

Phenotypic Variation of the Scarce Heath *Coenonympha hero* (L.) (Lepidoptera, Satyridae) from the Central Part of Its Range

E. Yu. Zakharova

Institute of Plant and Animal Ecology, Ural Branch, Russian Academy of Sciences, Yekaterinburg, 620144 Russia
e-mail: zakharova@ipae.uran.ru

Received April 1, 2015

Abstract—Variation of the fore and hind wing lengths and the diameters of wing eyespots in two subspecies of *Coenonympha hero* (L.) from the central part of the species range was analyzed. Clinal variation was revealed, manifested in a gradual increase of the wing size and eyespot diameters from west to east in the Urals. Both in *C. h. hero* in the Urals and in *C. h. perseis* in Siberia, the northern peripheral populations had a specific wing pattern with eyespots smaller than in more southern parts of the corresponding ranges. In most cases, such climatic factors as the mean annual air temperature, precipitation, duration of the frost-free period, and humidity were shown to affect significantly the variation of morphological traits of *C. hero*. Chrono-geographical analysis of variation showed that in some cases the differences between the samples collected in the same locality in different years were comparable to or greater than geographic variation within the subspecies range. Thus, the population as a whole is influenced by climatic factors and weather conditions in a particular part of the range during a particular season; *C. hero* may therefore be a suitable object for monitoring the impact of environmental changes on insects.

DOI: 10.1134/S0013873817040078

Coenonympha hero (Linnaeus, 1761) is a widespread Eurasian forest species whose range covers the temperate part of Eurasia as far northwards as the middle taiga, Sakhalin and the Southern Kuril Islands, and Japan (Davenport, 1941; Korshunov, 2002; Gorbunov and Kosterin, 2007). The ancestral form of *C. hero* probably originated in the Western Palaearctic, after which the species spread far to the east (Kodandaramaiah and Wahlberg, 2009).

The abundance of the species within the European part of its range is currently decreasing; the isolated endangered populations are often recognized as objects of monitoring and protection. The species is listed in the *Red Data Book of European Butterflies* (Van Swaay and Warren, 1999) with the “vulnerable” status (Spec 3). In some Western European states, such as Switzerland, *C. hero* has not been recorded since the 1980s and is considered extinct (Lütolf et al., 2006). One of the main reasons of the population decline of *C. hero* is believed to be transformation of its natural habitats into agrocenoses. Besides, an important factor of its current range reduction is the gradual climate warming in Europe. According to the results of model analysis of the potential species range depending on the combination of several climatic factors, such as the sum of degree-days, moisture content of the upper soil layers, the total annual temperature,

precipitation, etc., *C. hero* was placed in the HHR (very high climate change risk) category (Settele et al., 2008).

Within the territory of European Russia, *C. hero* is included in the regional Red Data Books of Pskov, Leningrad, Yaroslavl, Tver, Moscow, Ivanovo, Nizhny Novgorod, and Ryazan provinces, and also Mari El, Tatarstan, and Chuvash republics. It has the status of a rare species (category 3) in all these regions except Yaroslavl Province where *C. hero* is regarded as “probably extinct” (*Red Data Book of Yaroslavl Province*, 2004). In the Asian part of Russia *C. hero* is quite common and is not listed among protected species, with two exceptions: Chelyabinsk Province, where the species is included in the list of animals requiring special attention (*Red Data Book of Chelyabinsk Province*, 2005, Suppl. 2), and Krasnoyarsk Territory, where the species forms local though sometimes fairly large populations in the south of the region (*Red Data Book of Krasnoyarsk Territory*, 2011).

As can be expected, the species occupying such an extensive territory reveals considerable geographic variation, as the result of which a number of subspecies have been described by different authors. In particular, Davenport (1941) distinguished four subspecies: *C. h. hero* Linnaeus, 1761, *C. h. sabaesus* Fabri-

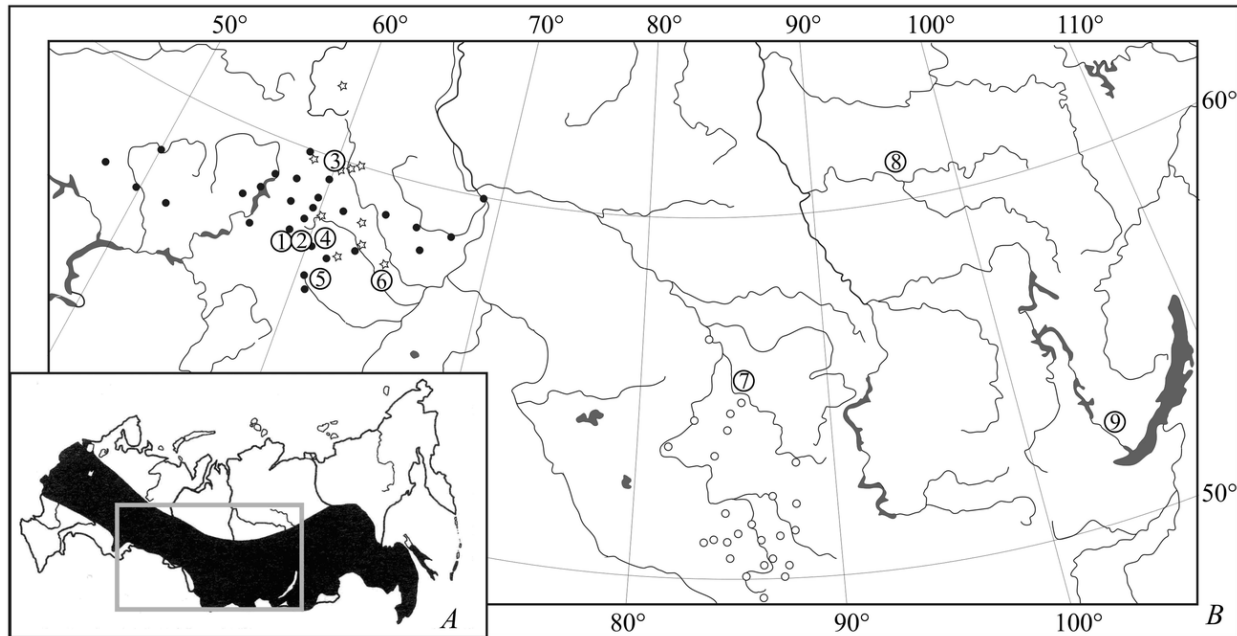


Fig. 1. The range of *Coenonympha hero* (L.) in the territory of Russia (after Gorbunov, 2001) (A) and its distribution in the Urals and Siberia according to different authors (B). Asterisks: localities of *C. hero* in the Urals (after Tatarinov and Gorbunov, 2014); filled circles: localities of *C. hero hero* (L.) in the Urals (after Lukhtanov and Lukhtanov, 1994); empty circles: localities of *C. hero perseis* Lederer in Western Siberia (after Lukhtanov and Lukhtanov, 1994). The material collection sites are numbered 1–9 (see Table 1).

cus, 1775, *C. h. perseis* Lederer, 1853, and *C. h. neo-perseis* Fruhstorfer, 1908. The status of some subspecies remains debatable; for example, *C. h. sabaeus* was regarded as a latitudinal (infrasubspecific) form of the nominotypical subspecies (Lvovsky and Morgun, 2007), while *C. h. sabaeus* is sometimes synonymized with *C. h. pilwonis* Matsumura, 1925 (Korshunov and Gorbunov, 1995).

In this work, I analyze the variation of the complex of morphological traits (the wing length and the wing eyespot size) in two subspecies of *C. hero* from the central part of its range. The chrono-geographic approach is used to estimate the impact of the different variation components (sexual, geographic, and chrono-graphic) and the influence of climatic factors on the phenetic aspect of the natural populations. The term “chronographic variation” is used herein to describe the manifestations of the variation of morphological traits in different years (seasons), which characterize the limits of modification variability in the given population (Vasiliev and Vasilieva, 2009).

MATERIALS AND METHODS

This work is based on samples of *C. hero* from the Urals and Siberia (Fig. 1). The size of the samples, coordinates of the sampling sites, and some climatic parameters according to the *Interactive Agricultural*

Ecological Atlas of Russia and Neighboring Countries (2008) are given in Table 1.

Sampling sites 1 (env. of Arakaevo, Bazhukovo settl.) and 2 (env. of Khomutovka, Ilmovka settl.) were located 50 km apart in the southern taiga subzone of the Middle Urals. *Coenonympha hero* were captured in forb meadows, floodlands of rivers and streams, and on the sides of forest roads. The northernmost sampling site 3 (env. of Karpinsk) was located in the North Urals, within the middle taiga subzone. Site 4 was the biological research station of the Ural Federal University, located near Fomino, Sverdlovsk Province, in the interfluvium of the rivers Iset and Sysert, in the pre-forest-steppe pine-birch forests of the taiga zone.

Two sites (5 and 6) were positioned within the northern forest-steppe subzone, in Chelyabinsk and Kurgan provinces, respectively.

The sample from the environs of Voronovo, Tomsk Province (site 7) was collected in a forb floodland meadow on the Ob bank. This territory belongs to the small-leaved forest (subtaiga) subzone, with the principal vegetation represented by the primary small-leaved (birch and aspen) forests, which have a well-developed grass-forb layer under the upland conditions. Such forests are often interspersed with dry meadows and bogged patches (Ilyina et al., 1985). All

Table 1. Size of samples of *Coenonympha hero* (L.), coordinates, and some climatic parameters of the species habitats in the Urals and Siberia

No.	Sampling locality	Coordinates, N, E	Natural zone (subzone)	Annual mean temperature, °C	Annual mean precipitation, mm	Mean duration of frost-free period, days	HTC	Year of sampling	Males, spec.	Females, spec.	Collector
1	Arakaevo, Bazhukovo	56° 44' 59° 22'	Taiga (southern taiga)	0.25	518	102	1.79	2002	10	0	E.Yu. Zakharova
2	Khomutovka, Ilmovka	56° 49' 59° 48'	Taiga (southern taiga)	0.34	519	102	1.71	2003	18	8	E.Yu. Zakharova
3	Karpinsk	59° 46' 59° 58'	Taiga (middle taiga)	-0.68	480	81	1.68	2006	7	5	A.O. Shkurikhin
4	Fomino	59° 46' 59° 58'	Taiga (middle taiga)	-0.68	480	81	1.68	2013	8	3	T.S. Oslina
5	Metlino	56° 36' 61° 03'	Taiga (pre-forest-steppe pine-birch forests)	0.98	473	102	1.46	2001	50	13	P.V. Rudoiskatel
6	Krasnyi Bor	56° 00' 64° 34'	Forest-steppe (northern forest-steppe)	1.08	427	102	1.37	2002	18	10	E.Yu. Zakharova
7	Voronovo	55° 47' 60° 59'	Forest-steppe (northern forest-steppe)	1.08	427	102	1.37	2005	8	4	E.Yu. Zakharova
8	Baikit	56° 00' 64° 34'	Forest-steppe (northern forest-steppe)	0.93	379	105	1.07	2008	9	4	E.Yu. Zakharova
9	Irkutsk	55° 59' 83° 48'	Taiga (small-leaved forests)	-0.58	442	103	1.34	2011	32	12	E.Yu. Zakharova
		61° 40' 96° 23'	Taiga (middle taiga)	-8.33	473	72	1.86	2014	29	35	E.Yu. Zakharova
		52° 27' 104° 31'	Taiga (southern taiga)	-2.93	309	83	1.48	2013	16	1	T.K. Tuneva
									9	0	ZIN collections
									8	0	ZIN collections

HTC is Selyaninov's hydrothermal coefficient

the material collected is kept in the museum of the Institute of Plant and Animal Ecology, Ural Branch, Russian Academy of Sciences (Yekaterinburg).

Two samples of *C. hero* from Krasnoyarsk Territory (site 8: Baikit) and Irkutsk Province (site 9: Irkutsk) comprised the material collected from 1892 to 1930 and kept in the main collection of the Zoological Institute of the Russian Academy of Sciences (ZIN) in St. Petersburg.

The laboratory processing of material included measuring the wing lengths (LF, fore wing; LH, hind wing) and the diameters of the eyespots in the wing pattern on the underside of the fore left and hind left wings. The length of the fore wing was measured from the base of vein *Sc* to the wing tip, and that of the hind wing, from the base of vein *Rs* to the apex of vein *Cu*₁. The fore wing pattern of *C. hero* may have as many as five eyespots, located in cells *R*₅-*M*₁, *M*₁-*M*₂, *M*₂-*M*₃, *M*₃-*Cu*₁, and *Cu*₁-*Cu*₂; they were designated as P1–P5, respectively. On the hind wing the eyespots are located in cells *R*_s-*M*₁, *M*₁-*M*₂, *M*₂-*M*₃, *M*₃-*Cu*₁, *Cu*₁-*Cu*₂, and *Cu*₂-2*A*; they were designated as G1–G6. Eyespot G7, when present, lies in cell *Cu*₂-2*A* near G6. Measurements of the material from sites 1–7 were carried out in dry detached wings, using an MBS-10 binocular microscope with an eyepiece micrometer at 8 × 0.6 magnification. The specimens from the ZIN collection (sites 8 and 9) were photographed with a Nikon Coolpix 4500 digital camera mounted via an adapter onto the MBS-10 microscope, at 8 × 0.6 magnification; measurements were carried out in ImageJ 1.48v software (Rasband, 2014).

Variation of the complex of metric traits (the eyespot sizes and the wing lengths) was assessed by discriminant analysis within the Statistica 5.5 software package. The hierarchy of sample similarities was studied by cluster analysis based on generalized Mahalanobis distances (D^2); the dendrogram was built by the unweighted pair group method with arithmetic mean (UPGMA) using the Past 2.14 software (Hammer et al., 2001). The influence of climatic factors on the variation of the studied traits was estimated by univariate ANOVA.

RESULTS

According to the literature data, the nominotypical subspecies *C. hero* is distributed in the Urals, the trans-Ural region, and Western Siberia as far eastwards as the Irtysh River (Fig. 1). The subspecies *C. h. perseis* is distributed in Siberia east of the Ob

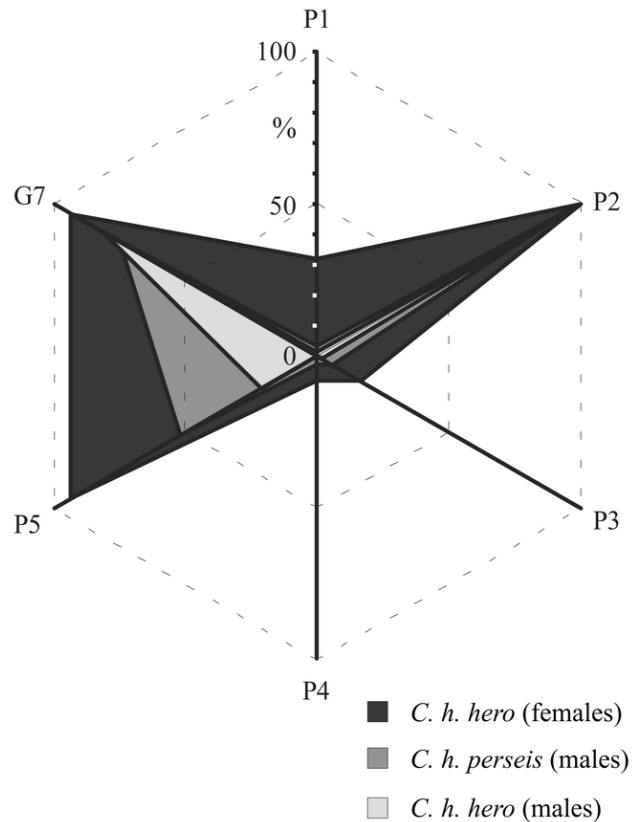


Fig. 2. Occurrence (%) of eyespots in the wing pattern of two subspecies of *Coenonympha hero* (L.). P1–P5, eyespots on the fore wing; G7, eyespot on the hind wing.

River (Lukhtanov and Lukhtanov, 1994; Gorbunov and Kosterin, 2007). Samples from the Urals and the trans-Ural region (sites 1–6) were assigned to the subspecies *C. h. hero*, and the Siberian samples (sites 7–9), to *C. h. perseis*. The results of statistical analysis of phenotypic variation confirmed the presence of considerable differences between the Ural and Siberian samples, which correspond to the level of subspecies. Discriminant analysis of the whole complex of studied traits (the lengths of the fore and hind wings and the diameters of the wing eyespots) revealed significant differences between the samples of *C. hero* from the Ural region and those from Siberia: the generalized Mahalanobis distance was $D^2 = 14.09$, the significance determined by Hotelling's T^2 statistic was $p < 0.01$ ($T^2 = 232.36$).

Similar to other species of the genus *Coenonympha* Hübner, some eyespots in the wing pattern of both subspecies of *C. hero* act as discrete phenes, so that the total number of eyespots on the wing may vary. In particular, from 0 to 5 eyespots may be present on the fore wing of *C. hero*. Only two variants are possible

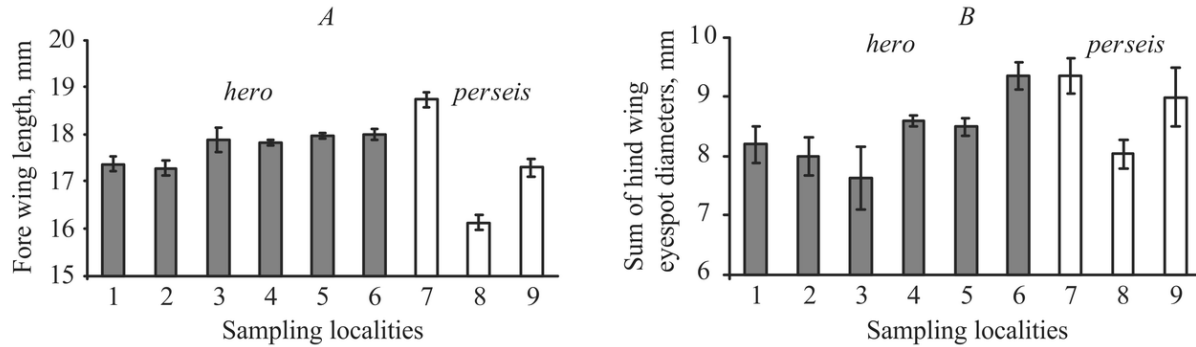


Fig. 3. Geographic variation in the length of the fore wing (A) and the sum of diameters of the hind wing eyespots (B) of males of *Coenonympha hero* (L.). The samples are numbered 1–9 as in Table 1.

for the hind wing: 6 or 7 eyespots, the 7th spot (G7) being located in cell Cu_2-2A . The different variants of phenetic combinations in the Ural populations of *C. hero* were described by us earlier (Zakharova et al., 2006).

It is known that *C. h. perseis* typically possesses larger and brighter eyespots on the wing underside as compared with the nominotypical subspecies (Davenport, 1941; Gorbunov and Kosterin, 2007). The latter authors noted the presence of additional small spots in cells $Rs-M_1$, M_2-M_3 , and M_3-Cu_1 in *C. h. perseis*. Analysis of the available samples showed that these eyespots, designated here as P1, P3, and P4, may be also present in *C. h. hero* though less frequently than in *C. h. perseis*. The frequency of occurrence of different phenes in the wing pattern of two subspecies of *C. hero* is shown in Fig. 2. Eyespot P2 in forewing cell M_1-M_2 was present in 100% of *C. h. hero* females but could be absent in males. On the whole, females were characterized by higher stability in the eyespot occurrence as compared with males. In turn, males of *C. h. perseis* showed higher stability of the eyespot pattern than males of the nominotypical subspecies. For example, phene P5 was found in 51.5% of males of *C. h. perseis* and only in 21.1% of males of *C. h. hero* (Fig. 2).

Geographic variation of the wing lengths and the eyespot sizes was analyzed using the samples of males from all the nine collection sites. Geographic variation of the eyespots was assessed not separately for each spot but for the sum of diameters of all the spots on the wing; this sum served as an integral estimate of “spottiness.” The factor “longitude” proved to be significant for all the analyzed traits in ANOVA: for the trait “fore wing length” $F(8, 310) = 19.69$, $p < 0.001$; for the trait “hind wing length” $F(8, 304) = 15.78$, $p < 0.001$; for the trait “sum of diameters of fore wing

eyespots” $F(8, 308) = 2.77$, $p < 0.01$; for the trait “sum of diameters of hind wing eyespots” $F(8, 289) = 3.44$, $p < 0.001$.

The populations of *C. h. hero* from the Urals and the trans-Ural area revealed clinal variation manifested by the adult body size and the eyespot diameter increasing from west to east (Fig. 3). The mean fore wing length of males from the Ural region was 17.7 ± 0.1 mm and exceeded the corresponding values for this subspecies in Sweden (15.7 ± 0.1 mm) and other parts of Western Europe (16.0 ± 0.2 mm) (Nylin and Svård, 1991). The larger specimens usually also had larger eyespots in the wing pattern. An exception was the northernmost sample from the environs of Karpinsk, where the mean fore wing length was 17.9 ± 0.3 mm but the eyespots were relatively small: the sum of diameters of fore wing eyespots was 0.5 ± 0.2 mm, that of hind wing eyespots was 7.6 ± 0.5 mm. Of the three studied samples of males of *C. h. perseis*, the specimens from the northernmost site (env. of Baikit) were the smallest and also had the smallest eyespots.

The effects of climatic features on the variation of morphological traits were assessed by MANOVA in which different climatic parameters (see Table 1) were used as independent factors. Females were excluded from analysis because they were absent in most of the samples. I analyzed the influence of four climatic parameters on the variation of the following metric traits of *C. hero* males: the lengths of the fore and hind wings and the sums of diameters of eyespots in the fore and hind wings. The influence of climatic factors on the variation of morphological traits of *C. h. perseis* was significant, whereas the influence of the annual mean air temperature and the duration of the frost-free period on the variation of the nominotypical subspecies within the Ural region was found to be statistically non-significant (Table 2).

Table 2. Results of MANOVA of the wing length and the sum of eyespot diameters in males of *Coenonympha hero* (L.)

Climatic parameter	Subspecies	Wilks's λ	F	df 1	df 2	p
Annual mean air temperature	<i>C. hero hero</i>	0.972	1.82	4	251	0.125
	<i>C. hero perseis</i>	0.191	8.38	8	52	< 0.0001
Annual mean precipitation	<i>C. hero hero</i>	0.809	4.57	12	659	< 0.0001
	<i>C. hero perseis</i>	0.191	8.38	8	52	< 0.0001
Mean duration of frost-free period	<i>C. hero hero</i>	0.972	1.82	4	251	0.125
	<i>C. hero perseis</i>	0.191	8.38	8	52	< 0.0001
Moisture content (HTC)	<i>C. hero hero</i>	0.783	3.94	16	758	< 0.0001
	<i>C. hero perseis</i>	0.191	8.38	8	52	< 0.0001

It is known that the distribution of insects in a given territory is determined not so much by the mean annual temperature and annual precipitation in themselves as by such important environmental parameters as the moisture content in the upper soil layers and the sum of degree-days during the frost-free period (Settele et al., 2008). In this research, the humidity (moisture content) of the territory was characterized by Selyaninov's hydrothermal coefficient (HTC), which varied from 1.07 to 1.86 in the Ural and Siberian parts of *C. hero* range (see Table 1). Analysis of phenotypic variation of *C. hero* in relation to humidity for the two subspecies revealed the following trend: specimens of *C. hero* were larger in regions with lower humidity, corresponding to the northern forest-steppe subzone, than in the more humid regions within the taiga zone (Fig. 4A). The trend of the eyespot size depending on the HTC values coincided with the same trend of the wing length (Fig. 4B).

As a rule, the size of the adults of univoltine lepidopteran species is clearly correlated with the duration of the vegetation period: the longer vegetation period allows the larvae to feed for a longer time, so that the adults can eventually reach a greater size (Nylin and Svård, 1991; Zakharova, 2012). Adults of *C. h. perseis* were significantly smaller in regions with short vegetation (frost-free) periods, and correspondingly larger in regions with longer vegetation periods (Fig. 4C, 4D). In analysis of the variation of *C. h. hero* from the Urals, the influence of the factor "mean duration of frost-free period" was found to be non-significant (Table 2), but the trend was still the same as in the Siberian subspecies.

In two localities (Fomino and Metlino) *C. hero* were sampled for several years, which made it possible to analyze the chronographic variation of these populations by the complex of morphological traits. Estima-

tion of the range of chronographic variation caused by the random fluctuations in the environment, allows these temporal differences to be compared with the range of the spatial, i.e., geographic variation. This chrono-geographic approach to analysis of intra- and interpopulation variation of morphological traits (Vasiliev et al., 2000; Vasiliev, 2005) was applied to studying the phenotypic variation in *C. hero*.

Based on the calculated matrix of Mahalanobis distances, the UPGMA dendrogram was built for all the available samples of *C. hero* with regard to sex, locality, and year of sampling (Fig. 5). As can be seen in the dendrogram, the samples of males and females formed two distinct clusters. Within the cluster of female samples, a separate group was formed by the samples made in Fomino in three different seasons (2001, 2002, and 2014). Somewhat separated from them were two phenotypically similar samples from the forest-steppe zone (Metlino and Krasnyi Bor).

Analysis of the hierarchy of relations in the male cluster showed the strongest manifestation of macro-geographic, i.e., subspecies-level differences. Among *C. h. perseis* males, the sample from the middle taiga subzone (env. of Baikit) was the most phenotypically distinct from the samples from more southern parts of the range in Siberia (env. of Voronovo and Irkutsk). The variation of males of the nominotypical subspecies from the Urals and trans-Ural area was characterized by significant differences in the complex of metric traits between populations from all the geographic localities. The chronographic differences were statistically non-significant in some cases, for example, for the samples from Fomino of 2001, 2002, and 2014, while in other cases they were significant and comparable with or even greater than geographic differences.

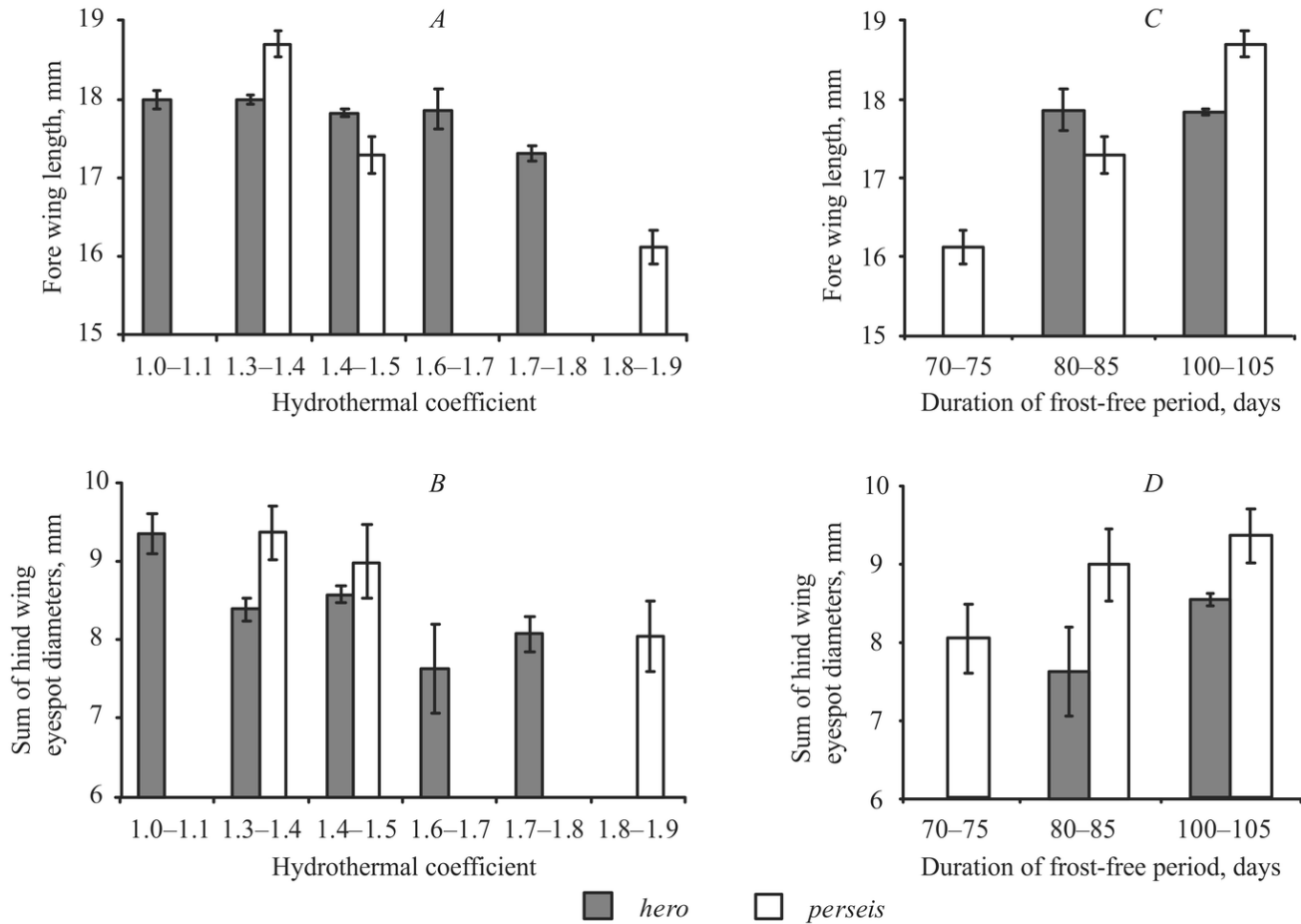


Fig. 4. Variation in the length of the fore wing (A, C) and the sum of diameters of the hind wing eyespots (B, D) in males of *Coenonympha h. hero* (L.) and *C. h. perseis* Lederer in relation to the moisture content (HTC; explained in the text) (A, B) and the duration of the frost-free period (C, D).

Thus, analysis of the clustering hierarchy indicated that individual variation components differently contributed to the total variation of the complex of metric traits of *C. hero* within the studied part of its range. The impact of the sex component was the greatest, followed by the geographic (in comparison of populations from such remote regions as the Urals and Siberia) and, finally, the chrono-geographic component.

DISCUSSION

The geographic variation of the adult size and the number of eyespots in different species of Nymphalidae and Satyridae (Lepidoptera) has been studied for a century. Research in this field was started by studies of eyespot polymorphism in *Maniola jurtina* (Linnaeus, 1758) by the British authors (Creed et al., 1962; Ford, 1965) and continued in the late XX and the early XXI centuries in the light of the new synthesis of genetics, evolutionary biology, and developmental biology (Nijhout, 1990; Brakefield et al., 1996; Bel-

dade et al., 2002; Dilão and Sainhas, 2004; Held, 2013, etc.). There is a variety of approaches to studying the wing pattern of Lepidoptera. Many of these studies are of considerable theoretical interest for various fields of modern entomology, ecology, and evolutionary biology. In particular, according to a number of authors, wing pattern variation in the local peripheral populations affected by shifts of the range boundary, for example in relation to climate changes, may be a convenient model for studying “evolution in action” (Parmesan, 2006; Monteiro and Prudic, 2010).

The specific features of distribution and habitats, and also some aspects of morphological and allozyme variation of *C. hero* in the European part of its range were studied by A. Cassel-Lundhagen and co-authors (Cassel et al., 2001; Cassel and Tammaru, 2003; Cassel-Lundhagen et al., 2008, 2009). Analysis of allozyme variation of European *C. hero* demonstrated a greater specificity of the peripheral populations (Estonia) as compared with the isolated (Sweden) or

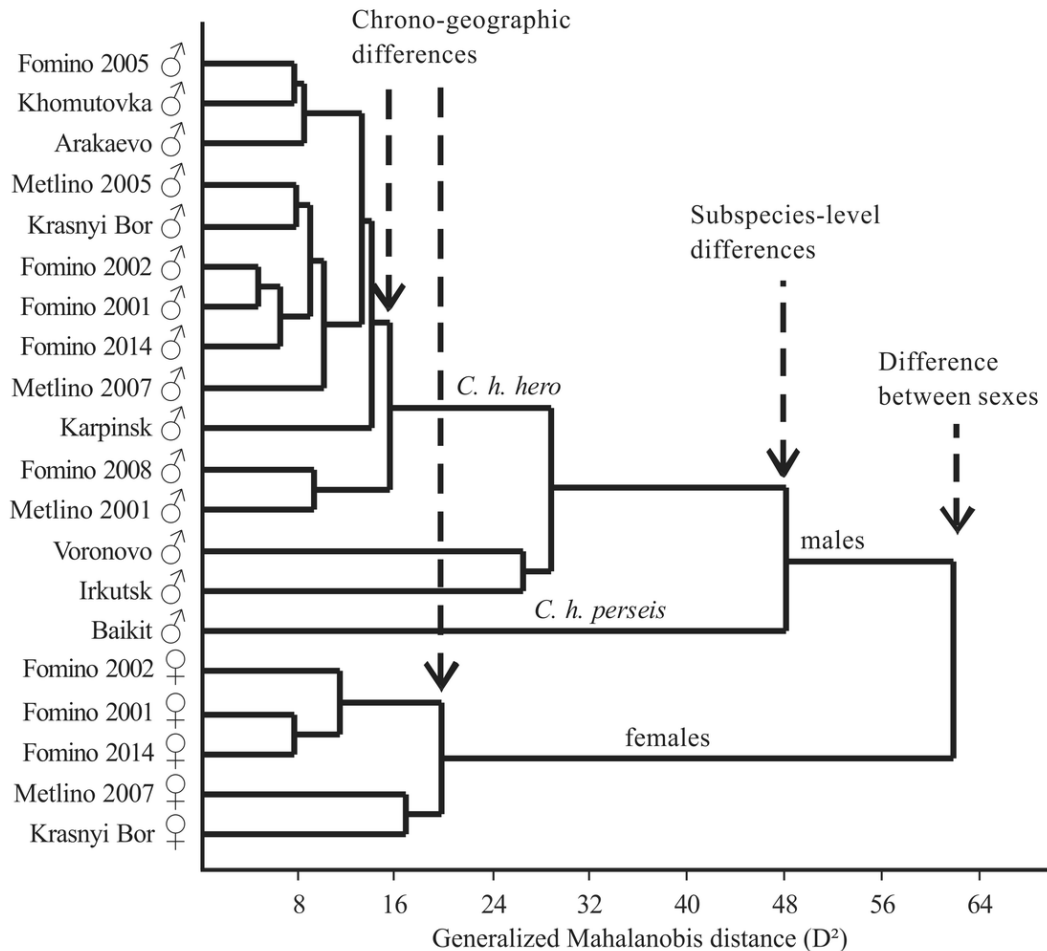


Fig. 5. Results of UPGMA clustering of generalized Mahalanobis distances (D^2) between the samples of males and females of *Coenonympha hero* (L.) by the complex of metric traits (wing lengths and eyespot diameters).

central (Russia: Middle Urals) populations (Cassel and Tammaru, 2003). However, analysis of the complex of morphological traits, such as the shape and size of wings, the diameter of some eyespots, and the size of the white band in the wing pattern, indicated a greater specificity of the isolated populations as compared with the central and peripheral ones. The cited authors suggested that the observed morphological differences resulted from the specific living conditions of the isolated populations and the ongoing selection in them, and considered the effects of inbreeding and manifestations of phenotypic plasticity to be a less probable cause (Cassel-Lundhagen et al., 2009).

The results of our study of variation of the complex of morphological traits (the wing length and the eyespot size) for *C. hero* populations from the Urals and Siberia partly agree with those obtained by A. Cassel-Lundhagen for the European populations. Although all the samples studied herein technically belong to the

central part of the vast Eurasian range of the species, the northernmost collection sites should be assigned to peripheral populations. It is these northern peripheral populations that are characterized by a peculiar wing pattern with smaller eyespots, as compared to the more southern samples. The greatest phenotypic specificity of a northern peripheral population was revealed both for the nominotypical subspecies in the Urals (env. of Karpinsk) and for the subspecies *C. h. perseis* (env. of Baikit). Both these peripheral populations occur at the boundary of the species range, within the middle taiga subzone.

Assessment of the role of climatic factors characterizing the ecological living conditions of a given population of *C. hero* in the variation of its morphological traits has demonstrated a significant influence (in most cases) of such parameters as the annual mean air temperature, the amount of precipitation, the duration of the frost-free period, and the moisture content. The

hypothesis of the considerable influence of abiotic environment and manifestation of phenotypic plasticity depending on external conditions is indirectly confirmed by the results of analysis of chronographic variation. In some cases, the differences between the samples collected in the same locality in different years are comparable to or greater than the geographic differences (within the subspecies range). Thus, the phenological aspect of the population as a whole is affected both by climatic factors and by weather conditions in a given part of the range during a particular season. Therefore, populations of *C. hero* represent a suitable object for monitoring the impact of environmental changes on insects.

ACKNOWLEDGMENTS

I am very grateful to S.Yu. Sinev and A.L. Lvovsky for the provided possibility of working with the butterfly collections of the Zoological Institute of Russian Academy of Sciences and for overall help and advice, and also to my colleagues T.S. Oslina, P.V. Rudoi-skatel, T.K. Tuneva, M.V. Chibiryak, Yu.M. Chibiryak, and A.O. Shkurikhin for help with material collection and the samples provided. This work was financially supported by the "Living Nature" program of the Ural Branch of Russian Academy of Sciences (project 15-12-4-25) and the Russian Foundation for Basic Research (project 16-04-01831a).

REFERENCES

- Beldade, P., Brakefield, P.M., and Long, A.D., "Contribution of Distal-less to Quantitative Variation in Butterfly Eyespots," *Nature* **415**, 315–317 (2002).
- Brakefield, P.M., Gates, J., Keys, D., Kesbeke, F., Wijngaarden, P.J., Monteiro, A., French, V., and Carroll, S.B., "Development, Plasticity and Evolution of Butterfly Eyespot Patterns," *Nature* **384**, 236–242 (1996).
- Cassel, A. and Tammaru, T., "Allozyme Variability in Central, Peripheral and Isolated Populations of the Scarce Heath (*Coenonympha hero*: Lepidoptera, Nymphalidae): Implications for Conservation," *Conservation Genetics* **4**, 83–93 (2003).
- Cassel, A., Windig, J., Nylin, S., and Wiklund, C., "Effects of Population Size and Food Stress on Fitness-Related Characters in the Scarce Heath, a Rare Butterfly in Western Europe," *Conservation Biology* **15** (6), 1667–1673 (2001).
- Cassel-Lundhagen, A., Sjogren-Gulve, P., and Berglind, S.A., "Effects of Patch Characteristics and Isolation on Relative Abundance of the Scarce Heath Butterfly *Coenonympha hero* (Nymphalidae)," *Journal of Insect Conservation* **12**, 477–482 (2008).
- Cassel-Lundhagen, A., Tammaru, T., Windig, J., Ryrholm, N., and Nylin, S., "Are Peripheral Populations Special? Congruent Patterns in Two Butterfly Species," *Ecography* **32**, 591–600 (2009).
- Creed, E.R., Dowdeswell, W.H., Ford, E.B., and McWhirter, K.G., "Evolutionary Studies on *Maniola jurtina*: the English Mainland, 1958–1960," *Heredity* **17**, 237–265 (1962).
- Davenport, D., "The Butterflies of the Satyrid Genus *Coenonympha*," *Bulletin of the Museum of Comparative Zoology at Harvard College* **87**, 215–349 (1941).
- Dilão, R. and Sainhas, J., "Modelling Butterfly Wing Eyespot Patterns," *Proceedings of the Royal Society of London B* **271**, 1565–1569 (2004).
- Ford, E.B., *Ecological Genetics*, 2nd Ed. (Methuen, London, 1965).
- Gorbunov, P. and Kosterin, O., *The Butterflies (Hesperioidae and Papilionoidea) of North Asia (Asian Part of Russia) in Nature. Vol. 2* (Rodina & Fodio, Moscow, 2007).
- Hammer, O., Harper, D.A.T., and Ryan, P.D., "PAST: Paleontological Statistics Software Package for Education and Data Analysis," *Palaeontologia Electronica* **4** (1), 1–9 (2001).
- Held, L.I. Jr., "Rethinking Butterfly Eyespots," *Evolutionary Biology* **40** (1), 158–168 (2013).
- Ilyina, I.S., Lapshina, E.I., Lavrenko, N.N., Meltser, L.I., Romanova, E.A., Bogoyavlensky, B.A., and Makhno, V.D., *Vegetation of the West Siberian Plain* (Nauka, Novosibirsk, 1985) [in Russian].
- Interactive Agricultural Ecological Atlas of Russia and Neighboring Countries: Economic Plants and Their Diseases, Pests and Weeds*, Ed. by A.N. Afonin et al. (2008). <http://www.agroatlas.ru>.
- Kodandaramaiah, U. and Wahlberg, N., "Phylogeny and Biogeography of *Coenonympha* Butterflies (Nymphalidae: Satyrinae) – Patterns of Colonization in the Holarctic," *Systematic Entomology* **34**, 315–323 (2009).
- Korshunov, Yu.P., *Rhopalocera (Lepidoptera) of Northern Asia* (KMK Scientific Press, Moscow, 2002) [in Russian].
- Lukhtanov, V. and Lukhtanov, A., *Die Tagfalter Nordwestasiens* (Herbipolina, Markleuthen, 1994).
- Lütolf, M., Kienast, F., and Guisan, A., "The Ghost of Past Species Occurrence: Improving Species Distribution Models for Presence-Only Data," *Journal of Applied Ecology* **43**, 802–815 (2006).
- Monteiro, A. and Prudic, K., "Multiple Approaches to Study Color Pattern Evolution in Butterflies," *Trends in Evolutionary Biology* **2** (1), 7–15 (2010).
- Nijhout, H.F., "A Comprehensive Model for Colour Pattern Formation in Butterflies," *Proceedings of the Royal Society of London Series B* **239** (1294), 81–113 (1990).
- Nylin, S. and Svärd, L., "Latitudinal Patterns in the Size of European Butterflies," *Holarctic Ecology* **14**, 192–202 (1991).

23. Parmesan, C., "Ecological and Evolutionary Responses to Climate Changes," *Annual Review of Ecology, Evolution and Systematics* **37**, 637–669 (2006).
24. Rasband, W.S., ImageJ: Image Processing and Analysis in Java (2014). <http://imagej.nih.gov/ij/>.
25. *Red Data Book of Chelyabinsk Province: Animals, Plants, and Fungi* (Ural University, Yekaterinburg, 2005) [in Russian].
26. *Red Data Book of Krasnoyarsk Territory, Vol. 1: Rare and Endangered Animal Species* (Siberian Federal University, Krasnoyarsk, 2011) [in Russian].
27. *Red Data Book of Yaroslavl Province* (Alexander Rutman Publ., Yaroslavl, 2004) [in Russian].
28. Settele, J., Kudrna, O., Harpke, A., Kühn, I., van Swaay, C., Verovnik, R., Warren, M., Wiemers, M., Hanspach, J., Hickler, T., Kühn, E., van Halder, I., Velling, K., Vliegthart, A., Wynhoff, I., and Schweiger, O., *Climatic Risk Atlas of European Butterflies. BioRisk No. 1* (Pensoft, 2008).
29. Van Swaay, C.A.M. and Warren, M.S., *Red Data Book of European Butterflies (Rhopalocera)* (Council of Europe Publishing, Strasbourg, 1999).
30. Vasiliev, A.G., *The Epigenetic Basis of Phenetics: Towards Population Meronomy* (Akademkniga, Yekaterinburg, 2005) [in Russian].
31. Vasiliev, A.G. and Vasilieva, I.A., *Homological Variation of Morphological Structures and Epigenetic Divergence of Taxa: Fundamentals of Population Meronomy* (KMK Scientific Press, Moscow, 2009) [in Russian].
32. Vasiliev, A.G., Vasilieva, I.A., and Bolshakov, V.N., *Evolutional and Ecological Analysis of Stability of the Population Structure of a Species: a Chrono-Geographic Approach* (Yekaterinburg, 2000) [in Russian].
33. Zakharova, E.Yu., "Phenotypic Variation in Ural and Siberian Populations of the Heath *Coenonympha amaryllis* (Stoll, 1782)," *Russian Journal of Ecology* **2**, 162–168 (2012).
34. Zakharova, E.Yu., Chibiryak, M.V., and Rudoiskatel, P.V., "The Use of Variation Spectra in Analysis of the Number and Size of Eyespots in the Wing Pattern of *Coenonympha hero* (Linnaeus, 1761) (Lepidoptera: Nymphalidae: Satyrinae)," *Izvestiya Chelyabinskogo Nauchnogo Tsentra* **4** (34), 85–90 (2006).