Variability of genitalia and pheromone communication channels of *Archips podana* (Scopoli) (Lepidoptera: Tortricidae)

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Abstract. The large fruit-tree tortrix *Archips podana* (Scopoli) is a widely distributed species in the whole of Europe. The species is variable in male genitalia. According to the different number and position of apical (A) and lateral (L) spikes on the aedeagus, A, L, 2L, AL, A2L, and 0 (without spike) phenotypes were discriminated. To determine the variability of pheromone communication of *A. podana*, field trap tests were conducted in different habitats and geographical regions in Estonia (Uhti and Otepää), northwestern Russia (Velikie Luki, Pskov Region), and the North Caucasus (Krasnodar Territory). The optimum content of Z-11-tetradecenyl acetate in pheromone blend, calculated using the Gaussian curve, was on average $61.3 \pm 1.3\%$. This is practically identical to the ratio of 60:40 in the mixture of (Z)- and (E)-11-tetradecen-1-yl acetates identified by Persoons et al. (1994, *J. Insect Physiol.*, **20**, 1181–1188). Experiments demonstrated that the optimal pheromone composition was the same in Krasnodar, where the L phenotype dominates, and in Velikie Luki and Estonia, where A phenotype males dominate. A deviation of attractive blend from optimum ratio causes a comparable decrease in trap catches for males of different aedeagus forms. The Caucasian subspecies with a lateral spike (male phenotype L), *A. podana meridiana* Kozl. et Esart., is placed in synonymy to nominotypical species in this paper. Calculation of pheromone communication parameters – channel width and optimal ratio – is an effective tool for ecochemical research and dispenser modelling.

Key words: normal distribution, pheromone communication channel, *Archips podana*, Tortricidae, phenotypes, population variability, (E)-11-tetradecenyl acetate, (Z)-11-tetradecenyl acetate.

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INTRODUCTION

The large fruit-tree tortrix (the omnivorous leafroller, apple surface eating tortricid) *Archips podana* (Scopoli) is a widely distributed species inhabiting the whole of Europe (Kuznetsov, 1978). Data from Asia Minor need confirmation (Razowski, 1977), whereas records from Siberia and the Far East belong to another species of the genus (Razowski, 1981; Kuznetsov, 1994). Polyphagous *A. podana* feeds on up to 28 plant species. The most preferable are *Betula* spp., *Fraxinus excelsior*, and *Ribes* spp. Fruit trees such as *Prunus*, *Malus*, and *Cerasus* are moderately inhabited (Litvinova, 1974). In regions with two generations of *A. podana* it is considered to be an important pest (Persoons et al., 1974), while in regions of one generation its damages are sporadic.

The species is highly variable in fore and hind wing coloration and venation in imagoes (Galetenko, 1964; Razowski, 1977). Ivanova was probably the first to show geographical variability for *A. podana* male genitalia (Ivanova & Mõttus, 1986a, 1986b), although Galetenko (1964) had earlier argued that the aedeagus of *A. podana* (from the Crimean population, Ukraine) had no apical spike (phenotype 0), contrary to many European authors who sketched the aedeagus with an apical spike (phenotype A) (Hannemann, 1963; Kuznetsov, 1978; Razowski, 1981).

Different authors have indicated from 2 to 6 phenotypes of the species (Ivanova & Mõttus, 1986a; Kozlov & Motorkin, 1987, 1988; Safonkin, 1987a, 1987b), depending on the number and position of apical (A) and lateral (L) spikes on the aedeagus (A, L, 2L, AL, A2L, 0 as main phenotypes). The combinations may be much more numerous than listed above (Kozlov & Motorkin, 1987). The presence of lateral and the missing of apical spikes is determined by dominant alleles of at least two nonlinked genes (Kozlov, 1989). Certainly, the number of spikes on the aedeagus has no taxonomic value, as it varies greatly (from 0 to 3 apical and from 0 to 7 lateral ones) in every geographical area and in brooding of one female (Kozlov, 1989; Kozlov & Motorkin, 1990). Brun et al. (1991) described a population of *A. podana* with a lateral spike as the Corsican variety.

The female sex pheromone of *A. podana* was identified as $60:40$ mixture of (E)- and (Z)-11-tetradecen-1-yl acetates (E11-14:Ac and Z11-14:Ac, respectively) on the basis of chromatography of pheromone gland extracts (Persoons et al., 1974). On the basis of field screening the optimum ratio was estimated at $1:1$. Numerous subsequent field screening experiments of the described attractant gave discordant results. In The Netherlands and England (Persoons et al., 1974), near Paris (Frérot et al., 1979), and in the Krasnodar Territory (Ivanova & Mõttus, 1986b), the most attractive was the blend of $1:1$ (Z/E). In Belarus (Bykhovets et al., 1986), Central Russia (Ryabchinskaya et al., 1986), and Carpathians region (Safonkin, 1989), the blend of $6:4$ (Z/E) was the most attractive. On the basis of published data Ivanova & Mõttus (1986a) hypothesized differences in the pheromone communication of different phenotypes of *A. podana*. Later Kozlov et al. (1991) found that for the Voronezh population (prevailingly A phenotype) the

mixture of 50:50 of Z11-14:Ac and E11-14:Ac was significantly more attractive than the 60:40 mixture; the latter was described as the best for the Lagodekhi (Georgia) population (L phenotype). This and some more differences were the basis for determining the Caucasian subspecies of *A. podana* (males phenotype L) as *A. podana meridiana* Kozl. et Esart. (Kozlov & Esartia, 1991).

The population's polymorphism and its relation to chemical communication of *A. podana* have been intensively discussed in Russian literature (Safonkin, 1987a, 1987b, 1988, 2000; Safonkin & Buleza, 1988; Kozlov & Motorkin, 1988, 1990; Kozlov, 1989, 1990, 1991; Kozlov & Kravchuk, 1991; Mõttus & Ivanova, 1991). Some dissimilarity in ethology and the EAG response of phenotypes AL and A, as well as different sensitivity of phenotype groups A+AL and L+0 have been found (Kozlov & Motorkin, 1990). Kozlov & Motorkin (1990) mapped the phenotype ratio for different regions revealed by means of pheromone trapping (attractant with Z/E ratio of 33:66 was used). Type L strongly dominates (more than 85%) in the Caucasus and the adjacent steppe zone, including Slavyansk-na-Kubani and Krasnodar. Consequently the Corsican variety described by Brun et al. (1991) belongs to the phenotype L, widespread in the Caucasus area. Azov and Volgograd have a large fraction of phenotypes L and AL and could be considered a transitional area of the domination of phenotype A. The Carpathians males of *A. podana* have approximately the same phenotype ratio as the rest of central Europe (more than 50% of phenotype A). Safonkin (1987a, 1987b, 1988, 1990) proposed some correlation with habitat (host plants), but data from Kozlov (1989) did not confirm it.

In case the phenotypes are signs of population varieties, some differences in pheromone communication may be expected. In this paper we report our results on comparison of pheromone communication channels of *A. podana* in several regions of Russia and in Estonia.

MATERIALS AND METHODS

Traps and field tests

Field trap tests were conducted in different habitats and geographical regions in Estonia (Uhti and Otepää), northwestern Russia (environs of Velikie Luki, Pskov Region), and the North Caucasus (environs of Krasnodar) using similar methodology. Traps were hung at least 20 m apart at a height of 1.5–2.0 m and were inspected every 5 to 10 days. In Russia cardboard or plastic deltatraps Atrakon® A with a sticky base area of 225 cm², produced by AS Tartu-Flora, Tartu, Estonia, were used. The entomological glue Pestifix® (Tartu-Flora) was used in the traps. All the experiments in Russia were carried out in five replicates. In Estonia tests were conducted in ten (forest at Otepää) or five replicates.

In trees traps were hung at a height of 1.5–1.8 m. Between the trees with traps at least two trees were left without traps.

Chemicals

Compounds used in Feroflor dispensers were assayed by gas chromatography on Carbowax 20 M capillary columns, 30 m, i.d. 0.25 mm. Z11-14:Ac used in Feroflor type dispensers contained about 0.8% of Z-11-tetradecenol (Z11-14:OH), and E11-14:Ac had about 0.4% of the corresponding alcohol (E11-14:OH). The accuracy of the ratio of the components and doses in the dispensers were checked using gas chromatography and was found as ±1%. E11-14:Ac used in Miniket dispensers did not contain a detectable amount of E11-14:OH. The content of Z11-14:OH was 0.1% in Z11-14:Ac.

Dispensers

Feroflor type dispensers were used in experiments before 1999 (Mõttus & Ivanova, 1991). In 2000 and later Miniket type dispensers were used. Miniket dispensers were loaded with 1 mg of a mixture of Z11-14:Ac and E11-14:Ac with a content of 20, 40, 50, 60, 70, or 80% of Z isomer. Feroflor dispensers were loaded with blends having different ratios of the isomers. The half-life of tetradecenyl acetate isomers exceeds 4 months. The evaporation rate of the mixture from the dispensers in field did not exceed 70 ng/h. The volatility of Z and E isomers of 11-tetradecenyl acetate from the dispensers was considered equal (Mõttus et al., 2001).

Calculation of the optimum ratio of a pheromone blend

The concept of communication channel width was introduced by Howse et al. (1998). Here we use the calculated optimum ratio of isomers as one of the quantitative characteristics of pheromone communication channels. Having trap catch data for dispensers with a different content of one component (x) we used the Gaussian curve

$$f(x) = \frac{A}{\sigma\sqrt{2\pi}} \exp\left(-\frac{(x-\mu)^2}{2\sigma^2} \right) + y_0, \tag{1}$$

where μ is the location of the maximum and σ is a parameter describing the width of the curve, to calculate the optimal content of one compound, x_{max}, in two-component attractant blend. For our purpose, Eq. (1) may be written as

$$y = \frac{A}{w_c\sqrt{\frac{\pi}{2}}} \exp\left(-\frac{(x_{max}-x)^2}{w_c^2} \right) + y_0, \tag{2}$$

where w_c is the width of the pheromone communication channel (approximately equal to two standard deviations) and x_{max} is used instead of the maximum location μ.

The width of the pheromone communication channel w_c characterizes the influence of component ratio on trap catches. As seen from Eq. (2), if the content of a substance is equal to $x_{max} \pm 0.5\,w_c$, the trap catch equals $y = e^{-0.5} = 0.61$ or 61% of the maximum trap catch. In case the change of the component ratio in effluvia equals $x_{max} \pm 0.4\,\sigma$, the mean trap catches are 10% lower than y_{max}. Obviously, w_c may be used as a measure of the pheromone communication channel width (Mõttus et al., 2001).

Statistical analysis and calculations

Trap catch data for the tested blends were subjected to ANOVA and, following a significant F value, differences between treatments were determined (Sokal & Rohlf, 1986). To calculate the optimal content of the attractive blend the built-in Gauss normal distribution function of the "Origin" program was used.

Morphological analyses of the male A. *podana* trapped by different attractant blends

Correlation between the attractant component ratio and the percentage of A, L, AL, and 0 phenotype males was tested by the χ^2-test.

RESULTS
Aedeagus variability

On the basis of the number of spikes on aedeagus, four phenotypes of *A. podana* were identified in field trials in 2000. Our study of the main phenotypes within the species (Table 1) revealed that the northern Caucasian population consists mainly of L phenotype males (89%), whereas A phenotype males dominate (69–89%) in Baltic populations in Estonia and northwestern Russia.

The results of morphological analysis of *A. podana* males trapped by different attractants are summarized in Table 2. There was no significant correlation between the attractant component ratio and the percentage of A, L, AL, and 0 phenotypes in trap catch at $p < 0.1$.

Table 1. Intraspecific variability of *Archips podana* in 2000 based on the position of spikes on the aedeagus. Males trapped by Z11-14:Ac and E11-14:Ac at a ratio 60:40

Collection locality	Country	Phenotypes, no. (and %) of males				Total no. of males
		A	AL	L	0	A+AL+L+0
Krasnodar	Russia	0	1(0.2)	423(89)	52(11)	476
Velikie Luki (orchard)	Russia	565(69)	87(11)	89(11)	72(9)	813
Velikie Luki (forest)	Russia	546(73)	66(9)	52(7)	84(11)	748
Pushkin	Russia	8(89)	1(11)	0	0	9
Uhti (orchard)	Estonia	282(84)	16(5)	16(5)	20(6)	334
Otepää (forest)	Estonia	337(84)	13(3)	34(8)	20(5)	404

Table 2. Phenotypes of *Archips podana* trapped by dispensers having variable ratio of 11-tetra-decenyl acetate isomers in Russia at Velikie Luki in 1990

Z11-14:Ac in attractant, %	Total trap catch, no. of males	Morphological forms, %			
		A	AL	0	L
41	13	75	0	25	0
51	17	45	18.2	27.3	9.1
55	29	89	0	11	0
59	97	45	10	32	12.5
66	58	62.5	6.3	25	6.3

## Optimum ratio of isomers and width of the pheromone communication channel

All the investigated *A. podana* populations had identical values of pheromone communication channel parameters. Optimal ratios of pheromone components and communication channel widths, calculated from the test results of 1990 and 1999 in different regions, are summarized in Table 3 and in Figs. 1–3.

Table 3. Optimum ratio of 11-tetradecenyl acetate isomers and the width of the pheromone communication channel of *A. podana* in different regions

Region	Year	Insect generation	Biotope	Optimum content of Z isomer, %	Channel width, %
Velikie Luki	1990	I	Orchard	62.2 ± 1.4	9.3
Krasnodar	1990	I	Orchard	60.2 ± 1.0	11.2
Krasnodar	1990	II	Orchard	62.9 ± 1.6	14.1
Uhti	1999	I	Orchard	61.2 ± 1.8	14.3
Otepää	1999	I	Forest	60.0 ± 0.9	9.8
Mean				61.3 ± 1.3	11.7 ± 2.3
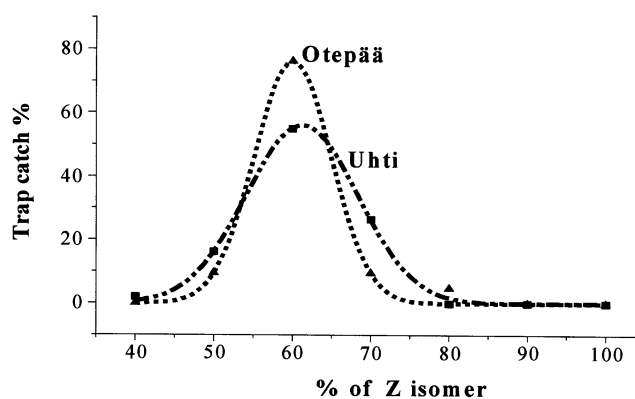
Fig. 1. Distribution of trap catches depending on the Z/E ratio in Estonia at Otepää (forest) and Uhti (orchard) in 1999.
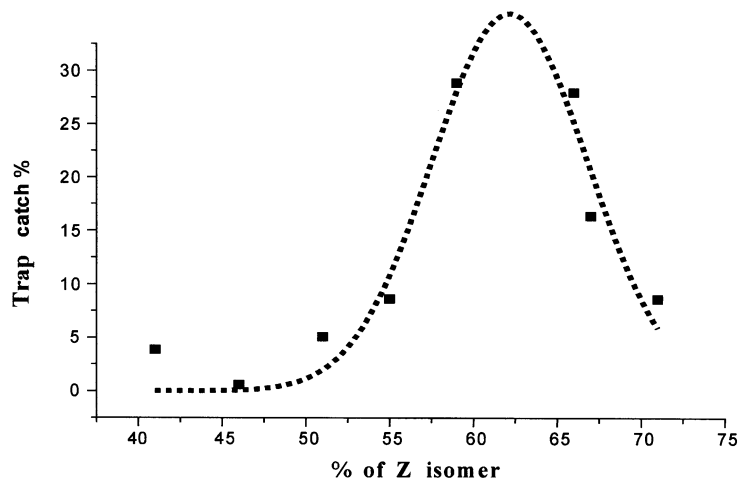
Fig. 2. Distribution of trap catches depending on the Z/E ratio in Russia at Velikie Luki (orchard) in 1990.
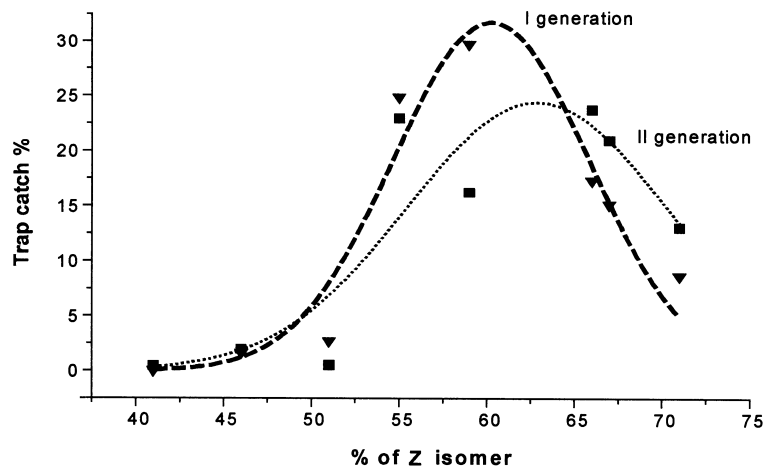
Fig. 3. Distribution of trap catches depending on the Z/E ratio in Russia at Krasnodar in 1990.

DISCUSSION

Genital variability

Insect genitalia are variable. In the monograph by Razowski (1981) on Tortricinae (including Archipini) we found at least 24 species for which he noted variability of male genitalia, especially the aedeagus. A great extent of variability (from 0 to 19 spikes on both sides of distal part) was also found on the aedeagus

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of *Pandemis heparana* Den. et Schiff. (Kozlov, 1991). Differences in genitalia of insects from different regions are the first step for speciation, and different forms are sometimes described as subspecies. Kozlov & Esartia (1991) separated a Caucasian subspecies of *A. podana* (males phenotype L) as *A. podana meridiana*, while Brun et al. (1991) described it as the "Corsican variety" of *A. podana*.

In our experiments in Estonia, northwestern Russia (Velikie Luki and Pushkin), and northern Caucasus, the ratio of *A. podana* male phenotypes in trap catches entirely coincides with those mapped by Kozlov & Motorkin (1990) (Table 1). The habitat (orchard or forest) had no influence in Estonia and northwestern Russia, and, as shown by Kozlov & Motorkin (1988), in western Georgia. A large proportion of phenotype L (5–8%) in the northern populations and the variability in size of apical and lateral spikes testify that we are dealing with only one taxon of specific range. According to Safonkin (1987b, 1988, 1990), a possible explanation of the distribution pattern of phenotypes is climatic adaptation. However, the adaptation of L phenotype males to southern and A phenotype males to northern climate has not been proven experimentally. The fraction of LD decreased from 87 to 71% during 5 generations of laboratory population in Kozlov's (1989) experiments with the material collected from Georgia. As supposed by Kozlov, the decrease may be due to worse adaptability to some laboratory conditions or heredity.

In case the different phenotypes of *A. podana* have differences in pheromone communication channels the females should emit different pheromone blends. The variation of the pheromone structure in mono- and polymorphic populations of some groups of Lepidoptera are known (Löfstedt & van der Pers, 1985; Löfstedt, 1990, 1991). The researches on the pheromone dialect of the noctuid *Scotia* (*Agrotis*) *segetum* (Den. et Schiff.), carried out in different countries of Europe, Asia, and Africa (Hansson et al., 1990; Tóth et al., 1992; Löfstedt, 1993; Wu et al., 1999) are of interest. In case of tortricids, Wen-jun et al. (1992) found sex pheromone polymorphism of *Adoxophyes orana* in China. Females taken from different cultures (apple and peach orchards, tea and cotton plantations) secrete sex pheromones with different blend component ratios.

Identity of pheromone communication channels of phenotypes

Optimal component ratio

Our experiments demonstrated the full identity of the pheromone communication channels of *A. podana* in the Krasnodar Territory, where the L phenotype dominates, and those in Velikie Luki and Estonia, where A phenotype males dominate. On average, the optimal ratio of 11-tetradecenyl acetate isomers was $61.3 \pm 1.3\%$ of Z11-14:Ac (Table 3). Analysis of the results of experiments carried out in Velikie Luki in 1990 demonstrated that a deviation of the attractive blend from the optimal ratio causes a comparable decrease in trap catches for males of different aedeagus forms (Table 2). The calculated percentages in trap catches scatter irregularly, but the differences are not significant.

In some papers, diverse values of the optimal isomer ratio have been published (Persoons et al. 1974; Frérot et al., 1979; Ivanova & Mõttus, 1986a). It may be due to insufficient purity of isomers used. Different load doses of a blend do not cause differences in trap catches in case of an optimal ratio of blend components (Liblikas et al., in prep.).

Communication channel width

The mean value of pheromone communication channel width was $11.7 \pm 2.3\%$ of Z11-14:Ac in all test locations (Table 3). This figure is typical of many Tortricidae moths (Ojarand et al., 2000; Mõttus et al., 2001). Shapes of activity curves for the *A. podana* populations were identical in orchards (Figs. 1–3) and in forest (Fig. 1).

The results described here demonstrate lack of variation in the optimal ratio of Z11-14:Ac and E11-14:Ac for different phenotypes of *A. podana*.

Influence of impurities

Commercial Z11-14:AC and E11-14:AC may contain some amount of the corresponding alcohol, Z11-14:OH and E11-14:OH. The synergistic activity of Z11-14:OH and E11-14:OH for *A. podana* was found in field tests in the Krasnodar and Pskov regions (Mõttus & Ivanova, 1991), Lagodekhi (Kozlov et al., 1991), and near Moscow (Safonkin, 2000), whereas no positive influence was recorded at Lipetsk and in the Voronezh area (Ryabchinskaya et al., 1986) and in Belarus (Mõttus & Ivanova, 1991). The effect of the corresponding alcohols depends probably on abiotic factors, dispenser design, etc., and it cannot be referred to differences among phenotypes. This aspect has been studied in our laboratories and results are in preparation (Liblikas et al., in prep.).

Taxonomic note

A new subspecies of *A. podana* (*A. p. meridiana*), inhabiting Caucasus, Krasnodar, and Stavropol areas as well as the Crimea, was defined by Kozlov & Esartia (1991) on the basis of three groups of characteristics: (1) frequency of the apical spike; frequency of the lateral spike; fraction of males having only an apical spike on the aedeagus; (2) size of the apical spike; distance of the apical spike from the apex of the aedeagus; direction of the apical spike; and (3) attractiveness of synthetic sex attractant blend (ratio of components, 5:5 or 6:4) and influence of 1:1 mixture of (Z11-14:AC):(E11-14:AC) (inhibitory or synergistic action). According to the authors, the subspecies differs from the nominotypical subspecies in absence of the apical spike on the aedeagus.

At the same time, *A. p. podana* populations vary greatly in the frequency of the apical spike, from 10 to 72% of the males in various samples have no apical spike or have it associated with the lateral spike (Kozlov & Esartia, 1991). The variation has been confirmed by our results. For example, the variation in different populations of Estonia and northwestern Russia is between 11 and 31% (Table 2).

According to the "75%-rule" (Mayr, 1971), at least 75% of the individuals in a population of one subspecies should differ from "all" (at least 97%) individuals

of another subspecies. In the case of *A. p. meridiana*, most specimens of *A. p. meridiana* population do not differ from at least 97% of *A. p. podana* males (89–100% of males have no apical spike). Other morphological characteristics, used by Kozlov & Esartia (1991), vary even to a greater extent than the frequency of the apical spike and have no taxonomic value. The identity of the optimal ratio of the pheromone components for Caucasian, northwestern Russian, and Estonian populations was demonstrated above. Therefore, a new subspecies of *A. podana* (*A. p. meridiana* Kozlov et Esartia), defined by Kozlov & Esartia (1991), is identical to *Archips podana* (Scopoli).

Normal distribution of attractivities

Regression analysis of the distribution of attractivities of different attractant blends by means of Gaussian or normal distribution enables to calculate the width and optimal composition of binary pheromone blends (Ojarand et al., 2000; Mõttus et al., 2001). It is evidently more informative than comparison of attractivities of different blends and enables quantitative prediction of trap catch results.

For instance, a pheromone dispenser for *A. podana* has maximum attractivity if the content of Z11-14:Ac in effluvia makes up 60%, in case the ratio of components differs by $\pm\sigma$ ($\pm6\%$), trap catch equals 61% of the maximum and in case of a difference of $\pm0.4\sigma$ (3% of Z11-14:Ac), the mean trap catch diminishes to 10%.

CONCLUSIONS

Evaluation of the pheromone communication channel within different dominating *A. podana* phenotypes in northwestern Russia, Estonia, the Caucasus, and the adjacent steppe zone revealed an identical optimal pheromone in all the tested areas. No evidence of pheromone dialect was established.

Fitting the normal distribution to field experiment data is an effective method for estimating the role of different blend components in chemical communication, for optimizing the composition of the blend, and for detecting intraspecific variability of pheromone communication.

A subspecies of *A. podana* (*A. p. meridiana* Kozlov et Esartia), defined by Kozlov & Esartia (1991), is identical to *Archips podana* (Scopoli).

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Archips podana (Scopoli) genitaalpreparaatide ja feromoonkommunikatsioonikanali varieeruvus

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Suur taramähkur *Archips podana* (Scopoli) on levinud kõikjal Euroopas. Selle liigi isaste genitaalpreparaadid varieeruvad aedeaguse kidade asendi ja arvu poolest. Kidad võivad asuda apikaalselt (vorm A) või lateraalselt (L), samuti võivad need puududa (0). On leitud ka mitme kidaga vorme 2L, AL ja A2L. Varasemates artiklites on viidatud võimalusele, et erinevate genitaalpreparaatidega taramähkurid võivad erineda ka feromoonkommunikatsiooni osas. Käesolevas töös on esitatud uurimistulemused *A. podana* isasloomade genitaalpreparaatide erinevusest Eestis (Uhti õunaaed ja segamets Otepää lähistel), õunaaedades Loode-Venemaal Leningradi oblastis ja Velikije Lukis (Pihkva oblast), samuti Lõuna-Venemaal Krasnodari krais Slavinski linna lähistel.

Feromoonainete segu aktiivsuste hindamisel Gaussi normaaljaotuse alusel selgus, et suure taramähkuri isasloomadele osutus kõikjal aktiivseimaks Z-11-tetradetsenüülatsetaadi (Z11-14:Ac) ja selle *trans*-isomeeri E11-14:Ac segu, mis sisaldas $61{,}3 \pm 1{,}3\%$ Z-isomeeri. See on Persoonsi jt poolt 1994. a identifitseeritud feromooni koostisega praktiliselt kokkulangev. Kuna Krasnodari krais domineerib L-tüüpi *A. podana*, Põhja-Euroopas aga A-tüüp, siis selle liigi isaste genitaalpreparaatide varieeruvus ei seondu muutustega reaktsioonis feromoonile. Tuginedes genitaalpreparaatide erinevusele ja oletatavale varieeruvusele feromooni retseptsioonis, kirjeldasid Kozlov ja Esartia (1991) isaste fenotüüpi L kui *A. podana* alamliiki *A. podana meridiana* Kozl. et Esart. Käesolevas artiklis toodud materjalide alusel puuduvad sellise alamliigi eraldamiseks alused. Üheks oluliseks järelduseks uurimusest loeme asjaolu, et feromoonkommunikatsiooni parameetrite, aktiivsuste maksimumi ja aktiivsuste jaotust saab kasutada nii putukate kui ka feromoondispenserite omaduste hindamiseks.