

**Reproduction of *Aphelinus albipodus* (Hymenoptera: Aphelinidae)
on Russian wheat aphid (Hemiptera: Aphididae) hosts**

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Abstract. Reproduction in *Aphelinus albipodus* (Hayat & Fatima) from China on *Diuraphis noxia* (Mordvilko) hosts was studied in the laboratory. Studies were conducted at three constant temperatures, 10.0, 21.1, and 26.7°C ($\pm 1.0^\circ\text{C}$), 14 L : 10 D photoperiod, and 50–70% R.H. The longevity of both males and females was greatest at 10.0°C (26.0 and 41.5 d, respectively); differences in longevity were not significant ($p > 0.05$) between 21.1 and 26.7°C in both sexes (males 13.1 vs. 10.0 d, females 20.9 vs. 16.4 d, respectively). Fecundity was greater at 26.7 (294.7 \pm 27.6 mummies) and 21.1°C (214.8 \pm 33.5 mummies) than at 10.0°C (56.9 \pm 11.7 mummies), but was not significantly different ($p > 0.05$) between the former two temperatures. *Aphelinus albipodus* did not successfully develop to adulthood at 10°C, thus r_m and R_0 values were zero, and T_g (generation time) could not be estimated. At 21.1°C, $r_m = 0.188$, $R_0 = 68.9$, and $T_g = 23.9$ d; those values were 0.288, 67.4, and 15.2 d, respectively, at 26.7°C. The offspring sex ratio (females) was male-biased at all three temperatures: 0.364 \pm 0.061 at 10.0°C, 0.437 \pm 0.029 at 21.1°C, and 0.341 \pm 0.002 at 26.7°C. Moreover, daily offspring sex ratio decreased with the age of the female parent at all three temperatures ($p < 0.05$). A pre-oviposition period of 1.5 d was observed in *A. albipodus* at 10°C, and female offspring were not produced during the first 7.5 d of adult life of mated females. The limited number of ovarian eggs, 6.5 \pm 2.5, in newly emerged females (< 6 h old) together with their fecundity schedule indicated synovigeny in *A. albipodus*. Results are discussed in relation to the colonization in North America of *A. albipodus* for biological control of *D. noxia*.

INTRODUCTION

Aphelinus albipodus (Hayat & Fatima) (Hymenoptera: Aphelinidae) [formerly *Aphelinus* sp. nr. *varipes*; see Hayat & Fatima (1992), González et al. (1994)] was collected from Russian wheat aphid, *Diuraphis noxia* (Mordvilko) (Hemiptera: Aphididae), hosts in the vicinity of Tahcheng, People's Republic of China, and imported to the USA in 1992 for biological control of the latter pest species. *Diuraphis noxia* presumably was introduced to the USA prior to 1986 when it was first discovered infesting cereal crops in Texas.

Following its discovery in Texas, *D. noxia* rapidly spread to most western states and to three Canadian provinces (Russian Wheat Aphid Task Force, 1992). At least two *Aphelinus* species have been reported parasitizing *D. noxia* in the USA prior to the successful colonization and spread of imported *Aphelinus* species (Feng et al., 1991; Lajeunesse & Johnson, 1991; Bernal et al., 1993). Indigenous natural enemies of *D. noxia*, including parasites, predators, and pathogens, are not effective at maintaining this pest at acceptable levels (Feng et al., 1991, 1992; Wraight et al., 1993; J. Bernal, unpubl. data). The importation and colonization of natural enemies with a long association with *D. noxia* has great potential as an effective method for its control. Such a long association may exist

between *D. noxia* and its natural enemies in north-western China, the presumed native range of this pest (González et al., 1990).

Natural enemy populations may reduce the growth rate, and thus the size, of their host populations by contributing to the total mortality suffered by the latter. The ability of a parasite population to increase in size, consequently causing greater mortality and therefore reducing the growth rate of its host population, is hence of special interest in biological control. The intrinsic rate of increase, r_m (Birch, 1948), is frequently used as a measure of a parasite population's potential rate of increase under specific environmental conditions. The parameter r_m combines reproduction and mortality estimates into a single value; thus, it is a practical measure of the potential performance of an organism in a given environment. Accordingly, r_m has been used as a relative measure of the potential impact that a parasite may have on its host's population (Force & Messenger, 1968; Messenger, 1970; Kambhampati & Mackauer, 1989). Ambient temperatures, among other factors, are known to affect the r_m of parasite populations (Force & Messenger, 1964b; Botto et al., 1988; Powell & Bellows, 1992; Steenis, 1993, 1994). Estimates of r_m obtained over a range of temperatures in the laboratory have been used to explain the distribution and abundance of parasites introduced for biological control (Force & Messenger, 1968; Messenger, 1970). The analyses of Force and Messenger support the use of the parameter r_m as an effective aide in assessing the potential relative performances of parasites imported for biological control of pests. Other studies (Kambhampati & Mackauer, 1989; Höller & Haardt, 1993), however, do not support the use of reproductive parameters, by themselves, as indices of the potential relative performances of introduced parasites.

The objective of the studies reported here was to examine under laboratory conditions the effect of different ambient temperatures on reproduction and reproductive parameters of *A. albipodus* (T92023*) from Tahcheng, PRC, on *D. noxia* hosts.

MATERIAL AND METHODS

Host and parasite cultures

Founder individuals for the parasite culture were collected in Tahcheng, PRC (46°42' N, 83°00' E, ca. 500 m), by D. González during 1992 and shipped to the Texas A & M University Quarantine Facility, College Station, Texas, USA. Rearing of *A. albipodus* at Riverside was initiated early in 1993. Rearing conditions and methods for the host and parasite were as described by Bernal et al. (1994).

Experimental methods

Two series of experiments were conducted at each of three constant temperatures, 10, 21.1, and 26.7°C ($\pm 1.0^\circ\text{C}$), inside small environmental chambers. Light intensity inside the chambers was ca. 500 Einstein. Photoperiod and humidity conditions inside the chambers were set at 14L : 10D, and 50–70% R.H., respectively.

In the first set of experiments, newly emerged male-female pairs of *A. albipodus* were offered 100 "large" (instars III, IV, and adults) *D. noxia* hosts daily. Large *D. noxia* were previously found to be suitable hosts for *A. albipodus* (Bernal & González, in press). Hosts were offered on two wheat seedlings (cv. MIT, 3 leaf stage, ca. 10 cm high) sown in plastic vials and enclosed in individual vial cages as previously described (Bernal et al., 1994). A streak of honey was provided on the inside of the vial cages as food for the parasites and was replenished as necessary. Parasite pairs were transferred daily to new vial pots containing 100 hosts until the death of the female parasite. Males usually died sooner than females and were replaced upon their death with males < 24 h old. Following exposure to the parasite pairs, the aphids on wheat seedlings were held inside an environmental chamber at 21.1°C ($\pm 1.0^\circ\text{C}$), 50–70% R.H., and

* Refers to Texas A & M University quarantine and taxonomic voucher number.

14L : 10D for formation of parasite mummies. Mummies were counted upon formation, and the wheat seedlings with live (i.e. potentially parasitized), and mummified aphids were cut at their base and transferred to small vials with mesh "windows". The vials containing the cut wheat seedlings and aphids were further held in the environmental chamber to allow formation of additional mummies and emergence of adult parasites. Adults were counted on emergence and their sex determined to estimate the offspring sex ratio (= proportion females). This set of experiments provided data on fecundity, offspring sex ratio, and adult survivorship and longevity in *A. albipodus* at each of the three study temperatures.

The second set of experiments was designed to provide data on pre-imaginal survivorship in *A. albipodus*. For each of the 3 study temperatures, groups of at least 350 large aphids on wheat leaf segments (ca. 1 cm) were exposed to groups of ca. 40, 0–2 day old mated female parasites for 4–6 h at 20–23°C. Following exposure to the parasites, the aphids were divided into 4 or 5 groups; each group was then transferred to potted wheat seedlings sown in plastic vials (described above). The aphids on wheat seedlings were held at one of the three study temperatures to allow development of the immature parasites. In the case of the 10.0°C experiment, one group of aphids was held at 21.1°C, the other groups at 10.0°C. On the day immediately following exposure to the female parasites, the aphids from one of the groups at each of the study temperatures (the group held at 21.1°C in the case of the 10.0°C experiment) were dissected to estimate the number of immature parasites (i.e. the size of the cohort) at the beginning of each experiment. The aphids of the remaining groups, except one group, were dissected at ca. equal intervals during the egg-mummy developmental period and the number of parasitized individuals (= immature parasites) was recorded. The duration of the egg-mummy developmental period had previously been determined (Bernal & González, in press). The aphids of the remaining, undissected, group were allowed to form mummies and produce adult parasites. This series of dissections, coupled with the known numbers of mummies and emerged adults allowed us to estimate the mortality suffered by the cohort of parasites from oviposition to emergence of adults.

The data obtained from the 2 sets of experiments were used to construct survivorship-fertility schedules for *A. albipodus* at each of the three temperatures studied. The iterative equation of Birch (1948), $\sum l_x m_x \exp(-r_m x) = 1$, was solved to obtain an estimate of the intrinsic rate of increase, r_m , at each of the temperatures studied. In Birch's equation, x = age in days (including the immature stages), l_x = age specific survival (including immature mortality), m_x = age specific number of female offspring per female parent, and r_m = the intrinsic rate of increase. The net reproductive rate was calculated as $R_0 = \sum l_x m_x$, and the mean generation time as $T_c = \sum l_x m_x x / R_0$.

A number of newly emerged females (< 6 h old) were dissected and the number of mature ovarian eggs counted in order to obtain information on a proovigenic or synovigenic status of *A. albipodus*. Mummies obtained from our parasite culture were placed individually in gelatin capsules and examined for emergence daily at 8:00 h and 14:00 h. Female parasites emerging during that period were killed by freezing and dissected in a droplet of soap water (10%). The number of mature ovarian eggs (= the egg load) and the length of the hind tibia were recorded for each female.

Statistical analyses

Unless otherwise indicated, means followed by their standard errors (S.E.) are presented. *t*-tests were used to test for significant differences in adult longevity between the sexes at each of the study temperatures. Analysis of variance (ANOVA) was used to test for significant differences ($p < 0.05$) in longevity and fecundity among the study temperatures. Student-Newman-Keuls tests ($p < 0.05$) were used to separate means where warranted. Bartlett's test for homogeneity of variances (Zar, 1974) revealed significant differences ($p < 0.05$) in the variances of the fecundity of *A. albipodus* among the study temperatures. Thus, fecundity data were transformed to Log_{10} values for ANOVA. Linear regression analysis was used to check for trends in daily offspring sex ratio with respect to female parent age. Comparisons among the overall offspring sex ratios (= total female offspring/total offspring) at the three study temperatures were made by examining for overlap between 98.3% confidence intervals. Confidence intervals were estimated at the 98.3% level in order that the comparisonwise error rate (3 comparisons) would result in a 95% confidence level for the experimentwise error rate for a Type I error.

RESULTS

Adult longevity

The mean longevity of female and male *A. albipodus* at each of the three study temperatures is given in Table 1. Females lived significantly longer ($p < 0.05$) than males at all three temperatures. ANOVA (females, $F_{2,35} = 17.625$, $p < 0.001$; males, $F_{2,27} = 9.128$, $p < 0.001$), followed by a Student-Newman-Keuls test ($p < 0.05$), revealed that both male and female adults lived significantly longer at 10.0°C relative to 21.1 or 26.7°C; longevity was not significantly different between 21.1 and 26.7°C. The longevities of males and females tended to be less variable as temperature increased.

TABLE 1. Mean longevity (\pm S.E.) in days of adult *A. albipodus* by sex, and fecundity (\pm S.E.) at three constant temperatures.

Temperature (°C)	Sex	Longevity ¹	Fecundity ²	n
10.0*	female	41.5 \pm 5.2A	56.9 \pm 11.7a	12
	male	26.0 \pm 4.9a	—	8
21.1**	female	20.9 \pm 1.9B	214.8 \pm 33.5b	12
	male	13.1 \pm 2.0b	—	11
26.7***	female	16.4 \pm 1.5B	294.7 \pm 27.6b	14
	male	10.0 \pm 1.2b	—	11

*, **, *** Females lived longer than males; *t*-test, $p = 0.05$, $p < 0.01$, $p < 0.005$, respectively.

¹ Values followed by same upper-case letter (females) or lower-case letter (males) within column are not significantly different, Student-Newman-Keuls test, $p \leq 0.05$.

² Values followed by same letter within column are not significantly different, Student-Newman-Keuls test, $p < 0.05$. Log₁₀-transformed values were used to separate means (see text).

Fecundity

All *A. albipodus* females produced eggs which developed to mummies during the first day of adult life at 21.1 and 26.7°C. However, only 1/3 of the females oviposited during the first day of adult life at 10°C. A pre-oviposition period, estimated as the number of days post adult emergence without production of mummies, in *A. albipodus* at 10°C was estimated as 1.5 \pm 0.6 d ($n = 12$). Moreover, only in few cases were female offspring produced on the first day following the pre-oviposition period at 10°C. The number of days immediately following adult emergence during which female offspring were not produced was estimated as 7.5 \pm 2.2 d ($n = 11$). Our observations at 21.1 and 26.7°C do not preclude the existence of a pre-oviposition period < 1 d in length at these temperatures.

The mean fecundity of *A. albipodus* at each of the three study temperatures is given in Table 1. Bartlett's test for homogeneity of variances (Zar, 1974) revealed that the variances of the fecundity of *A. albipodus* at the three temperatures were significantly different ($B_c = 10.531$, 35 *d.f.*, $p < 0.005$) thus further analyses were conducted on the Log₁₀-transformed values of the fecundity of individual females. ANOVA ($F_{2,35} = 30.298$, $p < 0.0001$), followed by a Student-Newman-Keuls test ($p < 0.05$), revealed that the fecundity of *A. albipodus* was greater at 21.1 and 26.7°C relative to 10.0°C, but was not significantly different between the former two temperatures (Table 1). The mean numbers of mummies produced by individual females at each of the temperatures were highly

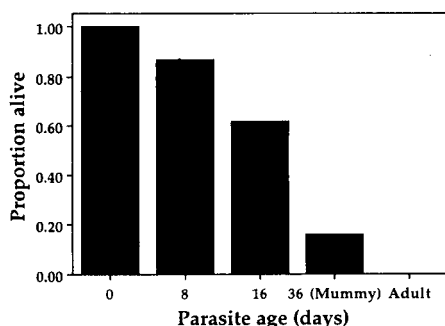


Fig. 1. Age-specific survivorship in *A. albipodus* at $10 \pm 1^\circ\text{C}$ (14L : 10D, 50–70% R.H.). Sample sizes used to estimate survivorship at each age were 141, 56, 50, 500 and 97 for the 0, 8, 16, 36, and adult columns, respectively. Age 0 indicates day on which hosts were parasitized (i.e. day of oviposition). Adults did not emerge from a total of 97 mummies.

at 10.0°C is shown in Fig. 2. Daily fecundity never exceeded 4 mummies and females had a maximum reproductive life of ca. 60 d (Fig. 2a). When fecundity was adjusted by daily offspring sex ratio, the number of female offspring did not exceed two on any day and exceeded one on only 8 d of the reproductive life of the females (Fig. 2b). The maximum reproductive life of female *A. albipodus* was ca. 50 d when adjusted for production of female offspring (Fig. 2b).

Data on survivorship and fertility in *A. albipodus* at 21.1°C are presented in Fig. 3a. Mortality in *A. albipodus* during the pre-imaginal stages was ca. 25% and was particularly notable during the early larval instars (age interval 0–8 d) where ca. 20% mortality

variable, with ca. 16-, 6-, and 4-fold differences between the lowest and highest fecundities at 10.0 , 21.1 , and 26.7°C , respectively.

The egg load of newly emerged females (< 6 h old) was 6.5 ± 2.5 ($n = 23$) mature ovarian eggs. Linear regression of the egg load of females against the length of their hind tibia was not significant ($F_{1, 21} = 2.511$, $p = 0.128$).

Demographic parameters

Data on daily fecundity and survivorship in *A. albipodus* at the three study temperatures are presented in Figs 1–3. Mortality during the larval stage at 10°C (i.e. up to age 36 d) was > 80% and adults did not emerge from mummies (i.e. 100% mortality by adult emergence) at this temperature (Fig. 1). The fecundity schedule of *A. albipodus* females

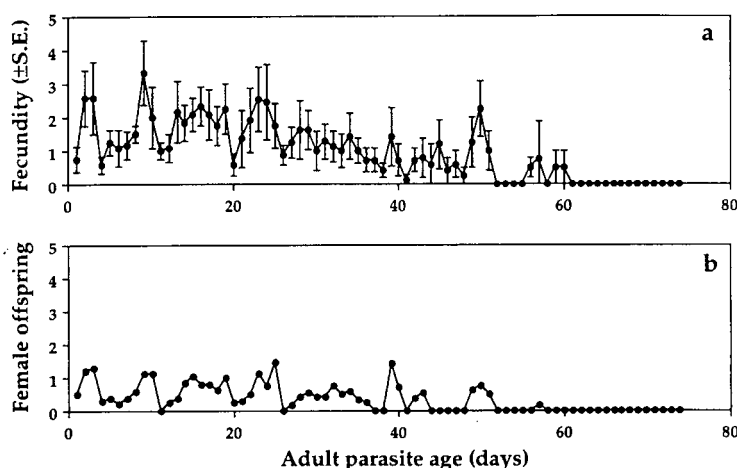


Fig. 2. Daily fecundity in *A. albipodus* at $10 \pm 1^\circ\text{C}$ (14L : 10D, 50–70% R.H.). a – mean numbers of mummies (\pm S.E.) produced daily; b – number of female offspring produced daily.

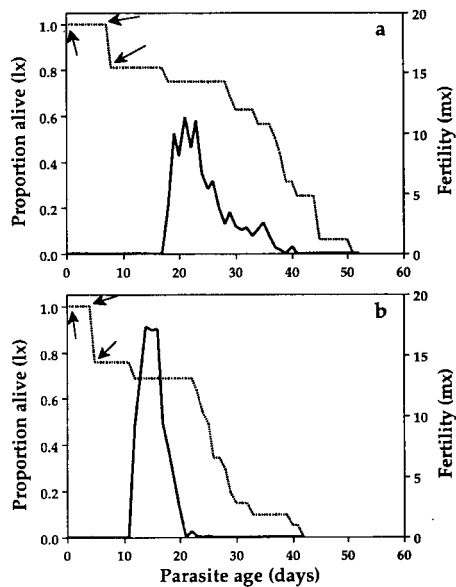


Fig. 3. Survivorship (l_x) (broken line) and fertility (m_x) (solid line) in *A. albipodus* at two constant temperatures (14L : 10D, 50–70% R.H.), a – $21.1 \pm 1.0^\circ\text{C}$; b – $26.7 \pm 1.0^\circ\text{C}$. Arrows indicate the parasite ages at which hosts were dissected to estimate parasite survivorship.

larval stage. Mortality did not occur during the first 11 d of adult life (age 11–22 d) after which survivorship steadily decreased to a small plateau (ca. 0.10) between 33 and 39 d of age, and then reached zero by 42 d. The fertility schedule of *A. albipodus* at 26.7°C was unlike that at 21.1°C . At 26.7°C it rapidly increased to a small plateau (ca. 17 female offspring per day) between 3 and 5 d after adult emergence followed by a fast decline to < 1 female offspring per day by 10 d. The maximum reproductive life of female *A. albipodus* was ca. 27 d; mummies and female offspring were not produced after 27 and 25 d, respectively.

TABLE 2. Life-table parameter values and offspring sex ratio ($\pm 98.3\%$ confidence intervals¹) in *A. albipodus* at three constant temperatures.

Temp. ($^\circ\text{C}$)	R_0	r_m	T_c	Sex ratio ²
10.0	0.000	0.000	—	$0.364 \pm 0.061\text{ab}^3$
21.1	68.913	0.1884	23.9	$0.437 \pm 0.029\text{a}$
26.7	67.391	0.2878	15.2	$0.341 \pm 0.002\text{b}$

¹ Confidence intervals were calculated as $[t_{(1-1-0.95)}^{1/3}, n] * (\text{S.E.})$ to allow comparisons (95% experimental error rate) among sex ratios.

² Expressed as proportion female offspring; sample sizes are $n = 357$, $n = 1695$, and $n = 2957$ for 10.0, 21.1, and 26.7°C , respectively.

³ Values followed by same letter within column are not significantly different ($p < 0.05$).

occurred, the remainder occurring during the mummy stage (age interval 8–18 d). Mortality did not occur during the first 11 d of adult life; it then steadily increased to 100% by age 51 d. The fertility schedule of *A. albipodus* was characterized by a succession of peaks and valleys with three similarly high peaks (ca. 10–11 female offspring per day) occurring during the first 6 d of adult life after which the peaks steadily became smaller; a final small peak (ca. 0.5 female offspring) occurred at 40 d. The maximum reproductive life of *A. albipodus* was ca. 40 d; mummies and female offspring were not produced after 43 and 40 d, respectively.

Data on daily survivorship and fertility in *A. albipodus* at 26.7°C are presented in Fig. 3b. Mortality during the pre-imaginal stages at 26.7°C , ca. 32%, was slightly greater than at 21.1°C . However, mortality was not detected during the early larval instars at 26.7°C ; all larval mortality occurred during the age interval 4–5 d. Mortality during the mummy stage (age interval 5–11 d) was ca. 8%; less than that which occurred during the

Intrinsic rate of increase, r_m , net reproductive rate, R_o , and generation time, T_c , values for *A. albipodus* at all three study temperatures were estimated from data presented in Figs 1–3 and are presented in Table 2. Values for R_o and r_m at 10°C were taken as zero since 100% mortality occurred during pre-imaginal development; the T_c value thus could not be estimated. R_o values were similar at 21.1 and 26.7°C, 68.9 and 67.4 respectively, while r_m values increased ca. 0.5-fold, from 0.19 to 0.29, with temperature in that interval.

Although *A. albipodus* did not develop successfully from egg to adult at constant 10°C, several adult parasites were obtained from mummies formed at this temperature but transferred to a higher temperature, 21.1°C, at 120 d from oviposition (= ca. 84 d in the mummy stage). Adults obtained under these conditions, referred to as “cold-type”, were mated in different combinations with each other or with adults from the insectary culture, referred to as “normal-type”. These adult parasites were then offered hosts for oviposition until the death of the female in order to gain insight to the effect of development at low temperature (10°C) on reproduction. The results of these mating and reproductive trials are presented in Table 3. The reproductive capacity of females and fertilization ability of males was not affected by the prolonged exposure to and development at 10°C, as shown by the production of mummies and female offspring when a cold-type male was mated with a similar female or a normal-type female. A cold-type female confined for its adult life with a cold-type male produced 202 mummies and the offspring sex ratio was 0.705; a normal-type female confined for 2 h with the latter cold-type male produced 285 mummies but only male offspring emerged (i.e. mating was not successful). However, in a separate trial a normal-type female confined for its adult life with a cold-type male produced male and female offspring; the sex ratio was 0.462.

TABLE 3. Results of reproductive trials involving “cold-type” *A. albipodus* mated with either a similar or “normal-type” individual at 21.1°C (Cm = “cold-type” male, Nf = “normal-type” female, and Cf = “cold-type” female). See text for explanation of “cold-type” and “normal-type”.

Trial/Cross	Female parent age	Total offspring		
		Mummies	Females	Males
1) Cm ¹ × Cf	0–6 days	107	65	32
	7–10 days	48	28	5
	11–20 days	47	0	2
	21 days–	0	0	0
	Totals	202	93	39
2) Cm ¹ × Nf	0–6 days	92	0	71
	7–10 days	81	0	58
	11–20 days	99	0	17
	21 days–	13	0	0
	Totals	285	0	146
3) Cm × 2 Nf ²	0–4 days	57	23	25
	5–14 days	60	7	10
	15 days–	4	0	0
	Totals	121	30	35

¹ The same male was used in Trials 1 and 2: Cm confined with Nf for ca. 2 h in Trial 2; then Cm confined with Cf for duration of experiment in Trial 1.

² Cm confined with 2 Nf for duration of experiment.

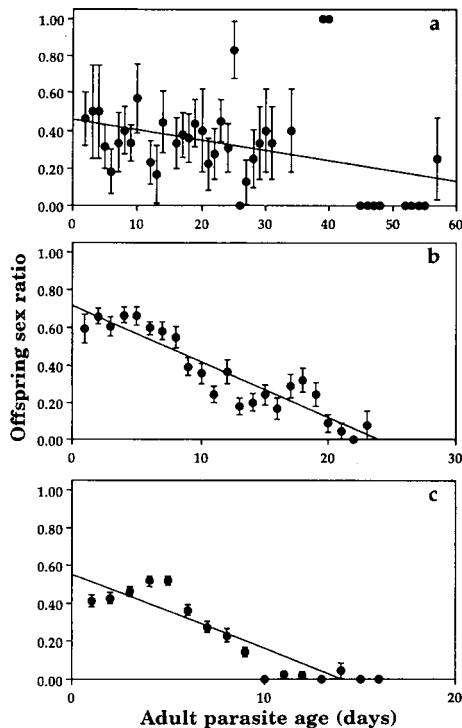


Fig. 4. Change in the offspring sex ratio (females) with parental female age in *A. albipodus* at three oviposition temperatures, a - $10.0 \pm 1.0^\circ\text{C}$; b - $21.1 \pm 1.0^\circ\text{C}$; c - $26.7 \pm 1.0^\circ\text{C}$. Adult parasites used in trials at all 3 temperatures were obtained from an insectary culture maintained at $20\text{--}25^\circ\text{C}$. Vertical bars indicate 95% confidence intervals. The linear regression curve for each temperature is shown superimposed. The equations, and F-values, describing the relationship between female parasite age and offspring sex ratio are: a - $Y = 0.45769 - 0.00557X$ ($r^2 = 0.136$), $F_{1,38} = 5.994$, $p < 0.02$; b - $Y = 0.71523 - 0.03012X$ ($r^2 = 0.862$), $F_{1,21} = 131.700$, $p < 0.001$; c - $Y = 0.55033 - 0.03963X$ ($r^2 = 0.830$), $F_{1,14} = 68.120$, $p < 0.001$. Only values where ≥ 4 offspring were produced at a given age ($n \geq 4$) were used for analyses and are shown. Note change of scale in X axes.

differences in longevity of *A. albipodus* reflect the influence of temperature on this attribute. These results are consistent with assertions that, within specific limits, longevity increases with decreasing ambient temperatures (Viggiani, 1984; Starý, 1988). The longevity of *A. albipodus* observed in this study is comparable to that of other *Aphelinus* species reported by various authors (Force & Messenger, 1964a; Bonnemaison, 1965;

The overall offspring sex ratio (= total female offspring/total offspring) was male-biased at all three study temperatures (Table 2). The lowest sex ratios occurred at 10.0 (0.364 ± 0.061) and 26.7°C (0.341 ± 0.020), while the highest occurred at 21.1°C (0.437 ± 0.029). However, the difference in sex ratio between 21.1 and 10.0°C was not significant ($p > 0.05$). Although the overall offspring sex ratio at all three study temperatures was male-biased, the age-specific offspring sex ratio varied with the age of the female parent (Fig. 4). In general, the offspring sex ratio tended to decrease with the age of the female parent at all three study temperatures ($p < 0.05$). At 10°C , the offspring sex ratio rarely exceeded 0.5 on any day during the life of the female parent but decreased in general with her age; however, the correlation between age and sex ratio was relatively poor at this temperature (Fig. 4a). At 21.1°C , the sex ratio was female-biased during the first 8 d of adult life, but then decreased to < 0.5 as the female parent aged (Fig. 4b). At 26.7°C , the offspring sex ratio initially increased from ca. 0.40 to ca. 0.55 by 5 d following adult emergence, and then rapidly decreased to < 0.10 by 10 d (Fig. 4c). Linear regression analyses revealed that the reductions in offspring sex ratio with the age of the female parents were highly significant ($p < 0.05$).

DISCUSSION

The longevity of aphelinids depends on various factors, among which food and temperature are of special importance. Food, in the form of honey and hosts, was available to all parasites during the course of the experiments at all three temperatures. Thus,

Raney et al., 1971). On the other hand, certain species such as *Aphelinus abdominalis* (Dalman) appear to be longer lived, different isofemale lines living > 50 d at 20°C (Höller & Haardt, 1993). The longevity of females may or may not be longer than that of males (Viggiani, 1984). In this study, females lived significantly longer than males at all three temperatures.

A pre-oviposition period of several hours (or less) is common in aphelinid females (Viggiani, 1984). In this study a pre-oviposition period > 1 day was detected at 10°C but not at 21.1 or 26.7°C. The frequency of our observations, i.e. once daily, did not allow us to detect shorter pre-oviposition periods that may have occurred at 21.1 and 26.7°C. Thus, we can not preclude the occurrence of a pre-oviposition period of < 1 day at higher temperatures (21–27°C) in *A. albipodus*. In addition, female *A. albipodus* held at 10°C delayed production of daughters for several days (> 7 d) following their emergence from mummies. Thus it is reasonable to expect that in the field, *A. albipodus* females emerging early in the season, i.e. late winter-early spring, will contribute less and later to decreasing the growth rate of *D. noxia* populations than their presence would suggest. Any significant impact of *A. albipodus* on *D. noxia* populations would necessarily be deferred until field temperatures are above 10°C for an appreciable length of time during the day. Target release areas in North America are within temperate zones where late winter-early spring temperatures are relatively cool.

Data concerning the fecundity of aphelinid species parasitic on aphids are relatively scarce if compared, for example, with the amount available in the case of aphidiid species. The fecundity of aphelinid females is known to vary with ambient temperatures and other factors (Stary, 1988). Moreover, aphelinids are mostly synovigenic (Viggiani, 1984); thus, the availability of adequate food is of particular importance. The fecundity of *A. albipodus* observed in this study is comparable to reports for certain other *Aphelinus* species (Bonnet-maison, 1965; Raney et al., 1971; Wahab, 1985; Bueno & Stone, 1987). However, other authors (Force & Messenger, 1964b; Höller & Haardt, 1993) reported considerably higher (as much as 4-fold higher) fecundity in species such as *Aphelinus semiflavus* Howard (= *asychis*) and *A. abdominalis*. The influence of temperature on the fecundity of insect parasites, including aphelinids, is well documented (Force & Messenger, 1964b; Raney et al., 1971; Powell & Bellows, 1992). Our observation that the fecundity of *A. albipodus* was lowest at 10.0°C, but relatively constant between 21.1 and 26.7°C is similar to the results of Raney et al. (1971) for *A. semiflavus*, but unlike those of Force & Messenger (1964b) where the fecundity of the latter species decreased at temperatures above 21°C. The latter possibly reflects inter-specific differences in responses to temperature between the *Aphelinus* species involved, including adaptation to distinct temperature regimes, since they originated in widely distinct climatic zones. As in the case of longevity, the availability of food was not a factor contributing to the differences in fecundity in *A. albipodus* among the study temperatures.

The results of this study, in particular at 21.1°C, indicate that *A. albipodus* is synovigenic. Fecundity schedules for individual female *A. albipodus* (not shown) typically show daily successions of peaks and valleys in the number of offspring produced due probably to alternate periods of oviposition and host-feeding/oogenesis. Moreover, adult females emerged with ca. 6 ovarian eggs available for oviposition; a small fraction, ca. 1/45 to 1/9, of the numbers of offspring produced at the different study temperatures.

Mortality during the pre-imaginal stages at 10°C was 100% in *A. albipodus*. The lethal effect of low temperature on *A. albipodus* is consistent with other reports concerning different species of *Aphelinus* (Force & Messenger, 1964b; Bernal & González, 1993; Bernal & González, in press). The rate of increase r_m and the net reproductive rate R_o at 10°C were thus equal to zero since they are functions of pre-imaginal survivorship. Even in the case of a small proportion of individuals surviving to the adult stage at 10°C, the r_m value would be negligible due to the extremely long developmental time (Bernal & González, in press) and high immature mortality at this temperature. Our results are similar to those of Force & Messenger (1964b) who determined that r_m and R_o were negligible in *A. semiflavus* at 10°C. Pre-imaginal mortality at 21.1 and 26.7°C was ca. 30% in *A. albipodus*. Force & Messenger (1964b) did not detect any significant pre-imaginal mortality at temperatures in the 21.1 to 29.4°C range, while ca. 20% pre-imaginal mortality occurred at 15.6°C in their study.

Life-table parameters are known to be affected by a number of environmental factors. In general, factors which affect the developmental time, survivorship, offspring sex ratio, or fecundity of parasites will affect parameters such as r_m , T_c , and R_o . In this study, the only variable was temperature which is known to have a strong effect on these parameters (Force & Messenger, 1964b; Botto et al., 1988; Powell & Bellows, 1992; Steenis, 1993, 1994). Despite the generally accepted influence of parameters such as r_m on the performance of natural enemies, few studies have been conducted where the r_m has been estimated for species of *Aphelinus* employed in various biological control programs. Force & Messenger (1964b) reported r_m values for *A. semiflavus* ranging from “very low” at 10.0°C, to 0.34 at 26.7°C, followed by a decline to a negative value by 32.2°C. Our estimates of r_m in *A. albipodus* at the three study temperatures were considerably lower than those of Force and Messenger. Similarly, they obtained estimates of the net reproductive rate, R_o , ca. 6.5- and 3.8-times higher than ours at 21.1 and 26.7°C, respectively.

Fecundity was not affected in female *A. albipodus* emerged from mummies formed at 10°C and transferred to 21.1°C at age 120 d from oviposition (ca. 84 d in the mummy stage). A cold-type female mated with a cold-type male and kept at 21.1°C produced > 200 mummies which is within the 95% confidence limits for the mean fecundity at 21.1°C. Likewise, the fertilization ability of males was not affected by development at 10°C. In two cases where a cold-type male was used to mate females (normal-, and cold-type) and female offspring were produced (i.e. mating was successful), the offspring sex ratios were 0.462 and 0.705. These sex ratios are greater than the overall offspring sex ratios at the three study temperatures. These results are similar to those of other authors involving aphelinid and aphidiid parasites of aphids in cases where mummies or adults produced at moderate temperatures were stored at low temperatures for varying lengths of time (Archer & Eikenbary, 1973; Archer et al., 1973, 1976; Scopes et al., 1973; Hofsvang & Hågvar, 1977).

The majority of aphelinids are biparental (arrhenotokous), although some uniparental (thelytokous) species are known, and certain otherwise biparental species have been found to include uniparental strains (Viggiani, 1984; Starý, 1988). *Aphelinus albipodus* is an arrhenotokous species (J. Bernal, unpubl. data). The offspring sex ratio of parasites is known to vary with a number of environmental and intrinsic (i.e. to the female parasite) factors (c.f. King, 1987). In the Aphelinidae, ambient temperatures have been shown to have a

significant effect on the offspring sex ratio (Stary, 1988). Commonly, offspring sex ratios (= proportion of females) in parasitic wasps are highest at intermediate temperatures and lowest at extreme temperatures (King, 1987). The latter assertion is, in general terms, consistent with our observations; offspring sex ratio was highest at 21.1°C (although not significantly different from that at 10°C). Reports concerning the offspring sex ratio of *Aphelinus* species show high variability. Reported sex ratios are in the range 0.00 to 0.84 (Force & Messenger, 1964b; Raney et al., 1971; Haardt & Höller, 1992; Höller & Haardt, 1993; this study), in some cases reflecting the effect of different temperatures, and in others the effect of different hosts or different parental isofemale lines. In addition to differences in offspring sex ratios due to temperature, we observed differences associated with the age of the parental parasites. In general, the offspring sex ratio decreased with the age of the parental female, and perhaps the male. King (1987) suggested that the offspring sex ratio commonly declined with age in female parasites and that such a reduction could result from sperm depletion or reduced sperm viability. In addition, King suggested that the age of the female's mate may also affect the offspring sex ratio. In our studies, males were continuously available for mating during the life of the female; when males died during the course of an experiment they were promptly replaced with young males. Thus, if female *A. albipodus* mate only once or very few times and at the beginning of their reproductive life, sperm depletion or loss of its viability are likely explanations for the reduction in offspring sex ratio with female age. Recent evidence involving *Trichogramma minutum* Riley (Leatemia et al., 1995) suggests that sperm depletion is the more likely of the latter two explanations. However, female *A. albipodus* occasionally mate more than once and later in their life (J. Bernal, pers. observ.); thus, the age of the male mate may also contribute to the reduction in offspring sex ratio with female parent age observed in this parasite.

The extremely detrimental effect of low temperature (10°C) on development in *A. albipodus* observed in this study (also see Bernal & González, in press) calls for further investigation of the effects of low temperature in this parasite. A potentially productive line of research is the investigation of overwintering adaptations, such as diapause, in *A. albipodus*. Our results indicate that without such an adaptation(s), *A. albipodus* would not be able to overwinter in its native range, nor in temperate zones such as those in North America where the parasite is currently being colonized for biological control of *D. noxia*.

As far as we are aware, our studies of *A. albipodus* together with limited data provided by Ramaseshiah & Dharmadhikari (1969) are the only sources of information available on this species; Ramaseshiah & Dharmadhikari misidentified *A. albipodus* and referred to it as *A. flavipes*. Recently, M. Hayat and K. Fatima described *A. albipodus* as a new species and synonymized it with Palearctic (including areas of the former USSR and China) *A. sp. nr. varipes* (Hayat & Fatima, 1992; González et al., 1994). Judging from the relatively widespread distribution of *A. albipodus* (see González et al., 1994), it is likely that biologically distinct populations (Caltagirone, 1985; González, 1988; Ruberson et al., 1989) exist and that these may be useful under different environmental conditions. The introduction to North America of such populations may prove to be a productive endeavor within biological control efforts against *D. noxia*.

The use of reproductive parameters as indicators of the potential performance of introduced natural enemies, or alternatively for explaining the performances of established

ones has produced mixed results (Force & Messenger, 1968; Messenger, 1970; Kambhampati & Mackauer, 1989; Höller & Haardt, 1993). In the case of *A. albipodus*, in addition to the impact that reproduction, through parasitism, may have on *D. noxia* populations, mortality caused by host-feeding must be considered when assessing its potential impact on host population levels. In many cases, female parasites are known to cause considerable additional mortality by host-feeding (DeBach, 1943; Flanders, 1953; Bartlett, 1964). *Aphelinus albipodus*, like other species of *Aphelinus* (e.g. Jervis & Kidd, 1986; Bai & Mackauer, 1990), host-feeds and oviposits in different hosts (J. Bernal, pers. observ.) and thus may cause considerable additional mortality through host-feeding. The present studies together with investigations on other performance criteria of *A. albipodus* as a natural enemy of *D. noxia* should provide a greater basis for comparative analyses of the potential performances of this and other parasites being imported to and colonized in the USA.

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REFERENCES

- ARCHER T.L. & EIKENBARY R.D. 1973: Storage of *Aphelinus asychis*, a parasite of greenbug. *Environ. Entomol.* **2**: 489–490.
- ARCHER T.L., MURRAY C.L., EIKENBARY R.D., STARKS K.J. & MORRISON R.D. 1973: Cold storage of *Lysiphlebus testaceipes* mummies. *Environ. Entomol.* **2**: 1104–1108.
- ARCHER T.L., BOGART R.K., EIKENBARY R.D. 1976: The influence of cold storage on the survival and reproduction by *Aphelinus asychis* adults. *Environ. Entomol.* **5**: 623–625.
- BAI B. & MACKAUER M. 1990: Oviposition and host-feeding patterns in *Aphelinus asychis* (Hymenoptera: Aphelinidae) at different aphid densities. *Ecol. Entomol.* **15**: 9–16.
- BARTLETT B.R. 1964: Patterns in the host-feeding habit of adult parasitic Hymenoptera. *Ann. Entomol. Soc. Am.* **57**: 344–350.
- BERNAL J. & GONZÁLEZ D. 1993: Temperature requirements of four parasites of the Russian wheat aphid *Diuraphis noxia*. *Entomol. Exp. Appl.* **69**: 173–182.
- BERNAL J.S. & GONZÁLEZ D. (in press): Thermal requirements of *Aphelinus albipodus* (Hayat and Fatima) (Hym.: Aphelinidae) on *Diuraphis noxia* (Mordvilko) (Hom.: Aphididae) hosts. *J. Appl. Entomol.*
- BERNAL J., GONZÁLEZ D., NATWICK E.T., LOYA J.G., LEÓN-LÓPEZ R. & BENDIXEN W.E. 1993: Natural enemies of Russian wheat aphid identified in California. *Calif. Agric.* **47**(6): 24–28.
- BERNAL J., BELLOWS T.S. JR. & GONZÁLEZ D. 1994: Functional response of *Diaeretiella rapae* (M'Int.) (Hym., Aphidiidae) to *Diuraphis noxia* (Mord.) (Hom., Aphididae) hosts. *J. Appl. Entomol.* **118**: 300–309.
- BIRCH L.C. 1948: The intrinsic rate of increase of an insect population. *J. Anim. Ecol.* **17**: 15–26.
- BONNEMAISON L. 1965: Observations écologiques sur *Aphelinus mali* Haldeman parasite du puceron lanigère (*Eriosoma lanigerum* Hausmann). *Ann. Soc. Entomol. Fr.* **1**: 143–176.
- BOTTO E.N., GONZÁLEZ D. & BELLOWS T.S. JR. 1988: Effect of temperature on some biological parameters of two populations of *Aphidius ervi* Haliday (Hymenoptera: Aphidiidae). In Gupta V.K. (ed.): *Advances in Parasitic Hymenoptera Research*. E.J. Brill, New York, pp. 367–377.
- BUENO R. JR. & STONE J.D. 1987: Reproductive response of *Aphelinus perpallidus* (Hymenoptera: Aphelinidae) to age of its parent and density of its host, *Monellia caryella* (Homoptera: Aphididae). *Environ. Entomol.* **16**: 877–880.
- CALTAGIRONE L.E. 1985: Identifying and discriminating among biotypes of parasites and predators. In Hoy M. & Herzog D. (eds): *Biological Control in Agricultural IPM Systems*. Academic Press, San Diego, pp. 189–200.

- DEBACH P. 1943: The importance of host-feeding by adult parasites in the reduction of host populations. *J. Econ. Entomol.* **36**: 647–658.
- FENG M.G., JOHNSON J.B. & HALBERT S.E. 1991: Natural control of cereal aphids (Homoptera: Aphididae) by entomophagous fungi (Zygomycetes: Entomophthorales) and parasitoids (Hymenoptera: Braconidae and Encyrtidae) on irrigated spring wheat in southwestern Idaho. *Environ. Entomol.* **20**: 1699–1710.
- FENG M.G., JOHNSON J.B. & HALBERT S.E. 1992: Parasitoids (Hymenoptera: Aphidiidae and Aphelinidae) and their effect on aphid (Homoptera: Aphididae) populations in irrigated grain in southwestern Idaho. *Environ. Entomol.* **21**: 1433–1440.
- FLANDERS S.E. 1953: Predation by the adult hymenopterous parasite and its role in biological control. *J. Econ. Entomol.* **46**: 541–544.
- FORCE D.C. & MESSENGER P.S. 1964a: Developmental period, generation time, and longevity of three parasites of *Therioaphis maculata* (Buckton) reared at various constant temperatures. *Ann. Entomol. Soc. Am.* **57**: 405–413.
- FORCE D.C. & MESSENGER P.S. 1964b: Fecundity, reproductive rates, and innate capacity for increase of three parasites of *Therioaphis maculata* (Buckton). *Ecology* **45**: 706–715.
- FORCE D.C. & MESSENGER P.S. 1968: The use of laboratory studies of three hymenopterous parasites to evaluate their field potential. *J. Econ. Entomol.* **61**: 1371–1378.
- GONZÁLEZ D. 1988: Biotypes in biological control—examples with populations of *Aphidius ervi*, *Trichogramma pretiosum*, and *Anagrus epos* (Parasitic Hymenoptera). In Gupta V.K. (ed.): *Advances in Parasitic Hymenoptera Research*. E.J. Brill, New York, pp. 475–482.
- GONZÁLEZ D., GILSTRAP F., ZHANG G., ZHANG J., ZAREH N., WHANG R., DIJKSTRA E., MCKINNON L., STARÝ P. & WOOLEY J.B. 1990: Foreign exploration, for natural enemies of Russian wheat aphid in China, Iran, Turkey, and The Netherlands. *Proceedings of the Fourth Russian Wheat Aphid Workshop*. Bozeman, Montana, pp. 154–165.
- GONZÁLEZ D., GILSTRAP F., ZHANG W., MCKINNON L., WOOLEY J.B., STARÝ P., WAGGONER M. & ZHANG G. 1994: Foreign exploration, for natural enemies of Russian wheat aphid in southern Xinjiang, People's Republic of China. In Peairs F.B., Kroening M.K. & Simmons C.L. (comp.): *Proceedings of the Sixth Russian Wheat Aphid Workshop*. Great Plains Agricultural Council, Fort Collins, pp. 208–222.
- HAARDT H. & HÖLLER C. 1992: Differences in life history traits between isofemale lines of the aphid parasitoid *Aphelinus abdominalis* (Hymenoptera; Aphelinidae). *Bull. Entomol. Res.* **82**: 479–484.
- HAYAT M. & FATIMA K. 1992: Taxonomic studies on *Aphelinus* (Hymenoptera: Aphelinidae). 5. Description of a new species and further records of *A. gossypii*, with a new synonymy. *Entomon* **17**: 103–107.
- HOFVANG T. & HÅGVAR E.B. 1977: Cold storage tolerance and supercooling points of mummies of *Ephedrus cerasicola* Starý and *Aphidius colemani* Viereck (Hym., Aphidiidae). *Norw. J. Entomol.* **24**: 1–6.
- HÖLLER C. & HAARDT H. 1993: Low field performance of an aphid parasitoid, *Aphelinus abdominalis*, efficient in the laboratory (Hym., Aphelinidae). *Entomophaga* **38**: 115–124.
- JERVIS M.A. & KIDD N.A.C. 1986: Host-feeding strategies in hymenopterous parasitoids. *Biol. Rev.* **61**: 395–434.
- KAMBHAMPATI S. & MACKAUER M. 1989: Multivariate assessment of inter- and intraspecific variation in performance criteria of several pea aphid parasites (Hymenoptera: Aphidiidae). *Ann. Entomol. Soc. Am.* **82**: 314–324.
- KING B.H. 1987: Offspring sex ratios in parasitoid wasps. *Q. Rev. Biol.* **62**: 367–396.
- LAJEUNESSE S.E. & JOHNSON G.D. 1991: New North American host records for *Aphelinus* sp. nr. *varipes* (Foerster) (Hymenoptera: Aphelinidae): the western wheat aphid, *Diuraphis tritici* (Gillette), and the Russian wheat aphid, *Diuraphis noxia* (Mordvilko) (Homoptera: Aphididae). *Can. Entomol.* **123**: 413–415.
- LEATEMIA J.A., LAING J.E. & CORRIGAN J.E. 1995: Production of exclusively male progeny by mated, honey-fed *Trichogramma minutum* Riley (Hym., Trichogrammatidae). *J. Appl. Entomol.* **119**: 561–566.
- MESSENGER P.S. 1970: Bioclimatic inputs to biological control. In Rabb R.L. & Guthrie F.E. (eds): *Concepts of Pest Management*. North Carolina State University, Raleigh, pp. 84–102.
- POWELL D.A. & BELLOWES T.S. JR. 1992: Development and reproduction of two populations of *Eretmocerus* species (Hymenoptera: Aphelinidae) on *Bemisia tabaci* (Homoptera: Aleyrodidae). *Environ. Entomol.* **21**: 651–658.

- RAMASESHIAH G. & DHARMADHIKARI P.R. 1969: Aphelinid parasites of aphids in India. *C.I.B.C. Tech. Bull.* **11**: 156–164.
- RANEY H.G., COLES L.W., EIKENBARY R.D., MORRISON R.D. & STARKS K.J. 1971: Host preference, longevity, developmental period and sex ratio of *Aphelinus asychis* with three sorghum-fed species of aphids held at controlled temperatures. *Ann. Entomol. Soc. Am.* **64**: 169–176.
- RUBERSON J.R., TAUBER M.J. & TAUBER C.A. 1989: Intraspecific variability in Hymenopteran parasitoids: comparative studies of two biotypes of the egg parasitoid *Edovum puttleri* (Hymenoptera: Eulophidae). *J. Kans. Entomol. Soc.* **62**: 189–202.
- RUSSIAN WHEAT APHID TASK FORCE 1992: Economic impact of the Russian wheat aphid in the western United States: 1989–1990. In Morrison W.P. (comp.): *Proceedings of the Fifth Russian Wheat Aphid Conference*. Great Plains Agricultural Council, Fort Worth, pp. 1–13.
- SCOPES N.E.A., BIGGERSTAFF S.M. & GOODALL D.E. 1973: Cool storage of some parasites used for pest control in glasshouses. *Pl. Pathol.* **22**: 189–193.
- STARÝ P. 1988: Aphelinidae. In Minks A.K. & Harrewijn P. (eds): *Aphids, Their Biology, Natural Enemies and Control*. Vol. B. Elsevier, Amsterdam, pp. 185–188.
- STEENIS M.J. VAN 1993: Intrinsic rate of increase of *Aphidius colemani* Vier. (Hym., Braconidae), a parasitoid of *Aphis gossypii* Glov. (Hom., Aphididae), at different temperatures. *J. Appl. Entomol.* **116**: 192–198.
- STEENIS M.J. VAN 1994: Intrinsic rate of increase of *Lysiphlebus testaceipes* Cresson (Hym., Braconidae), a parasitoid of *Aphis gossypii* Glover (Hom., Aphididae) at different temperatures. *J. Appl. Entomol.* **118**: 399–406.
- VIGGIANI G. 1984: Bionomics of the Aphelinidae. *Annu. Rev. Entomol.* **29**: 257–276.
- WAHAB W.A. 1985: Observations on the biology and behaviour of *Aphelinus abdominalis* Dalm. (Hym., Aphelinidae), a parasite of aphids. *J. Appl. Entomol.* **100**: 290–296.
- WRAIGHT S.P., PAPROWSKI T.J., MEYER W.L. & PEAIRS F.B. 1993: Natural enemies of Russian wheat aphid (Homoptera: Aphididae) and associated cereal aphid species in spring-planted wheat and barley in Colorado. *Environ. Entomol.* **22**: 1383–1391.
- ZAR J.H. 1974: *Biostatistical Analysis*. Prentice Hall, Engelwood Cliffs, New Jersey, pp. 131–133.

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