FAST−SLOW CONTINUUM IN THE LIFE HISTORY PARAMETERS OF LADYBIRDS REVISITED

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ABSTRACT

A previous study of the rate of development of larvae of aphidophagous and coccidophagous ladybirds indicated that they both had the same lower developmental threshold (Ldt) but that the coccidophagous species developed more slowly than the aphidophagous species. The current analysis of the rates of development of the eggs of 48 species belonging to 8 tribes, which were kept at a range of different temperatures, indicates that ladybirds do not all have the same Ldt, but that the of eggs of aphidophagous Coccinellini develop faster than those of coccidophagous Chilocorini and more importantly those of the aphidophagous genus *Scymnus* and the coccidophagous *Nephus*, both belonging to the same robust tribe, the Scymnini, also differ, with those of the latter genus developing more slowly. Possible reasons for this are discussed.

Keywords: aphidophagous, Coccinellidae, coccidophagous, development of eggs, fast and slow development, life history parameters

Introduction

The life history parameters of aphidophagous and coccidophagous ladybirds differ. The rate of larval development, relative growth rate, metabolic rate, speed of movement, reproductive investment, reproductive rate and rate of ageing of aphidophagous ladybirds are all faster than those of coccidophagous ladybirds, and this reflects the marked differences in the speed of life of their respective prey (Dixon 2000). As aphids are parthenogenetic and telescope their generations they have prodigious rates of increase compared with coccids. In addition, coccidophagous ladybirds are more successful biological control agents than aphidophagous species and this appears to be mainly a consequence of the former developing faster and the latter slower than their prey (Dixon 2000).

The rate of development of ladybirds is determined both by food quality and temperature. Each species tends to feed on relatively few species of prey in nature. For convenience, however, laboratory studies have depended on the mass production of a few species of aphids, which appear to be acceptable prey for the ladybirds studied. It is suggested, however, that prey animals differ in their content of limiting nutrients, like methionine, and Liebig's law applies (Cohen and Brummett 1997), or of toxic secondary plant substances they sequester from their host plants (Dixon 1998). Although a particular species of aphid is clearly not similarly suitable for all species of aphidophagous ladybirds it is more likely that the eggs of each species of ladybird are well provided with the nutrients necessary for embryonic development. In addition, as is recorded for many groups of organisms, large species of ladybirds lay larger eggs than small species but they are not proportionally larger (Stewart et al. 1991). If one assumes that the size of the cells of small and large species of ladybird are the same, then as the larvae that hatch from eggs laid by large species are larger than those that hatch from eggs laid by small species and both develop from a single cell, the expectation is that eggs laid by large species will take longer to hatch than those laid by small species. Metabolic theory also predicts that the development rate of eggs is proportional to $Wt^{0.25}$ (Brown et al. 2004).

Thus, it was decided to use the data available in the literature on the rate of development of eggs of ladybirds at different temperatures to determine whether the lower temperature threshold for the development of eggs is the same for all ladybirds (Dixon et al. 1997; Jarosik et al. 2002) and whether those of coccidophagous species develop more slowly than those of aphidophagous species (Dixon 2000).

Material and Methods

The relationship between rate of development and egg mass

In order to avoid the effect phylogeny might have on the rate of development, eggs of 12 species of ladybirds of the tribe Coccinellini were kept at 22 °C and their rate of development determined. Egg mass ranged from 0.1 (*Adalia decempunctata*) to 0.8 mg (*Anisolemnia dilatata*).

Lower temperature threshold for development

A survey of the literature provided 83 data sets of the time it takes the eggs of 48 species of ladybirds, belonging to 8 tribes, to hatch when kept at from 1 to 8 different temperatures falling within the range of the linear relationship between developmental rate and temperature. This data was first used to test the hypothesis that all ladybirds have the same lower developmental threshold (*Ldt*), 10 °C (Dixon et al. 1997).

Rate of development of the eggs of aphidophagous and coccidophagous species of ladybird

The above data was used also to determine whether the rates of development of the eggs of 23 species of Coccinellini, all of which feed on aphids, and 4 species of Chilocorini, all of which feed on coccids, differ. Then to factor out any effect that phylogeny might have, the rate of development of the eggs of 8 species of *Scymnus* and 3 of *Nephus*, which both belong to the tribe Scymnini, were compared.

Statistical analysis of the data:
a) **The relationship between rate of development and egg mass:** The exponential relationship between rate of development and egg mass was analyzed using a curve fitting routine and by regression after logarithmic transformation of the values on both axes.

b) **Lower temperature threshold for development of the eggs of ladybirds in general and that of the eggs of aphidophagous and coccidophagous species of ladybird in particular:** The hypothesis that all ladybirds have the same lower developmental threshold 10 °C was tested by expressing the rate of development (*RD*) and temperature (*t*) by a linear regression: $RD = a + bt$, where *a* is the intercept with the *y*-axis, and *b* the slope of the linear function. From this equation, the lower developmental threshold, i.e. the temperature when $RD = 0$ and $t = Ldt$, was estimated as $Ldt = -a/b$ (e.g. Jarošík et al. 2002). The 95% confidence interval of the *LDT* was used to determine whether the *Ldt* differs significantly from 10 °C. This was done by shifting the *y*-axis to the *Ldt* (at which point the developmental rate intercepts the temperature axis) by subtracting *Ldt* from temperature values and by calculating standard error of the shifted zero intercept (see e.g. Crawley 1993, p. 276–277).

To test the hypothesis that the rates of development of the eggs of aphidophagous and coccidophagous species differ, the data were evaluated by ANCOVA in which the rate of development was regressed on temperature with a different intercept and a different slope for aphidophagous and coccidophagous species. Parameters of this model were inspected for significance by deletion tests, following Crawley (1993). Deletion tests were repeated until a minimal adequate model (MAM) was established. In MAM, all non-significant parameters are removed, and all the remaining parameters are significantly ($P < 0.05$) different from zero and from one another (Crawley 1993).

Results

Rate of development and egg mass

The rate of development declines exponentially with increase in egg mass, with the eggs of the largest species (*Anisolemnia dilatata*) taking 1.3 times longer to hatch at 22 °C than those of the smallest species (*Adalia decempunctata*). The best fitting curve is significant but only accounts for 34% of the variation. The correlation coefficient of the relationship between the logarithmically transformed rates of development and egg masses is $r = 0.55$, which is significant ($P < 0.05$) if this is seen as a test of the prediction of a hypothesis and a one tailed test is used. That is, the hypothesis that the large eggs laid by the large species of ladybirds should take longer to hatch than the small eggs laid by the small species is well supported by these results but there is a lot of variability that remains to be accounted for, which may be partly resolved by more results, especially for large species.

Lower temperature threshold for development

The analysis of the relationship between rate of development and temperature for the eggs of 48 species belonging to 9 tribes of ladybirds revealed that ladybirds do not all have a lower developmental threshold of 10 °C (Fig. 1). The average value of the Ldt is 7.24 and the 95% confidence intervals (7.21–7.26 °C) do not overlap 10 °C. The previous analysis that indicated a common lower temperature threshold for development was based on the variation in rates of development of the larvae of aphidophagous and coccidophagous ladybirds that belonged mainly to two tribes, the Coccinellini and Chilocorini (Dixon et al. 1997). As the prediction of rate isomorphy is that all the developmental stages of a species will have the same lower developmental threshold (Jarošík et al. 2002) then the expectation was that if the different larval stages all have the same lower developmental threshold then so should the eggs. It is likely that the differences between species were obscured by the fact that as there was little data for each species the analysis was done on pooled data rather than by comparing data for different species. What is needed are extensive data sets recorded over a wide range of temperatures for many species. Comparison of this sort of data will undoubtedly reveal very big and highly significant differences between the lower developmental thresholds of the species.
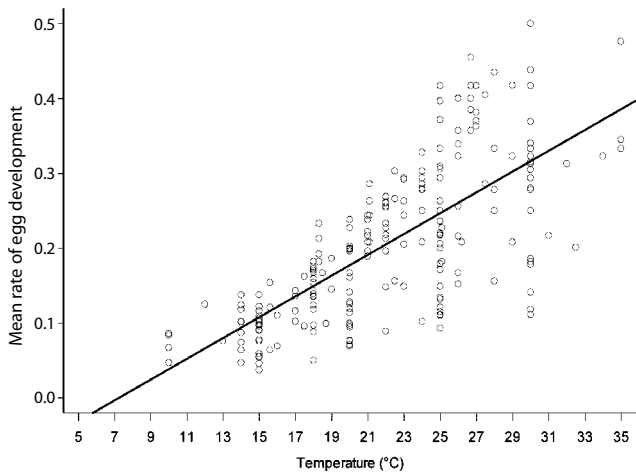
Fig. 1 The relationship between the average rates of development (*RD*) at different temperatures (*t*) of the eggs of 48 species of ladybirds belonging to 9 tribes. $RD = -0.10 + 0.014t$. The overall significance of the model is F = 238.4; d.f. = 1, 277; P < 0.001; R^2 = 0.51. (Data from: Allawi 2006; Atlihan and Chi 2008; Babu and Azam 1987; Brown 1972; Butler 1982; Cheah and McClure 1998; Chong et al. 2005; Grafton-Cardwell et al. 2005; Hämäläinen and Markkula 1977; Hodek 1958; Honěk and Kocourek 1988; Huang et al. 2008; Katsarou et al. 2005; Kontodimas et al. 2004; Kreiter and Iperti 1984; Kutuk and Yigit 2007; LaMana and Miller 1995,1998; M'Hamed and Chemseddine 2001; McMullen 1967; Michels and Bateman 1986; Michels and Behle 1991; Miller 1992; Miller and Paustian 1992; Mota et al. 2008; Naranjo et al. 1990; Obrycki and Tauber 1981, 1982; Omkar and Pervez 2004; Orr and Obrycki 1990; Ponsonby and Copland 1996; Ren et al. 2002; Roy et al. 2002; Schanderl et al. 1985; Shüder et al. 2004; Srivastra and Omkar 2003; Stathas 2000; Stathas et al. 2002; Uygun and Atlihan 2000; Wright and Laing 1978; Zhao and Wang 1987.)
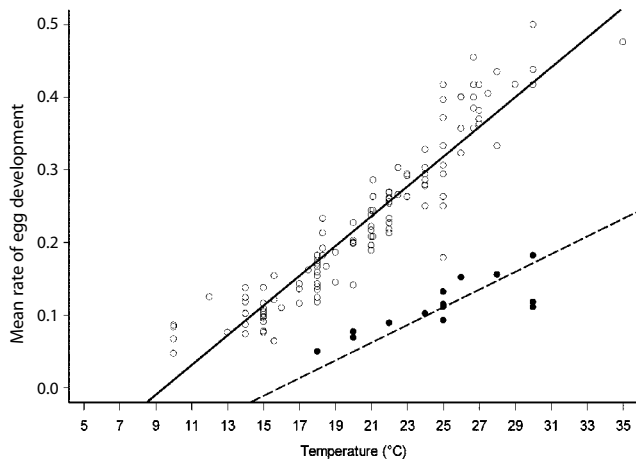

Fig. 2 The relationships between the average rates of development (RD) at different temperatures (t) of the eggs of aphidophagous Coccinellini (o) and coccidophagous (•) Chilocorini. Coccinellini: $RD = -0.19 + 0.020t$; Chilocorini: $RD = -0.19 + 0.012t$. The overall significance of the model is F = 536.5; d.f. = 2, 140; P < 0.001; R^2 = 0.88.

Interestingly, the data for the eggs of Coccinellini (aphid eaters) are at the upper bound and those of the Chilocorini (coccid eaters) at the lower bound of the distribution depicted in Fig. 1. Analysis of the data for these two tribes indicates that the eggs of Coccinellini

develop significantly faster than those of the Chilocorini (F = 370.85; d.f. = 1, 140; P < 0.0001) and that their average lower developmental thresholds (Ldts) also differ significantly (Fig. 2) The Ldt of Chilocorini (mean and 95% CI) is much higher, 15.92 (15.89–15.95), than that of Coccinellini, 9.47 (9.44–9.50). The clear difference in their rate of development cannot be attributed to egg size as the eggs of Chilocorini are not larger than those of Coccinellini.

Rate of development of the eggs of aphidophagous and coccidophagous species of ladybird belonging to the same tribe

The results of the above analyses of the whole data set, which includes information on species belonging to 9 tribes, or only two tribes, may be confounded by phylogenetic constraints (e.g. Harvey and Pagel 1991). In order to factor out the affects of phylogeny the data available for the aphid eating and coccid eating species of the tribe Scymnini were analyzed. Molecular data confirms that this is a robust tribe (Magro et al. 2010).
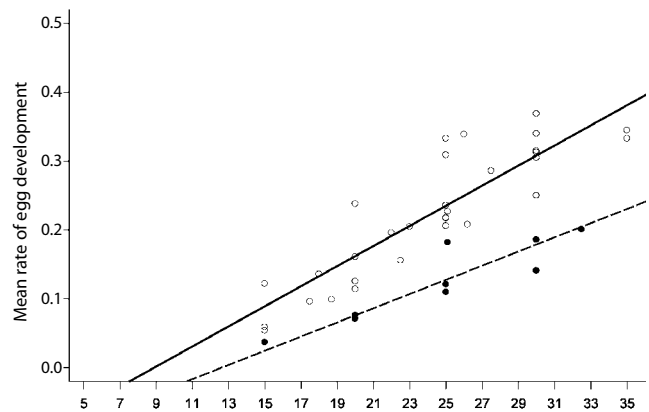

Fig. 3 The relationships between the average rates of development (RD) of eggs reared at different temperatures (t) of aphidophagous *Scymnus* (o) and coccidophagous *Nephus* (•), which both belong to the tribe Scymnini. *Scymnus: RD = -0.13 + 0.015t*; *Nephus: RD = -0.13 + 0.010t*. The overall significance of the model is F = 99.14; d.f. = 2, 38; P < 0.001; R^2 = 0.84.

This analysis indicates that the rate of development of the eggs of the coccid eating species of the genus *Nephus* is significantly slower than that of the aphid eating species of *Scymnus* (F = 52.20; d.f. = 1, 38; P < 0.001) and that their average lower developmental thresholds also differ (Fig. 3) (F = 99.14; d.f. = 2, 38; P < 0.0001; Ldt *Scymnus* = 8.90 [8.84–8.95]; Ldt *Nephus* = 12.61 [12.55–12.66]).

Discussion

This analysis of the time taken for the eggs of ladybirds to hatch when kept at different temperatures confirms the results of a previous similar analysis of the time taken by ladybirds to complete their larval development (Dixon et

al. 1997).The average rate of development of coccid eating species of ladybird is significantly slower than that of aphid feeding ladybirds. This study further indicates that this is unlikely to be due to a phylogenetic constraint as there are similar differences in the average rates of development of aphid eating and coccid eating species of ladybirds that belong to the same monophyletic tribe.

Interestingly, this marked difference in the rate of development is not mainly associated with size as is the case for Mammals (Bonner 1966; Sibly and Brown 2007). Metabolic theory predicts that small species will develop faster than large species but in the case of ladybirds coccidophagous species generally are smaller than aphidophagous species. The implication is that it must be advantageous for coccidophagous species to develop slower than would be predicted if their rate of development is mainly determined by metabolic constraints.

One possible explanation is that the food quality of the prey of the ladybirds that feed on coccids and aphids differs in terms of the limiting nutrients (Cohen and Brummett 1997) or toxic chemicals they contain (Dixon 1998). This is unlikely as the expectation is that the eggs are likely to be amply supplied with the nutrients required for embryonic development and, furthermore, it is possible to select ladybirds for improved performance on what are regarded as poor quality prey (Rana et al. 2002). However, this hypothesis needs to be rigorously tested.

Another possible explanation is that the lower developmental thresholds of aphid and coccid eating ladybirds differ. As the coccid eating ladybirds occur predominantly in subtropical and tropical regions and aphid eating ladybirds in temperate regions the prediction is that their Ldts will differ (Honěk 1996), which is supported by the results of this study. However, a preliminary analysis of the data for individual species indicates there is considerable overlap in the range of the Ldts of aphid and coccid eating ladybirds, but what is more significant is that relationships between the sum of the effective temperatures (SET) required for development and Ldt for coccid and aphid feeding ladybirds differ, with coccid eating species having considerably greater SET requirements than the aphid eating species. The SET requirement of a species is in part determined by food quality, which like temperature also affects the rate of development (Dixon 1998). Thus as concluded above it is important to determine to what extent, if any, food quality affects SET.

If the difference in the rates of development of coccidophagous and aphidophagous ladybirds is not attributable to differences in the food quality of their prey, which appears likely, then this poses a paradox that needs to be addressed. The intrinsic rate of increase (r_m) and developmental rate (1/D) are correlated and r_m is frequently used as a measure of fitness. Accepting this then the relatively slow rate of development of coccidophagous ladybirds is puzzling. Studies on *Drosophila* and fish indicate that the rate of development in these organisms is genetically controlled (Cruz do Nascimento et al. 2002; Devlin et

1994, 2001) and therefore subject to selection. The implication of this is that the reason why coccidophagous ladybirds don't develop faster is that they have been selected to develop slowly. It is likely the explanation is that it is advantageous for coccidophagous ladybirds to forage more slowly and consequently develop more slowly than aphidophagous ladybirds, but this needs further study.

Acknowledgements

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