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RESEARCH ARTICLE

# How do the consumption and development rates of the conifer specialist *Aphidecta obliterata* respond to temperature, and is it better adapted to limited prey than a generalist?

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## Abstract

This study aimed to address the effect of temperature on the consumption and development rates of *Aphidecta obliterata* and to compare the responses of *Ap. obliterata* (specialist) with that of *Adalia bipunctata* (generalist) to prey limitation. Temperature had a significant and positive effect on the time to egg hatch of *Ap. obliterata*. The duration of the larval instars was not affected by prey species at 15°C but was significantly shorter, 12.1 days at 20°C compared with 21.1 days at 15°C. The proportion of time spent in each instar, however, was not affected by temperature or prey species, but the duration of the pupal stage was significantly affected by temperature. The average daily consumption of prey aphids increased with instar and was significantly influenced by temperature. There was a significant difference in the length of the pupal stage between coccinellid species but not that of the larval stage. The duration of the larval period increased under conditions of prey shortage. The pupal period of *Ap. obliterata* was significantly affected by the food regime but not that of *Ad. bipunctata*. There was a significant interaction between species and food supply on the length of the pupal stage and the larval stage and the final fresh weight achieved by the newly emerged adults. Male adults weighed significantly less than the females in all regimes. Larvae of *Ap. obliterata* and *Ad. bipunctata* did not consume any of the alternative prey (Collembola or Psocoptera) provided. There was no significant difference in the consumption of prey between the two coccinellid species. The results suggest that both of these coccinellids are well adapted to low-density-specific prey. There were no obvious differences between the two, which would tend to favour either species in an environment of limited prey.

## Introduction

Coccinellids are important predators of coccid scale insects and aphids (Hodek, 1973; Majerus & Kearns, 1989; Dixon, 2000; Mann, 2002). A wide range of species occur naturally in association with these pests and a number have also been introduced as biological control agents with varying degrees of success (Hodek, 1973). The comparison between successful and failed attempts at classical biological control has led to certain characteristics being named as desirable attributes of a good natural enemy (Dixon, 2000). Among these are dietary specialisation, voracity and developmental rate relatively shorter than that of the prey (Mills, 1982; Dixon, 2000).

Some characteristics of a natural enemy are not fixed but can be influenced by external factors. For example, temperature can alter the consumption rate of prey by a predator (Frazer *et al.*, 1981; Mills, 1981; Sopp & Wratten, 1986; Chiverton, 1988) and the predator's rate of development (Hodek, 1973; Mills, 1981; Butler, 1982;

Alikhan & Yousuf, 1986). The developmental rate can also be modified by the prey species consumed and the amount of prey consumed (Beddington *et al.*, 1976; Michels & Behle, 1991; Dixon, 2000).

The green spruce aphid *Elatobium abietinum* (Walker) (Homoptera: Aphididae) is an important pest of susceptible spruce species grown in maritime climates (Carter & Halldórsson, 1998). It can cause serious damage to Sitka spruce [*Picea sitchensis* (Bong.) Carr.] (Straw *et al.*, 1998*a,b*), which is the predominant commercial tree species in the UK (Carter, 1990; Forestry Commission, 2002).

Samples from a wide geographical area of the UK, taken from Norway spruce (*Picea abies* L.), which is thought to be the original host of this aphid (Bejer-Peterson, 1962) and the more susceptible Sitka spruce, contained high numbers of *E. abietinum* (Timms, 2004). Associated with this pest were various natural enemy species, the most abundant group found were coccinellids and of the species present, the larch ladybird *Aphidecta obliterata* was by far the most common, with over 95% of all individuals present. This coccinellid was also overwhelmingly predominant at Radnor Forest, Wales; a commercial site mainly consisting of *P. sitchensis* (Timms, 2004).

With the predicted increase in the pest status of *E. abietinum* as a consequence of climate change (Straw, 1995; Zhou *et al.*, 1996), it is important to examine the consumption and developmental rates of individual *Ap. obliterata* and to investigate their response to an increase in temperature. It has been suggested that under hotter summer regimes and with elevated levels of $CO_2$ coccinellids may be more effective aphid predators (Awmack *et al.*, 1997; Skirvin *et al.*, 1997), but in general, our understanding of the likely impact of climate change on predator–prey interactions is limited and requires much further research.

This study aimed to investigate the potential of *Ap. obliterata* to control an aphid pest at a higher temperature to make predictions concerning the future relationship between this predator and *E. abietinum*. The temperatures compared were 15 and 20°C, a range that is large enough to produce detectable changes in the life histories of the insects involved. It is also representative of the range in which temperatures may increase in UK forestry in the summer months (Timms, 2004), although the actual differences are generally predicted to be smaller (Broadmeadow, 2002).

The effects of limiting prey supply on the development and survival of the conifer specialist *Ap. obliterata* were also studied, comparing it with a generalist coccinellid, the two-spot ladybird, *Adalia bipunctata* (L.). Although not always commonly associated with *E. abietinum*, *Ad. bipunctata* can be an important predator and was found to be the most abundant natural enemy on *P. abies* at Silwood Park, Ascot (Leather & Owuor, 1996; Day *et al.*, 2006). In addition, the potential for Collembola and Psocoptera to be utilised as alternative prey in times of scarcity was examined as these soft-bodied hexapoda were found in virtually all the canopy samples taken by thermal fogging at Radnor Forest and various other UK locations (Timms, 2004).

## Methods and materials

### The influence of temperature and prey species

The egg hatch times and larval consumption and developmental rates of *Ap. obliterata* were measured at two temperatures, using *Rhopalosiphum padi* (L.) (Homoptera: Aphididae) as an alternative prey species because of a lack of *E. abietinum* at the time when sufficient predator larvae were available. This aphid has been shown to be an acceptable alternative, in that it does not alter life-history parameters of *Ap. obliterata* relative to a pure diet of *E. abietinum* (Timms, 2004) or of arboreal specialists compared with generalist coccinellids (Jones, 1998). The consumption and developmental rates were also measured at the lower of the two temperatures with the natural prey species, *E. abietinum*. This allowed the additional comparison to be made between reproductive rates of *Ap. obliterata* on the two different prey species. All coccinellids were checked three to six times per day, including weekends.

The protocol used was as follows: 12 freshly laid (±1 h) *Ap. obliterata* eggs were collected from cultures maintained at 15°C, 16:8 h light : dark and ambient humidity and were reared under the same conditions. The eggs were checked at regular intervals throughout the day (three to six times per day), and time to hatching was recorded and the emerging larvae were transferred singly to 9-cm Petri dishes once they had left the egg sac. All larvae were then fed with an excess of third instar *E. abietinum* or *R. padi* as required (once or twice per day) and dead aphids removed. Although a Petri dish is an unnatural habitat, it provides a convenient and identical test arena for both species and is commonly used in studies of this nature (Majerus & Kearns, 1989; Hemptinne *et al.*, 1992; Evans, 2000).

The number of aphids eaten per day and per *Ap. obliterata* instar were recorded, as was the approximate duration of each instar. The duration of the pupal stage was also recorded, and the newly emerged adults were sexed and weighed. The same protocol was followed for an additional 12 *Ap. obliterata*, which were provided with similar-sized late-second and early-third instar *R. padi* instead of *E. abietinum*. This was repeated with a further 12 larvae at 20°C, 16:8 h light : dark and ambient humidity, these eggs having been collected from cultures maintained under the 20°C regime.

All individuals of the same instar were always provided with the same density of prey, regardless of treatment. The number of aphids provided were also well in excess of the daily aphid consumption. This was performed to limit any influence of prey density. The data were analysed using the statistical package, S-Plus (Version 6.0.2; Insightful Corp., Seattle, WA, USA).

### The influence of prey availability

Coccinellid eggs which had been laid at 15°C, 16:8 h light : dark and ambient humidity were collected. On leaving the egg sac, 20 *Ap. obliterata* and 20 *Ad. bipunctata* larvae were transferred singly to 9-cm Petri dishes, the sides of which were coated with Fluon®. Ten larvae of each species were provided with 3 aphids per day and the other 10 with 6 aphids per day, until pupation. The aphids supplied were all similar-sized late-second and early-third instar *R. padi*. Any dead or uneaten aphids were removed each morning and fresh ones supplied. All coccinellids were checked three to six times per day, including weekends. The length of the larval and pupal stages was recorded and newly emerged adults were weighed and sexed. The developmental data were analysed by ANOVA and *t*-tests and the weight data using the Student's *t*-test.

### Alternative prey

Psocoptera and Collembola were obtained by beating *P. sitchensis* branches collected from Radnor Forest (52°17′N, 3°10′W) and also from 3- to 4-year-old potted *P. sitchensis* maintained outdoors at Silwood Park, Ascot (51°23′N, 0°46′W). Psocoptera, Collembola and *E. abietinum* were placed in groups of five into 4.5-cm Petri dishes. A fourth instar *Ap. obliterata* larvae, which had been starved for 6 h, was then added to each of the dishes and was allowed to forage for a period of 24 h before removal. Twelve replicates of each treatment were carried out. The number of prey items consumed in each dish was recorded. This was repeated with fourth-instar *Ad. bipunctata* larvae. The data were analysed using a generalised linear model with binomial errors.

## Results

### The influence of temperature and prey species

#### *Egg hatch time*

Temperature had a significant effect on the time to egg hatch ($t = 65.1$, d.f. = 62, $P < 0.001$). The average time taken for the eggs of *Ap. obliterata* to hatch, after being laid, was 9.6 ± 0.07 days at 15°C. At 20°C, the time was reduced to 4.6 ± 0.03 days.

#### *Larval duration*

The durations of the larval instars were not affected by prey species at 15°C; however, those larvae fed *R. padi* had significantly shorter instar lengths at 20°C compared with those at 15°C (Fig. 1). Comparisons between individuals maintained on a diet of *R. padi*, at 15°C and 20°C, revealed that this was the case for all the individual instars ($t = 9.9$, d.f. = 22, $P < 0.001$ for the first instars; $t = 10.9$, d.f. = 22, $P < 0.001$ for the second instars; $t = 13.6$, d.f. = 22, $P < 0.001$ for the third instars and $t = 15.2$, d.f. = 22, $P < 0.001$ for the fourth instars). The overall duration of the larval stage increased from 12.1 days at 20°C to 21.1 days at 15°C.

The proportion of time spent in each instar, however, was not affected by temperature or prey species. The average percentages of the time spent as a first instar ranged from 28.4% to 29.6%, as second from 16.9% to 17.2%, as third from 17.8% to 19.6% and as fourth from 34.1% to 35.7%.

#### *Pupal duration*

The duration of the pupal stage was 15.0 ± 0.16 days for larvae fed with *E. abietinum* at 15°C, 15.3 ± 0.14 days for larvae fed with *R. padi* at 15°C and 7.5 ± 0.13 days for larvae fed with *R. padi* at 20°C. These durations were heavily

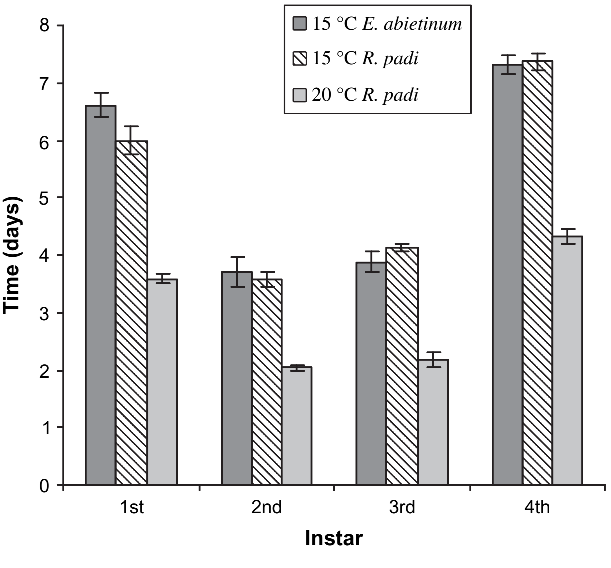

**Figure 1** The influence of temperature and prey species on the duration of each larval instar of *Aphidecta obliterata* (±1 SE).

dependent on temperature ($t = 40.5$, d.f. = 22, $P < 0.001$) but not food species at 15°C ($t = 1.54$, d.f. = 22, $P = 0.14$).

### *Prey consumption*

The average daily consumption of aphids increased with instar and was significantly influenced by temperature ($t = 9.4$, d.f. = 88, $P < 0.001$) but not the prey species provided ($t = 0.43$, d.f. = 88, $P = 0.67$) (Fig. 2).

The total number of aphids consumed over the entire larval lifespan ranged from 298.2 for larvae fed with *R. padi* at 15°C to 291.7 for larvae fed with *E. abietinum* at 15°C and to 239.0 for larvae fed with *R. padi* at 20°C. There was no significant difference between the total number of *E. abietinum* and *R. padi* aphids consumed at 15°C ($t = 0.58$, d.f. = 22, $P = 0.57$). Comparison of the two *R. padi* treatments, however, revealed that the temperature at which the larvae were maintained did significantly affect the overall consumption ($t = 6.08$, d.f. = 22, $P < 0.001$). Larvae consumed significantly fewer aphids in total at higher temperatures but developed significantly faster.

There was no significant effect of treatment on the percentage of the total larval aphid consumption. In this study, first instars consumed between 6.1% and 6.9%, second instars between 8.4% and 9.7%, third instars between 13.7% and 17.5% and fourth instars between 67.1% and 69.6%.

### *Adult weight*

Male adults weighed significantly less than the females in all regimes (Table 1) ($F = 152$, d.f. = 1,29, $P < 0.001$). There was, however, no significant difference between the weights achieved by the newly emerged adults as a consequence of prey species ($F = 0.005$, d.f. = 1,29, $P = 0.94$) or temperature ($F = 0.02$, d.f. = 1,29, $P = 0.90$).

**Table 1** The effect of larval diet and temperature on the weight achieved by newly emerged adult *Aphidecta obliterata*

| | | Weight (mg) (*n* = 6) | |
|---|---|---|---|
| Rearing Temperature | Prey Species | Male | Female |
| 15°C | *Elatobium abietinum* | 7.0 ± 0.1 | 8.8 ± 0.2 |
| 15°C | *Rhopalosiphum padi* | 6.7 ± 0.2 | 9.1 ± 0.2 |
| 20°C | *Rhopalosiphum padi* | 7.3 ± 0.2 | 8.6 ± 0.2 |

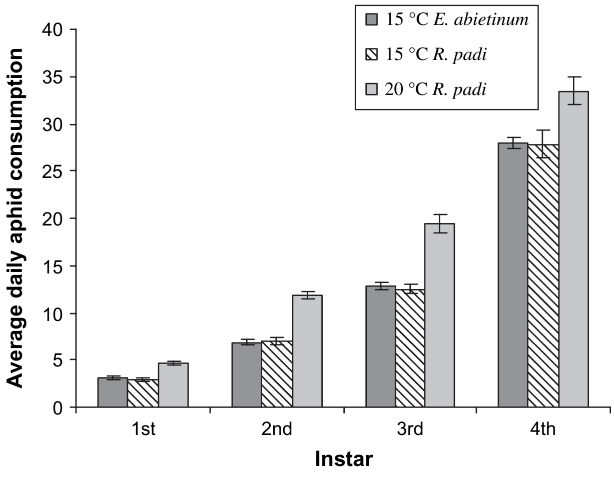

**Figure 2** The influence of temperature and prey species on the daily consumption of aphids by *Aphidecta obliterata* larvae (±1 SE).

## The influence of prey availability

There was a significant difference in the length of the pupal stage between coccinellid species ($F = 10.20$, d.f. = 1,24, $P < 0.0001$) but not the larval stage ($F = 0.23$, d.f. = 1,24, $P = 0.64$). The number of aphids supplied daily was significant in determining the larval period for both species ($F = 37.65$, d.f. = 1,24, $P < 0.0001$), with a decrease in prey availability increasing the duration of the larval stage (Table 2). The pupal period of *Ap. obliterata* was significantly affected by the food regime ($t = 4.56$, d.f. = 22, $P < 0.0001$) but that of *Ad. bipunctata* was not ($t = 1.34$, d.f. = 12, $P = 0.20$). There was a significant interaction between species and food supply on the length of the pupal stage ($F = 10.87$, d.f. = 1,24, $P = 0.003$) and the larval stage ($t = 5.57$, d.f. = 1, $P < 0.0001$). The final fresh weight achieved by the newly emerged adults was determined by food supply ($t = 7.24$, d.f. = 1, $P < 0.0001$) and an interaction between food supply and species ($t = 3.26$, d.f. = 1, $P = 0.004$).

Mortality rates were unaffected by species ($\chi^2 = 0.84$, d.f. = 1, $P > 0.05$) but were significantly influenced by the number of aphids supplied per day ($\chi^2 = 40.33$, d.f. = 1, $P \leq 0.01$).

## Alternative prey

The fourth instar larvae of *Ap. obliterata* did not consume any of the Collembola or Psocoptera provided but did consume *E. abietinum*. The same result was achieved for the fourth instar *Ad. bipunctata*. The average number of *E. abietinum* consumed over 24 h by *Ap. obliterata* was 4.5 ± 0.2 and by *Ad. bipunctata* was 4.2 ± 0.3. There was no significant difference in the consumption of prey between the two coccinellid species ($F = 3.16$, d.f. = 2, 66, $P = 0.08$). The Collembola and Psocoptera treatments could be combined without significant loss in explanatory power of the model ($F < 0.0001$, d.f. = 1,66, $P = 1.0$ ns),

**Table 2** Life-history parameters of *Aphidecta obliterata* and *Adalia bipunctata* provided with different daily aphid densities (*n* at start = 10 per treatment)

| Species | Food Regime (aphids/day) | Larval Duration (days ± 1 SE) | Pupal Duration (days ± 1 SE) | Emerged Adult Weight (mg ± 1 SE) | Number Reaching Adult Status | Overall Mortality (%) |
|---|---|---|---|---|---|---|
| *Ad. bipunctata* | 3 | 35.8 ± 1.2 | 20.4 ± 0.8 | 6.0 ± 0.2 ♂ | 2 | 50 |
| | | | | 6.7 ± 0.4 ♀ | 3 | |
| | 6 | 27.4 ± 0.4 | 19.8 ± 0.2 | 9.0 ± 0.3 ♂ | 4 | 20 |
| | | | | 9.8 ± 0.1 ♀ | 4 | |
| *Ap. obliterata* | 3 | 31.6 ± 1.0 | 27.3 ± 2.2 | 4.4 ± 0.04 ♂ | 2 | 60 |
| | | | | 4.6 ± 0.1 ♀ | 2 | |
| | 6 | 28.0 ± 1.1 | 22.2 ± 0.7 | 4.9 ± 0.3 ♂ | 4 | 20 |
| | | | | 6.2 ± 0.2 ♀ | 4 | |
| | Excess | 21.1 ± 0.3 | 15.3 ± 0.1 | 6.7 ± 0.2 ♂ | 4 | 10 |
| | | | | 9.1 ± 0.2 ♀ | 5 | |

while the consumption of *E. abietinum* was significantly higher ($F = 893$, d.f. = 1,66, $P < 0.001$).

## Discussion

### The influence of temperature and prey species

The species on which a coccinellid feeds has been shown to affect its rate of consumption and development (Michels & Behle, 1991; Dixon, 2000) and adult weight (Parry, 1992; Dixon, 2000). This was, however, not the case when comparing *R. padi* and *E. abietinum* as food sources for *Ap. obliterata*. This suggests that there was no difference in the quality of these two species as prey for this coccinellid. The two alternative non-aphid prey species provided (Collembola and Psocoptera) were, however, not suitable and did not provide a food source for either of the coccinellid species tested.

Temperature was an important factor in determining the daily consumption of prey and the developmental rate of the egg, larval and pupal stages of *Ap. obliterata*. This concurs with other studies of coccinellids (Hodek, 1973; Mills, 1981; Alikhan & Yousuf, 1986; Dixon, 2000). Coccinellids, like other insects, are poikilotherms, and as such, their developmental rates and activity levels are determined by external temperature (Trudgill *et al.*, 2005). Below a threshold temperature, a coccinellid will be inactive and will not consume prey (Frazer *et al.*, 1981). At temperatures above the threshold, the developmental and consumption rates of predatory coccinellids initially increase with temperature, rising to a maximum at the optimum temperature for the species, then falling as this temperature is exceeded (Hodek, 1973; Mills, 1981; Alikhan & Yousuf, 1986; Dixon, 2000). The results obtained in this study suggest that the optimum temperature for *Ap. obliterata* is above 15°C. It is not possible to determine whether or not the optimum is above or below 20°C because no intermediate or higher temperatures were tested.

Dixon (2000) suggested that the proportion of time spent in each stage of pre-imaginal development of aphidophagous coccinellids (i.e. egg, larva and pupa) will be unaltered by temperature. He summarises data from previous studies reporting on the time spent in each stage by several different species and gives estimates of the percentage of time generally spent in each stage to be 20% for the egg, 57% for the larva and 23% for the pupa. In this study, *Ap. obliterata* was found to spend 18.9–20.1% of the total development time in the egg stage, 45.9–50.0% in the larval stage and 31.0–33.2% in the pupal stage, depending on temperature. Hence, the amount of time spent in the egg stage was similar to that observed for other aphidophagous coccinellids but the larval and pupal stages were relatively shorter and longer, respectively. The different developmental stages of *Ap. obliterata* responded similarly but not identically to a rise in temperature from 15 to 20°C. The duration of the egg stage decreased by 52%, the pupal stage by 51% but the larval stage only exhibited a 43% decrease in duration. This lesser response may be because of limitations on growth rate caused by factors that are not related to temperature. The fact that it is the active feeding stage, which responds less positively to temperature, suggests that it is likely to be because of a factor other than an internal biological/chemical process.

Developmental rate also depends on the rate of food consumption (Beddington *et al.*, 1976; Mills, 1981), and it has been suggested that the increased rates of development exhibited by coccinellids in response to temperature are a direct consequence of their increased consumption rates, which accompany elevated temperatures (Mills, 1981). The average daily consumption rate of the larvae increased by 40% with the temperature rise from 15 to 20°C, but over the same range, the average rate of increase in development was slightly greater. It is therefore possible that the growth rate was limited by food consumption or that aphids are converted into ladybird tissues more efficiently at higher temperatures. The number of prey killed per unit time depends on handling time, prey density and attack rate (Holling, 1959; Dixon, 2000). Measures were taken in the experimental design to avoid prey density being a confounding factor; so the change seen in the consumption rates are likely to be because of altered attack rates and/or handling times.

Handling time is made up of the time spent pursuing, subduing, eating and digesting the prey (Eveleigh, 1981). An increase in temperature can produce an increase in the proportion of time spent pursuing prey by a predator (Chiverton, 1988) and the digestive rate would be expected to increase because it is a physiological process dependent on temperature. The time spent subduing and eating the prey, however, is less likely to respond to temperature because phytophagous prey have also been shown to be more active at higher temperatures (Everson, 1980), and the time spent eating is a function of the mouthparts of the predator. Therefore, the number of prey killed by *Ap. obliterata* at 20°C may be limited by these physical factors, which are unlikely to be favoured by temperature.

Mills (1981) found that the handling time of *Ad. bipunctata* larvae decreased between 32% and 44% depending on instar, in response to an increase in temperature from 15 to 20°C. If *Ap. obliterata* responds similarly, this would partly explain the fact that consumption rates only increased by 40% and the larval development rate by 43%, while the non-feeding stages of the ladybird showed a higher increase in developmental rate (51%) over the same temperature range. The handling time of prey by larvae of the damselfly *Ischnura elegans* (Van der Linden) has been shown to decrease exponentially with temperature up to 16°C, above which, it remains constant (Thompson, 1978). It is therefore possible that between 15 and 20°C, the prey handling time of *Ap. obliterata* larvae is approaching its minimum.

The effect of temperature on the total food consumption by coccinellid larvae during their development is in general, less clear, with both increases and decreases being reported (Hodek, 1973). A rise in predation rates with temperature would tend to have a positive effect on the total number of prey eaten, but accompanying increased developmental rates would have the opposite effect by limiting the number of days of the larval stage. Because the proportion of time spent in each instar and the total aphid consumption during each instar is apparently unaffected by temperature, the total consumption rate will depend on how the two rates increase relative to each other. For example, if the consumption rate of a coccinellid increased more proportionally over the temperature range studied than the developmental rate, an overall increase in the total consumption rate would be expected and vice versa.

The percentages of the total aphid consumption by each larval instar of *Ap. obliterata* were representative of those exhibited by other coccinellids (Hodek, 1973). The duration of the fourth instar was longer than the others and the consumption by this instar accounted for nearly 70% of the total larval prey eaten. The final instar and adult stages are therefore likely to have the most significant impact on prey in the field.

The adult weight achieved has been found to depend on rearing temperature (Dixon, 2000), increasing up to an optimum temperature and then decreasing after this point. The adult weights achieved by individuals in this study were not affected by temperature, although the larvae reared at 20°C ate significantly less overall. This suggests that *Ap. obliterata* functions more efficiently at 20 than 15°C. The lower weights achieved by the adult males is a common characteristic of coccinellids (Hodek, 1973; Majerus & Kearns, 1989; Dixon, 2000).

The results of this study suggest that *Ap. obliterata* would respond favourably to an increase in temperatures over the range 15–20°C, with increased consumption and developmental rates. Although the total number of aphids consumed by larvae at the higher temperature was lower, at this temperature, daily rates were higher and the time spent in non-feeding stages was shorter. Therefore, individuals are likely to spend an increased proportion of the time in feeding stages because adult status will be achieved more quickly. The shortened larval duration would also reduce the exposure of this vulnerable stage to predation. Meteorological data recorded from Radnor Forest in Wales showed that temperatures exceeded 15°C for periods during the summer but were generally lower (Timms, 2004). It is therefore possible that an increase in temperature in the range studied could occur as a consequence of climate change.

It is not possible to determine the overall effect of increased temperatures on the predator–prey relationship between *Ap. obliterata* and *E. abietinum* without detailed studies into the response of the host plant and prey species. This would be a productive area on which to concentrate future research efforts. Various scenarios have been put forward regarding the responses of aphid pests, host plants, natural enemies and interactions between these, to different aspects of climate change (Awmack *et al.*, 1997; Coviella & Trumble, 1999; Whittaker, 2001; Bale *et al.*, 2002; Newman, 2003). Modelling by Skirvin *et al.* (1997) focussed on the effects of temperature on a coccinellid–aphid system. The results suggested that the seven-spot ladybird, *Coccinella septempunctata* (L.), is likely to be a more effective control agent of the cereal aphid, *Sitobion avenae* (F.) in hotter UK summers. It was proposed that this was, at least in part, because of the fact that the coccinellid was expected to be better able to take advantage of the higher temperatures, the reproductive rate of the aphid decreasing more noticeably than that of the predator during daily temperature peaks.

### The influence of food availability

In addition to environmental variables, such as temperature, the developmental rates of predatory coccinellids are also dependent on the quality and availability of prey (Dixon, 2000). Beddington *et al.* (1976) predicted that the rate of larval development of predatory insects would increase with prey density until a plateau was reached. This hypothesis has been supported by several studies using different coccinellid species (Dixon, 1959, 1970; Hodek, 1973). Mills (1981) also demonstrated that a positive relationship exists between consumption rates and growth and developmental rates of *Ad. bipunctata*. The results of the present study concurred, showing that the developmental rates of both *Ap. obliterata* and *Ad. bipunctata* increased significantly as higher prey densities were provided, although the number of different densities used was too small to determine the shape of the relationship.

The length of the pupal stage appears to be less affected by larval food intake (Hodek, 1973). This was true for the pupae of *Ad. bipunctata* in this study but the pupal lifespan of *Ap. obliterata* was significantly decreased at the higher feeding rates, producing a significant food supply : species interaction. This implies that certain stages of the coccinellid life cycle can respond differently to altered food relations, depending on species.

The number of prey consumed by coccinellids in a given period is related to the density of the prey. This gives the functional response, which is typically type II for coccinellids (Carter *et al.*, 1984) as previously exhibited by both species in this study (Timms, 2004). At low densities, higher percentages of prey are therefore likely to be consumed but there is a minimum food requirement, below which larvae are unable to successfully attain adult status (Hodek, 1973). The minimum requirement varies between species (Hodek, 1973) and has been found to be as low as seven aphids per day for *C. septempunctata*. At this level of food supply, only 37.5% of the larvae survived to adulthood and the emerging adults were smaller and less fecund (Sundby, 1966). The survival rates of the two species in this study were slightly higher than this when limited to three aphids per day, suggesting that their minimum food requirement is three aphids per day or less, when provided with third instar *R. padi*. Time did not allow for investigation of the fecundity of the emerged adults but their relatively lower mortality rates imply that at least some individuals would reach sexual maturity and produce eggs.

When prey is supplied above the threshold amount, the larval stage can be completed but mortality rates may still be high and adult weights lower (Hodek, 1973). As the prey availability increases, so does survivorship until a maximum is reached (Dixon, 1959, 1970, 2000). Any further increase in food availability and consumption then serves to increase the adult size up to the maximum for the species (Dixon, 2000). An increase from three to six aphids more than doubled the survival rates of the two species used in this study and increased the average adult weight by up to 50%. The mortality rate of *Ap. obliterata* was further improved when prey was supplied to excess and the adult weight achieved rose by an additional 37% for males and 47% for females. The weights observed in the experiment spanned the range seen in the field (Parry, 1980; Zhou *et al.*, 1995), thus suggesting that the prey densities supplied reflected those experienced in the field.

As well as providing useful information concerning the effects of food supply on the life stages of two predators of *E. abietinum*, this experiment was designed to elucidate differences between the two which may affect their ability as control agents of this pest. *E. abietinum* is present in relatively low densities for much of the year, following the May/June population crash (Hussey, 1952; Bejer-Peterson, 1962; Day, 1984; Timms, 2004). During this time, many predators are still likely to be completing their larval stage (Timms, 2004). It is therefore vital that important natural enemies survive and continue to develop during periods of prey scarcity. Both *Ap. obliterata* and *Ad. bipunctata* were capable of completing their entire larval lifespan, producing viable pupae on as few as three aphids per day. The larval duration of *Ad. bipunctata* appeared to be more affected by prey scarcity than *Ap. obliterata* but its pupal duration was not affected, unlike *Ap. obliterata*.

The results of this study therefore suggest that both of these coccinellids are well adapted to low-density prey and do not appear to utilise other available prey groups. There were no obvious differences between the two, which would tend to favour either species in an environment of limited prey. The reason for the overwhelming predominance of *Ap. obliterata* and complete absence of *Ad. bipunctata* at Radnor Forest, Wales (Timms, 2004), must therefore be as a consequence of some other characteristic of the site or of the coccinellids.

This study has produced results that contribute to our understanding of how the pre-imaginal stages of two coccinellid predators of *E. abietinum* develop in times of prey scarcity. Although *E. abietinum* is expected to become a more serious pest in the future, with increased population peaks accompanying climate change (Straw, 1995; Zhou *et al.*, 1996), our comprehension of the consequences of climate change are limited because of the complex of factors involved. Modelling by Skirvin *et al.* (1997) predicted that within a temperature regime (cold, moderate and hot summers based on UK temperatures April to August, 1966–1993) an increase in temperature actually decreases aphid populations. It was proposed that this was because of a decrease in fecundity during the daily temperature maxima of hotter summers. Increased spring temperatures will also result in earlier development of aphid populations and if predators are not able to maintain current levels of synchrony, they will rely more heavily on the limited prey available following the population crash. Again, in order to address this possibility, further investigation into the response of *E. abietinum* to temperature increases are necessary.

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