RATE OF DEVELOPMENT OF PREDATORY INSECTS IS DEPENDENT ON THAT OF THEIR PREY

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ABSTRACT

In this study we analyzed data in the literature on the rates of development of parasitoids that parasitize aphids and coccids. The objective was to determine whether their rates of development, as is well documented for ladybirds, are also dependent on that of their prey. The analysis revealed that, like ladybirds, parasitoids that parasitize aphids develop faster than those that parasitize coccids. Parasitoids and ladybird predators show the same pattern in their rates of development: those attacking aphids develop faster than those attacking coccids. This is strong evidence that we are dealing with a general response rather than one specific to ladybirds. It also lends support to the concept that the development rates of these natural enemies are evolutionarily conserved rather than phylogenetically constrained.

Keywords: rate of development, parasitoids, aphids

Introduction

That the development of ladybirds attacking aphids is faster than that of those attacking coccids, and that this difference reflects the rate of development of their prey is well established (Dixon 2000; Dixon et al. 2011). The reason for the marked difference in the rate of development of aphids and coccids is generally assumed to be a consequence of aphids having achieved high rates of development by telescoping generations and feeding on better quality food (Dixon 1998). Modelling the interaction between predators and prey lends support to the idea that it is a consequence of optimizing their foraging for prey, and, if one assumes that it is the increase in predator biomass that is maximized by evolution then the optimum growth rate of a predator depends on that of its prey (Anthony F. G. Dixon, Satoru Sato and Pavel Kindlmann, unpublished). What is now important to establish, however, is that this is a general phenomenon and not one specific to ladybirds and that we are justified in generalizing that it applies, at least, to all insect predators.

Aphids and coccids are attacked by a wide range of predators, but except for ladybirds there are very few detailed studies on the rate of development at different temperatures of most of these predators. The only exceptions are hymenopterous wasps the larvae of which develop inside aphids and coccids. Although there is not the same sort of detailed information on their development as there is for ladybirds, nevertheless, there is sufficient to determine whether they similarly show prey related differences in their rates of development and so determine whether we are dealing with a general phenomenon rather than one specific to ladybirds.

Material and Methods

Source of Data

The literature was searched for papers that cited developmental times from oviposition to adult emergence for hymenopterous parasitoids of aphids and coccids. The sources are given in Table 1. Data for 17 species belonging to 2 families of parasitoids parasitizing 12 species of aphids and 9 species belonging to 3 families parasitizing 5 species of coccids were obtained from 33 papers, which provided data recorded at 3–6 temperatures for each parasitoid × host species combination.

Statistical Analysis

The linear relationship between the rate of development and temperature over the range below the maximum rate is a useful approximation (Trudgill et al. 2005). In studies of individual species a linear regression of development rate R (reciprocal of development time D, number of days from oviposition to adult emergence) on temperature T is calculated as $R = a + bT$. This equation can be used to calculate two characteristics of the thermal relationship of a species, its development threshold LDT = $-a/b$ and sum of effective temperatures SET = $1/b$ (Jarošík et al. 2011). Here we compare regression lines that characterize the thermal relationships of pooled data for groups of species of hymenopteran parasitoids with similar trophic specializations. Using a common plot for groups of species is justified because they are closely related taxonomically and ecologically similar in their requirements. In addition the number of values that

Table 1 List of data sets used for calculating development rate vs. temperature relationship of parasitoid species.

Parasitoid Species	Family	Parasitoid Species	Reference
Parasitoids of aphids			
Aphelinus asychis Walker	Aphelinidae	*Aphis gossypii* Glover	Schirmer et al. 2008; Byeon et al. 2011
Aphelinus gossypii Timberlake	Aphelinidae	*Toxoptera aurantii* (Boyer de Fonscolombe)	Tang and Yokomi 1995
Aphelinus spiraecolae Evans and Schauff	Aphelinidae	*Toxoptera aurantii* (Boyer de Fonscolombe)	Tang and Yokomi 1995
Aphelinus varipes (Förster)	Aphelinidae	*Aphis gossypii* Glover	van Steenis 1995; Röhne 2002
Aphelinus sp. nr. *varipes* (Förster)	Aphelinidae	*Diuraphis noxia* (Kurdjumov)	Lajeunesse and Johnson 1992
		Diuraphis tritici (Gillette)	Lajeunesse and Johnson 1992
		Rhopalosiphum maidis (Fitch)	Lajeunesse and Johnson 1992
Aphelinus sp.	Aphelinidae	*Diuraphis noxia* (Kurdjumov)	Prinsloo and duPlessis 2000
Aphidius colemani Viereck	Aphidiidae	*Myzus persicae* (Sulzer)	Zamani et al. 2007
Aphidius ervi Haliday	Aphidiidae	*Acyrthosiphon pisum* (Harris)	Campbell and Mackauer 1975
		Aphis pomi DeGeer	Malina and Praslicka 2008
		Myzus persicae (Sulzer)	Hofsvang and Hagvar 1975
Aphidius gifuensis Ashmead	Aphidiidae	*Myzus persicae* (Sulzer)	Ohta et al. 2001
Aphidius matricariae Haliday	Aphidiidae	*Diuraphis noxia* (Kurdjumov)	Miller and Gerth 1994
Aphidius platensis Brethes	Aphidiidae	*Myzus persicae* (Sulzer)	Hofsvang and Hagvar 1975
Aphidius smithi Sharma et Subba Rao	Aphidiidae	*Acyrthosiphon pisum* (Harris)	Campbell and Mackauer 1975
Aphidius sonchi Marshall	Aphidiidae	*Hyperomyzus lactucae* (Linnaeus)	Liu and Hughes 1984
Diaeretiella rapae (M'Intosh)	Aphidiidae	*Diuraphis noxia* (Kurdjumov)	Bernal and Gonzalez 1995
		Lipaphis erysimi (Kaltenbach)	Tripathi and Pandey 1994
Lysiphlebia japonica (Ashmead)	Aphidiidae	*Toxoptera citricida* (Kirkaldy)	Deng and Tsai 1998
Lysiphlebus testaceipes (Cresson)	Aphidiidae	*Schizaphis graminum* (Rondani)	Elliott et al. 1999; Royer et al. 2001
		Toxoptera aurantii (Boyer de Fonscolombe)	Tang and Yokomi 1995
		Toxoptera citricida (Kirkaldy)	Weathersbee et al. 2004
Praon pequodorum Viereck	Aphidiidae	*Acyrthosiphon pisum* (Harris)	Campbell and Mackauer 1975
Parasitoids of coccids			
Allotropa citri Muesebeck	Platygasteridae	*Pseudococcus cryptus* Hempel	Arai and Mishiro 2004
Anagyrus pseudococci (Girault)	Encyrtidae	*Planococcus citri* (Risso)	Tingle and Copland 1988
Aphytis chrysomphali (Mercet)	Aphelinidae	*Aonidiella aurantii* (Maskell)	Abdelrahman 1974; Kfir and Luck 1984
Aphytis lingnanensis Compère	Aphelinidae	*Aonidiella aurantii* (Maskell)	Kfir and Luck 1984
Aphytis melinus DeBach	Aphelinidae	*Aonidiella aurantii* (Maskell)	Abdelrahman 1974; Kfir and Luck 1984; Yu and Luck 1988
Encarsia citrina (Craw)	Aphelinidae	*Quadraspidiotus perniciosus* (Comstock)	Matadha et al. 2004
Encarsia perniciosi (Tower)	Aphelinidae	*Quadraspidiotus perniciosus* (Comstock)	McClain et al. 1990
Leptomastix abnormis (Girault)	Encyrtidae	*Planococcus citri* (Risso)	Tingle and Copland 1988
Metaphycus bartletti Annecke and Mynhardt	Encyrtidae	*Saissetia oleae* (Olivier)	Blumberg and Swirski 1982

each species x host combination contributes to the total number of values used to calculate the regression and the range of temperatures over which the development rates were recorded for each species are similar.

The differences between the data for groups of species with different trophic specializations, aphid and coccid parasitoids, were established using 1-way ANCOVA, with the host specialization (aphids and coccids) as a factor, development rate as a dependent variable and temperature as a covariate. The analysis was done using Statistica software (StatSoft 1994).

Results

Analysis of all the results clearly indicates that the parasitoids of aphids develop considerably faster than those of coccids. While the regression intercepts (and LDT) for the parasitoids of aphids and coccids differed greatly, the slopes (and SET) were nearly identical (Table 2) and as a consequence, the data for both groups differed significantly (ANCOVA: $F_{1,223} = 176.3$, $p < 0.001$). For example at 20 °C parasitoids of aphids develop on average twice as fast as parasitoids of coccids (Fig. 1). Remarkably and relevant to the hypothesis being tested here this figure is very similar to the relationships between the rates of development of aphidophagous and coccidophagous ladybirds (Fig. 1) in showing that those species attacking aphids develop faster than those attacking coccids.

In the data set analyzed the parasitoids of coccids belong to three families (Aphelinidae, Encyrtidae and Platygastridae) and those of aphids to two families (Aphelinidae and Aphidiidae) (Sharkey 2007), which raises the question: To what extent is the difference recorded above due to the phylogenetic histories of the parasitoids of aphids and coccids? Fortunately, there is one family, the Aphelinidae, common to the parasitoids of aphids and coccids. In the case of those attacking aphids they belong to only one genus (*Aphelinus*) and of those attacking coccids to two genera (*Aphytis* and *Encarsia*). Unfortunately in this case there is no genus of parasitoids that attacks both aphids and coccids, however, at the level of the family Aphelinidae there is a statistically significant difference in the rates of development of those attacking aphids and coccids: the former develop faster than the latter (Fig. 2). Also in this case the intercepts (and LDT) differed while the slopes (and SET) were nearly identical (Table 2) and the data for both groups differed significantly (ANCOVA: $F_{1,77} = 18.84$, $p < 0.001$).

Discussion

It is well documented that coccid eating ladybirds develop more slowly and as a consequence have much lower potential rates of population increase than similar sized aphid eating ladybirds. Analyses have revealed that this difference is not due to differences in body size, food quality, lower temperature thresholds for development or a phylogenetic constraint, but in the number of day degrees required to complete their development. In the case of coccid eating ladybirds the requirement is 3 times

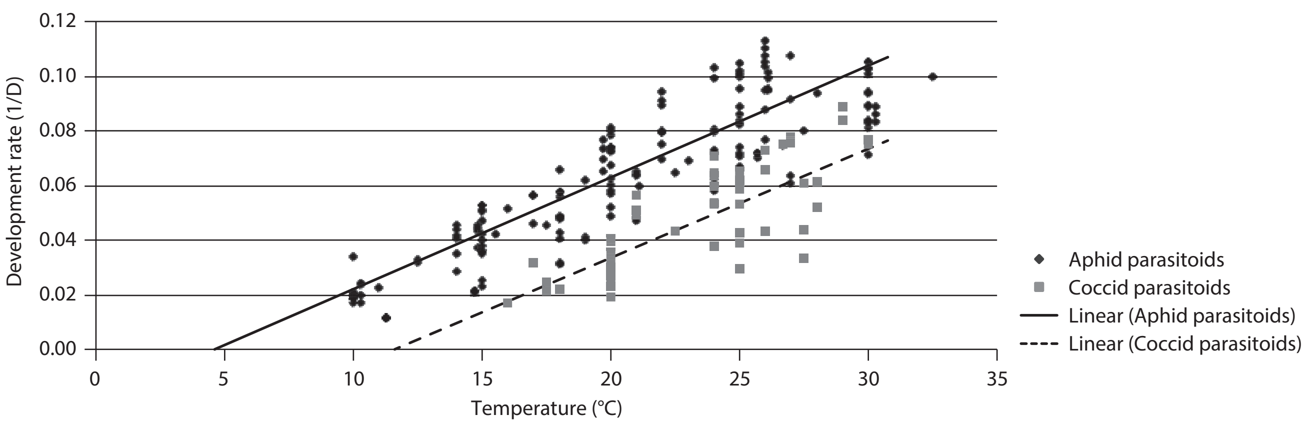

Fig. 1 Relationships between development rate (1/D) and temperature reported in the literature for hymenopterous parasitoids of aphids (♦) and coccids (■), respectively. D is the number of days from oviposition to adult emergence.

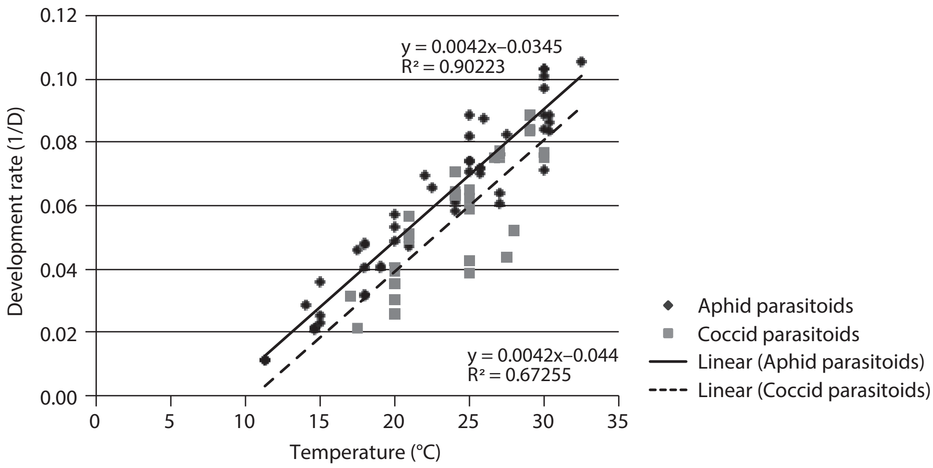

Fig. 2 Relationships between development rate (1/D) and temperature reported in the literature for hymenopterous parasitoids belonging to the subfamily Aphelinidae parasitizing aphids (♦) and coccids (■), respectively. D is the number of days from oviposition to adult emergence.

Table 2 Characteristics of the regression of development rate on temperature for the parasitoids of aphids and coccids using the data for all the taxa and that for only Aphelinidae.

Host species	N	a	b	R^2	F	P	LDT	SET
All taxa								
Aphids	164	−1.76E-02	3.93E-03	0.789	604.3	< 0.001	4.48	254.5
Coccids	55	−4.97E-02	4.19E-03	0.643	95.56	< 0.001	11.86	238.7
Aphelinidae								
Aphids	51	−3.45E-02	4.17E-03	0.902	452.2	< 0.001	8.27	239.8
Coccids	29	−4.40E-02	4.16E-03	0.673	55.5	< 0.001	10.57	240.4

greater than that of similar sized species of aphid eating ladybirds. This provides strong support for the concept that it is advantageous for coccid eating ladybirds to develop and forage more slowly than aphid eating ladybirds.

In addition to ladybirds there are several other groups of predatory and parasitic insects that attack both aphids and coccids. For a better understanding of the marked difference in the pace of life of ladybirds attacking aphids and coccids it is important to know whether other insect natural enemies also show similar differences in their pace of life. The analysis of the rate of development of parasitoids of aphids and coccids reveals that the same overall pattern as is well documented for ladybirds occurs in parasitoids with those attacking aphids also developing much faster than those attacking coccids. In this case, however, it is currently difficult to factor out completely the effect of phylogeny in determining the differences recorded in their rates of development. This is mainly because of the small size of the data set and lack of information on the relatedness of the genera for which there is data, or, put another way, how phylogenetically robust is the family Aphelinidae and to what extent do the genera in this family differ phylogenetically? Although limited the data for parasitoids is generally supportive of the hypothesis that we are dealing with a general phenomenon rather than and one restricted to ladybirds. That is the rates of development of insect natural enemies of aphids and coccids are more likely to be evolutionarily conserved rather than phylogenetically constrained.

The challenge now is not only to obtain more data on parasitoids but also for the other groups of insects that feed on both aphids and coccids, and for other insect predators that feed on prey with very different rates of development. This study of parasitoids also provides an insight into to why the rate of development of predators is so closely related to that of their prey. In this particular case the predator feeds on only one prey individual and all the foraging occurs within the body of that individual. The well-defined nature of this interaction provides strong evidence that the speed of development of the parasitoid larva relative to that of the host individual is critical in determining the maximum size it can achieve. If the parasite developed faster it would end up smaller, and if the host develops slowly then the parasite must also develop correspondingly slower than those that develop in fast developing hosts. That is, foraging in this case involves optimizing the trade-off between rate of development and adult size, which determines their fitness. In the case of predators the problem is similar but in this case they have to pursue and catch not one but many individuals and their availability in terms of biomass and the time for which they are available is determined by the speed at which they develop.

Acknowledgements

A.F.G.D. acknowledges support for this research from grants No. CZ.1.05/1.1.00/02.0073 of the MSMT and 14-36098G of the GA CR and A.H. from grant No. 14-26561S of the Grant Agency of the Czech Republic.

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