Spring emergence of Canadian *Delia radicum* and synchronization with its natural enemy, *Aleochara bilineata*

L.D. Andreassen, U. Kuhlmann, J.W. Whistlecraft, J.J. Soroka, P.G. Mason, O.O. Akinremi, N.J. Holliday[1]

Abstract—To characterize time of spring emergence following post-diapause development, *Delia radicum* (L.) (Diptera: Anthomyiidae) from Saskatchewan, Manitoba, and southwestern Ontario were collected in fall, maintained over winter at 1 °C, then transferred to higher constant temperatures until adult emergence. At each location there were "early" and "late" phenotypes. Truncated normal models of temperature dependency of development rate were fitted for each phenotype from each location. We provide the first evidence of geographic variation in the criteria separating these phenotypes. Separation criteria and models for early and late phenotypes at the two prairie locations, approximately 700 km apart, were indistinguishable, but differed from those for Ontario. Prairie phenotypes developed more slowly than Ontario phenotypes, and more prairie individuals were of the late phenotype. Poor synchronization of spring emergence could impair predation of *D. radicum* eggs by adult *Aleochara bilineata* Gyllenhal (Coleoptera: Staphylinidae). *Aleochara bilineata* from Manitoba were reared and development rates modelled as for *D. radicum*. Models of development rates for the two species, when combined with simulated soil temperatures for two prairie locations, suggest that emergence of adult *A. bilineata* is well synchronized with availability of *D. radicum* eggs in prairie canola.

Résumé—Afin de caractériser le moment de l'émergence printanière qui suit le développement d'après la diapause, nous avons récolté des *Delia radicum* (L.) (Diptera : Anthomyiidae) dans des cultures de Saskatchewan, du Manitoba et du sud-ouest de l'Ontario à l'automne, les avons conservés durant l'hiver à 1 °C, puis transférés à des températures constantes plus élevées jusqu'à l'émergence des adultes. À chaque site, il y avait des phénotypes « hâtif » et « tardif ». Des modèles normaux tronqués de la dépendance du taux de développement de la température ont pu être ajustés à chaque phénotype à chacun des sites. Nous présentons les premières données qui montrent une variation géographique des critères qui séparent ces phénotypes. Les critères de séparation et les modèles des phénotypes hâtifs et tardifs ne peuvent être distingués entre les sites des prairies distants d'environ 700 km, mais ceux-ci se démarquent de ceux de l'Ontario. Les phénotypes des prairies se développent plus lentement que les phénotypes de l'Ontario et un plus grand nombre des *D. radicum* des prairies appartiennent au phénotype tardif. Une faible synchronisation de l'émergence printanière pourrait entraver la prédation des œufs de *D. radicum* par les adultes d'*Alaeochara bilineata* Gyllenhal (Coleoptera : Staphylinidae). Nous avons fait des élevages d'*A. bilineata* du Manitoba et modélisé leur taux de développement comme nous l'avions fait pour *D. radicum*. Les modèles des taux de

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développement des deux espèces, combinés aux températures simulées des sols de deux sites des prairies, indiquent que l'émergence des adultes d'*A. bilineata* est bien synchronisée avec la disponibilité des œufs de *D. radicum* dans les cultures de colza des prairies.

[Traduit par la Rédaction]

Introduction

The root-feeding species of *Delia* Robineau-Desvoidy (Diptera: Anthomyiidae) have become more widespread and injurious to canola (oilseed cultivars of *Brassica napus* L. and *B. rapa* L. (Brassicacae)) on the Canadian prairies as the area planted has increased (Soroka *et al.* 2004). In regions of the prairies with more than 250 mm of rainfall from June to August, the cabbage maggot, *D. radicum* (L.), is the most abundant *Delia* species attacking canola (Griffiths 1986*b*).

A short photoperiod and low temperatures induce overwintering diapause in *D. radicum* (Hughes 1960; Read 1969) as pupae within puparia (Hughes 1960). In spring, pupae undergo post-diapause development culminating in adult emergence. Activity of adult *D. radicum* on the prairies peaks in early June (Bracken 1988) or mid-June (Griffiths 1986*b*), when females oviposit around canola roots and floral buds are raised above leaf rosettes (Griffiths 1986*a*). The duration of post-diapause development is temperature-dependent, but there are two types of response: individuals of the "early" phenotype complete post-diapause development within 14 days at 20 °C; emergence of adults of the "late" phenotype is delayed and protracted, with some individuals requiring 100 days at 20 °C to complete development (Finch and Collier 1983). Extended cold treatment does not induce late-phenotype individuals to commence post-diapause development more quickly after the temperature is increased to 20 °C (Finch and Collier 1983). Although Collier *et al.* (1989*a*) hypothesized that the late phenotype requires a second phase of diapause, it is now known that the traits of early and late emergence are exhibited in all pupae, regardless of their diapause state (Biron *et al.* 1998).

Whether a phenotype is early or late is a heritable trait (Walgenbach *et al.* 1993) that responds rapidly to selection (Finch and Collier 1983). Nevertheless, laboratory selection studies suggest that the early phenotype is not governed by a single dominant allele, that there are multiple loci for the late phenotype, and that these loci are expressed when the early allele is in the recessive state (Biron *et al.* 2002). Populations of *D. radicum* vary in the proportions of early and late phenotypes across North America (Walgenbach *et al.* 1993; Turnock and Boivin 1997) and Europe (Finch and Collier 1983; Finch *et al.* 1988), even when populations are separated by only a few kilometres (Finch *et al.* 1986).

The criterion for separating the two phenotypes has been variously defined as 224 day-degrees above 4 °C (DDC_4) (Finch and Collier 1983), 320 DDC_4 (Collier *et al.* 1989*a*, 1989*b*), and 256 DDC_4 (Turnock *et al.* 1985; Turnock and Boivin 1997). By any of these definitions, a large proportion of individuals in *D. radicum* populations in Alberta (Broatch *et al.* 2006) and Manitoba (Turnock and Boivin 1997) are of the late phenotype, whereas early phenotypes predominate in southern Ontario and Quebec (Turnock and Boivin 1997), Norway (Johansen and Meadow 2006), and some parts of the English Midlands (Finch and Collier 1983). Therefore, the characteristics of the late phenotype are the most important influences on the seasonal activity of *D. radicum* in western Canada, and the damage caused to canola crops there.

Aleochara bilineata Gyllenhal (Coleoptera: Staphylinidae) is an important natural enemy of *D. radicum* (Read 1962; Turnock *et al.* 1995; Soroka *et al.* 2002; Hemachandra *et al.* 2007). Adult *A. bilineata* feed on *D. radicum* eggs and larvae, and *A. bilineata* larvae parasitize *D. radicum* puparia (Wadsworth 1915). *Aleochara bilineata* larvae overwinter in puparia, then develop more slowly to emergence at low temperatures and more quickly at high temperatures than *D. radicum* (Read 1962). In spring in Ontario, adult *Aleochara* emerged up to three weeks later than adult *D. radicum* (Nair and McEwen 1975), but which *D.*

Table 1. Locations of *Delia radicum* puparia in Manitoba, Ontario, and Saskatchewan used for comparing post-diapause development.

	Crop*	Collection date	No. collected
2004–2005 experiment			
Prairie Provinces			
Shellbrook, Sask. (53°13′N, 106°23′W)	Canola	30 Sept.–6 Oct. 2004	384
Fort Whyte, Man. (49°49′N, 97°12′W)	Rutabaga, broccoli, cabbage	8–11 Oct. 2004	573
Southwestern Ontario			
London (42°59′N, 91°15′W)	Rutabaga	14 Nov. 2004	417
2005–2006 experiment			
Prairie Provinces			
Shellbrook, Sask. (53°13′N, 106°23′W)	Canola	29 Sept. 2005	375
Carman, Man. (49°30′N, 98°00′W)	Canola	14–31 Oct. 2005	385
Southwestern Ontario			
London (42°59′N, 91°15′W)	Rutabaga	8 Nov. 2005	415

*Cultivars of *Brassica* spp.

radicum phenotype was involved is not known, and the *Aleochara* were a mixture of species. Despite these uncertainties, Soroka *et al*. (2002) considered that poor synchronization in spring decreases the effectiveness of *A. bilineata* as a predator of *D. radicum* eggs, and recommended a search for better synchronized populations of *A. bilineata*. In prairie canola crops in late summer, parasitism of *D. radicum* puparia by *A. bilineata* larvae is also poorly synchronized: larvae are present too early to make optimal use of available hosts (Hemachandra *et al*. 2007). Broatch *et al*. (2008) suggested that *A. bilineata* emergence in Alberta is well synchronized with *Delia* oviposition; however, this conclusion was based on emergence in plots subjected to prolonged caging, which can affect microclimate and time of emergence (Southwood and Siddorn 1965).

The objectives of this research were to compare the response to temperature of rates of post-diapause development of *D. radicum* in populations from Manitoba, Saskatchewan, and southern Ontario and to determine whether poor synchronization can impair predation of *D. radicum* eggs by *A. bilineata* in prairie Canada. First, cold-exposed samples of diapausing pupae were reared at constant temperature, and nonlinear regression modelling was used to test for phenotypic differences among populations. Then, to assess the degree of synchrony of the predator with the

availability of prey eggs, the regression models and simulated soil temperatures were combined to allow the dates of spring emergence of *D. radicum* and *A. bilineata* at prairie locations, one each in Manitoba and Saskatchewan, to be predicted.

Materials and methods

Collection of development-rate data

In 2004–2005 and 2005–2006, individuals from three *D. radicum* populations and one *A. bilineata* population were exposed to different temperature regimes to assess post-diapause development rates. Larvae and puparia of *D. radicum* were collected from the field at three locations in the fall of both 2004 and 2005, at a time when diapause was assumed to have been induced. *Delia radicum* larvae were fed slices of rutabaga (a cultivar of *B. napus*) until they formed puparia. In the 2004–2005 experiment, *D. radicum* were collected from near Shellbrook, Saskatchewan, Fort Whyte, Manitoba, and London, Ontario (Table 1), and puparia were buried individually in 14 mL plastic vials half-filled with sand and vermiculite and maintained at 7 ± 0.5 °C with no light until all experimental material was assembled. Individuals from each population were then subjected to a cold treatment at 1 ± 0.5 °C for 16 weeks. One week before the end of cold treatment, the depth of substrate was reduced

to about 5 mm to facilitate detection of emerging adults. In the 2005–2006 experiment, *D. radicum* were collected from near Carman, Manitoba, Shellbrook, and London (Table 1), and were all maintained at $1 \pm 0.5°$ for 22 weeks. The same vials were used as in 2004–2005, but puparia were placed at 1 °C after collection or as they were formed; the volume of substrate was not reduced.

In both years, *A. bilineata* from a laboratory colony originating from collections made near Anola, Manitoba (49°53′N, 96°38′W), in 2002 were induced to diapause by exposing larvae to diapausing *D. radicum* puparia for 18–21 days at 14 °C with no light (Whistlecraft *et al.* 1985). Puparia containing *A. bilineata* were exposed to the same conditions as *D. radicum* except that in 2005–2006, half the *A. bilineata* were kept at 1 °C for 12 weeks and the other half for 22 weeks.

In both 2004–2005 and 2005–2006, following cold treatment, insects from each of the four populations were divided into groups of equal size and one group was assigned to each of five temperature regimes. Emergence was checked daily. In the 2004–2005 experiment the vials were moved from 1 °C to the treatment temperatures in 5 °C steps every 2 days. The final temperatures in 2004–2005 were 13.0, 16.0, 19.0, 22.0, and 24.0 $\pm$ 0.5 °C. In the 2005–2006 experiment, insects were moved directly from 1 °C to treatment temperatures 8.2, 12.2, 14.6, 17.0, and 20.0 $\pm$ 0.5 °C, and the *A. bilineata* were divided into 10 groups, 1 group for each temperature treatment after 12 or 22 weeks at 1 °C. All experiments were carried out in environmental chambers with a 16L:8D photoregime.

Voucher specimens from each population were identified to species (Brooks 1951; Griffiths 1991) and deposited in the J.B. Wallis Museum of Entomology at the University of Manitoba.

Analysis of development-rate data

The relationship between development rate and temperature for the 2005–2006 experiment was fitted to Taylor's (1981) truncated normal model:

$$R(T) = R_m e^{\left[-\frac{1}{2}\left(\frac{T-T_m}{T_\sigma}\right)^2\right]}$$

where $R(T)$ is the development rate (1/days) at temperature T (°C), R_m is the maximum development rate, which occurs at temperature T_m, and T_σ describes the spread of the normal curve. The simple model, shown above, was estimated for *A. bilineata* and compared with a model with separate parameters for beetles that spent 12 or 22 weeks at 1 °C. For *D. radicum*, the 2005–2006 data were used to estimate the parameters of a model that assigned the three populations different criteria, or "breakpoints" (*B*, measured as DDC_4), to separate the early and late phenotypes; different parameter values (R_m, T_m, T_σ) for the two phenotypes; and different parameters for the two phenotypes in the three populations. The full model, therefore, was

$$
R(T) = \left\{ \left(R_{mlE} e^{\left[-\frac{1}{2}\left(\frac{T-T_{mlE}}{T_{\sigma lE}}\right)^2\right]} \right) (DDC_4 \leq B_l) \right\}
$$
$$
+ \left\{ \left(R_{mlL} e^{\left[-\frac{1}{2}\left(\frac{T-T_{mlL}}{T_{\sigma lL}}\right)^2\right]} \right) (DDC_4 > B_l) \right\}
$$
$$
+ \left\{ \left(R_{msE} e^{\left[-\frac{1}{2}\left(\frac{T-T_{msE}}{T_{\sigma sE}}\right)^2\right]} \right) (DDC_4 \leq B_s) \right\}
$$
$$
+ \left\{ \left(R_{msL} e^{\left[-\frac{1}{2}\left(\frac{T-T_{msL}}{T_{\sigma sL}}\right)^2\right]} \right) (DDC_4 > B_s) \right\}
$$
$$
+ \left\{ \left(R_{mcE} e^{\left[-\frac{1}{2}\left(\frac{T-T_{mcE}}{T_{\sigma cE}}\right)^2\right]} \right) (DDC_4 \leq B_c) \right\}
$$
$$
+ \left\{ \left(R_{mcL} e^{\left[-\frac{1}{2}\left(\frac{T-T_{mcL}}{T_{\sigma cL}}\right)^2\right]} \right) (DDC_4 > B_c) \right\}
$$

where the parameter R_{mij} is for the *i*th population (*l* is London, *s* is Shellbrook, *c* is Carman) and *j*th phenotype (*E* is early, *L* is late), and terms of the form ($DDC_4 > B_i$) return a value of 1 when true and 0 when false.

Breakpoints were initially estimated for each population individually and, because

the distribution of DDC$_4$ values was discontinuous and non-integrable, manual iteration was used to estimate the most appropriate breakpoint for each population within the DDC$_4$ range 200–320, including 256 DDC$_4$ (Turnock and Boivin 1997), 320 DDC$_4$ (Collier *et al*. 1989*a*), and 224 DDC$_4$ (Finch and Collier 1983). An *F*-ratio test of error mean squares was used to determine whether including separate parameters and breakpoints for the different populations significantly improved the fit of the model (Gallant 1987). The fit of the final model was assessed by using the mean-corrected r^2 to assess the proportion of among-groups sums of squares explained by the model (Kvalseth 1985; Sokal and Rohlf 1995), where groups were all combinations of temperature, source population, and phenotype for *D. radicum* and all combinations of temperature and overwintering treatment for *A. bilineata*. Lamb's (1992) methods of estimating developmental-threshold temperature and day-degree requirement were followed.

Model effectiveness was tested by comparing median observed days to emergence with those predicted by the model, using linear regression and by examining the mean-corrected multiple r^2. Data from the 2004–2005 experiment could not be directly fitted to a model because of the complexity introduced by the stepped temperature increase, therefore they were analyzed by first estimating the proportion of development that occurred as the insects were gradually brought to the final treatment temperatures, using the appropriate parameters derived from the 2005–2006 experiment. The estimated development rate was used to predict days to emergence at the final temperature, which was then regressed on the observed median number of days. If the calculated intercept was not significantly different from 0 and the slope not significantly different from 1, the estimated parameters were considered unbiased (Lactin *et al*. 1995). The days to emergence for *D. radicum* from Fort Whyte (2004–2005 experiment) were compared with predicted days using the model developed for *D. radicum* from Carman (2005–2006 experiment).

Predicting spring emergence in the field

To place the laboratory results in a field context, meteorological data were used to estimate soil temperature at Prince Albert, Saskatchewan (53°12′N, 105°45′W), and Carberry, Manitoba (49°52′N, 99°22′W), from 2002 to 2006 and the soil-temperature data were used to predict spring emergence of each population, using the development-rate model. Daily maximum and minimum air temperatures, rainfall, and total precipitation (Environment Canada 2002) were used to estimate daily mean soil temperature at 5 cm depth with the soil-temperature algorithm in the modified versatile soil moisture budget (Akinremi *et al*. 1996). Because daily solar radiation for the two sites was required for the versatile soil moisture budget, we estimated this using the Hargreaves formula for calculating solar radiation (Hargreaves and Samani 1982):

$$R_s = K_{Rs}R_a\sqrt{(T_{\max}-T_{\min})}$$

where R_s is the daily solar radiation (MJ·m^{-2}·d^{-1}), R_a is the extraterrestrial radiation (MJ·m^{-2}·d^{-1}) at the latitude of the site, K_{Rs} is the adjustment coefficient for interior land mass (0.16 °C$^{-0.5}$), and $T_{\max}$ and $T_{\min}$ are the daily maximum and minimum air temperature, respectively. The temperature estimates were tested for bias as described in the previous section using the Carberry site, where actual measurements at 5 cm depth were available for 2003–2006 (O.O. Akinremi, unpublished data), for the period 1 April – 30 June of each year.

The estimates of daily mean soil temperature were used to predict the proportion of development of *D. radicum* and *A. bilineata* completed each day, starting on 1 April of each year. For *A. bilineata* and for each phenotype of each population of *D. radicum*, 500 parameter sets were selected for the equation

$$R(T)=R_m e^{\left[-\frac{1}{2}\left(\frac{T-T_m}{T_\sigma}\right)^2\right]}+\varepsilon$$

where ε is a random error term. For each parameter set, random normal values were drawn for R_m, T_m, and T_σ using the fitted parameter estimates from the model and their corresponding standard error (SE). Random normal values of ε were also drawn, with mean 0 and SE derived from the error mean square

for the model. The 500 parameter sets were applied to the soil-temperature data and the cumulative proportions of emergence completed per day used to provide 500 estimates of day of emergence at each location for *A. bilineata* and each *D. radicum* phenotype. Percentiles for day of emergence of *A. bilineata* were estimated directly; those for *D. radicum* populations were estimated after combining the early- and late-phenotype estimates, weighted by their proportion of occurrence in each population. Proportions of phenotype occurrence for London and Shellbrook were averages of the two years of data from these locations. For simulated soil temperatures for Carberry, the phenotype compositions of the Fort Whyte and Carman samples were averaged to represent the Manitoba population of *D. radicum*.

Results

Temperature and development rate

In both 2004–2005 and 2005–2006 the proportion of *D. radicum* emerging was higher for insects from London than for insects from the prairie populations (Fig. 1). Emergence of *A. bilineata* was low in both years and for both periods of exposure to 1 °C, especially at the lower treatment temperatures (Fig. 1).

There were two phenotypes (early and late) in the *D. radicum* populations. If *D. radicum* from all sources were considered to be a single population, the breakpoint between the two phenotypes that gave the highest mean corrected r^2 was 255 DDC$_4$. Estimating separate parameters for the two phenotypes using this breakpoint significantly improved the fit of the model (*a* in Table 2) over that of a model in which no phenotypes were distinguished.

A model with separate parameter estimates for each population, based on a breakpoint of 255 DDC$_4$, was not as good a fit to the data as a model using the same parameter estimates but the most appropriate breakpoint for each population (*b* in Table 2). These breakpoints were 224 DDC$_4$ for the London population and 280 DDC$_4$ for the prairie populations (Fig. 2). On the basis of these criteria, the early phenotype composed 71% of 210 individuals that emerged in 2004–2005 and 89% of

Fig. 1. Percent emergence at different temperatures and after different periods of cold exposure in 2004–2005 and 2005–2006 experiments on *Delia radicum* from London, Ontario (*a*); *D. radicum* from Shellbrook, Saskatchewan (*b*); *D. radicum* from Fort Whyte (2004–2005) and Carman, Manitoba (2005–2006) (*c*); and *Aleochara bilineata* from Manitoba (*d*). Emergence was based on the number of insects emerging divided by the number in each treatment, multiplied by 100; for field-collected *D. radicum*, the number of parasitoids that emerged was subtracted from the divisor.
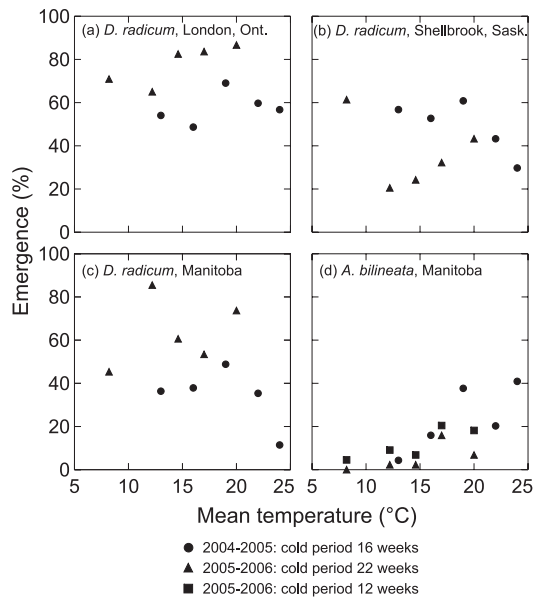
244 individuals that emerged in 2005–2006 in the London population. In the Shellbrook population, 32% of 183 in 2004–2005 and 45% of 124 in 2005–2006 were early phenotype. Of the 234 *D. radicum* from Fort Whyte in the 2004–2005 experiment, 31% were early phenotype. The Carman population in the 2005–2006 experiment (N.B. with 'en dash' between the years, instead of the normal dash. en dash does not seem to be available in Adobe) had the smallest proportion of early phenotype: 23% of 230.

Estimating distinct parameters for the late phenotype for each population yielded a significantly better fit than estimating a single set of parameters that were common to all populations. However, using separate parameters for the late phenotype for the two prairie populations was not significantly better

Table 2. Error sum of squares (SS$_{error}$) and degrees of freedom (df$_{error}$) for models relating rate of development of *Delia radicum* from London, Ontario, and the "prairies" (Shellbrook, Saskatchewan, and Carman, Manitoba) to temperature.

	Model	SS$_{error}$[a]	df$_{error}$	Numerator	F_{df}[b]
a					
1	All *D. radicum*, one phenotype	0.253156	577		
2	Early and late phenotypes separated at breakpoint 255 DDC$_4$	0.039589	573	*a*: 1–2	$F_{4,573} = 772.8$***
b					
1	All *D. radicum*, 255 DDC$_4$, population-specific parameters	0.027299	561		
2	Population-specific breakpoints, population-specific parameters based on 255 DDC$_4$	.026797	559	*b*: 1–2	$F_{2,559} = 5.2$*
c					
1	All *D. radicum*, population-specific breakpoints and parameters	0.025287	559		
2	Common parameters for late phenotype	0.027773	565	*c*: 2–1	$F_{6,559} = 9.16$***
3	Common parameters for late phenotype from the prairies	0.025335	562	*c*: 3–1	$F_{3,559} = 0.35$
d					
1	All *D. radicum*, population-specific breakpoint and early-phenotype parameters, late-phenotype parameters common for the prairies	0.025335	562		
2	Common parameters for early phenotype	0.039156	568	*d*: 2–1	$F_{6,562} = 51.10$***
3	Common parameters for early phenotype from the prairies	.025602	565	*d*: 3–1	$F_{3,562} = 1.97$

[a]Used in *F*-ratio tests to determine whether a model fit the data better with early and late phenotypes (*a*), population-specific breakpoints (*b*), or population-specific model parameters (R_m, T_m, T_σ) (*c* and *d*).

[b]*F* statistics denote comparisons of a difference in MS$_{error}$ (N.B. error could be in subscripts) (identified by line numbers in the numerator column), with MS$_{error}$ for the model with the lowest df$_{error}$ in the same section of the table (*a*, *b*, *c*, or *d*) (*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$).

than using pooled estimates for these populations (*c* in Table 2). Similarly, estimating separate parameters for each population for the early phenotype improved the model's fit relative to using a single set of early-phenotype parameters but not to using pooled parameter estimates for the two prairie populations (*d* in Table 2). Thus, the final model has common parameter estimates (Table 3) and breakpoints for the two prairie locations and these differ from those for the London population. The final model with these parameter estimates explained 98.5% of the (mean-corrected) among-groups sums of squares. The days to emergence predicted by a model with these parameters, and the actual number of days observed, are illustrated for early-phenotype *D. radicum* (Fig. 3) and for late-phenotype *D. radicum* and for *A. bilineata* (Fig. 4).

The developmental-threshold temperature of the early phenotype was nearly the same for the London and prairie *D. radicum* populations, but the day-degree requirement of the prairie early phenotype was higher by about 50 (Table 3). The developmental threshold temperature for the late phenotype from London was nearly 1 °C higher than for prairie *D. radicum* (Table 3), making a direct comparison of the day-degree requirement of this phenotype more difficult. However, late-phenotype *D. radicum* from prairie populations appeared to require the accumulation of more heat for post-diapause development than did those from London.

The basic model described *A. bilineata*'s development rate as accurately as a model with separate parameters for individuals assigned to 12 and 22 weeks' cold treatment at 1 °C (basic

Fig. 2. Observed cumulative emergence of *Delia radicum* from London, Carman, and Shellbrook at a constant temperature of 14.6 °C in relation to day-degrees above 4 °C (DDC_4) in the 2005–2006 experiment. The broken lines indicate the estimated breakpoints between early and late phenotypes for the London (224 DDC_4) and prairie (280 DDC_4) populations.
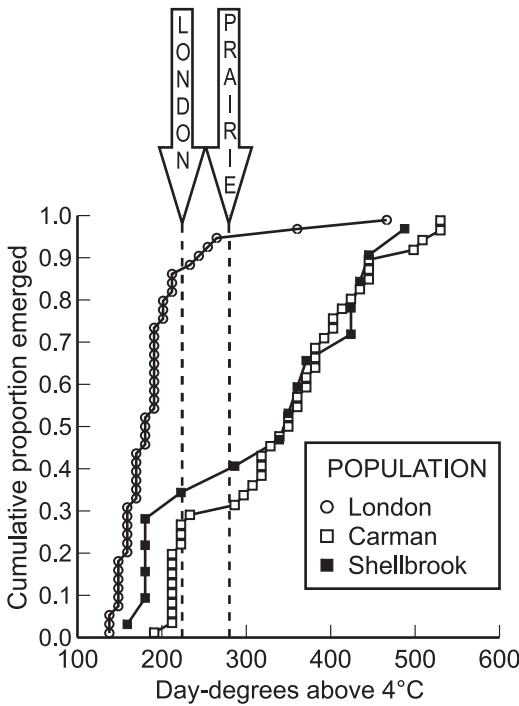
$SS_{error} = 0.000167287$, $df_{error} = 36$; separate $SS_{error} = 0.000151952$, $df_{error} = 33$; $F_{3,33} = 1.1$, $P = 0.36$). The rates of development of the two *A. bilineata* groups were therefore indistinguishable and a single set of the parameters R_m, T_m, and T_σ was estimated (Table 3). The three-parameter model explained 99.4% of the means-corrected among-groups sum of squares. *Aleochara bilineata* had a higher day-degree requirement than did any of the *D. radicum*.
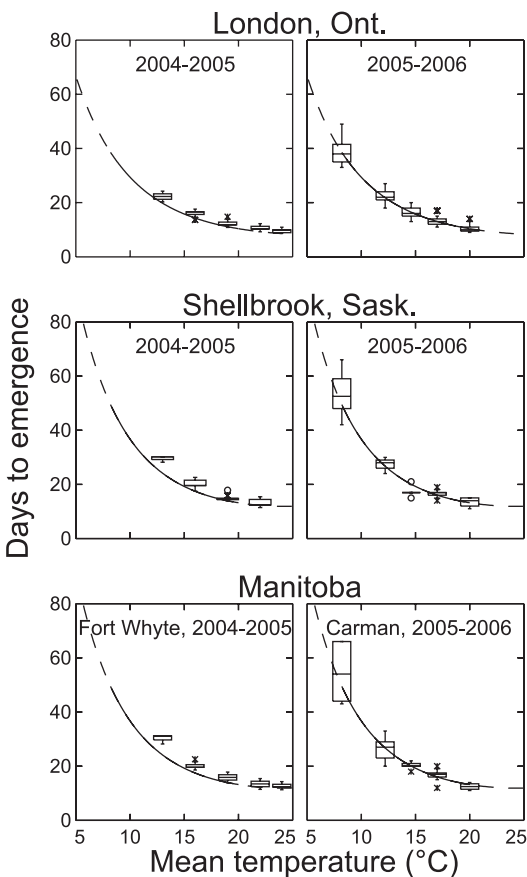
There were six combinations of year, phenotype, and population for which predictions of median observed days to emergence were inaccurate; all were in the 2004–2005 experiment, in which the temperature was gradually increased (Table 4). In four groups, bias was observed; that is, the regression slope was different from 1 or the intercept was different from 0 (Table 4). For *A. bilineata*, the lack of fit seemed to be at 13 and 16 °C (Fig. 4), temperatures at which few adults emerged (Fig. 1). For the early *D. radicum* phenotype from Fort Whyte and Shellbrook, the parameters estimated for the prairie *D. radicum* populations consistently underestimated days to emergence (Fig. 3). Of predictions for all populations studied, those for the late *D. radicum* phenotype from London were the poorest, particularly at 24 °C, where days to emergence was overestimated by about 100 (Fig. 4). In addition, there were two late-phenotype groups (Fort Whyte and Shellbrook) in 2004–2005 for which unbiased estimates of days to emergence were obtained but for which r^2 was relatively low (Table 4); in both cases, days to emergence of the late phenotype was underestimated at 13 °C and overestimated at 24 °C (Fig. 4).

Table 3. Estimated parameters for a truncated normal distribution model describing the rate of post-diapause development as a function of temperature, developmental threshold (TH_{08}), and day-degree requirement (DD_{80}) of early- and late-phenotype *Delia radicum* populations from London and the "prairies" (Shellbrook and Carman) and a population of *Aleochara bilineata* from Manitoba.

Population	R_m	T_m	T_σ	TH_{08}	DD_{80}
London, early phenotype	0.1246 ± 0.0144	28.0343 ± 2.4896	11.1942 ± 1.1317	3.1	186
Prairies, early phenotype	0.0841 ± 0.0061	24.4501 ± 1.7393	9.6243 ± 0.9631	3.0	237
London, late phenotype	0.0429 ± 0.0027	15.6767 ± 0.4065	4.3857 ± 0.5340	5.9	212
Prairies, late phenotype	0.0302 ± 0.0007	17.1913 ± 0.2267	5.4145 ± 0.2777	5.1	371
Aleochara bilineata	0.0349 ± 0.0021	22.5083 ± 1.2976	7.4820 ± 0.8420	5.8	444

Note: R_m is the maximum development rate, T_m is the temperature at which the rate is maximal, and T_σ is a shape parameter. All are given as the mean $\pm$ SE. $TH_{08} = T_m - 2.23\,T_\sigma$. $DD_{80} = T_\sigma/0.482R_m$
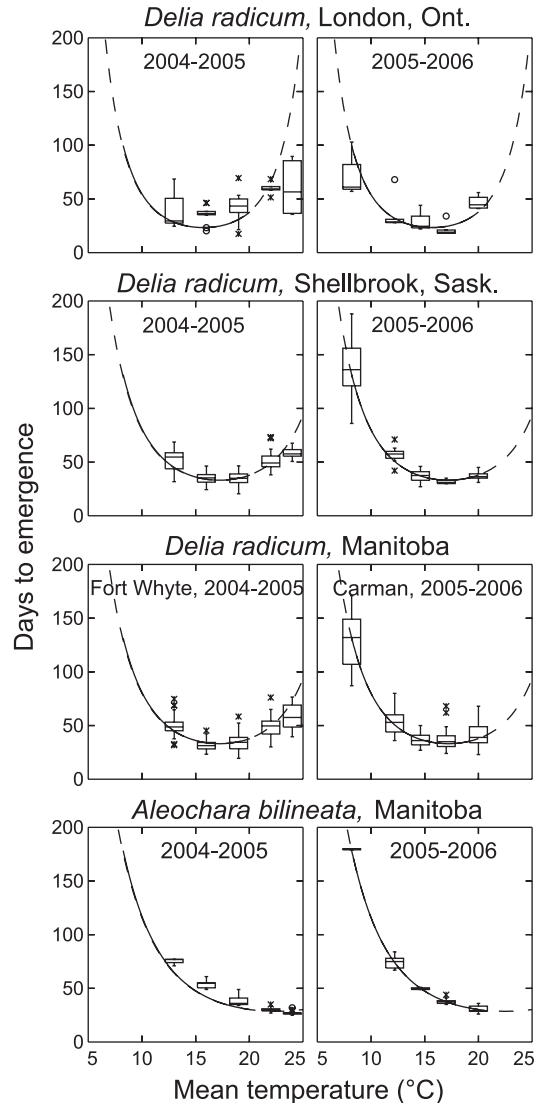
Fig. 3. Comparison of predicted and observed times from the end of cold exposure to the start of emergence for early-phenotype *Delia radicum* from Ontario, Manitoba, and Saskatchewan in two years. The solid curve represents predictions from the model fitted to 2005–2006 data; the extension (broken line) represents predictions beyond the temperature range used to fit the model. The upper and lower boundaries and midline of the boxes at each temperature represent lower and upper quartiles and median observed times, respectively. Whiskers attached to the boxes represent the range of values that fall within $1.5 \times$ the interquartile distance beyond quartiles. Extreme observations are represented by crosses ($\leq 3 \times$ the interquartile distance from the quartile) or circles ($> 3 \times$ the interquartile distance from the quartile).

Fig. 4. Comparison of predicted and observed times from the end of cold exposure to the start of emergence for late-phenotype *Delia radicum* from Ontario, Manitoba, and Saskatchewan and for *Aleochara bilineata* in 2 years (see Fig. 3 for details).

Predicting spring emergence in the field

Regressions of observed temperature on estimated temperature 5 cm below the soil surface revealed that much of the variance was explained ($r^2 > 0.75$). The intercept of the regressions, however, was significantly different from 0 for 2003–2005 but not in 2006; inspection of plots revealed that the versatile soil moisture budget slightly overestimated low temperatures early in the season. As a result, development started 0–4 days earlier in the simulation than was predicted from actual soil temperatures, depending on the year and group. Slope coefficients for these regressions

Table 4. Statistics for a test of model bias by linear regression of predicted on observed days to emergence, for *n* temperature treatments for populations of *Delia radicum* from Manitoba, Ontario, and Saskatchewan and for *Aleochara bilineata* from Manitoba.

Population	Year	Phenotype	Adjusted multiple r^2	n	Itercept	P^a	Slope	P^a
Aleochara bilineata, Manitoba	2004–2005		0.962	5	9.57 ± 3.01	ns	0.69 ± 0.07	*
	2005–2006		0.999	5	0.94 ± 0.57	ns	0.99 ± 0.01	ns
Delia radicum								
Fort Whyte, Man.	2004–2005	Early	0.996	5	-0.10 ± 0.44	ns	0.82 ± 0.03	*
		Late	0.774	5	-5.84 ± 12.83	ns	1.16 ± 0.30	ns
Carman, Man.	2005–2006	Early	0.997	5	2.10 ± 0.74	ns	0.88 ± 0.06	ns
		Late	0.999	5	-1.09 ± 1.31	ns	1.00 ± 0.02	ns
London, Ont.	2004–2005	Early	0.993	5	-1.20 ± 0.50	ns	0.89 ± 0.04	ns
		Late	0.568	5	123.73 ± 32.07	*	-2.42 ± 0.97	*
	2005–2006	Early	0.999	5	0.10 ± 0.35	ns	1.01 ± 0.02	ns
		Late	0.832	5	-16.70 ± 17.03	ns	1.70 ± 0.44	ns
Shellbrook, Sask.	2004–2005	Early	0.994	4^b	1.67 ± 0.77	ns	0.71 ± 0.04	*
		Late	0.541	5	0.89 ± 22.46	ns	0.97 ± 0.51	ns
	2005–2006	Early	0.984	5	1.69 ± 1.92	ns	0.90 ± 0.06	ns
		Late	0.993	5	1.59 ± 2.90	ns	0.95 ± 0.04	ns

[a]*t* test, df = $n - 2$; "ns", not significantly different from 0; *, significant at the 0.05 level.
[b]No early phenotype emerged at 24 °C.

were indistinguishable from 1 ($P > 0.05$) in all years except 2003 (slope = 1.19, SE = 0.035; t_{75} = 5.3, $P < 0.001$).

Delia radicum from London were predicted to emerge prior to those from the prairies, at both Carberry and Prince Albert (Fig. 5). At Carberry, predicted median emergence of adult *A. bilineata* was 13 ± 0.9 days (mean $\pm$ SEM) ($n = 5$) after that of Manitoba *D. radicum* and 34 ± 2.4 days after that of *D. radicum* from London. At Prince Albert, the predicted median emergence of *A. bilineata* was 16 ± 1.9 days after that of *D. radicum* from Saskatchewan and 33 ± 2.8 days after that of *D. radicum* from London. In both locations, median emergence of *A. bilineata* was predicted to be 9 ± 1 days after that of the prevailing late phenotype from prairie populations and much later than that of the majority of flies in the population from London, which was composed mainly of the early phenotype (Fig. 5).

Discussion

Development of *D. radicum*

This study is the first to model the temperature dependence of rates of development of *D. radicum* on canola in Canada and the first to demonstrate geographic variation in the criterion separating early and late phenotypes of this species. Differences in temperature-dependent development rates between Manitoba and eastern Canadian *D. radicum* populations have been observed previously (Turnock and Boivin 1997), but given the small geographic scale of such variation in some areas (Finch *et al.* 1986), we found surprising homogeneity in *D. radicum* from prairie localities as far apart as 700 km.

The timing of a species' seasonal cycle can vary both geographically, if a population from a specific location is better adapted to that area than another, and at the intrapopulation level, in which a population exhibits a range of responses to seasonal change (Danilevsky *et al.* 1970; Tauber and Tauber 1981). At the intrapopulation level, *D. radicum* phenotypes with rapid, intermediate, and slow development can be readily selected in the laboratory (Finch and Collier 1983; Walgenbach *et al.* 1993; Biron *et al.* 1998). It is hypothesized that two phenotypes persist because the early phenotype can complete more generations in warm years and the late phenotype is safer in

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Fig. 5. Predicted cumulative emergence in relation to Julian date for each of 5 years for the London and Manitoba populations of *Delia radicum* and *Aleochara bilineata* at Carberry (*a*) and of the London and Shellbrook populations of *D. radicum* and *A. bilineata* at Prince Albert (*b*).
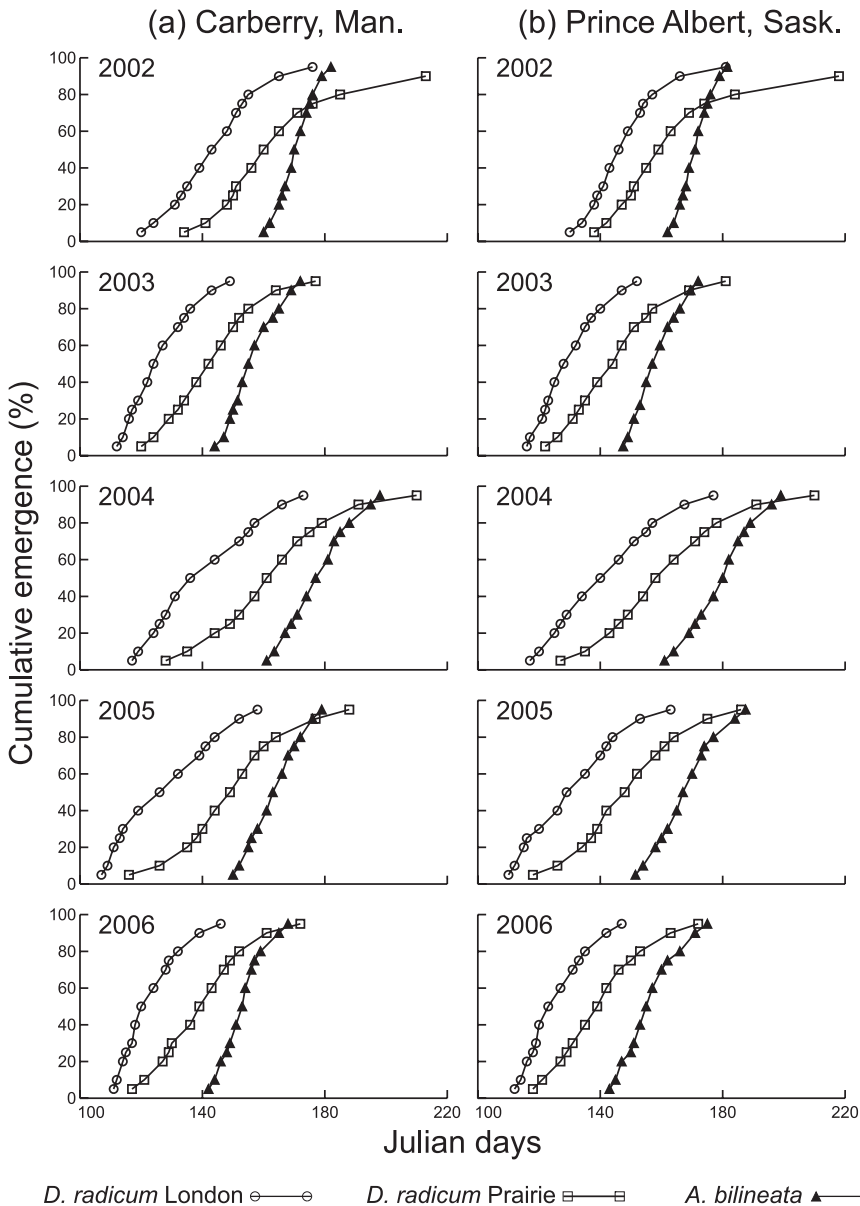
extreme spring weather that may kill early-emerging adults before they can reproduce (Finch and Collier 1983; Walgenbach *et al.* 1993; Biron *et al.* 1998). The positive correlation between the proportion of the early phenotype in a locality and thermal accumulation during the previous growing season

supports this hypothesis (Turnock and Boivin 1997). At the geographic level, the relative proportions of the two phenotypes (Finch and Collier 1983, 1985; Finch *et al.* 1986; Turnock and Boivin 1997) and the developmental response of both phenotypes to temperature (Turnock and Boivin 1997) can vary among

populations. Either phenotype could be selected naturally to synchronize emergence in spring with the availability of host plants in a particular area (Finch *et al.* 1986) as well as to respond to local climatic conditions (Turnock and Boivin 1997).

In previous studies a range of breakpoints has been applied to distinguish early and late phenotypes. This study demonstrates that the most appropriate criterion to use depends upon the population being studied. Specifically, samples collected around canola roots in Manitoba and Saskatchewan in our 2005–2006 experiment had the same breakpoint, which was higher than that for collections from the roots of rutabaga in London. If this difference is genetically based, selection pressure on prairie populations has favoured protracted emergence of the early phenotype, less protracted emergence of the late phenotype, or both.

For both early and late phenotypes, selection pressure on prairie populations has been uniform enough to cause responses of development to temperature to be the same over a large geographic area. These responses are distinct from those of corresponding phenotypes from London. The most obvious interpretation is that the most favourable time of emergence in spring depends on local availability of host plants. The principal host plant on the prairies is canola, and in the early 1980s gravid female *D. radicum* were present well before canola was in a stage preferred for oviposition (Griffiths 1986*a*). Perhaps emergence has become progressively later over the intervening years, thus minimizing the time female *D. radicum* spend waiting to lay eggs. Differences in climate may also favour differences in responses to temperature. London is about $7°$ south of the prairie areas studied, and the growing season starts about 2 weeks later and the frost-free period is 30–40 days shorter at the prairie locations than in London (Chapman and Brown 1966). Early-phenotype females would be more likely to die from weather-associated causes before laying eggs on the prairies than in the Ontario location. Both phenotypes from the prairies required more time to emerge than did the corresponding phenotypes from London, and also, the proportions of individuals in the prairie populations that were of the late phenotype were higher.

Turnock and Boivin (1997) studied *D. radicum* collected from rutabaga from the Canadian prairies and London using methods similar to those used here. Too few London individuals were of the late phenotype for analysis in their study, and the London early phenotype had a higher developmental threshold ($TH_{08} = 5.0$) and lower day-degree requirement ($DD_{80} = 160$) than in our study. The higher threshold may be accounted for in part by their use of different criteria to separate the phenotypes, and therefore by their inclusion as early phenotype of some individuals that perhaps would have been better considered late. The developmental threshold and day-degree requirement of our early-phenotype *D. radicum* from canola in Manitoba and Saskatchewan are similar to those of early *D. radicum* from *Brassica* vegetable plants from Winnipeg, Manitoba ($TH_{08} = 3.3$, $DD_{80} = 246$), reported in Turnock and Boivin (1997). Our prairie late phenotype had a higher developmental threshold and day-degree requirement than late *D. radicum* from Winnipeg reported in Turnock and Boivin (1997) ($TH_{08} = 4.4$, $DD_{80} = 316$). Our prairie late-phenotype *D. radicum* had an estimated developmental threshold similar to that of late *D. radicum* from England ($TH_{08} = 5.0$, $DD_{80} = 538$) and Prince Edward Island ($TH_{08} = 5.0$, $DD_{80} = 530$) (Turnock and Boivin 1997), but the day-degree requirement was much lower. Therefore, our prairie late-phenotype *D. radicum* did not emerge as late as those of some other populations and were similar to North Carolina (Walgenbach *et al.* 1993) and certain English (Finch *et al.* 1986) populations. The assumption that individuals in a *D. radicum* population will fall into one of two well-defined and universal phenotypes is a good first approximation, but is no doubt an oversimplification.

Data from the 2004–2005 experiment were not always well explained by the model developed using the 2005–2006 results, and this could be attributable to three methodological differences between the experiments: rate of temperature increase, duration of cold treatment, and range of temperatures used.

The rate at which post-diapause *D. radicum* pupae develop depends on the speed of the transition from low to higher temperatures (Hemachandra 2004). In this study, gradually raising the temperature caused early-phenotype *D. radicum* and *A. bilineata* to develop more slowly than predicted. The duration of cold treatment is expected to affect the proportion of pupae that complete diapause and can begin post-diapause development when the temperature is raised. At 0 °C, diapause is complete in about 60% of *D. radicum* individuals after 16 weeks, and this proportion reaches a maximum after 22 weeks (Collier and Finch 1983). Incomplete diapause would cause days to development to be higher than expected. As well, in the 2004–2005 experiment, two of the temperatures used were 22 and 24 °C; temperatures above 21 °C cause death or delayed development of pupae (Finch and Collier 1985; Johnsen *et al.* 1990), although this phenomenon seems to be specific to certain populations (Turnock and Boivin 1997). If mortality is an important factor, only rapidly developing individuals would emerge, giving the impression that development time had been overestimated. Also, no data collected above 20 °C were used in developing the model. Overestimation due to extrapolation of development rates at 22 and 24 °C (rather than to heat injury) is a reasonable explanation for deviations from predictions for *A. bilineata* in our 2004–2005 experiment because survival of *A. bilineata* was greater at higher temperatures.

Synchronization of *A. bilineata* emergence with prey availability

Adult *A. bilineata* are generally believed to emerge too late in spring to feed on *D. radicum* eggs laid by the overwintered generation (Read 1962; Jonasson 1994), even though in the laboratory, adult *A. bilineata* will eat immediately after emergence if provided with food. In southern Ontario, adult *Aleochara* (predominantly *A. bilineata*) emerged "no later than two weeks" (Nair and McEwen 1975, p. 349) after overwintered *D. radicum* in 1971 and about three weeks later than their hosts in 1972 (Nair and McEwen 1975), considerably later than the start of oviposition.

We used models of soil temperature at a typical depth for *D. radicum* pupation because there are insufficient observations of temperatures of prairie soils at the time of post-diapause development. Our models tended to overestimate soil temperatures near the time of snowmelt, when temperatures are low and increments of development minuscule. Thus, we expected there to be little influence of this bias on the predicted dates of emergence. Although the distributions of predicted days to emergence respond to variation in development rates detected in our modelling procedure, they do not capture variation due to differences in the pupal environment related to soil type, moisture level, or depth of pupae in soil. However, they do provide a way of assessing the relative time of emergence of insects experiencing the same environmental conditions. The predicted intervals between emergence of *A. bilineata* and prairie *D. radicum* suggest that emergence of *A. bilineata* on the prairies is well synchronized with availability of prey. Under optimal conditions, four or five days elapse between emergence of adult female *D. radicum* and commencement of oviposition (Finch 1974), and the oviposition rate is high for two–three weeks thereafter (Swailes 1961; Finch and Coaker 1969). Eggs hatch four−five days after oviposition (Finch and Coaker 1969). Thus, at the time of *A. bilineata* emergence, *D. radicum* eggs would recently have become available, and would be available for several weeks.

Emergence-cage studies in prairie canola stubble have shown that overwintered *A. bilineata* (Broatch *et al.* 2008) start to emerge about one week after peak *D. radicum* emergence in mid-June (Broatch *et al.* 2006), and most *A. bilineata* emerge two−three weeks following the *D. radicum* peak. Traps used in current-year crops in the same area, however, show both species to be present prior to their appearance in cages, and in one of two years for which comparable data have been published, the periods during which the two species were most active were coincident (Broatch *et al.* 2006, 2008). Broatch *et al.* (2008) argue that, as a predator, *A. bilineata* is better synchronized with the availability of of *D. radicum* eggs on the prairies than elsewhere.

The current study also shows that emergence of adult *A. bilineata* on the prairies is well synchronized with the availability of *D. radicum* eggs. The predominance of the late phenotype and the uniformity of the temperature dependence of rates of development of *D. radicum* on the prairies may have made synchronization of predator with prey more likely. Selection on prairie *D. radicum* to emerge earlier (and reduce the risk of egg predation by *A. bilineata*) seems to have been less strong than selection favouring later emergence, reduced weather-induced mortality, and better synchronization with host plants. Although adult *A. bilineata* potentially live much longer than the period required for a *D. radicum* egg to develop into a pupa (Read 1962), we expect that selection on *A. bilineata* development rates would tend to favour synchronization with the availability of host puparia rather than *D. radicum* eggs. Furthermore, we expect the strength of this selection to depend upon the importance of *D. radicum* eggs relative to other types of prey and of *D. radicum* puparia relative to those of other host species. Where early-phenotype *D. radicum* predominate and there are many potential host plants for *D. radicum*, springtime synchronization of *A. bilineata* predation with the availability of *D. radicum* eggs may remain imperfect.

Acknowledgements

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