

SHORT
COMMUNICATIONS

Changes in the Population Phenetic Structure of the Lacebug *Dictyla humuli* (Fabr.) (Heteroptera, Tingidae) in the Usman' Forest (Voronezh Oblast) in 1999–2001

O. A. Sherstneva¹, V. B. Golub¹, and A. S. Baranov²

¹Voronezh State University, Universitetskaya pl. 1, Voronezh, 394623 Russia

²Kol'tsov Institute of Developmental Biology, Russian Academy of Sciences,
ul. Vavilova 26, Moscow, 117808 Russia

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Analysis of the population phenetic structure of a species and its spatial and temporal variation is an important line of research in microevolution. The choice of the object (model species) and its characteristics to be estimated, as well as the determination of their quantitative and qualitative variations, plays an important role in these studies. The variant frequencies reflect the pattern of phenotypic and genotypic changes at the population level (Timofeeff-Ressovsky *et al.*, 1973; Yablokov, 1980). Although this field of research is of primary importance, few studies have dealt with variations in insect populations with time. In some insect species, the phenotypic characteristics of the populations have been found to remain stable during the study period. These are *Trichius fasciatus* (Novozhenov, 1977, 1989), *Brachyta interrogationis*, *Pachyta quadrimaculata* (Novozhenov, 1980, 1989), *Melolontha hippocastani* (Novozhenov, 1982), *Leptinotarsa decemlineata* (Kokhmanyuk, 1982), and *Philaenus spumarius* (Novozhenov, 1989). Specific, stable phenotypic characteristics are typical of the populations of some moths, such as *Argynnis paphia* and *Pararge aegeria*, notwithstanding their migrations (Novozhenov, 1989). Other insects, e.g., some Meloidae, are characterized by long-term variations in phenotypic characteristics from year to year (Bakirova, 1985).

Lacebugs (Heteroptera, Tingidae), a peculiar family of phytophagous insects, seem to be a promising model for phenetic studies. Their integuments have an areolate structure whose variation is clearly discrete and may be easily formalized based on the number of cells in the pattern. The geographic range of the lacebug *Dictyla humuli* (Fabr.) encompasses almost all of central Europe and a considerable part of southern Europe and spreads to Siberia as far east as the Angara River; the species is also abundant in Transcaucasia and has been found in Turkey and northern Iran (Péricart, 1983; Péricart and Golub, 1996; Golub, 1997). *Dictyla humuli* inhabits wet biotopes (floodplains, depressions, and waterlogged spots in forests, forest edges, and open places), where it lives on some representatives of the

family Boraginaceae (Bator, 1953; Puchkov, 1974; Péricart, 1983). *Symphytum officinale* L. is its main food plant in eastern European forest-steppe. The species is characterized by high abundance, low mobility, and confinement to specific food plants.

Adult *D. humuli* are small; their body length is only 3.1–3.8 mm. The pronotal disk has a coarse punctured pattern, which becomes areolate on the triangular hind process of the pronotum (Fig. 1). The lateral regions of the pronotum are areolate, considerably widened, and have edges rolled onto the disk (paranota). Three low, platelike carinae run along the pronotum. The hind portion of the pronotum is drawn into the areolate triangular process.

The areolate elytra are divided into fields by longitudinal veins protruding upward. The most lateral (costal) area has one row of cells over the greater part of its length and has two rows of cells at the base and near the apex. In some cases, there are a few second-row cells in the central part of the costal area, as an expression of variation. The subcostal area, which is located closer to the midline, has three rows of cells over the greater part of its length. The areolate discoid area is the most median. The vein dividing the subcostal and discoid areas ($R + M$) markedly protrudes in the form of a carina. In two points (in the middle and at the junction with the cubital vein (Cu)), it forms two distinct swellings, each enclosed in a blackish spot. The number of cells enclosed in the dark spots varies in different individuals.

To analyze the population phenetic structure of *D. humuli* and its changes with time, samples were collected during three growing seasons (1999–2001) in the lacebug population of the Usman' forest, 20 km north-northeast of the city of Voronezh. The lacebugs were collected on the leaves and flowers of *Symphytum officinale* in the same period (from June 23 to July 7) every year. The samples comprised 150–200 lacebugs. We randomly chose at least 35 lacebugs from each sample (50, 50, and 35 in 1999, 2000, and 2001, respectively).

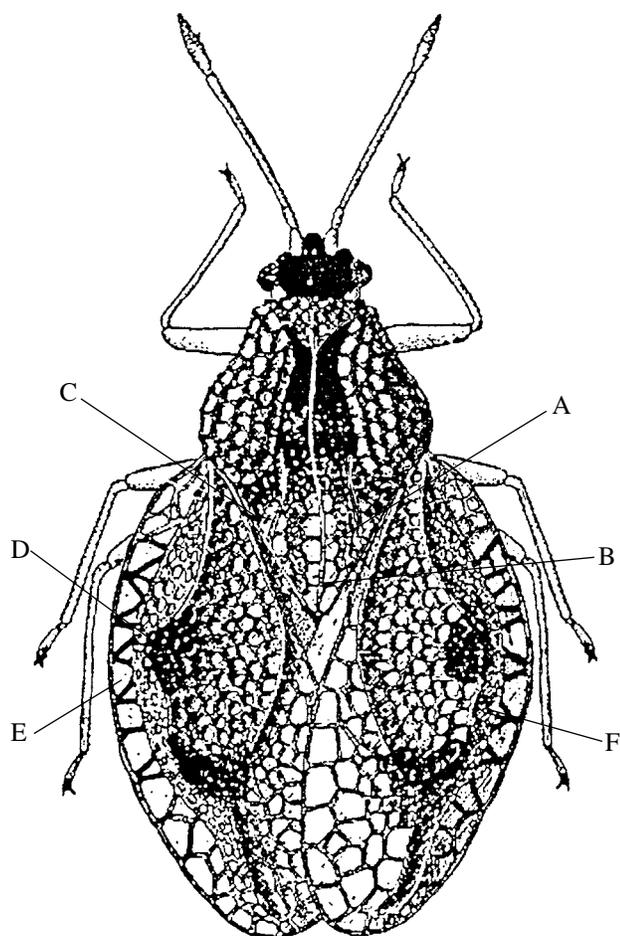


Fig. 1. General view of *Dictyla humuli* (Péricart, 1983): A–F, the morphological traits analyzed (for details, see the text).

The samples were compared with respect to six traits and their discrete variations (Fig. 1): trait A, the number of cells along the median carina of the pronotum, on its hind process (five, six, and seven cells were designated as A_1 , A_2 , and A_3 , respectively); trait B, the number of cells along the edge of the hind process of the pronotum (the presence of four, five, six, and seven cells was designated as B_1 , B_2 , B_3 , and B_4 , respectively); trait C, the number of cells between the lateral carina of the pronotum and the basal angle of the rolled paranotum, perpendicular to the midline of the body (the presence of two and three cells was designated as C_1 and C_2 , respectively); trait D, the number of longitudinal cell rows in the widest part of the subcostal field of the elytra (the presence of three rows was designated as D_1 ; the presence of three rows and one cell of the fourth row, D_2); trait E, the number of extra cells, in addition to the row of large cells, in the costal field of the elytra (the absence of such cells and the presence of zero, one, two, three, four, five, and six cells was designated as E_1 , E_2 , E_3 , E_4 , E_5 , E_6 , and E_7 , respectively); and trait F, the number of cells within the dark spots on the elytra (the presence of 4, 5, 6, 7, 8, 9, 10, and 11 cells was designated as F_1 , F_2 , F_3 , F_4 , F_5 , F_6 , F_7 , and F_8 , respectively).

In the material collected, we found a total of 26 quantitative variations. Each trait was analyzed separately using the intrapopulation diversity parameter (μ). To compare the population phenepools in different years, we calculated the mean parameter for all traits studied (Zhivotovsky, 1982).

Our analysis (table) showed that population phenotypic diversity considerably decreased during the three years of the study. The differences between mean values in both pairs of successive years (1999 and 2000; 2000 and 2001) were statistically significant ($t < 0.05$). The parameters of the phenetic diversity of individual traits also differed significantly. The vector of their changes in different years varied depending on the ratio between the frequencies of individual variants of each trait.

The changes in the μ values for traits A and D were synchronous, these values being lower in 2000 than in 1999 and 2001 (table). Apparently, the frequencies of different variants of both traits oscillated cyclically, which determined the decrease and subsequent increase in the μ values for these independent traits. For example, the frequencies of different variants of trait A changed as follows (Fig. 2): the frequency of variant A_1 decreased from 0.45 in 1999 almost to zero in 2000 and slightly increased (only to 0.11) in 2001; the frequency of variant A_2 permanently increased to 0.69 in 2001; and the frequency of A_3 gradually decreased from year to year.

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Values of phenetic diversity parameter for six traits in *Dictyla humuli* samples from the Usman' forest ($\mu \pm S_\mu$)

Year	N	Trait						$\mu_m \pm S_\mu$
		A	B	C	D	E	F	
1999	50	2.76 \pm 0.081	2.79 \pm 0.184	1.99 \pm 0.014	1.61 \pm 0.079	6.25 \pm 0.217	5.81 \pm 0.357	3.54 \pm 0.115
2000	50	2.34 \pm 0.124	2.59 \pm 0.191	1.99 \pm 0.014	1.54 \pm 0.084	3.76 \pm 0.349	6.86 \pm 0.279	3.18 \pm 0.128
2001	35	2.56 \pm 0.106	2.59 \pm 0.191	1.93 \pm 0.037	1.90 \pm 0.044	3.28 \pm 0.349	4.41 \pm 0.398	2.78 \pm 0.151

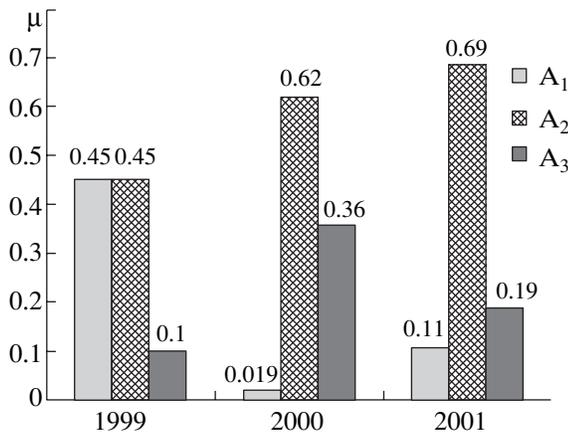


Fig. 2. Frequency distribution of the variants of trait A (the number of cells along the median carina of the pronotum, on its hind process). Variants A₁–A₃ correspond to numbers of cells from five to seven.

Thus, the frequency of the variant with the mean value of the trait increased during the three years of the study, and the variant with the minimum value almost disappeared.

The μ value for trait B was somewhat decreased in 2000 compared to 1999 (from 2.79 to 2.59) and remained approximately the same in 2001. As with traits A and D, the relative frequencies of the variants with average values of the trait tended to increase, and the frequency of one of the extreme variants (in this case, that with the maximum value) considerably decreased.

The phenetic diversity with respect to trait C was relatively stable: it was the same in the first two years and only slightly decreased (by 0.06) in the third year of the study. In 2001, the frequency of variant C₁ (i.e., the variant with the lower value of the trait) was somewhat increased.

The difference between the frequencies of two D variants slightly increased in 2000 compared to 1999 and decreased in 2001.

The diversity with respect to trait E distinctly decreased during the study period; it was almost twice as low in 2000 compared to 1999. The distribution of variant frequencies in 1999 was close to normal. In 2000, the frequencies of the variants with lower values of the traits tended to increase, whereas those of the variants with higher values drastically decreased, and the variant with the maximum value of the trait was eliminated. In 2001, one more variant (again, that which corresponded to the maximum value of the trait in that year) disappeared. The differences between the frequencies of the remaining variants decreased (Fig. 3). In morphological terms, the deviation from the normal distribution of the variants of trait E that occurred in the population studied during two years resulted in an increased proportion of lacebugs with a

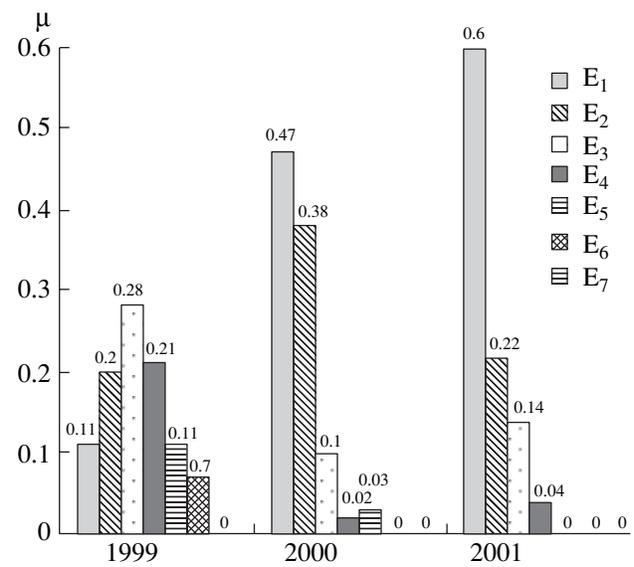


Fig. 3. Frequency distribution of the variants of trait E (the number of extra cells, in addition to the row of large cells, in the costal field of the elytra). Variants E₁–E₇ correspond to numbers of cells from zero to six.

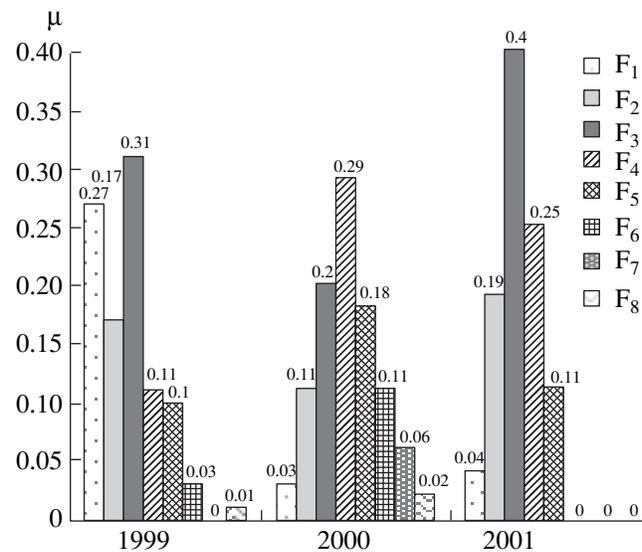


Fig. 4. Frequency distribution of the variants of trait F (the number of cells within the dark spots on the elytra). Variants F₁–F₈ correspond to numbers of cells from 4 to 11.

narrow costal field, because additional cells slightly widened it.

The μ value for trait F increased in 2000 compared to 1999 and decreased again in 2001. In 1999, the variants with lower values of the trait were considerably more frequent (Fig. 4). One of the variants (F₇) was absent altogether. In 2000, the proportion of variants with average values of the trait distinctly increased, and their distribution became close to normal. Therefore,

the phenetic diversity drastically decreased. In 2001, the normal distribution curve slightly shifted toward an increased proportion of variants with lower values of the trait, compared to the distribution observed in 2000. As in 1999, variant F₃ became prevalent, its frequency being even higher than in 1999. Three variants, F₆, F₇, and F₈, were eliminated altogether.

Thus, the comparative analysis of the population phenetic structure of *D. humuli* allowed us to determine some common patterns of changes in the phenetic diversity of different samples from the Usman' forest population of *D. humuli*. Traits B, E, and F were the most variable, with the dominant variants of these traits changing during the period studied. Traits E and F exhibited high intrapopulation diversity and considerable variation in the diversity parameters during the study period. Trait B was also variable; however, its μ value was lower and varied only slightly.

The population diversity with respect to traits A, C, and D was the most stable. Their diversity parameters insignificantly varied over three years.

The mean intrapopulation diversity gradually decreased during the three years of the study. Apparently, this was mainly accounted for by the decrease in μ for trait E during the last two years (2000 and 2001).

In general, the results of our study indicate that the general phenetic diversity of the population decreases with time due to changes in the frequencies of individual variants, with some of them being eliminated, resulting in differently directed variations of different traits. The droughty conditions of the three years of the study are a possible cause of the decrease in population phenotypic diversity, because they may have led to decrease in the frequencies or complete elimination of the phenotypes that were indirectly related to vitally important characteristics of the object.

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