CHAPTER 20

Sexual differences in insect development time in relation to sexual size dimorphism

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20.1 Introduction

In this chapter we address sexual differences in insect development time. Although sexual size dimorphism in insects is well documented and has been elaborated theoretically (see Chapter 6 in this volume), sexual differences in development time are understood imperfectly. Differences in development time between the sexes are one of the major proximate mechanisms to produce sexual size dimorphisms (growth rate differences being the other), as both traits are typically assumed to be highly correlated (it takes time to get large: Roff 1980; Fairbairn 1990; Blanckenhorn *et al*. 2007). In insects, sexual differences in development time are often small and their experimental determination difficult. An abundance of experimental data exists on the length of male and female pre-imaginal (i.e. pre-adult) development, largely on insects of economic importance (Honek 1997). However, error in estimating the duration of development prevents precise calculation of thermal constants, which are necessary for establishing the rate of development of the sexes over a range of ecologically relevant temperatures, and hence rigorous testing of real differences between males and females. By using the developmental-rate isomorphy concept of Jarošík *et al*. (2002, 2004) we here show that insect development is, on average, faster in males than females, and that this pattern is more pronounced in insects without a true pupal stage.

20.2 Development time and body size in insects

For any given insect species variation in adult body size is large (Honek 1993), and part of this variation is related to development time (Honek 1999). Given a particular growth rate, final size of an insect should be proportional to the duration of growth. We can thus expect a positive relationship between development time and body size, and a trade-off between these characteristics (Roff 1980). This means that an individual may either shorten its development at a cost of being small, or may grow large at a cost of long development.

In insects, female lifetime reproductive success (i.e. fecundity) is more closely correlated with body size (Honek 1993) than the major components of male reproductive success, in particular his mating ability. Thus, in terms of fitness females gain more than males from being large (Charnov *et al*. 1981). With few exceptions, insect males are therefore smaller (Chapter 6) and hence should develop faster than females. Protandry, i.e. the faster development of males, can also increase male mating success, thus further enhancing his fitness (Godfray 1994).

20.3 Temperature and insect development time

As ectotherms insects rely on external sources of heat. Consequently, we cannot say that ectotherms

require a certain length of time for development. They require a certain combination of time and temperature called physiological time. The concept of physiological time enables us to ask two central questions concerning the rate of development of males and females: (a) How to measure the rate of development of ectotherms? (b) How to analyse differences in the rate of development between males and females to reach a general conclusion?

20.3.1 How to measure the rate of development of ectotherms?

The rate of development of ectotherms is slow in the cold. As temperature increases, development rate increases up to an optimum temperature, and decreases again at high supraoptimum temperatures. In the wide range of ecologically relevant temperatures below the optimum the relationship between the rate of development and temperature is practically linear (Figure 20.1).

The linear approximation of the relationship between the rate of development and temperature enables us to calculate two constants: the sum of effective temperatures (*SET*)—that is, the amount of heat needed to complete a developmental stage—and the lower developmental threshold (*LDT*), the temperature below which development ceases. Thus the relationship between the rate of development, *RD*, and temperature, *T*, can be expressed as a linear equation in which a is the intercept with the y axis and b is the slope: $RD = a + bT$. The lower developmental threshold, at which the rate of development ceases (i.e. $RD = 0$), can then be calculated as $LDT = -b/a$. Furthermore, when development is completed (i.e. $RD = 1$), the sum of effective temperatures can be calculated as $SET = -1/b$. Then the number of day-degrees above the lower developmental threshold gives the sum of effective temperatures that is necessary for completion of a developmental stage (or total development). This linear relationship between the rate of development and temperature was first described by Ludwig (1928) and its suitability evaluated by Ikemoto and Takai (2000). Several non-linear models were also proposed (e.g. Logan *et al*. 1976; Lactin *et al*. 1995; Briére *et al*. 1999) and tested (Kontodimas *et al*. 2004). Here we use simple linear models which are convenient for meta-analysis (Jarošík *et al*. 2002).

Until recently it seemed that each developmental stage for each species had its own, specific lower developmental threshold (Honek and Kocourek 1990; Hodek and Honek 1996; Honek 1996; Kiritani 1997). This notion would change if, as shown in our example (Figure 20.2), the proportion of development time spent in individual developmental stages did not change with temperature; then the lower developmental threshold would remain the same for all developmental stages within a population of a given species.

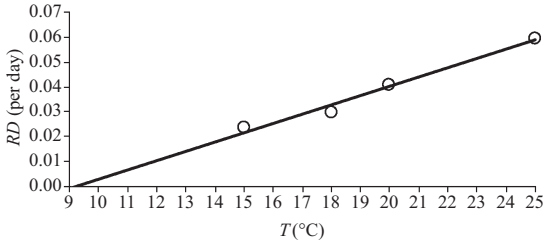

Figure 20.1 An example of a linear relationship between the rate of development (*RD*) and temperature (*T*) for the coccinellid beetle *Propylea japonica* (Thunberg). Data from Kawauchi (1983).

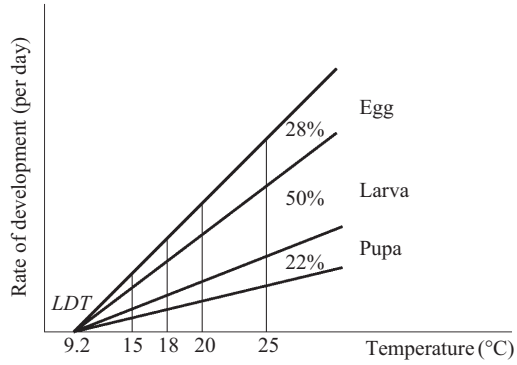

Figure 20.2 The concept of developmental isomorphy. Effect of temperature on the additively plotted rate of development, within the linear range of the relationship, for the coccinellid beetle *P. japonica*. The population is isomorphic and spent 28% of its total development in the egg, 50% as a larva, and 22% as a pupa at temperatures of 15, 18, 20, and 25°C. Therefore, all developmental stages have a common lower developmental threshold ($LDT = 9.2$). Because rate isomorphy implies no change with temperature in the proportion of time spent in a particular developmental stage, for assessment of the number of day degrees above the LDT necessary to complete a particular development stage, the sum of effective temperatures can be determined at any temperature within the linear range. Jarošík *et al.* (2003); data from Kawauchi (1983).

We call this notion *developmental-rate isomorphy* (Jarošík *et al*. 2002, 2004; Box 20.1).

The existence of developmental isomorphy thus facilitates measuring the rate of development of ectotherms to determine sexual differences more precisely. This is so because, as shown by Jarošík *et al*. (2002), the proportion of time spent in individual developmental stages typically does not change with temperature for males or females of a particular species (Figure 20.3a). Consequently, males and females must have the same lower developmental threshold, and the rate of development of males and females can be compared based on regression slopes of their rates of development on temperature (Figure 20.3b). Having an efficient tool for measuring the rate of development of males and females, we can now turn to the second question.

20.3.2 How to analyse differences in the rate of development between males and females to reach a general conclusion?

Reaching a general conclusion from particular experiments on any given species is an ambitious task because each experiment on the relationship between the rate of development and temperature is limited to those particular circumstances. We here use meta-analysis, a statistical synthesis of separate, independent experiments (Hedges and Olkin 1985; Hedges 1994; Shadish and Haddock 1994; Gurevitch and Hedges 2001) to analyse the differences in the rate of development between males and females as effect sizes that are independent of sample size and the scale of measurement (Box 20.2). We use the convention that negative effect size means shorter developmental time of males; that is, faster male than female development.

20.4 The data-set

Overall, we gathered data on the duration of non-dormant (i.e. direct) development of males and females, at two or more constant temperatures, for 132 populations of 122 insect species from 11 orders. All data fell within the range of the linear relationship between the *RD* and temperature. Because a previous study (Jarošík *et al*. 2002) has

Box 20.1 Concept of developmental-rate isomorphy in ectotherms

Rate isomorphy (Figure 20.2) means that the proportion of the development time spent in individual developmental stages does not change with temperature. Then the lower developmental threshold (*LDT*) remains the same for all developmental stages, and (1) the *LDT* can be established from data on any one developmental stage and (2) the sum of effective temperatures (*SET*) can be calculated from the duration of development at only one temperature.

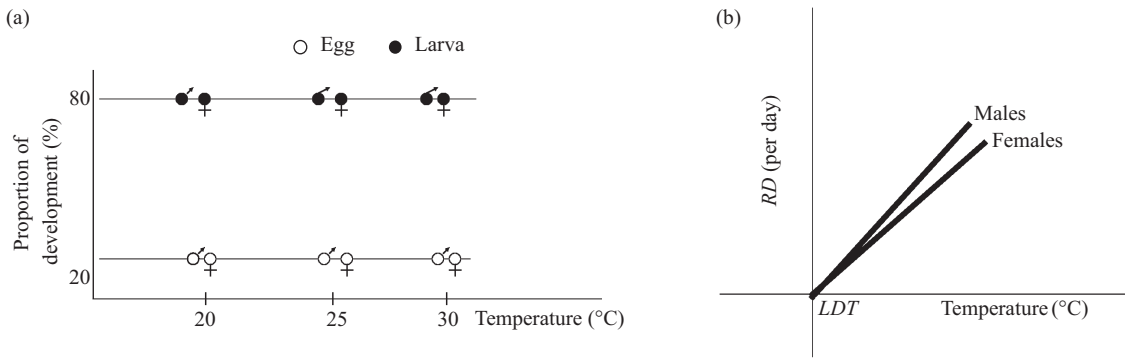

Figure 20.3 How to measure the rate of development of ectotherms. (a) The proportion of time spent in particular developmental stages of an ectotherm, exemplified by the cockroach *Periplaneta fuliginosa* (Serville), does not change with temperature for males and females. (b) Consequently, males and females must have the same lower developmental threshold (*LDT*), and the rate of development (*RD*) of males and females can be compared based on regression slopes of their rates of development on temperature. Data from Benson *et al.* (1994).

Box 20.2 Meta-analysis: statistical issues

Meta-analysis begins by representing the outcome of each experiment by a quantitative index of the effect size. This effect size is chosen to reflect differences between groups in a way that is independent of sample size and the scale of measurement used in the experiment. Meta-analytical techniques most commonly serve to test whether the effect size is significantly different from 0 and to examine potentially causative differences in the effect size among studies. The data necessary from each study to calculate the effect size and its variance are the means of the experimental groups, the standard deviations about these means, and the sample size of each group.

We estimated the mean development rates (*RD*) of males and females and the standard deviations from the regression slopes of *RD* on temperature (Figure 20.3b). The sample size of each group was equal to the number of temperatures used in each experiment. The data were corrected for small-sample bias following Hedges and Olkin (1985). To indicate significant variation in the rate of development between males and females, we used heterogeneity summary tables and contrasts among mean effect sizes, expressing the homogeneity of effect sizes between and within analysed groups by *Q-sums* (Hedges 1994; Gurevitch and Hedges 2001); these approaches are principally similar to classical ANOVAs and orthogonal contrasts among means (e.g. Sokal and Rohlf 1995).

shown that developmental-rate isomorphy is not affected by factors such as genetic differences between populations and differences in geographical origin, food, humidity, photoperiod, or number of instars, the data on the duration of development were averaged across these factors for each population.

Some controversy exists about whether all studies on a topic should be included in the analysis, or whether low-quality studies (e.g. data for only a part of pre-imaginal development) should be excluded. Following Gurevitch and Hedges (2001) we included all studies unless the results of the low-quality studies differed from those of higher-quality studies. We had reliable data for the insect orders Blattodea and Thysanoptera, for which all the data on developmental time were available for the whole (egg-to-adult) pre-imaginal development. We also had reliable data for the insect orders Diptera and Hymenoptera, for which all the effect sizes covering just a subset of the developmental stages (i.e. egg, larva, or pupa) showed the same trend as for the whole (egg-to-adult) pre-imaginal development. However, this was not so for Coleoptera, Homoptera, and Lepidoptera. For the Coleoptera and Homoptera the effect sizes covering the total pre-imaginal development differed from those covering only some of the developmental stages. However, these differences were not significant, and therefore all data were used in the analyses. For the Lepidoptera the data for pupal development differed significantly from those for the other developmental stages and the total pre-imaginal development and were therefore excluded.

There was no possibility to evaluate the quality of the data *a priori* for the insect orders Aphaniptera (= Siphonaptera), Heteroptera, Neuroptera, and Orthoptera, because all available data were for one developmental stage only, so we used all of the data. However, the Aphaniptera, for which only data on the pupal stage were available, appeared to be a very strong outlier, showing a reverse trend compared with all the other data (Table 20.1). Therefore, in the *a priori* planned comparison between holometabolous and heterometabolous insects (i.e. insects having and lacking the true pupal stage, respectively), and in our comparison of groups within the Holometabola, the Aphaniptera data were excluded.

20.5 Results

The mean effect across all studies indicated that males develop significantly ($P < 0.05$) faster than females. Following a conventional interpretation of the magnitude of effect sizes (Cohen 1969), the

Table 20.1 Sample size (number of species, *N*), rate of development of males and females (per day), effect sizes (d_+; see Box 20.2) with their 95% confidence intervals (CI) of the differences between the rate of development of males and females within insect orders, and the corresponding test statistics (*Z*, *P*) for the null hypotheses of no differences. Negative effect sizes mean faster development of males and positive effect sizes the converse. 95% Confidence intervals ($d^L - d^U$) that do not include 0 and *Z* statistics with $P < 0.05$ indicate statistically significant differences between males and females.

Order	Sample size *N*	Rate of development (per day)		Effect size	95% CI		Statistic	Probability
		Males	Females	d_+	d^L	d^U	*Z*	*P*
Aphaniptera	2	0.00534	0.00651	7.16	3.65	10.67	4.00	<0.001
Blattodea	1	0.000201	0.000195	−2.53	−4.68	−0.38	−2.31	0.028
Coleoptera	15	0.0043	0.00410	−0.80	−1.27	−0.34	−3.38	0.001
Diptera	15	0.00529	0.00517	−0.41	−0.80	−0.03	−2.12	0.042
Heteroptera	7	0.00376	0.00372	−0.33	−0.94	0.27	−1.08	0.223
Homoptera	13	0.00334	0.00338	−0.10	−0.57	0.37	−0.40	0.368
Hymenoptera	43	0.00474	0.00450	−0.80	−1.05	−0.56	−6.50	<0.001
Lepidoptera	30	0.00336	0.00329	−0.52	−0.84	−0.21	−3.23	0.002
Neuroptera	1	0.00295	0.00292	−0.25	−1.86	1.36	−0.31	0.381
Orthoptera	2	0.00141	0.00122	−3.90	−5.96	−1.84	−3.71	<0.001
Thysanoptera	3	0.00433	0.00419	−0.63	−1.27	0.01	−1.93	0.062

overall effect size, $d_+ = -0.598$ (variance, $s^2_{d+} = 0.0053$), is considered to be "medium". Most insect orders, namely the Blattodea, Coleoptera, Diptera, Hymenoptera, Lepidoptera, and Orthoptera, exhibit significantly faster development of males than females (Table 20.1). A similar difference was only marginally significant ($P < 0.1$) for the Thysanoptera. No such difference between males than females was apparent in the Heteroptera, Homoptera, and Neuroptera. Only in the Aphaniptera did female pupae develop significantly faster than male pupae.

A heterogeneity summary table (Table 20.2) indicates significant variation in the rate of development between males and females, both within and between insect orders. Most variation (85%) appeared within insect orders, suggesting that the systematic differences in the rate of development between males and females are not strongly affected by phylogenetic relatedness; thus the results should remain similar if the analysis were repeated using phylogenetically independent contrasts. The strong within-order variability evident in Table 20.2 also suggests that the overall average effect across all studies is of limited value.

An *a priori* planned comparison between Holometabola (insects having the true pupal stage) and Heterometabola (insects without the true pupal stage) demonstrated that males of the Heterometabola develop significantly faster ($Q = 6.56$; $df = 1$; $P = 0.01$) relative to females (effect size of the difference between males and females $d_+ = -7.50$) than males of the *Holometabola* ($d_+ = -2.80$). In search for further patterns, we first repeated the meta-analysis just for the *Holometabola*, with parasitoid/non-parasitoid insects as a grouping factor: no significant differences were found ($Q = 0.29$; $df = 1$; $P = 0.59$), as almost all variability remained within groups ($Q = 132.1$; $df = 71$; $P < 0.0001$), clearly suggesting that the traits related to a parasitoid life history do not crucially affect the differential rate of development of males and females. When repeating the meta-analysis just for the Heterometabola, subdivided into the three distinct subgroups of postembryonic development type Pauro-, Para-, and Remetabola (Box 20.3), the results again indicated no significant variation between these groups ($Q = 3.80$; $df = 2$; $P = 0.15$). Significant variability appeared only within the group with parametabolic

Table 20.2 Heterogeneity summary table, expressing the homogeneity of effect sizes (Box 20.2) between the rate of development of males and females within and between insect orders. The test statistic (*Q-sums*) with corresponding degrees of freedom (df) and probability (*P*) indicates statistically significant results.

Source of heterogeneity in effect sizes	Q-sums	df	*P*
Between orders	41.727	10	<0.001
Within orders			
Aphaniptera	1.478	1	0.224
Blattodea	–	0	–
Coleoptera	35.036	14	0.001
Diptera	17.751	14	0.218
Heteroptera	3.829	6	0.700
Homoptera	29.267	12	0.004
Hymenoptera	76.547	42	0.001
Lepidoptera	61.613	22	<0.001
Neuroptera	–	0	–
Orthoptera	2.951	1	0.086
Thysanoptera	1.171	2	0.557
Total within orders	229.644	114	<0.001
Total	271.371	124	<0.001

Box 20.3 Postembryonic development types of heterometabolous insects

Paurometabola are insects with a classic postembryonic development of Heterometabola: insects lacking a true pupal stage and having several larval instars that are gradually more similar to adults (orders Orthoptera, Blattodea, Heteroptera, and most Homoptera in our analysis). Parametabola include males of Coccoidea (coccids; mealybugs, and scales) and Remetabola thrips (Thysanoptera); these two latter groups, similar to Paurometabola, do not have a true pupal stage, but include quiescent stages, ecologically similar to the true pupal stage of Holometabola (Heming 2003).

development (i.e. the Coccoidea; $Q = 23.08$; $df = 6$; $P = 0.001$).

20.6 Discussion

Our work shows that in insects, males on average develop faster than females, indicating protandry, but this difference varies strongly among taxa. This result seems little affected by phylogenetic relatedness, except by the existence of a pupa in holometabolous insects, which seems to limit the rate (i.e. speed) of male development relative to females, as in holometabolous insects the difference in the length of pre-imaginal development of males and females is significantly smaller than in heterometabolous insects. In heterometabolous insects the gonads develop gradually during all larval stages, thus providing longer time for development. In contrast, holometabolous insects undergo a complete histolysis of larval tissues during pupation, with a new development of adult tissues starting from imaginal discs. Assuming similar patterns of sexual dimorphism in holo- and heterometabolous insects, it is therefore possible that particularly in holometabolous insects the pre-imaginal development of male gonads is more costly than that of female gonads (Blanckenhorn *et al*. 2007), potentially explaining the limitation in male development rate in holometabolous relative to heterometabolous insects found here.

A second potential explanation for our finding relates to possible systematic differences in mortality risk of males relative to females in heterometabolous and holometabolous insects, as in the latter group larvae and adults often live in completely different environments (Blanckenhorn *et al*. 2007). Thus it could be adaptive for a male to remain longer in the larval stage if this increases its survivorship to reproductive age, whereas for a female it may be adaptive to emerge earlier because adult female insects typically need to feed to mature their eggs before reproduction. Again assuming similar patterns of sexual dimorphism in holo- and heterometabolous insects, we would in this case expect a smaller difference in the development times of males and females in heterometabolous insects, in which larvae and adults live in the same environment, than in holometabolous insects. As we obtained the opposite result, however, we can reject this hypothesis.

20.7 Summary and conclusions

Using the concept of developmental rate isomorphy, meaning that the proportion of time spent in individual developmental stages does

not change with temperature for males and females of any particular species, we compared the rate of development of males and females based on regression slopes of their rates of development on temperature. To reach general conclusions, we compared these rates for 122 insect species from 11 orders using meta-analysis, a statistical synthesis of separate, independent experiments. On average, males develop significantly faster than females. However, this overall effect is accompanied by large variation within insect orders, suggesting that the systematic differences in the rate of development between males and females are not strongly affected by phylogenetic relatedness. The faster male relative to female development is more pronounced in heterometabolous insects without a true pupal stage than in holometabolous insects with a true pupal stage, perhaps related to pre-imaginal development of male gonads being more costly than that of female gonads in the latter group. In contrast, the pattern was not affected by other life-history traits such as a parasitoid life history or the existence of quiescent stages in insects lacking the true pupal stage.

20.8 Acknowledgments

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20.9 Suggested readings

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