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BIOLOGICAL COMPARISON OF DIFFERENT POPULATIONS OF ARGAS (PERSICARGAS) PERSICUS (OKEN)

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Abstract. Characteristic features of the developmental cycle of *Argas* (*P.*) *persicus* (Oken, 1818) populations and their hybrids from Czechoslovakia and Azerbaijan were compared. It was proved that the phenotypic differences found earlier (Dusbábek 1984) are also accompanied by genotypic differences reflected in the peculiarities of developmental cycle. However, no traces of genetic incompatibility were detected. The heaviest losses in the course of developmental cycle were found in homogamic crosses and are considered to be due to the inbreeding depression during laboratory culturing. Some biological properties seem to have been inherited in the matroclinal form and may therefore be connected with extrachromosomal inheritance.

Experimental interspecific hybridization is one of the basic methods of biological analysis of the systematic validity of related species. The study of a species at the level of gamma-taxonomy (Mayr 1969) i.e. at the intraspecific level, requires a deeper analysis of interpopulation relationships (McDonald 1976). Remarkable results were obtained when developmental cycles of different argasid populations were compared, different populations were crossbred and the geographic variability of the phenotype was studied.

Balashov (1971), while crossbreeding 14 different populations of *Ornithodoros* (*Pavlovskyella*) *tartakovskyi* Olenev, 1931, in some combinations found a modified fertility in F_1 generation of hybrids, manifesting itself in a lesser number of eggs, unfinished embryogenesis, reduced viability of larvae and even complete genetic incompatibility in several crosses. These biological differences were much more distinct than the differences in the phenotype of individual populations (Balashov 1972, 1975a). During similar crossbreedings of the F_1 generation of hybrids in *Ornithodoros* (*Pavlovskyella*) *verrucosus* Olenev, Zassukhin et Fenynk, 1934 a slight genetic incompatibility appeared between the northern and southern groups of populations, but it was lacking inside these groups (Balashov 1975b). Hoogstraal et al. (1975) found differences in the course of developmental cycle in five studied populations of *Argas* (*Persicargas*) *robertsi* Hoogstraal, Kaiser et Kohls 1968, and likewise did Gothe et Koop (1974), who studied pre-larval stage in reciprocal hybrids of two populations of *Argas* (*Persicargas*) *arboreus* Kaiser, Hoogstraal et Kohls, 1964.

The studies on geographic variability of phenotype in three populations of *Argas* (*Persicargas*) *persicus* (Oken, 1818) revealed that out of 48 randomly selected characters these populations were similar only in 21 of them (Dusbábek 1984). Therefore, we decided to compare biologically two of these three populations, in order to find genetic differentiation of species and to establish the relationship between the phenotype and genotype in these populations.

MATERIALS AND METHODS

The *A. persicus* populations from Czechoslovakia and Azerbaijan were used for biological comparison. The first one was collected from henhouses in the village Ipeľský Sokolec, district of Levice, Czechoslovakia, on 28 June 1972. The second one was obtained by courtesy of RNDr. J. Řeháček, D.Sc., of the Virological Institute of the Slovak Academy of Sciences in Bratislava, and was collected from henhouses in the villages Arad and Shlelyan of the district Yevlakh, the Azerbaijan SSR, on 16 and 22 October 1979. The argasids of both populations were colonized for a number of years and several generations in the laboratory at temperature of 27 ±1 °C and 75 ±5 % RH in darkness. Our experiment was conducted under the mentioned conditions.

The biological comparison of populations consisting of homogamic and heterogamic crosses of adults of both populations was conducted parallel and was started on 12 June 1981; brother-sister mating of F_1 hybrids and backcrossing of F_1 hybrids with pure males and females of both populations were also conducted parallel and were started in the period between 4 and 6 June 1982. Each group tested consisted of five virgin females and five virgin males obtained from isolated 2nd and 3rd instars of nymphs. Males and females fed separately and after the first feeding were placed one pair each in a culture jar. Controls were daily made in the periods of oviposition and hatching of larvae, without interfering with the argasids, later twice weekly. The size and state of egg batch were assessed after hatching and feeding of larvae on the remains of the egg batch kept in 70 % alcohol. Groups of 50—100 larvae from each egg batch, aged four weeks, were fed on 2-8-week-old chickens each placed in a wire cage above a dish filled with water. The chickens were used for larval feeding only once. Nymphs and imagoes were fed one month after the moulting of last specimens on older chickens and cocks previously used for tick feeding, by method of Kaiser (1966). Evaluated were only those specimens whose development continued following the first blood-meal. The duration of pre-oviposition was assessed from the day on which the engorged females and males were placed in pairs in culture jars, after the first eggs appeared, and the duration of pre-eclosion from the first eggs laid until the appearance of first larvae. As diapausing specimens were considered those argasids whose premoulting period in the winter months exceeded 30 days. As the onset of diapause was considered the date of last feeding, as the end of winter diapause was regarded the moulting for the next developmental stage.

The total assessed material of P_1 generation consisted of 2,822 eggs, 1,500 unfed larvae, 764 engorged larvae, 626 nymphs I, 483 nymphs II, 90 nymphs III, 3 nymphs IV, 204 ♀ and 219 ♂. The assessed material of F_1 generation included 5,859 eggs and 4,625 unfed larvae.

For statistical evaluation of differences in the duration of individual stages of development and further quantitative characteristic features in homogamic and heterogamic crosses of parents (Tables 1 and 2) Student's t-test was used, while the numbers of diapausing nymphs I and II were compared by χ^2 test. The differences in viability of the prelarval and larval developmental stages of F_1 generation (Tables 4 and 5) were compared by using the statistical test equality of parameters of Poisson random variables after Suzhatme and Hald (Fabián 1963) and χ^2 test; for the comparison of the duration of pre-oviposition and pre-eclosion Student's t-test was used. For the implementation of these tests the author is indebted to RNDr. J. Železný of the Department of Biomathematics of the South Bohemian Biological Centre at České Budějovice. The following abbreviations are used in the text and tables:

Aa = progeny of ♀ from Azerbaijan and ♂ from Azerbaijan
Ac — progeny of ♀ from Azerbaijan and ♂ from Czechoslovakia
Cc = progeny of ♀ from Czechoslovakia and ♂ from Czechoslovakia
Ca = progeny of ♀ from Czechoslovakia and ♂ from Azerbaijan

RESULTS

The results obtained by biological comparison of populations are summed up in Tables 1—5. The duration of respective developmental stages (Table 1), the egg output and percentage of developing larvae and nymphs (Table 2), and numbers of diapausing specimens (Table 3) were studied in parental generations. Only prelarval and larval stages of development (Tables 4 and 5) were compared in filial generations.

Table 1. Duration of periods in the life cycle of homogamic and heterogamic crosses of Azerbaijan and Czechoslovak populations of *Argas persicus* (in days, $\bar{x} \pm$ SD)

		Aa	Ac	Cc	Ca
♀	Pre-oviposition	17.0 ± 8.3	24.2 ± 18.4	15.6 ± 5.4	7.0 ± 1.9
Egg	Incubation	14.0 ± 2.9	16.0 ± 2.4	18.0 ± 0	16.6 ± 2.6
Larva	Feeding	4.9 ± 0.6	4.5 ± 0.5	5.2 ± 0.5	4.9 ± 0.5
	Premoulting	10.6 ± 3.1	11.8 ± 7.8	9.9 ± 1.8	9.8 ± 2.1
N I	Premoulting	17.8 ± 14.2	29.7 ± 25.4	65.2 ± 46.6	54.4 ± 38.0
N II	Premoulting to N III	19.3 ± 9.5	14.1 ± 0.5	14.3 ± 2.0	17.2 ± 4.5
	to ♀	20.0 ± 7.3	16.3 ± 1.9	18.1 ± 2.5	15.9 ± 1.9
	to ♂	23.4 ± 10.1	18.1 ± 2.0	17.5 ± 2.1	17.1 ± 1.4
N III	Premoulting to N IV	15.0 ± 0.0	18.0 ± 0.0	14.0 ± 0.0	—
	to ♀	20.7 ± 3.6	18.9 ± 3.2	17.0 ± 1.4	16.4 ± 2.7
	to ♂	20.7 ± 3.6	18.2 ± 2.0	17.6 ± 1.2	17.6 ± 2.4
N IV	Premoulting to ♂	22.0 ± 0.0	16.0 ± 0.0	19.0 ± 0.0	—

Table 2. Productivity of different developmental stages in the life cycle of homogamic and heterogamic crosses of Azerbaijan and Czechoslovak populations of *Argas persicus*

		Aa	Ac	Cc	Ca
Egg	Mean number in a batch	118.5 ± 51.1	180.0 ± 61.1	124.0 ± 35.3	142.7 ± 12.6
Larva	% of hatched	59.2	80.9	43.5	97.2
	% of fed	53.9	46.9	37.3	46.0
	% of moulted	91.5	76.6	49.4	80.8
N I	% of moulted	96.7	96.8	59.0	87.3
N II	% of moulted to N III	18.2	16.8	40.4	21.9
	to ♀	40.9	44.5	25.5	30.5
	to ♂	35.5	38.7	27.7	45.1
N III	% of moulted to N IV	2.9	5.0	5.3	—
	to ♀	38.2	45.0	15.8	50.0
	to ♂	50.0	50.0	68.4	50.0
% of total productivity		32.2	31.9	10.4	32.0

a) Homogamic and heterogamic crosses of parents (P_1)

A comparison of the duration of respective developmental stages in homogamic and heterogamic crosses (Table 1) shows a conspicuous agreement in most indices and only minimum statistically significant differences. The most conspicuous differences appeared in the premoulting period of nymphs I, which significantly differed ($P < 0.01$) in most of the combinations tested. These differences are connected with the unequal number of engorged nymphs I in respective crosses which have entered the winter diapause and with the relevant prolongation of their premoulting period. While the differences in the number of diapausing and non-diapausing nymphs I between crosses Cc and Ca proved to be not significant, the differences in the remaining crosses were stastistically significant ($P < 0.01$) (Table 3). The diapause of nymphs I in the cross Cc occurred between 22 October 1981 and 20 April 1982, in the cross Ca in the period from 16 October 1981 to 15 April 1982, in the cross Aa between 9 December 1981 and 8 March 1982 in the cross Ac in the period from 30 November 1981 to 22 February 1982. In crosses Aa and Ac the period of

Table 3. Diapause incidence in nymphs I and II of homogamic and heterogamic crosses of Azerbaijan and Czechoslovak populations of *Argas persicus*

	Not diapaused		Diapaused		Total
	n	%	n	%	n
			Nymphs I		
Aa	178	92.2	15	7.8	193
Ac	71	61.2	45	38.8	116
Cc	26	41.3	37	58.7	63
Ca	41	36.6	71	63.4	112
			Nymphs II		
Aa	163	86.7	25	13.3	188
Ac	108	100	0	0	108
Cc	44	100	0	0	44
Ca	84	100	0	0	84

Table 4. Duration of periods in prelarval stage of life cycle and survival of larvae of brother-sister crosses and backcrosses of F_1 hybrids of Azerbaijan and Czechoslovak populations of *Argas persicus* (in days, $\tilde{x} \pm$ SD)

	Pre-oviposition	Pre-eclosion	Survival of larvae
Aa ♀ × Aa ♂	17.0 ± 10.6	16.5 ± 2.4	88.5 ± 38.2
Aa ♀ × Ac ♂	16.7 ± 3.8	15.0 ± 0.8	124.5 ± 36.9
Aa ♀ × Ca ♂	26.2 ± 13.9	15.6 ± 2.5	94.2 ± 43.3
Ac ♀ × Aa ♂	19.2 ± 6.7	17.0 ± 1.6	154.6 ± 52.7
Ac ♀ × Cc ♂	26.6 ± 16.3	15.2 ± 1.8	102.2 ± 28.6
Ac ♀ × Ac ♂	19.8 ± 3.8	15.2 ± 1.1	139.0 ± 31.7
Cc ♀ × Cc ♂	8.5 ± 1.7	20.3 ± 2.1	21.0 ± 10.4
Cc ♀ × Ca ♂	11.2 ± 2.9	17.4 ± 1.9	41.4 ± 15.4
Cc ♀ × Ac ♂	11.5 ± 9.0	17.3 ± 1.5	40.0 ± 13.5
Ca ♀ × Cc ♂	13.2 ± 3.3	16.2 ± 1.8	130.4 ± 51.6
Ca ♀ × Aa ♂	22.6 ± 10.8	17.2 ± 2.3	224.4 ± 39.6
Ca ♀ × Ca ♂	19.2 ± 3.2	16.0 ± 2.0	153.8 ± 31.8

diapause of nymphs I was consequently shorter and its onset considerably delayed. The premoulting period of nymphs II, moulted to nymphs III, females and males was definitely longer in the cross Aa ($P < 0.01$), similarly as in nymphs III moulted to females and males but only at the level of $P < 0.05$. Also here it became evident that only in this cross the winter diapause of nymphs II occurred (Table 3). The pre-oviposition in crosses Cc and Ca was shorter than in crosses Aa and Ac, but only the shorter duration of pre-oviposition in the cross Ca was significant ($P < 0.01$). In this cross and in the cross Cc as well, also the premoulting period in larvae ($P < 0.01$) was significantly shorter than in crosses Ac and Aa, while crosses Cc and Ca did not differ from each other significantly, similarly as the differences between Aa and Ac were not significant.

The differences in the egg output (Table 2) between respective crosses were not significant, but the two homogamic crosses (Aa and Cc) significantly differed ($P < 0.01$) in a lesser number of hatched larvae. In comparison with Table 5 where crosses Aa and Cc served as controls, it is evident that the lesser number of hatched larvae also occurred in these crosses. The cross Cc yielded explicitly a lower percentage of engorged larvae ($P < 0.05$) than the cross Aa and a significantly lower ($P < 0.05$) production of nymphs I and II (Table 2). There were no significant differences in the percentage of moulted nymphs II and III, only in the number of nymphs II moulting to nymphs III there was a significant difference between crosses Cc and Ac. All these differences resulted in a lower total productivity of homogamic cross Cc, representing the percentage of unfed larvae able to complete their development to imago.

b) Brother-sister crosses and backcrosses of F_1 hybrids

The investigation of crosses in F_1 hybrid generation was restricted to the studies on prelarval and larval stages of development only (Tables 4, 5). The period of the preoviposition was significantly shorter ($P < 0.01$) in all three crosses of females from the Czechoslovak tick population (Cc × Cc, Cc × Ca, Cc × Ac), similarly as in crosses Ca × Cc. In other crosses there were no significant differences in the duration of preoviposition. Likewise in the duration of pre-eclosion the individual crosses showed no significant differences.

Table 5. Fertility of brother-sister crosses and backcrosses of F_1 hybrids of Azerbaijan and Czechoslovak populations of *Argas persicus*

	Mean egg number in a batch	% of hatched larvae	% of unhatched developed larvae	% of sterile eggs
Aa ♀ × Aa ♂	91.0 ± 52.3	54.4	12.1	33.5
Aa ♀ × Ac ♂	113.3 ± 25.8	92.9	4.0	3.1
Aa ♀ × Ca ♂	87.8 ± 51.7	94.5	1.1	4.4
Ac ♀ × Aa ♂	87.0 ± 42.0	89.4	4.1	6.5
Ac ♀ × Cc ♂	81.0 ± 21.1	87.9	1.5	10.6
Ac ♀ × Ac ♂	88.8 ± 23.7	89.9	5.0	5.1
Cc ♀ × Cc ♂	96.0 ± 34.7	49.0	32.7	18.3
Cc ♀ × Ca ♂	125.0 ± 33.3	67.2	29.8	3.0
Cc ♀ × Ac ♂	140.0 ± 31.6	28.8	67.0	4.2
Ca ♀ × Cc ♂	107.8 ± 63.7	95.2	0.2	4.6
Ca ♀ × Aa ♂	118.2 ± 15.4	91.5	4.2	4.3
Ca ♀ × Ca ♂	104.8 ± 46.5	91.0	4.2	4.8

The comparison of the egg output in F_1 experimental crosses mostly revealed a lesser number of eggs in batches laid by females from Azerbaijan and by females coming from crosses of females Ac with different males. On the other hand, in females Cc and Ca the numbers of eggs were significantly higher ($P < 0.01$) in most cases. The only exception is the backcross Aa × Ac, where the number of eggs was significantly higher ($P < 0.01$) than in the other females of the group Aa and Ac, between which no significant differences appeared. In the control crosses Cc × Cc the number of eggs was significantly lower ($P < 0.01$) than in the other crosses in female groups Cc and Ca, which showed no significant mutual differences in the number of eggs.

The percentage of hatched larvae in most crosses was approximately at a same level (87.9—95.2 %). Only the two control crosses (Aa × Aa and Cc × Cc), showing no significant differences between each other, and back crosses with females from Czechoslovak populations (Cc × Ca and Cc × Ac) differed significantly from remaining crosses in the lesser number of hatched larvae. The cross Cc × Ca yielded a significantly higher number of hatched larvae than crosses Cc × Cc and Cc × Ac which showed no significant mutual differences.

Differentiated were also the eggs in which the development had started but no hatching of larvae occurred from sterile eggs where the embryo did not develop at all. While the number of unhatched developed larvae was significantly higher in those crosses, in which the number of hatched larvae was significantly lower (Aa × Aa, Cc × Cc, Cc × Ca and Cc × Ac), the number of sterile eggs was significantly higher only in the two control crosses, namely Aa × Aa and Cc × Cc.

The comparison of the life span of larvae clearly demonstrated the lower viability of the progeny of females from the Czechoslovak population (Cc × Cc, Cc × Ca, Cc × Ac) which survived a shorter period ($P < 0.01$) than the progeny from other crosses. Likewise the larvae from crosses Aa × Aa and Aa × Ca survived a shorter period than those from of Aa and Ac females other crosses, but these differences were not evident enough. However, unlike the survival of larvae from females Cc, the larvae from females Aa survived significantly longer ($P < 0.01$).

DISCUSSION

Although the developmental cycle of *Argas persicus* has been in recent years revised in populations from different geographic regions (Frolov 1970a, b, Frolov et Dazhiev 1970a, b, Frolov et Kachekova 1972, Gothe and Koop 1974, Petrov and Gecheva 1975, Dusbábek and Rosický 1976, Khalil 1979, El Kammah and Wahab 1979, Srivastava et al. 1981), the results are comparable with difficulty due to different conditions of tick culturing, primarily temperature, host species used for their feeding, date of the onset of developmental cycle and the relevant date of the onset of winter diapause as well as the methods used in the assessment of experiments. The course of developmental cycle in homogamic and heterogamic crosses of parental populations of *A. persicus* in our experiment agrees in most indices with the data of the above mentioned authors and the differences, if any, can be explained by the differences in the arrangement and assessment of experiment.

Among the statistically significant differences in the course of developmental cycle of respective homogamic and heterogamic crosses the biologically most significant difference appears to be in the number of diapausing nymphs I and consequently also in the duration of their premoulting period (Tables 1 and 3). The longest premoulting period in crosses Cc and Ca is an evident result of the highest percentage of nymphs I which underwent the winter diapause. The shortest premoulting period of nymphs I was encountered in the cross Aa where the least number of specimens diapaused. In that cross only the winter diapause also appeared in nymphs II, resulting in the significantly longer premoulting period while moulting into nymphs III, males and females, than in other crosses, where nymphs III did not diapause any more. Consequently, the onset of winter diapause in the homogamic cross Aa is distinctly delayed, affecting a lower number of nymphs I and also some nymphs II undergo the diapause. In homogamic cross Cc the onset of winter diapause is earlier, appearing in a major portion of nymphs I and the diapause does not affect nymphs II.

The progeny of females in the homogamic cross Cc is most similar to the heterogamic cross Ca both in the duration of premoulting period of nymphs I and the number of diapausing nymphs I. Likewise, the progeny of females of the homogamic cross Aa is most similar to the heterogamic cross Ac in those characteristics, both homogamic crosses Cc and Aa mutually differing significantly. In both cases the progeny of females from Czechoslovak population mated with males from the Czechoslovak or Azerbaijan tick populations significantly differed ($P < 0.01$) from the progeny of females from the Azerbaijan population mated with Czechoslovak or Azerbaijan males. A similar situation is encountered in the duration of premoulting period of larvae (Table 1) where crosses Aa and Ac do not significantly differ mutually, just as crosses Cc and Ca do not significantly differ either, but the differences between the two groups are significant ($P < 0.01$). Also in the backcross and brother-sister cross of F_1 hybrids (Tables 4 and 5) there appears to be a mutual similarity of females of each respective group irrespective of males in the duration of pre-oviposition and egg output, and moreover, a mutual similarity between female groups Cc and Ca on the one hand and Aa and Ac on the other. The properties of progeny in these cases seem to be determined mostly by the properties of mother, irrespective of the properties of father. Similar results were obtained by Hunt and Drummond (1983) who compared reproduction biology of the laboratory and wild populations of lone star tick *Amblyomma americanum* (L., 1758) and noted that most reproduction characteristic features of wild females mated with colony males were similar to those of wild females mated with wild males; and colony females mated with wild males had reproduction characteristics similar to those of colony females mated with colony males. Consequently adaptations to long-lasting conditions of environment passed on to progeny in the form of matrocliny and thereby connected with cytoplasmatic heredity, may be involved here.

The characteristic features of viability of the individual developmental stages and the total productivity (summed up in Table 2) indicate the heaviest losses suffered during ontogenesis in cross Cc, in the percentage of hatched larvae as well as in cross Aa, consequently in both homogamic crosses. In the first series of experiments this phenomenon did not become manifest in heterogamic crosses (Table 3), but it did manifest itself again in homogamic backcrosses of F_1 generation of pure males with pure females (Tables 4, 5) in a lesser average number of eggs laid in the cross Cc × Cc, as opposed to heterogamic crosses of females with different males, lower percentages of hatched larvae in homogamic crosses Aa × Aa and Cc × Cc, as well as in a shorter life span of unfed larvae in the female group Cc. These characteristics may be connected with long-term inbreeding of a small number of specimens in the laboratory colony, which is reflected in the manifestation of recessive sublethal and lethal genes, resulting in a lower viability of the laboratory population (McDonald 1976). Similar conclusions were drawn by Steward et al. (1982), after interpreting their results obtained by comparing developmental cycles of feral and laboratory populations of *Boophilus microplus* (Canestrini, 1888).

It may be therefore concluded that the phenotypic differences found in the argasid populations from Czechoslovakia and Azerbaijan (Dusbábek 1984) are also accompanied by differences in genotype. However, no traces of genetic incompatibility were detected. The heaviest losses in the course of developmental cycle were found in homogamic crosses and are considered to be due to inbreeding during laboratory culturing. Some biological characteristic features seem to have been inherited in the matroclinal form and may be connected with extrachromosomal inheritance.

БИОЛОГИЧЕСКОЕ СРАВНЕНИЕ РАЗНЫХ ПОПУЛЯЦИЙ *ARGAS* (*PERSICARGAS*) *PERSICUS* (OKEN)

Ф. Дусбабек

Резюме. Дано сравнение характеристик цикла развития популяций *Argas* (*P.*) *persicus* (Oken, 1818) из Чехословакии и Азербайджана и их гибридов. Установлено, что раньше обнаруженные разницы фенотипа (Дусбабек 1984) существуют наравне также с разницами в генотипе, отражающимися в особенностях цикла развития. Однако, не обнаружены никакие признаки генетической несовместимости. Самые высокие потери в течение цикла развития обнаружены у гомогамных скрещиваний и их считают результатом инбредного влияния при лабораторном разведении. Некоторые биологические свойства по всей вероятности унаследованы в матроклинном виде и могут быть следовательно связаны с внеядерной наследственностью.

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