

Effects of Temperature, Host Instar, and Adult Feeding on Progeny Production by the Endoparasitoid *Venturia canescens* (Gravenhorst) (Hymenoptera: Ichneumonidae)

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ABSTRACT Laboratory studies were conducted on the effect of temperature and host instar on lifetime and age-specific fertility of honey-fed and starved adults of *Venturia canescens* Gravenhorst (Hymenoptera: Ichneumonidae) parasitizing larvae of *Ephestia kuehniella* Zeller (Lepidoptera: Pyralidae). The relationships between the number of progeny produced with adult longevity and body size also were investigated. Highest mean fertility of honey-fed wasps was recorded at 20°C, followed, in decreasing order, by 25, 30, and 15°C, with most offspring emerging during the first 5 d. In contrast, temperature did not have a strong effect on progeny production in the case of starved adults. Provision of adult parasitoids with honey resulted in a significant increase in production of total offspring at all temperatures. Wasps that parasitized second-instar hosts produced significantly fewer descendants than those that oviposited in third- to fifth-instar hosts, which produced similar numbers of offspring. Interactions between temperature and feeding were significant. The total number of offspring produced by honey-fed adults increased with longevity and body size, regardless of temperature or host instar. Conversely, number of progeny produced by starved wasps was correlated only with body size.

KEY WORDS parasitoid, fertility, offspring, biological control, stored products

fecundity (total number of laid eggs) and fertility (number of viable progeny) are variable features of an insect, influenced by a plethora of intrinsic and extrinsic factors. The evaluation of a natural enemy as biocontrol agent requires a thorough study of the main effects and possible interactions of such factors on these characteristics (Jervis and Copland 1996). In the case of endoparasitoids, however, fecundity is relatively difficult measure, because the eggs are laid inside the bodies of multiple hosts. Moreover, fertility is a more reliable criterion for evaluation anyway, representing the net number of progeny, after elimination of individuals that fail to complete development (Jervis and Copland 1996). Thus it is preferable to study fertility rather than fecundity in endoparasitoids.

Venturia canescens is a thelytokous, koinobiont, solitary endoparasitoid of lepidopterous larvae. Its host range includes many moth species, mainly pyralids, whose larvae are pests of stored products (Salt 1976). The number of progeny it produces has been the subject of very few studies (Beling 1932, Kurstak 1966). The most complete ones are those of Ahmad (1936) and Harvey et al. (2001), who provide some

experimental data on the effects of temperature, adult nutrition, and host density.

This study deals with the main effects and interactions of temperature, adult feeding, and host instar on lifetime and age-specific fertility of *V. canescens*. The relationship of number of progeny to adult longevity and body size also was investigated.

Materials and Methods

Host and Parasitoid Cultures

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 and 65 ± 5% RH under a 16:8 L:D photoperiod. Host eggs (250–300) were placed in clear plastic boxes (17 by 11 by 5 cm) containing 200–250 g of semolina, which provided excess food throughout larval life.

The original population of the parasitoid was collected in flour mills near Athens, Attiki Co., Greece. *V. canescens* also was reared in plastic boxes as described for *E. kuehniella*. Approximately 200 fourth-fifth instars from the host culture were placed in each box together with 10 adult wasps. This procedure was repeated every 4 d. Boxes were left until adult wasps enclosed. To segregate parasitoids for experiments, par-

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Table 1. Range of head capsule width of second to fifth instars of *E. kuehniella*

Host instar	N	Head capsule width (mm)	
		Min	Max
2	25	0.26	0.38
3	25	0.48	0.61
4	25	0.71	0.83
5	25	0.96	1.31

N, no. of individuals examined.

asitized host pupae were removed from the culture and placed individually in petri dishes at 20°C.

Effect of Temperature, Host Instar, and Adult Feeding

Instars were distinguished by the criterion of maximum head capsule width, according to the method of Harvey and Thompson (1995a). Preliminary experiments were conducted to estimate the range of maximum head capsule widths for our moth population. Moth larvae were reared individually from egg to pupation and daily observations were made to record molts (head slippage) as verification of instar change. Measurements of maximum head width of 25 larvae each of second, third, fourth, and fifth instars were taken under a calibrated stereomicroscope (Table 1).

Larvae of the same instar were placed in groups of 100 into a large modified petri dish (12 cm diameter). Air circulation was achieved through a hole (4 cm diameter) in the lid, covered with nylon mesh. The dishes were left undisturbed for 24 h before being presented to parasitoids to permit release of mandibular secretions (e.g., silk), which contain kairomones that elicit probing behavior by *V. canescens* (Corbet 1971).

The following day, newly emerged adults were collected and placed individually in a dish and either were given no access to food or were provided with honey ad libitum smeared on the inside of the dish, depending on the experimental design. Each parental wasp was transferred daily to another petri dish identical with the previous one. Larvae in the previous dish were transferred at 25°C to large glass jars containing excess food medium to complete development, and emerging adult parasitoids or moths were counted.

The procedure was carried on until the parental wasp died. Longevity (days from eclosion until death) and body size of parental wasps of all cohorts at death were measured. Body size was indexed by measuring hind tibia length under a calibrated stereomicroscope.

To study the main effects and interactions of honey-feeding and temperature on the number of progeny produced, the offspring of 10 honey-fed and 10 starved adults, supplied daily with 100 full-grown host larvae, were counted at four constant temperatures (15, 20, 25, and 30°C). The effect of host instar was measured by counting the number of progeny produced by 10 honey-fed wasps supplied daily with 100 host larvae of the same instar (second, third, fourth, or fifth) at 25°C.

Statistical Analysis

Effects of Adult Longevity and Body Size. Data were subjected to analysis of variance (ANOVA) at $\alpha = 0.05$. Means were separated using the Tukey-Kramer honestly significant difference (HSD) test (Sokal and Rohlf 1995), and all statistical analyses were performed using the statistical package JMP v.4.0.2 (SAS Institute 1989). To determine the relationship between number of progeny and longevity or body size, correlation coefficients were calculated for all pairs of data. The coefficients' values were tested for departure from zero using a two-tailed *t*-test at $n-2$ df (Sokal and Rohlf 1995).

Effects of Temperature, Host Instar, and Adult Feeding. Data were subjected to two-way ANOVA at $\alpha = 0.05$ to determine the significance of main effects and possible interactions. The main effects were temperature, presence or absence of food, and host instar. Comparisons of means were performed as above.

Results

Effect of Temperature

Feeding Adults. Temperature had a significant effect on fertility of honey-fed wasps (Table 2). The number of progeny differed significantly among temperatures ($F = 43.32$; $df = 3, 36$; $P < 0.0001$). The highest mean fertility was recorded at 20°C, followed, in decreasing order, by 25, 30, and 15°C.

In the case of age-specific fertility, most offspring were produced during the first five days at 20, 25, and

Table 2. Mean no. progeny produced by female *V. canescens* at various constant temperatures, supplied daily with 100 full-grown larvae of *E. kuehniella* (65 ± 5% RH, 16:8 L:D)

Temperature (°C)	n	No. progeny			
		Honey-fed		Starved	
		Mean ± SE ^a	Range	Mean ± SE ^a	Range
15	10	35.7 ± 3.62aA	22–58	20.3 ± 0.82a ^b B	16–25
20	10	108.6 ± 6.89bA	78–136	24.0 ± 0.73bB	19–26
25	10	82.9 ± 4.58cA	67–108	23.1 ± 0.54bB	19–25
30	10	51.8 ± 3.51dA	36–71	24.4 ± 1.14bB	20–30

N, no. of parental females.

^aValues followed by the same lowercase letter are not significantly different; means in a row followed by the same capital letter are not significantly different (Tukey-Kramer HSD test, $\alpha = 0.05$).

^bDifferences proved to be significant but were minor and biologically meaningless.

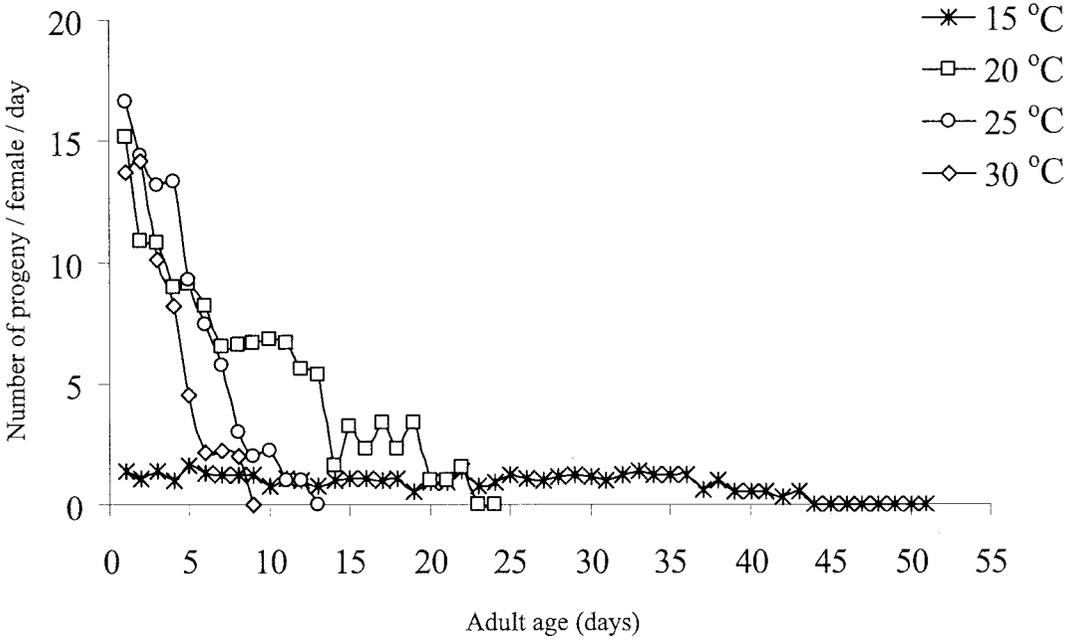


Fig. 1. Age-specific fertility of honey-fed *V. canescens* adults supplied daily with 100 full grown larvae of *E. kuehniella* at various constant temperatures ($n = 10$ adults, $65 \pm 5\%$ RH, light period:16:8 L:D).

30°C (50.6, 80.6, and 94.6% of total progeny, respectively). In contrast, progeny emergence at 15°C did not vary notably with parental age (Fig. 1). The relationship between temperature and number of progeny of *V. canescens* is described satisfactorily by a simple second-degree equation ($R^2 = 0.8627$; Fig. 2).

Starved Adults. The influence of temperature on progeny production differed significantly when adults

were deprived of food ($F = 4.81$; $df = 3,36$; $P = 0.006$). However, the differences concerned only adults who lived at 15°C (Table 2). Fertility was similar among wasps held at higher temperatures (20–30°C).

The effect of temperature on age-specific fertility of starved adults was similar to that of honey-fed ones (Fig. 3). The rate of offspring emergence declined with age, with most offspring being recorded during

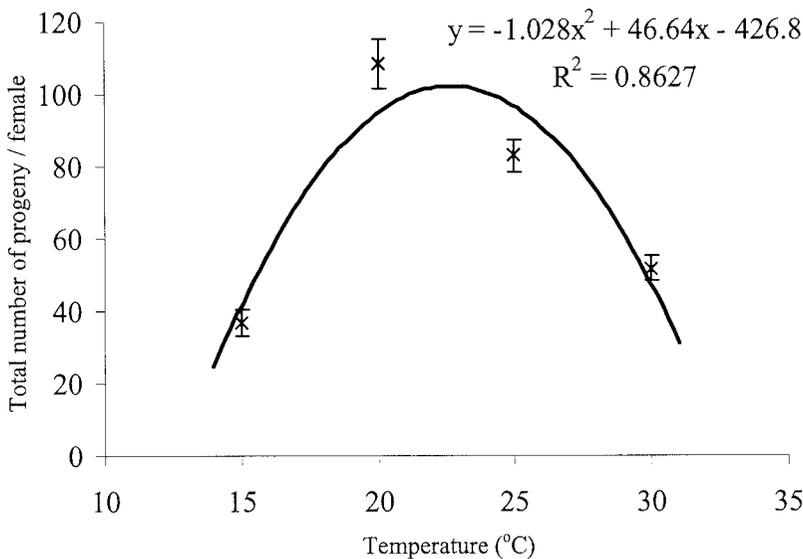


Fig. 2. Effect of temperature on total progeny produced by honey-fed *V. canescens* adults supplied daily with 100 full grown larvae of *E. kuehniella* ($n = 10$ adults, $65 \pm 5\%$ RH, 16:8 L:D; bars represent SEM).

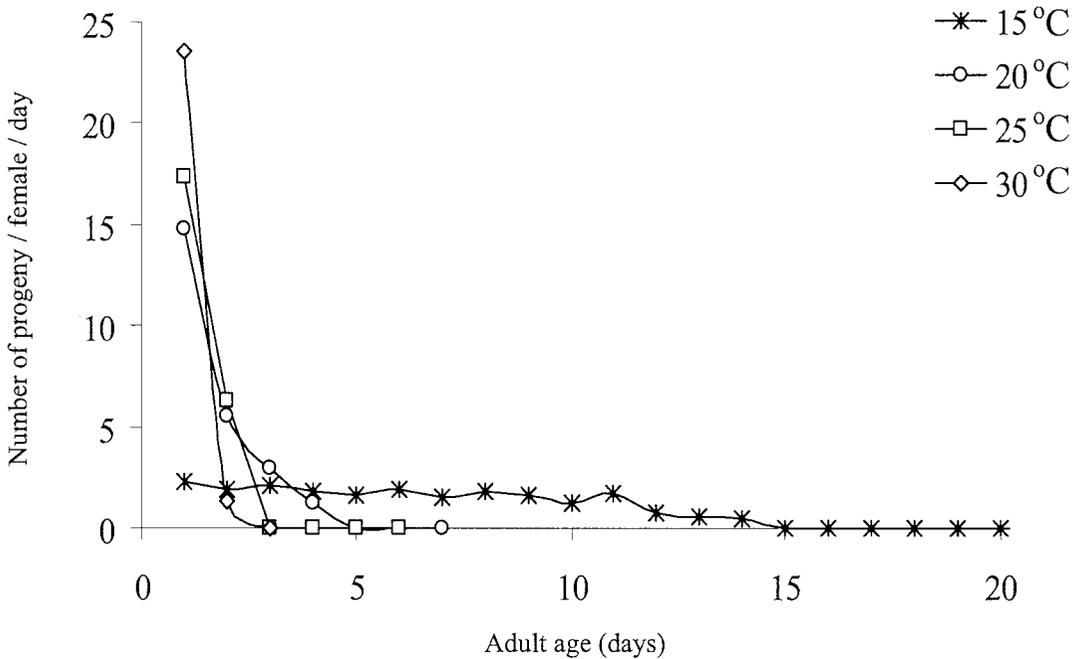


Fig. 3. Age-specific fertility of starved *V. canescens* adults supplied daily with 100 full grown larvae of *E. kuehniella* at various constant temperatures ($n = 10$ adults, $65 \pm 5\%$ RH, 16:8 L:D).

the first day at 20, 25, and 30°C (61.7, 75.3, and 96.7% of total progeny, respectively) and 85–100% having emerged by the second day. In contrast, the trend was constant at 15°C.

Effect of Adult Feeding

Feeding on honey resulted in a remarkable increase in offspring over those starved at 15 (75.8%), 20 (352.9%), 25 (258.8%), and 30°C (112.3%). The differences in number of progeny among fed and starved wasps were significant at all temperatures (Table 2; 15°C: $F = 18.71$; $df = 1,18$; $P = 0.0004$, 20°C: $F = 149.02$; $df = 1,18$; $P < 0.0001$, 25°C: $F = 167.64$; $df = 1,18$; $P < 0.0001$, 30°C: $F = 55.02$; $df = 1,18$; $P < 0.0001$).

Effect of Host Instar

Number of progeny of *V. canescens* varied significantly among different host instars ($F = 42.51$; $df = 3,36$; $P < 0.0001$). Wasps that parasitized second-instar hosts produced significantly fewer descendants than those that oviposited in third- to fifth-instar hosts (Table 3). Mean number of progeny produced per day decreased with age irrespective of host instar (Fig. 4); 58.6, 66.2, 74.3, and 80.6% of the total offspring from second, third, fourth, and fifth host instars, respectively, were recorded by the fifth day.

A two-way ANOVA was performed on the data sets in Tables 2 and 3 to determine the effects of temperature, food access, and host instar on number of progeny. It revealed that fertility varied significantly with

all factors. In addition, the interaction between temperature and feeding was significant (Table 4).

Effect of Adult Longevity and Body Size

The total number of offspring produced by honey-fed adults increased with parent longevity as well as with its body size, regardless of temperature and host instar (Table 5). The respective correlations were significant ($P < 0.05$). In contrast, the number of progeny produced by starved wasps was correlated only with body size (Table 5).

Discussion

Effect of Temperature

Temperature had a significant effect on the number of progeny produced by *V. canescens* only in the case

Table 3. Mean no. progeny produced by honey-fed *V. canescens* females supplied daily with 100 fifth-instar larvae of *E. kuehniella* (25°C, $65 \pm 5\%$ RH, 16:8 L:D)

Host instar	n	No. of progeny	
		Mean \pm SE ^a	Range
2	10	28.5 \pm 1.34a	21–34
3	10	86.8 \pm 4.45b	67–116
4	10	73.2 \pm 5.01b	54–97
5	10	82.9 \pm 4.58b	67–108

n, no. parental adults.
^aValues followed by the same letter are not significantly different (Tukey-Kramer HSD test, $\alpha = 0.05$).

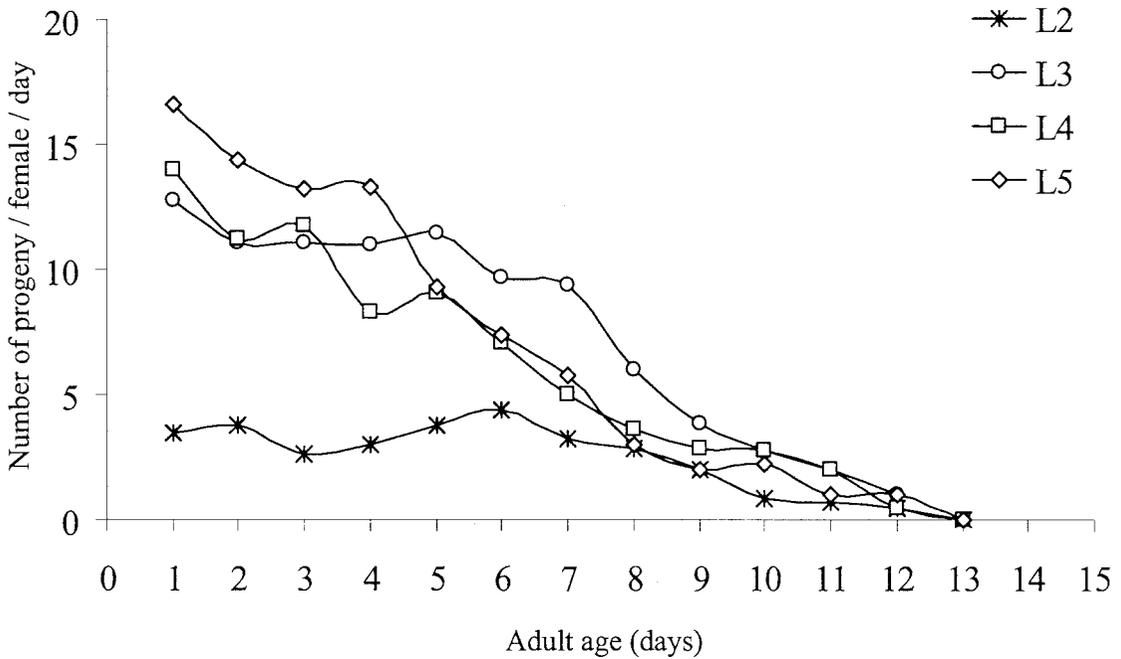


Fig. 4. Age-specific fertility of honey-fed *V. canescens* adults supplied daily with 100 larvae of *E. kuehniella* of various instars (temperature: 25°C, $n = 10$ adults, $65 \pm 5\%$ RH, 16:8 L:D).

of honey-fed adults. Ahmad (1936) did not record significant variation in production of offspring by *V. canescens* with temperature, either in feeding or starved adults. This can be attributed to a high overall reduction in progeny (mean, 31.1–38.7), because Ahmad supplied 300 host larvae once without replenishment. Consequently, there was a great loss of offspring because of superparasitism, a common phenomenon in *V. canescens* and a significant cause of “egg waste” (e.g., Simmonds 1943, Harvey et al. 1993, Sirot 1996).

The total number of progeny per female ranged from 20.3 to 108.6 depending on feeding regimen and temperature. There are contradictory experimental data concerning this feature of *V. canescens* in the literature. Ahmad (1936) claimed that maximum total offspring per female reached 75 with *E. kuehniella* as host, whereas it exceeded 400 in a recent study with *Plodia interpunctella* (Hübner) (Lepidoptera: Pyralidae) (Harvey et al. 2001). The maximum in this study was 136.

Total offspring of honey-fed adults averaged 251 ± 45 on *Cadra cautella* (Walker) (Lepidoptera: Pyralidae) (35 larvae/d) at 27°C (Trudeau and Gordon

1989), 53.8 on *E. kuehniella* (200 larvae/d) at 23°C (Ahmad 1936), and almost 260 on *P. interpunctella* (200 larvae/d) at $25 \pm 2^\circ\text{C}$ (Harvey et al. 2001). When adults were deprived of food, the respective numbers were 52.25 (Ahmad 1936) and almost 50 (Harvey et al. 2001). Our data differ substantially from some of the results referred to above. The differences may be credited to external (host species, temperature, host habitat, and others) or internal factors (genetic variation among populations of *V. canescens* of different origins), which can affect parasitoid fertility (Godfray 1994, Jarvis and Copland 1996).

Age-specific fertility did not change appreciably with temperature except at 15°C. Rate of offspring emergence was highest during the first days of the adult life, and declined thereafter, irrespective of food presence. It should be noted that this decline started from the first day. A similar trend of age-specific fertility in *V. canescens* has been noted in other studies as well (Ahmad 1936, Trudeau and Gordon 1989, Harvey et al. 2001). The exception at 15°C, where emergence rate did not change with time, can be attributed to the greatly reduced number of progeny and indicates that this temperature is extreme for *V. canescens*. A remarkably low number of progeny at 15°C was also reported by Ahmad (1936) (2–5 progeny/d/female).

The relationship of fertility of *V. canescens* with temperature is well described by a simple second-degree equation. Lower values were observed at extreme temperatures (15 and 30°C), whereas the largest numbers of progeny emerged at moderate temperatures (20 and 25°C). This is a common pattern for the relationship between temperature and parasitoid

Table 4. Two-way ANOVA for main effects and interactions of temp (T), feeding (Fd), and host instar (I) on no. progeny produced by *V. canescens* ($\alpha = 0.05$; $df = 102$)

	Main effects			Interactions
	Fd	I	T	Fd \times T
df	1	3	3	3
F	164.94	25.49	20.45	13.12
P	<0.0001	<0.0001	<0.0001	<0.0001

Table 5. Correlation of total no. *V. canescens* progeny produced by honey-fed and starved adults with adult longevity and body size at various constant temperatures (65 ± 5% RH, 16:8 L:D)

Temperature (°C)	Longevity (days)			Body size (hind tibia length in mm)		
	Mean ± SE	<i>r</i>	<i>P</i>	Mean ± SE	<i>r</i>	<i>P</i>
Honey-fed						
15	36.10 ± 2.79	0.89	<0.001	1.76 ± 0.03	0.80	<0.01
20	15.20 ± 1.68	0.76	<0.02	1.81 ± 0.03	0.77	<0.01
25	8.70 ± 0.70	0.74	<0.02	1.81 ± 0.03	0.76	<0.02
30	6.00 ± 0.53	0.74	<0.02	1.77 ± 0.03	0.76	<0.02
Starved						
15	14.4 ± 1.14	0.37	0.28	1.77 ± 0.03	0.73	<0.02
20	4.50 ± 0.50	0.24	0.49	1.82 ± 0.03	0.71	<0.05
25	3.00 ± 0.37	0.28	0.43	1.74 ± 0.04	0.70	<0.05
30	1.60 ± 0.16	0.04	0.92	1.79 ± 0.03	0.62	<0.05

r, correlation coefficient; *n* = 10 parental wasps.

toid fertility (e.g., Force and Messenger 1964, van Lenteren et al. 1987), and is consistent with the general presumption that insects cannot mature their eggs or are unable to oviposit outside a range of tolerable temperatures (Force and Messenger 1964, Greenfield and Karandinos 1976).

This is the first time the effect of temperature on the number of progeny produced by starved *V. canescens* adults has been studied. Many synovigenic species, like *V. canescens*, emerge with a small number of eggs stored in their lateral oviducts. However, feeding on nonhost food such as nectar and honey is necessary to compensate for the increased metabolic requirements of further ovogenesis (Flanders 1942, Jervis and Copland 1996). Previous studies have shown that oogenesis in *V. canescens* is a nutrient-limited process and is triggered only when sufficient nourishment is available (Kurstak 1966, Harvey et al. 2001, 2003). This may explain the nonsignificant effect of temperature on the fertility of starved adults, in that they would not have had any eggs available for oviposition beyond those present at emergence. This is supported by the concurrence of the number of progeny produced by starved adults (6–30) with the egg load of newly emerged wasps reported by Kurstak (1966) (20 eggs), Trudeau and Gordon (1989) (23.7 ± 1.1 eggs), Harvey et al. (1994) (≈30 eggs), and Eliopoulos (2003) (5–49 eggs).

Effect of Feeding

Wasps with access to honey produced significantly more progeny than starved ones. Similar conclusions have been made not only for *V. canescens* (Harvey et al. 2001) but for many other synovigenic parasitoids (e.g., Wäckers 1996, Wäckers et al. 1998, Schmäle et al. 2001). Beling (1932) was the first to suspect the importance of adult feeding on *V. canescens* when she observed newly emerged wasps leaving and then returning to the host habitat with nectar droplets in their mouthparts.

Adult feeding (on sugar or hosts) can have strong effects on parasitoid fitness parameters such as longevity, lifetime fecundity, survival, searching efficiency, overall activity, and other related parameters

(e.g., Godfray 1994, Jervis et al. 1996, Jervis and Kidd 1999). This has been verified not only for *V. canescens* (e.g., Ahmad 1936, Harvey et al. 2001, Eliopoulos 2003), but also for many other parasitoids of stored product pests, such as *Uscana lariophaga* Steffan (Trichogrammatidae) (van Huis et al. 1990), *Anisopteromalus calandrae* Howard (Wäckers 1996, Wäckers et al. 1998, Schmäle et al. 2001), *Dinarmus basalis* Rondani (Schmäle et al. 2001) (Pteromalidae), *Heterospilus prosopidis* Viereck (Wäckers et al. 1998, Schmäle et al. 2001), and *Habrobracon hebetor* Say (Nickle and Hagstrum 1981) (Braconidae).

These conclusions, and knowing that lack of suitable carbohydrate food sources has long been suspected as an important cause of poor performance of many biocontrol agents (Wolcott 1942), may justify the use of food supplements in suitable release sites to augment the efficacy of released parasitoids and other natural enemies (Wäckers et al. 1998, Schöller et al. 1997, Schöller 1998). Such food supplements promise substantial improvement in biological control efficacy in storage ecosystems.

Effect of Host Instar

Wasps that oviposited in second-instar hosts produced significantly fewer progeny than those that parasitized more mature hosts. This might be attributed to several reasons: the wound from the oviposition hole sometimes cannot be healed by a very young host (Harvey et al. 1994); normally high mortality of *E. kuehniella* during this instar (Harvey and Vet 1997); low acceptance of small larvae by the wasp for parasitism, given the preference of *V. canescens* for ovipositing in larger hosts (e.g., Harvey et al. 1994, Harvey and Thompson 1995b, Harvey and Vet 1997). Similar behavior has been observed in many koinobiont parasitoids of lepidopteran larvae (Beckage and Templeton 1985, Wani et al. 1994, Harvey 2000, Harvey et al. 2000). Our results establish that progeny production by *V. canescens* is not significantly influenced by host instar when older than second instar.

Host instar did not have much effect on age-specific fertility of *V. canescens*. In all cases (except 15°C), a decline in the rate of offspring emergence was re-

corded from the first day. Most lifetime progeny production had been recorded by the second day.

Effect of Body Size and Longevity

Larger wasps produced more progeny than their smaller conspecifics. The same results were observed when *V. canescens* parasitized larvae of *P. interpunctella* (Harvey et al. 2001). Fertility also was positively correlated with adult longevity. Longer-lived parasitoids had more time to access and parasitize host larvae and consequently produced more progeny. A positive correlation between number of progeny and longevity was reported previously for *V. canescens* (Harvey et al. 2001), as well as for other parasitoids of stored products pests (Wäckers 1996, Wäckers et al. 1998, Schmüle et al. 2001).

It should be noted that fertility was positively correlated with body size but not with longevity when wasps were deprived of food. Longer-lived, but starved, adults were unable to use their extra time because they ran out of mature eggs soon after emergence and could not replace them.

Our study shows conclusively that production of progeny by *V. canescens* is significantly enhanced, not only when wasps are supplied with honey and/or with mature hosts, but also by mild temperature conditions (20–25°C). These findings are of crucial importance when *V. canescens* is reared indoors or released as a classical biocontrol agent against lepidopterous pests of stored products.

References Cited

- Ahmad, T. 1936. The influence of ecological factors on the Mediterranean flour moth, *Ephesia kuehniella*, and its parasite *Nemeritis canescens*. *J. Anim. Ecol.* 5: 67–93.
- Beckage, N. E., and T. J. Templeton. 1985. Temporal synchronization of emergence of *Hyposoter exiguae* and *H. fugitivus* (Hymenoptera: Ichneumonidae) with apolysis preceding larval molting in *Manduca sexta* (Lepidoptera: Sphingidae). *Ann. Entomol. Soc. Am.* 78: 775–782.
- Beling, I. 1932. Zur biologie von *Nemeritis canescens* Grav. (Hymen. Ophion.). I. Züchtungserfahrungen und ökologische beobachtungen. *Z. Angew. Entomol.* 19: 223–249.
- Corbet, S. A. 1971. Mandibular gland secretion of larvae of the flour moth, *Anagasta kuehniella*, contains an epideictic pheromone and elicits oviposition movements in a hymenopteran parasite. *Nature (Lond.)*. 232: 481–484.
- Eliopoulos, P. A. 2003. Study of the parasitoid *Venturia canescens* (Gravenhorst) (Hymenoptera: Ichneumonidae) as a biocontrol agent against lepidopterous pests of stored products. PhD thesis, Agricultural University of Athens, Athens, Greece.
- Eliopoulos, P. A., J. A. Harvey, C. G. Athanassiou, and G. J. Stathas. 2003. Effect of biotic and abiotic factors on reproductive parameters of the synovigenic endoparasitoid *Venturia canescens*. *Physiol. Entomol.* 28: 268–275.
- Flanders, S. E. 1942. Oosorption and ovulation in relation to oviposition in the parasitic Hymenoptera. *Ann. Entomol. Soc. Am.* 35: 251–266.
- 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.
- Godfray, H.C.J. 1994. Parasitoids—behavioral and evolutionary ecology. Princeton University Press, Princeton, NJ.
- Greenfield, M. D., and M. G. Karandinos. 1976. Fecundity and longevity of *Synthedon pictipes* under constant and fluctuating temperatures. *Environ. Entomol.* 5: 883–887.
- Harvey, J. A. 2000. Dynamic effects of parasitism by an endoparasitoid wasp on the development of two host species: implications for host quality and parasitoid fitness. *Ecol. Entomol.* 25: 267–278.
- Harvey, J. A., and D. J. Thompson. 1995a. Developmental interactions between the solitary endoparasitoid *Venturia canescens* (Hymenoptera: Ichneumonidae), and two of its hosts, *Plodia interpunctella* and *Coryra cephalonica* (Lepidoptera: Pyralidae). *Eur. J. Entomol.* 92: 427–435.
- Harvey, J. A., and D. J. Thompson. 1995b. 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., and L.E.M. Vet. 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., I. F. Harvey, and D. J. Thompson. 1993. The effect of superparasitism on development of the solitary parasitoid wasp, *Venturia canescens* (Hymenoptera: Ichneumonidae). *Ecol. Entomol.* 18: 203–208.
- Harvey, J. A., I. F. Harvey, and D. J. Thompson. 1994. Flexible larval growth allows use of a range of host sizes by a parasitoid wasp. *Ecology*. 75: 1420–1428.
- Harvey, J. A., K. Kodash, and M. R. Strand. 2000. Differences in larval feeding behavior correlate with altered developmental strategies in two parasitic wasps: implications for the size-fitness hypothesis. *Oikos*. 88: 621–629.
- Harvey, J. A., I. F. Harvey, and D. J. Thompson. 2001. Lifetime reproductive success in the solitary endoparasitoid, *Venturia canescens*. *J. Insect Behav.* 14: 573–593.
- Jervis, M. A., and M.J.W. Copland. 1996. The life cycle, pp. 63–161. In M. A. Jervis and N.A.C. Kidd (eds.), *Insect natural enemies—practical approaches to their study and evaluation*. Chapman & Hall, London, UK.
- Jervis, M. A., and N.A.C. Kidd. 1999. Parasitoid adult nutritional ecology: implications for biological control, pp. 131–151. In B. A. Hawkins and H. V. Cornell (eds.), *Theoretical approaches to biological control*. Cambridge University Press, Cambridge, UK.
- Jervis, M. A., N.A.C. Kidd, and G. E. Heimpel. 1996. Parasitoid adult feeding behaviour and biocontrol—a review. *Biocont. News Inf.* 17:11N–26N.
- Kurstak, E. S. 1966. Le rôle de *Nemeritis canescens* Gravenhorst dans l'infection à *Bacillus thuringiensis* Berliner chez *Ephesia kuehniella* Zeller. Première partie. *Ann. Epiph.* 17: 335–383.
- Nickle, D. A., and D. W. Hagstrum. 1981. Provisioning with pre-paralyzed hosts to improve parasite effectiveness: a pest management strategy for stored commodities. *Environ. Entomol.* 10: 560–564.
- Salt, G. 1976. The hosts of *Nemeritis canescens*, a problem in the host specificity of insect parasitoids. *Ecol. Entomol.* 1: 63–67.
- SAS Institute. 1989. JMP: a guide to statistical and data analysis. v. 4.02. SAS Institute, Cary, NC.
- Schmüle, I., F.L. Wackers, C. Cardona, and S. Dorn. 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. 1998. Integration of biological and non-biological methods to control arthropods infesting stored products. IOBC/WPRS Bull. 21: 13–26.
- Schöller, M., S. Prozell, A. G. Al-Kirshi, and Ch. Reichmuth. 1997. Towards biological control as a major component of integrated pest management in stored product protection. J. Stored Prod. Res. 33: 81–97.
- Simmonds, F. J. 1943. The occurrence of superparasitism in *Nemeritis canescens* Grav. Rev. Can. Biol. 2: 15–49.
- Sirof, E. 1996. The pay-off from superparasitism in the solitary parasitoid *Venturia canescens*. Ecol. Entomol. 21: 305–307.
- Sokal, R. R., and F. J. Rohlf. 1995. Biometry, 3rd ed. Freeman, New York.
- Trudeau, D., and D. M. Gordon. 1989. Factors determining the functional response of the parasitoid *Venturia canescens*. Entomol. Exp. Appl. 50: 3–6.
- van Huis, A., N. K. Kaashoek, and H. M. Maes. 1990. Biological control of bruchids (Col.: Bruchidae) in stored pulses by using egg parasitoids of the genus *Uscana* (Hym.: Trichogrammatidae): a review, pp. 99–108. In F. Fleurat-Lassard and P. Ducom (eds.), Proceedings of the 5th International Working Conference on Stored Products Protection. Imprimerie du Midoc Bordeaux, Bordeaux, France.
- van Lenteren, J. C., A. van Vianen, H. F. Gast, and A. Kortenhoff. 1987. The parasite-host relationship between *Encarsia formosa* Gahan (Hym., Aphelinidae) and *Trialeurodes vaporariorum* (Westwood) (Hom., Aleyrodidae). XVI. Food effects on oogenesis, oviposition, life-span and fecundity of *Encarsia formosa* and other hymenopterous parasites. J. Appl. Entomol. 103: 69–84.
- Wäckers, F. 1996. Can food provision increase the efficacy of biological control in storage systems, p. 551. In A.A. Balkema (ed.), Proceedings of the 20th International Congress of Entomology. Museo Regionale di Scienze Naturali, Firenze, Italy.
- Wäckers, F. L., K. Schmäle, C. M. Cardona, and S. Dorn. 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.
- Wani, M., K. Iwabuchi, and J. Mitsuhashi. 1994. Developmental responses of *Galleria melonella* (Lepidoptera: Pyralidae) larvae to parasitism by a braconid parasitoid, *Apanteles galleriae* (Hymenoptera: Braconidae). Appl. Entomol. Zool. 29: 193–201.
- Wolcott, G. N. 1942. The requirements of parasitoids for more than hosts. Science. 96: 317–318.

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