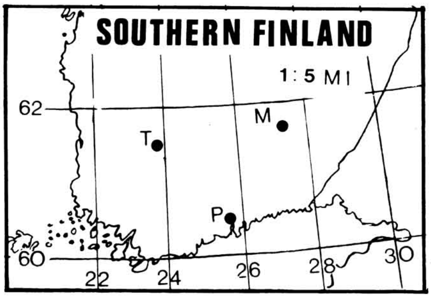


Fig. 1. Map of southern Finland. The letters show the study area as follows: M = Mikkeli district, P = Porvoo district and T = Tampere district.

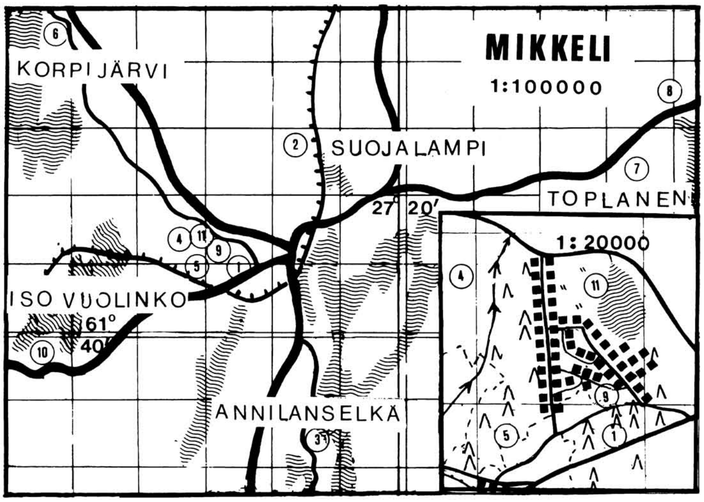


Fig. 2. Map of the Mikkeli district. The numbers indicate the sites of the Mikkeli populations.

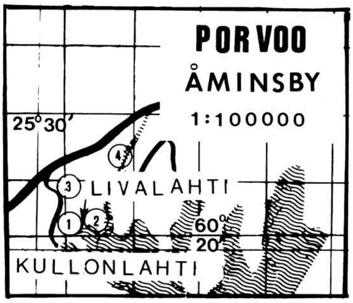


Fig. 3. Map of the Porvoo district. The numbers indicate the sites of the Porvoo populations.

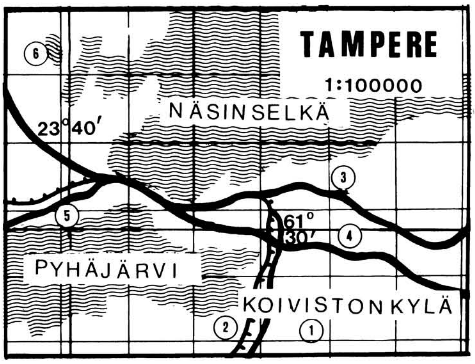


Fig. 4. Map of the Tampere district. The numbers indicate the sites of the Tampere populations.

Table 1. The numbers of *Aphantopus hyperantus* in 1958, 1960—64 and 1968—75 in the Mikkeli, Porvoo and Tampere districts.

	Mikkeli											Porvoo					Tampere								
	M1	M2	M3	M4	M5	M6	M7	M8	M9	M10	Tot.	P1	P2	P3	P4	Tot.	T1	T2	T3	T4	T5	T6	T7	Tot.	
	Males																								
1958																	72	85	89	84	89	69	77	565	
1960												28	12	15		55									
1961	69	54	53	76							252	11	10	—		21									
1962	—	—	—	—								20	—	8	11	39									
1964	—	—	—	—								—	—	9	—	9									
1968	98	101	85	2	90	104	106				586	—	—	—	—	—									
1969	104	63	81	1	121	100	124				594	—	—	—	—	—									
1970	9	15	11	—	67	1	—				103	—	—	—	—	—									
1971	27	21	31	—	64	13	79	34	25	14	308	3	—	—	—	3									
1972	15	9	42	—	122	10	49	30	50	84	411	63	—	16	—	79									
1973	101	66	91	—	125	18	82	75	94	95	747	100	—	43	—	143									
1974	47	18	10	—	115	—	—	—	55	—	245	—	—	—	—	—									
1975	25	—	—	—	59	—	—	—	—	—	84	—	—	—	—	—									
Tot.	495	347	404	79	763	246	440	139	224	193	3330	225	22	91	11	349	72	85	89	84	89	69	77	565	4244
	Females																								
1958																	23	16	24	11	15	28	16	133	
1960												18	16	8		42									
1961	52	49	51	19							171	9	14	—	23										
1962	—	—	—	—							—	18	—	—		18									
1964	—	—	—	—							—	—	—	—		—									
1968	51	53	56	—	43	61	52				316	—	—	—		—									
1969	49	48	52	—	57	42	25				273	—	—	—		—									
1970	—	11	5	—	5	—	—				20	—	—	—		—									
1971	16	5	15	—	21	8	11	8	—	21	105	22	—	15		37									
1972	14	1	12	—	54	1	12	19	27	43	183	67	—	13		80									
1973	38	40	23	—	63	11	19	15	20	53	282	18	—	15		33									
1974	9	3	2	—	31	—	—	—	3	—	48	—	—	—		—									
1975	10	—	—	—	15	—	—	—	—	—	25	—	—	—		—									
Tot.	239	210	216	19	289	123	119	42	50	117	1424	152	30	51		233	23	16	24	11	15	28	16	133	1790
																									6034

For comparison, in 1971—73 Ringlets were examined from Åminsby in Porvoo (= P, Fig. 3) (60°20′ N), where Ringlets were collected from Livalahti (P1) and Kullo (P3). They were compared with earlier samples collected by Prof. E. Suomalainen from the same district in 1960—64. His samples, 207 Ringlets, originated not only from Livalahti and Kullo but also from populations in Kesälä (P2) and Karleby (P4).

The material of this study also included Ringlets from seven populations near Tampere (= T, Fig. 4) (61°30′ N). These were collected by Mrs. E.-L. Kanerva, M.A., in 1958. Six of these samples were from the Tampere district, and one from Mouhijärvi 30 km west of Tampere.

For the sake of comparison, in 1970—74 I collected *Erebia ligea* (L.) (Table 4) and in 1971—73 *Coenonympha glycerion* (Bkh) from the Mikkeli district (Table 5). All scientific names are according to the catalogue of the Macrolepidoptera of Finland (Jalava 1977).

2.2. Biotopes of the Aphantopus hyperantus populations in the Mikkeli district

The bulk of the material was collected in Mikkeli. Sites for populations in the Mikkeli district (M) are shown in Fig. 2.

Population M1. The meadow inhabited by population M1 is about 250 m long in the NE-SW direction and 200 m broad, sloping southwest and bordered on the SE side by a main regional highway. During the first half of the study period, the meadow was flanked by forest to the east, north and west. The southwestern part of the meadow was an abandoned field, the rest a natural meadow, and neither part was grazed in 1961 or 1968—75.

The highway, which was constructed in the mid-60s, had an unfavourable effect on the soil water balance of the meadow. As a result of industrial building activity the meadow grew smaller piece by piece during the 1970s.

Population M2. The meadow inhabited by M2 is about 200 m long in the NW-SE direction and 300 m broad, sloping towards the southeast. It is surrounded by woods on all but the southeast side, where a railway runs. The National Railway Company owns a safety belt 12—40 m broad, and periodically treats this with herbicides. The herbicide "Vesakkotuho 500" (2,4-D 333gr, 2,45-T 167gr, H_2O 500gr) killed the dicotyledons in the southeastern part of the meadow. At times withering and death of plants was observed up to 100 m from the railway. The herbicide was always applied in early June, at which time *Aphantopus* was at the larval stage.

The detruction caused by the poisoning was most intensive in 1969 and 70 when, at the beginning of the flight period of *Aphantopus*, large parts of the meadow turned yellowish or brown. In 1971—73 the vegetation recovered, except near the railway, where it was always dead or withering.

Population M3. This population occupied a meadow, originally about 100 × 50 m in size, which was reduced by forest plantations to a small wayside area and in the late 1960s was only about 40 m^2 in area. The afforestation caused an ecological change (Table 2).

Population M4. This population lived about 4 km northwest of meadows M1, M5 and M9, on the shore of the river Sirkkapuro. In summer 1961 the area was still a pasture, but the meadow was then abandoned and was soon invaded by bushes and trees.

Population M5. The site occupied by M5 lies about 2 km southwest of the previous area. The meadow was originally divided by ditches into 8 sections about 150 m long in the NW-SE direction and about 50 m broad. The meadow slopes towards the southwest.

The eastmost edge was investigated with the sweep-net. This part of the meadow was surrounded by woods. In 1973 a tall stand of pines was clear-cut, after which, northerly winds could blow freely across the meadow. This certainly affected the microclimatic and ecological conditions, including the plant coverages.

The meadow slopes very gently, and the vegetation belts generally found on hillsides are not present in M5.

Population M6. At the beginning of the study period the site of population M6 was a large isolated wayside meadow about 100 × 50 m in area in the vicinity of a lake, Korpijärvi (Fig. 2). In 1968 the meadow was planted with large seedlings of *Picea abies*. With time the meadow was invaded by spruces. This ecological change destroyed many of the food plants of *Aphantopus* larvae, especially reducing the coverage of *Phleum pratense* and *Poa* ssp.

Population M7. This population occupied a woodland glade supporting low, sparse growths of such plants as *Deschampsia caespitosa, Calamagrostis* spp. and *Poa* spp. Along the forest edges these grasses were tall and dense. The dominant tree was *Pinus sylvestris*.

In 1970—71 the sheltering woods were almost totally felled and part of the study area was covered with logs. The study still continued, however, in 1971—73.

Population M8. This meadow is surrounded by woods and slopes towards the south; it lies slightly more than 2 km northeast of M7. In places there are scattered *Pinus* and *Betula*. Ecologically the meadow remained practically unchanged throughout the study period.

Population M9. The meadows inhabited by populations M1, M5 and M9 were once parts of a large meadow complex, which was split up by roads and human settlements long before this study began.

The meadow, about 200 × 100 m, was protected by a dense spruce forest in the south but bordered by human settlements on all other sides. Thus the area was exposed to north winds. The meadow was dominant by *Alopecurus pratensis, Dactylis glomerata, Agrostis tenuis* and *Poa* ssp. During dry periods (e.g. in 1972) many of the plants tended to wither and die more rapidly than in the other meadows. The area was studied in 1971—74, during which parts of the meadow were partly destroyed by human activity. This activity was most intense at the edges of the northern part, which originally had the most suitable food plants for *Aphantopus* and shady sites for the larvae.

Population M10 inhabited a meadow surrounded by pinewoods on all but the southeast side, where it was bordered by *Alnus incana*. The meadow lies in a narrow valley, its northern end rising rather steeply towards a wooded hillside. The meadow itself is about 350 m long in the NE-SW direction and 40—100 m broad. The dominant plants are grasses (Table 2).

2.3. Biotopes of the populations in the Porvoo district

In 1971—73 Ringlets in the Porvoo district (P) were caught with a sweep-net (Fig. 3). The samples were collected in two of the meadows in which the *Aphantopus* samples of 1960—64 were encountered. The meadows were the following: *Aphantopus hyperantus* population P1 inhabited a shore meadow at the inner end of Livalahti, a bay on the gulf of Finland. The meadow was carrying a very dense hay crop.

The habitat of P2 was separated from P1 by a belt of spruce forest.

P3 lived in the Kullo area about 1 km northwest of the sites of P1 and P2. The meadow slopes towards the southeast and is covered with grasses (e.g. *Poa* and *Deschampsia* spp).

P4 inhabited a shore meadow on the west bank of the Mustijoki river, about 3 km from P2.

The ecology of the populations of the Porvoo district was not investigated in detail. Here, however, in contrast to Mikkeli, the vegetation for the meadows remained practically unchanged throughout the study period 1971—73.

2.4. Biotopes of the populations in the Tampere district

The area investigated comprised six populations living in both sides of the isthmus that joins the lakes Näsijärvi and Pyhäjärvi (Fig. 4). For comparison, a population (T7) was also investigated in Mouhijärvi about 30 km from T1—T6. The area occupied by this population was an old clearing left after a forest fire in the middle of woods, about 4 km from the railway station at Nohkua.

The sites of the populations in the T district were ecologically relatively similar. The populations in the T district proper were situated as follows:

The habitat of T1 was a fallow in a suburb, Koivistonkylä. The very small population T2 lived in a meadow about 2.5 km west of T1. Population T3 lived in a small meadow situated along the edge of the forest. Population T4 occupied a relatively large meadow about 2 km from T3. All these four populations lived on the southeast side of the isthmus (Fig. 4).

Population T5 lived in a meadow on the southwestern side of the isthmus, near Pyhäjärvi, and T6 occupied a glade in the middle of woods, on the northwest side of the isthmus. All the populations were isolated from each other.

Table 2. The coverages of the most important plants in the areas occupied by the populations of the Mikkeli district. The coverages are shown as percentages. A = 1971, B = 1978.

	M1		M2		M3		M5		M6		M7		M8		M9		M10	
	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B
Aegopodium podagraria	20	30	14	14	5	3	20	20	6	—	—	15	5	20	6	10	6	5
Agrostis tenuis	20	—	15	10	20	25	15	6	15	6	12	14	15	4	15	13	15	8
Alchemilla "vulgaris"	15	3	35	25	25	6	30	25	6	3	10	3	10	12	10	6	10	6
Alopecurus pratensis	35	25	30	15	—	3	20	6	4	3	5	5	20	20	6	4	6	15
Anthoxanthum odoratum	9	—	15	9	3	—	35	14	3	3	—	—	5	5	6	—	6	—
Anthriscus sylvestris	5	14	5	6	6	10	5	5	5	3	3	3	10	8	6	10	10	15
Calamagrostis arundinacea	4	—	5	6	4	10	5	—	5	14	20	14	4	3	4	—	4	—
Leucanthemum vulgare	5	—	3	3	5	5	7	6	4	3	—	3	15	6	15	6	4	3
Dactylis glomerata	4	8	10	12	8	8	4	—	7	—	7	4	15	10	14	14	7	5
Deschampsia flexuosa	7	—	10	14	12	25	9	7	12	25	14	20	10	7	7	9	12	15
Deschampsia cespitosa	—	—	3	4	—	—	3	3	—	—	—	—	—	4	—	—	—	3
Elymus repens	—	3	—	6	—	5	—	—	—	3	—	9	—	—	—	—	—	—
Epilopium angustifolium	3	—	5	5	10	3	4	—	6	14	6	6	6	3	3	—	35	25
Festuca pratensis	3	—	6	10	—	—	3	—	—	—	—	—	—	6	—	5	—	—
Filipendula ulmaria	20	40	12	10	—	—	6	14	5	—	—	—	15	14	6	—	4	—
Lathyrus pratensis	15	—	10	7	4	—	15	6	5	4	—	—	15	12	7	—	6	6
Milium effusum	7	3	10	4	6	—	9	—	3	—	—	—	3	4	—	—	—	—
Phleum pratense	15	6	15	12	7	10	14	6	4	3	14	5	10	6	10	9	14	14
Poa pratensis	25	5	30	20	30	15	20	6	28	14	15	15	30	20	28	20	30	25
Trifolium pratense	12	—	12	10	10	4	9	6	5	—	—	—	12	9	6	6	3	10
Vicia cracca	5	3	7	6	6	3	10	7	5	3	4	3	5	5	8	6	4	5
Vicia sepium	10	5	8	4	6	—	14	5	—	—	—	—	7	5	3	3	5	3

2.5. Vegetation in the Mikkeli district

Analyses of vegetation were made in 1971—72, the coverages of the most important plant species being estimated as percentages in each meadow in the M district. The tree coverage was also estimated to obtain some idea of the shade afforded and of the general character of the meadow.

The vegetation of the meadows was analysed once more in June 1978, in plots of 2×2 m^2. Coverages of the plant species were estimated on the following scale: , , 1, 2, 3, . . . 15, 20, 30 . . . 100 %. The most prevalent plants outside the plots were also recorded both for the community concerned and for the whole meadow complex.

The coverages of the most important plants are given in Table 2.

2.6. Material of Aphantopus hyperantus

Practically all the samples were collected with sweep-nets, mainly between 08.30 — 15.30 hours, in sunny or sometimes moderately rainy weather in 1968 — 74. The total number of individuals collected was 6034, of which 1790 (29.7 %) were females.

The phenotypes of the butterflies collected were recorded on cards bearing outlines of the upper- and undersides of the butterfly. In addition to the number, shade and position of the spots, the cards had spaces for recording the number of the meadow, the date of collecting and the sex of the individual. In 1968 and 1969, the size of each individual was also recorded.

The left wings of each butterfly were selected to represent the individual and thus all tables and pictures in this study are based on observations made from the left wings.

All the meadows investigated lie fairly close to one or other of the two weather stations in the M district: the Mikkeli airport and Suosaari. Thus the weather data from these two stations give a fairly good picture of the general climatic conditions prevailing in the meadows. In Figs. 5—9 daily recordings of mean temperature and total precipitation are given to provide a background for the analysis of weather conditions favourable for flight.

2.7. The modified humidity index, MHI

Temperature may well be one of the limiting factors for *Aphantopus*, but variations in temperature were not very great during the study period. Precipitation was much more variable than mean temperature. To take into account both temperature and precipitation, a humidity index designed for the purposes of the present work was calculated. In designing this modified humidity index, *MHI*, the weather statistics of the M district were studied to find the highest and lowest sums of the daily mean temperatures for 5-day periods (June 7—11, 12—16, etc., see Table 3). The highest sums found never exceeded the value of 120 day-degrees Celsius.

Precipitation for 5-day periods was calculated simply as a sum of the daily precipitations. The *MHI* was calculated from the following formula, in which T is the daily mean temperature and P the daily precipitation:

$$MHI = (120 - 5T) + 5P$$

Wind velocity was not taken into account, since it varied very little and in June and July the mean velocity was generally between 2 and 4 m/s. In Finland daily mean temperatures very seldom lie at 24°C for 5 consecutive

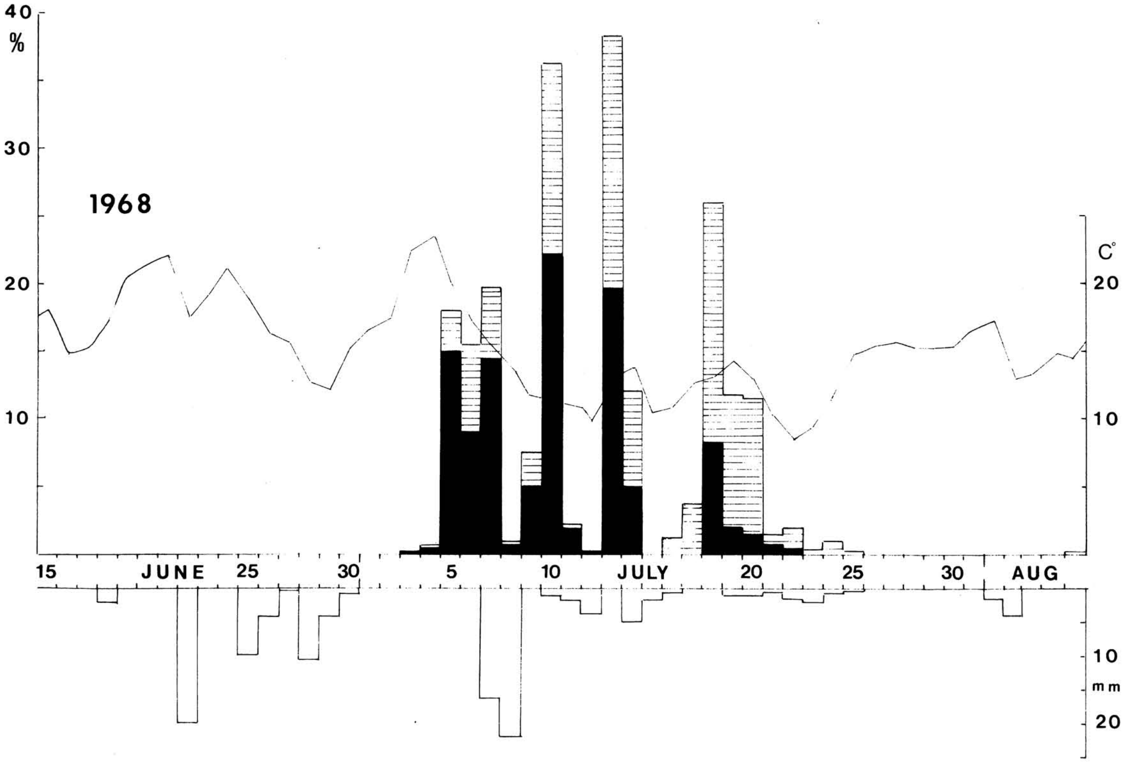


Fig. 5. Time-course of captures of *Aphantopus hyperantus* in 1968 in the Mikkeli district. The black histograms show the daily numbers of males and the hatched histograms show the numbers of females. The line shows the daily mean temperatures (C°), and the white histograms the daily precipitations (mm).

days. If this were to happen in a period completely without rain, then *MHI* = 0 and thus the value 0 may be considered to signify extreme aridity. The more humid and cool the period, the higher the *MHI*. In practice, *MHI* usually lies between 0 and 100 and so serves as a useful reference variable for any possibly correlated biological variable expressed as percentages. The word "modified" indicates that humidity is expressed in a such a way that the whole range tends to lie between 0 and 100.

The *MHI* has been used in investigations on *Philaenus spumarius* (Homoptera) by Halkka (personal communication about the use of the modified humidity index for the purposes of the present study).

2.8. Biology and appearance of Aphantopus hyperantus

Haunts

The Ringlet flew in meadows and woodland openings and along the edges of ditches and roadsides. The butterfly avoided moist meadows, but in the openings it favoured the microclimatically damper parts, where the vegetation

Table 3. The modified humidity index (*MHI*) in 1968—74 in the Mikkeli district.

	1968	1969	1970	1971	1972	1973	1974
7—11.VI	60.8	45.4	28.1	72.3	59.7	43.1	69.9
12—16.VI	37.9	39.6	55.6	60.1	54.2	70.5	36.4
17—21.VI	26.7	35.2	36.7	45.6	33.8	46.1	18.4
22—26.VI	62.4	54.2	34.4	56.9	45.8	22.3	47.2
27— 1.VII	63.3	69.9	19.7	62	0.3	62.9	64.5
2— 6.VII	20.2	84.8	54.8	39	27.8	7.5	63.8
7—11.VII	93.7	40.7	62.5	35.7	20.9	25.8	50.7
12—16.VII	71.3	59.5	90.4	61	26.6	19.9	47.3
17—21.VII	58.5	61.5	47	73.2	27.5	26.7	42
22—26.VII	62.6	68.2	47.9	40.9	46.6	37.8	39.9
27—31.VII	42.6	21.2	41.9	52.8	33	37.4	79.3
1— 5.VIII	52.4	38.8	34.7	48.9	38.2	40	90.6
6—10.VIII	51.7	39.7	60.5	68.7	23.5	47.1	115.6
11—15.VIII	72.9	30.4	52.6	74.4	100.9	40.8	109.9
7.VI—15.VIII	55.5	49.2	47.6	52.3	38.5	37.7	62.5
12.VI—15.VIII	55.1	49.5	49.1	50.7	36.9	37.3	62.0
17.VI—15.VIII	56.5	50.3	48.6	49.9	35.4	34.5	64.1
Annual temperature	2.3	2.2	2.7	2.9	4.2	3.4	4.8
Annual precipitation	623	535.7	578.7	557.7	474.2	559.7	823.8

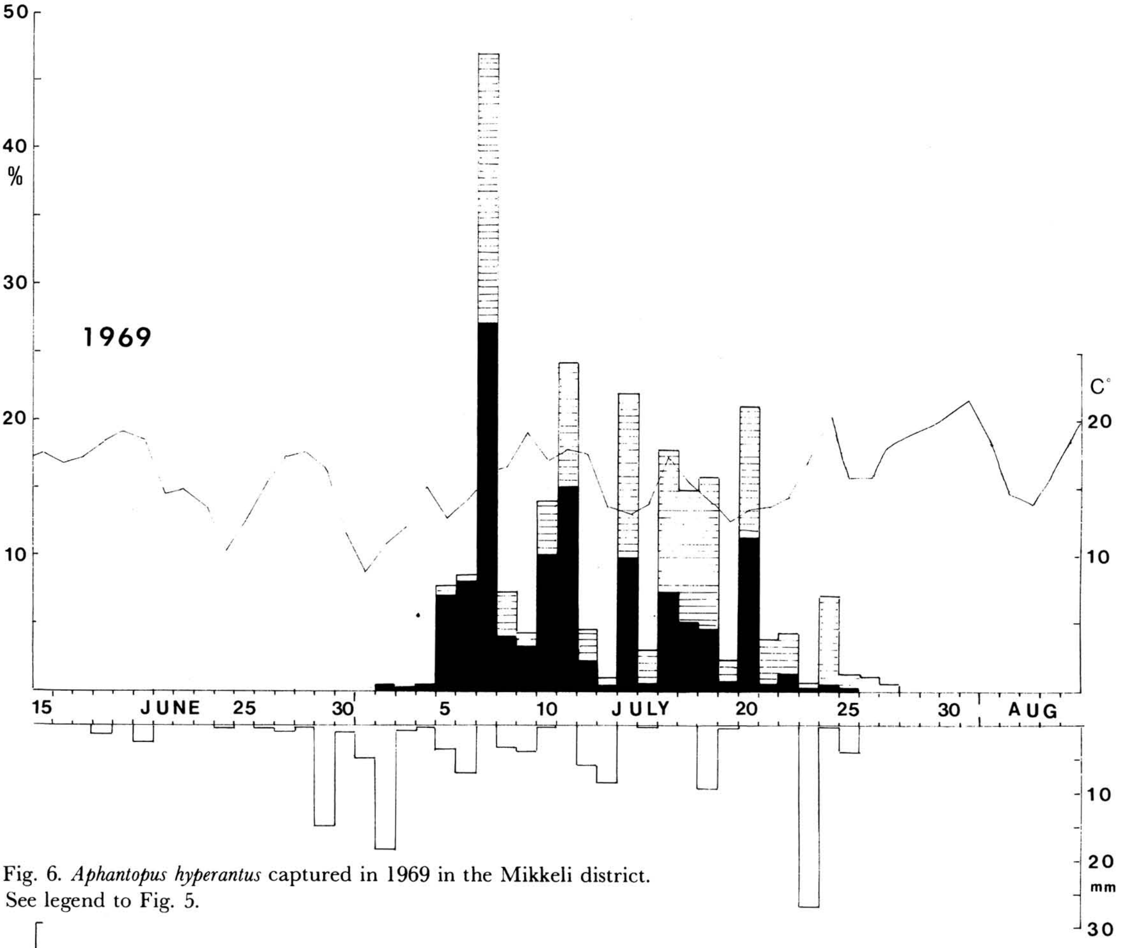


Fig. 6. *Aphantopus hyperantus* captured in 1969 in the Mikkeli district. See legend to Fig. 5.

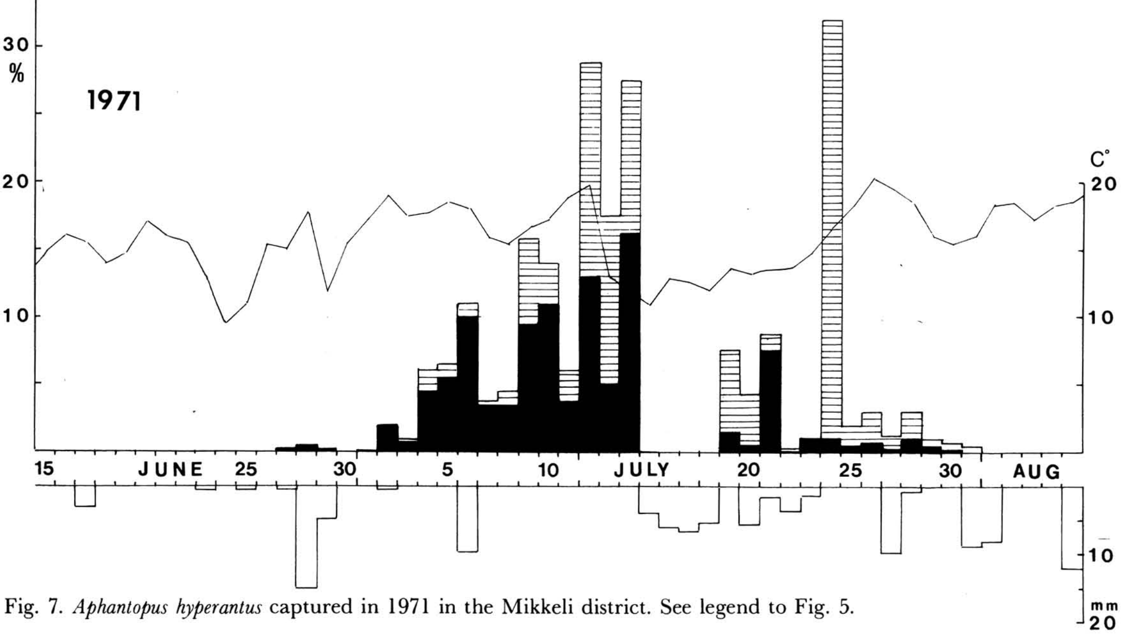


Fig. 7. *Aphantopus hyperantus* captured in 1971 in the Mikkeli district. See legend to Fig. 5.

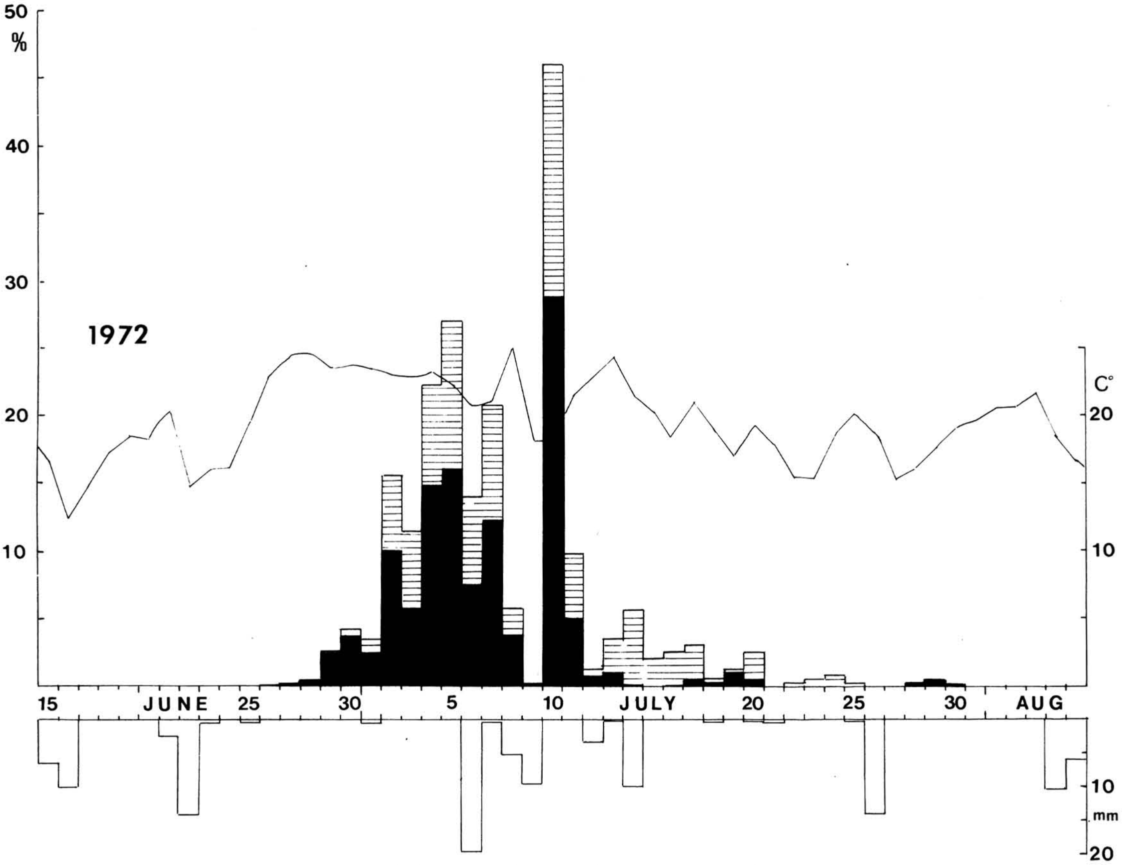


Fig. 8. *Aphantopus hyperantus* captured in 1972 in the Mikkeli district. See legend to Fig. 5.

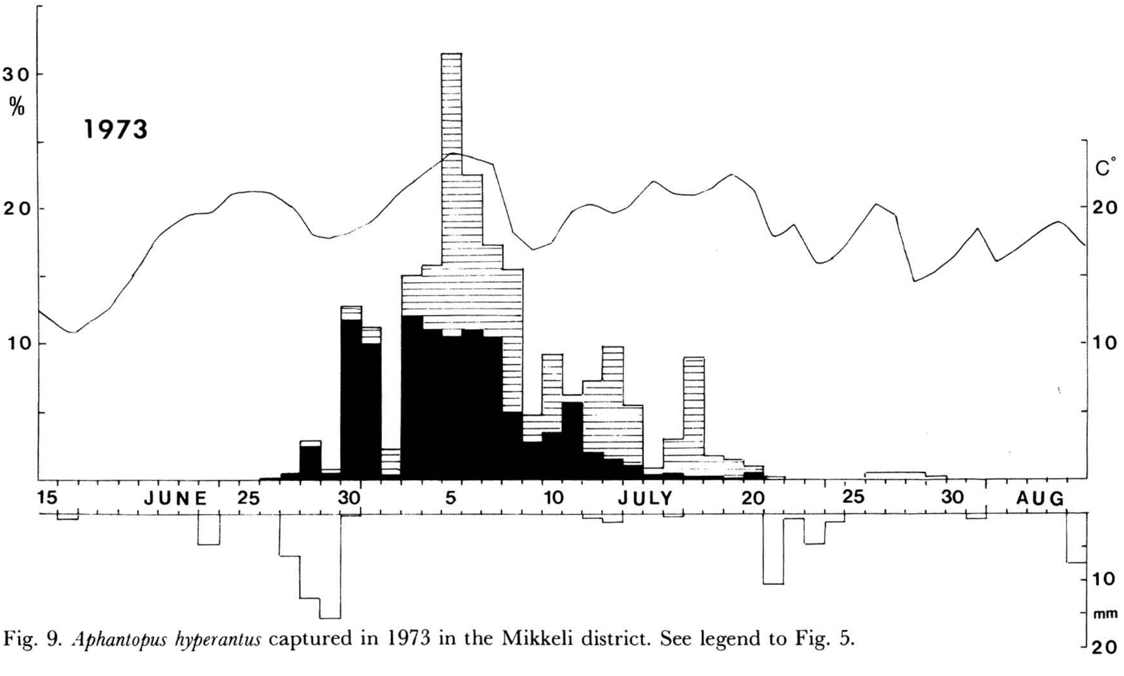


Fig. 9. *Aphantopus hyperantus* captured in 1973 in the Mikkeli district. See legend to Fig. 5.

was more lush. All this made it difficult to draw limits between the areas occupied by populations.

The Ringlet females, unlike many other butterflies, seldom show a strict preference for certain plants when laying their eggs, but simply drop them on blades of grass. Thus the eggs are laid over a large and varied area. This is in accord with the feeding habits of the larvae, which live on a great many grasses, especially *Poa pratensis* and *Poa annua*, or other *Poa* spp., *Milium effusum*, and even *Carex* spp. (Valle 1935, Higgins & Riley 1970, Seppänen 1970).

Other plants on which the larvae have been found feeding include *Phleum pratense* (Valle 1935, Seppänen 1970), *Calamagrostis* spp. and *Phalaris* spp. (Seppänen 1970). The favourite food-plants seems to be *Poa pratensis* and *Poa annua.*

Development and hatching

The eggs of *Aphantopus hyperantus* are smooth over most of their surface, but around the top there are low ridges. The egg, which is almost round, is at first light yellow but later becomes darker.

The females lay eggs from about the last quarter of July to the first few days of August. According to studies made in England, the larval period lasts about 280 days (Frohawk 1934). It is very difficult to find the larva of *Aphantopus* (Frohawk 1934) as "upon the slightest disturbance it falls from its food and rolls into a complete ring, remaining motionless over a minute or more; it then straightens itself to its former position."

In Finland, according to E. Peltonen (personal communication to E. Suomalainen), it seems probable that the species is univoltine, generally overwintering as the larva. As evidence of this E. Peltonen has found fairly large larvae of *Aphantopus* in late May and early June.

The larvae of the Ringlet feed only at night. They reach a final length of about 20 mm (Valle 1935).

The pupa, which rests on the ground, is light brown and rather short and thick. The pupa is about 11.7 mm long in the males and about 12.7 mm in the females (Frohawk 1934). According to studies in England, the pupal period lasts about 14 days.

The first adults emerge during the last quarter of June (Figs. 5—9) in Finland. The time is nearly the same as in England (Goodden 1978). The life span of adult *Aphantopus hyperantus* is probably not more than 21 days (see Frohawk 1934). A hypothetical scheme for the average life cycle in Finland is given in Fig. 10.

Flight

In the study area the Ringlets are on the wing in June — July (Figs. 5—9). During the study period flying began between 25 June — 5 July. The males appeared first and the females took wing a couple of days later.

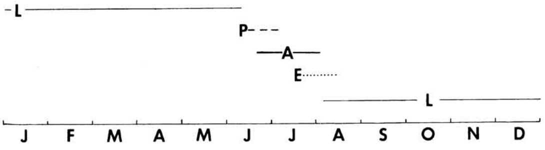


Fig. 10. Hypothetical scheme for the average life cycle of *Aphantopus* in Finland. In the summer months, the periods overlap and may, in different years and different meadows be shifted by 1—2 weeks, depending on weather conditions. A = adult, E = egg, L = larva, P = pupa.

The length of the flight period of a population varied from 30 to 35 days. At first the populations include more males than females.

Because the butterflies were collected between the same hours (see p. 5), the results for different years are quantitatively comparable (Figs. 5—9). The differences between years may have been causally connected with annual changes in the *MHI* (Table 3).

The flight period is influenced by the *MHI* of the larval period, which also affects the size and the gene pool of the next generations. Further, the diagrams show the flight behaviour of *Aphantopus.*

Flight activity was maximal when the sun was shining, and the weather was neither very windy nor cloudy. In the warm evening *Aphantopus* flies towards evenings (21 hours). Wind was obviously an influential factor, since when it became stronger, the height of flights decreased and the butterflies flew where the vegetation afforded shelter. At wind speeds of over 10 m/s no Ringlets could be seen on the wing.

In studies made in England *Aphantopus* was found to fly "during gloomy weather or even in a gentle summer shower" (Frohawk 1934). Observations during the present study indicated that the Ringlets seek shelter from showers of rain either between stalks of grasses or on the underside of leaves of such plants as *Pteridium aquilinum* or *Rubus idaeus*, the latter being especially favoured in M7.

In the morning the Ringlets crawled out of the grass on to the leaves of small herbs (e.g. *Alchemilla*), and spread their wings. Perhaps the butterflies were trying to absorb into their dark wing surfaces as much radiant heat from the sun as possible before they took wing. Flying was at first somewhat slow (particularly the first flights), but towards noon it gradually became more rapid. At the same time the numbers in flight increased. The normal flight of this butterfly is somewhat slow and fluttering, but it usually follows a zigzag course and is able to change direction rapidly.

The males flew at greater heights than the females. The flight of the female was heavier and the females often flew close above the grass stems or among them. When both sexes were flying low it was more difficult to see the light-coloured females than the dark males.

If a Ringlet was chased, it flew a short distance and dropped down quickly among the vegetation. The butterfly pressed itself against the yellow tussocks and was immobile. The adaptive colouring caused by the spotting on the underside created such a good camouflage that the outline of the butterfly was difficult to discern. The females made use of their protective colouring more often than the males.

The females, when laying eggs, tended to keep to the edges of the meadows. For instance, in M9 the females were never seen laying eggs in the centre of the meadow. The caterpillars probably move very little, as all the emerging adults were found along the edges of this meadow. The same conclusion could be drawn from the number of newly emerged individuals, which was higher along the edges of the meadow than in the centre. The reason for this may have been a shading effect, which created suitable conditions for the food plants of *Aphantopus.*

Eye-spots

All the wing areas of *Aphantopus* are adorned with eye-spots (Fig. 11). Their size, form and number varies with the sex and with the area of the wing and is also individually variable. As a rule individuals were symmetrical in their spotting patterns.

In this study the eye-spots were divided, according to form and size, into two main classes (Fig. 12):

1A) The largest eye-spots consisted of a white dot surrounded by a black or dark brown ring. The breadth of this ring was variable. Surrounding it was another ring, which was light or dark yellow in colour or sometimes even orange. These eye-spots were biggest in those individuals in which the outer ring was light yellow. The large eye-spots were often oval or rhomboid (f. *lanceolata* see Collier 1956, 1957, Lincome 1967).

On the underside of the fore wings in the females the eye-spots were often wide enough for the outer rings to touch each other, like a string of beads.

1B) The same main size class included eye-spots in which the central white dot was absent. Eye-spots with and without the central white dot were both classed in the study as rings.

2) The second main type of eye-spot was a small yellow dot without a surrounding ring.

The arrangement of eye-spots on the fore and hind wings was recorded for each butterfly captured, the possible sites of spots being numbered for identification (Fig. 11).

The two main types of eye-spots were treated together. In the males however, small spots seem to occur at sites in which they are not commonly found in the females. In individuals with many eye-spots, the "extra" spots are usually small.

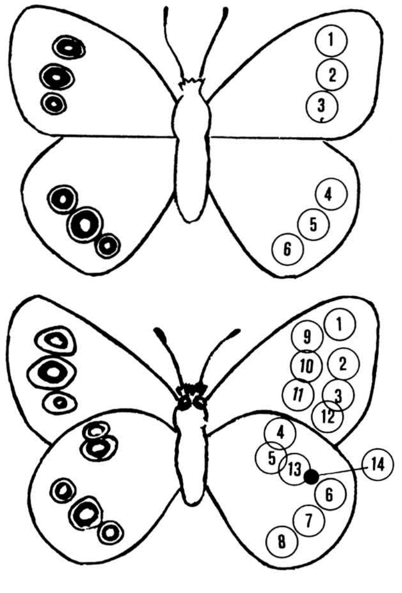


Fig. 11. The sites of eye-spots in *Aphantopus hyperantus*.

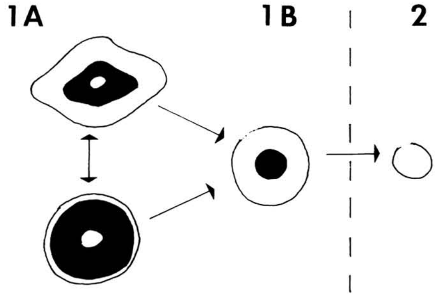


Fig. 12. The two main classes of eye-spots in the Ringlet, 1A) or 1B) all the rings persist and 2) the dots.

2.9. Species for comparison

Erebia ligea

The geographical range of this butterfly stretches across Eurasia from the Atlantic coast eastwards to the Pacific coast. The species is absent from the Iberian Peninsula, the islands of the Mediterranean, the southern Balkans, northern Germany and the southeast of Europe (Higgins & Riley 1970).

Erebia ligea, the Arran Brown, is one of the commonest butterflies in Scandinavia. In Norway, Sweden and Finland its geographical range extends into Lapland (Valle 1935, Nordström 1958, Higgins & Riley 1970). In Finland the range of *Erebia* is connected with the sphere of influence of the Arctic Ocean. In the Åland Islands the Arran Brown is very rare.

Studies on the flight periodicity of *Erebia ligea* began in Finland towards the end of the 19th century. At the beginning of the 20th century studies on the butterfly were undertaken in many regions in Finland, in particular in the Karelian Isthmus (Muolaa) and the northwest and north shores of Lake Ladoga (Sortavala) and Ostrobothnia (Seinäjoki, Vaasa). The results of these and many studies on *Erebia* were summarized by Suomalainen (1937), who published a study on the occurrence of the species during 11 years in the Porvoo district (See also Douwes 1980).

In these studies Suomalainen noted that the numbers of *Erebia* fluctuated with a periodicity of 2 years. In even years the butterfly was absent or very rare, but in odd years it was common. These differences between odd and even years have not been seen in all districts. In some districts the differences have been very clear.

Federley (1938) showed that the chromosome number of *Erebia* is $n = 29$. This is the same number as he found in the Ringlet.

Collecting. In 1970—74 *Erebia ligea* was sampled with a sweep-net in the habitats of the *Aphantopus* populations M1, M2, M6, M7 and M10 in the Mikkeli district and in P3 in the Porvoo district (Table 4).

By collecting the Arran Brown and the Ringlet from the same areas it was possible to make comparisons between related satyrid species with regard to ecological variation and trends in the populations.

Records were made of the sex and arrangement of eye-spots on the under- and uppersides of the fore and hind

Table 4. The numbers of *Erebia ligea* in 1970—74 in the Mikkeli (M) and Porvoo (P) districts.

	Males (M)							Females (F)							Tot. M+F
	M1	M2	M6	M7	M10	P3	Tot.	M1	M2	M6	M7	M10	P3	Tot.	
1970	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
1971	79	50	89	78	59	11	366	14	16	13	16	25	—	84	450
1972	—	—	2	3	4	—	9	—	—	1	—	—	—	1	10
1973	84	70	89	74	67	—	384	18	49	27	32	51	—	177	561
1974	—	—	—	1	2	—	3	—	—	—	—	1	—	1	4
Tot.	163	120	180	156	132	11	762	32	65	41	48	77	—	263	1025

wings of each butterfly captured. The spots were numbered as shown in Fig. 13.

To be able to follow changes in spotting on the wings, the Arran Brown was card-indexed in the same way as the Ringlet (see p. 5).

Development. The egg of *Erebia* is ovoid, with longitudinal ridges. It is light yellow, the grooves being brownish. In the study years egg-laying females were observed in early August.

The larva is short and stout. Its food-plants consist of grasses such as *Deschampsia* spp. and *Milium effusum* (Higgins & Riley 1970, Seppänen 1970). The larva overwinters for 2 successive years (Seppänen 1969). According to E. Peltonen (personal communication), this species passes the first winter as tiny larvae within the eggs and the second as large larvae. The pupa rests on the ground. In the study meadows the first adults emerge during the first quarter of July.

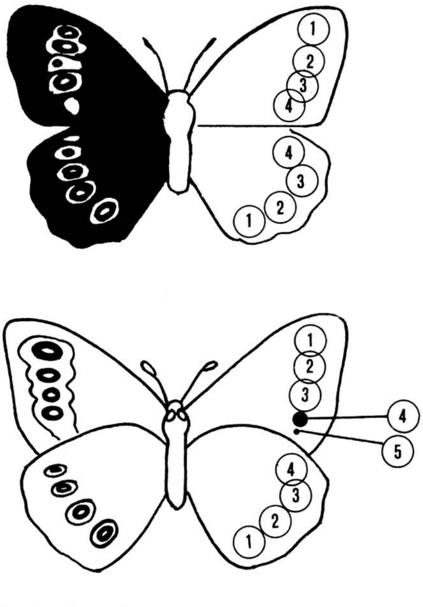


Fig. 13. The sites of eye-spots in *Erebia ligea.*

Flight. The Arran Brown flies in July and August. The butterfly usually appears during the first week of July. In 1971 the first males were seen on 8 July and most of the butterflies were flying between 21 and 26 July. In 1971 the flight period of the Ringlets was almost over when the Arran Brown appeared. In 1973 *Erebia* males started their flight period on 4 July and most individuals were collected between 11 and 20 July 1973.

The butterfly flies along the edges of forests and above wooded pastures, forest glades and rough hill slopes. Its favourite haunts are stands of spruce, but it is also found flying in more open woodlands dominated by pine or birch. In M2 and M7 the species was seen on hill slopes with sparse stands of pine. *Erebia* takes off suddenly, flying along a zigzag course, and so it is difficult to catch with a sweep-net. It is quite a powerful flier. In 1973 it was found in the streets of the town Mikkeli far from any meadows.

The Arran Brown is "an arrant sun-worshipper". The butterfly stopped flying if even a small cloud momentarily eclipsed the sun, but as soon as the sun came out again it was on the wing. In dull weather the butterflies seek shelter in the grass. The eye-spots afford it camouflage against its environment, so that its enemies have difficulty in finding it. In this respect the behaviour of the Arran Brown and the Ringlet is very similar.

Coenonympha glycerion

Coenonympha glycerion (Fig. 14) is a tiny butterfly of meadows. The species inhabits much of Central Europe but is absent from the northwestern part of the Continent. Thus Norway, Sweden and Denmark lie mainly outside its area. Eastwards the area of distribution of the butterfly extens as far as the Pacific coast (Langer 1958).

The Chestnut Heath, *Coenonympha glycerion* (Borkhausen) (= *iphis* (Denis & Schiffermüller)), another member of the Satyridae, has spread into Finland from the east. The butterfly was mentioned in the catalogue of Finnish butterflies by Sahlberg 1819 (see Kaisila 1959).

During the last century the species lived in the regions around Lake Ladoga. Towards the end of the century it spread slowly over most of the mainland of Finland. The geographical range of *Coenonympha* nowadays extends to the western part of Ostrobothnia in western Finland (Kaisila 1962). Possibly the butterfly will occupy larger areas in Sweden and Norway before long. Nowadays it is common in southern and central Finland up to 64°N

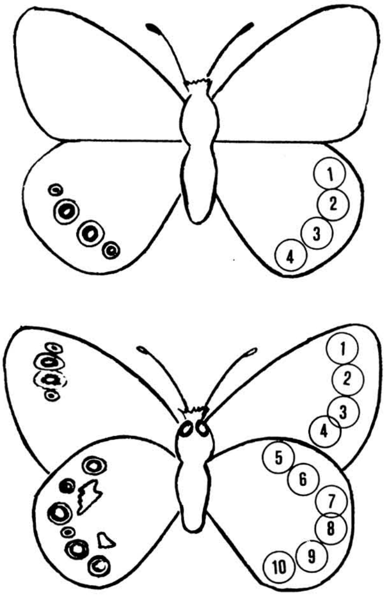


Fig. 14. The sites of eye-spots in *Coenonympha glycerion.*

(Langer 1958, Higgins & Riley 1970). One of its northernmost localities is in Kittilä (67°45′ N).

The related species *Coenonympha tullia* Muller shows "a wide, chiefly clinal geographical variation, expressed in the number of eye-spots on the wings" (Turner 1963). Thus *Coenonympha glycerion* might possibly be used for studies of clinal and other geographical variation. Earlier the populations of *Coenonympha glycerion* have not been studied in Finland.

However, observations on wing spotting and other features have been collected from museum samples. Thus we have information about the spots (Valle 1935) and also about the larval and the adult food-plants (Seppänen 1969, 1970). Moreover, we know the chromosome number, n = 29 (Federley 1938).

Collecting. *Coenonympha glycerion* was collected in the Mikkeli district in 1971—73. At the beginning the butterflies were sampled with a sweep-net at every site where studies were being made on populations of the Ringlet. Most of the samples were very small, and only those populations which were investigated during all 3 years (M5, M9 and M11; Table 5) are treated here. M11 was also inhabited by *Aphantopus* but only in very small numbers.

The sex, date of capture, locality and eye-spot pattern of each butterfly captured were recorded on butterfly cards.

Development. The eggs of *Coenonympha glycerion* and spherical and their colour is light reddish yellow. Larvae of *Coenonympha glycerion* have been found in Finland only on *Deschampsia caespitosa*; however rearing *ex ovo* has been successful on other grasses, e.g. *Dactylis glomerata* (Seppänen 1970). It seems probably that the species overwinters as a larva in the same way as *C. tullia* and *C. pamphilus* (Goodden 1978). The development of the butterfly is univoltine, according to Seppänen (1969, 1970). The green pupa rests on the ground (Valle 1935). During the study years egg-laying females were observed in the Mikkeli district from the end of June to mid-July.

Flight. The Chestnut Heath flies in June—July. In the study areas flight began about mid-June. Males emerged slightly earlier than females. Most of the butterflies appeared on the wing between 26 June and 6 July. Like the other species studied, the butterfly appeared earlier in 1973 than in the other years.

The Chestnut Heath, like the Ringlet, flies just above the grass, and the mode of flight is much the same, though somewhat heavier. When the Chestnut Heath senses danger it first makes rapid twists and turns in its flight, and soon dives into the grasses.

The preferred habitat of *Coenonympha glycerion* is damp meadows on shores and openings in woods. The samples from the Mikkeli district originated from relatively dry hill slopes, which may account for their small size.

3. Results on Aphantopus

3.1. Size and ground colour of the wings

The length of the fore wings in the adult varied from 19 to 25 mm, and the wing spread from 36 to 43 mm. Females were somewhat larger than males. The upperside of the wings was blackish or dark brown. The males were darker than the females. The underside in the males was greyish yellow and a little darker than in the females, whose wings were sometimes even pure yellow. The colour tones varied individually. The Finnish

Table 5. The numbers of *Coenonympha glycerion* in 1971—73 in the Mikkeli district.

	Males (M)						Females (F)						
	M3	M5	M8	M9	M11	Tot.	M3	M5	M8	M9	M11	Tot.	Tot. M+F
1971	6	66	21	77	26	196	3	15	8	12	23	50	246
1972	7	105	3	27	54	196	—	43	2	12	25	80	276
1973	—	49	—	29	17	95	—	9	—	8	16	33	128
Tot.	13	220	24	133	97	487	3	67	10	32	64	176	663

specimens seem to resemble specimens from the northern part of the English cline (see p. 1).

3.2. Eye-spots

The eye-spots were grouped on the wings in such a way that on the upperside of the fore (UF) and hind wings (UH) there were six (3 + 3) sites, and on the underside of the fore (LF) and hind wings (LH) fourteen (7 + 7) sites in which eye-spots were either present or absent. The specimens from the Mikkeli district were scored for spot placing, and the frequencies of occupancy of the different sites recorded (Table 6).

In the females the sites of the eye-spots tended to be occupied more frequently than in the males. Sites 10 and 11 were exceptions.

Only at site 7 on the LH did the presence of an eye-spot in both sexes reach a probability approaching 100 %. The sole exception to this was one male from the Porvoo district. The sites on the upperside in which eye-spots were almost always present were site 5 (87.6 %) on the UH and site 1 (73.7 %) on the UF.

The large number of possible sites for eye-spots and their variable tendency to be occupied meant that many butterflies, despite different spot placing, had the same number of eye-spots. But owing to the large number of possible combinations with regard to the position and size of the spots, practically every individual was unique. The commonest types on the basis of occupancy of spot sites were as shown in Table 7 and the numbers of eye-spots as in Tables 8—9.

Table 6. The sites of the eye-spots in *Aphantopus hyperantus* and the observed frequencies with which they were occupied.

	Upperside						
	Fore wings			Hind wings			
	1	2	3	4	5	6	
Males	47.4 %	26.0 %	0.7 %	48.0 %	75.2 %	0.0 %	
Females	99.9 %	99.8 %	48.5 %	97.3 %	100 %	5.4 %	
	Underside						
	Fore wings						
	1	2	3	9	10	11	12
Males	99.4 %	50.4 %	35.8 %	0.1 %	0.1 %	0.1 %	0.0 %
Females	100 %	100 %	96.0 %	0.1 %	0.0 %	0.0 %	0.3 %
	Hind wings						
	4	5	6	7	8	13	14
Males	98.4 %	99.9 %	99.9 %	100 %	99.9 %	0.7 %	0.0 %
Females	100 %	100 %	100 %	100 %	100 %	2.4 %	0.1 %

Table 7. The most frequent spotting types among 3555 males and 1574 females of *Aphantopus hyperantus* as percentages in the Mikkeli (1961, 1968—75) and Porvoo (1971—73) districts. The types are described by the site numbers occupied (000000 = no spots, 120450 = spots sites 1, 2, 4 and 5) on the respective sides. With regard to the underside, rare types are omitted.

Upperside (6 sites)

Males		Females	
000000	23.23	123450	52.50
120450	18.90	120450	40.01
000050	15.06	123456	3.56
000450	14.21	120050	1.95
100450	10.65	123050	1.01
100050	6.46	120456	0.53
120050	4.07	020450	0.20
020450	2.45	120000	0.12
020050	1.02	100450	0.06
123450	0.82		
120000	0.68		
020000	0.20		
000400	0.20		
120400	0.06		
100400	0.06		
123050	0.06		
023450	0.03		

Underside (14 sites)

Males		Females	
12045678000000	53.31	12345678000000	94.01
12345678000000	38.00	12045678000000	4.79
10040678000000	6.65		
00045678000000	0.70		
02045678000000	0.23		

The number of spots on the UF varied in the males from none to three and in the females two to three. In most populations males with three spots were extremely rare. The highest frequency observed was in M5, about 1 %.

The variation in the number of eye-spots on the UH was none to two in the males one to three in the females. The occurrence of only one eye-spot in the females was rather unusual (2.5 %) and nearly always asymmetrical.

The variation on the LF was nought to five in the males and two to five in the females. The presence of more than three eye-spots was very uncommon in both sexes. Those few individuals which had four (3 males and 5 females) or five (1 male) eye-spots on the wing were asymmetrical, the other wing always having three spots.

On LH the most common spot number was five. In both sexes, however, a few individuals were found with up to six (24 males and 44 females) or seven (1 male and 1 female) eye-spots.

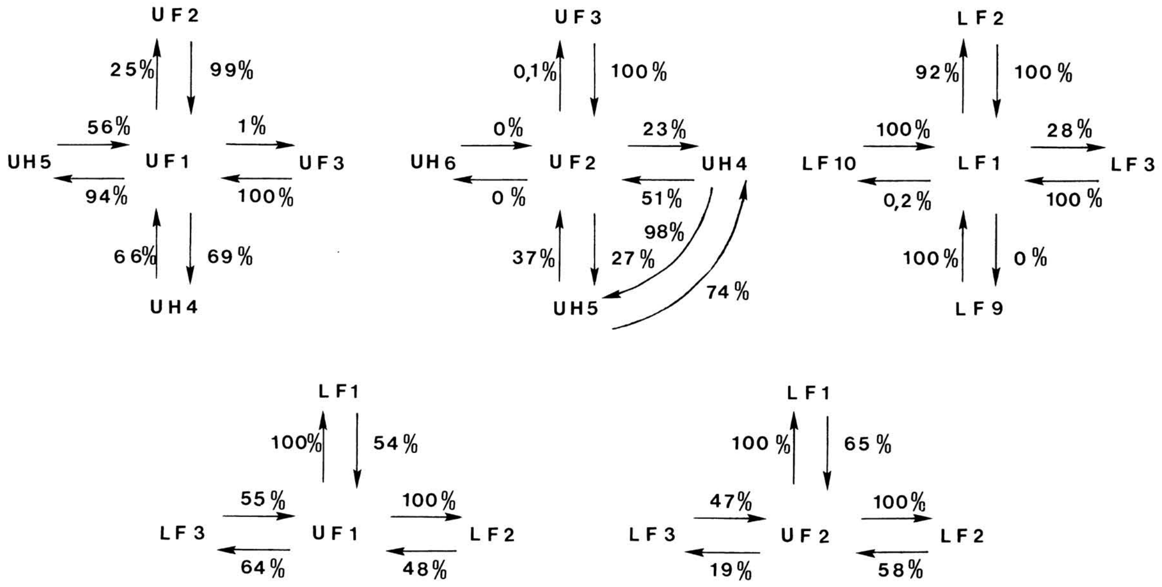


Fig. 15. The probability that the presence of a certain eye-spot would be linked with the presence of other eye-spots in males of *Aphantopus*.

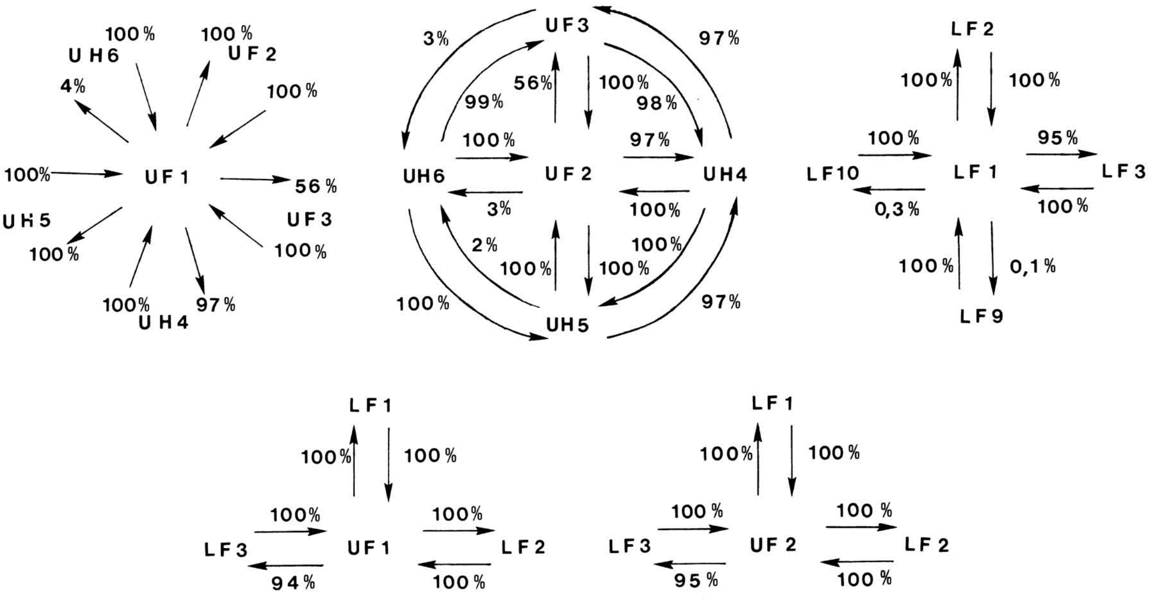


Fig. 16. The probability that the presence of a certain eye-spot would be linked with the presence of other eye-spots in females of *Aphantopus*.

	UF	UH	LF	LF	UF UH	UF UH	LF UF
1973	1 2	5 4	1 2	1 3	1 4	1 5	1 1
M 1	17%	71%	87%	41%	84%	97%	33%
M 2	14%	59%	87%	27%	87%	100%	24%
M 3	15%	56%	88%	26%	55%	97%	33%
M 5	21%	77%	95%	39%	78%	94%	34%
M 6	49%	99%	87%	7%	100%	98%	27%
M 7	19%	65%	94%	42%	55%	95%	39%
M 8	18%	53%	96%	53%	54%	89%	36%
M 9	8%	52%	86%	38%	67%	83%	26%
M10	27%	85%	97%	51%	95%	100%	42%
P 1	33%	63%	97%	47%	44%	88%	50%
P 3	29%	67%	98%	55%	81%	100%	38%

Fig. 17. The observed frequencies with which, in 1973, the presence of one eye-spot was linked with that of another eye-spot in the males of *Aphantopus*. UF 1 → LF 2 and UH 4 → UH 5 always 100 %.

These counts include butterflies caught in Porvoo in 1971—73. The reason for this was that small spots were often present at sites 13 and 14 (Fig. 11). These small eye-spots were either dots (2) or ringlets of types 1A and 1B.

The eye-spots were nearly always larger on the underside than on the upperside.

During the study no butterflies totally without dots or ringlets were found, and, in fact, such an individual has been described only by Newman (Ford 1945).

Eye-spots are expressed at the different possible sites in a definite order. The observed frequency of an eye-spot was greatest at site 1 on the anterior margins of both the UF and LF (order of appearance: sites 1 → 2 → 3) in both sexes (Figs. 15—16).

On the UH on the other hand, the frequency was greatest at the posterior margin (order of appearance: sites 5 → 4 in males; Fig. 15, and sites 5 → 4 → 6 in females; Fig. 16). The frequency with which the presence of one eye-spot was linked with the presence of an other eye-spot depended on the wing-area (Fig. 15), the site of the eye-spot (Fig. 15), the sex (Figs. 15, 16), the population (Fig. 17) and the year (Fig. 18).

	UF	UF	UH	LF	LF	UF UH	UF UH	LF UF
M5	1 2	1 3	5 4	1 2	1 3	1 4	1 5	1 1
1968	34%	1%	75%	98%	40%	76%	95%	62%
1969	19%	1%	75%	93%	34%	78%	94%	40%
1970	21%	0%	63%	96%	29%	65%	93%	38%
1971	31%	2%	63%	97%	46%	85%	93%	42%
1972	14%	0%	74%	88%	33%	7 %	89%	24%
1973	21%	2%	77%	95%	39%	79%	94%	34%
1974	36%	2%	67%	92%	32%	82%	95%	36%
1975	44%	0%	69%	92%	29%	93%	98%	49%

Fig. 18. The observed frequencies with which the presence of an eye-spot at one site was linked with the presence of another eye-spot in 1968—75 in population M5 in the males of *Aphantopus* in Mikkeli district. UF 1 → LF 1, UF 1 → LF 2 are always 100 %, UH 4 → UH 5 100 % except in 1970 97 %.

The presence of a given eye-spot was generally accompanied by the presence of spots at certain sites in the other wing areas. For example, the presence of UF 1 seems to be linked with the presence of LF 1 and LF 2 with about the probability of 100 %.

3.3. Patterns of spot numbers

The data obtained may be analysed in several ways, none of which is satisfactory by itself, but taken together they give a good picture of the variability of the populations. In the present study, the delineation of phenotypes (morphs) is based on the combinations of the numbers of eye-spots present in the four wing areas (Tables 8 and 9).

According to these combinations or spotting patterns the males could divided into 33 classes and the females into 12 classes. In this classification, however, the number of eye-spots on the LH was treated as constant, because otherwise the number of classes would have become very large and the number of individuals in each class would have been very small (one or two butterflies). Among the males captured none represented the classes 2—1—1—5, 2—2—1—5 or 2—0—1—5.

3.4. Differences between the sexes

The *Aphantopus* males and females differed constantly from each other in mean spot number (Tables 8—9). The differences were greater for the upper- than for the underside and greater for the fore than for the hind wings. The differences were very small indeed on the LH and as a rule not statistically significant (Fig. 19).

This figure shows the variation of spot distribution in the two sexes. One of the greatest differences between the sexes is in the number of spots on the UF (averaging 1.88 spots more in the females than in the males but, depending on years and populations, varying between 1.3 and 2.2).

Table 8. The phenotypes in the males of *Aphantopus hyperantus* in order of frequency. Spot numbers were counted on wing areas in the following order: UF—UH—LF—LH, given in the columns. The percentage frequency of each combination was calculated. The material for this table comprises all the individuals captured in the Mikkeli district and the 1971—73 individuals from the Porvoo district, totalling 3555 males and 1547 females. Because the underside of the hind wings varied very little, well over 90 % of the individuals having 5 spots, this number is used throughout to reduce the number of spot frequency classes included.

1.	0 — 0 — 2 — 5	14.14	18.	0 — 2 — 1 — 5	0.71
2.	2 — 2 — 3 — 5	12.54	19.	1 — 0 — 3 — 5	0.68
3.	0 — 1 — 2 — 5	9.38	20.	3 — 2 — 3 — 5	0.53
4.	0 — 2 — 2 — 5	7.93	21.	2 — 0 — 2 — 5	0.35
5.	1 — 2 — 2 — 5	7.27	22.	2 — 0 — 3 — 5	0.29
6.	2 — 2 — 2 — 5	7.07	23.	1 — 1 — 1 — 5	0.26
7.	0 — 0 — 3 — 5	4.95	24.	1 — 0 — 1 — 5	0.20
8.	1 — 2 — 3 — 5	4.95	25.	0 — 0 — 0 — 5	0.20
9.	0 — 1 — 3 — 5	4.83	26.	1 — 2 — 1 — 5	0.08
10.	0 — 0 — 1 — 5	4.22	27.	1 — 1 — 4 — 5	0.02
11.	0 — 2 — 3 — 5	3.91	28.	0 — 2 — 0 — 5	0.02
12.	1 — 1 — 2 — 5	3.88	29.	1 — 2 — 0 — 5	0.02
13.	1 — 1 — 3 — 5	3.37	30.	0 — 1 — 0 — 5	0.02
14.	2 — 1 — 3 — 5	1.82	31.	0 — 0 — 4 — 5	0.02
15.	1 — 0 — 2 — 5	1.43	32.	0 — 0 — 5 — 5	0.02
16.	0 — 1 — 1 — 5	1.31	33.	3 — 1 — 3 — 5	0.02
17.	2 — 1 — 2 — 5	1.10			

Table 9. The most common phenotypes in the females of *Aphantopus hyperantus*. See legend to table 8.

1.	3 — 2 — 3 — 5	50.63	7.	2 — 3 — 3 — 5	0.47
2.	2 — 2 — 3 — 5	37.42	8.	2 — 1 — 2 — 5	0.33
3.	2 — 2 — 2 — 5	4.78	9.	1 — 2 — 3 — 5	0.26
4.	3 — 3 — 3 — 5	3.42	10.	3 — 2 — 2 — 5	0.20
5.	2 — 1 — 3 — 5	1.67	11.	2 — 2 — 4 — 5	0.06
6.	3 — 1 — 3 — 5	0.84	12.	2 — 3 — 2 — 5	0.06

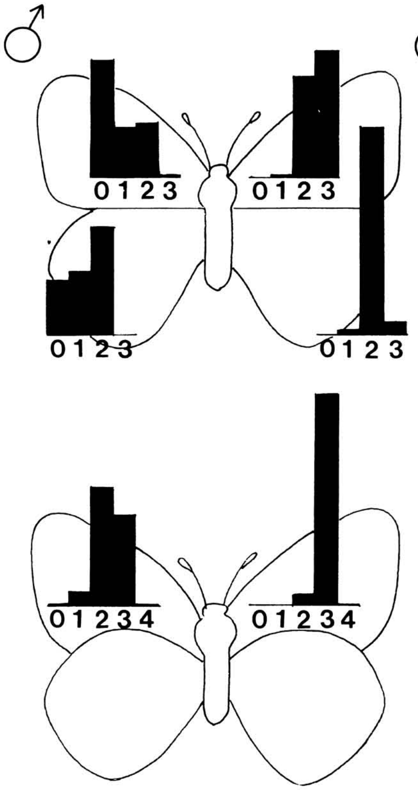


Fig. 19. Comparison of the total numbers of eye-spots in males and females of *Aphantopus hyperantus* in the Mikkeli district.

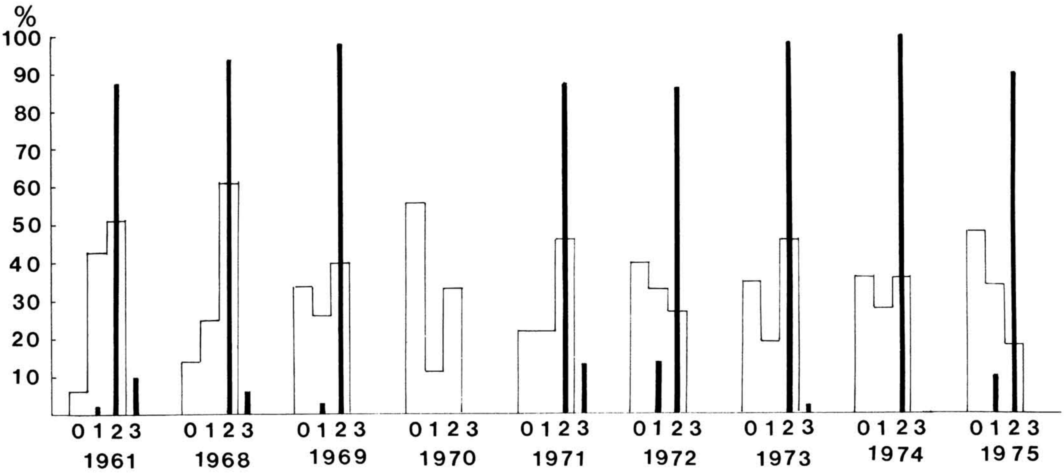


Fig. 20. The variation in the number of eye-spots on the UH in males and females of *Aphantopus* in M1 in 1961—75. The white histograms show the number of males as percentages and the black histograms show the number of females as percentages.

A comparison of Tables 3 and 4 shows the great differences in the number of spots between the sexes. For instance, the frequency of 2—2—3—5 is 12.5 % in the males but 37.4 % in the females. The frequency of 3—2—3—5 is zero in the males but 50.6 % in the other sex. None of the morphs with no spots on UF are found in the females, although some of them are frequent in the males (e.g. 0—0—2—5 and 0—1—2—5).

The sexes show similar trends from generation to generation. If, for example, the mean spot number in a given year is high for one sex, the same is generally true for the other sex (Fig. 20).

3.5. Variation in spotting on the upperside of the fore wing among the early- and later-flying males

In *Aphantopus* the possibility that phenotype frequency is correlated with date of emergence was investigated in 1968 and 1969. The number of males with 0, 1 or 2 spots on the UF were compared in the χ^2 test (Table 10), which did not reveal any differences between the early- and late-flying fractions of the population.

Table 10. The number of males of *Aphantopus hyperantus* with 0, 1 or 2 spots in 1968 and 1969 in relation to their time of emergence.

		0	1	2		
1968	2— 6.VII	38	35	25	$df = 2$	
	17—21.VII	29	18	22	$\chi^2 = 1.88$	$P > 0.30$
1969	2— 6.VII	29	14	13	$df = 2$	
	17—21.VII	32	23	28	$\chi^2 = 2.68$	$P > 0.20$

3.6. Changes in the frequencies of spotting patterns

Populations in the Mikkeli district

Upperside of fore wings (UF) in males. In the samples the number of males with no spots on the UF increased significantly from 1968 to 1972 ($\chi^2 = 191.33$, $df = 1$, $P < 0.001$) and decreased somewhat thereafter (Fig. 21). In 1972 such males were in the majority in every population but one. In populations M1, M2 and M6 they formed over 78 % and in populations M3, M5, M9 and M10 from 60 to 78 %. In population M8 the frequency of males with no UF spots was only 51 % in this year and in M7 only 46 %.

During the same period, 1968—72, the frequency of males with one and two UF spots decreased.

A trend towards higher frequencies of males with one or two spots was observed in 1972—73 in populations M1, M6 and M10. At the same time, the populations M7, M8 and M9 the trend towards an increase in the frequency of males without spots on UF continued.

The change in UF spotting pattern frequencies in the males was statistically highly significant

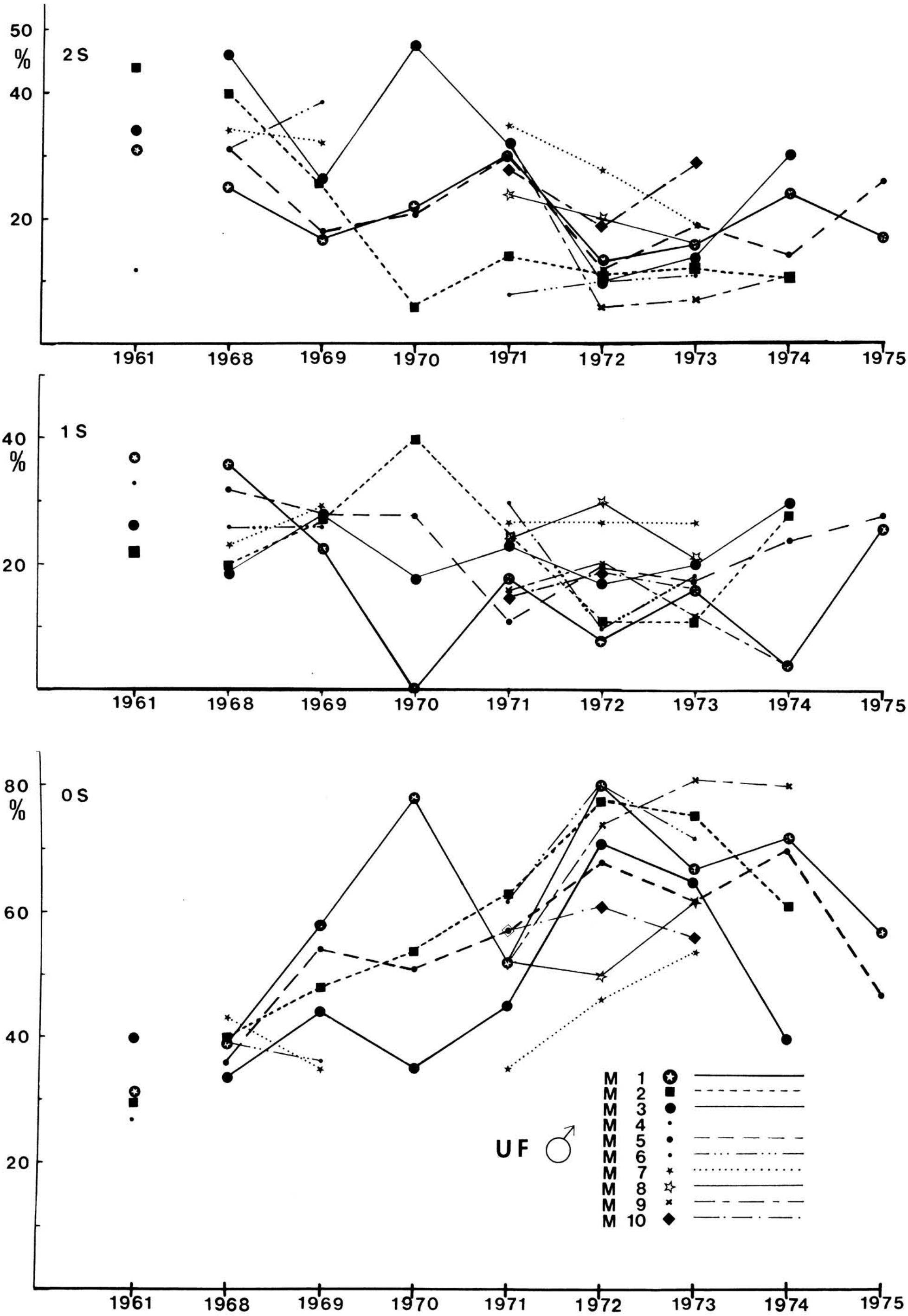


Fig. 21. The proportions of males of *Aphantopus* with no (0S), one (1S) or two (2S) eye-spots on the upperside of the fore wings (UF) in 1961 and 1968—75 in the populations of the Mikkeli district.

from 1961 to 1974, especially in populations M2 ($\chi^2 = 54.25$, $df = 21$, $P < 0.001$). In some populations, on the other hand, the change was statistically significant at the level $P < 0.01$, e.g. M1 ($\chi^2 = 45.87$, $df = 24$), M5 ($\chi^2 = 39.72$, $df = 21$), or at the level $P < 0.05$, e.g. M7 ($\chi^2 = 18{,}92$, $df = 12$).

Interesting changes in the frequency of UF spotting patterns in the males were found for example, in populations M3. In the males spotting was bimodal in 1968, with a large mode at two and a smaller one at no spots, and unimodal with a large mode at no spots in 1969 ($\chi^2 = 16.6$, $df = 1$, $P < 0.001$). This spotting changed again in 1970 into a bimodal frequency two — none. The frequencies of the UF spotting phenotypes were almost the same as in 1968.

Males with no UF spots formed 34 % in 1968 and 35 % in 1970, males with one UF spot formed 19 % in 1968 and 18 % in 1970, and males with two UF spots 46 % and 47 % in 1970. In 1971 the UF spot frequency was still bimodal, but now it was of type none — two (with a large mode at no spots and a smaller one at two spots). From 1972 the population was unimodal. Males with no UF spots were in the majority. The change from 1968 over the interesting years to 1974 was statistically highly significant (M3: $\chi^2 = 43.59$, $df = 21$, $P < 0.001$).

In the populations investigated the spotting on the UF was almost always symmetrical and in most populations unimodal (with a mode at none).

Upperside of hind wings (UH) in males. On the upperside of the hind wings (UH), as on that of the fore wings, lack of spots slowly increased in frequency among the males in the samples of the Mikkeli district. Males with no UH spots reached a maximum in 1972 (Fig. 22). The tendency towards a higher proportion of such males took place at the expense of males with two spots. This was because in the first study year, 1968, the commonest type of spotting on the upperside of the hind wings was two UH spots. Populations M1 and M9 formed exceptions to this rule. In population M9, over 50 % of the males were always without UH spots except in 1971, when the males with no spots amounted to only 24 % (the males with two spots were then 44 %).

The variation in population M1 is shown in Fig. 20. All this variation in population M1 resulted in statistically highly significant changes between 1961—74 ($\chi^2 = 77.60$, $df = 14$, $P < 0.001$).

Significant changes of this type also occurred in other populations, e.g. M3 ($\chi^2 = 47.15$, $df = 14$, $P < 0.001$), M5 ($\chi^2 = 42.08$, $df = 14$, $P < 0.001$) and M10 ($\chi^2 = 11.53$, $df = 4$, $P < 0.05$) during the study period.

In other populations, however, for example M7 the changes were not statistically significant ($\chi^2 = 8.85$, $df = 14$, $P > 0.30$).

In population M6 significant changes occurred not only in the number of UH spots (M6: $\chi^2 = 22.85$, $df = 8$, $P < 0.01$) between 1968 and 1973 but also in the size of the eye-spots between 1968 and 1969 ($f = 202$, $t = 3.21^{**}$). This population had a considerable number of dots. The number of rings and dots varied, and statistically significant differences were observed for both ring number ($f = 202$, $t = 5.17^{**}$) and dot number ($f = 202$, $t = 2.18^{**}$).

Underside of fore wings (LF) in males. The commonest number of LF spots was two (Fig. 23). This number of spots was retained very stably in population M5 during the years of the study ($\chi^2 = 2.95$, $df = 7$, $P > 0.90$). In all the other populations, the number of eye-spots varied between two and three. Two LF spots was generally the most frequent phenotype, but three was in the majority in population M2 in 1961 and 1974, in M6 in 1969, in M7 and M9 in 1971, and in M3 in 1968 and 1974. In populations M8 and M9, on the other hand, males with three LF spots were in the majority without interruption. In most populations the frequency of males with one LF spot was constantly below 20 %.

As in the case of the upperside the changes from year to year were particularly striking in populations M1 and M2. In M1 the frequency of males with one LF spot increased from 5 % of 1968 to 52 % of 1971 and in 1972 suddenly fell to zero. Because, in addition, there were changes in the frequencies of males with two and three LF spots, the between-years comparison was statistically highly significant ($\chi^2 = 125.80$, $df = 24$, $P < 0.001$). In M2 the changes were similar ($\chi^2 = 49.78$, $df = 21$, $P < 0.001$). In M3, for example, changes in the frequencies of the different types of males were much less marked ($\chi^2 = 23.42$, $df = 21$, $P > 0.30$).

In populations M5 and M7 one male was found in which there were four LF spots; the spotting of the wings was asymmetrical, four-three. One male of this M1 population had no LF spots.

Underside of hind wing (LH) in males. There were as a rule five LH spots, occasionally four, there being no spot in site 4 (Fig. 11). Males with four spots were very rare and thus there were no statistically significant differences in the spotting on the underside of the hind wings. In nearly all the populations there were also males with two,

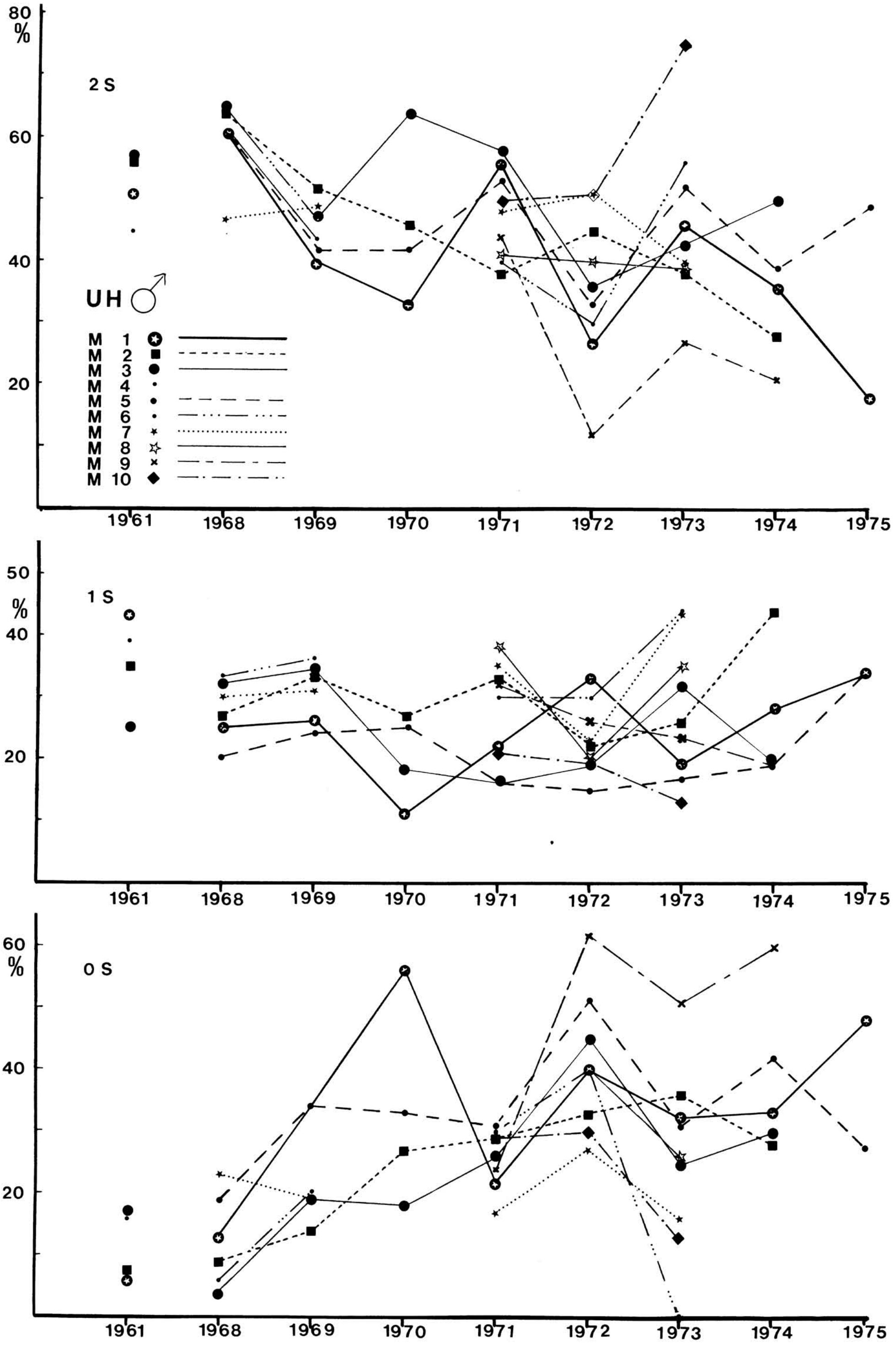


Fig. 22. The proportions of males of *Aphantopus* with no (0S), one (1S) or two (2S) eye-spots on the upperside of the hind wings (UH) in the populations of the Mikkeli district in 1961 and 1968—75.

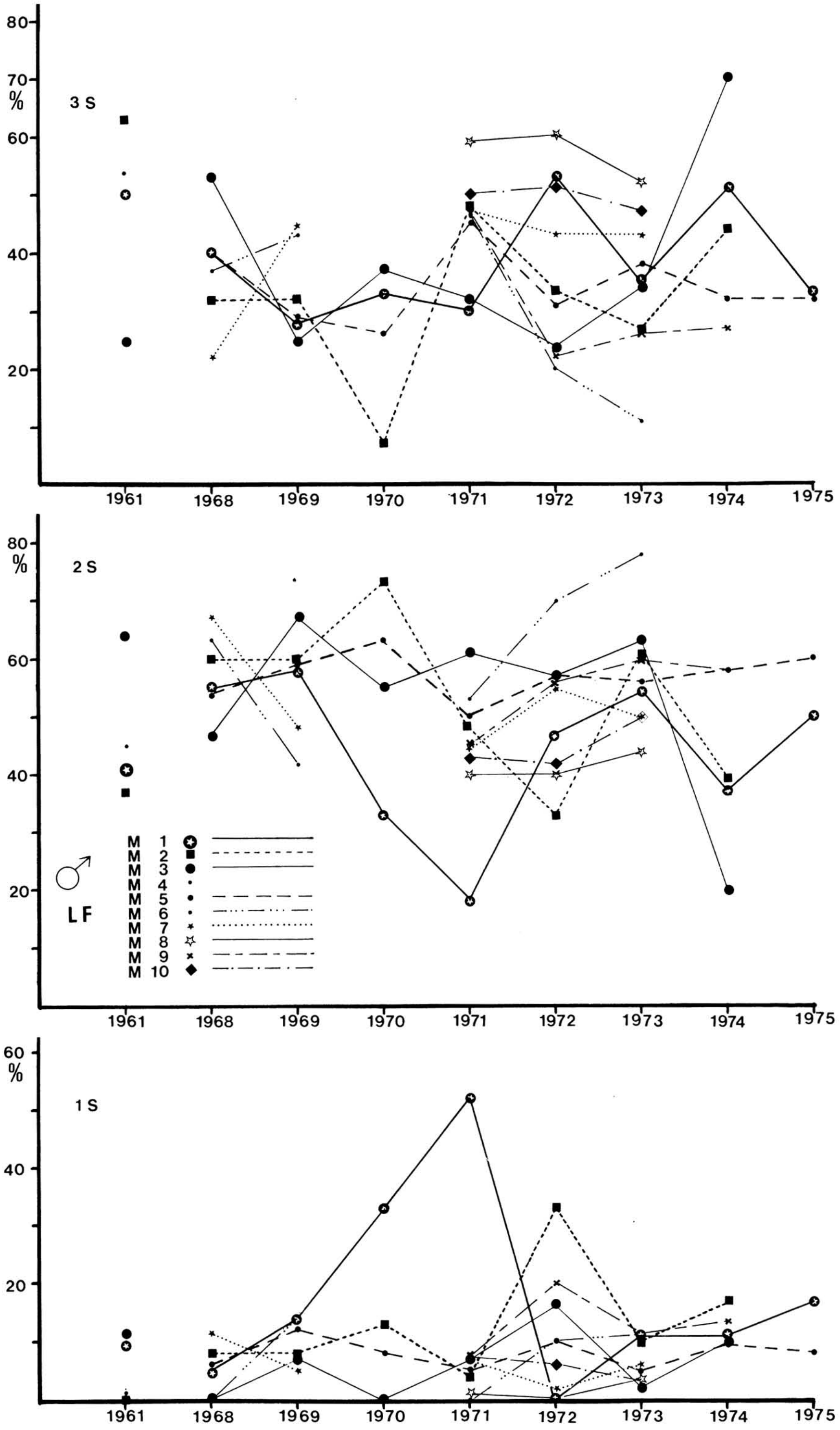


Fig. 23. The proportions of males of *Aphantopus* with one (1S), two (2S) or three (3S) eye-spots on the underside of the fore wings (LF) in the populations of the Mikkeli district in 1961 and 1968—75.

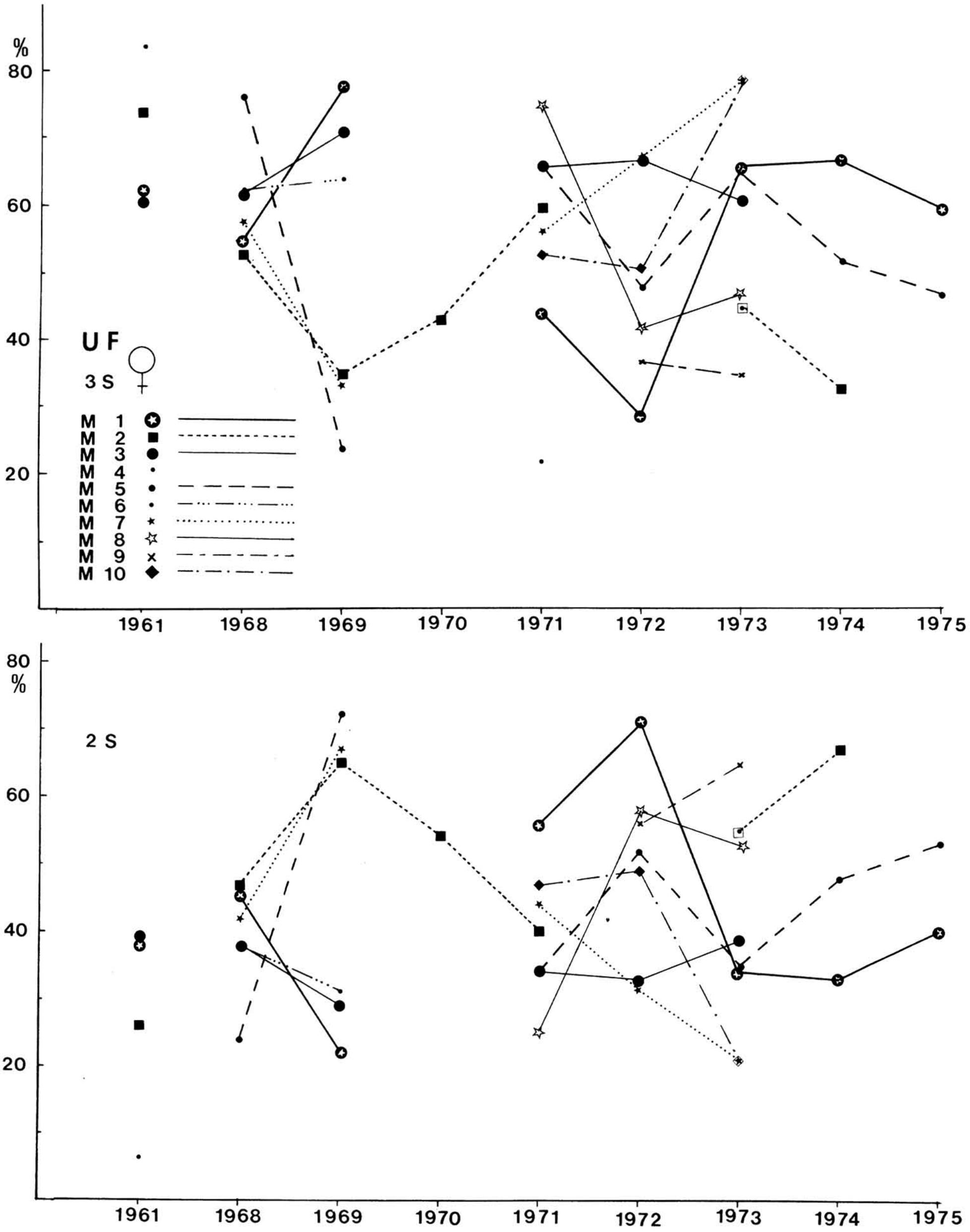


Fig. 24. The proportions of females of *Aphantopus* with two (2S) or three (3S) eye-spots on the upperside of the fore wings (UF) in the populations of the Mikkeli district in 1961 and 1968—75.

three, six and seven LH spots. But population M6 consisted exclusively of males with five LH spots.

Upperside of fore wing (UF) in females. Females had either two or three UF eye-spots (Fig. 24). The most stable population was M3, where the fluctuation in the frequency of the females with three UF spots was at most only 10 %. In the same way the frequencies in population M5 did not change significantly ($\chi^2 = 10.63$, $df = 12$, $P > 0.50$).

In 1972 the number of females with two spots increased and the number with three spots decreased in every population. It should be recalled that 1972 was the year when the number of males

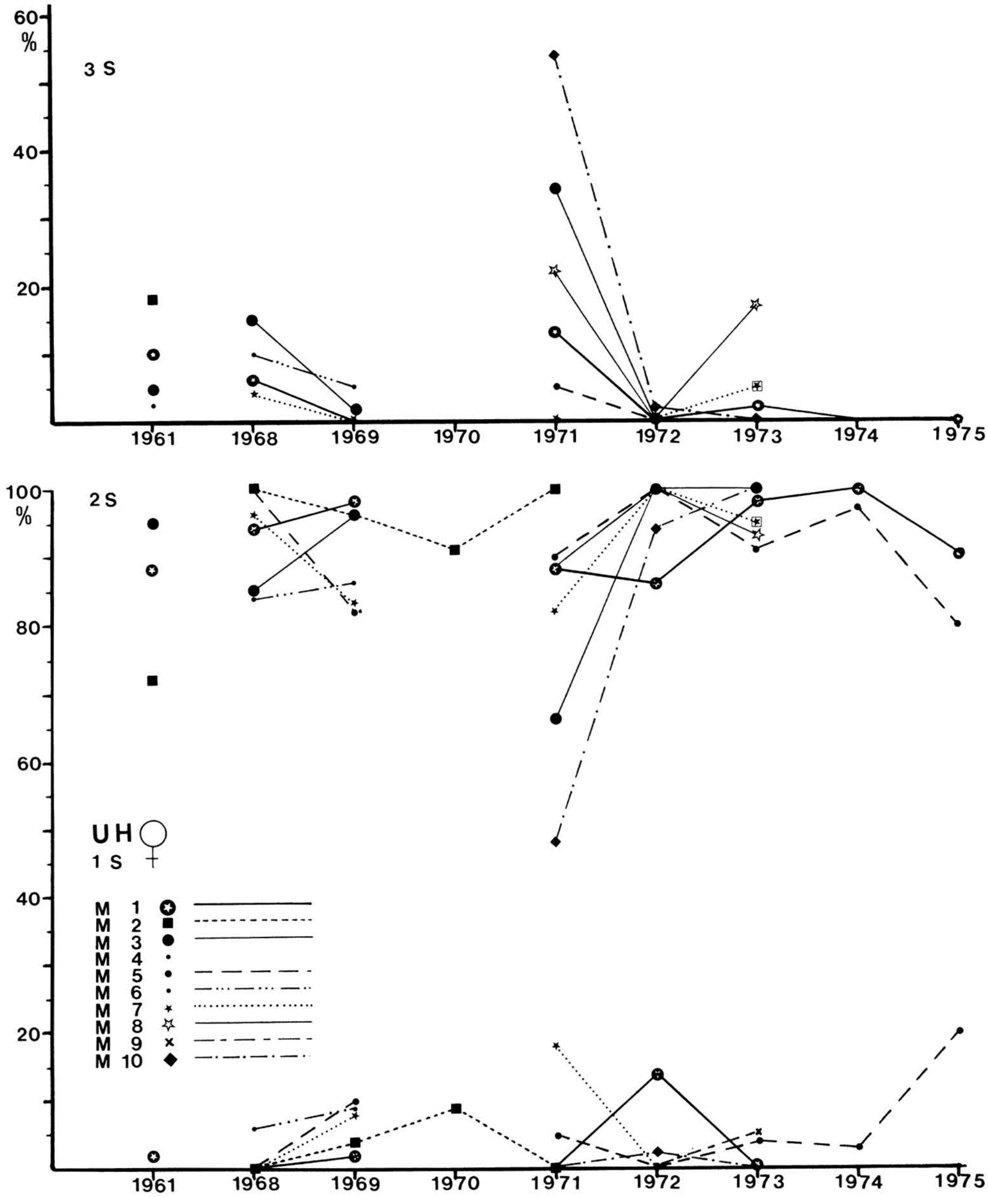


Fig. 25. The proportions of females of *Aphantopus* with one (1S), two (2S) or three (3S) eye-spots on the upperside of the hind wings (UH) in the populations of the Mikkeli district in 1961 and 1968—75.

with no UF spots increased considerably in every population studied. This and the fluctuation in the number of females with two or three UF spots led to chi-square values that were significant as, for example, in populations M1 ($\chi^2 = 19.02$, $df = 6$, $P < 0.001$) and M2 ($\chi^2 = 15.31$, $df = 4$, $P < 0.001$) during the study years. Again the changes were most clearly statistically significant in those populations in which man's influence was strongest.

Upperside of hind wings (UH) in females. From year to year females with two UH spots were in the majority (Fig. 25), amounting to over 80 % in 1971 in populations M3 and M10, while the proportion of females of this kind was 66 % in M3 and 48 % in M10. In 1972 the reduction in the number

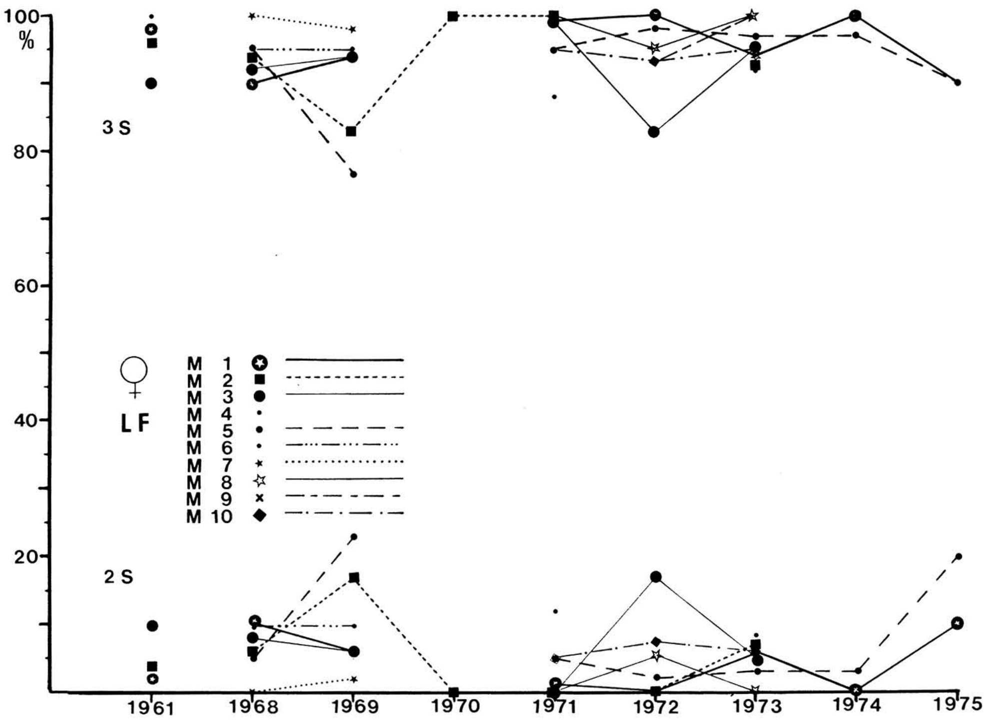


Fig. 26. The proportions of females of *Aphantopus* with two (2S) or three (3S) eye-spots on the underside of the fore wings (LF) in the populations of the Mikkeli district in 1961 and 1968—75.

of UH spots resembled the change on the UF. Females with three UH spots were either altogether lacking or their number had decreased strongly. The change in the frequencies of eye-spots during the study years was statistically highly significant in population M2 ($\chi^2 = 159.90$, $df = 12$, $P < 0.001$), significant in others, e.g. in M3 ($\chi^2 = 24.40$, $df = 10$, $P < 0.01$) and fairly significant in others, e.g. in M7 ($\chi^2 = 22.06$, $df = 12$, $P < 0.05$). In the same way there was a statistically highly significant change in population M10 ($\chi^2 = 29.5$, $df = 4$, $P < 0.001$). This was due to the depletion of females with three UH spots (from 58 % to 3 %). On the other hand, there was no statistically significant change in population M5 ($\chi^2 = 17.32$, $df = 12$, $P > 0.10$) during the study period.

The frequency of the females with one UH spot in the populations investigated never exceeded 20 %.

It might be noted that there were statistically significant changes in the females, but variability was less extreme than in the males.

Underside of fore (LF) and hind (LH) wings in females. Changes in LF spotting in the females were not statistically significant in some populations, e.g. M1 ($\chi^2 = 2.53$, $df = 6$, $P > 0.80$) and M2 ($\chi^2 = 7.29$, $df = 4$, $P > 0.10$), but highly significant in others, e.g. M5 ($\chi^2 = 29.93$, $df = 6$, $P < 0.001$).

The commonest LF spot number was three (Fig. 26). In all the populations females with two LF spots were found at frequencies of under 25 %. In populations M5 one asymmetrical female with four and five spots was recorded.

The number of LH eye-spots was usually five, but occasional individuals were found with six and seven LH spots.

Populations in the Porvoo district

Wing spot numbers in males in the four wing areas. In all years except 1961 the majority of males in the populations of the P district had no spots on the UF. The frequency of males with no UF spots was greatest in 1972. Males with one UF spot were relatively frequent in 1961. In most populations, however, the differences in the number of UF spots between the study years were negligible, e.g.

P1 ($\chi^2 = 26.92$, $df = 12$, $P < 0.01$) and P3 ($\chi^2 = 11.0$, $df = 6$, $P < 0.05$).

In 1971 and 1973 the modal type in the males had two UH spots and in 1972 no UH spot. This and the fluctuation in spot frequency in the 1960s caused highly significant differences in spotting pattern frequency in population P1 ($\chi^2 = 31.50$, $df = 8$, $P < 0.001$). In the other populations, in contrast, no significant changes occurred, e.g. in P3 ($\chi^2 = 5.74$, $df = 4$, $P > 0.20$).

Most of the males had two eye-spots on the LF. The number of spots in this wing had thus become stabilized and the same was true of the LH, in which there were nearly always five spots.

Wing spot numbers in females in the four wing areas. The spotting on the UF in the females was very labile in the P district. In populations P1 and P2 the numbers of females with two and three UF spots varied. In the odd-numbered years females with three UF spots were mostly in the majority. The difference between odd and even years was statistically significant (e.g. P1: $\chi^2 = 14.93$, $df = 5$, $P < 0.05$).

In the same population significant variability was also noted on the UH ($\chi^2 = 29.9$, $df = 12$, $P < 0.01$). In contrast, on the LH there was considerable stability.

Populations in the Tampere district

Every population was found to show internal variation. The sex differences were very marked, affecting spotting both in general and in the separate wing areas. The only exception was no sex differentiation was recorded on the LF.

In the populations of the T district (Table 1) there were numerous males with no LH spots or with only LH spots. In this district spot size was very small and the number of spots was usually low.

3.7. Synopsis of observations on the M and other districts

The populations varied considerably in size and density from year to year, the maxima being about seven time the minima in the M district.

Statistically significant differences between populations during the study period were observed in UF and UH spotting patterns in both sexes. As a rule they were strongest in the males.

From 1968 to 1972 the frequency of individuals with no spots on the UF and UH increased in the males. Simultaneously, the frequency of males with two spots on the UF and UH decreased. A trend in the same direction was also found with regard to the spotting pattern on the LF, the number of the males with three spots decreasing. Thus 1972 was exceptional as compared with the other study years. In 1973 there was again a trend towards spotting patterns with many eye-spots. After this the males with no UF spots increased in frequency in some populations and decreased in others.

In the females such population trends towards fewer spots between 1968—72 was not so clear as in the males. However, 1972 was also exceptional for the number of the eye-spots in the females.

In the males the distribution of the spotting patterns on the UF was unimodal being as a rule at no spots, and on the UH mostly unimodal at two spots, except in M1 and M5, which were nearly always bimodal, with peaks at two and none.

In the females the pattern was unimodal on the UF at two or three spots and on the UH at two spots.

On the LF the mode was at two spots in the males and at three spots in the females. On the LH there were five eye-spots as a rule in both sexes.

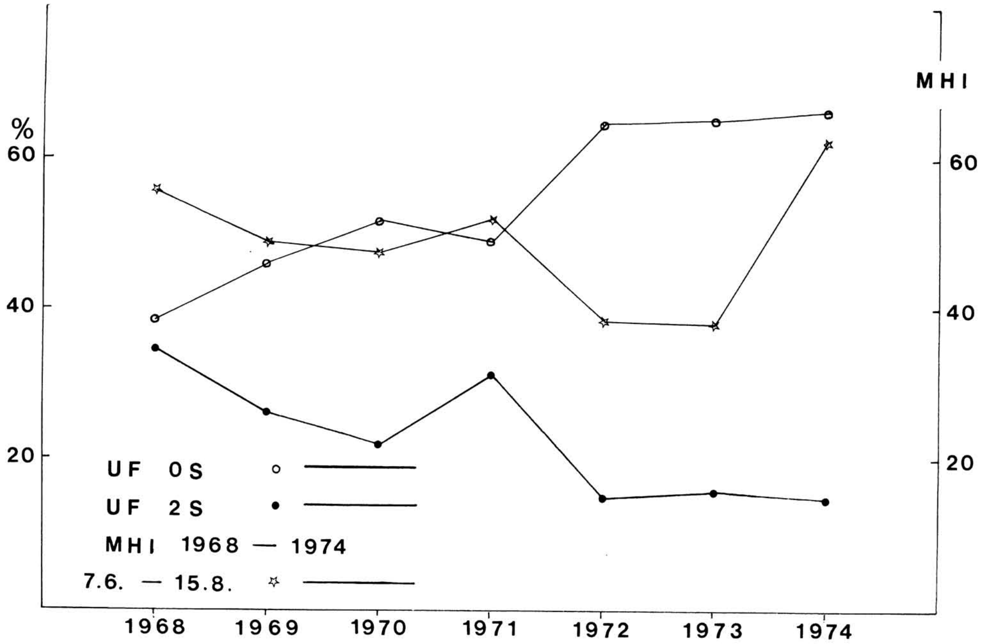
In these studies it was noticed that in some populations the eye-spots differed considerably in size from year to year.

The results for the populations in the Porvoo district were very similar to those for the Mikkeli district populations in the distribution of the spotting patterns on the different wing areas. The observations in the Tampere district emphasize that every population is somewhat different from the others with regard to spotting patterns.

3.8. Climate and eye-spots

On comparison of the temporal variation in spotting with the variability of climatic conditions in different years, certain correlations emerge. The coefficient of correlation (r) was calculated by plotting the percentages of different types of individuals against the modified humidity index (*MHI*) values. The significance of the correlation was tested using the t-test as described by Bonnier & Tedin (1962: 145—166).

The correlation between climate and number of eye-spots seemed strongest on the UF in the males with none ($t = 10.733$, $P < 0.001$) or with two ($t = 7.512$, $P < 0.001$) eye-spots (Fig. 27) from 1968 to 1973. The correlations between *MHI* and eye-spots on UH was weaker in the males with none ($t = 4.051$, $P < 0.01$) or two ($t = 3.803$, $P <$



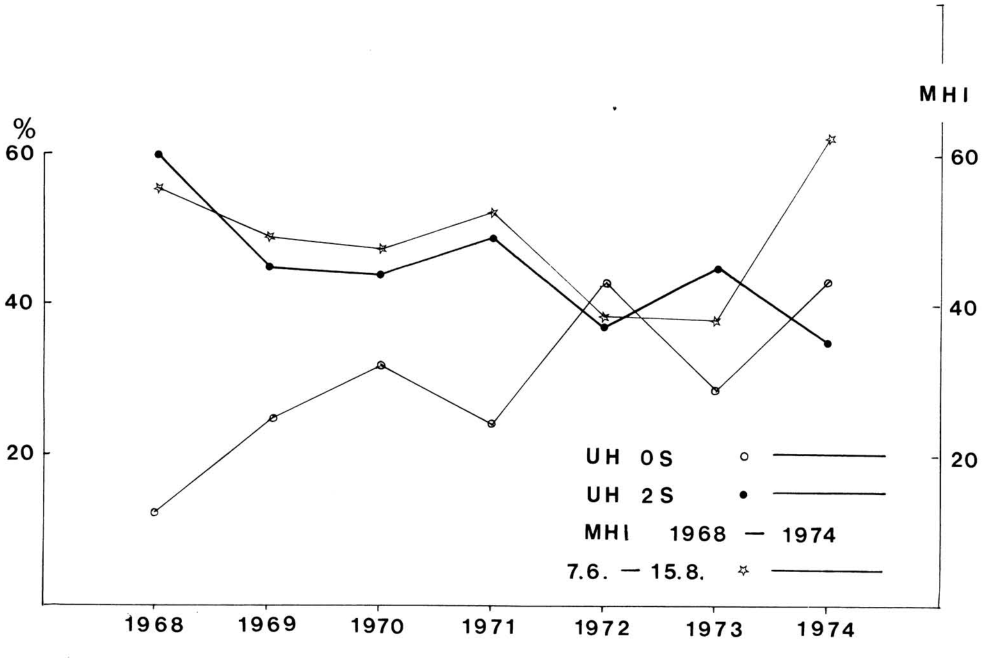


Fig. 27. The relation, in the Mikkeli district, between the modified humidity index (*MHI*) and the frequencies of the different spotting phenotypes on the upperside of the fore wings (UF) and hind wings (UH) in the males of *Aphantopus*.

0.01) spots. From 1968 to 1974 the correlation between *MHI* and none UF ($t = 1.499$, $P > 0.20$), *MHI* and two UF ($t = 1.466$, $P > 0.20$), *MHI* and none UH ($t = 1.587$, $P > 0.20$) and *MHI* and two UH ($t = 1.098$, $P > 0.30$) was not significant.

In addition to these specific comparisons correlation between climate and the average number of the eye-spots on the UF in the males was investigated in the Mikkeli district. The results show that at higher temperatures the number of eye-spots is smaller. It was so in all the study years except 1974.

4. Results on species used for comparison

4.1. Erebia ligea

Spotting

In the brownish red submarginal band of the wings there are eye-spots, usually four in number (Fig. 13; 91 % of samples). The third eye-spot, reckoned from the edge of the fore wings, is either absent or smaller than the others. Two exceptional males were found which did not have the lowest of the four eye-spots. Six of the males studied had five spots (0.8 %). This extra eye-spot always lacked the white central dot usually present in the other spots.

On the UH there were as a rule three to four eye-spots. These occasionally consisted of a white dot surrounded by a black circle, but mostly simply of a black dot.

On the LF the number of eye-spots varied in the males from two to four, and in the females from three to five. In both sexes the predominant number was three.

The number of eye-spots on the LH varied in the males from none to four and in the females from one to four. The numbers none, one and two were very seldom observed, the commonest number being three.

In *Erebia*, as in *Aphantopus*, the females tended to have more spots than the males. In both species the majority of butterflies in the samples were males (Tables 1 and 4).

The spots were numbered as shown in Fig. 9. To be able to follow the changes in the spotting on the wings, the frequencies of spotting types were expressed as percentages (Table 11).

In both *Aphantopus* and *Erebia* the frequency with which the eye-spot sites were occupied was greater near the top of the fore wings than in the more central areas.

In general, in *Erebia* the sites of the eye-spots were occupied with a higher frequency than in *Aphantopus*.

Table 11. The observed frequencies (%) with which the sites of eye-spots in *Erebia ligea* were occupied.

	Fore wings				
	Upperside				
	1	2	3	4	5
Males	100	100	78.3	99.7	0.7
Females	100	100	93.4	99.6	0.3
	Underside				
	1	2	3	4	5
Males	100	100	39.0	98.8	—
Females	100	100	50.0	100	0.6
	Hind wings				
	Upperside				
	1	2	3	4	5
Males	99.2	98.7	93.5	9.6	0.0
Females	100	100	95.7	13.6	—
	Underside				
	1	2	3	4	
Males	99.6	98.7	96.8	8.0	
Females	99.6	99.2	97.6	14.6	

Comparison in the populations investigated

The *Erebia* populations, although often inhabiting areas slightly different from those of the *Aphantopus* populations, are numbered by the same designations.

In 1971 and 1973 the Arran Brown was abundant in the Mikkeli district (Table 4). In 1970 not a single individual was found, and in 1972 the butterfly was sparsely represented in populations M6, M7 and M10; altogether ten individuals were captured. In 1974 one male was caught from M7, and from 10 two males and one female were taken.

Thus *Erebia ligea* was abundant in the odd years (98.5 %) and scarce in the even years (1.5 %) in both the Mikkeli and the Porvoo district (Table 4). For this reason comparisons of the frequencies of spotting types were made only between odd years.

It seems that, for the UF in the males, the relative numbers of spotting types changed very little. For example, in M1 ($\chi^2 = 4.93$, $df = 3$, $P > 0.10$) and M2 ($\chi^2 = 1.24$, $df = 2$, $P > 0.50$), no changes came anywhere near to being statistically significant. The situation was the same in the females (e.g. for M2: $\chi^2 = 1.77$, $df = 2$, $P > 0.30$).

In M1 a statistically highly significant change was recorded on the UH ($\chi^2 = 14.64$, $df = 2$, $P < 0.001$). In the other populations the change was not significant (e.g. for M2: $\chi^2 = 1.17$, $df = 2$, $P > 0.30$). The same was true with regard to the changes on the UH in the females (e.g. for M10: $\chi^2 = 0.53$, $df = 1$, $P > 0.30$).

Thus in *Erebia* as a rule no significant changes in spotting type occurred.

4.2. Coenonympha glycerion

Spotting

The hind wings of the males are dark brown on the upperside, and the fore wings coppery brown. The ground colour of the males is either orange or coppery yellow. The fore wings of the butterfly become darker towards the wingtips. There are no eye-spots on the UF (Fig. 14).

On the UH there may be up to four eye-spots. The spots were divided into two classes: those in which some or all the rings (black inner ring with an outer orange-brown ring) are either present or persist in a reduced state, and those in which the rings are totally lost and only yellow dots remain. Some of the eye-spots were very obscurely coloured.

The LH is brownish grey in the males and yellowish grey in the females. In both sexes this ground colour is darker in the proximal part than along the outer margin. There are two small white areas, the anterior one being somewhat larger (Fig. 14). Close to the outer margin of the wings is a lead-coloured streak on which there may be up to six eye-spots. Especially in the females the spots shine like silver.

On the LF the spots are quite small. They are surrounded by an outer ring of yellowish or brownish red. The inner ring is black. The spots, up to three in number, were numbered as shown in Fig. 14.

The frequency with which the eye-spot sites were occupied increased towards the anterior margin of the fore wing (Table 12). In the males as the table shows spots were present at site 1 in 36.0 % and at site 4 in 0.4 % of all the males studied. In the females the frequencies was 86.9 % at site 1 and 0.6 % at site 4.

On the UH eye-spots were present most frequently at site 4 and least frequently at site 1.

On the LH eye-spots were more frequently absent from site 6 than from the other sites. The frequency with which a spot was present at site 6 was 71 % in the males and 100 % in the females. In M9 one male was caught in which there were no spots. In *Aphantopus* I have not observed any such individuals.

Table 12. The observed frequencies (%) with which the sites of eye-spots in *Coenonympha glycerion* were occupied.

	Fore wings					
	Underside					
	1	2	3	4		
Males	36.0	11.9	4.1	0.4		
Females	86.9	44.0	26.2	0.6		
	Hind wings					
	Upperside					
	4	3	2	1		
Males	44.0	22.3	14.5	1.4		
Females	94.6	85.7	69.0	32.1		
	Underside					
	5	6	7	8	9	10
Males	92.8	71.0	96.1	99.8	99.6	96.9
Females	100	100	100	100	100	100

The frequency with which the site of an eye-spot was occupied clearly varied from population to population and from year to year.

Comparison in the populations investigated

The numbers of spotting types in the *Coenonympha* populations varied from year to year. The majority of males had no spots on the UH. Significant differences in the frequency of males were found between 1971 and 1973 in M9 ($\chi^2 = 20.91$, $df = 8$, $P < 0.01$) and sub-significant differences in M5 ($\chi^2 = 14.80$, $df = 8$, $P < 0.05$).

In the males spots were also often absent from the LF. The frequency of these individuals was maximal in 1972. In that year the proportion of such males was over 59 % in all populations, their frequency being highest in M9 (91 % in 1972). However, the differences between the study years were not statistically significant (e.g. in M9: $\chi^2 = 4.55$, $df = 6$, $P > 0.50$).

The inter-year differences in the frequency of males were likewise not significant with regard to the LH (e.g. in M9: $\chi^2 = 15.84$, $df = 10$, $P > 0.10$). It is true, however, that on this wing area the differences came closer to significance than on the LF.

In the females the number of eye-spots varied very little on either the UH or LH, and temporal variation was not statistically significant. The same was noted with regard to LF (e.g. M5: $\chi^2 = 2.49$, $df = 6$, $P > 0.80$).

In 1972 the females in all the populations had smaller average numbers of spots than in the other study years.

The results show that the frequencies of the spotting phenotypes of *Coenonympha* fluctuate from year to year, the temporal fluctuations being stronger in the males than in the females.

5. Discussion

5.1. The possible role of gene flow

It is difficult to estimate the significance of gene flow, but the fact that males have been seen flying above the level of the treetops makes gene flow between populations a definite possibility. Such hich flights have been observed only once or twice each summer; they were always made by butterflies disturbed by the use of the sweep-net.

Three of the populations studied, M1, M5 and M9, were situated near to each other (distance 1—2 km), but were partly isolated by islets of woodland. Movement between the meadows was never observed, although there are roadsides and other potential migration routes between the three meadows, especially between M1 and M5. Creed et al. (1959), working with *Maniola,* pointed out that, if the differences in the selection factors acting on two populations are sufficiently large, selection can maintain differences in spite of gene flow. Recent studies on clines (Endler 1977) have shown that very small differences in the environment can cause a difference in spotting pattern between populations of nearby areas.

5.2. Size of the populations

The *Aphantopus* populations P1 and M5 may be considered large in terms of the numbers of individuals daily in flight. Until 1970 M1 was another population comparable with these. At the other extreme are populations M3 and M7, inhabiting very small meadows and comprising perhaps one-third of the number of individuals found in M5 and P1.

When I started this study I tried to select tiny populations that were well isolated from their nearest neighbours. On the other hand, from our knowledge of the range of *Aphantopus* (Higgins & Riley 1970), the populations investigated can be regarded as peripheral. This might explain their low densities.

Similar observations have been made by Brakefield (1979) in his recent study of *Maniola* in peripheral populations of Scotland.

Every single meadow was visited at intervals of 2—3 days and the average percentage removal was roughly estimated at less than 20. It seems improbable that the collecting procedure caused any significant qualitative effects in the populations. Probably most of the males were taken after they had already inseminated the females. Many of the females had already laid most of their eggs at the time of capture and thus the next generation was not severely affected.

Sjösted (1936), when catching butterflies in South Ostrobothnia with a sweep-net, noted a considerable variation in the abundance of the *Aphantopus* populations from year to year.

In the Mikkeli populations, the numbers of individuals were maximal in 1968, 1969 and 1973 and minimal in 1970. In the Mikkeli and Porvoo districts the changes in numbers showed the same trends in the different populations. This may have been due to climatic and ecological factors that fluctuated similarly in the two areas from year to year.

This hypothesis gains some support from the parallel observations of the members of the Finnish Lepidopterological Society (FLS). In the pooled observations, the numbers, of species and individuals recorded each summer were related to the general climate. For example, in 1973 the summer in central Finland was exceptionally warm and dry, and butterflies were numerous. Similarly the summer of 1968 was very fine and the Rhopalocera were plentiful (FLS). In contrast, the cool, moist summer of 1970 was noted in the records as a "very poor summer with regard to butterflies".

The results of lepidopterological investigation performed in Mäntyharju, about 50 km SW of Mikkeli, by Mr. O. Peltonen, M.A., are extremely useful here as reference data. Peltonen made phenological observations on *Aphantopus* in 1968—80, and recorded numbers of all the Macrolepidoptera at light traps in 1968—75 (O. Peltonen, unpublished).

The flight periods of the Mäntyharju and Mikkeli populations of *Aphantopus* coincided closely in 1968—75. In three years, 1968, 1972 and 1973, the largest number of individuals daily in flight was observed on exactly the same day in both Mäntyharju and Mikkeli (10 July, 11 July and 6 July, respectively). Another similarity between the *Aphantopus* populations in Mäntyharju and Mikkeli is the timing of the fluctuations in population size, there being minima around 1969—71 and maxima in 1973 in both regions.

Macrolepidoptera were captured at light traps in Mäntyharju in 1968—75 by Peltonen in the following rounded numbers, adjusted with due regard to intensity of collecting:

1968	11200	1972	9100
1969	7100	1973	6300
1970	8000	1974	7600
1971	8800	1975	9400

The records show that the number of Macrolepidoptera individuals increased steadily in 1969—72, then decreased and increased again. The factors underlying the increase in 1969—72 remain obscure, but one of the causes may well be a change in the general climate.

Such a change did, in fact, take place in 1969—72, at least in regard to the summer months (p. 3, Tab. 1). The number of spots on the wings of *Aphantopus* was found to correlate with a climatic parameter, the modified humidity index (Fig. 27). Perhaps the abundance of Macrolepidoptera in Mäntyharju likewise correlated with the MHI, but of course the possibility cannot be ruled out that the correlations discussed are fortuitous.

In addition to the "natural" and "climatic" fluctuations with all their capriciousness, another factor to be considered is human influence. This led to a reduction in the size of the meadows M1, M3, M7 and M9, the planting of trees in M3 and M6, and the destruction of the woods alongside M5 and M7. All this affected the ecology of the vegetation and the density of the food-plants in the meadows. There were changes in the microclimatic conditions and possibly also the intensity of selection. These changes were reflected in the size of the populations. In 1970, at a time when the average climatic and human influence upon the study meadows was very strong, the numbers of butterflies suddenly decreased. It is possible that random genetic drift may have operated during the bottleneck phase.

Fluctuations, in density were greatest in the *Aphantopus* population in meadow M2. The herbicide, which was applied when *Aphantopus* was at the larval stage, effectively decimated the population. The poisoning was most intensive in 1969 and 1970. The poison caused the withering and death of many of the food-plants, and many *Aphantopus* larvae probably destroyed. However, not all the Ringlets were killed in population M2. The population escaped extinction because of the large size of the meadow, the sections farthest from the railway affording the larvae a sufficient habitat unaffected by the poisoning.

The populations of *Erebia ligea* varied in abundance in a different way from those of *Aphantopus.* In the odd years the *Erebia* populations were large in every locality, but in the even years the species was very infrequent in some communities (M6, M7 and M10) and totally absent from others (M1 and M2). One reason for this variation was the biennial development of the larvae. Another reason might be the same as Mikkola (1976) hypothetized for northern *Xestia* species: "The phenomenon can be explained more satisfactorily if it is regarded as an adaptive strategy, i.e. as a feature that benefits the populations. It is easy to understand what kind of advantage the populations gain from alternate-year flight: the parasites, predators and micro-organisms living on the larvae lack their prey or substrate in the flight year and are therefore at a low level in the next year, which is that of the larval population. A similar two-year cycle is presumably extremely difficult for a parasite or predator to attain, needing a very high degree of specialization."

In the abundant years 1971 and 1973, the size of the *Erebia* populations was roughly the same. Only in population M2 did the results show a clear difference between these years. The reason for this might have been poisoning by a herbicide, which destroyed the food-plants of the *Erebia* larvae in meadow M2 in 1971.

The *Erebia* populations were generally larger than the *Aphantopus* populations in all the meadows in the Mikkeli district. It is possible that *Erebia* was less affected by the poisoning than *Aphantopus,* because it tended to live in habitats relatively little treated by herbicides.

In contrast, the size of the *Coenonympha glycerion* populations fluctuated irregularly. The reason for this may have been the strong human influence affecting the *Coenonympha* meadows and, on the other hand, perhaps variations, in climate between different years.

5.3. Polygenism and polymorphism

As reported by Sheppard and Ford (Ford 1945, 1955), the eye-spots in the Ringlet are probably controlled on a multifactorial or polygenic basis.

However, it seems possible that the genetic basis of the polymorphism is more complex. The occurrence of an eye-spot at a given site is an all-or-none phenomenon, and some switch determinant may well be necessary for starting the train of gene activities that lead to the presence of a certain eye-spot. Although the genetic basis is unknown, the all-or-none principle makes it legitime to call spot number variability a polymorphism.

When natural selection changes, the polymorphism may enable *Aphantopus* to adapt to the new conditions by changing the frequencies of the genes determining eye-spot number. This change sometimes occurs very rapidly. Indeed, it is more effective for a species to adapt according to the demands, of natural selection by changing the frequencies of existing alleles than by altering the composition of the gene complex (e.g. Halkka 1970).

The probability that an eye-spot will be expressed varies for the different eye-spot sites. The eye-spots were found in certain combinations. The same has been noted in *Maniola* (McWhirter & Creed 1971).

Polymorphism has been defined by Ford (1940) "as an occurrence together in the same habitat of two or more distinct forms of a species in such proportions that the rarest of them cannot be maintained by recurrent mutation" (Ford 1945). Colour polymorphisms are usually due to variability in the frequency of alleles within the population.

The former is valid with regard to the morph frequencies in all the three species *Aphantopus hyperantus, Erebia ligea* and *Coenonympha glycerion.* The polymorphisms in *Aphantopus, Erebia* and *Coenonympha* are colour polymorphisms expressed as variability in the number of eye-spots (pigmented spots). This kind of polymorphism has been found previously in other butterflies, e.g. *Maniola jurtina* L. (Creed et al. 1962, 1964, 1970 and subsequently), *Polyommatus icarus* (Dowdeswell et al. 1940), *Utetheisa ornatrix* (Pease 1968) and *Pyronia* species (Frazer & Willcox 1975).

Earlier studies have shown that polymorphism confers a considerable advantage on a species, enabling it to adapt rapidly to its surroundings, and so to extend its range into new climatic areas and to maintain the range already occupied when faced with climatic changes.

Such species as *Aphantopus, Erebia* and *Coenonympha* have to keep their phenotypic variability as extensive as possible. Only thus can they defend their position among their competitors, as pointed out by Shapiro & Carde (1970). As a rule the degree of polymorphic variability expressed by the spotting patterns tends to remain unchanged, as shown by the evolutionary studies in *Maniola jurtina* L (Creed et al. 1959, 1970; Dowdeswell et al. 1967).

5.4. Selection

How does *Aphantopus* maintain a sufficiently versatile variability?

According to Dobzhansky (1970), temperature, light and food resources are among the factors that have notable effects upon the genetic composition of insect populations.

Studies on *Maniola jurtina* have shown beyond doubt that ecological factors can cause very rapid changes in butterfly populations (Dowdeswell et al. 1957, 1960; Dowdeswell 1961). The work on *Melitaea chalcedona* has shown that "... the greatest change in colour takes place where the climatic change is greatest..." (Le Gare & Hovanitz 1951).

Studies on *Maniola jurtina* (McWhirter 1969, Ford 1971) have also shown that "... heritability of spotting in the butterflies increases when the temperature rises" (Ford 1971). The reason might be that most of the genes express themselves only at high temperatures.

It seems worth while seriously to consider the possibility that ecological fluctuations are responsible for maintaining the variations in the number and size of the eye-spots on the different wing areas of *Aphantopus, Erebia* and *Coenonympha.*

In 1976 Ford reported that in *Maniola:* "The spot-number is under multifactorial control, and its heritability lies within the range of 49 to 77 % at 22°C. That is to say, taking the average value, 63 % of the variation in spot-frequency is genetic and 37 % environmental". Thus the number of eye-spots depends mainly on genes.

Climatic selection

Constant differences in all the frequencies often seem to exist between populations of insects or other invertebrates from different geographical areas. They "can be understood as responses to local variations in factors maintaining a particular polymorphic balance over a wide region" (Halkka et al. 1974). Cain & Currey (1963) named such differences "area effects". Many workers believe that "area effects" can often be traced to regional variability in climatic factors.

In *Aphantopus* the main factor regulating eye-spot variation appears to be climate. The frequencies of the spot numbers in this species seem to depend on changes in the MHI. The reaction was strongest in the UF and weaker in the UH of the *Aphantopus* males. In the UF the curves for the males with two spots and for the MHI ran parallel from 1968 to 1973 ($P < 0.001$) (Fig. 27). The frequencies of the males with no UF spot showing opposite trends ($P < 0.001$). The individuals with one or three spots were too rare for adequate investigations of temporal changes.

The diagrams did not follow these rules after 1973, the reason being the strong diminution in population size. After 1970 the stochastic changes caused by the decrease in population size may have been further intensified through the influence of man.

The year 1974 was also very different from the other study years with regard to annual temperature and precipitation.

The hypothesis that variation is correlated with MHI received some support from the parallel results of the studies on *Coenonympha*. In the *Coenonympha* population temporal variation in the eye-spots was strongest on the UH. In every *Coenonympha* population the number of eye-spots was smallest in 1972.

Bengtson in his study on *Maniola jurtina* in 1973—77 in southern Sweden, wrote: "Climate seems a likely candidate for the ultimate selective agent probably acting through other ecological factors" (Bengtson 1978). Now we must remember that both *Maniola* and *Aphantopus* are polymorphic for wing spotting. In the females Bengtson (1975, 1978) observed significant differences in spotting between 1973+1974 or 1976+1977, on the one hand, and 1975, on the other. In the hot, dry summer of 1975 he noted a significant decrease in the average spot number. Thus the general trend was the same as in the *Aphantopus* populations of the Mikkeli district: a rise in the mean temperature of the summer was associated with a decrease in the average number of spots.

Natural selection can be intensive with regard to many characters at the same time only if these are controlled by the same genes (Haldane 1957). We must suppose that in *Aphantopus* the genes which enable the species to adapt to the climate are either the same ones that regulate spotting or are linked with these within a supergene. Inside a supergene, crossing over is partially suppressed or totally absent (see e.g. Turner 1967, Ohte & Kimura 1970, Halkka et al. 1976).

Thus it seems likely that in *Aphantopus* selection did not exert its action specifically on the genes determining the eye-spots but on the whole gene pool and perhaps mainly through genes determining other characteristics. In *Aphantopus* the climate had its strongest effect upon the "marker" phenotype on the upperside of the fore wings and in *Coenonympha* on the upperside of the hind wings.

Although there were clear correlations between colour phenotype frequencies and microclimate, it is possible that, as in *Philaenus* (Halkka 1974), the different phenotypes have different microclimatic optima. This might explain the abrupt changes in spotting frequencies sometimes seen in successive generations.

In *Cepaea nemoralis* microclimatic conditions affect the polymorphism of the species and thus "Responses to microclimate may also depend on the genetic background of local populations..." (Jones et al. 1977).

In the present study we must remember that the microclimatic conditions varied greatly because man influenced these by planting or cutting tree stands, cutting down forests and applying herbicides.

It seems that in *Aphantopus* and possible also *Coenonympha* and *Erebia*, in contrast to *Maniola jurtina*, males are more variable than females and serve as a better indication of ecological changes in the environment.

In *Maniola jurtina* differences in the size of the butterflies have been found between years (Tudor & Parkin 1979). The same study showed significant differences in size in both sexes between individuals flying early and late. As a possible cause for this dissimilarity Tudor & Parkin suggested, a change in the ecology during the period of larval and pupal development.

Aphantopus hyperantus was studied with regard to its size in the Mikkeli district in 1968 and 1969. No differences in mean size were found between these years. However, the MHI was very similar 1968 and 1969.

In *Maniola* Tudor & Parkin (1979) found that females without spots are more frequent during the first quarter of the season than later on; however, the difference was not statistically significant. This conclusion is the opposite of that reached by Dowdeswell (1961) in his study of *Maniola.*

It seems probable that in the *Aphantopus* populations there are no differences in phenotype frequencies between the early- and later-flying fractions. In the abundant populations of 1968 and 1969 no seasonal differences were observed (Table 10).

Other selective factors

Another important selective factor in the *Aphantopus* populations might be visual selection, especially of the apostatic subtype (Clarke 1969). In apostatic selection predators that prey on a polymorphic species learn to attack the commonest morph, and the rare morphs gain an advantage. Such polymorphism enables uncommon morphs to survive, although climatically they may be the least adapted of all. Then if an opportunity should arise for the species to expand into an area with a different climate it can take advantage of these uncommon morphs (Clarke 1969, Shapiro & Carde 1970).

In *Aphantopus*, visual selection might pertain to the underside of the hind wings, which are displayed during the escape reaction. In this species the LH is perhaps the most important wing area with regard to adaptation.

Further, it is possible that the underside of the fore wings is important in connection with sexual selection, for in these wing areas there is a considerable difference in eye-spot size between males and females. Perhaps this accounts for the constancy of the spot distribution on the underside of the hind wings in *Aphantopus* males and females throughout the study period.

In studies on *Maniola jurtina* it was suggested that parasites (Dowdeswell 1961, 1962) and bacteria (Beaufoy et al. 1970) may play some part as selective agents.

Although no one appears to have studied the incidence of infection, it seems unlikely that parasites and bacteria could have caused the temporal variation in phenotype frequencies in *Aphantopus*. A look at the variation curves reveals that they are all alike. These curves, which represent many different populations, would hardly be so similar if there were dissimilarities among populations in the incidence of parasitism. Moreover it seems highly unlikely that parasitism could exert its influence on the wing pairs separately.

And then we have human activities causing many changes that may affect selection pressures. Such changes may be the reason that, in the populations strongly exposed to human influence changes in UF spotting pattern frequencies in males were often different from the changes in less exposed populations (e.g. M1, M2).

5.5. Random genetic drift

Could natural selection alone bring about these irregular changes, which often fluctuate from year to year about an average value?

Regarding temporal variability, the curves in population M1 seem not to conform to the general pattern, deviating from the rest in several respects, especially in 1970—71 (Figs. 21, 23).

However, the apparently random changes may perhaps be the result of human influence, which operates through the use of pesticides and herbicides, the planting or felling of forests, reduction in the areas of meadows and so on. These measures, which produce secondary effects upon selection pressures, were greatest with regard to M1. In area effects and other local effects, a large number of selection pressures may be acting in opposite directions (Lewontin 1974, Semenoff 1977), and it is often very difficult to be sure when changes depend on local effects and when on random genetic drift.

In the present study area, however, local effects seem to act side by side with chance. Chance, in turn, results partly from the haphazard influence of man, and this may explain the sudden changes which manifest themselves in the frequencies of the phenotypes.

6. Summary

1. The populations of *Aphantopus hyperantus* varied considerable in size. The variation was probably dependent on climatic factors, as in the most populations the number of butterflies changed very similarly from year to year. Exeptions to this rule were seen in populations living in meadows strongly affected by human activities.

2. It seems that as regards the expression of eye-spots at different sites on the upperside of the fore wings the factors responsible mostly operate in such a way that a spot is present at site 1 whenever there are spots as other sites. Similarly a spot is unlikely to appear at site 3 unless spots are fairly well developed at sites 1 and 2. Similar relations can be traced in the other wing areas.

3. In both sexes the appearance of an eye-spot at a given site depends on the microenvironment of the population and on the year of sampling.

The numbers of eye-spots on the upper- and underside of the fore wing are interdependent. In the same way the numbers of eye-spots on the upperside of the fore and hind wing are interdependent.

4. In *Aphantopus*, variability in the numbers and types of eye-spots produced about 33 different phenotypes in the males and 12 in the females.

The spotting pattern on the upperside of the fore wing of the males was unimodal at no spots and on the upperside of the hind wing of the males unimodal at two spots.

In females the pattern was unimodal on the upperside of the fore wing at two or three spots, and on the upperside of the hind wing at two spots.

On the underside of the fore wing the modal number was two spots in the males and three spots in the females. On the underside of the hind wing there were five eye-spots in both sexes.

5. The frequencies of the eye-spot patterns and the modal numbers of spots were found to fluctuate. It seems probable that this variability in spotting is ultimately due to climatic factors. The correlation between eye-spot patterns and climate was strongest in the males. The lower the "modified humidity index" (*MHI*), i.e. the drier the climate, the larger the number of males with no spots.

6. Every one of the *Aphantopus* populations studied lived in surroundings in which ecological factors, such as temperature, humidity, soil and general characters of vegetation, were site-specific. Thus, every population probably lived under unique microclimatic conditions. Hence, differences in the site-specific effects might explain why in some of the populations trends in spotting frequencies were sometimes reversed apparently haphazardly in successive generations.

7. In some populations, changes in the environment during the study period were due to human influence. Poisoning with herbicides, clear-cutting of forests, reduction of meadow areas and other human activities affected the populations, causing drastic reductions in their size which left the populations open to chance variation in spotting frequencies.

8. Selection in *Aphantopus* probably does not act directly upon the spotting patterns, but upon other characters. Thus it seems possible that the genes which enable *Aphantopus* to adapt to the climate are closely linked with the genes that regulate spotting within an alleged supergene.

9. The results concerning the *Erebia* and *Coenonymphia* populations afforded some support for certain of the conclusions reached regarding the *Aphantopus* populations.

Acknowledgements. I am greatly obliged to Mrs. Eeva-Liisa Kanerva, M.A., and my sincere thanks are also to Mr. Osmo Peltonen, M.A., for loaning material for this study. I am grateful to the former Head of the Department of Genetics Prof. Emer. Esko Suomalainen for suggesting investigation of satyrid butterflies as the theme for my graduate and doctoral studies. I thank Dr. Juhani Lokki for criticism during the early phases of the work. Dr. Kauri Mikkola has during later phases of the study likewise given valuable criticism. For guidance, especially regarding the technical aspects of my doctoral work, I am thankful to the Head of the Department of Genetics, Professor Olli Halkka. Dr. Samuel Panelius offered valuable comments on many aspects of the manuscript. Mrs. Jean Margaret Perttunen, B.Sc. kindly checked the English of the manuscript.

References

Baletto, E. & Tosco, G. 1975: Reports of Rhopalocera in the Liguirian Alps. — Boll. Soc. Entomol. Ital. 107: 160—163.

Beaufoy, E. M., Beaufoy, S., Dowdeswell, W. H. & McWhirter, K. G. 1970: Evolutionary studies on Maniola jurtina (Lepidoptera Satyridae). The southern English stabilisation, 1961—68. — Heredity 25: 105—113.

Bengtson, S.-A. 1975: Fläckpolymorfism hos Maniola jurtina L. (Lep.) i södra Sverige och Norge. — Entomologen 4:2: 29—36.

—»— 1978: Spot-distribution in Maniola jurtina (Lepidoptera) on small islands in southern Sweden. — Holarct. Ecol. 1: 54—61.

Brakefield, P. 1979: Spot-number in Maniola jurtina-variation between generations and selection in marginal populations. — Heredity 42: 259—266.

Cain, A. J. & Currey, J. D. 1963a: Area effects in Cepaea. — Phil. Trans. R. Soc. Lond. (B2) 46: 1—81.

—»— 1963b: The causes of area effects. — Heredity 26: 277—298.

Clarke, B. 1969: The evidence for apostatic selection. — Heredity 24: 347—352.

Collier, A. E. 1956: Rearing of Aphantopus hyperantus Linn. ab lanceolata Shipp. — Entomol. Rec. 68: 1—2.

—»— 1967: A new aberration of Aphantopus hyperantus (Lep. Satyridae). — Entomol. Rec. 79: 4.

Creed, E. R., Dowdeswell, W. H., Ford, E. B. & McWhirter, K. G. 1959: Evolutionary studies on Maniola jurtina: The English mainland 1956—57. — Heredity 13: 363—391.

—»— 1962: Evolutionary studies on Maniola jurtina: The English mainland 1958—60. — Heredity 17: 237—265.

—»— 1970: Evolutionary studies on Maniola jurtina

(Lepidoptera, Satyridae). The "boundary phenomenon" in Southern England, 1961 to 1968. — In: Hecht, M. K. & Steere, W. C. (ed.), Essays in Evolution and Genetics in Honor of Theodosius Dobzhansky: 594 pp. Amsterdam.

Creed, E. R., Ford, E. B. & McWhirter, K. G. 1964: Evolutionary studies on Maniola jurtina: The Isles of Scilly 1958—59. — Heredity 19: 471—488.

Dobzhansky, T. 1970: Genetics of the Evolutionary Process. — 505 pp. New York.

Dobzhansky, T. & Pavlovsky, O. 1957: An experimental study of interaction between genetic drift and natural selection. — Evolution 11: 311—319.

Douwes, P. 1980: Periodical appearance of species of the butterfly genera Oeneis and Erebia in Fennoscandia (Lepidoptera: Satyridae). — Entomol. Generalis 6: 151—157.

Dowdeswell, W. H. 1961: Experimental studies on natural selection in the butterfly, Maniola jurtina. — Heredity 16: 39—52.

—»— 1962: A further study of the butterfly Maniola jurtina in relation to natural selection by Apanteles tetricus. — Heredity 17: 513—523.

Dowdeswell, W. H., Fisher, R. A. & Ford, E. B. 1940: The quantitative study of populations in the Lepidoptera I. Polyommatus icarus Rott. — Ann. Eugenics 10(2): 123—136.

Dowdeswell, W. H. & Ford, E. B. 1955: Ecological genetics of Maniola jurtina L. on the Isles of Scilly. — Heredity 9: 265—272.

Dowdeswell, W. H., Ford, E. B. & McWhirter, K. G. 1957: Further studies on isolation in the butterfly Maniola jurtina L. — Heredity 11: 51—65.

—»— 1960: Further studies on the evolution of Maniola jurtina in the Isles of Scilly. — Heredity 14: 333—364.

Dowdeswell, W. H. & McWhirter, K. G. 1967: Stability of spot distribution in Maniola jurtina throughout its range. — Heredity 22: 187—210.

Endler, J. A. 1977: Geographical variation, speciation and clines. — 246 pp. Princeton, New Jersey.

Federley, H. 1938: Chromosomenzahlen finnländischer Lepidopteren. I. Rhopalocera. — Hereditas 24: 397—464.

Frazer, J. F. D. & Willcox, H. N. A. 1975: Variation in spotting among the close relatives of the butterfly Maniola jurtina. — Heredity 34: 305—322.

Ford, E. B. 1945: Butterflies. — 368 pp. London.

—»— 1955: Moths. — 266 pp. London.

—»— 1965: Genetic polymorphism. — 101 pp. London.

—»— 1971: Ecological genetics. — 410 pp. London.

—»— 1976: Genetics and adaptation. — 58 pp. Southampton.

Frohawk, F. W. 1934: The complete book of British butterflies. — 384 pp. London.

Goodden, R. 1978: British butterflies. A field Guide. — 141 pp. — London.

Haldane, J. B. S. 1957: The cost of natural selection. — J. Genet. 55: 511—524.

Halkka, O. 1970: Sattuman vaikutuksesta sylkikaskaspopulaatioiden geenifrekvensseihin. — Luonnon Tutkija 74: 33—43.

Halkka, O., Halkka, L. & Raatikainen, M. 1975: Transfer of individuals as a means of investigating natural selection in operation. — Hereditas 80: 27—34.

Halkka, O. & Kohila, T. 1976: Persistence of visual polymorphism, despite a low rate of predation in Philaenus spumarius (L.) (Homoptera, Aphrophoridae). — Ann. Zool. Fennici 13: 185—188.

Halkka, O., Raatikainen, M. & Halkka, L. 1974: The founder principle, founder selection, and evolutionary divergence and convergence in natural populations of Philaenus. — Hereditas 78: 73—84.

—»— 1976: Conditions requisite for stability of polymorphic balance in Philaenus spumarius (L.) (Homoptera). — Genetica 46: 67—76.

Halkka, O., Raatikainen, M. & Vilbaste, J. 1976: Transition zone between two clines in Philaenus spumarius (L.) (Hom., Aphrophoridae). — Ann. Entomol. Fennici 42: 105—111.

Higgins, L. G. & Riley, N. D. 1970: A field guide to the butterflies of Britain and Europe. — 380 pp. London.

Hämet-Ahti, L., Jalas, J. & Ulvinen, T. 1977: Suomen alkuperäiset ja vakiintuneet putkilokasvit. — 77 pp. Dept. Botan., Univ. Helsinki.

Jalava, J. 1977: Suomen perhosten luettelo. — 70 pp. Helsingin hyönteisvaihtoyhdistys.

Jones, J. S., Leith, B. H. & Rawlings, P. 1977: Polymorphism in Cepacea. A problem with too many solutions. — Ann. Rev. Ecol. Syst. 8: 109—143.

Kaisila, J. 1959: Vanhimmat tiedot Suomen päiväperhoslajistosta. — Ann. Entomol. Fennici 25: 80—102.

—»— 1962: Immigration und Expansion der Lepidopteren in Finnland in der Jahren 1869—1960. — Acta Entomol. Fennica 18: 1—452.

Kanerva, E.-L. 1959: Eräiden tesmaperhospopulaatioiden välisestä muuntelusta. — Laudatur thesis, Dept. Genet., Univ. Helsinki.

Langer, T. W. 1958: Päiväperhosten parissa. — 187 pp. Porvoo.

Le Gare, S. M. J. & Hovanitz, W. 1951: Genetic and ecological analysis of wild populations in Lepidoptera. II. Color pattern variations in Melitaea chalcedone. — Washman J. Biol. 9: 257—310.

Lewontin, R. C. 1974: The genetic basis of evolutionary change. — 346 pp. New York.

Lincome, C. B. 1967: Variation in Aphantopus hyperantus Linn. — Entomol. Rec. 79: 127—129.

McWhirter, K. 1969: Heritability of spot number in Scillonian strains of the Meadow brown butterfly (Maniola jurtina L.). — Heredity 24: 314—318.

McWhirter, K. G. & Greed, E. R. 1971: An analysis of spot placing in the Meadow brown butterfly Maniola jurtina. — In: Creed, R. (ed.), Logical genetics and evolution. Essays in honour of E. B. Ford: 275—288. Oxford.

Mikkola, K. 1976: Alternate-year flight of northern Xestia species (Lep., Noctuidae) and its adaptive significance. — Ann. Entomol. Fennici 42: 191—199.

Murray, J. & Clarke, B. 1976: Supergenes in polymorphic land snails. II Partula suturalis. — Heredity 37: 271—282.

Nordström, F. 1919: Bidrag till kännedomen on Sveriges dagfjärilar. — Entomol. Tidskr. 40: 120—142.

Nordström, F. 1955: De Fennoskandiska dagfjärilarnas utbredning. — Kungl. Fysiograf. Sällsk. Handl., N. F.66. N1.

Ohta, T. & Kimura, M. 1970: Development of associative overdominance throughout linkage disequilibrium in finite populations. — Genetics 69: 247—260.

Pease, R. W. Jr. 1968: Evolution and hybridisation in the Utetheisa ornatrix complex (Lepidoptera: Arctiidae). I. Inter- and intrapopulation variation and its relation to hybridization. — Evolution 22: 719—735.

Robinson, R. 1971: Lepidoptera genetics. — 687 pp. London.

Semenoff, R. 1977: Can polymorphism be maintained by selection favouring in intermediate optimum phenotype? — Heredity 39: 373—381.

Seppänen, E. J. 1954: Suomen suurperhostoukkien ravintokasvit. — Animalia Fennica 8: 1—415.

—»— 1969: Suurperhosten talvehtimisasteet. — Ann. Entomol. Fennici 35: 129—152.

—»— 1970: Suomen suurperhostoukkien ravintokasvit. — Animalia Fennica 14: 1—179.

Shapiro, A. M. & Carde, R. T. 1970: Habitat selection and competition among sibling species of satyrid butterflies. — Evolution 24: 48—54.

Sjöstedt, J. 1936: Havaintoja perhosten esiintymisestä Etelä-Pohjanmaalla (Oa). — Notulae Entomol. 16: 12—20.

Suomalainen, E. 1937: Über das periodische Auftreten von Erebia ligea L. (Lep. Satyridae) in Finland. — Ann. Entomol. Fennici 3: 78—83.

Tudor, O. & Parkin, D. T. 1979: Studies on phenotypic variation in Maniola jurtina (Lepidoptera: Satyridae) in the Wyre forest, England. — Heredity 42: 91—104.

Turner, J. R. G. 1963: A quantitative study of a welsh colony of the large heath butterfly Coenonympha tullia Muller (Lepidoptera). — Proc. R. Entomol. Soc. Lond. 38: 101—112.

—»— 1967: On supergenes. I. The evolution of supergenes. — Amer. Naturalist 101: 195—221.

Valle, K. J. 1935: Suurperhoset, Macrolepidoptera. I. Päiväperhoset, Diurna. — Animalia Fennica 2: 1—174.

Wahlgren, E. 1930: Dagfjärilar. Diurna. Svensk Insektfauna. 10 Fjärilar. Lepidoptera. I. Storfjärilar. Macrolepidoptera: 1—84.

Received 1. II. 1981
Printed 5. VI. 1981