Res. Popul. Ecol. 36(1), 1994, pp. 121-124.

Researches on POPULATION ECOLOGY Original paper

Genetic Estimations for Body Size Characters, Development Period and Development Rate in a Coccinelid Beetle, *Harmonia axyridis*

Hideki UENO

Graduate School of Environmental Earth Science, Hokkaido University, Sapporo 060, Japan

Abstract. Heritabilities and genetic correlations for body size characters and development period in a coccinellid beetle, *Harmonia axyridis* were estimated by a sib-analysis experiment. Positive genetic correlations were detected between size characters and development rate. If this is upheld in the field, genetic variation would be eliminated, as the loci affecting the characters are supposed to be fixed. However, the results indicated moderate heritabilities for all characters. Possible explanations for the results are discussed.

Key words: *Harmonia axyridis*, heritability, genetic correlation, pleiotropy.

Introduction

The genetic variation of traits connected to fitness components is supposed to be low because continuous selection is expected to eliminate most of the mutant genetic variability (Falconer 1989), unless it is maintained by a selection-mutation balance (Lande 1976). However, considerable heritability estimates are often reported for the traits such as development period (Dawson 1977; Dingle et al. 1977), body size (Stearns 1984), survival (Roberts 1961) and fertility (Jinks and Broadhurst 1963; Perrins and Jones 1974). How the genetic variation of the traits under selection is maintained has been the central focus of ecological genetics. For the maintaining mechanism, several explanations are discussed (Stearns 1992). Among them, the antagonistic pleiotropy hypothesis is concerned with the genetic relationship among the traits connected to different fitness components (Rose 1982). It occurs in the situation where the traits are antagonistically coded by the genes, resulting in homogeneous total genotypic fitness and allowing the alleles to be unfixed. Even though some genetic analyses seem to support this hypothesis, the evidence is rather mixed (Bell and Koufopanou 1986).

Larger males of the ladybird beetle *Harmonia axyridis* may have an advantage in mating. Comparison of body size of non-mating and mating beetles showed significant differences in the males in spring copulations (Osawa and Nishida 1992; Ueno unpublished). Thus, positive directional selection seems to act on male body size in this life history episode, and it would be worth measuring how much genetical variation is maintained for body size characters in this species.

Body size characters achieved at the adult stage are influenced by the performance during the immature stages. Larger body size may be achieved by taking a longer time to develop into adults. During the larval stages high mortality is indicated (Osawa 1991). Thus, development period and development rate are possible candidate traits on which antagonistic selection with body size characters is expected.

This study is designed to estimate heritabilities for body size characters, development period and development rate, and genetic correlations between them.

Materials and Methods

Pupal beetles were collected from a suburb of Gifu City and used as sires and dams in a sib-analysis experiment. Beetles were reared individually under 25°C and 16L-8D conditions. Freeze-dried honeybee larvae were supplied *ad libitum*. Rearing conditions were the same throughout this experiment. After eclosion adult males were introduced to females. Copulated females were kept isolated thereafter and oviposition was checked every 12 hours (12 : 00 and 24 : 00). In order to avoid cannibalism larvae were reared individually. Molting, pupation and eclosion were also checked every 12 hours. Dry adult weight was measured to 1 μg with a microbalance. Body size

characters, body length, body width and elytral length were also measured. Development rate was calculated as $\log_e$(dry adult weight)/larval period, assuming an exponential growth curve for simplicity.

A nested ANOVA for unbalanced design decomposes the total variance into the following components; $V_p = k_1V_s + k_2V_d + V_e$, where V_p is total phenotypic variance, V_s is between-sire variance, V_d is between-dam variance and V_e is residual variance. Coefficients, k_1 and k_2, were calculated according to Snedecor and Cochran (1967). These variances connect to causal components as; $4V_s = V_a$, and $4V_d = V_a + V_n$, where V_a is additive genetic variance and V_n is dominance variance. Covariance components were calculated as; $\mathrm{Cov}(x, y) = [\mathrm{Var}(x+y) - \mathrm{Var}(x) - \mathrm{Var}(y)]/2$. This analysis had an unbalanced design, and therefore F-tests based on balanced data may be unreliable. Instead, Tukey's Jackknife procedure was employed to obtain the standard errors of the heritability estimate (Sokal and Rohlf 1981). Resampling units were set as paternal families. Environmental correlations were calculated by subtraction using the following formula; $r_p = h_x h_y r_a + e_x e_y r_e$, where h is the square root of the heritability of the trait and $e^2 = 1 - h^2$, r_p, r_g and r_e are phenotypic, genetic and environmental correlations, respectively (Falconer 1989).

Results

I obtained 558 male and 618 female individuals which were assigned both to 13 paternal and 46 maternal families. Because correlation patterns are not necessarily the same between males and females, the statistical analyses were performed separately for each sex.

Body size characters showed significant difference between males and females (body length, 6.278±0.297 [mean±SD] mm for males, 6.821±0.317 for females, $F=942.070$, $P<0.001$; body width, 5.189±0.298 for males, 5.701±0.301 for females, $F=882.694$, $P<0.001$; elytral length, 5.148±0.289 for males, 5.397±0.315 for females, $F=205.262$, $P<0.001$; dry weight, 7.983±2.349 μg for males, 9.195±2.377 for females, $F=79.209$, $P<0.001$). Development period did not differ significantly (larval period, 13.415±1.403 [mean±SD] days for males, 13.489±1.355 for females, $F=0.890$, $P=0.346$), while development rate showed significant difference (0.131±0.033 for males, 0.153±0.014 for females, $F=232.678$, $P<0.001$). Thus, females achieved larger body size than males though they took about the same development periods as males.

The three correlation patterns, phenotypic, genetic and environmental correlations, were similar among themselves and for both males and females. There were large phenotypic correlations among size characters. Negative correlations were indicated between body size characters and development period (a positive correlation in fitness terms), and positive correlations between body size characters and development rate (Table 1).

Heritabilities for all characters were moderate. Rather higher genetic estimates were obtained for females. Jackknife procedure indicated that heritabilities for all characters were significantly larger than zero (Table 2). Thus, some amounts of genetic variation for size characters, development period and development rate were maintained in the population. Size characters were also correlated genetically. Body size characters showed

Table 2. Heritability estimates in body size characters and development period in *Harmonia axyridis*. Figures in parentheses indicate jackknife estimates.

Trait	Heritability	
	Male	Female
Body length	0.324 (0.343±0.079)	0.563 (0.571±0.093)
Body width	0.238 (0.258±0.087)	0.417 (0.423±0.089)
Elytral length	0.324 (0.342±0.048)	0.440 (0.441±0.064)
Dry weight	0.321 (0.341±0.082)	0.383 (0.393±0.108)
Larval period	0.376 (0.376±0.108)	0.313 (0.314±0.077)
Development rate	0.361 (0.373±0.085)	0.409 (0.413±0.106)

Table 1. Estimates of phenotypic correlations for males (upper triangle) and for females (lower triangle).

	BL	BW	EL	DW	LP	DR
BL		0.790	0.670	0.553	−0.429	0.631
BW	0.809		0.572	0.504	−0.325	0.552
EL	0.735	0.636		0.409	−0.388	0.491
DW	0.203	0.440	0.433		−0.331	0.956
LP	−0.387	−0.310	−0.401	−0.271		−0.721
DR	0.535	0.445	0.474	0.838	−0.677	

BL: body length, BW: body width, EL: elytral length, DW: dry weight, LP: larval period, DR: development rate.

Table 3. Estimates of genetic correlations for males (upper triangle) and for females (lower triangle).

	BL	BW	EL	DW	LP	DR
BL		0.947	0.857	0.731	−0.471	0.725
BW	0.975		0.723	0.616	−0.236	0.550
EL	0.509	0.905		0.657	−0.472	0.651
DW	0.736	0.685	0.825		−0.446	0.918
LP	−0.519	−0.428	−0.539	−0.591		−0.760
DR	0.725	0.650	0.802	0.928	−0.852	

BL: body length, BW: body width, EL: elytral length, DW: dry weight, LP: larval period, DR: development rate.

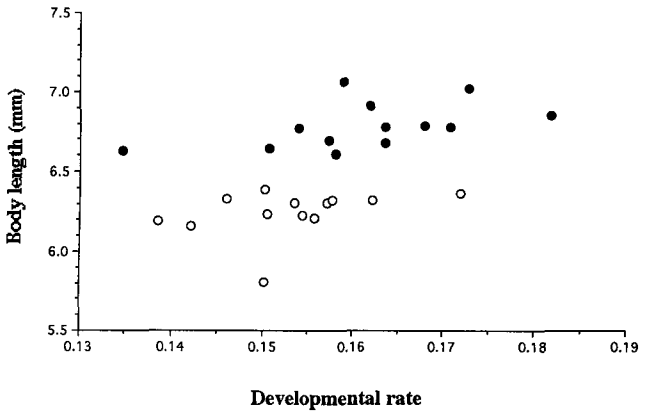

Fig. 1. Relationship of the half-sib family means of development rate and adult body length. Open and closed circles represent males and females, respectively.

negative genetic correlations with development period and positive with development rate (Table 3). Figure 1 shows half-sib family means of development rate plotted against body length. Even though they were statistically not significant ($r=0.359$, $F=1.625$, $P=0.229$, for males; $r=0.500$, $F=3.665$, $P=0.082$, for females), the same genetic associations were suggested. Thus genetically, longer development period and slower development rate were possibly connected to smaller body size, and shorter development period and faster development rate to larger body size. Environmental correlation showed a similar pattern to phenotypic and genetic correlations (Table 4).

Discussion

Genetic correlation among the traits can both increase and decrease the rate of evolutionary change and they can also change the trajectories (Lande 1982). Positive genetic correlations between development rate and body size characters obtained in the results would facilitate faster evolutionary change of both traits than when no correlation between the two traits exists. If the genetic relationships indicated in the present results are upheld in the field, intensive directional force is expected accelerating evolutionary change to the optima limited by physiological and phylogenetic designs, and this is supposed to drive genetic variation to the exhaustion. Thus, the positive correlation patterns in the results is inconsistent with the situation which the antagonistic pleiotropy hypothesis proposes. Genetic variation of these traits, on the other hand, were still maintained in the population. This would need some explanations.

Possible explanations for why genetic variation is maintained and for why positive, instead of negative, genetic

Table 4. Estimates of environmental correlations for males (upper triangle) and for females (lower triangle).

	BL	BW	EL	DW	LP	DR
BL		0.735	0.580	0.468	−0.408	0.583
BW	0.668		0.517	0.464	−0.368	0.560
EL	0.973	0.434		0.291	−0.343	0.408
DW	−0.268	0.277	0.160		−0.270	0.977
LP	−0.309	−0.246	−0.324	−0.102		−0.699
DR	0.368	0.302	0.232	0.780	−0.518	

BL: body length, BW: body width, EL: elytral length, DW: dry weight, LP: larval period, DR: development rate.

correlations between characters connected to fitness components were obtained in the results are as follows. 1) Selections may not be consistent. Especially in the case where environmental conditions are uncertain and fluctuating, they may be insufficient to eliminate the genetic variation (though larger body size advantages were detected for males in two different populations for successive seasons; Kyoto population [Osawa and Nishida 1992] and Gifu population [Ueno unpublished]). 2) Recent studies revealed that genetic structure is not as consistent as supposed. Different populations may show different genetic structure between traits (Berven and Gill 1983; Berven 1987). Also environmental factors have been reported to affect genetic structure (Via 1984; Groester and Dingle 1987; Lynch et al. 1989). Especially, novel environments such as laboratory conditions are suggested to reduce the degree of antagonistic associations because fortuitously pre-adapted individuals would enhance their general fitness (Service and Rose 1985).

These environmental-genetic interactions are worth examining, since recent studies indicating their connection to phenotypic plasticity have been accumulating (Stearns 1992). Several studies found the sign changes in genetic correlations between age and maturity size according to the environmental conditions (Giesel et al. 1982; Gebhardt and Stearns 1988; Newman 1988a, b). In the results, negative correlations were involved with poor growth conditions and positive with rich conditions. Stearns (1989, 1992) proposed two possible hypothetical situations for the observations of the sign change. In one situation, the largest and latest maturing genotype under good growth conditions is the largest but earliest maturing genotype under poor conditions. In the other situation, growth rate and asymptotic size have negative genetic correlations, where the growth curves of different genotype cross if followed far enough. The present results were obtained with artificial freeze-dried honey bee larvae. Okamoto (1978) reported longer elytral length for the same species reared with several kinds of aphids, and negative relationships between elytral length and total development period

across the aphid species. Thus the artificial diet seemed to be inferior to natural aphid resources, and the hypothetical situations proposed by Stearns (1989, 1992) may be likely and are worth testing. The same experimental sets would thus be needed across a range of environments.

Since genetic structure is affected by various factors, we cannot simply exclude other genetic associations in different experimental conditions. Though they do not come out, at genetic levels other relationships might be possible. So far, little is known about intermediate processes which connect genotypic to phenotypic levels. The similarity between genetic and environmental correlation patterns obtained in the present study may indicate that both genetic and environmental factors affect the phenotypic expression through the same sort of physiological and developmental pathways.

Ackowledgements: I would like to express my sincere thanks to K. Tsuji for critical consultations throughout this study. I am grateful to R. Thornhill, Y. Tanaka, S. Kudo and S. Higashi for discussion on the earlier drafts. Comments from the referee improved the manuscript.

References

Bell, G. and V. Koufopanou (1986) The cost of reproduction. *Oxford Surv. Evol. Biol.* **3**: 83–131.

Berven, K. A. (1987) The heritable basis of variation in larval developmental patterns within populations of the wood frog (*Rana sylvatica*). *Evolution* **41**: 1088–1097.

Berven, K. A. and D. E. Gill (1983) Interpreting geographic variation in life history traits. *Am. Zool.* **23**: 85–97.

Dawson, P. S. (1977) Evolutionary adjustment of development time in mixed populations of flour beetles. *Nature* **270**: 340–341.

Dingle, H., C. K. Brown and J. P. Hegmann (1977) The nature of genetic variance influencing photoperiodic diapause in a migrant insect, *Oncopeltus fasciatus*. *Am. Nat.* **111**: 1047–1056.

Falconer, D. S. (1989) *Introduction to quantitative genetics*, 3rd ed. Longman, New Yolk.

Gebhardt, M. D. and S. C. Stearns (1988) Reaction norms for developmental time and weight at eclosion in *Drosophila mercatorum*. *J. Evol. Ecol.* **1**: 335–354.

Giesel, J. T., P. A. Murphy and M. N. Manlove (1982) The influence of temperature on genetic interrelationships of life history traits in a population of *Drosophila melanogaster*: what tangled data sets we weave. *Am. Nat.* **119**: 464–479.

Groester, F. R. and H. Dingle (1987) Genetic and maternal influences on life history plasticity in response to photoperiod by milkweed bugs (*Oncopeltus fasciatus*). *Am. Nat.* **129**: 332–346.

Jinks, J. L. and P. L. Broadhurst (1963) Diallel analysis of litter size and body weight in rats. *Heredity* **18**: 319–336.

Lande, R. (1976) The maintenance of genetic variability by mutation in a polygenic character with linked lici. *Genet. Res.* **26**: 221–235.

Lande, R. (1982) A quantitative genetic theory life history evolution. *Ecology* **63**: 607–615.

Lynch, M. L., K. Spitze and T. Crease (1989) The distribution of life-history variation in the *Daphnia pulex* complex. *Evolution* **43**: 1724–1736.

Newman, R. A. (1988a) Genetic variation for larval anuran (*Scaphiopus couchii*) development time in an uncertain environment. *Evolution* **42**: 763–773.

Newman, R. A. (1988b) Adaptive plasticity in development of *Scaphiopus couchii* tadpoles in desert ponds. *Evolution* **42**: 774–783.

Okamoto, H. (1978) Laboratory studies on food ecology of aphidophagous lady beetles (Coleoptera: Coccinellidae). *Memories of Faculty of Agriculture, Kagawa University* **32**: 1–94 (in Japanese with English summary).

Osawa, N. (1991) *Ecological studies on the ladybird beetle* Harmonia axyridis *Pallas in a natural population*. Ph. D. Thesis, Kyoto University.

Osawa, N. and T. Nishida (1992) Seasonal variation in elytral colour polymorphism in *Harmonia axyridis* (the ladybird beetle): the role of non-random mating. *Heredity* **69**: 297–307.

Perrins, C. M. and P. J. Jones (1974) The inheritance of clutch-size in the great tit (*Parus major* L.). *Condor* **76**: 225–229.

Roberts, R. C. (1961) The lifetime growth and reproduction of selected strains of mice. *Heredity* **16**: 369–381.

Rose, M. R. (1982) Antagonistic pleiotropy, dominance, and genetic variation. *Heredity* **48**: 63–78.

Service, P. M. and M. R. Rose (1985) Genetic covariation among life-history components: The effect of novel environments. *Evolution* **39**: 943–945.

Snedecor, G. W. and W. G. Cochran (1967) *Statistical methods*, 6th ed. Iowa State University Press.

Sokal, R. R. and F. J. Rohlf (1981) *Biometry*, 2nd ed. Freeman, San Francisco.

Stearns, S. C. (1984) Heritability estimates for age and length at maturity in two populations of mosquito-fish that shared ancestors in 1905. *Evolution* **38**: 368–375.

Stearns, S. C. (1989) Tradeoffs in life history evolution. *Func. Ecol.* **3**: 259–268.

Stearns, S. C. (1992) *The evolution of life histories*. Oxford University Press.

Via, S. (1984) The quantitative genetics of polyphagy in an insect herbivore. II. Genetic correlations in larval performance within and across host plants. *Evolution* **38**: 896–905.

Received 29 March 1994; Accepted 14 June 1994