INTRINSIC RATE OF INCREASE AND TEMPERATURE COEFFICIENTS OF THE APHID PARASITE *EPHEDRUS CALIFORNICUS* BAKER (HYMENOPTERA: APHIDIIDAE)

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Abstract

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The demographic statistics and the temperature requirements for development of *Ephedrus californicus* Baker were determined under constant laboratory conditions. At 23°C, females provided each day with forty 2nd-instar pea aphids, *Acyrthosiphon pisum* (Harris), lived for 13.4 days and laid 1193 eggs on average; the highest fecundity of any female was 1762 eggs. For an assumed population sex ratio of 1:1 males to females, the intrinsic rate of increase, r, was 0.371 females·female^{-1}·day^{-1} when all eggs laid were counted. The lower temperature threshold for development, t, was estimated as 6.83°C, and the time-to-adult, K, as 228.9 degree-days. The potential use of *E. californicus* in the biological control of the lupine aphid, *Macrosiphum albifrons* Essig, in England is considered.

Résumé

On a déterminé les statistiques démographiques et les besoins thermiques pour le développement chez *Ephedrus californicus* Baker, maintenu sous des conditions constantes de laboratoire. A 23°C, des femelles ayant eu journalièrement accès à 40 larves de stade 2 du puceron du pois, *Acyrthosiphon pisum*, ont survécu pendant 13,4 jours et ont pondu 1193 oeufs, en moyenne; la fécondité maximale observée pour une femelle est de 1762 oeufs. Si on suppose que le rapport mâles:femelles est 1:1, le taux intrinsèque d'accroissement naturel est de 0,371 femelles femelle^{-1} jour $^{-1}$ lorsque tous les oeufs pondus sont comptés. On a estimé le seuil thermique du développement t, à 6,83°C, et la constante thermique du développement de l'adulte, K, à 228,9 degrés-jours. On discute de la possibilité d'utiliser *E. californicus* pour la lutte biologique contre le puceron *Macrosiphum albifrons* Essig en Angleterre.

Introduction

The genus *Ephedrus* Haliday (Hymenoptera: Aphidiidae) includes several economically important parasites of aphids. For example, *E. cerasicola* Starý is used in Norway to control the green peach aphid, *Myzus persicae* (Sulzer), in glasshouses (Hofsvang and Hagvar 1978, 1979). And *E. plagiator* (Nees) was released in the United States for the biological control of the greenbug, *Schizaphis graminum* (Rondani) (Dureseau *et al.* 1972; Jackson *et al.* 1974).

During 1983–1984, we studied the lupine aphid, *Macrosiphum albifrons* Essig, and its parasites in southern British Columbia. Our objective was to obtain background information for a possible biological control program against the lupine aphid in England, where the aphid has caused extensive damage to lupines grown in gardens and on reclamation sites after its recent introduction (Carter *et al.* 1984). Here we report on the fecundity, longevity, and developmental rate of *E. californicus* Baker under laboratory conditions. This parasite was consistently reared from, but not abundant on, the lupine aphid in British Columbia (Cohen and Mackauer 1986). Other hosts of *E. californicus* include various *Dactynotus* species and the rose aphid, *Macrosiphum rosae* (L.) (Mackauer and Starý 1967). The parasite also attacks the pea aphid, *Acyrthosiphon pisum* (Harris), but has been rarely collected from this host in British Columbia (S. Kambhampati, pers. commun.).

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Materials and Methods

A laboratory colony of *E. californicus* was established from specimens that had emerged from mummified lupine aphids collected in the vicinity of Vancouver, BC, in 1983. Because lupine aphids are difficult to maintain year-round in the laboratory, the parasites were transferred to pea aphids, which they accepted readily as hosts. Both the parasites and the aphids, which were reared on broad-bean plants, *Vicia faba* L. cv. "Broad Windsor", were maintained at an average temperature of 23–25°C in the insectary.

Life-table statistics. We estimated the fecundity and longevity of *E. californicus* for a cohort of 12 females which were 0–10 h old at the beginning of the experiment and of approximately equal size. The females were fed honey and caged with males for 4 h, after which they were placed individually in 15.5-cm-diameter plastic rearing cages (Mackauer and Bisdee 1965). Each cage contained forty 2nd-instar pea aphids feeding on a broad-bean shoot; the cages were kept in a growth chamber at 23 ± 1°C, 65 ± 10% RH, and a 16L:8D diel cycle.

Each female was transferred to a new cage with 40 unparasitized 2nd-instar pea aphids every 24 h, until dead. The aphids were reared in their cages for 4 days and then preserved in 70% ethanol for later dissection. We dissected a sample of 20 preserved aphids from each 24-h period and doubled the number of parasite eggs and larvae found. These were totalled over all days (i.e. cages) alive to estimate a female's lifetime fecundity. We estimated the intrinsic rate of increase, r, by an iterative solution of the Lotka-Euler equation

$$\sum_x l_x m_x \, e^{-rx} = 1$$

where l_x and m_x are, respectively, the age-specific survival and fecundity rates for the cohort on day x (Andrewartha and Birch 1954). For the calculation, we assumed that all births and deaths during day x had taken place at the pivotal time. We assumed further that no mortality occurred between oviposition and adult eclosion from mummified hosts; this time was estimated as 14 days from regression equations given below. For comparison with previous life-table studies of aphidiids, we calculated r for different assumed population sex ratios by multiplying all m_x values with a constant p, which is the proportion of females among all offspring.

Temperature coefficients. We used quantal response analysis (Finney 1971) to estimate the time-to-adult of *E. californicus* at each of four constant temperatures, 17.6, 20.9, 24.0, and 26.4 ± 1°C. We exposed 72 ± 4-h-old (at 21.1°C) aphids to a single attack by a mated parasite female, held individually in a clear 00-gelatin capsule. For each temperature experiment, five groups, comprising 22–45 aphids which had been parasitized during a 30-min interval, were set up. Aphids were reared to mummification on bean shoots in 8.5-cm-diameter plastic cages (Mackauer and Bisdee 1965), then transferred to covered wax paper cups. At predetermined times, spaced approximately evenly around the expected median eclosion time ET_{50}, one randomly selected group was removed from the constant-temperature chamber, and the numbers of emerged males and females were counted. The proportions of eclosed adults among those in each group, transformed to their probit values, were plotted against the $\log_{10}$ values of the emergence times. We estimated the ET_{50} values from the regression, fitted by an iterative maximum likelihood procedure to the empirical data in accordance with procedures given by Finney (1971).

For average temperatures, the relationship between the temperature and the rate of development can be described by a linear regression equation of the form $\hat{y} = a + bT$, where $y = 1/ET_{50}$ is the rate of development, T is the temperature, and a and b are constants fitted by least-squares regression (Campbell *et al.* 1974). Letting $y = 0$, we can obtain

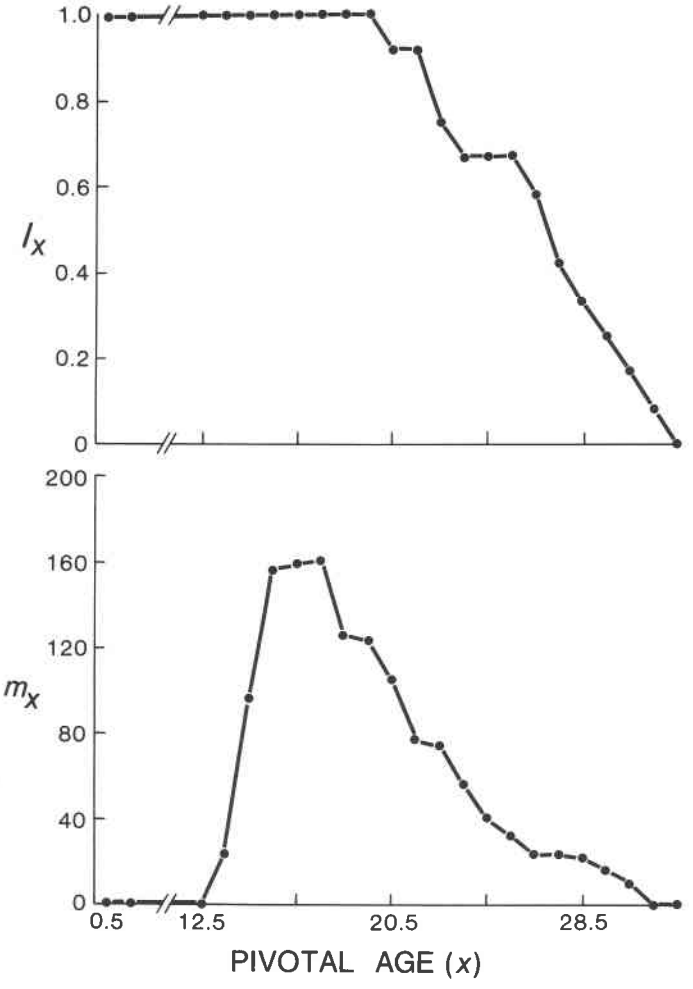

FIG. 1. Age-specific survival (l_x) and fecundity rate (m_x) of *Ephedrus californicus* reared on 2nd-instar pea aphids (40 aphids per day) at 23°C in the laboratory. (Mortality during larval and pupal development was assumed to be zero.)

from the equation the lower threshold temperature for development, t, as well as the time-to-adult, K, in degree-days above t, which is in fact the reciprocal of the regression coefficient b.

Data analysis. For the statistical tests, we followed procedures described by Sokal and Rohlf (1981), except where otherwise indicated.

Results

At 23°C, adult females of *E. californicus* survived an average of 13.4 ± 3.9 (SD) days in the laboratory. All but one female started to lay eggs on the 1st day after eclosion, with a mean of 23.5 ± 17.5 eggs per female. The age-specific fecundity rate reached a maximum of about 160 eggs per day on days 3–5 and declined gradually thereafter (Fig. 1).

During their lifetime, females laid an average of 1193.0 ± 306.3 eggs, of which 99.5% (1187.2 ± 303.7 eggs) were laid during the period of intensive egg laying, PIEL; this period

Table 1. Performance characteristics of *Ephedrus californicus* ($n = 12$) provided with forty 2nd-instar pea aphids per day. All data refer to period of intensive egg laying, PIEL

Variate	$\bar{x} \pm$ SD
Length of PIEL (days)	12.1 ± 3.7
No. of eggs laid·female^{-1}	1187.2 ± 303.7
No. of eggs laid·female^{-1}·days of PIEL^{-1}	101.6 ± 20.1
Prop. of eggs laid during first 4 days	0.391 ± 0.144
No. of aphids parasitized	399.8 ± 120.2
No. of aphids parasitized·egg laid^{-1}	0.336 ± 0.053
No. of aphids escaping parasitization	83.5 ± 44.1
Overall proportion of aphids escaping	0.170 ± 0.063
No. of eggs laid·host attacked^{-1}	3.048 ± 0.492

can be defined (Mackauer 1983) as the period from day 1 of adult life to the day when reproductive activity essentially ceased and less than half of the available hosts were parasitized. The number of eggs laid during PIEL was correlated with the length of PIEL ($r = 0.750$; $t_s = 2.952$ by Hotelling's modified z-transformation; $P < 0.01$). Except during the 1st and the last days in each parasite's life, when few eggs were laid, many aphids were attacked repeatedly (Table 1). The highest number of parasite eggs and larvae found in a single aphid was 19, with an average of 3.05 ± 0.49 eggs during PIEL.

Estimates of the intrinsic rate of increase, r, and of other life-table statistics are given in Table 2, based on the total numbers of eggs laid. At a sex ratio of 0.66, which is the ratio observed in the field (Cohen 1985), $r = 0.389$ when possible egg losses due to superparasitism were ignored.

The time from oviposition to adult eclosion was inversely correlated with the temperature. As male and female *E. californicus* did not differ in their development times ($P > 0.05$; by median test), we calculated the rate of development at each temperature from the pooled data (Table 3). At 26.4°C, significantly fewer parasites emerged than at any of

Table 2. Effect of population sex ratio on reproductive rate and intrinsic rate of increase of *Ephedrus californicus* at 23 ± 1°C, based on total number of eggs laid

Sex ratio*	GRR†	R_0†	r‡
0.50	664.6	596.5	0.371
0.66	877.4	801.4	0.389
1.00	1329.3	1193.1	0.414

*Assumed sex ratio, p = proportion of females among all offspring produced.
†Gross (*GRR*) and net reproductive rate (R_0), in females·female^{-1}·generation^{-1}.
‡Intrinsic rate of increase, r, in females·female^{-1}·day^{-1}.

Table 3. Percentage adult eclosion, median developmental time, and statistics of probit regression line* of *Ephedrus californicus* reared at four constant temperatures

Temp.	No. mummies	Percentage eclosion†	ET_{50}‡	95% CL of ET_{50}	Slope ± SE	y-intercept
17.6	198	92.4a	21.37	21.25–21.48	84.76 ± 15.52	−224.71
20.9	218	95.4a	16.13	16.10–16.22	132.22 ± 16.53	−337.58
24.0	208	94.2a	13.38	13.30–13.44	99.22 ± 15.09	−243.71
26.4	200	82.5b	12.34	12.15–12.51	35.56 ± 6.10	− 83.93

*Regression of probit emergence on $\log_{10}$ time after oviposition.
†Percentage values sharing the same letter form homogenous subsets, $P \leq 0.05$ (Sokal and Rohlf 1981, p. 728).
‡Median emergence time, in days.

the lower temperatures, a fact suggesting that the upper deleterious temperature range was approached; these data were therefore not included in our calculations. The relationship between the rate of development, y, and the temperature, T in °C, can be described by a linear regression equation, $\hat{y} = 0.00437\ T - 0.02984$ ($r^2 = 0.999$; $P = 0.009$). By extrapolation, the lower temperature threshold for development, t, is 6.83°C (SE = 0.38°C), and the time-to-adult, K, is 228.9 degree-days.

Discussion

Estimates of lifetime fecundity of aphidiid species vary from much less than 100 to about 800 eggs (Hagen and van den Bosch 1968), with *Ephedrus* species generally being placed among the less fecund species. For example, from the number of mummies produced, the average fecundity of *E. cerasicola* was estimated as 51 offspring (Hofsvang and Hagvar 1975), that of *E. incompletus* Provancher as 53.2 offspring (Withington 1909), and that of *E. plagiator* (Nees) as 255 offspring (Jackson *et al.* 1974). Sorokina (1970) found between 340 and 370 eggs in the ovaries of *E. persicae* Froggatt, whereas Starý (1962) reported for the same species about 70 developed and "a big quantity of undeveloped eggs ... in each ovary". Our data on *E. californicus* suggest that the potential fecundity of these parasites probably has been underestimated because of unsuitable experimental methods. Mummy counts do not disclose cases of superparasitism, and dissection of ovaries is appropriate only for proovigenic species, i.e. species in which oogenesis is largely complete before oviposition begins (Flanders 1950). In synovigenic species such as Aphidiidae (Force and Messenger 1964; Liu and Carver 1985; Shirota *et al.* 1983), oogenesis is a continuous process, and therefore dissection is not a reliable method for the estimation of lifetime fecundity.

Although we reared *E. californicus* on the pea aphid, which is less often attacked than the lupine aphid in nature, both species were equally acceptable and suitable as hosts in the laboratory (Cohen 1985). Thus, any differences between these aphids presumably had no effect on parasite fecundity or development time.

Ephedrus californicus shares several characteristics with other aphidiid species that have been rated as effective natural enemies (Clausen 1978). Its intrinsic rate of increase, r, which can be used as an index of its fitness, is comparable to that of *A. smithi* Sharma and Subba Rao (Mackauer 1983) and *Trioxys complanatus* Quilis (Force and Messenger 1964); but the rate is considerably higher than that of the lupine aphid, which was estimated by Frazer and Gill (1981) as 0.278 at 24.2°C. The age-specific fecundity (m_x) curve of *E. californicus* is skewed to the right (Fig. 1). This pattern indicates that females in older age classes (> 5–6 days after eclosion) contributed very little to the cohort's growth rate (Fig. 2). As a result, longevity could be much shorter in the field than in the laboratory without causing a corresponding reduction in the ultimate population growth rate, r.

The high level of superparasitism observed in our experiments was a consequence of the limited host supply, which was kept constant at 40 aphids per day regardless of variations in the age-specific fecundity rate. As *E. californicus* females can discriminate between unparasitized and parasitized hosts (Chow and Mackauer 1986), oviposition constraint could have affected the number of eggs laid and thus caused the fecundity to be underestimated. Any such bias was probably minor. In a detailed study of the relationship between fecundity and host density, Mackauer (1983) showed that, in *A. smithi*, lifetime fecundity was not significantly reduced except in parasites provided with 20 or fewer pea aphids per day.

However, *E. californicus* differs in two important aspects from *A. smithi* and other effective biological control agents: its host range is relatively broad, and its lower temperature threshold for development is considerably higher than that of the lupine aphid and of several other aphid parasites found in the Vancouver area (Table 4). A high developmental threshold in parasites may be advantageous as their spring emergence will be

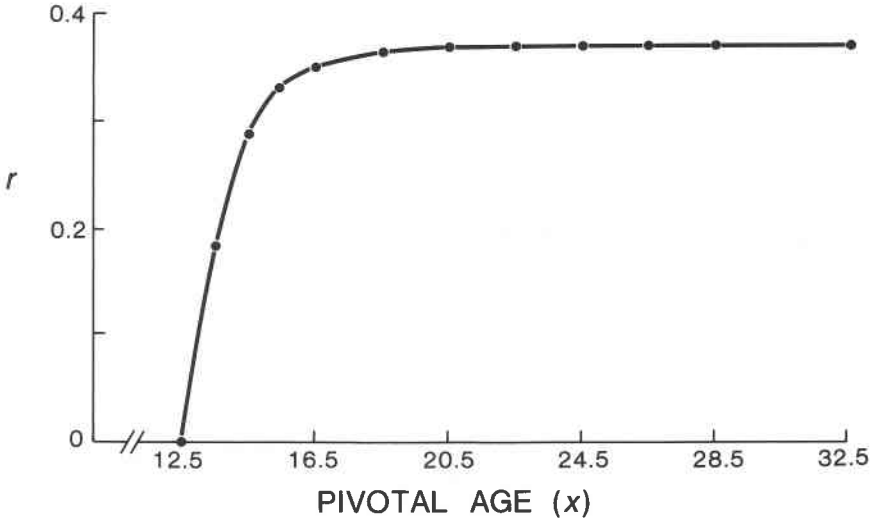

FIG. 2. Cumulative contribution to the intrinsic rate of increase (r) of *Ephedrus californicus* by females in successive age classes. (Sex ratio, $p = 0.5$; m_x values based on total no. eggs laid.)

Table 4. Lower developmental threshold, t(°C), of some aphids and their parasites in the Vancouver area

Aphid	$t \pm$ SE	Parasite	$t \pm$ SE
Acyrthosiphon pisum	4.0 ± 0.28*	*Aphidius ervi*	4.2 ± 0.38*
Brevicoryne brassicae	4.7 ± 0.80*	*Diaeretiella rapae*	4.9 ± 0.94*
Macrosiphum albifrons	4.0 ± 0.59†	*Ephedrus californicus*	6.8 ± 0.38
Masonaphis maxima	3.9 ± 0.47*	*Aphidius rubifolii*	5.3 ± 0.41*

*Campbell *et al.* (1974).
†Frazer and Gill (1981).

delayed until hosts are available. But this characteristic makes *E. californicus* a poor biological control agent because early season synchrony, and impact on the first aphid generation, is important in preventing pest outbreaks (Campbell *et al.* 1974; Hagen and van den Bosch 1968).

Polyphagous natural enemies are, in general, not synchronized with any particular host or prey. Various authors (e.g. Doutt and DeBach 1964; Huffaker *et al.* 1971; Murdoch *et al.* 1985) have suggested that polyphagy by itself is not a sufficient reason for rejecting a natural enemy as a possible agent for biological control. They noted that, in contrast with specialized parasites and predators, polyphagous natural enemies are not solely dependent on one host or prey species for survival and reproduction. Yet dispersal to other aphids, together with its relatively late appearance in summer (Cohen and Mackauer 1986), may be the chief reasons why *E. californicus* has little impact on the lupine aphid in British Columbia. Although our findings, and their interpretation on the basis of ecological theory, must be extrapolated with caution to a different situation, they suggest that *E. californicus* may not be a good candidate for the biological control of this pest in England. This hypothesis can be tested by an actual release and performance study under field conditions.

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