Life Tables of *Venturia canescens* (Hymenoptera: Ichneumonidae) Parasitizing the Mediterranean Flour Moth (Lepidoptera: Pyralidae)

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ABSTRACT Effects of temperature, adult feeding, and host instar on life table parameters of *Venturia canescens* Gravenhorst (Hymenoptera: Ichneumonidae) parasitizing larvae of *Ephestia kuehniella* Zeller (Lepidoptera: Pyralidae) were studied in the laboratory. Experimental adults lived under various regimes of temperature (15, 20, 25, and 30°C), food supply (with or without access to honey), and host instar (second, third, fourth, and fifth). Temperature increase resulted in higher values of the intrinsic rate of natural increase (r_m), the net reproductive rate (R_o), the finite capacity of increase (λ), and the gross reproductive rate (*GRR*), whereas it was followed by decrease of the mean generation time (*G*) and the doubling time (*DT*) values. Feeding on honey caused remarkable increase of r_m, R_o, and *GRR*, whereas r_m and λ reached their maximum when full-grown hosts (fifth instar) were parasitized. This is the first time life table parameters of *V. canescens* have been studied. The findings of the current study are discussed on the basis of improving *V. canescens* performance as a biological agent against moth pests of stored products.

KEY WORDS *Venturia canescens*, life tables, biological control, stored products

INSECT PESTS OF STORED PRODUCTS are attacked by a variety of natural enemies, such as predatory insects and mites, hymenopterous parasitoids, other vertebrates, and pathogenic microorganisms. Although the use of beneficial insects to control pests is well established in agriculture and horticulture, their use against postharvest pests was very limited until recently. During the last decade, however, biological control has come to occupy a significant part in stored product integrated pest management (IPM) for many reasons, such as IPM's many advantages over traditional chemical methods, pest resistance to conventional pesticides, the phase out of methyl bromide, the favorable conditions of the stored-product environment for beneficial insects, and its compatibility with other management methods (Arbogast 1984, Brower et al. 1996, Schöller et al. 1997, Schöller and Flinn 2000).

Hymenopterous parasitoids are natural components of stored grain ecosystem and some species are of potential value as biocontrol agents. *Venturia canescens* Gravenhorst (Hymenoptera: Ichneumonidae) is a solitary, koinobiont endoparasitoid that is known to attack and develop successfully in the larvae of many lepidopterous pests of stored products (Frilli 1965, Salt 1975). Effects of temperature (Ahmad 1936; Nakahara and Iwabuchi 2000; Eliopoulos and Stathas 2003, 2005; Eliopoulos et al. 2003), host species (Harvey and Thompson 1995; Harvey et al. 1995, 1996; Harvey 1996, 2000; Harvey and Vet 1997), and host instar or size (Harvey et al. 1994, Harvey and Thompson 1995, Sait et al. 1995, Harvey and Vet 1997, Hemerik and Harvey 1999, Eliopoulos et al. 2003, Eliopoulos and Stathas 2005) on features of its preimaginal developmental and adult life, have been the subject of many previous studies. However, no experimental data concerning its life table parameters are available.

Life table parameters are often used by biological control workers (Messenger 1964) when the problem of choosing the most effective biocontrol agents is faced. Especially, in the absence of other criteria, the species with the greatest value of r_m would be usually selected. Moreover, knowing how r_m varies in relation to factors such as temperature and host density or instar can be very helpful in deciding on the timing of introduction, for example, in an inoculative release program.

The current study was undertaken to investigate the effects of temperature, adult feeding, and host instar on life table parameters of *V. canesens* against the Mediterranean flour moth, *Ephestia kuehniella* Zeller (Lepidoptera: Pyralidae), to provide useful information for its future use as biocontrol agent against moth pests in stored-product facilities.

Materials and Methods

Data regarding the number of progeny, duration, and survival of preimaginal development of *V. canescens* from Eliopoulos (2003) and Eliopoulos and Stathas (2003, 2005) were combined for the estimation of several demographic parameters and life table con-

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Table 1. Demographic parameters of *V. canescens*

Parameter	Description
x (d)	Age class of females from egg stage
n_x	No. of surviving females entering age class x
ℓ_x	Probability to survive from birth to the beginning of age class x
m_x (females/female/d)	Mean no. of female progeny per female of age class x
R_o (females/female/generation)	$G = \frac{\ln R_o}{r_m}$
G (d)	$R_o = \sum \ell_x m_x$
λ (females/female/d)	$\lambda = e^{r_m}$
DT (d)	$DT = \frac{\ln 2}{r_m}$
r_m	$\sum \ell_x m_x e^{-r_m x} = 1$
V_x	$V_x = \frac{\ell_t}{\ell_x} m_t$ where $m_t = \sum_x^w m_x$ and $\ell_t = \sum_x^w \ell_x$
e_x (d)	$e_x = \frac{T_x}{L_x}$ where $T_x = \sum L_x$ and $L_x = \frac{\ell_x + \ell_{x+1}}{2}$
GRR (females/female/generation)	$GRR = \sum m_x$

struction. The estimated parameters were the intrinsic rate of natural increase (r_m), net reproductive rate (R_o), mean generation time (G), finite capacity of increase (λ), gross reproductive rate (GRR), doubling time (DT), reproductive value (V_x), and life expectancy (e_x). Their calculation was conducted according to the equations presented on Table 1. Equations and life table construction method were adopted from Birch (1948), Krebs (1994), and Jervis and Copland (1996).

r_m Comparison. For the r_m comparison of adults reared under different conditions, the statistical procedure of Meyer et al. (1986) and Hulting et al. (1990) was used. This pairwise test is based on the comparison

Table 2. Demographic parameters of honey-fed adults of *V. canescens* at 25°C, supplied daily with 100 larvae of *E. kuehniella* of various instars

L_2						L_3					
x	n_x	l_x	m_x	e_x	V_x	x	n_x	l_x	m_x	e_x	V_x
1	77	1.000	0.000	3.092	70.1	1	21	1.000	0.000	6.806	509.6
35	10	0.130	3.500	9.100	299.5	29	10	0.476	12.800	9.000	876.4
36	10	0.130	3.800	8.100	238.2	30	10	0.476	11.100	8.000	675.4
37	10	0.130	2.600	7.100	181.6	31	10	0.476	11.100	7.000	512.7
38	10	0.130	3.000	6.100	140.6	32	10	0.476	11.000	6.000	372.2
39	10	0.130	3.800	5.100	102.5	33	10	0.476	11.500	5.000	254.4
40	10	0.130	4.400	4.316	66.7	34	10	0.476	9.700	4.000	156.4
41	9	0.117	3.222	3.706	40.4	35	10	0.476	9.400	3.158	87.7
42	8	0.104	2.875	3.067	23.2	36	9	0.429	6.000	2.563	43.5
43	7	0.091	2.000	2.385	10.9	37	7	0.333	3.857	2.083	22.1
44	6	0.078	0.833	2.000	4.0	38	5	0.238	2.800	1.625	10.4
45	3	0.039	0.667	1.800	2.3	39	3	0.143	2.000	1.250	4.0
46	2	0.026	0.500	1.333	0.8	40	1	0.048	1.000	1.000	1.0
47	1	0.013	0.000	1.000	0.0						

L_4						L_5					
x	n_x	l_x	m_x	e_x	V_x	x	n_x	l_x	m_x	e_x	V_x
1	18	1.000	0.000	7.357	486.9	1	11	1.000	0.000	8.810	794.7
27	10	0.556	14.000	8.900	735.6	25	10	0.909	16.600	8.200	776.0
28	10	0.556	11.200	7.900	539.8	26	10	0.909	14.400	7.200	559.0
29	10	0.556	11.800	6.900	392.6	27	10	0.909	13.200	6.200	389.9
30	10	0.556	8.300	5.900	264.1	28	10	0.909	13.300	5.200	256.5
31	10	0.556	9.100	4.900	178.0	29	10	0.909	9.300	4.200	149.0
32	10	0.556	7.100	3.900	105.0	30	10	0.909	7.400	3.556	82.9
33	10	0.556	5.000	3.222	57.0	31	8	0.727	5.750	3.286	50.6
34	8	0.444	3.625	2.857	35.3	32	6	0.545	3.000	2.909	29.3
35	6	0.333	2.833	2.364	21.7	33	5	0.455	2.000	2.333	16.3
36	5	0.278	2.800	1.875	10.6	34	4	0.364	2.250	1.714	8.5
37	3	0.167	2.000	1.400	4.2	35	3	0.273	1.000	1.250	2.7
38	2	0.111	0.500	1.000	0.5	36	1	0.091	1.000	1.000	1.0

Table 3. Demographic parameters of honey-fed adults *V. canescens* supplied daily with 100 full-grown larvae of *E. kuehniella* at various constant temperatures

15°C

x	n_x	l_x	m_x	e_x	V_x
1	61	1.000	0.000	11.000	302.0
105	10	0.164	1.400	35.500	568.8
106	10	0.164	1.100	34.500	550.6
107	10	0.164	1.400	33.500	536.3
108	10	0.164	1.000	32.500	518.1
109	10	0.164	1.600	31.500	505.1
110	10	0.164	1.300	30.500	484.3
111	10	0.164	1.200	29.500	467.4
112	10	0.164	1.200	28.500	451.8
113	10	0.164	1.200	27.500	436.2
114	10	0.164	0.800	26.500	420.6
115	10	0.164	1.100	25.500	410.2
116	10	0.164	1.000	24.500	395.9
117	10	0.164	0.800	23.500	382.9
118	10	0.164	1.000	22.500	372.5
119	10	0.164	1.100	21.500	356.7
120	10	0.164	1.100	20.500	337.2
121	10	0.164	1.000	19.500	318.1
122	10	0.164	1.100	18.500	298.3
123	10	0.164	0.500	17.500	275.5
124	10	0.164	0.900	16.500	258.2
125	10	0.164	0.900	15.500	237.1
126	10	0.164	1.400	14.500	216.8
127	10	0.164	0.800	13.500	192.6
128	10	0.164	0.900	12.500	175.3
129	10	0.164	1.200	11.500	158.0
130	10	0.164	1.100	11.053	137.4
131	9	0.148	1.000	11.235	132.2
132	8	0.131	1.125	10.875	130.0
133	8	0.131	1.250	10.533	113.3
134	7	0.115	1.143	11.000	108.7
135	6	0.098	1.000	11.818	105.8
136	5	0.082	1.200	11.900	107.4
137	5	0.082	1.400	10.900	89.3
138	5	0.082	1.200	9.900	70.8
139	5	0.082	1.200	8.900	55.7
140	5	0.082	1.200	7.900	41.1
141	5	0.082	0.600	7.667	28.3
142	4	0.066	1.000	7.500	26.7
143	4	0.066	0.500	6.500	16.3
144	4	0.066	0.500	5.500	11.0
145	4	0.066	0.500	5.143	6.7
146	3	0.049	0.333	5.800	4.4
147	2	0.033	0.500	6.000	3.3
148	2	0.033	0.000	5.000	0.0
149	2	0.033	0.000	4.000	0.0
150	2	0.033	0.000	3.000	0.0
151	2	0.033	0.000	2.667	0.0
152	1	0.016	0.000	2.500	0.0
153	1	0.016	0.000	1.500	0.0
154	1	0.016	0.000	1.000	0.0

20°C

x	n_x	l_x	m_x	e_x	V_x
1	20	1.000	0.000	10.800	1,093.2
38	10	0.500	15.200	14.700	1,932.2
39	10	0.500	10.900	13.700	1,589.3
40	10	0.500	10.800	12.700	1,333.5
41	10	0.500	9.000	11.700	1,100.7
42	10	0.500	9.100	10.700	909.7
43	10	0.500	8.200	9.700	735.6
44	10	0.500	6.500	8.700	588.1
45	10	0.500	6.600	7.700	470.9
46	10	0.500	6.700	6.700	365.9
47	10	0.500	6.800	6.000	273.6
48	9	0.450	6.667	5.938	215.6
49	7	0.350	5.571	6.583	188.3
50	5	0.250	5.400	6.700	180.6
51	5	0.250	1.600	6.333	122.0
52	4	0.200	3.250	6.857	117.5
53	3	0.150	2.333	6.833	108.8
54	3	0.150	3.333	5.833	79.2
55	3	0.150	2.333	4.833	48.9
56	3	0.150	3.333	4.600	29.6
57	2	0.100	1.000	4.500	17.5
58	2	0.100	1.000	3.500	10.0
59	2	0.100	1.500	2.500	4.5
60	2	0.100	0.000	1.500	0.0
61	2	0.100	0.000	1.000	0.0

25°C

x	n_x	l_x	m_x	e_x	V_x
1	11	1.000	0.000	8.810	794.7
25	10	0.909	16.600	8.200	776.0
26	10	0.909	14.400	7.200	559.0
27	10	0.909	13.200	6.200	389.9
28	10	0.909	13.300	5.200	256.5
29	10	0.909	9.300	4.200	149.0
30	10	0.909	7.400	3.556	82.9
31	8	0.727	5.750	3.286	50.6
32	6	0.545	3.000	2.909	29.3
33	5	0.455	2.000	2.333	16.3
34	4	0.364	2.250	1.714	8.5
35	3	0.273	1.000	1.250	2.7
36	1	0.091	1.000	1.000	1.0

30°C

x	n_x	l_x	m_x	e_x	V_x
1	11	1.000	0.000	6.238	368.5
20	10	0.909	13.700	5.500	342.5
21	10	0.909	14.200	4.500	216.9
22	10	0.909	10.100	3.684	116.8
23	9	0.818	8.222	3.000	63.6
24	8	0.727	4.500	2.429	28.5
25	6	0.545	2.167	1.818	13.8
26	5	0.455	2.200	1.286	5.9
27	2	0.182	2.000	1.000	2.0

of respective Jacknife estimates (r_J) and their standard errors (σ_J). Specifically, Jacknife "pseudo-values" (r_j) were computed as follows:

$$\tilde{r}_j = n \cdot r_m - (n - 1) \cdot r_{mj}$$

where n is the number of parental adults ($n = 10$ during the current study), r_m is the intrinsic rate of increase, and r_{mj} ($j = 1, \dots n$) is the intrinsic rate of increase of j adults dropping individual j out of the data set. The pseudo-values were used to calculate the Jacknife estimate:

$$\hat{r}_J = \frac{1}{n} \cdot \sum_{j=1}^{n} \tilde{r}_j$$

and an estimate of its standard error:

$$\hat{\sigma}_J = \sqrt{\frac{1}{n \cdot (n - 1)} \cdot \sum_{j=1}^{n} (\tilde{r}_j - \hat{r}_J)^2}$$

If ${r_m}^{(1)}$ and ${r_m}^{(2)}$ represent the true population growth rates of two different *V. canescens* cohorts, then the

Table 4. Demographic parameters of starved adults of *V. canescens* supplied daily with 100 full-grown larvae of *E. kuehniella* at various constant temperatures

15°C					
x	n_x	l_x	m_x	e_x	V_x
1	61	1.000	0.000	4.915	71.6
105	10	0.164	2.300	13.900	259.8
106	10	0.164	1.900	12.900	224.1
107	10	0.164	2.100	11.900	193.2
108	10	0.164	1.800	10.900	160.4
109	10	0.164	1.600	9.900	130.6
110	10	0.164	1.900	8.900	105.5
111	10	0.164	1.500	7.900	79.5
112	10	0.164	1.800	6.900	59.8
113	10	0.164	1.600	6.211	40.9
114	9	0.148	1.222	5.824	28.8
115	8	0.131	1.750	5.125	20.1
116	8	0.131	0.750	4.400	8.4
117	7	0.115	0.571	3.923	4.4
118	6	0.098	0.500	3.455	1.8
119	5	0.082	0.000	3.000	0.0
120	4	0.066	0.000	3.000	0.0
121	2	0.033	0.000	3.000	0.0
122	2	0.033	0.000	2.667	0.0
123	1	0.016	0.000	2.500	0.0
124	1	0.016	0.000	1.500	0.0
125	1	0.016	0.000	1.000	0.0

20°C					
x	n_x	l_x	m_x	e_x	V_x
1	20	1.000	0.000	3.667	79.8
38	10	0.500	14.800	4.000	110.5
39	10	0.500	5.500	3.158	34.1
40	9	0.450	3.000	2.412	11.8
41	8	0.400	1.250	2.000	2.5
42	4	0.200	0.000	2.000	0.0
43	2	0.100	0.000	1.500	0.0
44	2	0.100	0.000	1.000	0.0

25°C					
x	n_x	l_x	m_x	e_x	V_x
1	11	1.000	0.000	3.381	88.5
25	10	0.909	17.400	2.632	71.2
26	9	0.818	6.333	1.938	14.1
27	7	0.636	0.000	1.500	0.0
28	3	0.273	0.000	1.250	0.0
29	1	0.091	0.000	1.000	0.0

30°C					
x	n_x	l_x	m_x	e_x	V_x
1	11	1.000	0.000	2.048	61.2
20	10	0.909	23.600	1.375	39.9
21	6	0.545	1.333	1.000	1.3

approximate $100(1-\alpha)\%$ confidence interval (CI) for $r_m^{(1)}$-$r_m^{(2)}$ is as follows:

$$\hat{r}_J^{(1)} - \hat{r}_J^{(2)} \pm t(f,\ \alpha/2) \cdot \sqrt{(\hat{\sigma}_J^{(1)})^2 + (\hat{\sigma}_J^{(2)})^2}$$

where t $(f, \alpha/2)$ is the point of the Student's t-distribution for level of significance $\alpha/2$ (=0.025 during the current study) and with f degrees of freedom:

$$f = \frac{[(\hat{\sigma}_J^{(1)})^2 + (\hat{\sigma}_J^{(2)})^2]^2}{\dfrac{(\hat{\sigma}_J^{(1)})^4}{n_1 - 1} + \dfrac{(\hat{\sigma}_J^{(2)})^4}{n_2 - 1}}$$

where n_1 and n_2 are the number of parental wasps in the data sets from the two comparing cohorts ($n_1 = n_2 = 10$). A confidence interval that does not include zero indicates significant difference between the two r_m.

Results

Demographic parameters of cohorts of *V. canescens* adults lived at different conditions of temperature, feeding, and host instar are presented in Tables 2–6.

Effect of Temperature. Temperature increase resulted in higher values of r_m, R_o, λ, and *GRR*, whereas it was followed by decrease of *G* and *DT* values (Table 5). Differences of values of r_m among different temperatures proved to be significant after the comparison of Jacknife estimates. Intrinsic rate of increase of honey-fed adults lived at 15°C was calculated 23 times smaller than the respective value at 30°C. This decline was less intense when adults did not feed on honey (15 times).

Highest R_o was obtained at 25°C for feeding adults and at 30°C for starved adults (75.36 and 22.18, respectively). The lowest value of this parameter was recorded at 15°C for both starved and honey-fed adults (2.34 and 3.21, respectively). Generation time (*G*), was 110.15 and 109.65 d, respectively, at 15°C and was decreased at almost 5 times when temperature was 30°C. Lowest λ value was calculated at 15°C irrespective of access to food and was positively correlated with temperature.

Feeding *V. canescens* adults presented maximum *GRR* at 20°C, whereas the lowest value was recorded at 15°C (≈65.6% decrease). Temperature rise did not

Table 5. Demographic parameters of adults of *V. canescens* supplied daily with 100 full-grown larvae of *E. kuehniella* at various constant temperatures and host instars

	Honey-fed adults				Starved adults			
	15°C	20°C	25°C	30°C	15°C	20°C	25°C	30°C
r_m	0.0077aA	0.0933bA	0.1586cA	0.1793dA	0.0106aA	0.0644bB	0.1206cB	0.1547dB
R_o	2.34	49.85	75.36	47.09	3.21	12.00	21.00	22.18
G	110.15	41.89	27.25	21.48	109.65	38.56	25.24	20.03
$\lambda[\rho]$	1.008	1.09	1.17	1.19	1.01	1.06	1.13	1.17
GRR	43.75	127.12	89.20	57.09	21.29	24.55	23.73	24.93
DT	89.62	7.43	4.37	3.86	65.11	10.75	5.74	4.48

r_m values of same feeding treatment followed by the same lowercase letter are not significantly different. r_m values (of same temperature) followed by the same uppercase letter are not significantly different.

Table 6. Demographic parameters of honey-fed adults of *V. canescens* at 25°C supplied daily with 100 larvae of *E. kuehniella* of various instars

	Host instar			
	Second	Third	Fourth	Fifth
r_m	0.0338a	0.1160b	0.1252c	0.1586d
R_o	3.70	41.33	40.66	75.36
G	38.67	32.07	29.59	27.25
$\lambda[\rho]$	1.03	1.12	1.13	1.17
GRR	31.19	92.25	78.25	89.20
DT	20.48	5.97	5.53	4.37

r_m values followed by the same letter are not significantly different.

cause appreciable change to the value of this parameter in starved wasps. Doubling time was minimized at 30°C and increased as temperature declined, reaching its maximum at 15°C.

Effect of Host Instar. Intrinsic rate of increase was higher at more grown hosts (Table 6). The value of r_m was almost 5 times higher in late instar compared with early instar hosts. Waps that laid their eggs inside second instar hosts had a very low R_o (3.7), compared with those that parasitized older hosts (40.66–75.35). Finally, later instar hosts resulted in increase of λ (0.8–19%) and decrease of *DT* (7–78%). However, values of *G* and *GRR* showed noteworthy change only in the second instar hosts. A decrease of 17–30% was recorded for the former, and an increase of 150–195% for the latter parameter when hosts older than second instar were parasitized.

Effect of Feeding. Honey-fed parasitoids presented significantly higher r_m than starved parasitoids, within the temperature range 20–30°C. This value rise varied from 16% (30°C) to 45% (20°C). At 15°C, r_m values between starved and feeding wasps were statistically equivalent.

Feeding on honey caused remarkable increase of R_o at 20–30°C (112–315%), whereas differences on this parameter between starved and honey-fed wasps were insignificant at 15°C. Another result of adult feeding was the significant increase of *GRR* at all temperatures (105–417%). On the contrary, the values of λ, *G*, and *DT* did not change notably. The only exception was the parasitoids which lived at 15°C, where feeding adults had 37% higher doubling time.

Discussion

The determination of life history parameters requires laboratory studies, thus implying artificial conditions, despite the fact that insects are subjected to more complex and fluctuating situations in their natural environment. Nevertheless, life tables remain a very useful tool for evaluating a parasitoid against a host under various climatic conditions and host habitats (Birch 1948, Leslie and Park 1949, Jervis and Copland 1996). Especially, a parameter such as r_m is of great interest because it integrates the effects of mortality and fertility in a single value.

The intrinsic rate of increase (r_m) of *V. canescens* increases significantly with temperature rise. As pointed out by Graham (1959) and Force and Messenger (1964), temperature is shown to affect strongly the value of r_m, limiting the environment where an insect can be expected to persist and increase in numbers, within the temperature range where its r_m is greater than zero. *V. canesecens* seems unable to survive at temperatures below 15°C given that r_m approaches zero at that temperature (honey-fed, 0.0077; starved, 0.0106). The positive correlation between r_m and temperature, from 15 to 30°C, has been recently recorded for other parasitoids as well (Pratissoli and Parra 2000, Schöller and Hassan 2001).

Highest values of r_m, R_o, and *GRR* and lowest of *G* and *DT* were calculated at 25 and 30°C, indicating that *V. canescens* performs best in warm, southern temperate regions.

Because the demographic parameters of *V. canescens* are estimated for the first time, there are no other experimental data for compare comparison. However, an indirect comparison with life table features of other natural enemies of Pyralidae, which compete with *V. canescens* for storage moths, would be interesting. The ectoparasitoid *Habrobracon hebetor* Say (Hymenoptera: Braconidae) presented r_m equal to 0.215 when parasitizing larvae of *Corcyra cephalonica* Stainton (Lepidoptera: Pyralidae) at 22°C and 54% RH (Nikam and Pawar 1993), whereas that of the predatory mite *Blattisocius tarsalis* (Berlese) (Acari: Ascidae) was 0.242 when feeding on eggs of *Cadra cautella* (Walker) at 27°C and 73% RH (Haines 1981), whereas the r_m of the egg parasitoid *Trichogramma evanescens* Westwood (Hymenoptera: Trichogrammatidae) was estimated 0.299, 0.366, and 0.476 at 20, 26, and 30°C, respectively, ovipositing in eggs of *E. elutella* at 73% RH. (Schöller and Hassan 2001).

Despite the fact that respective r_m values of *V. canescens* are lower than those of its competitors, they should not be directly compared because they have been estimated under very different conditions (e.g., temperature, relative humidity, and host species). Moreover, Huffaker et al. (1977) cautioned that concluding that a natural enemy having lower r_m than that of its host or prey would be a poor biological control agent is a common error. The parasitoid or predator only needs to have an r_m high enough to offset that part of the pest's r_m that is not negated by parasitism.

V. canescens presented maximum e_x in the first two classes of x (immature stages or newly emerged adults), and decreased steadily as wasp aged. Slight fluctuations observed at 15 and 20°C in adults with access to food, is probably because of unusually long life span.

Maximum value of V_x also was recorded for individuals of age class $x = 1$ (parasitized larvae) or for the following class (newly emerged adults). The biological meaning of this result is that these individuals will offer more progeny to the next generation than their conspecifics of other classes. A similar conclusion also has been reported for other parasitoids (Morales-Ramos and Cate 1993, Doury and Rojas-Rousse 1994). Thus, it may be concluded the newly emerged adults would be ideal individuals for release, given that releasing parasitized host larvae is impracticable. This holds true especially for biological programs that use inoculative releases of *V. canescens* where control is achieved by the offspring of released individuals.

The results of the current study provide information that will help to facilitate more effective control of moth pests of stored products by *V. canescens.* The wasp is mostly unable to survive in temperatures below 15°C, as revealed by the r_m tables, and it would therefore not be a suitable candidate species for the control of stored-products pests in cold northern climates or in nontemperature-controlled facilities. However, because many stored-product facilities regulate their temperatures from 20 to 27°C, the wasp may be released even in cold climates. This conclusion is based on the results for wasps from the population tested in this study, which were collected from a warm region. Populations of the wasp acclimated to colder climates may prove more tolerant to low temperatures. In inoculative releases of *V. canescens,* an effort should be made for the introduction of newly emerged wasps because they not only live long and also produce more progeny than older conspecifics.

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