

Heritability of progeny size in a terrestrial isopod: transgenerational environmental effects on a life history trait

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Maternal effects, the environment that mothers provide to their offspring, their provision of nutrients and the environment that offspring of the same clutch share, have come to be recognized as an important influence on offspring fitness. In addition, in invertebrates, maternal effects and common environment may change according to a mother's diet. We tested for the changes in quantitative genetic parameters in a half-sib design where mothers were fed diets varying in nutrient content. Surprisingly, we found that not only maternal and common environmental variance changed with

experimental diets but also there were significant changes in narrow-sense heritabilities, with corresponding h^2 values of 0.61 (high protein), 0.08 (high carbohydrate) and 0.001 (equal carbohydrate:protein). Our results show how an environmentally driven evolutionary process could occur in nature, since the response to selection could change dramatically according to the composition of the diet that females are ingesting.

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Introduction

Animals live and reproduce in changing environments (Endler, 1986). Organisms face this environmental fluctuation in a variety of ways, and frequently they demonstrate phenotypic plasticity in several of their organismal attributes (Via *et al.*, 1995). However, environment can also affect the way that traits are inherited; maternal and general environmental effects are a known example. The environment that mothers provide to their offspring, as well as their provision of nutrients, has been recognized to be an important influence on offspring performance (Mousseau and Fox, 1998, 2000). This is especially true for animals with direct development including a maternal care period, as in many arthropods (Fox and Czesak, 2000).

The environmental effect on the additive genetic variances of life history traits in invertebrates has received extensive treatment (Ebert *et al.*, 1993; Barata and Baird, 1998; Mousseau *et al.*, 2000; Pfrender and Lynch, 2000; Hunt and Simmons, 2002). Nevertheless, few studies have explored the effect of the mother's specific environment (eg mother's diet) on offspring phenotype (Fox, 1997; Fox *et al.*, 2001). A little known, yet interesting, phenomenon is the modification of genetic parameters (ie heritabilities and maternal–environmental

variance) due to changes in the mother's diet. Such a case would provide support for the hypothesis that the response to selection would change as a function of available diets, which, in turn, may change both spatially and seasonally. As far as we know, only one study has been published suggesting this pattern (Kause *et al.*, 2001).

A key life history trait for many arthropods is progeny size, since it has an important effect on starvation resistance of larvae (Torres-Vila and Rodriguez-Molina, 2002), locomotor performance (Gibert *et al.*, 2001), defense against predators (Fox and Czesak, 2000) and the determination of subsequent growth rate (Lawlor, 1976). Hence, progeny size (measured either for eggs or offspring) has effects on individual performance, and therefore on fitness (Fox, 2000; Fox and Czesak, 2000). Parental care is a strong determinant of progeny size in invertebrates (Lawlor, 1976; Fox and Czesak, 2000; Hunt and Simmons, 2002; Rauter and Moore, 2002; Torres-Vila and Rodriguez-Molina, 2002), particularly for isopods, where the marsupium provides a microenvironment where nutrients and minerals are translocated to offspring (Warburg, 1993; Helden and Hassall, 1998). Being detritivores, terrestrial isopods usually face low protein diets and fluctuating food availability (Warburg, 1993; Lavy *et al.*, 2001). It is known that the proportion of protein in offspring diet can exert important effects on their performance (Torres-Vila and Rodriguez-Molina, 2002). In this paper, we go one step further by hypothesizing that mothers provided with experimental diets varying in protein content will change the genetic parameters of their progeny. According to the model proposed by Hartl *et al.* (1985) and reviewed in Hoffmann

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and Merilä (1999), morphological traits increase their additive genetic variance under low nutrient conditions since phenotypic differences among genotypes are increased in limiting resource conditions. Since the carbohydrate content of diets is important for the formation of exoskeleton (Harrison, 1990; Helden and Hassall, 1998), low carbohydrate diets could be considered as an unfavourable environment for this species. Consequently, we predict that the offspring of females fed with low carbohydrate will exhibit higher additive genetic variance than those under control and high carbohydrate treatments.

Materials and methods

Animals and study site

Porcellio laevis is widely distributed in Chile and in several other areas throughout the world (Leistikow and Wägele, 1999). The individuals utilized for this experiment were obtained from Estación de Investigaciones Ecológicas Mediterráneas, the University terrestrial station in San Carlos de Apoquindo (33°23'S; 70°31'W). The station is located 20 km to the east of Santiago, in the Andean foothills, and encompasses roughly 835 ha (for a complete description of the study site see Jaksic, 2001). Isopods were collected by hand from under stones, pieces of wood and soil litter. All specimens were placed in plastic containers and transferred to the laboratory in the Department of Ecology of the Pontificia Universidad Católica de Chile.

Maintenance and culture

Individuals were sexed and later assigned to one of three different diet treatments (see Table 1). The gross energy of each diet was determined using a Parr 1261 computerized calorimeter, with three replicates per treatment. Diets were isocaloric (ie differences in calories between treatments were less than 3%), with average values of 18.8 ± 0.12 , 18.1 ± 0.07 and 18.9 ± 0.14 kJ/g for the control (equal carbohydrate:protein), high carbohydrate and high protein diets, respectively. For diet treatments and before pairings, each female was maintained isolated during 2 months. Three females and one male (a half-sib design) were placed in a Petri dish (50 mm of diameter; base layer of plaster of Paris). In all, 30 replicate Petri dishes were placed in each experimental condition. All treatments were maintained in an environmental chamber (21°C, 14L:10D). We placed females and males together to allow fertilization and

egg extrusion by the females. Given that females of terrestrial isopods can store sperm from several males (Moreau *et al*, 2002), we used only the second clutch of each isolated female (the first one was discarded to avoid any possibility of sperm storage after the isolation).

Offspring were fixed in 50% alcohol immediately following emergence from the maternal marsupium. We measured offspring size as the total length of offspring (ie the distance between the mid-dorsal anterior margin of the carapace and the distal margin of the pleotelson). Females and their offspring were measured using a compound microscope equipped with a calibrated ocular micrometer.

Estimation of heritability

We used an animal model (MTDFREML software) procedure (Boldman *et al*, 1995). This procedure yields direct heritabilities and genetic additive and environmental variances. We followed the general notations and model fitting procedures outlined in Dohm *et al* (2001). Our breeding design allowed us to estimate three variance components: A, the additive variance; C, the postnatal common environmental variance, including nonadditive effects; and E, the environmental variance. We present results for the complete model (ACE), which includes maternal effects (both prenatal and postnatal, see Dohm *et al*, 2001) and nonadditive components, and the reduced model (AE) without maternal effects or nonadditive components, in each case we include real variance component values (ie not as a proportion of the total phenotypic variance).

To test the significance of maternal effects, we constrained the ACE model to the AE model and performed a likelihood ratio test (LRT). According to Shaw and Geyer (1997), the appropriate LRT for variance components is a one-tailed test. In this case, the critical χ^2 at $P=0.05$ is 2.706 and 4.605, with one and two degrees of freedom, respectively (Shaw and Geyer, 1997; Dohm *et al*, 2001). For genetic effects: (1) we constrained the ACE model to a CE model to test the significance of additive genetic effects, (2) we constrained the AE model to an E model to test the significance of additive genetic effects without considering maternal effects on the full model, and (3) we constrained the ACE model to an E model to test the significance of animal effects with two degrees of freedom (ie total genetic effects + maternal effects) (Dohm *et al*, 1996, 2001).

To compare statistically genetic parameters between treatments, we followed a procedure modified from (Shaw, 1991; see also Roff, 1997, p 103). We proceeded in

Table 1 Composition of the experimentally purified control, high carbohydrate and high protein diets

Ingredients	Control		High carbohydrate		High protein	
	Grams	%	Grams	%	Grams	%
Soy protein	137.5	27.5	25	5	250	50
Cornstarch	137.5	27.5	250	50	25	5
α -Cellulose	189	37.8	189	37.8	189	37.8
Vitamin mix	1	0.2	1	0.2	1	0.2
Vegetable oil	35	7	35	7	35	7
Total	500	100	500	100	500	100

For each ingredient weights are expressed in grams on an air-dry basis and percentages (%) are based on total dry weight.

a manner analogous to a one-way ANOVA where all effects are evaluated first, and then the specific means are compared in an *a posteriori* test. The overall analysis consisted in comparing the log likelihood (LL) of the pooled sample (ie all three treatments considered as a single population) with the sum of the three LL values estimated separately (see Shaw, 1991). The difference between the sum of likelihoods and the pooled likelihood was compared with a χ^2 distribution with one degree of freedom, with a significance level of 0.05. Next, we performed the '*a posteriori*' test, using pairwise sequential Bonferroni-corrected comparisons (Rice, 1989) with the same LRT procedure to evaluate which pairs of treatments were statistically different.

Results and discussion

The proportion of protein in the mother's diet had significant effects on offspring size ($H_{2,1263} = 18.7$; $P = 0.0001$, Kruskal–Wallis test). Multiple comparisons of mean ranks showed that individuals born from mothers fed with equal proportions of protein and carbohydrates (ie control diet) were larger than those born from mothers fed with a lower proportion of protein to carbohydrate (ie low protein diet treatment), which, in turn, were larger than those that born from mothers fed with a higher proportion of protein to carbohydrate (ie high protein diet treatment; $P < 0.001$ for all pairwise comparisons). The reduced size of the

offspring in the high protein treatment is expected, given the known effect of carbohydrate on exoskeleton in the young (Harrison, 1990; Helden and Hassall, 1998). Since our high protein treatment was low in carbohydrates, this probably produced comparatively smaller individuals. Genetic analysis showed that both narrow-sense heritabilities (h^2) and maternal and common environmental variance (c^2) changed with the composition of diets (Table 2). Only the high protein diet yielded a large and significant h^2 , whereas both the control diet and low protein diet treatment produced low and nonsignificant h^2 , and high c^2 (Table 2). Significant differences were found among the three genetic analyses (overall $\chi^2 = 13.5$; $P = 0.0002$) with the high protein treatment differing significantly from the control treatment ($\chi^2 = 12.2$; $P = 0.0003$), following sequential Bonferroni correction. Neither low protein versus high protein nor low protein versus control treatment comparisons were significant following sequential Bonferroni correction (although both were significant at $\alpha = 0.1$).

Life history traits have low h^2 , either as a result of Fisher's fundamental theorem of natural selection, according to which 'the rate of increase of fitness of any organism at any time is equal to its genetic variance in fitness at that time', thus, fitness traits are expected to have low levels of additive genetic variance due to rapid fixation of alleles conferring highest fitness (Fisher, 1930; Gustaffson, 1986) or because fitness-related traits may have higher residual variance (ie environmental and

Table 2 (a) Heritabilities (h^2) and maternal effect (c^2) values for each treatment, (b) statistics of the fit to the animal model procedure and (c) significances computed by likelihood ratio tests

Treatment	High carbohydrate	High protein	Control	Total (diet as a fixed effect)
$h^2 \pm SE$	0.08 \pm 0.36	0.61 \pm 0.39*	0.001 \pm 0.29	0.06 \pm 0.12
$c^2 \pm SE$	0.47 \pm 0.19**	0.11 \pm 0.17	0.38 \pm 0.15***	0.41 \pm 0.07***
$e^2 \pm SE$	0.46 \pm 0.19	0.28 \pm 0.24	0.62 \pm 0.16	0.53 \pm 0.07
V_A	0.0023	0.0153	0.00001	0.0017
V_C	0.0143	0.0028	0.0111	0.0118
V_E	0.0141	0.0070	0.0180	0.015
V_P	0.031	0.025	0.029	0.029
$-2*LL$				
ACE	-1248.4	-1079.0	-1337.3	-3631.7
CE	-1248.3	-1076.2	-1337.3	-1631.4
AE	-1240.1	-1078.6	-1326.8	-1513.2
E	-1059.7	-975.6	-1209.8	-3210.4
<i>Descriptive data</i>				
Sires	25	18	23	66
Dams	54	45	59	158
Offsprings	349	296	394	1039
Total animals	428	359	476	1263
Mean \pm SD (offspring, mm)	1.76 \pm 0.18	1.73 \pm 0.17	1.79 \pm 0.17	1.76 \pm 0.17
Min–Max (offspring, mm)	1.19–2.19	1.19–2.15	1.15–2.35	1.15–2.35

h^2 = (direct) narrow-sense heritability; c^2 = common environmental and maternal proportion of total variance; e^2 = environmental proportion of total variance; SE = asymptotic standard error; V_A = additive genetic variance; V_C = common environmental and maternal variance; V_E = residual variance; ACE model = full model including additive genetic variance+common environmental and maternal variance+environmental (residual) variance; CE = reduced model excluding additive genetic effects; AE = reduced model excluding common environmental and maternal variance; E = reduced model excluding both additive genetic effects and common environmental and maternal variance (assuming purely environmental effects). Twice the LL value approximates a χ^2 distribution. Likelihood ratio tests (Lynch and Walsh, 1998) were performed to evaluate whether estimates were significantly different than zero, with degrees of freedom equal to the number of parameters dropped from the model. According to Shaw and Geyer (1997) (see also Dohm *et al*, 2001) this is a one-tailed test, where critical χ^2 values are 2.706 and 4.605 with one and two degrees of freedom, respectively.

* $P < 0.05$.

** $P < 0.01$.

*** $P < 0.001$.

nonadditive genetic variances) and consequently low heritability due to more complex genetic architecture than traits more distantly associated with fitness (Price and Schluter, 1991; Merilä and Sheldon, 1999). Overall, our results (ie considering the entire data set and including diets as a fixed effect) are in agreement with this general pattern.

However, we did find a surprisingly high value of heritability in one of our experimental diets (ie high protein, $h^2=0.61$), which contrasts with the general pattern observed in life history traits (Mousseau and Roff, 1987), but is in agreement with what is known for crustaceans (Pfrender and Lynch, 2000). This may be due, in part, to the low maternal effects obtained in the high carbohydrate and control treatments. Alternatively, the expression of additive genetic variation could increase in unfavourable conditions (Hoffmann and Merilä, 1999). Actually, the high protein diet presented an additive genetic component one order of magnitude larger than any of the other treatments. Since the amount of carbohydrate in the diet is important for the formation of exoskeleton (Helden and Hassall, 1998; Harrison, 1990), the diet with low content of carbohydrate could be considered as a 'stressful environment'. This condition could increase the expression of additive genetic variance by reducing environmental variance as results suggest (see Table 2; Hoffmann and Merilä, 1999).

Our results support the generalized view of maternal/common environmental effects as strong determinants of progeny size (Mousseau and Fox, 1998, 2000), and these findings may apply to other herbivorous arthropods, since the proportion of nitrogen in animal biomass is usually much higher than that of plants (Awmack and Leather, 2002). For herbivorous arthropods, available dietary nitrogen (in the form of protein and free amino acids) can potentially limit many important processes (McNeill and Southwood, 1978; White, 1993; Joern and Behmer, 1997). A potential shortcoming of our conclusions may arise from two facts. First, we forced individuals to consume the experimental diets. Second, our design cannot distinguish from pure maternal and common environmental variance.

With regard to the first issue, Joern and Behmer (1997) showed that a grasshopper species could select diets with more carbohydrate content, and both Hassall and Rushton (1984) and Warburg (1993) describe behavioural diet selection by terrestrial isopods. Whether *P. laevis* selects its diets according to the nutrient content is not known. However, this phenomenon would be important for determining the potential for selection on progeny size of *P. laevis*, depending on three main facts: (1) the annual reproductive pattern of this species, (2) according to this pattern, the seasonal basis of nitrogen and carbohydrate availability in the environment, which, in turn, depends on the plant species present in the ambient, and (3) the scale of spatial heterogeneity that *P. laevis* experiences. Most of this information has not been collected, which incites a call for more field studies with regard to the physiological ecology of this species.

With regard to the second issue (the differentiation between maternal and common environmental effects), the proportional contributions of maternal and common environmental effects to progeny size do not change our general conclusion: diet consumed by the mother could change dramatically the form of inheritance in progeny

size. Certainly, we cannot draw conclusions with regard to the extent of variance in progeny size that is due to translocations of nutrients from the mother (a prenatal maternal effect), or the contrary, how important is the shared environment of the offspring in determining their size (a pure common environmental effect). Such information would be valuable especially in the scenario of the effects of favourable and unfavourable environments on response to selection (see Hoffmann and Merilä, 1999).

Maternal and common environmental effects were highly variable among experimental diets, which, in turn, induced strong differences in heritabilities. Differences in genetic variances due to environment have been reported for *Daphnia* (Ebert *et al*, 1993), the seed beetle (Fox *et al*, 1999) and the sawfly (Kause *et al*, 2001). Furthermore, our results are in concordance with studies that report changes in maternal effects with the specific environment of the mother (Barata and Baird, 1998; Rauter and Moore, 2002). Some authors have reported intergenerational effects of mothers on life history patterns and trade-offs (Ebert *et al*, 1993; Fox, 1994, 1997; Rauter and Moore, 2002); nevertheless, our results suggest a rather different outcome: intergenerational effects can interfere with genetic effects. With regard to standard evolutionary theory, this would mean that the environment experienced by a mother, which may change on a seasonal and/or unpredictable basis (Kause *et al*, 2001), could determine how and when a trait responds to natural selection (Hoffmann and Merilä, 1999). Several lines of evidence are in agreement that progeny size could be a target of selection (Lawlor, 1976; Barata and Baird, 1998; Fox and Czesak, 2000; Fox *et al*, 2001; Torres-Vila and Rodriguez-Molina, 2002) and that maternal and common environmental effects could modify the response to selection (Fox and Czesak, 2000; Rauter and Moore, 2002), both in favourable and unfavourable environments (Hoffmann and Merilä, 1999). Hence, our initial hypothesis suggesting the existence of environmentally driven evolutionary processes would be supported by our results.

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