

Effects and interactions of temperature, host deprivation and adult feeding on the longevity of the parasitoid *Venturia canescens* (Hymenoptera: Ichneumonidae)

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Abstract. A laboratory study was carried out to determine the effects and interactions of temperature, host deprivation and adult feeding on the longevity of the parasitoid *Venturia canescens* (Gravenhorst) (Hymenoptera: Ichneumonidae). The effect of body size was also examined. Large wasps (hind tibia length > 1.96 mm) lived significantly longer than smaller conspecifics (hind tibia length < 1.89 mm). Adults reared at 15°C lived longer regardless of whether supplied with hosts or food. Correspondingly, adults had a shorter life at 30°C. Honey-fed adults lived significantly longer than starved adults at all temperatures and irrespective of host presence, while access to hosts resulted in a decrease in longevity at all temperatures, regardless of food supply. The Weibull distribution was used to describe the age specific survival, which in *V. canescens* is of “Type I”, as the risk of death increases with age. Despite the significant effect of host presence on survival it was less than either temperature or feeding. The interactions between feeding, host presence and temperature proved to be significant. The objective of the study was to improve the effectiveness of *V. canescens* as a biological control agent of stored product pests.

INTRODUCTION

Adult longevity is an important factor in the population dynamics of parasitoids and influences their effectiveness in exploiting host populations. The longer a male wasp lives the more females it can inseminate, while the longer a female can live the more eggs it can lay (Tingle & Copland, 1989; Jervis & Copland, 1996; Jervis et al., 1996). Longevity is a variable species specific characteristic, which is influenced by a range of biotic (host, body size, mating, adult feeding, etc.) and abiotic (temperature, humidity, photoperiod) factors (Jervis & Copland, 1996).

The present study deals with the effect of some of the above factors on the longevity of *Venturia canescens* (Gravenhorst) (Hymenoptera: Ichneumonidae), a thelytokous, koinobiont, solitary, endoparasitoid of lepidopterous larvae. Its host range includes many moth species, mainly pyralids attacking stored products (Frilli, 1965; Salt, 1975, 1976). The influence of adult feeding, host presence and temperature on the longevity of *V. canescens* has been well studied (Candura, 1928; Beling, 1932; Ahmad, 1936; Frilli, 1965; Kurstak, 1966; Shikrenov, 1970; Matsumoto, 1974). However, the use of variable temperatures and different types of adult food has resulted in contradictory results. In addition, it is unknown whether interactions between these factors affect the longevity of *V. canescens*.

In the present study, the effect of biotic (body size, presence of adult food and / or host) and abiotic (temperature) factors on the longevity and survival of *V. canescens*

was examined. The interactions among those factors on the longevity of *V. canescens* were also analyzed. Moreover, the Weibull distribution was fitted to experimental results and the survival scale and shape parameters were calculated. The findings are analyzed on the basis of improving the efficiency of *V. canescens* as biocontrol agent against stored product pests.

MATERIAL AND METHODS

Full-grown larvae of the Mediterranean Flour Moth *Ephestia kuehniella* Zeller (Lepidoptera: Pyralidae) were used as hosts. The host species was reared in incubators at 25°C with a photoperiod of 16L : 8D and 65 ± 5% R.H. Cultures were maintained in clear plastic boxes (17 × 11 × 5 cm) containing 200–250 g of semolina with 250–300 host eggs. This arrangement ensured that larvae had an excess of food throughout their larval life.

The original population of the parasitoid was collected in flourmills near Athens, Attiki. *Venturia canescens* was also reared in same type of plastic boxes as *E. kuehniella*. Approximately, 200 4th–5th instar moth larvae from the stock culture were placed in each box together with 10 adult wasps. This procedure was repeated every 4 days. The boxes were left until the wasps emerged.

Effect of temperature, host presence and adult feeding on longevity

To segregate parasitoids for experiments, parasitoid pupae were removed from the culture, placed individually in Petri dishes and kept at 20°C. Newly emerged adults were reared without access to food or were provided with honey ad libitum smeared on the inside of the dish, with or without access to hosts, according to the experimental design. A uniform size of

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wasp was achieved by selecting adults whose hind tibia length were between 1.85 and 1.95 mm long.

Adult longevity of cohorts of 35 honey-fed or starved individuals exposed to a range of constant temperatures (15, 20, 25 and 30°C), with or without access to hosts, was measured. The daily supply of honey and hosts (50 mature L5 larvae of *E. kuehniella*) was achieved by the transferring of each experimental adult to a Petri dish identical with the initial one. Daily observations (every 8 h for cohorts at 30°C) were made to determine whether the parasitoids were still alive.

Effect of body size on longevity

The effect of body size on adult longevity was investigated using 92 newly emerged adult wasps of various sizes. In order to obtain adults of different sizes they were collected daily from cultures of host larvae parasitized at the 2nd up to the 5th instar. In koinobiont parasitoids, which consume the entire host before pupation (like *V. canescens*) adult parasitoid size is often strongly correlated with host size (instar) at time of parasitism (Harvey & Thompson, 1995; Harvey & Vet, 1997; Hemerik & Harvey, 1999) or there is a consistent relationship between host size at oviposition and death (Mackauer & Sequeira, 1993). Thus, adults that emerge from hosts parasitized in different instars vary in body size. Adult wasps were fed on honey and kept isolated from hosts at 20°C. After death the body size of experimental wasps was determined by measuring the length of a hind tibia under a calibrated stereomicroscope. Experimental adults of almost equal size were grouped so as to create a total of seven groups with hind tibial lengths of: <1.76, 1.77–1.83, 1.84–1.89, 1.90–1.95, 1.96–2.01, 2.02–2.09 and >2.1 mm.

Statistical analysis of experimental data

Effect of body size on longevity

Data were submitted to an analysis of variance with $\alpha = 0.05$. Means were separated using the Tukey-Kramer HSD Test (Sokal & Rohlf, 1995). Statistical analysis was performed using the statistical package JMP v. 4.0.2 (SAS, 2000). In addition, for pairs of data between two variables correlation coefficients were calculated. The coefficients' were tested for departure from zero using two-tailed t-test with n-2 df (Sokal & Rohlf, 1995).

Effect of temperature, host presence and adult feeding on longevity

Data were submitted to a 3-way ANOVA with $\alpha = 0.05$ to determine whether the main effects and various interactions were significant. The main effects were a) temperature (15, 20, 25 and 30°C), b) presence or absence of food and c) presence or absence of hosts. The comparison of the means was performed as above.

Weibull distribution

The Weibull frequency distribution was used to describe the age specific survival of individuals in each regime. The proportion surviving at time t is given by:

$$S(t) = e^{-(t/b)^c}, t, b, c > 0$$

where b and c are the scale and shape parameters of the distribution, respectively. The value of the shape parameter $c > 1$, $= 1$, and < 1 correspond to Deevy's (1947) type I, II and III survivorship curves, respectively (Pinder et al., 1978). The estimation of these parameters was done using JMP statistical program (SAS, 2000). LT_{50} values (the time interval after which the population of the parasitoid was reduced to half) were also calculated from the fitted Weibull curves. Furthermore, coefficients of non-linear regression (R^2) were calculated for each Weibull curve using a SPSS statistical program. The b and c values of the cohorts of adults reared at different temperatures,

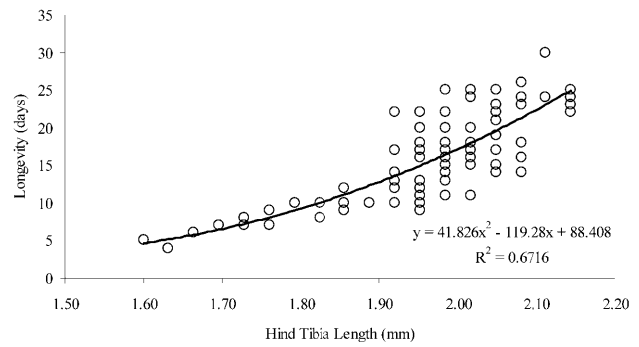


Fig. 1. Correlation between body size and longevity of honey-fed adults of *V. canescens* that did not have access to hosts (n = 92 adults, temperature: 20°C).

host and feeding regimes were compared using the tables of Thoman & Bain (1969) and Thoman et al. (1969).

RESULTS

Effect of body size

Parasitoid longevity covaried significantly with adult wasp size (n = 92, $r = 0.80$, $P < 0.001$, Fig. 1). The differences among adult groups were statistically significant (df = 6, 85; $F = 30.03$; $P < 0.0001$) (Fig. 2), with large adults (hind tibia length > 1.96 mm) living considerably longer (mean ≈ 19.3 days) than small adults (hind tibia length < 1.89 mm) (mean ≈ 8.1 days), at 25°C.

Effect of temperature, feeding and host presence

In all cases longevity decreased with increase in temperature (Table 1). The differences among different temperatures were statistically significant irrespective of feeding treatment and host presence: fed adults without hosts (df = 3, 136; $F = 146.55$; $P < 0.0001$) and with hosts (df = 3, 136; $F = 206.28$; $P < 0.0001$), starved adults with hosts (df = 3, 136; $F = 199.21$; $P < 0.0001$) and without hosts (df = 3, 136; $F = 94.93$; $P < 0.0001$). Differences between two successive temperatures were significant only between 15 and 25°C (Table 1).

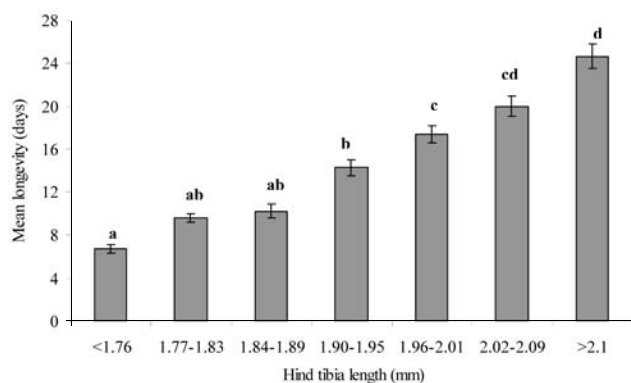


Fig. 2. Longevity of honey-fed adults of *V. canescens* of different body size that did not have access to hosts (Bars represent the standard error of the mean, numbers followed by the same letter are not significantly different (Tukey-Kramer HSD Test, $\alpha = 0.05$), sample sizes: $n_{<1.76} = 12$; $n_{1.77-1.83} = 5$; $n_{1.84-1.89} = 4$; $n_{1.90-1.95} = 24$; $n_{1.96-2.01} = 23$; $n_{2.02-2.09} = 18$; $n_{>2.1} = 6$, temperature = 20°C).

TABLE 1. Longevity in days (mean \pm S.E.) of honey-fed and starved adults of *V. canescens* with or without access to host at various constant temperatures (65 \pm 5% R.H., photoperiod: 16L : 8D, n = 35 adults).

Temperature ($^{\circ}$ C)	Honey-fed adults		Starved adults	
	without hosts	with hosts	without hosts	with hosts
15	50.00 \pm 1.95a ¹ A ²⁺³ [24–71]	42.80 \pm 1.54a ^F A ⁺ [21–55]	17.46 \pm 1.01bA* [9–29]	14.00 \pm 0.67cA* [9–21]
20	17.51 \pm 0.86aB ⁺ [11–31]	15.60 \pm 1.10aB ⁺ [5–30]	9.40 \pm 0.61bB* [2–14]	5.26 \pm 0.39 cB* [2–9]
25	8.00 \pm 0.35aC ⁺ [5–13]	7.37 \pm 0.38aC ⁺ [5–13]	4.60 \pm 0.36bC* [1–9]	2.19 \pm 0.23cC* [1–6]
30	5.71 \pm 0.34aC ⁺ [3–10]	4.19 \pm 0.31a ^F C ⁺ [0.5–8]	1.94 \pm 0.15bC* [0.5–4]	1.29 \pm 0.11cC* [0.3–2.3]

[] – value range; ¹ – for each feeding treatment, values in rows followed by the same small letter are not significantly different; ² – values in columns followed by the same capital letter are not significantly different; ³ – for each host treatment, values in rows followed by the same symbol (+ or *) are not significantly different; ^F – differences were significant but small and biologically meaningless.

The longevity of honey-fed parasitoids maintained at the same temperature showed no dependence on access to hosts (15 $^{\circ}$ C: df = 1, 68; F = 8.40, P = 0.0051, 20 $^{\circ}$ C: df = 1, 68; F = 1.88, P = 0.1752, 25 $^{\circ}$ C: df = 1, 68; F = 1.47, P = 0.2298 and 30 $^{\circ}$ C: df = 1, 68; F = 10.90; P = 0.0015; differences found at 15 and 30 $^{\circ}$ C proved to be significant but were small and biologically meaningless). Starved wasps with no access to hosts lived significantly longer than those that had access to hosts (15 $^{\circ}$ C: df = 1, 68; F = 8.15, P = 0.0057, 20 $^{\circ}$ C: df = 1, 68; F = 32.57, P < 0.0001, 25 $^{\circ}$ C: df = 1, 68; F = 31.54, <0.0001 and 30 $^{\circ}$ C: df = 1, 68; F = 12.26; P = 0.0008) (Table 1).

Host deprived wasps experienced ~73–186% increase in longevity when they were supplied with honey (15 $^{\circ}$ C: df = 1, 68; F = 219.99; P < 0.0001, 20 $^{\circ}$ C: df = 1, 68; F = 59.31; P < 0.0001, 25 $^{\circ}$ C: df = 1, 68; F = 45.49; P < 0.0001 and 30 $^{\circ}$ C: df = 1, 68; F = 101.34; P < 0.0001). The respective increase for ovipositing wasps was ~196–236% (15 $^{\circ}$ C: df = 1, 68; F = 293.62; P < 0.0001, 20 $^{\circ}$ C: df = 1, 68; F = 78.14; P < 0.0001, 25 $^{\circ}$ C: df = 1, 68; F = 134.62; P < 0.0001 and 30 $^{\circ}$ C: df = 1, 68; F = 76.93; P < 0.0001) (Table 1).

A 3-way ANOVA revealed that the main effect of host presence and its interaction with temperature were insignificant, whereas all other main effects and interactions proved to be significant (Table 2).

Weibull distribution

The survival curves of adults of all cohorts are shown in Fig. 3. The proportion surviving at each time interval is presented, along with the fitted Weibull curve. Non-linear regression coefficient values (R^2) ranged between 0.85–0.99 (Table 3). The values of Weibull parameters

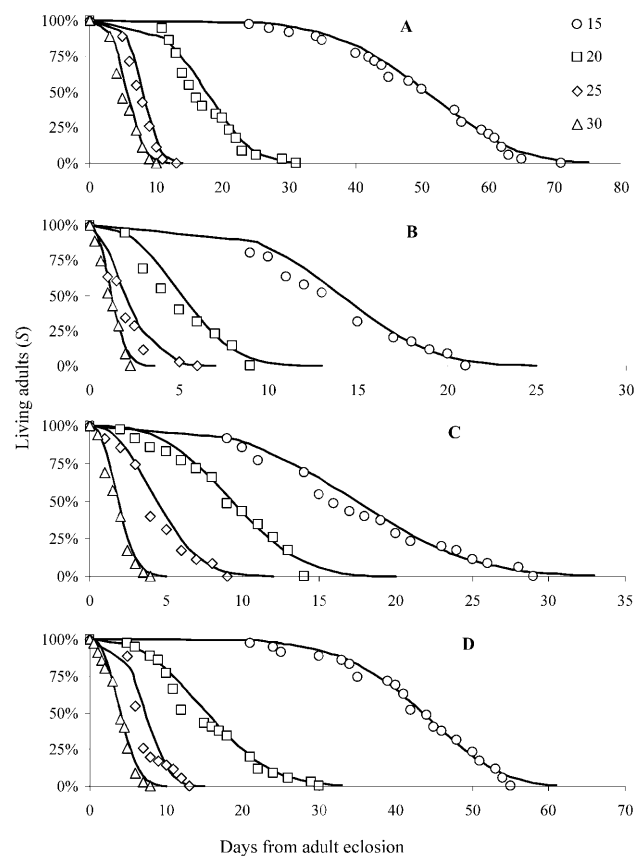


Fig. 3. Survival curves of adults of *V. canescens* with: A – access to hosts; B – access to food; C – deprived of both food and hosts; D – access to both food and hosts, at a range of constant temperatures.

TABLE 2. Analysis of variance (3-way ANOVA) for main effects and interactions of temperature (T), access to food (F) and host presence (H) on longevity of *V. canescens* (α = 0.05, error df = 546).

	Main effects			Interactions			
	T	H	F	T \times H	T \times F	F \times H	T \times F \times H
df	3	1	1	3	3	1	3
F	265.65	2.45	248.34	1.41	190.74	33.47	4.99
P	<0.0001	0.1178	<0.0001	0.2377	<0.0001	<0.0001	0.0020

TABLE 3. Weibull parameter values for survival curves of *V. canescens*.

		Temperature (°C)				
		15	20	25	30	
Honey-fed adults	without hosts	n	35	35	35	35
		b	54.408a	19.394b	8.789c	6.405c
		c	5.303a	3.641a	4.287a	3.130a
		LT _{50W}	50.77	17.53	8.06	5.69
		LT _{50O}	50–55	15–16	7–8	4–5
	Type	I	I	I	I	
	R ²	0.98	0.94	0.95	0.93	
	with hosts	n	35	35	35	35
		b	46.302a	17.614b	8.197c	4.700c
		c	5.944a	2.626a	3.306a	2.451a
LT _{50W}		43.53	15.32	7.33	4.04	
LT _{50O}		42–44	12–15	6–7	3–4	
Type	I	I	I	I		
R ²	0.98	0.97	0.85	0.98		
Starved adults	without hosts	n	35	35	35	35
		b	19.518a	10.535b	5.190c	2.198c
		c	3.246a	2.972a	2.290a	2.347a
		LT _{50W}	17.42	9.31	4.42	1.88
		LT _{50O}	15–16	8–9	3–4	1.5–2
	Type	I	I	I	I	
	R ²	0.96	0.96	0.96	0.96	
	with hosts	n	35	35	35	35
		b	15.485a	5.950b	2.477c	1.452c
		c	3.945a	2.538a	1.789a	2.154a
LT _{50W}		14.11	5.15	2.02	1.22	
LT _{50O}		13–15	4–5	1.5–2	1–1.3	
Type	I	I	I	I		
R ²	0.94	0.93	0.89	0.95		

Values of b and c of the same feeding treatment and host presence followed by the same letter are not significantly different [Tables of Thoman & Bain (1969) and Thoman et al. (1969), $\alpha = 0.05$]; n – sample size; LT_{50W} – LT₅₀ value calculated using the Weibull equation; LT_{50O} – LT₅₀ value range estimated from experimental data; R² – coefficient of non linear regression.

(b,c) and LT₅₀ are included in Table 3. The shape parameter (c) was always significantly >1. Both feeding and access to host did not influence the c value significantly.

DISCUSSION

Several authors have proposed that intra-specific variation in parasitoid life histories can be classified according to their mode of development: ectoparasitoids and idiobionts have one suite of traits, and endoparasitoids and koinobionts (such as *V. canescens*) another. Longevity is strongly correlated with mode of development given that shorter adult lifespan is associated with endoparasitism and/or koinobiosis (Mayhew & Blackburn, 1999).

Effect of body size

Body size influences many ecological and biological parameters of parasitoids, including longevity (e.g. Godfray, 1994; Jarvis & Copland, 1996). This was verified for *V. canescens* as the large wasps (hind tibia length > 1.96 mm) lived significantly longer than the small ones (hind tibia length < 1.89 mm). A positive correlation between body size and longevity is recorded for adults of *V. canescens* reared on *Plodia interpunctella* (Hübner) (Lepidoptera: Pyralidae) (Fletcher et al., 1994; Harvey et al., 1994), as well as for other parasitoids of stored product pests, like *Lariophagus distinguendus* Förster

(Hymenoptera: Pteromalidae) (Bellows, 1985), *Trichogramma evanescens* Westwood (Hymenoptera: Trichogrammatidae) (Waage & Ng, 1984) and *Goniozus nephantidis* (Muesebeck) (Hymenoptera: Bethyidae) (Hardy et al., 1992).

In contrast, Blackburn argued that very few life history traits correlate with parasitoids' body size, emphasizing that longevity was not one of them (Blackburn, 1991).

Effect of temperature

There is an optimum temperature range for every insect species outside of which survival is severely reduced (Jackson, 1966; Krishnamoorthy, 1989). Longevity of most insect species decreases with increasing temperature within the optimum range. This phenomenon was recorded for *V. canescens* during the present study. Adults maintained at 15°C lived much longer than wasps kept at other temperatures under all food regimes. Correspondingly, reduced longevity was recorded in adults maintained at 30°C.

Corbet & Rotheram (1965), report that fed *V. canescens* adults lived 20–25 days at 25°C. In the present study it ranged between 11–31 days. When adults supplied with food kept in fluctuating temperatures of 17.6–22°C and 15.4–16.9°C, they live for 17–28 and 38–59 days, respectively (Shikrenov, 1970). However, these results cannot be compared with those of the present study as they were

not recorded at constant temperatures. Fletcher et al. (1994), observed that starved adults of *V. canescens* did not live longer than 3 days at 25°C (9 days in the present study) and half the population did not survive to the 2nd day (3–4 days in the present study).

Kurstak (1966) reports that wasps fed on sugar solution lived 43 days at 15°C, 22 days at 20°C and 15 days at 25°C, and starved adults for 4, 8 and 17 days, respectively. Our results agree with those of Kurstak only for starved adults (17.46 days at 15°C, 9.40 days at 20°C and 4.60 days at 25°C). In contrast, our results for fed wasps differ from those of Kurstak. This can be attributed to the different types of food (sugar solution – honey) in these two studies. Food type is known to influence parasitoid longevity (Jervis & Copland, 1996; Jervis et al., 1996; Schmäle et al., 2001; Wäckers, 2001).

Effect of feeding

Fed adults lived significantly longer than starved conspecifics at all temperatures, irrespective of whether hosts were available or not. Many studies have shown that parasitoids supplied with carbohydrate-rich foods such as honey, sugar, honeydew, nectar etc., lived longer than adults that were either starved or given only water (Wäckers, 1996; McDougall & Mills, 1997; Wäckers et al., 1998; Schmäle et al., 2001). The importance of adult nutrition for *V. canescens* was first suggested by Beling (1932), when she observed newly emerged wasps leaving the habitat and host environment soon after emergence, and that the “returning” wasps had nectar droplets on their mouthparts.

In the present study supplying honey significantly increased the longevity of *V. canescens* adults in all cases. Similar observations are recorded in earlier studies (Beling, 1932; Ahmad, 1936; Frilli, 1965; Kurstak, 1966; Shikrenov, 1970; Matsumoto, 1974). Starved and host deprived adults lived for 3.5 days at 23°C while those that were fed lived as long as 40 days (Ahmad, 1936). Furthermore, Beling (1932) records that food type has a significant effect on longevity, with adults fed a sugar solution living up to 57 days and honey up to 72 days.

The same relation between feeding and longevity is recorded for parasitoids with completely different biology such as *Aphytis melinus* DeBach (Hymenoptera: Aphelinidae) (Heimpel et al., 1997), *Trichogramma platneri* Nagarkatti (Hymenoptera: Trichogrammatidae) (McDougall & Mills, 1997), *Catolaccus grandis* (Burks) (Hymenoptera: Pteromalidae) (Morales-Ramos & Cate, 1992), and others.

The effect of feeding depends on temperature and availability of hosts and interactions between these factors (Table 2). This can be attributed to the fact that the time available for feeding is reduced either when temperature declines (due to inactivity) or time-consuming parasitism occurs. Consequently, the wasp is undernourished in both cases.

Adult feeding can have a strong effect on parasitoid fitness measured in terms of longevity, lifetime fecundity, survival, searching efficiency, overall activity etc. (Godfray, 1994; Jervis & Copland, 1996; Jervis et al., 1996;

Jervis & Kidd, 1999). This is the same not only for *V. canescens* (Ahmad, 1936; Matsumoto, 1974; Harvey et al., 2001; Eliopoulos, 2003) but also for many parasitoids of stored product pests (van Huis et al., 1990; Wäckers, 1996; Wäckers et al., 1998; Schmäle et al., 2001).

The above plus the fact that a lack of suitable carbohydrate food sources in man-made ecosystems has long been suspected to be an important cause of failure of many biological control programs (Wolcott, 1942; Hocking, 1967), justifies the use of food supplements at release sites to augment the efficacy of released parasitoids and other biocontrol agents, especially in storage facilities (Schöller et al., 1997; Wäckers et al., 1998). The use of food supplements could greatly improve the efficacy of biological control of stored product pests.

Effect of host presence

Providing hosts resulted in the parasitoid having a short life at all temperatures, regardless of food supply. Beling (1932), attributes this to energy consumption for parasitism needs. Reduced longevity associated with parasitism is recorded for many non-host feeding parasitoids (Jervis et al., 1996) and is recorded for *V. canescens* by Ahmad (1936) (40 to 20 days) and Matsumoto (1974) (35 to 22 days).

Host deprivation also results in a longer adult life in *Gryon pennsylvanicum* (Ashmead) (Hymenoptera: Scelionidae) (Vogt & Nechols, 1993), *Diadromus subtilicornis* (Gravenhorst) (Hymenoptera: Ichneumonidae) (Tran & Takasu, 2000), *Telenomus isis* (Polaszek) (Hymenoptera: Scelionidae) (Chabi-Olaye et al., 2001).

However, temperature and feeding had a greater effect on adult longevity than availability of hosts (Table 2). Irrespective of treatment, wasps supplied with food and deprived of hosts did not live significantly longer than adults with food and hosts. Similar results are presented by Harvey et al. (2001).

Longevity of koinobiont endoparasitoids, which are mostly *r*-strategists, appears to be correlated with host availability (Blackburn, 1991). According to some interpretations of the theory of the *r-k* continuum, small species should be *r*-selected, with short generation times and high reproductive capacities, while large species should be *k*-selected, with long life spans and low rates of reproduction (Pianka, 1970; Blackburn, 1991). *Venturia canescens* is one of the biggest parasitoids, has a moderate life span and a copious egg production and seems to be a classic example of a compromise between *r* and *k* selection (J.F. Harvey, pers. commun.).

However, it should be mentioned that there is no convincing evidence of a trade-off between reproduction and life expectancy given that host density has no effect upon adult survival in koinobionts (Jervis & Copland, 1996).

Weibull distribution

The Weibull distribution is an effective way of representing longevity data and describing survival curves. It enables the shape and scale of different survival curves to be compared statistically and provides valuable informa-

tion that is lost if results are presented in the form of a mean with a standard deviation.

High values for the non-linear regression coefficients (R^2 : 0.85–0.99) indicate that the distribution very satisfactorily described the data. The LT_{50} values calculated using the distribution equation (LT_{50W}) fall within the range of observed values (LT_{50O}) or are slightly higher (Table 3).

As Jervis & Copland (1996) note longevity data are best presented as cohort survival curves so that biologically meaningful comparisons between treatments can be made. Value of the shape parameter (c) was always significantly >1 irrespective of temperature, food and host presence, indicating that the survival curve of *V. canescens* is of Type I, in which the risk of death increases with age. Estimates of c for different cohorts of *V. canescens* adults indicate that all the survivorship curves are similarly shaped.

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REFERENCES

- AHMAD T. 1936: The influence of ecological factors on the Mediterranean Flour Moth, *Ephestia kühniella* and its parasite *Nemeritis canescens*. *J. Anim. Ecol.* **5**: 67–93.
- BELING I. 1932: On the biology of *Nemeritis canescens*. I. Breeding experiences and ecological observations. *Z. Angew. Entomol.* **19**: 223–249 (in German, English abstr.).
- BELLOWS T.S. 1985: Effects of host age and host availability on developmental period, adult size, sex ratio, longevity and fecundity in *Lariophagus distinguendus* Förster (Hymenoptera: Pteromalidae). *Res. Pop. Ecol.* **27**: 55–64.
- BLACKBURN T.M. 1991: A comparative examination of life span and fecundity in parasitoid hymenoptera. *J. Anim. Ecol.* **60**: 151–164.
- CANDURA G.S. 1928: A contribution to the knowledge of the moth infesting foodstuffs, *Ephestia kuehniella* Zeller, and of its parasite, *Nemeritis canescens*, Gravenhorst. *Boll. Lab. Zool. Portici* **21**: 149–214.
- CHABI-OLAYE A., SCHULTHESS F., POEHLING H.M. & BORGE-MEISTER C. 2001: Factors affecting the biology of *Telenomus isis* (Polaszek) (Hymenoptera: Scelionidae), an egg parasitoid of cereal stem borers in West Africa. *Biol. Control* **21**: 44–54.
- CORBET S.A. & ROTHERAM S. 1965: The life history of the ichneumonid *Nemeritis (Devorgilla) canescens* (Gravenhorst) as a parasite of the Mediterranean flour moth, *Ephestia (Anagasta) kuehniella* Zeller, under laboratory conditions. *Proc. R. Entomol. Soc. Lond. (A)* **40**: 67–72.
- DEEVEY E.S. 1947: Life tables for natural populations of animals. *Quart. Rev. Biol.* **22**: 283–314.
- ELIOPOULOS P.A. 2003: *Study of the Parasitoid Venturia canescens (Hymenoptera: Ichneumonidae) as a Biocontrol Agent Against Lepidopterous Pests of Stored Products*. Ph.D. Thesis, Agricultural University of Athens, 181 pp. (in Greek, English abstr.).
- FLETCHER J.P., HUGHES J.P. & HARVEY I.F. 1994: Life expectancy and egg load affect oviposition decisions of a solitary parasitoid. *Proc. R. Soc. Lond. (B, Biol. Sci.)* **258**: 163–167.
- FRILLI F. 1965: Studies on the Ichneumonid Hymenoptera. I. *Devorgilla canescens* (Grav.). *Entomologica* **1**: 119–209 (in Italian, English abstr.).
- GODFRAY H.C.J. 1994: *Parasitoids – Behavioral and Evolutionary Ecology*. Princeton Univ. Press, Princeton, NJ, 473 pp.
- HARDY I.C.W., GRIFFITHS N.T. & GODFRAY H.C.J. 1992: Clutch size in a parasitoid wasp: a manipulation experiment. *J. Anim. Ecol.* **61**: 121–129.
- HARVEY J.A. & THOMPSON D.J. 1995: Host behaviour and its influence on foraging and acceptance by the solitary parasitoid wasp, *Venturia canescens* (Hymenoptera: Ichneumonidae). *Entomophaga* **40**: 193–210.
- HARVEY J.A. & VET L.E.M. 1997: *Venturia canescens* parasitizing *Galleria mellonella* and *Anagasta kuehniella*: differing suitability of two hosts with highly variable growth potential. *Entomol. Exp. Appl.* **84**: 93–100.
- HARVEY J.A., HARVEY I.F. & THOMPSON D.J. 1994: Flexible larval growth allows use of a range of host sizes by a parasitoid wasp. *Ecology* **75**: 1420–1428.
- HARVEY J.A., HARVEY I.F. & THOMPSON D.J. 2001: Lifetime reproductive success in the solitary endoparasitoid, *Venturia canescens*. *J. Insect Behav.* **14**: 573–593.
- HEIMPEL G.E., ROSENHEIM J.A. & KATTARI D. 1997: Adult feeding and lifetime reproductive success in the parasitoid *Aphytis melinus*. *Entomol. Exp. Appl.* **83**: 305–315.
- HEMERIK L. & HARVEY J.A. 1999: Flexible larval development and the timing of destructive feeding by a solitary parasitoid: an optimal foraging problem in evolutionary perspective. *Ecol. Entomol.* **24**: 308–315.
- HOCKING H. 1967: The influence of food on longevity and oviposition by *Rhyssa persuasoria* (L.) (Hymenoptera: Ichneumonidae). *J. Austr. Entomol. Soc.* **6**: 217–223.
- HUIS VAN A., KAASHOEK N.K. & MAES H.M. 1990: Biological control of Bruchids (Col.: Bruchidae) in stored pulses by using egg parasitoids of the genus *Uscana* (Hym.: Trichogrammatidae): a review. In Fleurat-Lassard F. & Ducom P. (eds): *Proceedings of 5th International Working Conference on Stored Product Protection*, Bordeaux, France, pp. 99–108.
- JACKSON D.J. 1966: Observations on the biology of *Caraphractus cinctus* Walker (Hymenoptera: Mymaridae), a parasitoid of the eggs of Dytiscidae (Coleoptera). III. The adult life and sex ratio. *Trans. R. Entomol. Soc. Lond.* **118**: 23–49.
- JERVIS M.A. & COPLAND M.J.W. 1996: The life cycle. In Jervis M.A. & Kidd N. (eds): *Insect Natural Enemies – Practical Approaches to their Study and Evaluation*. Chapman and Hall, London, pp. 63–161.
- JERVIS M.A. & KIDD N.A.C. 1999: Parasitoid adult nutritional ecology: implications for biological control. In Hawkins B.A. & Cornell H.V. (eds): *Theoretical Approaches to Biological Control*. Cambridge University Press, Cambridge, pp. 131–151.
- JERVIS M.A., KIDD N.A.C. & HEIMPEL G.E. 1996: Parasitoid adult feeding behaviour and biocontrol – a review. *Biocontr. News Inform.* **17**: 11–26.
- KRISHNAMOORTHY A. 1989: Effect of cold storage on the emergence and survival of the adult exotic parasitoid, *Leptomastix dactylopii* How. (Hym., Encyrtidae). *Entomon* **14**: 313–318.
- KURSTAK E.S. 1966: The role of *Devorgilla canescens* in infection by *B. thuringiensis* in *E. kühniella* – First Part. *Ann. Epi-phyt.* **17**: 335–383 (in French, English abstr.).
- MACKAUER M. & SEQUEIRA R. 1993: Patterns of development in insect parasites. In Beckage, N.E., Thompson S.N. & Frederick B.A. (eds): *Parasites and Pathogens of Insects. Vol. 1*. Academic Press, London, pp. 1–23.
- MATSUMOTO B.M. 1974: On the adult longevity of the entomophagous parasite, *Venturia canescens* (Hymenoptera: Ichneumonidae). *Entomophaga* **19**: 325–329.

- MAYHEW P.J. & BLACKBURN T.M. 1999: Does development mode organize life-history traits in the parasitoid hymenoptera? *J. Anim. Ecol.* **68**: 906–916.
- MCDUGALL S.J. & MILLS N.J. 1997: The influence of hosts, temperature and food sources on the longevity of *Trichogramma platneri*. *Entomol. Exp. Appl.* **83**: 195–203.
- MORALES-RAMOS J.A. & CATE J.R. 1992: Rate of increase and adult longevity of *Catolaccus grandis* (Burks) (Hymenoptera: Pteromalidae) in the laboratory at four temperatures. *Environ. Entomol.* **21**: 620–627.
- PIANKA E.R. 1970: On r and k selection. *Am. Nat.* **104**: 592–596.
- PINDER J.E., WIENER J.G. & SMITH M.H. 1978: The Weibull distribution: a new method of summarizing survivorship data. *Ecology* **59**: 175–179.
- SALT G. 1975: The fate of an internal parasitoid, *Nemeritis canescens*, in a variety of insects. *Trans. R. Entomol. Soc. Lond.* **127**: 141–461.
- SALT G. 1976: The hosts of *Nemeritis canescens*, a problem in the host specificity of insect parasitoids. *Ecol. Entomol.* **1**: 63–67.
- SAS INSTITUTE. 2000: *JMP, User's Guide, Version 4*. SAS Institute Inc., Cary, N.C., 280 pp.
- SCHMÄLE I., WÄCKERS F.L., CARDONA C. & DORN S. 2001: Control potential of three hymenopteran parasitoid species against the bean weevil in stored beans: The effect of adult parasitoid nutrition on longevity and progeny production. *Biol. Control* **21**: 134–139.
- SCHÖLLER M., PROZELL S., AL-KIRSHI A.G. & REICHMUTH C. 1997: Towards biological control as a major component of integrated pest management in stored product protection. *J. Stored Prod. Res.* **33**: 81–97.
- SHIKRENOV D. 1970: The morphological and biological characteristics of *Nemeritis canescens* Grav., a parasite of *Ephestia kuehniella* Zell. *Rast. Zash.* **18**: 22–24.
- SOKAL R.R. & ROHLF F.J. 1995: *Biometry – The Principles and Practice of Statistics in Biological Research*. 3rd ed. W.H. Freeman, New York, 887 pp.
- THOMAN D.R. & BAIN L.J. 1969: Two sample tests in the Weibull distribution. *Technometrics* **11**: 805–815.
- THOMAN D.R., BAIN L.J. & ANTLE C.E. 1969: Inferences on the parameters of the Weibull distribution. *Technometrics* **11**: 445–460.
- TINGLE C.C.D. & COPLAND M.J.W. 1989: Progeny production and adult longevity of the mealybug parasitoids *Anagyrus pseudococci*, *Leptomastix dactylopii*, and *Leptomastidea abnormis* (Hym.: Encyrtidae) in relation to temperature. *Entomophaga* **34**: 111–120.
- TRAN T.V. & TAKASU K. 2000: Life history of the pupal parasitoid *Diadromus subtilicornis* (Gravenhorst) (Hymenoptera: Ichneumonidae) as influenced by temperature, photoperiod, and availability of food and hosts. *Entomol. Sci.* **3**: 255–264.
- VOGT E.A. & NECHOLS J.R. 1993: The influence of host deprivation and host source on the reproductive biology and longevity of the squash bug egg parasitoid *Gryon pennsylvanicum* (Ashmead) (Hymenoptera: Scelionidae). *Biol. Control* **3**: 148–154.
- WAAGE J.K. & NG S-M. 1984: The reproductive strategy of a parasitic wasp. I. Optimal progeny and sex allocation in *Trichogramma evanescens*. *J. Anim. Ecol.* **53**: 401–416.
- WÄCKERS F. 1996: Can food provision increase the efficacy of biological control in storage systems? *Proceedings of 20th International Congress of Entomology, Firenze, Italy, 25–31 August 1996*. p. 551.
- WÄCKERS F.L. 2001: A comparison of nectar- and honeydew sugars with respect to their utilization by the hymenopteran parasitoid *Cotesia glomerata*. *J. Insect Physiol.* **47**: 1077–1084.
- WÄCKERS F.L., SCHMÄLE K., CARDONA C.M. & DORN S. 1998: The effect of food supplements on the longevity of the bean weevil parasitoids *Anisopteromalus calandrae* and *Heterospilus prosopidis*. *IOBC/WPRS Bull.* **21**: 75–82.
- WOLCOTT G.N. 1942: The requirements of parasitoids for more than hosts. *Science* **96**: 317–318.

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