FECUNDITY, LONGEVITY, AND INTRINSIC NATURAL RATE OF INCREASE OF *EPIDINOCARSIS LOPEZI* (DE SANTIS) (HYMENOPTERA: ENCYRTIDAE)

Y. IZIQUEL
E.N.S.A.T., Laboratoire d'Entomologie, 145 Avenue de Muret, 31076 Toulouse cédex, France

and B. LE RÜ
O.R.S.T.O.M., Laboratoire d'Entomologie Appliquée, B.P. 181, Brazzaville, R. Congo

Abstract

Can. Ent. 124: 1115–1121 (1992)

A laboratory study of the fecundity, longevity, and intrinsic natural rate of increase of *Epidinocarsis lopezi* (De Santis) (Hymenoptera: Encyrtidae) was performed at 26°C, the average temperature observed in the Congo during pullulation of its host *Phenacoccus manihoti* Mat.-Ferr. (Homoptera: Pseudococcidae). With 30 mealybugs per female per day, the parasitoid lives for an average of 41.4 days and lays 558.5 eggs. The net reproduction rate (R_0) was calculated to be 269.9 females per female per generation, the average duration of a generation (T) was 33.9 days, and the intrinsic natural rate of increase of the parasitoid (r_m) was 0.213. The fecundity observed in *E. lopezi* in this study was much higher than the figures previously reported. The r_m of the parasitoid appeared to be higher than that determined by other authors for the mealybug. The limits of such a comparison are discussed.

Iziquel, Y., et B. Le Rü. 1992. Fécondité, longévité, et taux intrinsèque d'accroissement naturel d'*Epidinocarsis lopezi* (De Santis) (Hymenoptera: Encyrtidae). *Can. Ent.* **124**: 1115–1121.

Résumé

Une étude au laboratoire a été réalisée sur *Epidinocarsis lopezi* (De Santis) (Hym. Encyrtidae) à la température de 26°C, moyenne des températures qu'il rencontre au Congo durant la phase de pullulation de son hôte *Phenacoccus manihoti* Mat.-Ferr. (Hom. Pseudococcidae). En présence de 30 cochenilles par femelle et par jour, le parasitoïde vit en moyenne 41,4 jours et pond 558,5 oeufs. Le taux net de reproduction (R_0) a été évalué à 269,9 femelles par femelle et par génération, la durée moyenne d'une génération (T) à 33,9 jours et le taux intrinsèque d'accroissement naturel du parasitoïde (r_m) à 0,213. Il apparaît que la fécondité trouvée pour *E. lopezi* dans notre étude est très supérieure aux valeurs rapportées jusqu'ici, et que plusieurs facteurs peuvent l'expliquer. Par ailleurs, le r_m du parasitoïde est semble-t-il plus élevé que celui de la cochenille déterminé par d'autres auteurs. On discute des limites d'une telle comparaison.

Introduction

Epidinocarsis lopezi (De Santis) is an Encyrtidae introduced into Africa in 1981 to control the cassava mealybug *Phenacoccus manihoti* Mat.-Ferr. (Homoptera: Pseudococcidae) (Herren and Neuenschwander 1991). The data published to date attributed it with low fecundity (Odebiyi and Bokonon-Ganta 1986; Umeh 1988; Biassangama et al. 1988; Löhr et al. 1989). Examination of these data led us to believe that the experimental procedures used may have influenced the results. The study presented here was thus performed under conditions (especially host density) that would enable the parasitoids to express maximum fecundity at the temperature observed during the 3 months of pullulation of *P. manihoti* in the Congo. We also evaluated the intrinsic natural rate of increase (r_m) of the parasitoid. The r_m of *P. manihoti* has been estimated by several authors (Iheagwam 1981; Lema and Herren 1985; Le Rü and Fabres 1987; Le Rü and Papierok 1987; Schulthess et al. 1987); that of *E. lopezi* has been the subject of one study (Löhr et al. 1989).

Material and Methods

Mealybugs were reared on *Talinum triangularae* Jacq. (Portulacaceae) at 25±1°C (except when otherwise specified, all the averages are given ± SD), 70±3% RH, 12L:12D photoperiod. This common weed is a good, though not preferred, host of *P. manihoti* in the field (Neuenschwander and Madojemu 1986). The fecundity, longevity, and r_m of *P. manihoti* are similar on the substitute plant to those on *Manihot esculenta* Crantz (Le Rü et al. 1992). The plants were infested with neonatal larvae (less than 12 h) to achieve synchronous development of individuals and thus limit size variations. For the experiment, the mealybugs were presented to the parasitoid on rooted cuttings of *T. triangularae*.

A cutting was placed in a ventilated chamber (height 13 cm, diameter 9 cm). Thirty reared mealybugs were placed on the leaf of this cutting: 10 second-instar larvae (L2), 10 third-instar (L3), and 10 fourth-instar (L4). Stages L2, L3, and L4 are the preferred host stages for the parasitoid and maximum fecundity is expressed with a density of 30 mealybugs per female wasp (Iziquel 1990). The mealybugs were placed at 26±0.5°C, 64±2% RH, 12L:12D photoperiod, 25–26 h before presentation to the parasitoid so that they had time to start feeding. The next day, at the start of the scotophase, a male and a female *E. lopezi* 3–10 h old were introduced and the chamber immediately returned to dark conditions. Every day, at the start of the scotophase, the couple were introduced to a new batch of 30 healthy mealybugs. The female was supplied with honey and left in the presence of the male throughout the experiment. The experiment continued until the death of each female. A total of 11 females was obtained from mummies collected in cassava fields in the Congo from September to December when the average temperature was 26°C (Iziquel and Le Rü 1989). As size may affect fecundity (van Dijken et al. 1991), females of similar size were chosen (1.6±0.3 mm body length).

The mealybugs were dissected 4 days after exposure to parasitism when parasitoid larvae were large enough (stage L2–L3) to be recovered easily. In this way, possible egg and L1 mortality may have been missed. The intrinsic natural rate of increase (r_m) was obtained by:

$$\Sigma_x \, e^{-r \cdot m_x} \cdot l_x \cdot m_x = 1$$

where (l_x) is the probability of survival and (m_x) is the number of female eggs laid per unit of time for a female of age (x) (Birch 1948). The duration of parasitoid development at 26°C was 17 days (Giordanengo and Nénon 1990). The pre-imago death rate, evaluated to be 5% by Löhr et al. (1989), was assumed to be zero. In the laboratory, about 60% of the parasitoids emerging from stages L2, L3, and L4 are female (Iziquel 1990). Under natural conditions the sex ratio fluctuates considerably, varying from extremes of 10 to 90% females (unpublished data). The average is about 50% and this figure was used to calculate the r_m.

Results

Of a total of 13328 mealybugs presented to 11 *E. lopezi* females, 5292 (39.7%) were parasitized and 718 (13.6%) were superparasitized. Female parasitoids lived for an average of 41.4±15.5 days with a range from 15 to 64 days. The egg-laying period averaged 36±13.2 days (range 14–47), resulting in 558.5±220.2 eggs laid (range 230–853). There is a correlation between fecundity and longevity of the parasitoid ($r^2=0.609$; $F=14.05$; $p=0.0046$). On the last day of the egg-laying period, 64% of the females were still alive, but 3 days later only 18% were still alive. The average number of female eggs laid per female per day (m_x) peaked at about 11 on the 7th day after eclosion and then decreased (Fig. 1). The *E. lopezi* population was multiplied by $R_0=269.9$ in one generation, T lasting 33.9 days. The intrinsic natural rate of increase (r_m) was calculated to be 0.213.

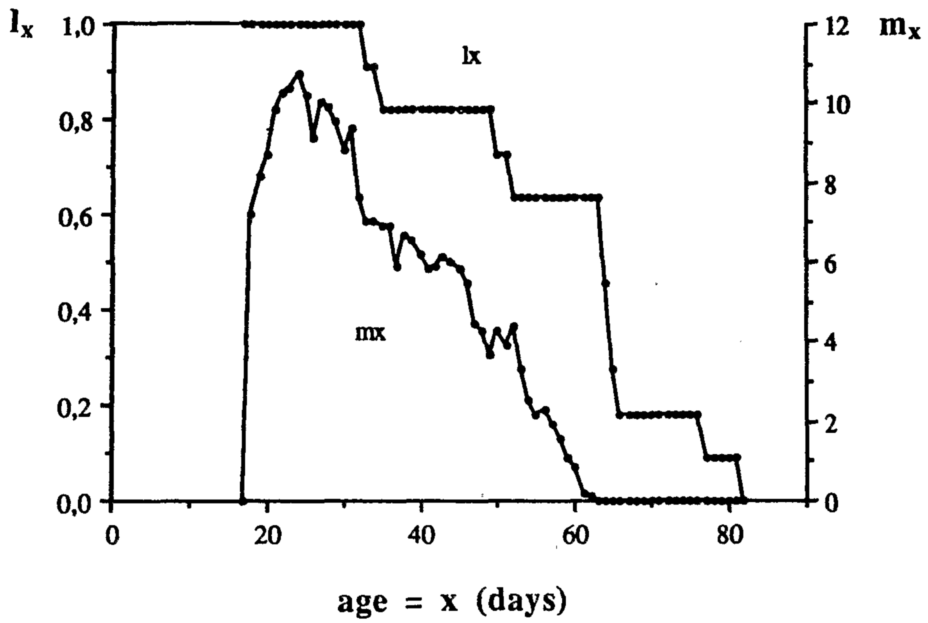

FIG. 1. Age-specific survival (l_x) and fecundity rate (m_x) of *Epidinocarsis lopezi* at 26±0.5°C, 64±2% RH, 12L:12D photoperiod.

Discussion

Fecundity, Longevity. The parasitoid fecundity found in our study was 3- to 16-fold higher than fecundities hitherto reported (Table 1). Parasitoid longevity was 2- to 7-fold higher too, except for the study of Biassangama et al. (1988) where it was the same as in our study. Several factors may affect the fecundity and longevity, or both, of the parasitoid: host density; method used for assessing fecundity; lack of food supply for adult females; temperature of the experiment; host plant; and existence of ecotypes in the species *E. lopezi* or *P. manihoti*.

The functional response of *E. lopezi* to host density was demonstrated by Iziquel (1990), who showed that there is a correlation between the number of eggs laid by the parasitoid and host density; seven eggs are laid per female per day with 10 mealybug hosts and 19 eggs with 30 mealybugs. The ratio between fecundities is 2.7 and the ratio between host densities is 3. The same ratios can be obtained in comparing fecundities and densities from our study with Biassangama et al. (1988) (Table 1). The limited host density explains the fecundity obtained by Biassangama et al. (1988) and it partially explains the results of Löhr et al. (1989) and Umeh (1988).

Table 1. Fecundity and longevity of *Epidinocarsis lopezi* from the literature

Reference	Temp. (°C)	Host density (mealybugs per day)	Fecundity	Longevity (days)
Odebiyi and Bokonon-Ganta (1986)	24–31	50	67 mummies	13
Umeh (1988)	26–34	20	34 eggs	6
Biassangama et al. (1988)	26	10	208 eggs	42
Löhr et al. (1989)	22	10	84 mummies	19
This study	26	30	559 eggs	41

Table 2. Comparison of the net reproduction rate (R_0), the generation time (T), and the intrinsic rate of natural increase (r_m) of *Epidinocarsis lopezi* and *Phenacoccus manihoti* at temperatures close to 26°C

	R_0 (♀/♀/gener.)	T (days)	r_m (♀/♀/day)
E. lopezi			
26°C, 64% RH (this study)	269.9	33.9	0.213
27°C, 60% RH (Löhr et al. 1989)	24.6	19.9	0.166
P. manihoti			
27°C, 72% RH (Lema and Herren 1985)	443.2	32.9	0.2
28°C, 65–95% RH (Schulthess et al. 1987)	485.7	36.5	0.183
25°C, 75% RH (Le Rü and Fabres 1987)	412	40.9	0.147

Three methods can be used to assess parasitoid fecundity: dissection of ovaries; dissection of parasitized hosts; and host mummy counts. Only the two latter methods were used in the studies reported in Table 1. Because *E. lopezi* is a solitary parasitoid, dissection of parasitized hosts will take into account the supernumerary eggs resulting from superparasitism whereas mummy counts do not. Mummy counts underestimate fecundity in proportion to superparasitism, which depends on host density. Iziquel (1990) showed that with a density of 30 mealybugs per female per day, 12% of the eggs laid by the parasitoid were supernumerary; with a density of 8 mealybugs, 38% of eggs were supernumerary.

Parasitoid longevity, and consequently fecundity, may be influenced by the lack of a carbohydrate source for females. None of the three studies that report short longevities (Table 1) mention if carbohydrates were provided for the parasitoid. Carbohydrates are essential in *E. lopezi* as in all synovogenic species (Jervis and Kidd 1986). In addition, the type of carbohydrates is important. van Lenteren et al. (1987), on the aphelinid *Encarsia formosa* Gahan, and Idoine and Ferro (1988), on the eulophid *Edovum puttleri* Grissell, showed that the longevity of the parasitoids increased with honey compared with honeydew.

The temperatures used by Odebiyi and Bokonon-Ganta (1986) and Umeh (1988) sometimes exceeded 30°C (Table 1). Löhr et al. (1989) showed that at 30°C the longevity of the parasitoid was reduced by 60% compared with longevity at 22°C.

Some authors have shown that the host plant species or variety may modify parasitoid fecundity and longevity (Ruberson et al. 1989; Bhatt and Singh 1989). No such studies are available on *E. lopezi*. Nevertheless, if host density had been the same in the Biassangama et al. (1988) study and in ours, fecundity probably would have been the same. Experimental temperatures were the same in both studies, leading to similar parasitoid longevities. It therefore seems that parasitoid longevity and fecundity are similar whether the mealybugs are reared on *M. esculenta* or *T. triangularae*.

Several authors have observed differences in parasitoid longevity among different ecotypes of the same species (Ruberson et al. 1989). No information is available on the existence of ecotypes in *E. lopezi* or its host *P. manihoti*. Both species are from the Paraguay river basin (Herren and Neuenschwander 1991). *Phenacoccus manihoti* was introduced in Africa in the early 1970s and *E. lopezi* about a decade later. Löhr et al. (1989) worked on parasitoids from Brazil. Other studies (Table 1) were performed on specimens descended from parents whose origin is not known; they were introduced in 1981–1982 in Nigeria (Umeh 1988; Odebiyi and Bokonon-Ganta 1986) and the Congo (Biassangama et al. 1988; and this study).

Intrinsic Natural Rate of Increase. Löhr et al. (1989) determined the intrinsic natural rate of increase of *E. lopezi* at five temperatures between 20 and 30°C. The maximum rate was obtained at 27°C. At this temperature, female longevity was 9 days with total fecundity of 42 mummies, and a net reproduction rate (R_0) almost 10-fold less than ours; the generation period (T) was reduced by 14 days and the intrinsic natural rate of increase (r_m) was 0.166 in comparison with 0.213 in our study (Table 2). These differences in the assessment of R_0, T, and r_m are accounted for by fecundity and longevity of the parasitoid. The intrinsic natural rate of increase also integrates other parameters, such as the duration of pre-imago development and the sex ratio, which vary slightly between the two studies.

The results of three studies performed on *P. manihoti* at temperatures of about 26°C are shown in Table 2. The net reproduction rate (R_0) observed in *E. lopezi* was 34–44% that of the mealybug, and the generation time (T) was almost the same or slightly shorter [data from Löhr et al. (1989) were not included]. The intrinsic natural rate of increase of the parasitoid appeared to be slightly higher than that of the mealybug.

The r_m of a parasitoid is sometimes compared with that of other parasitoids with the same host (Force and Messenger 1964) or hosts that are systematically close (Hagvar and Hofsvang 1990), with a hyperparasitoid (Singh and Srivastava 1989), or with its phytophagous host (Messenger 1964). In biological control, some authors consider that a parasitoid may be effective when, among other criteria, its r_m is the same or greater than that of the pest (Huffaker et al. 1976; van Lenteren and Woets 1988; Bigler 1989). Tripathi and Singh (1990) note that such comparisons are difficult, as the r_m can be affected by many factors and because the studies are not always performed under identical conditions. The effectiveness of beneficial insects predicted from laboratory results must be supplemented by studies under natural conditions (Bigler 1989). The effectiveness of *E. lopezi* has been demonstrated both by exclusion experiments (Neuenschwander et al. 1986) and by monitoring mealybug population dynamics after introduction of parasitoids (Neuenschwander et al. 1989; Hammond and Neuenschwander 1990). Nevertheless, Iziquel and Le Rü (1989) and Le Rü et al. (1991) showed that under certain conditions in the Congo (high host densities, extremely high rates of hyperparasitism), the parasitoid cannot control *P. manihoti* populations.

Acknowledgments

The authors thank J.P. Dipietro and J.S. Pierre (Ecole Nationale Supérieure Agronomique de Rennes) for their help with data processing.

References

Bhatt, N., and R. Singh. 1989. Bionomics of an aphidiid parasitoid *Trioxys indicus*. 30. Effect of host plants on reproductive and development factors. *Biological Agriculture and Horticulture* **6**: 149–157.

Biassangama, A., G. Fabres, and J.P. Nénon. 1988. Parasitisme au laboratoire et au champ d'*Epidinocarsis* (*Apoanagyrus*) *lopezi* (Hym.: Encyrtidae) auxiliaire exotique introduit au Congo pour la régulation de l'abondance de *Phenacoccus manihoti* (Hom.: Pseudococcidae). *Entomophaga* **33**: 453–465.

Bigler, F. 1989. Quality assessment and control in entomophagous insects used for biological control. *Journal of Applied Entomology* **108**: 390–400.

Birch, L.C. 1948. The intrinsic rate of natural increase of an insect population. *Journal of Animal Ecology* **17**: 15–26.

Force, D.C., and P.S. Messenger. 1964. Fecundity, reproductive rates, and innate capacity for increase of three parasites of *Therioaphis maculata* (Buckton). *Ecology* **45**: 706–715.

Giordanengo, P., and J.P. Nénon. 1990. A study of the life cycle of *Epidinocarsis* (=*Apoanagyrus*) *lopezi* (Hymenoptera: Encyrtidae) introduced parasitoid on the cassava mealybug *Phenacoccus manihoti* (Homoptera: Pseudococcidae) in Africa. *Journal of African Zoology* **104**: 549–555.

Hagvar, E.B., and T. Hofsvang. 1990. Fecundity and intrinsic rate of increase of the aphid parasitoid *Ephedrus cerasicola* Stary (Hym., Aphidiidae). *Journal of Applied Entomology* **109**: 262–267.

Hammond, W.N.O., and P. Neuenschwander. 1990. Sustained biological control of the cassava mealybug *Phenacoccus manihoti* (Hom., Pseudococcidae) by *Epidinocarsis lopezi* (Hym. Encyrtidae) in Nigeria. *Entomophaga* **35**: 515–526.

Herren, H.R., and P. Neuenschwander. 1991. Biological control of cassava pests in Africa. *Annual Review of Entomology* **36**: 257–283.

Huffaker, C.B., F.J. Simmonds, and J.E. Laing. 1976. The theoretical and empirical basis of biological control. pp. 41–78 *in* Huffaker, C.B., and P.S. Messenger (Eds.), Theory and Practice of Biological Control. Academic Press, New York, NY. 788 pp.

Idoine, K., and D.N. Ferro. 1988. Aphid honeydew as a carbohydrate source for *Edovum puttleri* (Hymenoptera: Eulophidae). *Environmental Entomology* **17**: 941–944.

Iheagwam, E.U. 1981. The influence of temperature on increase rates of the cassava mealybug, *Phenacoccus manihoti* Mat.-Ferr. (Homoptera, Pseudococcidae). *Journal of African Zoology* **95**: 959–964.

Iziquel, Y. 1990. Le parasitisme de la cochenille du manioc par l'Encyrtidae *Epidinocarsis lopezi*: un exemple d'interactions hôte–parasitoïde chez les insectes. Thèse d'Université, Rennes 1. 75 pp.

Iziquel, Y., and B. Le Rü. 1989. Influence de l'hyperparasitisme sur les populations d'un Hyménoptère Encyrtidae, *Epidinocarsis lopezi*, parasitoïde de la cochenille du manioc *Phenacoccus manihoti* introduit au Congo. *Entomologia Experimentalis et Applicata* **52**: 239–247.

Jervis, M.A., and N.A.C. Kidd. 1986. Host feeding strategies in Hymenopteran parasitoids. *Biological Review* **61**: 395–434.

Lema, K.M., and H.R. Herren. 1985. The influence of constant temperature on population growth rates of the cassava mealybug *Phenacoccus manihoti*. *Entomologia Experimentalis et Applicata* **38**: 165–169.

Le Rü, B., and G. Fabres. 1987. Influence de la température et de l'hygrométrie relative sur la capacité d'accroissement de la cochenille du manioc *Phenacoccus manihoti* (Hom. Pseudococcidae) au Congo. *Acta Oecologica, Oecologia Applicata* **8**: 165–174.

Le Rü, B., Y. Iziquel, A. Biassangama, and A. Kiyindou. 1991. Variations d'abondance et facteurs de régulation de la cochenille du manioc *Phenacoccus manihoti* (Hom.: Pseudococcidae) cinq ans après l'introduction d'*Epidinocarsis lopezi* (Hym.: Encyrtidae) parasitoïde néotropical au Congo en 1982. *Entomophaga* **36**: 499–511.

Le Rü, B., and B. Papierok. 1987. Taux intrinsèque d'accroissement naturel de la cochenille du manioc, *Phenacoccus manihoti* Matile-Ferrero (Homoptère, Pseudococcidae). Intérèt d'une méthode simplifiée d'estimation de r_m. *Acta Oecologica, Oecologia Applicata* **8**: 3–14.

Le Rü, B., M. Tertuliano, and P.A. Calatayud. 1992. Les différentes catégories de résistance des plantes–hôtes de la cochenille du manioc *Phenacoccus manihoti* (Hom. Pseudococcidae), perspectives d'études. Résumé du 4è Atelier du Réseau CORAF Manioc: Biocénose des principaux ravageurs du manioc et lutte biologique. I.I.T.A., Bénin, Cotonou, 4–9 mars 1991. In press.

Löhr, B., A.M. Varela, and B. Santos. 1989. Life-table studies on *Epidinocarsis lopezi* (De Santis) (Hym., Encyrtidae), a parasitoid of the cassava mealybug, *Phenacoccus manihoti* Mat.-Ferr. (Hom., Pseudococcidae). *Journal of Applied Entomology* **107**: 425–434.

Messenger, P.S. 1964. Use of life tables in a bioclimatic study of an experimental aphid–braconid wasp host–parasite system. *Ecology* **45**: 119–131.

Neuenschwander, P., W.N.O. Hammond, A.P. Gutierrez, A.R. Cudjoe, R. Adjakloe, J.U. Baumgärtner, and U. Regev. 1989. Impact assessment of the biological control of the cassava mealybug, *Phenacoccus manihoti* Matile-Ferrero (Hemiptera: Pseudococcidae), by the introduced parasitoid *Epidinocarsis lopezi* (De Santis) (Hymenoptera: Encyrtidae). *Bulletin of Entomological Research* **79**: 579–594.

Neuenschwander, P., and E. Madojemu. 1986. Mortality of the cassava mealybug, *Phenacoccus manihoti* Mat.-Ferr. (Hom.: Pseudococcidae), associated with an attack by *Epidinocarsis lopezi* (Hym.: Encyrtidae). *Bulletin de la Société Entomologique Suisse* **59**: 57–62.

Neuenschwander, P., F. Schulthess, and E. Madojemu. 1986. Experimental evaluation of the efficiency of *Epidinocarsis lopezi*, a parasitoid introduced into Africa against the cassava mealybug *Phenacoccus manihoti*. *Entomologia Experimentalis et Applicata* **42**: 133–138.

Odebiyi, J.A., and A.H. Bokonon-Ganta. 1986. Biology of *Epidinocarsis* (=*Apoanagyrus*) *lopezi* (Hymenoptera: Encyrtidae) an exotic parasite of the cassava mealybug, *Phenacoccus manihoti* (Homoptera: Pseudococcidae) in Nigeria. *Entomophaga* **31**: 251–260.

Ruberson, J.R., M.J. Tauber, and C.A. Tauber. 1989. Intraspecific variability in hymenopteran parasitoids: Comparative studies of two biotypes of the egg parasitoid *Edovum puttleri* (Hymenoptera: Eulophidae). *Journal of the Kansas Entomological Society* **62**: 189–202.

Schulthess, F., J.U. Baumgärtner, and H.R. Herren. 1987. Factors influencing the life table statistics of the cassava mealybug *Phenacoccus manihoti*. *Insect Science and its Application* **8**: 851–856.

Singh, R., and P.N. Srivastava. 1989. Life table studies of an aphid hyperparasitoid *Alloxysta pleuralis* (Cameron) (Hym., Alloxystidae). *Journal of Applied Entomology* **107**: 351–356.

Tripathi, R.N., and R. Singh. 1990. Fecundity, reproductive rate, longevity and intrinsic rate of increase of an aphidiid parasitoid *Lysiphlebia mirzai*. *Entomophaga* **35**: 601–610.

Umeh, E.-D.N. 1988. Development, oviposition, host feeding and sex determination in *Epidinocarsis lopezi* (De Santis) (Hymenoptera: Encyrtidae). *Bulletin of Entomological Research* **78**: 605–611.

van Dijken, M.J., P. Neuenschwander, J.J.M. van Alphen, and W.N.O. Hammond. 1991. Sex ratios in field populations of *Epidinocarsis lopezi*, and exotic parasitoid of the cassava mealybug in Africa. *Ecological Entomology* **16**: 233–240.

van Lenteren, J.C., A. van Vianen, H.F. Gast, and A. Kortenhoff. 1987. The parasite–host relationship between *Encarsia formosa* Gahan (Hymenoptera: Aphelinidae) and *Trialeurodes vaporariorum* (Westwood) (Homoptera: Aleyrodidae). XVI. Food effects on oogenesis, oviposition, life-span and fecundity of *Encarsia formosa* and other hymenopterous parasites. *Journal of Applied Entomology* **103**: 69–84.

van Lenteren, J.C., and J. Woets. 1988. Biological and integrated control in greenhouses. *Annual Review of Entomology* **33**: 239–269.

(Date received: 22 October 1991; date accepted: 10 August 1992)