

Age and size at maturity: a quantitative review of diet-induced reaction norms in insects

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Running title: Reaction norms for age and size at maturity

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This article has been accepted for publication and undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the Version of Record. Please cite this article as doi: 10.1111/evo.12518.

ABSTRACT

Optimality models predict that diet-induced bivariate reaction norms for age and size at maturity can have diverse shapes, with the slope varying from negative to positive. To evaluate these predictions, we perform a quantitative review of relevant data, using a literature-derived data base of body sizes and development times for over 200 insect species. We show that bivariate reaction norms with a negative slope prevail in nearly all taxonomic and ecological categories of insects as well as in some other ectotherm taxa with comparable life histories (arachnids and amphibians). In insects, positive slopes are largely limited to species, which feed on discrete resource items, parasitoids in particular. By contrast, with virtually no meaningful exceptions, herbivorous and predatory insects display reaction norms with a negative slope. This is consistent with the idea that predictable resource depletion, a scenario selecting for positively sloped reaction norms, is not frequent for these insects. Another source of such selection – a positive correlation between resource levels and juvenile mortality rates – should similarly be rare among insects. Positive slopes can also be predicted by models which integrate life history evolution and population dynamics. As bottom-up regulation is not common in most insect groups, such models may not be most appropriate for insects.

KEY WORDS: amphibians, catch-up growth, compensatory growth, meta-analysis, phenotypic plasticity, spiders

Introduction

Age and size at maturity are of particular interest for evolutionary ecologists because of the pervasive effects of these variables on individual fitness (Blanckenhorn 2000) and demographic parameters of the populations. Within species, larger size confers a fitness advantage in many organisms: larger females are often more fecund, whereas larger males may gain advantage in competition for resources or mates (Andersson 1994). However, everything else being equal, larger size requires a longer juvenile development, which may increase the risk of dying without leaving any progeny.

The basic theoretical models of life-history evolution have addressed the question of optimal development time and body size across environments of different quality (Stearns 1992; Roff 1992). In these models, environmental quality has been defined in terms of resource levels available for the growing juveniles. Variability in the environmental conditions enters the models as variation in growth rates, which are thus assumed to be environmentally determined (for a different approach, see Abrams et al. 1996). A common prediction of such models is that, in favorable conditions, individuals reach their large adult size in a short time, whereas in poor conditions they remain smaller in spite of a longer development time. In other words, there is a negative correlation between size and time at maturity, and the corresponding bivariate reaction norm has a negative slope.

Nonetheless, such a monotonically decreasing size vs. age reaction norm is not the only predicted pattern: from the earliest (Stearns and Koella 1986) to the most recent (Marty et al. 2011) approaches, a wide variety of different shapes appear among the predictions of theoretical models. Indeed, under certain environmental conditions, it can also be adaptive to mature early at a small size, which thus results in the bivariate reaction norm with a positive slope. This is most clearly the case when the resource can become completely depleted or

when growth conditions rapidly deteriorate (Blanckenhorn 1999; Harvey et al. 2005). Nothing is then to be gained by prolonging juvenile development. Another general scenario that can lead to positively sloped reaction norms for size and development time is a predictable association of growth rate with mortality rate. Indeed, all other things equal, higher juvenile mortality rates invariably select for earlier maturation (Stearns 1992; Marty et al. 2011): it should always pay to leave the unsafe juvenile environment quickly enough. If growth rate is predictably positively correlated with mortality risk, organisms may have evolved the ability to use certain growth rates as a cue for high mortality, and to adaptively respond by maturing early at the cost of lower size.

In some contrast to the solid body of modelling work, studies confronting the theoretical predictions with empirical data appear to be relatively scarce, which means that various predicted shapes of the age vs. size reaction norms may not be actually recorded. Indeed, we are not aware of any systematic attempts to organize the empirical evidence on diet-induced reaction norms for development time and body size across any larger taxonomic group. This is different from the situation with comparable phenotypic responses to varying temperatures, reviewed and synthesized in a number of works (e.g. Atkinson 1994; Angilletta et al. 2004). Nevertheless, for insects in particular, there is plenty of empirical data available to evaluate the predictions of theoretical models. In addition to studies specifically addressing the reaction norms in response to food quality and quantity (Tammaru 1998; Blanckenhorn 1999; Fischer and Fiedler 2000; Plaistow et al. 2004; Berner et al. 2005, for some examples), there is an abundance of relevant data gathered for other purposes, such as, e.g. for evaluating performance of various pests on different cultivated plants. Indeed, it is a common practice in experimental insect ecology to subject different samples of conspecifics to different food quality treatments, and to record growth parameters such as final (pupal or adult) weights, and development times. This kind of data can be used to examine the response of final body

size and development time to variation in food quality and quantity. Even if the results of any individual study should be treated with caution when interpreted in a context other than the original one (see Discussion), a statistical pattern emerging from a high number of case studies will still most likely deliver a correct signal.

In this paper, we make use of this large bulk of available data and conduct a quantitative analysis of diet-induced reaction norms for body size and development time. The analysis is based on a comprehensive, original literature-derived data base of final body sizes and larval development times for over 200 species of insects, with a broad taxonomic and ecological coverage. We first aimed at an explorative examination of the relative frequency of negatively versus positively sloped reaction norms across different taxonomic and ecological categories. We proceeded with examining the hypothesis that negatively sloped bivariate reaction norms for size and development time should dominate among species in which both food depletion and predictable correlations between food availability and mortality risk are unlikely. Finally, we discuss possible reasons why the shapes of reaction norms for size and development time may systematically differ between insects and some other animals.

Materials and Methods

DATA BASE

A systematic literature survey was conducted to address reaction norms for body size and development time in insects. Google Scholar and Thomson Reuters Web of Science were searched to acquire case studies reporting data on final body size and larval development time of conspecific insects under two or more different food manipulation treatments (Appendix S1 in Supporting Information). A variety of combinations of different synonyms of development time (development time, developmental time, larval/nymphal period, larval/nymphal time, etc) and body size (body/pupal/adult size, body/pupal/adult mass,

body/pupal/adult weight, etc) were used as search terms. No restrictions were set on years of publication. The resulting data base was further extended by data collected for several earlier studies (Teder and Tammaru 2005; Blanckenhorn et al. 2007; Teder et al. 2008; Stillwell et al. 2010; Molleman et al. 2011; Teder 2014). We primarily used numerical presentations of relevant data. Graphical presentations were considered for those insect groups for which studies with numerically presented data were scarce.

Both pupal and adult sizes were accepted as measures of final body size. If several measures of final body size had been reported, measures of pupal size were preferred over those of adult size. With regard to development time, for most insect groups we considered only studies reporting data on the actual growing phase, i.e. larval development time. Larval development time was defined as the time from egg hatching to pupation (or, rarely, formation of a prepupa) in holometabolous insects, and the time from egg hatching to adult emergence in hemimetabolous insects. In a subset of species with concealed juvenile development, parasitoids and xylophages in particular, development time was also allowed to include the duration of egg and/or pupal development.

In this study, the examination of reaction norms was limited to manipulative experiments in which food quality or food amount had been varied in otherwise uniform conditions. In the source studies, variation in food quality had been typically achieved by rearing different subsets of insect larvae on, e.g., different host/prey species, different artificial diets, etc (= different treatments). In studies manipulating food quantity, most typically, individuals of the control treatment with *ad libitum* access to food had been compared to those with limited access to food (food deprivation, food shortage, starvation periods, either temporarily or permanently). Studies in which variation in food amount or quality had been caused by crowding of the larvae were not considered in the present analysis. This was because crowding *per se* appears to often induce specific responses in

developmental variables (Peters and Barbosa 1977; Tammaru et al. 2000; Vellau and Tammaru 2012), not of direct relevance in the present context. Similarly, we did not include studies in which larval development had been modified in response to the cues of predator presence (Higginson and Ruxton 2010), or a seasonal cue such as photoperiod (Gotthard 2004; Teder et al. 2010).

For the purpose of the analyses, data retrieved from different studies were always treated as different data sets. Data retrieved from a single study were divided into multiple data sets, if these were obtained from different experiments, or from using different genotypes / populations. Data from multifactor experiments were split into different data sets so that the focal environmental factor (i.e. food quality / quantity) was allowed to vary while the non-focal environmental factor (e.g. temperature) was kept constant. Depending on the particular study, data to assess reaction norms had been reported for males and females separately, or males and females combined. If relevant data for males and females had been presented separately, we used data on females. Such an approach was justified by similarity of qualitative patterns in males and females: in 87% of 184 data sets, the sign of the slope of bivariate reaction norms did not differ between sexes, neither was there a systematic pattern in the rest of the data sets that could have biased our main conclusions.

For comparison, a representative (but not comprehensive) sample of case studies was collected for two other ectotherm taxa in which reaction norms for age and size at maturity have frequently been addressed. In particular, arachnids (spiders, opilionids, mites) were chosen to compare reaction norms in insects with those in another large group of arthropods. We also compared insect reaction norms with those in amphibians, a group of organisms resembling insects in that their life cycle includes distinct larval and adult stages, separated by metamorphosis.

DATA TRANSFORMATION AND ANALYSIS

Prior to analyses, the following transformations of the data were performed. First, to make measures of body weight comparable with linear measures of body size, all measurements of weight were linearized using the cube-root transformation. Second, in order to make different data sets comparable, all treatment-specific values of body size and development time were standardized by dividing each value by the cross-treatment average. Neither of these transformations did affect the sign of the correlation between size and development time.

Original articles were examined to find out, if among-treatment differences in body size, development time or both were statistically significant. If this had not been made explicit, the significance of among-treatment differences was determined by calculating 95% confidence intervals for treatment-specific mean values (using SE, SD and N for this purpose). The data sets with no significant among-treatment difference in both parameters (48 out of 430 data sets; 11%) were ignored in the analyses. This was done because any trend emerging from data sets with uncertain differences between treatments is necessarily strongly affected by chance.

As a further step, the Pearson correlation coefficient between body size and development time was calculated for each data set to describe respective bivariate reaction norms. Treatment-specific mean values of the two parameters were treated as individual observations in these analyses. Statistics derived for individual data sets were used to evaluate qualitative consistency of the reaction norms for body size and development time across different taxonomic and ecological categories. Vote counting was used for this purpose: a vote cast by a particular data set was determined by the sign (positive/negative) of respective correlation coefficient, irrespective of its statistical significance (Wang and Bushman 1999). As no species was represented by supernumerous data sets in the data base,

we treated each individual data set as providing independent piece of evidence. The qualitative results did not change when, in alternative analyses, a single most representative data set was chosen for each species.

The individual (i.e. data set specific) correlation coefficients were meta-analytically combined to obtain respective weighted mean correlations, and their 95% confidence intervals. A random-effects model (instead of a less conservative, fixed-effects model) was used for this purpose. The meta-analyses of correlation coefficients were performed with Metacor package (Laliberté 2009) in R (R Development Core Team 2013), which implements the DerSimonian-Laird random-effects meta-analytic approach (Schulze 2004). Due to computational limitations, correlations based on less than four data points (four treatments in our case) could not be included in the meta-analytic calculations (variance for the Fisher's r -to- z transformed correlation coefficients cannot then be calculated).

Due to our particular interest in the occurrence of positive correlations between size and development time, bivariate reaction norms with a positive slope were subjected to closer scrutiny. To sort out individual studies potentially providing most reliable evidence, special attention was given to the 'strong cases' of positive correlations, defined as such by the following criteria: 1) among-treatment differences in both variables were statistically significant, 2) there was at least 5% difference in (linearized) size between the extreme treatments, and 3) treatment groups were reared under constant temperature (excluding thus any field data). The latter was done to avoid the possibility that a positive correlation between size and development time could arise in response to among-treatment differences in rearing temperature (cf. Atkinson 1994) rather than that in resource levels.

Accounting for phylogenetic relationships among the species in our data set was limited to comparing different insect orders. Phylogenetically explicit comparative methods (Martins 1996) could not be used because of the unsystematic character of the data that were

retrieved, and because reliable phylogenies are still available only for a limited number of insect taxa. However, our main focus was to detect patterns that are invariant across taxa, and any argument of invariance is robust to disregarding phylogenetic relationships.

Results

As a result of the literature search, we retrieved a total of 382 data sets (214 insect species, spanning 9 orders and 63 families) containing mean values of final body size and larval development time for two or more treatments (Appendix S1 in Supporting Information). Of these, the treatment imposed had significant effects on both body size and development time in 283 data sets (74%), whereas treatment-induced differences in just one of the two variables were significant in 92 data sets (24%): development time in 47 data sets, and body size in 45 data sets (Appendix S1 in Supporting Information). For 7 data sets (2%), there was not sufficient data to determine significance of the treatment effect; however, as the absolute effect of manipulations on either one or both of the two variables in these data sets was high, we treated these data sets as if the effect of treatment had been significant.

Diet-induced bivariate reaction norms for body size and development time had predominantly negative slopes (284 of 382 data sets; 74%; Figs 1, 2; Appendix S1 in Supporting Information). A positively sloped reaction norm was found for 98 data sets (26%, three data sets with flat reaction norms were also included here; Appendix S1 in Supporting Information). The fraction of positively sloped reaction norms was significantly lower in the experiments explicitly manipulating the amount of food available than in the experiments varying food quality (11% vs. 27%; Fisher's exact test: $p = 0.03$). There was no difference in the proportion of positive slopes when reaction norms derived from manipulations involving artificial/seminatural diets were compared with those using natural diets only (27% vs. 25%; Fisher's exact test: $p = 0.87$). Reaction norms with a negative slope were prevalent in most ecological categories (Fig. 2). However, idiobiont parasitoids clearly deviated from this

general pattern (idiobiont parasitoids vs. all others – Fisher’s exact test: $p = 0.0001$), showing mostly positive correlations between size and development time (Fig. 2). A somewhat higher share of positive correlations, compared to other ecological categories, was also found in koinobiont parasitoids (Fig. 2). Negatively sloped reaction norms prevailed in all insect orders for which sufficient data could be obtained (Fig. 1). Positively sloped reaction norms were somewhat more frequent among holometabolous than in hemimetabolous insects (28% vs. 15%; Fisher’s exact test: $p = 0.03$). Nevertheless, this difference almost disappeared when parasitoids (which occur only among holometabolous insects) were omitted from the analysis (Fisher’s exact test: $p = 0.29$).

Positive correlations between size and development time were generally limited to the data sets in which diet-induced variability in development time was relatively low (Fig. 3). In particular, the average ratios of maximum and minimum (treatment-specific) development times for data sets with negative and positive correlations were 1.33 and 1.17, respectively (t -test: $df = 378$, $t = 4.1$, $p < 0.0001$; Fig. 3). By contrast, respective ratios of maximum and minimum body size were nearly equal (1.12 for negative and 1.10 for positive correlations; t -test: $df = 378$, $t = 1.6$, $p = 0.12$; Fig. 3).

Convincing evidence for positive body size vs. development time correlations among insects other than parasitoids was scarce. Altogether, just 14 data sets (out of 299, i.e. parasitoids excluded) were considered to represent ‘strong’ (see Materials and Methods, for criteria) cases of a positively sloped reaction norm (Table 1). This number is nearly twelve times lower than the number of equivalent strong cases (165) among bivariate reaction norms with a negative slope. With a single exception of a dipteran saprophage (Blanckenhorn 1999), all strong cases of a positively sloped reaction norm were those of lepidopteran and orthopteran herbivores. In case of predatory insects, not a single data set (out of 59) provided strong evidence for a positively sloped reaction norm (Table 1).

Across the data sets, the meta-analytically weighted Pearson correlation coefficient between body size and development time was -0.65, differing highly significantly from zero (95% confidence interval: -0.73 to -0.55; $N = 144$, $p < 0.0001$). Meta-analytically weighted mean correlations for most taxonomic and ecological categories were rather similar in magnitude (Table 2, 3). As an exception, in idiobiont parasitoids positive and negative correlations balanced each other, resulting in a meta-analytic correlation coefficient close to zero (Table 3). In general, negative correlations between body size and development time were much stronger than positive correlations. The absolute values of respective mean Pearson correlation coefficients were 0.75 and 0.54 (t -test: $df = 221$; $t = 4.9$; $p < 0.0001$).

In most data sets (79%), development time was more variable than linearized body size across treatments. While average size difference (i.e. the ratio of maximum and minimum treatment-specific mean values) across all data sets was 1.11, average time difference was 1.29 (paired t -test: $df = 379$; $t = 11.3$; $p < 0.0001$). This pattern was qualitatively consistent across major taxonomic and ecological categories (Tables 2, 3). Again, however, idiobiont parasitoids formed a remarkable exception to this pattern: development time showed a higher variability in just 38% of the data sets (idiobiont parasitoids vs. all others – Fisher's exact test: $p < 0.0001$; Table 3).

Respective patterns in the bivariate reaction norms in arachnids and amphibians were largely consistent with those in insects. In both groups, negative correlations between body size and development time prevailed (9 out of 10 in arachnids; 11 out of 12 in amphibians; Table 4).

Discussion

We found overwhelming empirical support for those life-history models which predict a negative relationship between age and size at maturity in response to varying resource levels. Indeed, a vast majority of the 382 diet-induced bivariate reaction norms for size vs. development time had a negative slope (Fig. 1, 2; Appendix S1 in Supporting Information). Insects on lower resource levels may considerably prolong their juvenile periods but they still remain somewhat smaller than their conspecifics experiencing more favorable conditions. This is in contrast to the predominantly positively sloped size vs. time reaction norms in response to variation in ambient temperature in ectotherms (Atkinson 1994; Angilletta et al. 2004). Convincing evidence of diet-induced positive correlations between size and development time were scarce, and largely limited to the insects feeding on discrete resources, parasitoids in particular. The overall picture thus suggests that the negative environmentally induced relationship between size and development time is the general case for insects. Reaction norms derived from a representative sample of studies for arachnids and amphibians are consistent with those in insects.

Nevertheless, meaningful exceptions to this rule can occur under special circumstances. The disproportionally high incidence of positive slopes among parasitoids of different insect orders, and idiobiont parasitoids (Fig. 2, for the definition) in particular, is probably a straightforward consequence of the commonly occurring food depletion in this ecological group. Larvae of these insects are confined to particular host individuals, which frequently become fully consumed, causing a typically strong dependence between body sizes of the host, and the emerging adult parasitoid (Harvey et al. 2005). Seed-feeding insects should represent a quite similar case (e.g. Fox et al. 1996). Nonetheless, positive slopes in seed eaters do not abound in our data base, probably because the frequent target species of

such studies are often not confined to individual seeds, and for those species which are (e.g. Bonal and Muñoz 2009) no comparable data are available. Insects feeding on animal dung provide another example of predictable food depletion (or deterioration), with indeed some positively sloped reaction norms reported (Blanckenhorn 1999; Shafiei et al. 2001; Teuschl et al. 2007).

By contrast, we found those insects that are not confined to discrete resource items not to be likely to display positive correlations between size and development time. The proportion of positive correlations was particularly low among predatory insects, ranging from dragonflies to ladybird beetles. In fact, no single size vs. development time relationship for this ecological group could be regarded as a ‘strong’ case (Table 1) of a positively sloped reaction norm. In Odonata (all predatory), all of the 16 reaction norms were negatively sloped. One possible explanation may rest on the following reasoning. In particular, even if facing food shortage should not be exceptional for predatory larvae (Ives et al. 1993), it hardly is predictable in general (Evans 2003; Ueno 2003). This is partly due to high mobility of both the predators and their prey. Moreover, many predatory insects are long-lived as larvae, possessing efficient anti-predator strategies themselves, and are thus well adapted to survive periods of transient food shortage. Intuitively, therefore, for a predator, it should pay less to ‘give up’ and mature early at small size than for an insect larva with different nutritional ecology. This same logic can be extended to explain the nearly uniformly negatively sloped reaction norms in spiders (Table 4), which are perhaps even more adapted to withstand periods of nutritional stress.

In line with our expectations, positively sloped reaction norms were also scarce among herbivores, the ecological group with the largest share of entries in our data base. Indeed, as “the world is green” (Hairston et al. 1960), the resources of insect herbivores become fully used only exceptionally, precluding the realization of food depletion scenario.

Slightly less obviously perhaps, in herbivores, there is also little reason to expect predictable positive cross-environment associations between growth rate (host quality) and mortality risk, another general scenario predicted to lead to positive correlations between size and age at maturity (Stearns and Koella 1986; Perrin and Rubin 1990; Abrams and Rowe 1996; Marty et al. 2011). Indeed, even though examples of mortality risk differences between several host plant species exist (reviewed in Remmel et al. 2011), such effects are hardly consistent enough in time and space to have shaped life-history responses. Moreover, using host plant species as a cue of mortality risk is expected to evolve when the herbivore is oligophagous, i.e. utilises a low number of distinct host species to which specific adaptations can evolve. This is not a common situation, however. More frequently, the herbivores are either (functionally) monophagous or broad generalists (Bernays and Chapman 1994).

Driven apparently both by tradition (Roff 1986; Stearns and Koella 1986) and practical needs (e.g. Ernande et al. 2004; Dunlop et al. 2009; Enberg et al. 2009), a large share of the theoretical work on the age vs. size reaction norms has been focusing on fish. Accordingly, in addition to the assumption of cross-environment correlation between growth rate and mortality risk, phenomena like density-dependent growth (Marty et al. 2011), and the effect of predation rate on food availability in juveniles (Abrams and Rowe 1996) enter the approach as essential elements. Incorporating such population- and community-level processes increases the complexity of the models so that a wide array of different predictions becomes possible. Consistently, in fish, there is indeed some empirical support for reaction norms for size and age at maturity, which are not monotonically decreasing (Alm 1959; Jonsson et al. 2013).

For most herbivorous insects, in contrast, population- and community-level phenomena hardly interact with selective pressures on life-history traits to a notable extent. This is primarily because density dependence via bottom-up regulation is not common in

herbivorous insects (Speight et al. 1999; Price et al. 2011). By contrast, the relatively simple approach taken by Day and Rowe (2002) relies on assumptions, which can be believed to be the most essential ones in shaping selective pressures on body size and development time. Indeed, in insects, the dependence of realized fecundity on female body size is frequently so strong (Honek 1993), and mortality of the juveniles due to predation so high (Cornell and Hawkins 1995, Rimmel et al. 2011) that there is hardly much space for any other general ecological factors to set the scene. Importantly, consistent with the critical assumption of the overhead threshold model of Day and Rowe (2002), the fecundity vs. body size relationship clearly has a negative intercept (e.g. Tammaru et al. 1996, 2002). The few studies explicitly addressing the size vs. age reaction norms in arthropods (Tammaru 1998; Plaistow et al. 2004) have found shapes closely resembling the predictions of the overhead threshold model. Unfortunately, the majority of the data sets analysed in the present paper did not allow us to evaluate parameters of the reaction norms more complex than the overall slope. However, as the key parameters of the model by Day and Rowe (2002) can be determined for various insects, the adequacy and sufficiency of the overhead threshold model can be tested by quantitatively comparing the shapes of predicted and recorded reaction norms.

Another obvious difference between fish and insects lies in the contrast between the indeterminate vs. determinate character of their growth. Intuitively, the costs of early maturation at smaller size should be lower if there is an opportunity to compensate for small initial size later in the adult life. Nevertheless, modelling results do not suggest that the shapes of reaction norms should qualitatively differ among organisms with determinate and indeterminate growth (Stearns 1992). Moreover, the ‘insect-like’ reaction norms typically recorded in amphibians (Table 4) further undermine the idea that the ability to grow after maturation is a decisive determinant of the shape of the reaction norms. Instead, the similarity of reaction norms between amphibians and insects rather suggests that ecological

characteristics shared by these groups may have the decisive role. Such shared characteristics include the distinctly separated larval and adult stage as well as limited chances to outgrow the primary predators. The failure to reach such a size refugium translates into a positive rather than negative dependence between body size and the risk of being preyed upon. Positive size dependence of mortality risk is characteristic of insects (Rommel et al. 2011) which should strongly select against growing large if growth rates are low.

So far, actually, we are unaware of any exemplary cases of positively sloped reaction norms in herbivorous insects, in response to variation in diet quality. A closer examination of the few ‘strong’ positive correlations (see Material and Methods, for criteria) shows that there was just one case (Shen et al. 2006) where the positive correlation was consistent across all treatments (Table 1). This is in strong contrast to the total number of data sets (139) for herbivores in which there were more than 2 treatments. A further reason for caution is that all the studies yielding ‘strong’ positive correlations were performed in contexts other than the study of reaction norms of size at maturity, and with a single exception (Bossart 1998) other than evolutionary ecology of larval growth. This implies that the original authors might have paid less attention to methodological details, which are critical from our perspective but were not necessarily so from the perspective of the original studies.

Quality of the data aside, it is interesting to note that a number of strong positive correlations between size and development time stem from comparisons among artificial diets, or when artificial diet was compared to a natural host plant (larvae tend to grow for a longer time and attain larger size on artificial substrates): (e.g. Allsopp et al. 1983; Hunter et al. 1994; Shen et al. 2006; Table 1). Obviously, in the strict sense, the insects cannot be adapted to artificial diets, which may be a problem if the proximate cue for the maturation decision is other than growth rate or body size itself (the mechanistic basis of the maturation decision is not known for certain, Kemirembe et al. 2012; Andersen et al. 2013). If chemical

composition (or just water content) of the diet directly interferes with the cue, the positive correlations found among artificial diets may result from proximate physiological mechanisms rather than adaptive decision making. The possibility of a direct physiological, i.e. non-adaptive, effect of chemical composition of the host is supported by the tendency of larvae on nitrogen-rich substrates to pupate earlier at smaller size (Chen et al. 2004; Fischer and Fiedler 2000; but see Tigreros et al. 2013).

In summary, we found that negative correlations between size and development time in response to variations in diet quality are ubiquitous. The cases of – presumably adaptive – positive correlations are largely limited to insects feeding on discrete food items. It requires further study whether such reaction norms ever occur in insects that are not typically faced with resource depletion (primarily herbivores). So far, however, the data appear are consistent with the idea that the negative slope of the reaction norm for size and time at maturity may come close to be a general rule for most ecological groups of insects. At a more general level, our results suggest that key evolutionary forces shaping reaction norms for age and size at maturity may radically and predictably differ among taxa with different ecology. This suggests that a variety of approaches may be needed to reach an evolutionary explanation for plasticity in body size and development time.

ACKNOWLEDGMENTS

We thank Wolf Blanckenhorn, Robert Davis, Toomas Esperk, Cecilia Ronnås, Anu Tiitsaar, and two anonymous reviewers for helpful comments, and Ants Kaasik for statistical advice. The study was supported by the Estonian Research Council (grants no 8413, 9294 and IUT20-33), and the EU through the European Regional Development Fund (Centre of Excellence FIBIR).

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Table 1. Strong cases (see Materials and Methods, for criteria) of a positively sloped bivariate reaction norm for body size and development time among insects other than parasitoids. N refers to the number of treatments in the data set, r is the Pearson correlation coefficient.

| Species | Taxonomic category | Ecological category | N | r | Reference |
|--------------------------------|-----------------------|------------------------|-----|------|--------------------------|
| <i>Chorthippus brunneus</i> | Orthoptera | Herbivore | 2 | na | Hassall and Grayson 1987 |
| <i>Chorthippus brunneus</i> | Orthoptera | Herbivore | 2 | na | Hassall and Grayson 1987 |
| <i>Epiphyas postvittana</i> | Lepidoptera | Herbivore | 5 | 0.01 | Mo et al. 2006 |
| <i>Heliothis subflexa</i> | Lepidoptera | Herbivore | 2 | na | Laster et al. 1982 |
| <i>Lymantria dispar</i> | Lepidoptera | Herbivore | 4 | 0.23 | Joseph and Kelsey 1994 |
| <i>Lymantria xyliana</i> | Lepidoptera | Herbivore | 4 | 0.99 | Shen et al. 2006 |
| <i>Merophyas divulsana</i> | Lepidoptera | Herbivore | 5 | 0.05 | Allsopp et al. 1983 |
| <i>Mussidia fiorii</i> | Lepidoptera | Herbivore | 3 | 0.95 | Muli et al. 2011 |
| <i>Papilio glaucus</i> | Lepidoptera | Herbivore | 3 | 0.86 | Bossart 1998 |
| <i>Phthorimaea operculella</i> | Lepidoptera | Herbivore | 16 | 0.48 | Horgan et al. 2007 |
| <i>Pieris canidia</i> | Lepidoptera | Herbivore | 2 | na | Chen et al. 2004 |

| | | | | | |
|--------------------------------|-------------|------------|---|------|-------------------------|
| <i>Platynota idaeusalis</i> | Lepidoptera | Herbivore | 3 | 0.69 | Hunter et al. 1994 |
| <i>Scathophaga stercoraria</i> | Diptera | Saprophage | 2 | na | Teuschl et al. 1999 |
| <i>Spodoptera litura</i> | Lepidoptera | Herbivore | 5 | 0.77 | Kiyoku and Tsukuda 1967 |

Table 2. Meta-analytically weighted average Pearson correlation coefficients between development time and body size for different taxonomic categories (95% confidence intervals and *p*-values in parentheses). Among-treatment differences in body size and development time represent average values of ratios of maximum and minimum treatment-specific values calculated for each data set. Data for other taxonomic categories were too scarce for meaningful averaging.

| Taxonomic category | Meta-analytically weighted mean <i>r</i> | Among-treatment differences in body size | Among-treatment differences in development time |
|--------------------|--|--|---|
| Lepidoptera | -0.63 (-0.73...-0.50, <0.0001) | 1.12 | 1.35 |
| Coleoptera | -0.56 (-0.78...-0.21, 0.002) | 1.08 | 1.24 |
| Diptera | -0.71 (-0.89...-0.35, 0.0004) | 1.09 | 1.26 |
| Hymenoptera | -0.48 (-0.70...-0.16, 0.002) | 1.13 | 1.20 |
| Hemiptera | -0.83 (-0.93...-0.58, <0.0001) | 1.08 | 1.26 |
| Orthoptera | -0.96 (-0.997...-0.55, 0.002) | 1.18 | 1.42 |
| Odonata | na [*] | 1.08 | 1.14 |
| Total | -0.65 (-0.73...-0.55, <0.0001) | 1.11 | 1.29 |

* na = not available. All reaction norms for Odonata were derived from experiments with two treatments, in which case calculating a correlation coefficient (or its mean across studies) was not meaningful.

Table 3. Meta-analytically weighted average Pearson correlation coefficients between development time and body size for different ecological categories (95% confidence intervals and p -values in parentheses). Among-treatment differences in body size and development time represent average values of ratios of maximum and minimum treatment-specific values calculated for each data set. Data for other ecological categories (saprophages, fungivores, frugivores, detritivores) were too scarce for meaningful averaging. For the definition of herbivores, koinobiont and idiobiont parasitoids, see Fig. 2.

| Ecological category | Meta-analytically weighted mean r | Among-treatment differences in body size | Among-treatment differences in dev. time |
|------------------------|--|--|--|
| Herbivores | -0.67 (-0.76...-0.56, <0.0001) | 1.11 | 1.32 |
| Predators | -0.79 (-0.93...-0.45, 0.0002) | 1.10 | 1.27 |
| Seed-eaters | -0.59 (-0.15...-0.83, 0.006) | 1.06 | 1.24 |
| Koinobiont parasitoids | -0.70 (-0.84...-0.47, <0.0001) | 1.09 | 1.24 |
| Idiobiont parasitoids | 0.32 (-0.12...0.66, 0.08) | 1.17 | 1.12 |
| Total | -0.64 (-0.73...-0.55, <0.0001) | 1.11 | 1.29 |

Table 4. Sources of data used to derive diet-induced bivariate reaction norms for body size vs. development time in arachnids and amphibians.

RN slope refers to the sign of the slope of the bivariate reaction norm. *N* indicates the number of treatments in each particular data set.

| Species | Order | Family | Ecological category | N | RN slope | Reference |
|----------------------------------|----------------|--------------|----------------------|----|-------------|-------------------------------|
| Arachnida | | | | | | |
| <i>Sancassania berlesei</i> | Sarcoptiformes | Acaridae | predator / fungivore | na | neg | Plaistow et al. 2004 |
| <i>Phalangium opilio</i> | Opiliones | Phalangiidae | predator | 2 | neg | Allard and Yeargan 2005 |
| <i>Holocnemus pluchei</i> | Araneae | Pholcidae | predator | 3 | neg | Jakob and Dingle 1990 |
| <i>Hygrolycosa rubrofasciata</i> | Araneae | Lycosidae | predator | 2 | neg | Vertainen et al. 2000 |
| <i>Larinioides sclopetarius</i> | Araneae | Araneidae | predator | 3 | neg | Kleinteich and Schneider 2011 |
| <i>Lycosa tarantula</i> | Araneae | Lycosidae | predator | 2 | flat | Moya-Laraño et al. 2003 |
| <i>Nephila clavipes</i> | Araneae | Nephilidae | predator | 2 | neg | Vollrath 1998 |
| <i>Nephila clavipes</i> | Araneae | Nephilidae | predator | 3 | neg | Higgins and Goodnight 2011 |
| <i>Pholcus phalangioides</i> | Araneae | Pholcidae | predator | 2 | neg | Uhl et al. 2004 |

| | | | | | | |
|---------------------------------|---------|----------------|----------|---|-----|------------------------|
| <i>Zygiella x-notata</i> | Araneae | Araneidae | predator | 2 | neg | Mayntz et al. 2003 |
| Amphibia | | | | | | |
| <i>Ambystoma maculatum</i> | Caudata | Ambystomatidae | predator | 2 | neg | Walls 1998 |
| <i>Bufo terrestris</i> | Anura | Bufonidae | predator | 2 | neg | Beck and Congdon 2000 |
| <i>Bufo woodhousei</i> | Anura | Bufonidae | predator | 2 | neg | Alford and Harris 1988 |
| <i>Discoglossus galganoi</i> | Anura | Alytidae | predator | 2 | neg | Nicieza et al. 2006 |
| <i>Hyla cinerea</i> | Anura | Hylidae | predator | 2 | neg | Blouin 1992 |
| <i>Hyla gratiosa</i> | Anura | Hylidae | predator | 2 | neg | Blouin 1992 |
| <i>Hyla regilla</i> | Anura | Hylidae | predator | 6 | neg | Kupferberg et al. 1994 |
| <i>Hyla squirella</i> | Anura | Hylidae | predator | 4 | neg | Beck 1997 |
| <i>Pseudacris crucifer</i> | Anura | Hylidae | predator | 5 | neg | Hensley 1993 |
| <i>Scaphiopus couchii</i> | Anura | Scaphiopodidae | predator | 3 | pos | Morey and Reznick 2000 |
| <i>Scaphiopus couchii</i> | Anura | Scaphiopodidae | predator | 2 | neg | Newman 1998 |
| <i>Scaphiopus intermontanus</i> | Anura | Scaphiopodidae | predator | 3 | neg | Morey and Reznick 2000 |

Figure 1. Breakdown of bivariate reaction norms for final body size vs. development time into those with negative and positive slopes by taxonomic categories. Numbers within the bars refer to the number of data sets analyzed.

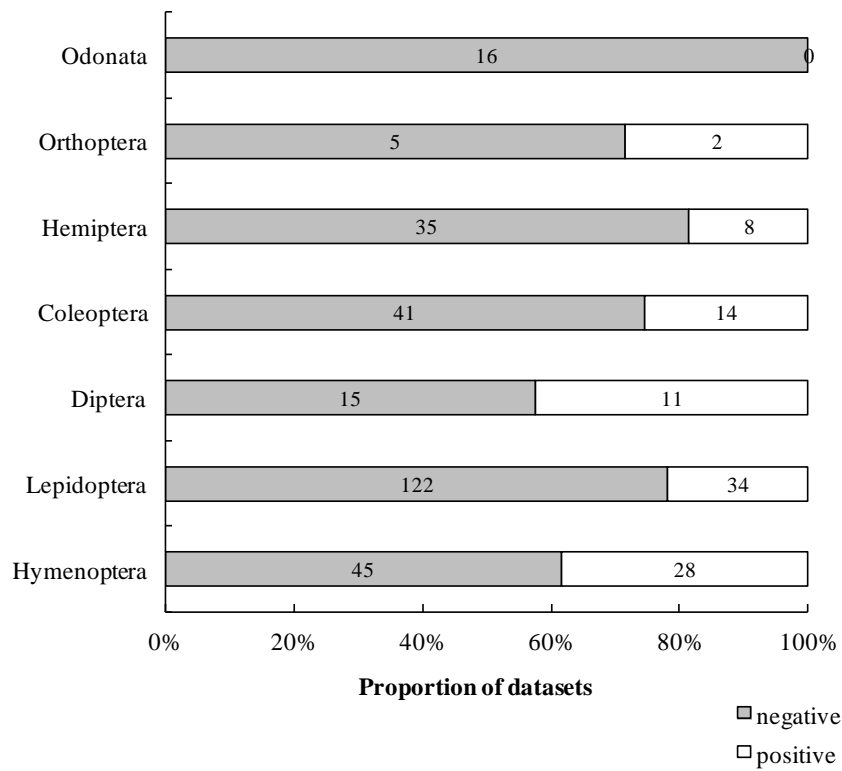


Figure 2. Breakdown of bivariate reaction norms for final body size and development time into those with negative and positive slopes by ecological categories. The category of herbivores includes species feeding on leaves (most data sets in this category), flowers, stems and roots of living plants; seed-eaters are classified as a separate group. Koinobiont parasitoids are those which allow their insect hosts to continue growth. Idiobiont parasitoids parasitize non-growing stages of the host, or growing stages in which they inhibit further growth by paralysis. Numbers within the bars refer to the number of data sets analyzed.

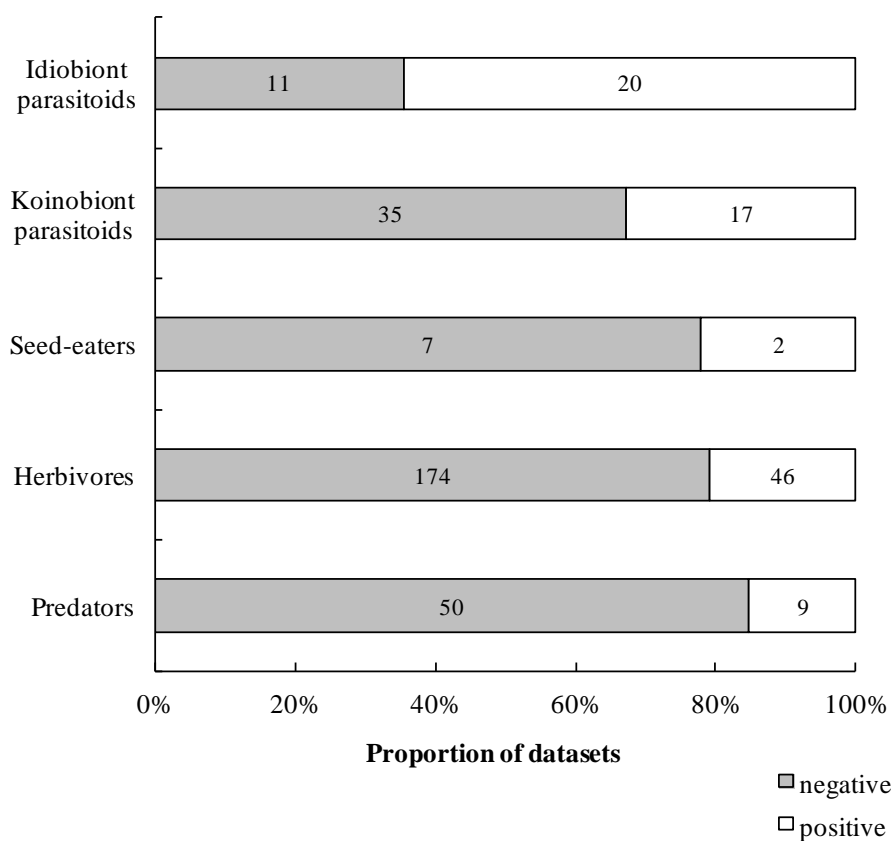


Figure 3. Diet-induced variability in development time and body size in data sets, from which A) negatively or B) positively sloped reaction norms for body size vs. development time were derived. Each point represents one data set. Among-treatment differences in size and time are expressed as the ratio of maximum and minimum treatment-specific values for each data set. Both axes have the same scaling to facilitate comparison of the differences in body size and development time.

