

GENETIC VARIATION AND CORRELATIONS OF LIFE-HISTORY TRAITS IN GYPSY MOTHS (*LYMANTRIA DISPAR* L.) FROM TWO POPULATIONS IN SERBIA

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Abstract — Periodic fluctuations in density impose different selection pressures on populations of outbreaking Lepidoptera due to changes in their nutritional environment. The maternal effects hypothesis of insect outbreak predicts the transmission of this nutritional «information» to subsequent generations and alterations in offspring life-history traits. To test for these time-delayed effects of the parental generation, we compared life-history traits and their variation and covariation among laboratory-reared gypsy moths hatched from egg masses collected from low- and medium-density populations. Decreased individual performance was recorded in offspring from the medium-density population, indicating reduced egg provisioning under crowding conditions. Genetic variance and covariance were also shown to be sensitive to density of the parental generation. In gypsy moths from the medium-density population, quantitative genetic analysis revealed significantly higher broad-sense heritabilities for development duration traits and demonstrated a trade-off between development duration and body size.

Key words: Life-history traits, population density, maternal effects hypothesis, broad-sense heritability, genetic correlations, *Lymantria dispar*

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INTRODUCTION

The gypsy moth is a folivorous insect species with outbreaking population dynamics. Periodic fluctuations in its population density include several phases: latency (low density), progradation (increase in density), culmination (high density), and retrogradation (decrease in density) (Elkinton and Liebhold, 1990). In Serbia, 3-6 years of outbreak periods are followed by latency which may last from 2 to 10 years (Marović et al., 1998). During outbreaks, this generalist pest causes economic damage due to defoliation of forests and orchards over large areas. Explaining mechanisms underlying the cyclic density changes may help in predictive modelling for gypsy moth management. Host-plant quality, temperature, humidity, natural enemies (parasites, pathogens, predators), and other environmental factors affect gypsy moth population dynamics (Valentin et al., 1983; Elkinton and Liebhold, 1990; Berryman, 1996).

Overpopulation also depends on gypsy moth quality, i.e., its biochemical, physiological, developmental, and behavioral traits, which further influence fitness components, stress resistance and tolerance, dispersal ability, etc. (Rossiter, 1994). Maternal effects as one aspect of population quality have been incorporated in theoretical and mathematical models of gypsy moth population dynamics (Sharov and Covert, 1994).

High density populations of the gypsy moth are characterized by shortened development time, decreased pupal mass and fecundity, and supernumerary molts (Leonard, 1974); decreased egg size with unchanged vitellin content (Diss et al., 1996); broadened host-plant range (Barbosa, 1978); decreased proportion of females (Myers et al., 1998); increased dispersion of first-instar larvae (Barbosa et al., 1981); disturbed circadian feeding rhythm (Lance et al., 1986); increased proportion of dark coloration (Ponomarev, 1994);

and changes in resistance to parasites and viruses (Martemyanov and Bakhvalov, 2007).

Changes in gypsy moth performance can be attributed to changes in leaf quality during defoliation, such changes including increased phenol content (Rossiter et al., 1988) and decreased water, nitrogen and free sugar content (Valentin et al., 1983). Additionally, periodicity of gypsy moth populations strongly depends on the species composition of forest stands (Johnson et al., 2006). Since leaf quality affects egg quality (Rossiter et al., 1993), nutritionally-based environmental influences are expected to transmit to the next generation through maternal effects. If this is so, then population differences in performance should be revealed under laboratory conditions. Such results have been obtained in the gypsy moth (Rossiter, 1991 a; Myers et al., 1998) and other insects (Carisey and Bauce, 2002; Zehender and Hunter, 2007; Chapuis et al., 2008).

During periodic fluctuations, gypsy moth populations are exposed to different density-dependent selection regimes: r-selection at low density and K-selection at high density. It is theoretically predicted (MacArthur and Wilson, 1967) that different sets of life-history traits will occur under these regimes, and that sensitivity of life-history traits to density will be subject to genetic variation. Under crowded conditions, K selection favors increased efficiency in resource use and resistance to starvation, viruses, and other stressors, leading to changes in inter-family variance/covariance of life history traits.

This study deals with the question of whether maternal nutrition (or environment) affects life-history traits in the gypsy moth. Life-history traits and their variation and covariation were compared between laboratory-reared gypsy moths from egg masses collected from low- and medium-density populations.

MATERIAL AND METHODS

Populations and rearing conditions

Gypsy moth egg masses were collected from two

oak populations with distinctly different population densities: a low-density population at the Ražanj locality (150 km southeast of Belgrade), with 10 egg masses/ha; and a medium-density population at the Despotovačke Šume locality (116 km southeast of Belgrade), with 100 egg masses/ha. Thus, egg-mass density was approximately 10 times higher at the Despotovačke Šume than at the Ražanj locality. The Ražanj population was in the latency phase, while the Despotovačke Šume population was in the progradation phase, one year before outbreak. The localities were 50 km apart, which exceeds the migration distance of gypsy moth. Forests at both localities consisted mainly of oak trees as a suitable host plant for the gypsy moth.

Twenty-two egg masses sampled from Ražanj and twenty six egg masses sampled from Despotovačke Šume were surface-sterilized in 0.1% sodium hypochlorite and set out for hatching. In view of the great differences between first- and last-laid eggs (Rossiter, 1991 b), only eggs from the central area of an egg mass were set out for hatching. The hatched larvae were reared under conditions of low density, 23°C, and 16:8 light:dark photoperiods. They were daily supplied with fresh oak leaves (*Quercus cerris*) collected from unattacked sites. Five larvae in the first instar and only one or two larvae in the late larval instars were cultured in 200-ml plastic cups. Pupae were separated by sex and kept individually in the same cups until adult eclosion. Plastic cups were also used as mating chambers. One male was mated with one to three females.

Determination of life-history traits

The following life-history traits were measured in gypsy moths originating from two populations: pre-adult viability (V), larval duration (LD), pupal duration (PD), preadult development duration (PAD), pupal mass (PM), and adult longevity (L). Preadult viability was determined by daily count of dead individuals and calculation of the percentage of larvae which complete their development. Pupal mass was measured on the second day of pupal development. Pupation, adult eclosion, and adult mortality were also recorded daily. As revealed by our previous investigations (Lazarević, 1994), male longevity

was not affected by mating, while mated females live significantly longer than virgin ones. Thus, longevity was determined in males regardless of their mating status, but in females only mated individuals were taken into account. The analysis included 255 females and 263 males hatched from 22 egg masses collected at the Ražanj locality and 426 females and 470 males hatched from 26 egg masses collected at the Despotovačke Šume locality.

Statistical analyses

Given apparent sexual dimorphism, the mean values and standard errors for life-history traits were calculated for females and males separately. Comparison of life-history traits between the two populations was carried out by one-way ANOVA (Sokal and Rohlf, 1981). Following examination of normality and homogeneity of the variance assumption, the appropriate ANOVA models were applied to arcsin-square root-transformed viability and log-transformed values of other life-history traits. Broad-sense heritabilities (h^2) were calculated according to standard formulae for the unbalanced full-sib design (Becker, 1984). Larvae hatched from an egg mass represent full-sibs, since gypsy moth females lay a single egg mass, which is the product of a single mating. Significant between-population differences in broad-sense heritabilities were revealed by the z-test (Sokal and Rohlf, 1981). Genetic correlations were calculated either as Pearson's product-moment

correlations of family means (r_m) or as «component» correlations (r_g), i.e., genetic covariance between two traits standardized by the genetic variances (Via, 1984; Becker, 1984). Analysis of covariance involved partition of phenotypic covariance into environmental and (broad-sense) genetic components. The significance of «component» genetic correlation cannot be estimated for the unbalanced full-sib design. Family means correlations contain not only inter-family, but also intra-family «error» variance/covariance. Similar values of r_m and r_g correlations can be obtained if family size is large (Via, 1984). Correlations between populations were compared by the z test.

RESULTS

The data presented in Table 1 show significantly lower preadult viability in offspring from the medium-density compared to low-density population. The population from the Despotovačke Šume locality is characterized by prolonged pupal duration in both females and males, decreased pupal mass and longevity in females, and prolonged preadult development duration in males.

A significant level of expression of genetic variation was revealed for most life-history traits within both populations (Table 2). With the exception of pupal duration, most heritability estimates were low in females from the Ražanj population, while

Table 1. Means (\bar{x}) and standard errors (\pm SE) for life-history traits in gypsy moths reared on oak leaves at low density and originated from two populations: Ražanj (low density, latency) and Despotovačke Šume (medium density, progradation). The significance of the difference between the populations was tested by one-way ANOVA. V - preadult viability, LD - larval duration, PD - pupal duration, PAD - preadult development duration, PM - pupal mass and L - longevity * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Trait	Ražanj			Despotovačke Šume			F
	\bar{x}	\pm	SE	\bar{x}	\pm	SE	
V (%)	97.830		0.071	94.920		1.011	4.933*
♀ LD (days)	37.231		0.184	37.000		0.210	0.774
PD (days)	11.545		0.046	12.014		0.053	44.210***
PAD (days)	48.777		0.195	49.014		0.225	0.600
PM (mg)	1347.280		14.410	1306.822		19.310	4.701*
L (days)	8.841		0.085	8.431		0.094	10.420**
♂ LD (days)	32.336		0.194	32.506		0.165	0.533
PD (days)	12.741		0.049	13.229		0.050	24.657***
PAD (days)	45.076		0.205	45.736		0.182	3.503*
PM (mg)	441.762		3.191	449.202		13.051	0.087
L (days)	5.093		0.079	5.355		0.089	2.200

Table 2. Broad-sense heritabilities ($h^2 \pm SE$) for life history traits in gypsy moths from two populations. Significant heritability was revealed by the t-test. Population differences were examined by applying the t-test to z-transformed values of heritabilities. Other abbreviations are explained in Table 1. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Trait	Ražanj			Despotovačke Šume			t
	h^2	\pm	SE	h^2	\pm	SE	
♀ LD (days)	0.3529		0.1316*	0.7657		0.1729***	2.162*
PD (days)	0.0054		0.0070	0.1307		0.1015	0.985
PAD (days)	0.3642		0.1334*	0.82584		0.1740***	2.650*
PM (mg)	0.2131		0.1060*	0.4273		0.1484**	0.911
L (days)	0.2642		0.1166*	0.4515		0.1517**	0.794
♂ LD (days)	0.7144		0.1703***	0.4612		0.1466**	1.328
PD (days)	0.0057		0.0069	0.4803		0.1486**	2.509*
PAD (days)	0.6658		0.1671***	0.6022		0.1593***	0.353
PM (mg)	0.6287		0.1643**	0.2475		0.1172*	1.720
L (days)	0.1384		0.0089	0.1013		0.9009	0.197

medium-to-high estimates are characteristic for females from Despotovačke Šume. Significantly higher broad-sense heritability was noticed for larval and preadult development duration in females and pupal duration in males from the medium-density population.

Phenotypic correlations (r_p) of life-history traits are mainly weak, with the exception of moderate correlation between larval/preadult development duration and pupal mass in females from Despotovačke Šume (Table 3). Strong positive environmental correlations (r_e) between these traits were noticed for Ražanj gypsy moths, in both females and males. Seven out of 18 comparisons of r_p between the populations showed significantly higher values in the medium-density population, although correlation structures were similar between the populations as revealed by product-moment correlation between arcsin-square root-transformed r_p -values ($r=0.7358$, $P<0.001$). Ten out of 18 comparisons of r_e showed a significant difference between the populations, and there was no similarity between environmental correlation structures at the two densities ($r=0.3315$, $P<0.173$). Genetic correlations (both «component» and Pearson's) between larval/preadult development duration and pupal mass were negative in gypsy

moths from Ražanj, while an antagonistic correlation (trade-off) was recorded in the Despotovačke Šume population. Significant positive genetic correlation between female size and longevity was evident in both populations. In males, these life-history traits were not correlated. Among 18 correlation comparisons, five Pearson's and 13 «component» correlations differed significantly between the populations. Additionally, four Pearson's and eight «component» correlations differed in sign. The structure of genetic correlations was sensitive to population density in the parental generation only for «component» correlations ($r=0.4166$, $P<0.085$ for r_g and $r=0.5835$, $P<0.011$ for r_m).

DISCUSSION

Many papers have confirmed the dependence of insect life-history traits and trade-offs between them and both the past and current environment (Rossiter 1991a, 1994; Mousseau and Fox, 1998; Kim and Thorp, 2001; Carisey and Bouce, 2002; Baldal et al., 2005; Chapuis et al., 2008). Environmentally-based maternal effects may alter means and variance/covariance in individual insect performance (Mousseau and Dingle, 1991).

Table 3. Genetic correlations of life-history traits determined by analysis of covariance (r_g) or product-moment correlations of family means (r_m) in gypsy moths from the Ražanj (R) and Despotovačke Šume (D) localities. Environmental (r_e) and phenotypic correlations (r_p) were obtained from analysis of covariance. Population differences were tested by the z-test. Other abbreviations are explained in Table 1. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. Significant population differences are marked as A ($P < 0.05$), B ($P < 0.01$), and C ($P < 0.001$).

Correlation	r_g		r_e		r_p			
	R	D	R	D	R	D		
♀	LD	-PD	0.732	1.059	0.041	-0.380 C	0.132*	0.163*
			0.276	0.496**				
		-PM	-0.858	0.659 C	0.626	0.511	0.211***	0.564*** C
			-0.236	0.587** B				
		-L	-0.760	-0.010 B	-0.029	0.251 C	-0.252***	0.084 C
			-0.514*	0.010				
	PD	-PAD	0.767	1.053	0.329	0.114 A	0.363***	0.390***
			0.411	0.604***				
		-PM	-0.601	0.502 C	0.301	0.279	0.196**	0.316***
			-0.100	0.333				
		-L	-0.348	-0.564	-0.040	0.207 B	-0.075	0.006
			-0.115	-0.229				
	PAD	-PM	-0.863	0.643 C	0.682	0.696	0.242***	0.601*** C
			-0.248	0.590** B				
		-L	-0.750	-0.064 B	-0.035	0.386 C	-0.257***	0.081 C
			-0.514	-0.025				
	PM	-L	0.986	0.418 C	-0.091	0.105 A	0.165*	0.242***
			0.602**	0.499*				
♂	LD	-PD	0.111	0.789 B	0.110	-0.308 C	0.080	0.208**
			0.103	0.560**				
		-PM	-0.669	0.302 C	0.639	-0.047 C	-0.240***	0.072 C
			-0.469*	0.210 A				
		-L	-0.772	0.050 B	-0.125	-0.157	-0.304***	-0.098 A
			-0.576**	-0.086				
	PD	-PAD	0.191	0.873 C	0.502	0.001 C	0.319***	0.470***
			0.257	0.728*** A				
		-PM	1.029	0.781	0.183	0.018	0.304***	0.281***
			0.573**	0.595**				
		-L	0.501	-0.156 A	-0.205	-0.331	-0.140*	-0.261***
			-0.010	-0.133				
	PAD	-PM	-0.592	0.434 C	0.641	-0.042 C	-0.157*	0.144* C
			-0.374	0.331 A				
		-L	-0.719	0.001 B	-0.192	-0.273	-0.321***	-0.163*
			-0.554**	-0.107				
	PM	-L	0.526	0.264	-0.197	-0.063	0.044	-0.010
			0.205	0.199				

The parental environment influences offspring performance directly through the selection of parents that better match the environment (e.g., resistance to starvation and toxic allelochemicals) or through egg provisioning (differential allocation of nutrients, defensive agents, hormones, and enzymes for egg development). If there is a negative covariance between direct additive genetic effects and maternal effects, low food quality of the parental generation will be transformed into increased performance of the offspring generation (Rossiter, 1991a). This negative maternal effect compensates for a deteriorating environment and, according to Rossiter's (1994) maternal effects hypothesis, «... could build gradually over several generations as population density (and host damage) moves from low to moderate levels». Delayed life-history effects and trade-offs between the current and future environment can give rise to population variability and delayed density dependence, which can further promote cyclic population dynamics (Beckerman et al., 2002).

The present study, like some others before (Dis et al., 1996; Yerger and Rossiter, 1996; Myers et al., 1998; Erelli and Elkinton, 2000), compares gypsy moth performance between populations in different phases of growth. The populations used in our experiment were at low and medium (moderate) density, and we therefore expected that the medium-density population would express a negative maternal effect under optimal laboratory conditions. However, we found a weak but statistically significant effect of parental density on offspring life-history traits, and gypsy moth performance was reduced in offspring from the medium-density population, contrary to expectations (Table 1). On the other hand, Rossiter (1991a) showed that larger female and male pupae were attained if the parental generation experienced higher defoliation. However, she analyzed the first five females and five males pupated from each egg mass, while we set out for hatching only a sample of eggs from the central area of an egg mass. Faster development and larger pupae are characteristic of females hatched from larger, first-laid eggs (Rossiter, 1991b). Although egg size-number trade-off is predicted

under stressful conditions (Parker and Begon, 1986), only first-laid eggs was found to increase size in response to high density in *Callosobruchus maculatus* (Kawecki, 1995), and vitellogenin content of only first-laid eggs of the gypsy moth was affected by the parental host plant (Rossiter et al., 1993). It is possible that parental density and nutrition (defoliation of host plants) have different influence on early and late reproduction in such a way that only first-laid eggs increase in size and/or quality under crowding conditions.

In any case, we may suppose that maternal effects represent a significant component of broad-sense genetic variation and covariation of gypsy moth life history traits. Estimated heritabilities (Table 2) and genetic correlations (Table 3) in full-sib analysis of variance and covariance therefore do not give information about possible evolutionary responses to selection. Significant differences of egg-masses (full-sib families) were discovered for gypsy moth life-history traits in previous investigations (Rossiter, 1987; Myers et al., 1998; Lazarević et al., 1998, 2002), as well as in the present study (Table 2). Maintenance of a significant level of genetic variability is, among other factors, made possible by the eruptive population dynamics of the gypsy moth. The succession of low-, medium-, and high-density phases of population growth expose the gypsy moth to different selection pressures (r and K selection), which may lead to differences in expression of genetic variability. Broad-sense heritabilities for some development duration traits were significantly higher in the medium-density compared to the low-density population (Table 2). Phenotypic plasticity and parental effects modulate the expression of genetic variability by changing intra- and/or inter-family variance (Mousseau and Dingle, 1991; Stearns 1992). It has been shown that increased broad-sense heritabilities in a medium-density population of the gypsy moth are the result of increased genetic variance (Lazarević, 2000), which can be attributed to differential gene expression and disturbed development canalization in a stressful environment (Hoffmann and Parsons, 1991). In agreement with our results, Myers et al. (1998) obtained increased inter-family differences in high density populations.

The succession of r- and K-selection regimes requires fast adaptive responses to temporal variation in the environment. Such responses are facilitated by physiological trade-offs between genes determining acquisition and allocation of limited resources for different functions. Increased density favors individuals with fast consumption and molting at the expense of large body size, leading to a positive correlation between development duration and body mass. Such a positive genetic correlation represents a trade-off, since prolonged development is usually associated with reduced fitness, while large body size means a higher reproductive potential. This was obtained for gypsy moth females hatched from egg masses collected from the medium-density population and reared under optimal laboratory conditions (Table 3). Genetic trade-offs contribute to the maintenance of genetic variability of life-history traits in natural populations and are a fundamental presumption of their evolution (Reznick, 1992). No development duration-body size trade-off was found in previous investigations on gypsy moths reared on different host plants (Miller et al., 1991; Lazarević et al., 1998). Moreover, the trade-off obtained in the present study (Table 3) was lost in the next generation of rearing under laboratory conditions (Lazarević, 2000), indicating a low additive component in broad-sense genetic correlations. Insect species with a fixed number of instars usually show negative genetic correlation between development time and body size under stressful conditions (Gebhardt and Stearns, 1993). Plasticity of the number of instars in response to high density (Leonard, 1974) may account for positive correlations under mild stress, since supernumerary molts can enable the insect to overcome the harmful effects of stress and attain larger body size. On the other hand, maximization of the growth rate is a strategy of some outbreaking Lepidoptera (Tammara et al., 2000). Under optimal conditions, maximal body size can be attained in shorter development time. We obtained such a negative genetic correlation between larval duration and pupal mass in males from the low-density population (Table 3). Under severe density stress, outbreaking lepidoptera had shorter development

time and attained lower pupal mass (Leonard, 1974; Tammara, 1998; Tammara et al., 2000).

Although our results do not accord with Rossiter's hypothesis, they emphasize the importance of parental nutrition for variation and covariation of offspring life-history traits. Increased variation under crowded conditions represents the raw material that natural selection acts upon, while trade-offs facilitate fast adaptive responses to selection.

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ГЕНЕТИЧКА ВАРИЈАБИЛНОСТ И КОРЕЛАЦИЈЕ ИЗМЕЂУ ОСОБИНА ЖИВОТНОГ ЦИКЛУСА ГУБАРА (*LYMANTRIA DISPAR* L.) ПОРЕКЛОМ ИЗ ДВЕ ПОПУЛАЦИЈЕ ИЗ СРБИЈЕ

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Лепидоптере са еруптивном популационом динамиком су изложене различитим селективним притисцима током периодичних флукуација бројности услед промена у нутритивном квалитету њихове животне средине. Хипотеза о улози материнског ефекта у појави пренамножења инсеката предвиђа пренос ове нутритивне «информације» на следеће генерације и промену особина животног циклуса код потомака. Да бисмо тестирали овај временски одложен утицај паренталне генерације упоредили смо особине животног циклуса, њихову варијабилност и међусобне корелације између губа-

ра гајених у лабораторији пореклом из популација ниске и средње бројности. Потомство пореклом из популације средње бројности показало је смањење индивидуалне перформансе што указује на редукцију квалитета јаја са порастом густине популације. Генетичка варијанса и коваријанса су такође биле осетљиве на густину родитељске генерације. Квантитативно-генетичком анализом је добијена већа херитабилност у ширем смислу за особине трајања развића као и узајамно ограничење између трајања развића и масе лутки губара које су пореклом из популације средње бројности.