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Environment-dependent genetic correlations between development time and body mass in a scorpionfly

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Abstract

Development time and body mass at maturation are two important fitness traits fundamental for our understanding of life history theory. Generally, fast development is associated with small adult body mass, as it will take longer to grow large. However, the strength of this trade-off may depend on average food availability, as the potential benefit of long development will depend on the rate of food intake. Here, I report results of a food manipulation experiment during larval development of the scorpionfly *Panorpa cognata* (Insecta, Mecoptera). Development time showed considerable genetic variation, yet food level had no influence and there was a strong genetic correlation in development time across environments. As expected, larval and adult body weight was significantly affected by food availability. Furthermore, body mass was influenced by a highly significant genotype-by-environment interaction. The reaction norm for body mass in response to food treatment was much stronger in families with long development time compared with rapidly developing genotypes. This effect was accompanied by a shift in the genetic correlation between development time and body size when comparing the two food levels. Specifically, the genetic correlation between body mass and development time changed from being positive at high food levels to a negative genetic correlation at low food levels. These results are consistent with other empirical findings demonstrating a similar shift in genetic correlations between body mass and development time when comparing favourable and unfavourable environmental conditions.

Keywords: *Panorpa cognata*; Food availability; Life history evolution; Genotype-by-environment interaction; Reaction norms

Introduction

The study of life history theory is concerned with the effects of variation in the timing of events and energy expenditure on traits important for an organism's growth, development, survival and reproduction (e.g. Roff, 1992; Stearns, 1992). An assumption fundamental for life history theory is that evolution is constrained by universal trade-offs between different traits affecting fitness. The strength of these trade-offs will be shaped by abiotic and biotic interactions, which of course may be very different between species, populations and individuals. An organism's life history can thus be seen as the sum of several strategic decisions over an organism's life time.

Two key life history traits are duration of growth (or development time) and body size or mass at maturity (Stearns and Koella, 1986; Rowe and Ludwig, 1991; Roff, 1992; Stearns, 1992). Whereas there is a large body

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of evidence suggesting that in numerous species adult body mass is closely associated with female fecundity (Roff, 1992; Blanckenhorn, 2000) and male mating success (Andersson, 1994), development time is usually thought to be negatively correlated with fitness, for several reasons. During longer development, individuals will be exposed to predators for a longer time span, decreasing the chances of survival until sexual maturity (Sibly and Calow, 1986). Furthermore, variation in climatic variables during the year will set constraints on development time. Time horizons due to seasons unsuitable for growth and reproduction will often set upper limits for the duration of development (Roff, 1980; Nylin and Gotthard, 1998; Gotthard, 2001). Nevertheless, all other things being equal, it will take longer to grow to a larger size, and large body size is, therefore, typically positively correlated with development time. Thus, organisms must usually trade off fast development for large adult body mass and vice versa (Stearns and Koella, 1986; Roff, 1992; Stearns, 1992; Nylin and Gotthard, 1998).

Environmental factors, such as temperature or food availability, will have profound effects on the suitability of a given life history strategy (Roff, 1992; Stearns, 1992). Yet, organisms often will face an environment that varies in time and space. Furthermore, genotypes may be differentially adapted to distinct environmental settings, and therefore show genotype-specific reaction norms in response to them (Via and Lande, 1985; West-Eberhard, 1989; Pigliucci, 2005). Hence, the widespread occurrence of such genotype-by-environment interactions has several important implications for the study of life history evolution. First, such interactions may help understand the maintenance of genetic variability in important fitness traits such as life history traits (see Gillespie and Turelli, 1989; Jia et al., 2000). Second, the strength of life history trade-offs is often affected by environmental conditions (Reznick et al., 2000; Sgrò and Hoffmann, 2004). Longer development time may, for instance, have a larger effect on adult body mass when food resources for growth are abundant or are of high quality compared with situations of food stress (e.g. Gebhardt and Stearns, 1988; Kause and Morin, 2001; Kause et al., 2001). Thus, under unfavourable conditions, genotypes with long development time may not be able to exploit and convert food resources into large body size as effectively as under conditions with ample food availability. The magnitude of the genetic correlation between life history traits which has been widely used as a measure of the strength of trade-offs (see Roff, 1996, 2000; Sgrò and Hoffmann, 2004) can thus differ considerably between different environments and even change sign (van Noordwijk and de Jong, 1986; Gebhardt and Stearns, 1988; Newman, 1988; Simons and Roff, 1996; Blanckenhorn, 1998; Tessier et al., 2000; Kause and Morin, 2001; Messina and Fry, 2003; Ernande et al., 2004; Uhl et al., 2004; Blanckenhorn and Heyland, 2005). Such genotype-environment interactions can therefore result in environment-dependent genetic correlations between life history traits (van Noordwijk and de Jong, 1986; Stearns et al., 1991; Reznick et al., 2000; Sgrò and Hoffmann, 2004).

Here, I examine the effect of genotype and larval food availability on development time and growth in the scorpionfly *Panorpa cognata*. At the site of the study population near Freiburg i. Br. (47°57′N, 07°38′E) in south-western Germany, *P. cognata* has two generations a year. Adults of the spring generation emerge and reproduce in May/June. Larvae of the second annual generation develop in June/July. Following pupation, adults emerge and reproduce in July/August. The offspring develop in late summer and hibernate as last instar larvae. This population is presumably somewhere at the edge of the geographic distribution where this bivoltine development mode is possible. More northerly located populations, in Bonn (50°46′N) and Gießen (50°34′N) for instance, with somewhat shorter seasons, are characterised by a single annual generation (Sauer, 1970; L. Engqvist, pers. obs.). A transition from a univoltine life cycle to bivoltinism will drastically shorten the time available to attain maturity in each generation (Roff, 1980; Rowe and Ludwig, 1991; see also Blanckenhorn, 1994; Blanckenhorn and Fairbairn, 1995). This implies that time horizons due to seasonality may strongly constrain the development of individuals in this particular study population of *P. cognata*. Individuals of the second generation will have to develop rapidly in order for them to reproduce in time for their offspring to complete development before the time of the first freeze in autumn. Furthermore, *Panorpa* scorpionflies are scavengers (Byers and Thornhill, 1983; Bockwinkel and Sauer, 1994), and there are strong indications that availability of food resources is declining in the course of the season (Bockwinkel and Sauer, 1994). Thus, in order to exploit higher food resources in the second adult generation, fast larval development seems even more favourable. Nevertheless, longer development time may affect body mass positively and in scorpionflies body condition strongly influences female fecundity (Engqvist and Sauer, 2003a, b) and male reproductive success (Sauer et al., 1998; Engqvist and Sauer, 2003b). In nature, food levels may differ considerably between years, and, as outlined above, this may strongly affect the genetic correlations between development time and body mass. Hence, the benefit of long development time may be different at different food levels.

In this study, I investigated larval development during the diapause-free developing, summer generation of *P. cognata*. The main objective was to study the overall and genotype-specific effects of food availability during larval development on development time and body mass

in *P. cognata*. Accordingly, I aimed at measuring the heritability of development time and body mass at two different food levels and to determine the reaction norm of these traits in response to food shortage. Particularly, I examined if development time and body growth showed heritable phenotypic plasticity in response to food level, that is whether there are genotype-by-environment interactions and whether different genotypes follow different growth strategies. Finally, my aim was to estimate and compare the genetic correlations between development time and final body size in the different environments.

Materials and methods

Genetic variance, genotype-by-environment interactions and genetic correlations between traits were analysed using a split-brood full-sib design. Full-sib offspring were randomly assigned to be reared individually in one of two different treatments differing in food availability.

Breeding of the parent generation

The parent generation in the breeding experiment were all F_1 offspring of animals caught near Freiburg i. Br. in south-western Germany in August 2002. Field-caught males and females were held in pairs in plastic boxes ($10 \times 10 \times 7\,cm^3$) containing moist filter paper, peat-filled petri dishes for oviposition and food ad lib. Food consisted of small cut mealworms (*Tenebrio molitor*). Boxes were inspected daily for egg laying. Larvae were reared on a 12L:12D photoperiod and, as third larval instars, transferred to soil-filled, open-bottomed plastic cylinders (∅ 40 cm, depth 1 m) placed outdoors in the ground, where they overwintered. Adults were collected at the day of emergence. For details of breeding protocols see Sauer (1970, 1977), Thornhill and Sauer (1992) and Engqvist and Sauer (2003a).

Breeding of offspring generation

A full-sib design was used. Parents were generally randomly paired but with restrictions. As I wanted the genetic pool to be as diverse as possible, I used descendants from as many field-caught pairs as possible. Furthermore, pairings between siblings were avoided. Parents were paired and copulations lasted at least 2 h. Females were thereafter kept individually in oviposition boxes identical to the breeding boxes used for the parent generation. Boxes were inspected daily for egg laying. I used a pair of fine and flexible tweezers to carefully transfer egg batches from the egg-laying box to a petri dish containing moist tissue paper. In total I collected fertilized eggs from 28 families.

Following larval hatching, broods were split and the larvae were randomly assigned to two different treatments. Initially, I intended to assign seven larvae from each family to each treatment, but unfortunately, in some families not enough larvae hatched or died during larval development. In total, 317 larvae reached the fourth larval stage and 280 emerged as adults.

Larvae were fed on a diet that consisted of either 10 or 30 mg freeze-dried mosquito larvae (Astra® Aquaria) every seventh day. Larvae were kept individually in small plastic petri dishes (∅ 5.2 cm) containing moist filter paper and food at 18 °C on a 18L:6D photoperiod enabling diapause-free development (see Sauer, 1970, 1977). Before feeding, Petri dishes were changed to avoid fungi invasion. Larvae from both treatments invariably consumed all food between feeding events, except for the last feeding before pupation, which always seemed untouched on inspection. On the 26th day, fourth instar larvae were weighed to the nearest 0.1 mg and transferred to peat-filled cylinders (8×3.5 cm, approximate peat depth: 4 cm) where they entered the pupal stage and finally emerged. No food was provided during this phase. On emergence, individuals were sexed, and once again weighed to the nearest 0.1 mg. The mean length of the left and right forewing was used as a measure of body size. Measurements were made to the nearest 0.1 mm with a dissecting microscope at 10× magnification.

Statistical analysis

I used mixed model ANOVAs to estimate genetic variation and the effects of food treatment and gender as well as the family × treatment interaction on development time, larval mass, adult mass and size. In these analyses family was entered as a random factor and gender and treatment were entered as fixed factors. In the initial analyses gender × treatment as well as gender × family interactions were included. However, no trait displayed significant gender interactions (all $F<1.9$, all $P>0.05$), indicating that all potential gender effects were homogeneous over families and treatments. These non-significant interactions were, therefore, removed prior to the final analyses. Yet, in all subsequent analyses and calculations, gender differences were controlled for by adjusting the trait values by the corresponding gender effect.

I used three different measures of growth during larval development: larval weight of fourth instar larvae on the 26th day of age, adult hatch weight, and adult body size. There were strong and positive correlations between all these measures (larval weight/adult weight: $R = 0.755$, $P<0.001$; larval weight/adult size:

$R = 0.621$, $P < 0.001$; adult hatch weight/adult size: $R = 0.710$, $P < 0.001$). I, therefore, performed a principal component analysis in order to obtain a one-dimensional variable of larval body growth, which was then used for subsequent analyses. Prior to the principal component extraction, I cube-root transformed the weight measures in order to obtain the same linear scale as in the measure of body size.

Heritabilities were estimated for full-sib designs using the formulas in Roff (1997). Standard errors were calculated using a formula accounting for unequal family sizes (Swiger et al., 1964; referred to in Roff, 1997, p. 41).

The genetic correlations between traits within environments, r_g, can be computed as

$$r_g = \frac{\mathrm{COV}(x, y)}{\sqrt{\mathrm{VAR}(x)\,\mathrm{VAR}(y)}},$$

where COV and VAR are the genetic components of covariance and variance of traits x and y (Falconer and Mackay, 1996; Roff, 1997). For a full-sib breeding design, the genetic covariance component is calculated as

$$\mathrm{COV}(x, y) = \frac{\mathrm{MC_{AF}} - \mathrm{MC_{WF}}}{k},$$

where $\mathrm{MC_{AF}}$ is the mean cross product among families, $\mathrm{MC_{WF}}$ the mean cross product within families and k the weighted family size (cf. Roff, 1997, p. 82) The standard errors of the genetic correlations between traits were estimated using the jackknife as described by Roff and Preziosi (1994). Subsequently, t-tests were used to test for significant deviances of the genetic correlations from zero and for differences between treatments in the magnitude of genetic correlations.

Similarly, the genetic correlation of a trait x across environments, $r_{g(a)}$, was calculated as

$$r_{g(a)} = \frac{\mathrm{COV}(x_L, x_H)}{\sqrt{\mathrm{VAR}(x_L)\,\mathrm{VAR}(x_H)}},$$

where $\mathrm{COV}(x_L, x_H)$ is the covariance of trait x in the two treatments, and the genetic variance components for the trait in the treatments with low and high food levels are given by $\mathrm{VAR}(x_L)$ and $\mathrm{VAR}(x_H)$, respectively (see Fry, 1992; Roff, 1997). The covariance term is given by

$$\mathrm{COV}(x_L, x_H) = \frac{\mathrm{MS_{AF}} - \mathrm{MS_{F\times E}}}{2n'},$$

where MS equals the mean sum of squares and n' corresponds to the number of progeny per family assigned to each treatment. In the case of varying numbers of progeny per family and treatment, n' can be derived from the expected mean squares of the F × E variance (cf. Fry, 1992). The jackknife was used to estimate standard errors of the different $r_{g(a)}$, but significant deviations from $r_{g(a)} = 0$ were tested using a two-tailed F-test, with $F = \mathrm{MS_{AF}}/\mathrm{MS_{F\times E}}$ (see Fry, 1992).

In 2 out of 28 families, I only obtained values for larval development and growth in one of the two treatments. These data were discarded in all analyses regarding G × E interactions (mixed model ANOVA, $r_{g(a)}$), but were taken into account in the heritability and genetic correlation estimates within treatments (r_g). Thus, the heritabilities and genetic correlations between traits (r_g) are based on 27 families within each treatment and the analyses concerning G × E interactions are based on 26 families.

The statistical analyses were performed using SPSS 12.0.1 except for the jackknives which were programmed in R 2.4.1. The major axis (MA) regressions (see Figs. 1 and 2) were calculated using the program Model II regression (Legendre and Legendre, 2001), available from ⟨http://www.bio.umontreal.ca/casgrain/en/labo/model-ii.html⟩.

Results

Development time

Mean ± SD development time from larval hatching until adult emergence was 52.76 ± 3.24 days. There was no difference in development time between males and females (males: 52.76 ± 3.25 days; females: 52.76 ± 3.24;

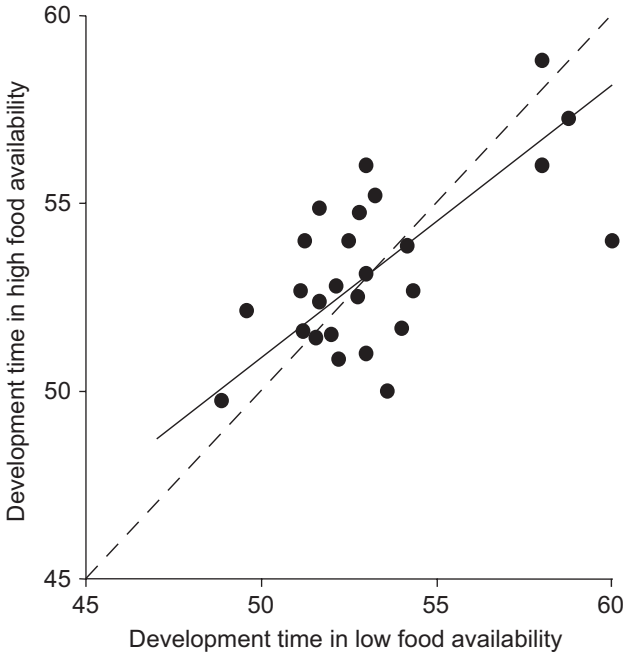

Fig. 1. Family mean correlation in development time across treatments, illustrating both the genetic variance present in development time as well as the lack of effect of food level on development time. The data points represent the family means in both treatments. The dashed line depicts the expected values assuming no difference between treatments. The solid line is from an MA regression.

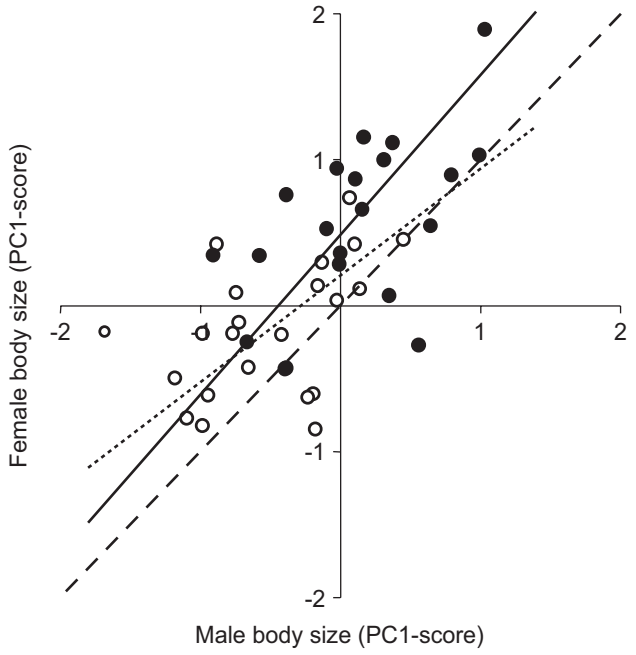

Fig. 2. Influence of gender, food treatment and family on larval body growth (PC1 score). The data points represent the family means in both treatments (high food availability: solid circles and solid line, low food availability: open circles and dotted line). The dashed line depicts the expected values assuming no difference between females and males. The other lines are MA regression lines.

Table 1), nor had food treatment any significant effect (low food availability: 52.56 ± 3.24; high food availability: 52.94 ± 3.23; Table 1, Fig. 1). However, family explained a significant amount of the variance in development time (Table 2). Hence, there were substantial and significant heritabilities of development time in both food treatments (Table 1). The flat shape of the norm of reaction in response to food level was also consistent across treatments. This was evident from the non-significant family × treatment interaction and the relatively strong genetic correlation across treatments (Table 2). As there was no genotype-by-environment interaction, it is also possible to compute an overall estimate of heritability, which amounted to 0.601 ± 0.149.

Body mass and size

The principal component analysis on the measure of individual body measures (larval weight, adult hatch weight and adult size) yielded a single significant factor (PC1, eigenvalue: 2.39; proportion of variance: 79.7%). This principal component 1 is a combined score of body size and weight; thus, high scores are associated with both heavy and large individuals (factor loadings: larval weight 0.885; adult hatch weight 0.922; adult size 0.870).

Despite receiving the same amount of food and having the same average development time as males, females were significantly larger and heavier, both as larvae and as adults (Table 1, Fig. 2).

As expected, larval food availability had an effect on all measures of larval body growth. Larvae receiving more food were, on average, both significantly heavier and significantly larger (Tables 1 and 2, Fig. 2). All measures of body growth consistently showed a statistically significant genotype × food treatment interaction (Table 2) indicating that the effect of food availability on larval growth is different for different genotypes. Thus, there is a heritable phenotypic plasticity in larval growth in response to food levels. Comparing mean family development times with the mean differences in PC1 scores between treatments within each family (Fig. 3) made obvious that in families with a long larval development time the plasticity in response to food availability is higher than in faster developing genotypes ($R = 0.445$; $P = 0.026$). Due to the strong genotype-by-environment interaction, the genetic correlations across treatments were relatively weak compared with the across-treatment correlation of development time (cf. Table 2). For all traits related to body size, the estimated $r_{g(a)}$ was positive, but only significantly so for larval weight (Table 2).

As different genotypes responded differently to food availability, separate heritabilities were estimated for the two treatments, correcting for the variance due to differences in body mass and size between males and females. In both environments, all measures of body growth displayed a consistently large and significant amount of genetic variance, demonstrated by heritability estimates ranging between 0.367 and 0.608 (cf. Table 1).

Genetic correlations between traits

The genetic correlation between development and body growth was also estimated in both treatments separately. At low food availability, there was a significant negative genetic correlation between larval development time and body growth (PC1 score) ($r_g = -0.283 \pm 0.087$, $t_{26} = -3.27$; $P = 0.003$; Fig. 4). In contrast, in the high food availability treatment there was a positive but non-significant correlation between family mean development time and family mean PC1 score ($r_g = 0.057 \pm 0.130$, $t_{26} = 0.44$; $P > 0.6$; Fig. 4). The difference in genetic correlations between environments was statistically significant ($t_{52} = 2.10$; $P = 0.04$). However, in the high food availability treatment, a curvilinear relation between family mean development time and family mean PC1 score became evident upon inspection (Fig. 4) as the inclusion of a quadratic term improved the statistical model significantly ($t_{25} = -2.40$;

Table 1. Estimates of trait means (±SE) and heritabilities (±SE) under low and high food availability for development time and the different measures of body growth (PC1, larval weight, adult weight and size)

		Development time		PC1		Larval weight		Hatch weight		Adult size	
		Low food availability	High food availability	Low food availability	High food availability	Low food availability	High food availability	Low food availability	High food availability	Low food availability	High food availability
Trait size	Males	52.3±0.35	53.1±0.44	−0.73±0.10	0.06±0.10	25.2±0.41	27.4±0.43	19.5±0.31	22.2±0.37	11.3±0.05	11.7±0.05
	Females	52.8±0.43	52.8±0.33	−0.19±0.10	0.70±0.11	26.2±0.39	29.7±0.46	20.9±0.36	24.0±0.38	11.9±0.08	12.2±0.08
h^2		0.68±0.19**	0.59±0.18**	0.59±0.19**	0.61±0.19**	0.45±0.18*	0.53±0.18**	0.39±0.18*	0.37±0.18*	0.58±0.19**	0.54±0.19**

*$P<0.05$, **$P<0.01$.

Table 2. Output of the mixed-model ANOVA and the jackknife estimates (±jackknife SE) of the genetic correlation across treatments for all measured traits

	Source of variation	Development time			PC1			Larval weight			Hatch weight			Adult size		
		d.f.	F	P	d.f.	F	P	d.f.	F	P	d.f.	F	P	d.f.	F	P
Mixed-model ANOVA	Gender	1, 222	2.55	0.11	1, 221	46.5	<0.001	1, 225	16.5	<0.001	1, 222	26.9	<0.001	1, 224	76.0	<0.001
	Treatment	1, 43.9	0.01	0.99	1, 36.4	45.9	<0.001	1, 40.8	31.6	<0.001	1, 38.1	47.20	<0.001	1, 34.5	24.4	<0.001
	Family	25, 24.9	4.56	<0.001	25, 24.9	2.18	0.029	25, 24.9	2.59	0.01	25, 24.9	1.64	0.11	25, 24.9	1.74	0.09
	Family × treatment	25, 222	1.25	0.20	25, 221	1.98	0.005	25, 225	1.51	0.06	25, 222	1.76	0.01	25, 224	2.41	<0.001
Genetic correlation	$r_{g(a)}$	0.767±0.15			0.271±0.13			0.366±0.15			0.193±0.18			0.206±0.15		
across environment	$MS_G/MS_{G\times E}$	$F_{25,25}=4.56$		$P<0.001$	$F_{25,25}=2.17$		$P=0.06$	$F_{25,25}=1.71$		$P=0.02$	$F_{25,25}=1.63$		$P=0.22$	$F_{25,25}=1.74$		$P=0.16$

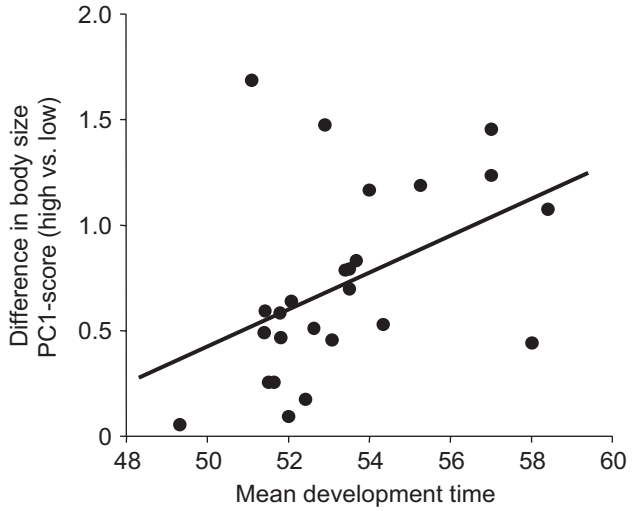

Fig. 3. Correlation between family mean development time and the reaction norm of body growth (PC1 score) in response to food availability.

$P = 0.02$). Specifically, the genetic correlation between development time and body size (PC1 score) was significantly positive for families with a mean development time of fewer than 52.2 days (post-hoc comparison, see Aiken and West, 1991).

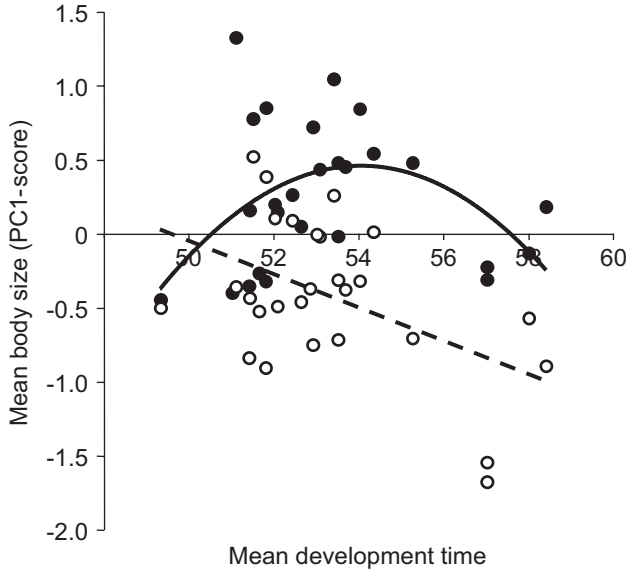

Fig. 4. Genetic correlations between development time and larval body growth (PC1 score) at two different food levels. Data points represent the family means at each food level (high food availability: solid circles and solid line, low food availability: open circles and dashed line). Lines indicate the weighted least square regressions including a quadratic term (which is significant only for the high food level).

Discussion

This study investigated the impact of genotype and food availability on larval development in the scorpionfly *P. cognata*. In order to estimate the additive genetic variances and covariances, a full-sib design was employed. Estimates of additive genetic variance derived from full-sib studies are generally augmented because they potentially also contain variance due to maternal effects, dominance and/or common larval environment (Falconer and Mackay, 1996; Roff, 1997). In this study, variance due to common larval environment and maternal effects is improbable as larvae were reared individually and parents had been held in the laboratory under identical and standardized conditions for at least one generation. Yet a slight overestimation due to dominance variance is possible (Roff, 1997).

With respect to development time, food availability had no considerable effect, resulting in consistently flat reaction norms (i.e. fixed time option, cf. Blanckenhorn, 1998). This was unexpected insofar as resource limitation generally results in a longer development time (Stearns and Koella, 1986), though cases where food shortage induces earlier maturation are also sometimes observed (see e.g. Blanckenhorn, 1998, 1999). The lack of a food effect on development time may indicate that, at least during the summer generation of this population, developing *P. cognata* larvae may be severely time constrained. An already fast growth rate may constrain an even more accelerated larval development (see e.g. Blanckenhorn, 1999 for a discussion) and time horizons due to seasonality may restrain individuals from growing longer when food is scarce.

However, there was considerable heritable variation in both development time and body mass in both treatments. Most importantly, however, the genetic correlation between these traits changed from being negative at low food availability to predominantly positive at higher food availability. Evidently, genotypes with different development times show different reaction norms for body mass in response to larval food availability, as revealed by a significant family × treatment interaction. These data suggest that the potential benefit of a long development time in terms of increased growth will be fundamentally different with differing food availability. A long development time will be beneficial if it allows an individual to grow larger. Apparently, this is only realised at higher food availability. If food is scarce, genotypes with long development time seem not to be able to exploit and convert food resources into large body sizes as effectively as under conditions with ample food.

The relationship between development time and body size revealed an interesting pattern. While at low food availability the genetic correlation was unambiguously negative, the correlation between these two traits was

more complex at high food availability. The genetic correlation between development time and body size was positive only for families with short to intermediate development time, whereas the correlation diminished at increasing development times of families. There may be at least two explanations for this result. First, the sib-families with the longest development times may represent genotypes with low overall viability that take a long time to develop and are unable to grow large despite sufficient food supply. Mutation-selection balance might explain the incidence of such maladapted genotypes within a population despite strong selection (e.g. Houle et al., 1996). Another possibility that might have caused this outcome is that the food supply used in the high food availability treatment was not necessarily the highest possible. In other studies using more relaxed larval dietary conditions, adult *P. cognata* scorpionflies were on average larger (mean ± SD female size: 12.7 ± 0.29 mm, Engqvist and Sauer, 2001) than in the present study. Hence, in this scenario the selected high food level would only be sufficient for intermediate genotypes, whereas families with longer development time may require even more food to grow effectively, and as a result a positive time-size relationship may only be realised when food availability is relatively unlimited (see Fig. 5).

Previous studies have shown that environmental changes altering the levels of nutrition can lead to shifts in genetic correlations between life history traits (for reviews see Reznick et al., 2000; Sgrò and Hoffmann, 2004). The results presented here are supported by a number of similar findings in previous studies and add to a growing body of evidence demonstrating nutrition- or environment-dependant trade-offs, as revealed by changes in the genetic correlations between development time and body growth. In *Drosophila mercatorum*, the genetic correlation between development time and weight changed from being significantly positive in an environment with high levels of yeast to significantly negative in a low-yeast environment (Gebhardt and Stearns, 1988), in accordance with the present study. Similarly, in a study of a birch-feeding sawfly, *Priophorus pallipes*, with larvae being fed on diets differing in quality, the genetic correlation between body size and development time switched from positive on a high-quality diet to negative on a low-quality diet (Kause and Morin, 2001). Furthermore, in an inter-specific study using different sawfly species feeding on the same host plant, it was shown that in species where the timing of larval development coincides with high and stable birch leaf quality, longer development time results in larger body mass. Yet, in species feeding on senescing leaves the phenotypic and genetic correlations between development time and final mass were negative or zero, as the rapidly deteriorating foliage quality prevented the larvae from gaining high body mass even after a long development time (Kause et al., 2001). Quite the opposite was found in studies of cellar spiders *Pholcus phalangioides* (Uhl et al., 2004) and yellow dung flies *Scatophaga stercoraria* (Blanckenhorn, 1998), where the genetic correlations between development time and body size were positive only at low food availability and were considerably weaker when food was abundant. This highlights that the way the amount of genetic covariation between life history traits changes as an effect of environmental stress is far from completely understood (see also Hoffmann and Merilä, 1999). Van Noordwijk and de Jong (1986) demonstrated elegantly that the magnitude and even the sign of the genetic covariance between life history traits between which trade-offs are expected is affected by the amount of genetic variation for resource acquisition. If genetic variation in acquisition is large, apparent trade-offs will be concealed, because genotypes with high acquisition ability may be able to develop faster and still become larger than inferior genotypes. Thus, the results here may indicate that genetic variation in acquisition is higher under larval food stress.

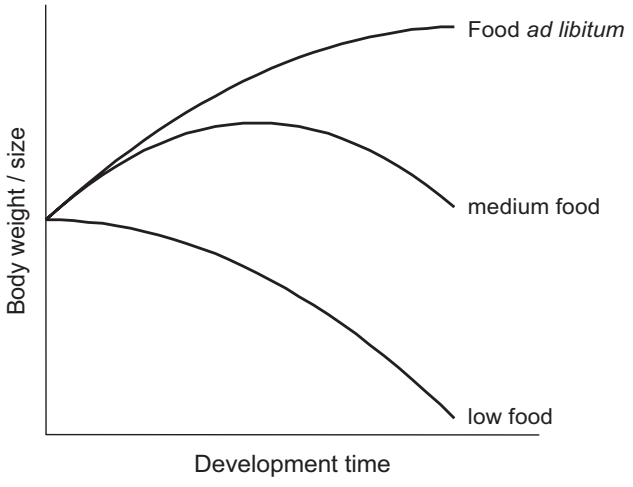

Fig. 5. Curves showing hypothetical genetic correlations between development time and larval body weight with increasing food availability.

On the other hand, it has been argued that life history trade-offs may be stronger or even only apparent in resource-poor environments, as the expression of allocation trade-offs may require resources to be scarce (Hoffmann and Parsons, 1991; Reznick et al., 2000; Tessier et al., 2000). This contrasts with the findings of the present study where the life history trade-off between fast development and body size was noticeable at the most favourable food level only. Genotypes with a longer development time resulting in a larger body size at high food levels seem to be more susceptible to food shortage. This indicates costs of increased development rate and resource utilisation in terms of a greater sensitivity to food limitation, in other words, a trade-off

between resource utilisation and minimum resource requirements (Reznick et al., 2000; Tessier et al., 2000). Hence, in this scorpionfly species there seems to be a pronounced polymorphism with regard to food utilisation during larval development. There appears to be a continuum of genotypes adapted to different levels of food availability. This genotype-by-environment interaction may provide an answer to why some genotypes which would seem superior if one only studies larval performance in one environmental condition fail to spread to fixation. This explanation rests on the assumption that conditions are heterogeneous in either space or time (Gillespie and Turelli, 1989). This presumption is likely to be fulfilled in the present study system, given that scorpionflies are scavengers both as larvae and as adults (Byers and Thornhill, 1983; Bockwinkel and Sauer, 1994) and food availability is likely to vary in both space and time (see for instance Thornhill, 1980; Bockwinkel and Sauer, 1994).

For the aims of the present study, larval breeding conditions were chosen so that larvae showed diapause-free development. In the study population from which the individuals were sampled, *P. cognata* has two discrete generations a year. Thus, in every second generation larval development includes a hibernating diapause stage. The constraints on larval development under these conditions are likely to be different from those during the fast diapause-free development (see e.g. Blanckenhorn, 1994). Both food availability and the time horizon for suitable growth are likely to differ. Diapausing individuals of the first annual generation are in general considerably larger than individuals with diapause-free development (Engqvist and Sauer, 2001, 2003a). Furthermore, preliminary results indicate that individuals on a hibernating development program are able to transform the same amount of food much more effectively into weight gains than those under a diapause-free development. This might indicate that constraints on development time are much more relaxed under these conditions, resulting in different trade-offs. Future studies should therefore aim at incorporating this additional environmental dimension in order to more completely understand the temporal environmental changes in life history trade-offs in this interesting study system.

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