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Praon volucre (Hymenoptera: Braconidae: Aphidiinae), a natural enemy of *Macrosiphum euphorbiae* (Hemiptera: Aphididae): Life table and intrinsic rate of population increase

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Abstract. Life table data of natural enemies are often used to understand their population dynamics and estimate their potential role in the biological control of pests. *Macrosiphum euphorbiae* (Thomas) (Hemiptera: Aphididae) is an important pest of several crops and its intrinsic rate of population increase (r_m) is 0.282 at 22°C. The life table parameters (immature mortality, developmental time, sex ratio of emerging adults, fecundity and longevity) of *Praon volucre* (Haliday) (Hymenoptera: Braconidae: Aphidiinae) parasitizing *M. euphorbiae* were estimated in a climatic chamber at 22 ± 1°C, RH 70 ± 10% and 12 h photophase. Immature mortality was 8.2%, developmental time of males and females was 13.9 and 14.4 days, respectively, and the sex ratio was 0.55 (= fraction of females). Parasitoid fecundity was 504 eggs and longevity 11 days. The net rate of reproduction (R_0) was 207.5 females and the intrinsic rate of population increase (r_m) 0.281 females/female/day. The time for doubling the population (TD) was 2.45 weeks. *P. volucre* has a population growth rate similar to that of its host *M. euphorbiae* and might therefore be a good candidate for the biological control of this aphid.

INTRODUCTION

In the selection and evaluation of natural enemies, determination of population growth parameters is important for understanding their population dynamics. Life table fertility data provide an integrated view of these population biological characteristics under certain environmental conditions and life table fertility data can be used to estimate the potential of a biological control agent for reducing the abundance of a pest (Bellows et al., 1992). Life table fertility data can also be used to calculate the intrinsic rate of population increase (r_m), which is an important selection criterion for identifying potential biological control agents (van Lenteren, 2009).

Aphids have a high reproductive capacity and short developmental time resulting in rapidly increasing populations, which make them important pests in several crops, both in the field and in protected cultivation (Bueno, 2005). The aphid *Macrosiphum euphorbiae* (Thomas) (Hemiptera: Aphididae) originates from North America, but is now distributed throughout most of the world. It is a polyphagous aphid that can damage more than 200 species of plants belonging to more than 20 families (Blackman & Eastop, 1985). In addition to being a serious pest of field crops, this aphid also infests crops in greenhouses in Brazil. According to Boll & Lapchin (2002), this species is able to disperse and reproduce very quickly in protected environments like greenhouses.

There are few natural enemies that can control aphids in greenhouses, e.g., the parasitoid *Aphidius colemani* Viereck (Hymenoptera: Braconidae, Aphidiinae) (Bueno & Sampaio, 2009), the predator *Aphidoletes aphidimyza* (Rondani) (Diptera: Cecidomyiidae) (Rabasse & van Steenis, 1999) and many other species that have much lower reproductive rates than the aphids (Bueno, 2005). To find aphid parasitoids with a sufficiently high rate of reproduction for use as biocontrol agents is a great challenge. Currently, studies are being conducted in this laboratory on identifying parasitoids that can be used to control *M. euphorbiae* (e.g. De Conti et al., 2008; Sidney et al., 2010a). According to Starý et al. (2007), the parasitoids *Praon volucre* (Haliday) and *Aphidius ervi* Haliday (Hymenoptera: Braconidae, Aphidiinae) parasitize *M. euphorbiae* in the field and greenhouses. Both aphidiines parasitize *M. euphorbiae* on a wide range of host plants in various ecosystems with different climatic conditions (Kavallieratos et al., 2004a, 2005, 2010; Tomanović et al., 2009). Sidney et al. (2010a) state that *P. volucre* is superior to *A. ervi* in terms of larval competition, which results in a greater probability of establishment after release when compared with *A. ervi*.

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Life table parameters of Brazilian *M. euphorbiae* populations were determined by De Conti et al. (2010) who report an intrinsic rate of population increase of 0.282 females/female/day at 22°C. These authors also report high rates of parasitism of the aphids *M. euphorbiae*, *Uroleucon ambrosiae* (Thomas) and *Aulacorthum solani* (Kaltenbach) (Hemiptera: Aphididae) by *P. volucre* (De Conti et al., 2008; Silva et al., 2009). Currently, the commercially available parasitoid for *M. euphorbiae* control is *A. ervi* and as there are many cases of the control of this aphid by this parasitoid being insufficient there is certainly a need for a more efficient natural enemy (J. van Schelt, 2010, pers. commun.).

In this paper, the life table fertility parameters of *P. volucre* are determined and compared with those of the aphid *M. euphorbiae* in order to estimate the biological control potential of this parasitoid.

MATERIAL AND METHODS

Colonies of *M. euphorbiae* were collected from lettuce (*Lactuca sativa* L.) in the field. Lettuce leaves infested with aphids were transported to the laboratory in Petri dishes (15 cm diameter) sealed with organza. After identification (Peña-Martinez, 1992), the aphids were reared on lettuce plants grown in pots placed in acrylic cages (60 × 30 × 30 cm) maintained in a climatic room (22 ± 2°C, RH 70 ± 10% and 12 h photophase).

Sowthistle plants, *Sonchus oleraceus* L., infested with *Uroleucon sonchi* (L.) and containing parasitoid mummies were collected in the field and transported to the laboratory inside paper bags. The plants were placed in a pot containing water, inside an acrylic cage (30 × 30 × 60 cm), and all the mummies developing on these plants were collected during 1 week. The mummies were individually placed in glass tubes (100 mm × 8 mm) in a climate room (22 ± 2°C, RH 70 ± 10% and 12 h photophase) until emergence of adults. The adults of *P. volucre* were identified using the characteristics provided by Tomanović et al. (2003). The adult parasitoids were released on lettuce plants infested with *M. euphorbiae* in acrylic cages. In order to obtain sufficient parasitoids for the experiments, field collected parasitoids were reared for 3 generations in the laboratory. The fourth generation of the laboratory reared population was used in the experiments

To assess immature mortality, females of *P. volucre* (n = 10) up to 24 h old, mated, with no prior oviposition experience and fed with honey and water were used in the experiments. Each female was released into a Petri dish (5 cm diameter) containing a lettuce leaf disc with 40 nymphs of *M. euphorbiae* on a layer of 1% water-agar. The Petri dishes were kept in a climatic chamber at 22 ± 1°C, RH 70 ± 10% and 12 h photophase. To standardize the age of the nymphs, 30–50 adults of *M. euphorbiae* were maintained for 24 h in Petri dishes (15 cm diameter) containing a lettuce leaf disc on a layer 1% water-agar. Nymphs of the second and third instars (approximately 24 to 36 h old) were used in the experiments. After the first oviposition, each *P. volucre* female was allowed to lay eggs for 40 min. The Petri dishes with nymphs remained in the climatic chamber. After 4 days, 20 aphid nymphs were dissected under a stereomicroscope (Olympus-SZ40, Olympus Corporation, Japan) to determine the number of aphids with parasitoid larvae inside. The other 20 nymphs remained in the climatic chamber until mummification, after which the mummies were placed individually in glass tubes (100 mm × 8 mm), containing honey and water, until adult emergence. The number of adult parasitoids, the developmental time (from oviposition to emergence) and the sex ratio were determined. Percentage immature mortality of *P. volucre* was estimated by the difference between the number of aphids with parasitoid larvae inside (NL) and the number of emerged adult parasitoids (NA) (% M = [(NL – NA) / NL] × 100).

Reproduction and longevity of *P. volucre* were determined using the method used by van Steenis (1994). Fifteen *P. volucre* 24 h old females, mated and fed with honey and water, were used. Each female parasitoid was released in a Petri dish (15 cm diameter) containing a lettuce leaf disc on a layer of 1% water-agar and honey and water as food and second and third instar nymphs of *M. euphorbiae*. The parasitoid females remained in the Petri dish for 24 h. The Petri dishes were sealed with organza and kept in a climatic chamber. The number of nymphs offered daily to the parasitoid females during their life cycle was: 300 nymphs on the first day, 250 nymphs on the second day, 200 nymphs on the third day, 150 nymphs on the fourth day, 100 nymphs on the fifth day and 50 nymphs on all the subsequent days until the females died. The parasitized nymphs were kept for three days in a climatic chamber to allow the parasitoid to develop to the larval stage. After this period, the aphids were transferred to a slide on which there was a drop of sodium chloride solution (1%) and dissected under a stereomicroscope (Olympus-SZ40, Olympus Corporation, Japan). The number of parasitoid larvae per aphid nymph was recorded. The number of parasitoid larvae found was considered to be equivalent to the number of eggs laid by the *P. volucre* females, although some parasitoid mortality may have occurred during the first three days after oviposition.

Parasitoid life table fertility was determined by using the growth parameters age interval (x), age-specific fecundity (m_x) and age-specific survival (l_x). The net reproductive rate (R_0), the time interval between generations (T), the intrinsic rate of population increase (r_m), the finite rate of increase (λ) and the time needed for the population to double in size (TD) were calculated using the methods described in Andrewartha & Birch (1954).

RESULTS

Average immature mortality of *P. volucre* was 8.2% (Table 1). Male and female developmental times were 13.9 ± 0.13 and 14.4 ± 0.14 days, respectively, and the sex ratio, expressed as the proportion of females, was

TABLE 1. Percentage mortality of immature stages of *Praon volucre* in *Macrosiphum euphorbiae* (22 ± 1°C, RH 70 ± 10% and 12 h photophase).

Female	No. of nymphs with parasitoid larvae (NL) in a sample of 20 nymphs	No. of adults (NA) that emerged from 20 aphids
1	3	10
2	4	5
3	4	2
4	9	5
5	1	2
6	10	5
7	7	4
8	2	6
9	11	11
10	10	6
Total	61	56
% Immature mortality*	8.2%	

* % Immature mortality = [(NL – NA) / NL] × 100

TABLE 2. Daily fecundity of *Praon volucre* ovipositing in *Macrosiphum euphorbiae* (22 ± 1°C, RH of 70 ± 10% and 12 h photophase).

Age of females (days)	Number of females living	Number of aphids offered / female	Total larvae / female (± SE)	Cumulative percentage eggs / female	Aphids not parasitized (± SE)	Dead aphids (± SE)
1	15	300	98.3 ± 5.75	19.5	178.2 ± 5.62	25.7 ± 5.55
2	15	250	58.8 ± 4.68	31.1	166.3 ± 4.74	26.1 ± 5.51
3	15	200	52.7 ± 5.08	41.5	127.8 ± 4.62	20.9 ± 4.35
4	14	150	44.7 ± 4.56	50.4	92.1 ± 5.03	14.7 ± 3.36
5	12	100	42.7 ± 3.63	58.8	52.7 ± 3.67	6.0 ± 2.07
6	12	50	27.7 ± 3.39	64.3	20.9 ± 3.45	2.3 ± 1.22
7	11	50	28.1 ± 3.40	69.9	19.8 ± 3.26	3.9 ± 1.52
8	10	50	26.4 ± 2.89	75.1	22.7 ± 2.88	1.6 ± 1.22
9	10	50	22.6 ± 2.88	79.6	24.4 ± 3.07	3.5 ± 2.21
10	10	50	23.0 ± 3.16	84.1	25.4 ± 3.27	2.5 ± 1.64
11	9	50	18.5 ± 2.81	87.8	29.6 ± 2.89	2.8 ± 1.41
12	7	50	14.8 ± 2.63	90.8	35.3 ± 2.76	1.3 ± 1.26
13	6	50	15.3 ± 2.47	93.8	33.2 ± 2.61	1.6 ± 1.58
14	6	50	13.8 ± 2.37	96.5	35.2 ± 2.68	2.8 ± 2.00
15	5	50	7.6 ± 2.93	98.1	40.6 ± 2.85	1.8 ± 1.52
16	5	50	3.2 ± 1.82	98.7	45.0 ± 2.19	1.8 ± 1.55
17	3	50	4.0 ± 1.89	99.6	46.0 ± 1.89	0.0 ± 0.0
18	3	50	2.3 ± 1.05	100.0	47.0 ± 2.28	0.7 ± 1.04
19	2	50	0 ± 0.0	100.0	50.0 ± 0.0	0.0 ± 0.0
20	1	50	0 ± 0.0	100.0	50.0 ± 0.0	0.0 ± 0.0
21	0	–	–	–	–	–
Total			504.5	100%	1142.2	120.0

TABLE 3. Number and percentage of *Macrosiphum euphorbiae* nymphs containing larvae of *Praon volucre* (22 ± 1°C, RH 70 ± 10% and 12 h photophase).

Age of females (days)	Number of live females	Number of aphids containing parasitoid larvae	
		1 larva (± SE)	2 larvae (± SE)
1	15	93.9 ± 10.37	2.2 ± 0.55
2	15	56.5 ± 5.45	1.1 ± 0.36
3	15	50.0 ± 6.85	1.3 ± 0.46
4	14	41.9 ± 5.14	1.3 ± 0.54
5	12	40.0 ± 3.46	1.4 ± 0.46
6	12	25.9 ± 2.85	0.9 ± 0.44
7	11	25.9 ± 3.43	1.1 ± 0.29
8	10	25.0 ± 2.72	0.7 ± 0.35
9	10	21.6 ± 2.45	0.5 ± 0.26
10	10	21.2 ± 2.74	0.9 ± 0.59
11	9	16.9 ± 2.26	0.8 ± 0.57
12	7	14.6 ± 2.71	0.1 ± 0.06
13	6	15.3 ± 2.51	0.0 ± 0.00
14	6	12.4 ± 1.89	0.7 ± 0.34
15	5	7.6 ± 3.85	0.0 ± 0.00
16	5	3.2 ± 1.58	0.0 ± 0.00
17	3	3.7 ± 1.85	0.3 ± 0.11
18	3	2.3 ± 1.55	0.0 ± 0.00
19	2	0.0 ± 0.00	0.0 ± 0.00
20	1	0.0 ± 0.00	0.0 ± 0.00
21	0	–	–
Total number of aphids parasitized		477.9	13.3
Percentage of aphids with 1 or 2 parasitoid larvae		97.2%	2.8%

0.55. Females of *P. volucre* oviposited until the 18th day of their lifespan, resulting in a total fecundity of 504 eggs (Table 2). Cases of superparasitism (i.e. more than one parasitoid per host) occurred during almost the whole life span of *P. volucre* females, but at a very low rate and only 2.8% of all host nymphs contained more than one parasitoid larva (Table 3). Maximum longevity of *P. volucre* females was 20 days and average longevity 11 days. After the third day a gradual decrease in survival was recorded (Fig. 1).

The growth parameters calculated from the life table fertility data of *P. volucre* were: a net reproductive rate (R_0) of 207.5 females, an intrinsic rate of population increase (r_m) of 0.281 females/female/day, a finite rate of increase (λ) of 1.32 females/day, a time interval between generations (T) of 18.9 days and a time period for the parasitoid population to double (TD) of 2.45 weeks.

DISCUSSION

Survival of immature parasitoids is highly dependent on host survival (Jervis & Copland, 1996). Climatic factors (Rodrigues et al., 2004), nutritional quality (Silva et al., 2008a; Sidney et al., 2010b) and host defences (Brodeur & Boivin, 2004) are among the main causes of mortality in immature parasitoids. The low percentage immature mortality recorded in this study (8.2%) indicates that *M. euphorbiae* is a good host for *P. volucre*. Stilmant et al. (2008) report that immature mortality of the same parasitoid developing in *Sitobion avenae* (Fabricius), *Metopolophium dirhodum* (Walker) and *Rhopalosiphum padi* (L.) (Hemiptera: Aphididae) is 35.3, 38.7 and 38.7%, respectively.

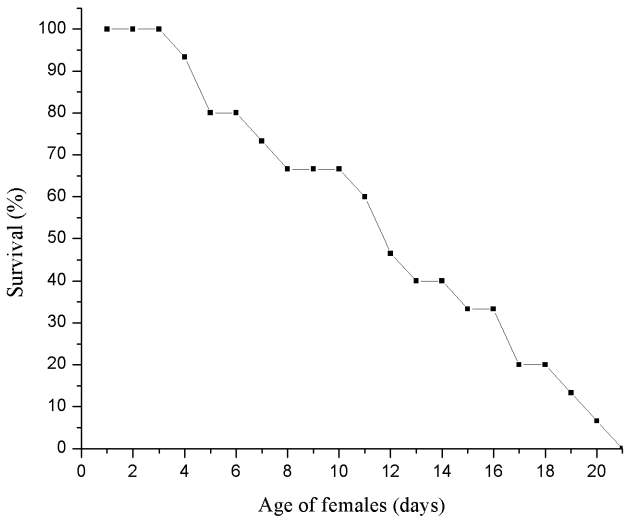

Fig. 1. Survival of *Praon volucre* females when provided with nymphs of *Macrosiphum euphorbiae*.

The developmental time of males and females of *P. volucre* in *M. euphorbiae* was similar (13.9 and 14.4 days, respectively) to the values reported by De Conti et al. (2008) in the same aphid host (15.2 and 15.9 days, respectively) and in *U. ambrosiae* (15.8 and 15.9 days, respectively).

The sex ratio of *P. volucre* in this study was 0.55. The sex ratio of the same species developing in *M. euphorbiae* is 0.44 (De Conti et al., 2008), in *A. solani* 0.49 (Silva et al., 2009) and in *S. avenae* 0.7 (Langer et al., 2004). According to Shukla & Triphathi (1993), climatic conditions, size and host density have a direct influence on the sex ratio of parasitoids and female biased sex ratios are common in Aphidiinae populations.

The rates and patterns of oviposition recorded for *P. volucre* parasitizing *M. euphorbiae* are similar to those reported by Messenger (1964) for *Praon palitans* Muesebeck (Hymenoptera: Braconidae: Aphidiinae) parasitizing *Therioaphis trifolii* form *maculata* (Buckton) (Hemiptera: Aphididae). Both parasitoids oviposit for periods exceeding 15 days and approximately 50% of the eggs are laid within the first four days of a female's life. However, *P. volucre* has a higher total fertility (504 eggs) than *P. palitans* (298.8 eggs; Messenger, 1964). In other Aphidiinae, such as *A. colemani* and *Lysiphlebus testaceipes* (Cresson) (Hymenoptera: Braconidae: Aphidiinae), about 85–90% of the offspring is produced during the first three days after female emergence and females oviposit for an average of 8 days (Rodrigues et al., 2003; Torres et al., 2007; Silva et al., 2008b). Reproduction in *A. colemani* and *L. testaceipes* seems to be limited by time because females of these species parasitize a very high number of hosts during the first three days of their life. Indeed, Rasekh et al. (2010) report that females of *Lysiphlebus fabarum* (Marshall) (Hymenoptera: Braconidae: Aphidiinae) are more likely to be time-limited than egg-limited because they lay most of their eggs early in life. In contrast, the parasitoids *P. volucre* and *P. palitans* appear to be egg-limited, i.e., these females need a long lifespan to maximize offspring production. This feature of a long oviposition period leads to long persistence of *P. volucre* in crops. Interestingly, Kavallieratos et al. (2004b) record the long presence of *P. volucre* in tobacco crops infested with *Myzus persicae* (Sulzer).

A low rate of super-parasitism of *M. euphorbiae* nymphs by *P. volucre* was recorded in this study. Host discrimination, i.e. the ability to recognize an already parasitized host determines the extent of super-parasitism (van Lenteren, 1981). Chow & Mackauer (1986) report that parasitoids recognize recently parasitized aphids on antennal contact. With the development of the parasitoid inside the host, physiological changes occur that can be recognized by sensillae on the ovipositor of the aphid parasitoids. According to Mackauer (1990), external marking of aphid hosts is species-specific, whereas the physiological changes that occur after oviposition are more general and can be recognized by other species of parasitoids.

Super-parasitism by solitary parasitoids is usually seen as a waste of eggs and time (van Lenteren, 1981). However, there are situations in which super-parasitism can be beneficial for a parasitoid, such as when it results in higher survival (van Alphen & Visser, 1990; Bai & Mackauer, 1992; Mackauer & Chau, 2001). *Praon volucre* is apparently able to discriminate between non-parasitized and parasitized hosts, because only a very small proportion of the hosts were super-parasitized. In those cases where it is doubtful if host discrimination occurs, the actual distribution of eggs by each female should be tested against the Poisson distribution, which supposes random egg distribution (van Lenteren et al., 1978). Here a simpler approach was used as the pooled data indicated an ability to discriminate. According to the pooled data (Table 2 and 3) 1442 aphids contained no parasitoid eggs, 478 one egg and only 13 aphids had 2 eggs. If the parasitoids had distributed their eggs at random (i.e. without the ability to discriminate) the expected Poisson distribution, predicts 1210 aphids without eggs, 363 with one egg, 54 with two eggs and 6 with three or more eggs. The actual egg distribution differs significantly from the Poisson distribution (Chi-Square = 77.70, df = 3, $P < 0.00000$).

The experimental set-up used might have led to super-parasitism, but the number of hosts offered to the parasitoid was two to three times more than the daily oviposition capacity of *P. volucre*, so host limitation and time available for oviposition cannot explain superparasitism. That a small proportion of the hosts was super-parasitized when ample hosts were available is also recorded for *A. colemani* (van Steenis, 1993; Torres et al., 2007) and *L. testaceipes* (van Steenis, 1994; Rodrigues et al., 2003; Silva et al., 2008b). Although *P. volucre* shows intraspecific discrimination, it is apparently not able to discriminate interspecifically as Sidney et al. (2010a) show it is unable to distinguish between unparasitized hosts and hosts already parasitized by *A. ervi*. Chow & Mackauer (1984) mention that females of *Praon pequodorum* Viereck did not distinguish hosts already parasi-

tized by *Aphidius smithi* Sharma & Subba Rao and report that *P. pequodorum* out competes *A. smithi.*

The longevity of *P. volucre* is affected by the presence of hosts. In the absence of hosts, *P. volucre* females live for 14.1 days (Silva et al., 2009) and of 20.4 days (De Conti et al., 2008). In this study a shorter longevity of 11 days in the presence of hosts was recorded and this is thought to be due to the costs of egg laying (Roitberg et al., 2001).

One of the parameters used to evaluate the potential biological control capacity of a parasitoid is its intrinsic rate of population increase (r_m). According to van Lenteren (2009), a parasitoid will be an effective control agent if, in addition to other factors, its r_m is equal or greater than that of the target pest. De Conti et al. (2010), using the same experimental conditions as used in this study for *P. volucre*, observed that the r_m for the host aphid *M. euphorbiae* was 0.282, which is only slightly higher than the r_m of *P. volucre*. A positive characteristic in addition to high r_m is the long reproductive period of *P. volucre*: they parasitize hosts for up to 18 days. However, it should be realized that the experiments were conducted in confined spaces under optimal conditions. Thus the findings still need to be validated under more practical greenhouse conditions.

The results of this study demonstrate that *P. volucre* has an innate capacity of population increase similar to that of its host. This suggests that *M. euphorbiae* might be controlled by *P. volucre* by regular inundative releases. Furthermore, these results provide important basic data for developing methods of mass production, quality control and of releasing parasitoids.

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