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Phenotypic Variation in Ural and Siberian Populations of the Heath *Coenonympha amaryllis* (Stoll, 1782)

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Abstract—Phenotypic variation in the widespread Siberian and Mongolian butterfly species *Coenonympha amaryllis* (Stoll, 1782), an indicator of undisturbed steppe communities, is analyzed. It is shown that its size variation is influenced by a complex of climatic factors, the most important of them being the average starting date of the frost-free period and average annual temperature in the region. Longitude-dependent variation in size is described by a "sawtooth curve" characteristic of species with changing voltinism.

Keywords: geographic variation, climatic factors, natural populations, butterflies, Siberian and Mongolian species, *Coenonympha.*

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Problems in studies on the population structure of a species and intraspecific differentiation and stability of the phenetic pattern of populations are closely related to the problem of analyzing population biodiversity, since the formation of the population structure of a species is a historically long process (Vasil'ev, Vasil'eva, and Bol'shakov, 2000). The study of insular or local populations living at margins of the species range in comparison with populations from the main part of the range is especially interesting in this respect. Insects are convenient model organisms for various population ecological studies. In this study, the phenotypic variation of a widespread species of diurnal Lepidoptera is analyzed.

The heath *Coenonympha amaryllis* (Stoll, 1782) is a Siberian and Mongolian species that prefers open and moderately forested dry steppe landscapes of the steppe and forest–steppe zones (*Cheshuekrylye Buryatii*, 2007). The main part of its range in Russia covers areas of Southern and Eastern Siberia to the Kolyma basin in the northeast, the Upper Amur region, and southwestern Primorye (Korshunov and Gorbunov, 1995). In Western Siberia, the species has local distribution (Gorbunov and Kosterin, 2007); e.g., it does not currently occur in Omsk oblast, where it had the status of a "common" species in the early 20th century (Knyazev, 2009). According to the catalog of Russian lepidopterans (*Katalog cheshuekrylykh* ..., 2008), *C. amaryllis* inhabits the Middle and Southern Urals. There are published data on habitats of this species in Chelyabinsk oblast, Orenburg oblast, and Bashkortostan (Gorbunov et al., 1992; Gorbunov and Olschwang, 1997; L'vovskii and Morgun, 2007), while the presence of this species in northern areas of this part of its range, such as Perm, Sverdlovsk, and Tyumen oblasts, is very doubtful. In Chelyabinsk oblast (Verkhneural'sk district), a local population of *C. amaryllis* was reliably identified in the Leonovskie Mountains; its size remains unknown, and therefore *C. amaryllis* was included in the regional Red Data Book as a rare and poorly studied species (category IV) (*Krasnaya kniga* ..., 2005).

Despite the large range occupied by *C. amaryllis*, relatively few its subspecies have been described, compared to other species of the genus, e.g., *C. pamphilus* (Linnaeus, 1758) and *C. tullia* (Müller, 1764). In the classic study by Davenport (1941), in addition to the nominotypical *C. amaryllis*, four other subspecies are listed: *C. a. accrescens* Staudinger from China and Korea, *C. a. rinda* Ménétries from Amur oblast, *C. a. tydeus* Leech from eastern Tibet, and the new subspecies *C. a. emmonsi* Davenport from the environs of Lhasa and adjacent areas. The subspecies *C. a. borisovi* Korshunov et Ivonin, 1996 was described from the Baikal region (Listvyanka, Severobaikal'sk, and Kultuk). It is distinguished by a relatively large size, deeper gray background coloration of the wings, and enlarged eye spots in the wing pattern. Korshunov (2002) advanced this subspecies to the species rank and regarded it as a Baikal endemic on the basis of large eye-spots in its wing pattern and a specific structure of the male genitalia. However, according to other authors (Gorbunov and Kosterin, 2007; Tuzov et al., 1997), this subspecies, or even species, is nothing more than a geographic form living under the specific microclimatic conditions of the southern bank of Lake

Table 1. Sizes of *Coenonympha amaryllis* samples and the coordinates and some climatic parameters of species habitats in Russia

City or village	*N*, ind.		Coordinates (N; E)	Annual average temperature, °C	Average date of the start of frost-free period	Average duration of frost-free period	Annual average percipitation, mm	Aridity index
	Males	Females						
Verkhneural'sk	57	23	53°52′; 59°13′	1.0	May 1 – June 1	90–120	363	3.3
Ongudai	10	–	50°44′; 86°12′	–5.8	June 21 or later	60–90	608	14.5
Minusinsk	15	–	53°42′; 91°42′	0.7	June 11 – June 21	90–120	361	3.4
Krasnoyarsk	9	–	56°00′; 92°47′	0.5	May 1 – June 1	90–120	476	4.5
Maritui	6	–	51°47′; 104°12′	–1.1	June 11 – June 21	60–90	475	5.3
Irkutsk	12	8	52°27′; 104°31′	–1.1	June 1 – June 11	90–120	475	5.3
Kyakhta	6	–	50°35′; 106°45′	0.1	June 11 – June 21	90–120	343	3.4
Ulan-Ude	5	–	51°30′; 107°30′	–0.5	June 1 – June 11	90–120	240	2.5
Nerchinsk	24	12	52°04′; 116°35′	–3.5	June 11 – June 21	60–90	423	6.5
Sretensk	41	–	52°24′; 117°43′	–3.2	June 11 – June 21	60–90	354	5.2

Baikal. A large part of the *C. amaryllis* range, including the Urals, is occupied by the nominotypical subspecies.

In this study, the morphological variation of the forewing and hindwing length and eye-spot diameter in the wing pattern is analyzed for the nominotypical subspecies of *C. amaryllis*, which occurs in the forest-steppe and steppe zones of Russia from 59°E (Chelyabinsk oblast) to 117°E (Chita oblast), depending on the climatic conditions of a given region.

MATERIAL AND METHODS

Samples of *C. amaryllis* from different parts of its range in Russia were collected over the period from 1892 to 1930 and are stored in the archival collection of the Zoological Institute of the Russian Academy of Sciences, St. Petersburg. The author has also used her own materials of this species collected in the Southern Urals (the Leonovskie Mountains, Verkhneural'sk district, Chelyabinsk olbast) between June 23 and 28, 2009.

Since the geographic variation of the species was analyzed over a large part of its range, it was necessary to take into account climatic conditions in various habitats. Table 1 shows data on sample sizes, coordinates of areas, average starting dates and duration of the frost-free period (*Klimaticheskii atlas SSSR*, 1960), and annual average temperatures and precipitation (http://meteo.ru/climate/). As an integrated parameter characterizing climate, the de Martonne aridity index was calculated: $I = P/(T + 10)$, where P is the average annual precipitation and T is the average annual temperature in a given area.

Laboratory processing of the material included measurements of the forewing length (LF), hindwing length (LH) and the diameters of eye-spots in the wing pattern on the ventral surface. The measurements were made with an MBS-10 binocular microscope using an ocular micrometer at a magnification of 8 × 0.6, recalculating the results in millimeters. The scheme of measurements and nomenclature of the spots in the wing pattern are shown in Fig. 1.

Variation in metric characters (eye-spot size and wing length) was analyzed using discriminant analysis; the influence of climatic factors on individual size was estimated by one-way ANOVA in the Statistica 5.5 program package.

RESULTS AND DISCUSSION

Table 2 shows average values of the forewing and hindwing lengths and the diameters of eye spots in the wing pattern for samples of male and female *C. amaryllis*. As in most other species of the genus *Coenonympha* Hübner, female *C. amaryllis* are somewhat larger than males: their wing length is on average 0.5–1.0 mm greater. The size parameters of the Irkutsk sample proved exceptional: the forewing length was 16.3 ± 0.7 mm in females and 16.4 ± 1.1 mm in males. In addition, females had a greater average number of eye spots, which were also larger than in males. This is also characteristic of other heath species, e.g., *C. hero* (Linnaeus, 1761) (Zakharova, Chibiryak, and Rudoiskatel', 2006), *C. oedippus* (Fabricius, 1787) (Zakharova and Ivanov, 2009), and *C. pamphilus* (Linnaeus, 1758) (Zakharova, 2008).

Because of sexual dimorphism in morphological characters of *C. amaryllis*, subsequent analysis of geographic variation was performed taking into account

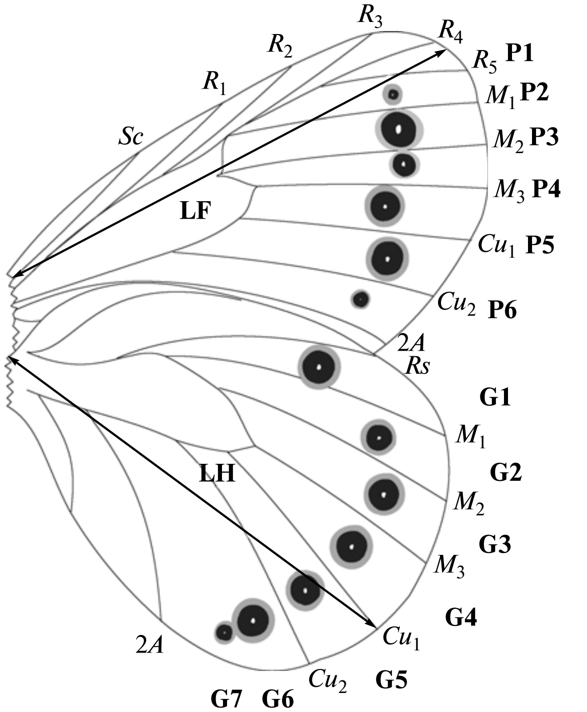

Fig. 1. Maximum numbers of eye spots in the wing pattern of *Coenonympha amaryllis* (Stoll, 1782) and scheme of forewing (LF) and hindwing (LH) measurements: P1–P6, spots of forewing pattern; G1–G7, spots of hindwing pattern.

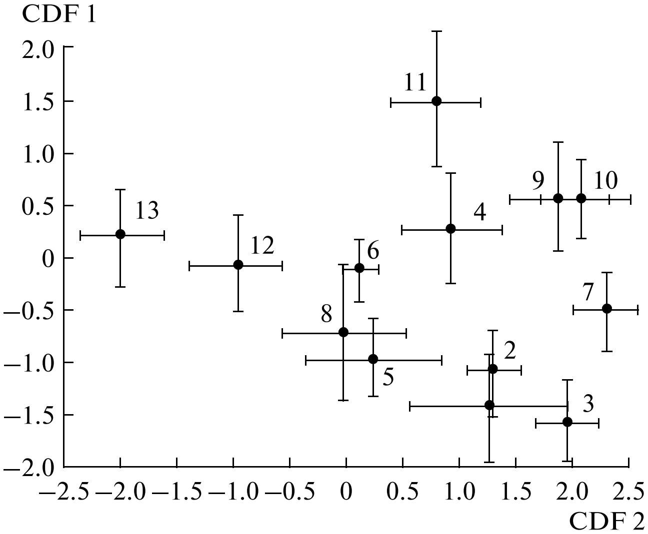

Fig. 2. Results of discriminant analysis of wing length and eye-spot size in the wing pattern of *C. amaryllis* (standard deviations for sample centroids in the space of two canonical discriminant functions, CDF, are shown). Samples: (1) Ongudai, males; (2) Minusinsk, males; (3) Krasnoyarsk, males; (4) Irkutsk, males; (5) Irkutsk, females; (6) Kyakhta, males; (7) Ulan-Ude, males; (8) Maritui, males; (9) Sretensk, males; (10) Nerchinsk, males; (11) Nerchinsk, females; (12) Verkhneural'sk, males; (13) Verkhneural'sk, females.

the sex of individuals. Figure 2 shows the results of discriminant analysis for the complex of metric characters (forewing and hindwing length and diameters of eye spots). Two characters, the sizes of eye spot P6 in the forewing and eye-spot G7 in the hindwing, were excluded from analysis because of their rare occurrence. Eye-spot P6 was found only in the sample of males from Verkhneural'sk, in 1.6% individuals; and the occurrence frequency of eye-spot G7 is at most 20%, while in some samples it is totally absent (Zakharova, 2010).

The results of discriminant analysis show that the sample from the local Southern Ural population (Verkhneural'sk) is very peculiar phenotypically and significantly differs from samples collected in other regions of Siberia. The values of Mahalanobis distances between the Verkhneural'sk and other samples are in most cases maximal and statistically significant (Table 1). The geographic remoteness and isolation from the main part of the range explains the differences found in the complex of metric characters. The samples of males from Kyakhta and Ulan-Ude proved similar to those from other habitats (the differences between them are not significant), which is probably explained by the small sample size (Table 1). The first canonical discriminant function (CDF 1), reflecting geographic differences, accounts for 69.64% of the intergroup variance, while CDF 2 accounts for 12.45%.

The largest spots are found in the wing pattern of butterflies from Maritui station (Table 2). They are probably similar to the form *C. a. borisovi* Korshunov et Ivonin, 1996, described on the basis of a full set of large spots in the wing pattern. The author's data confirm the presence of a specific geographic form of *C. amaryllis* on the southern bank of Lake Baikal.

To elucidate the pattern of clinal variation in the size of *C. amaryllis* over a large part of its range, we used one-way ANOVA with some climatic parameter as the independent factor. Female samples were excluded from analysis because of their small size, and the pattern of geographic variation was estimated using exclusively male samples.

There is a distinct correlation between the size of *C. amaryllis* individuals and the average starting date of the frost-free period (Fig. 3a). The influence of this factor on the forewing and hindwing length is significant (Wilks's $\lambda = 0.651$, $F = 16.786$, $p = 0.0001$) and readily explicable: the earlier the frost-free period starts, the longer is the growing season as a whole, which allows larvae to feed for longer than in areas with shorter summers. This rule is also confirmed by other data: the largest *C. amaryllis* individuals studied by the author are from the Southern Urals, where the frost-free period starts relatively early; the smallest are from the Altai, where this period starts after June 21 (Tables 1, 2; Fig. 3a). The influence of the average annual temperature on the wing length variation in

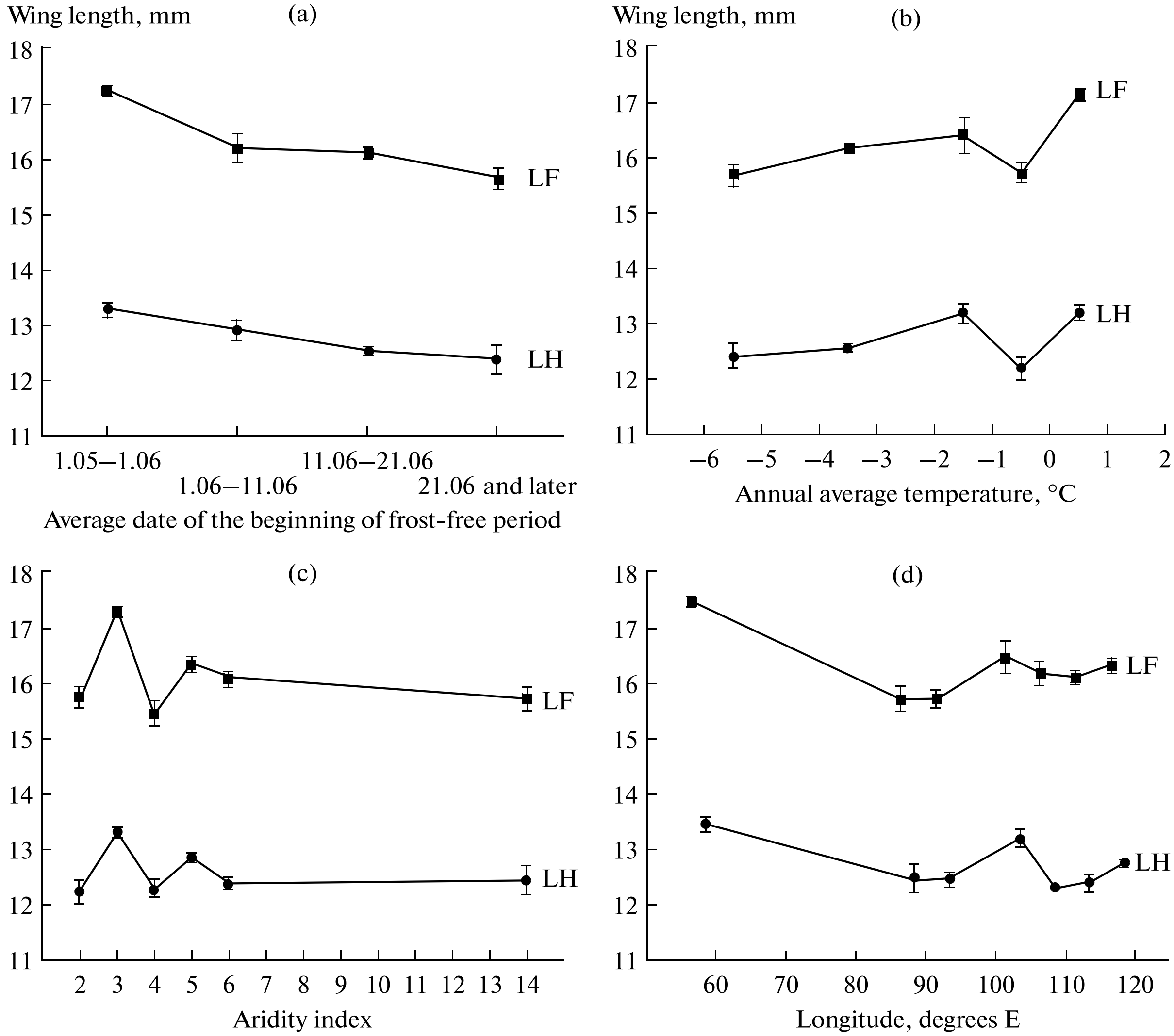

Fig. 3. Variation of forewing length (LF) and hindwing length (LH) in male *C. amaryllis* (mm), depending on (a) the beginning of frost-free period, (b) annual average temperature, (c) aridity index, and (d) longitude of the area.

C. amaryllis is also significant (Wilks's $\lambda = 0.492$, $F = 22.69$, $p = 0.0001$) and can be characterized as follows: in areas with lower average annual temperatures, butterflies of this species are smaller than in areas with higher temperatures (Fig. 3b). One exception is the male sample from Ulan-Ude, where, despite a relatively high annual average temperature (–0.5°C), the forewing length in *C. amaryllis* averages 15.7 ± 0.2 mm.

The results of the analysis of variation in *C. amaryllis* size depending on the degree of climate aridity (the value of aridity index) are shown in Fig. 3c. ANOVA confirmed a significant influence of this factor on variation in wing length (Wilks's $\lambda = 0.601$, $F = 12.30$, $p = 0.0001$), but no distinct trend could be revealed in this case. It is known from the literature (Gorbunov and Kosterin, 2007) that *C. amaryllis* in the eastern part of its range occurs in habitats differing in moisture supply (forest-steppe, tundra, and waterlogged areas, including swamped sparse larch stands), but is strictly xerophilous in the western parts of its range. The degree of climate aridity probably limits the distribution of the species beyond the boundaries of the steppe and forest–steppe zone, but the size of *C. amaryllis* does not directly depend on this factor.

The longitude-dependent geographic variation in the size of *C. amaryllis* has a "sawtooth" pattern (Fig. 3d). As shown for diurnal lepidopterans of some families (Lycaenidae, Nymphalidae, and Satyridae), this type of latitudinal or longitudinal geographic variation in size is found in species with voltinism changing over their ranges. It is believed that the body size of insects living in southern habitats is larger than that of insects living in northern habitats because the period favorable for their development is relatively longer. A considerable amount of recent data on clinal variation in the size of insects provide evidence either for or

Table 2. Average values of wing length and eye-spot diameters in the wing-pattern of *C. amaryllis*, mm

Sample	Forewing length, LF	Spots in cells of forewing					Hind-wing length, LH	Spots in cells of hindwing						
		R_5-M_1	M_1-M_2	M_2-M_3	M_3-Cu_1	Cu_1-Cu_2		Rs-M_1	M_1-M_2	M_2-M_3	M_3-Cu_1	Cu_1-Cu_2	Cu_2-$2A$	Cu_2-$2A$
		P1	P2	P3	P4	P5		G1	G2	G3	G4	G5	G6	G7
Verkhneural'sk, males	17.4 ± 0.7	0.3 ± 0.4	1.8 ± 0.2	1.1 ± 0.5	1.5 ± 0.3	1.5 ± 0.2	13.4 ± 1.4	1.8 ± 0.3	1.6 ± 0.2	1.5 ± 0.2	1.7 ± 0.2	1.7 ± 0.2	1.3 ± 0.2	0.1 ± 0.2
females	17.7 ± 0.6	0.7 ± 0.5	2.0 ± 0.2	1.4 ± 0.3	1.7 ± 0.2	1.8 ± 0.2	14.1 ± 0.5	1.9 ± 0.2	1.7 ± 0.2	1.5 ± 0.3	1.9 ± 0.2	1.8 ± 0.2	1.3 ± 0.3	0.1 ± 0.1
Ongudai, males	15.7 ± 0.7	0.4 ± 0.4	1.7 ± 0.1	1.2 ± 0.2	1.4 ± 0.3	1.4 ± 0.2	12.4 ± 0.8	1.7 ± 0.3	1.3 ± 0.3	1.3 ± 0.2	1.6 ± 0.3	1.6 ± 0.2	1.3 ± 0.2	0.1 ± 0.1
Minusinsk, males	15.9 ± 0.6	0.3 ± 0.4	1.5 ± 0.1	0.8 ± 0.3	1.2 ± 0.2	1.3 ± 0.2	12.5 ± 0.6	1.6 ± 0.1	1.4 ± 0.1	1.2 ± 0.1	1.5 ± 0.1	1.5 ± 0.1	1.1 ± 0.1	0.1 ± 0.1
Krasnoyarsk, males	15.4 ± 0.7	0.3 ± 0.3	1.6 ± 0.1	0.9 ± 0.3	1.1 ± 0.2	1.4 ± 0.2	12.3 ± 0.5	1.6 ± 0.4	1.3 ± 0.3	1.2 ± 0.2	1.5 ± 0.3	1.6 ± 0.2	1.2 ± 0.2	0.1 ± 0.2
Maritui, males	17.1 ± 0.3	1.6 ± 0.1	2.1 ± 0.2	1.7 ± 0.1	1.8 ± 0.1	1.8 ± 0.1	13.3 ± 0.4	2.2 ± 0.1	1.8 ± 0.2	1.6 ± 0.2	2.0 ± 0.1	2.0 ± 0.1	1.7 ± 0.1	0.6 ± 0.1
Irkutsk males	16.4 ± 1.1	0.4 ± 0.4	1.6 ± 0.1	1.0 ± 0.4	1.3 ± 0.2	1.2 ± 0.3	13.2 ± 0.6	1.7 ± 0.1	1.2 ± 0.2	1.2 ± 0.2	1.4 ± 0.2	1.4 ± 0.3	1.1 ± 0.2	0.2 ± 0.3
females	16.3 ± 0.7	0.9 ± 0.2	1.7 ± 0.2	1.2 ± 0.4	1.5 ± 0.2	1.4 ± 0.2	13.3 ± 0.9	1.8 ± 0.1	1.5 ± 0.2	1.5 ± 0.2	1.6 ± 0.2	1.5 ± 0.1	1.2 ± 0.1	0.1 ± 0.1
Kyakhta, males	16.6 ± 0.3	0.5 ± 0.3	1.8 ± 0.1	1.0 ± 0.4	1.4 ± 0.2	1.5 ± 0.2	12.4 ± 0.3	1.8 ± 0.2	1.5 ± 0.1	1.3 ± 0.1	1.6 ± 0.1	1.5 ± 0.1	1.2 ± 0.1	0.3 ± 0.3
Ulan-Ude, males	15.7 ± 0.2	–	1.3 ± 0.1	0.6 ± 0.3	1.0 ± 0.1	1.1 ± 0.1	12.2 ± 0.2	1.4 ± 0.1	1.2 ± 0.1	1.1 ± 0.0	1.2 ± 0.1	1.4 ± 0.1	1.0 ± 0.1	–
Sretensk, males	16.3 ± 0.7	0.3 ± 0.3	1.5 ± 0.2	0.8 ± 0.3	1.2 ± 0.3	1.3 ± 0.2	12.7 ± 0.4	1.4 ± 0.2	1.1 ± 0.2	1.1 ± 0.2	1.2 ± 0.2	1.3 ± 0.2	1.1 ± 0.2	0.1 ± 0.2
Nerchinsk, males	16.1 ± 0.5	0.3 ± 0.4	1.5 ± 0.2	0.9 ± 0.4	1.2 ± 0.3	1.3 ± 0.3	12.4 ± 0.6	1.3 ± 0.2	1.0 ± 0.2	1.0 ± 0.1	1.2 ± 0.2	1.3 ± 0.2	1.0 ± 0.2	–
females	16.9 ± 0.7	0.6 ± 0.3	1.5 ± 0.2	0.8 ± 0.3	1.3 ± 0.2	1.3 ± 0.4	13.4 ± 0.6	1.5 ± 0.3	1.2 ± 0.3	1.1 ± 0.2	1.3 ± 0.4	1.4 ± 0.3	0.9 ± 0.4	0.1 ± 0.1

Table 3. Generalized Mahalanobis distances between samples of *C. amaryllis* according to a complex of metric characters

Sample no.	1	2	3	4	5	6	7	8	9	10	11	12
	Ongu-dai	Mi-nusinsk, males	Krasno-yarsk, males	Irkutsk, males	Kyakh-ta, males	Ulan-Ude, males	Sretensk, males	Nerchinsk, males	Verkhneu-ral'sk, males	Irkutsk, females	Nerchin-sk, fe-males	Verkhneu-ral'skfe-males
1	0.00	3.82	2.10	4.64	5.85	7.20	**5.96**	**5.72**	**9.28**	6.01	**11.13**	**14.91**
2		0.00	2.44	**5.56**	3.76	3.66	**4.40**	**5.10**	**8.04**	4.89	**7.49**	**14.57**
3			0.00	**7.11**	7.23	5.28	**5.87**	**6.30**	**12.82**	8.31	**12.20**	**20.39**
4				0.00	5.21	6.63	3.39	4.56	5.61	5.15	4.96	11.02
5					0.00	9.61	6.11	6.53	3.25	5.16	6.22	6.47
6						0.00	3.22	4.69	**13.00**	**11.65**	9.77	**23.81**
7							0.00	0.91	**8.92**	**8.63**	**4.30**	**16.86**
8								0.00	**11.05**	**10.09**	**4.11**	**18.15**
9									0.00	**7.07**	**7.90**	**3.26**
10										0.00	**8.76**	**9.63**
11											0.00	**10.44**
12												0.00

Note: Differences statistically significant at $p < 0.05$ according to F-test are boldfaced.

against Bergmann's rule, which was originally formulated for vertebrates (Blanckenhorn et al., 2006).

A gradual increase in the size of adult insects size in the north–south direction can be expected in univoltine species, or in bi- and multivoltine species that can switch to univoltinism. In cases where the shift from uni- to bivoltinism takes place, the dependence of body size on latitude has a sawtooth pattern (Nylin and Svärd, 1991; Karl et al., 2008). Indeed, according to this author's results, the decreasing size of *C. amaryllis* in areas located at 90–95° E can be explained by the presence of the bivoltine life cycle in this part of the range. Korshunov observed in 1969 the flight of two generations of *C. amaryllis* in Khakassia; the emergence of adults of the first generation started during the second half of June, and the emergence of adults of the second generation took place during the last ten days of July and in August (Korshunov, 2002). Several generations during the warm season (flight of adults from the first ten days of June to early September) were also observed in Dauria (115–116°E) (Dubatolov and Kosterin, 1999). According to published data, the species is univoltine in Eastern Siberia and the Russian Far East, as well as in the Southern Urals.

CONCLUSIONS

The heath *Coenonympha amaryllis* (Stoll, 1782), along with the sulphur *Colias heos* (Herbst, 1792) and the lycaenid *Agrodiaetus damon* ([Dennis & Schiffermüller], 1775), is an indicator species of undisturbed steppe communities. The abundance of these species decreases due to plowing of virgin lands, overgrazing by livestock, mowing, and springtime burning of dry grass in steppes and steppe-like biotopes (Berlov and Berlov, 2006).

Analysis of a complex of metric characters (the wing length and the size of spots in the wing pattern) has revealed a considerable level of geographic variation in the nominotypical subspecies of *C. amaryllis* over a large part of its range. Two of the populations studied have a distinctive phenetic image (large individual size and relatively large eye spots in the wing pattern): in the Leonovskie Mountains near Verkhneural'sk (Chelyabinsk oblast) and on the southern coast of Lake Baikal (Maritui station, Irkutsk oblast). The sample from Maritui station can possibly be attributed to the subspecies *C. a. borisovi* Korshunov et Ivonin, 1996. The longitude-dependent geographic variation in the size of *C. amaryllis* is described by a sawtooth curve, which, according to the literature, reflects the clinal variation of species capable of switching from univoltinism to bivoltinism in both longitudinal and latitudinal directions. The results of this study on *C. amaryllis* populations agree with published data (Nylin and Svärd, 1991; Karl et al., 2008). It has been found that the size variation in *C. amaryllis* is significantly dependent on the average starting date of the frost-free period and annual average temperature in a given area. The influence of the degree of aridity on the size of *C. amaryllis* is ambiguous but appears to play an important role, because the distribution of the species is limited to the forest-steppe and steppe zones.

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