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Oviposition, Development, and Feeding of *Scymnus* (*Neopullus*) *sinuanodulus* (Coleoptera: Coccinellidae): A Predator of *Adelges tsugae* (Homoptera: Adelgidae)

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ABSTRACT The hemlock woolly adelgid, *Adelges tsugae* Annand, is a major threat to hemlocks in the eastern United States. As part of efforts to control this pest, *Scymnus* (*Neopullus*) *sinuanodulus* Yu et Yao, a potential predator, was collected from hemlocks in Yunnan, China. Three shipments were imported during 1996 and 1997 to a quarantine laboratory to study the beetle's biology. Beetles began oviposition immediately after transferal from 5°C in the spring, ceased oviposition by June, and laid the same number of eggs, whether egg laying began in February or in April. Two-year-old beetles laid as many eggs per year as 1-yr-old beetles. We observed only one generation per year. Yearly fecundity averaged 130 eggs with a maximum of 200 per female. Newly emerged beetles remained preovipositional until the following spring, but could be induced to oviposit in the fall by prior exposure to 5 or 10°C for 1.5 mo. The egg, larval (four instars), and pupal stages lasted 10, 20, and 10 d, respectively, at 20°C. From egg to adult took 73, 40, and 35 d at 15, 20, and 25°C, respectively. Larval survival was only 5% at 25°C. Both larvae and adults fed on all stages of *A. tsugae*, but larvae grew faster with much higher survival on adelgid eggs, and could not complete development on adelgid nymphs alone. When given adelgid eggs, the beetles laid more eggs initially; however, adelgid nymphs seem to satisfy nutritional requirements for oviposition. Laboratory-reared beetles were similar to field-collected beetles in oviposition, fecundity, feeding, survival, and development.

KEY WORDS *Scymnus sinuanodulus*, *Adelges tsugae*, hemlocks, oviposition, development, feeding

THE HEMLOCK WOOLLY adelgid, *Adelges tsugae* Annand, is native to Asia, occurring in China, Japan, and India (Inouye 1953, Ghosh 1983, Wang et al. 1997). First described from western North America in the 1920s (Annand 1924, 1928) and subsequently identified in Asia (Takahashi 1937), it was not reported in eastern North America until the 1950s (Souto et al. 1996). It is believed to have been accidentally introduced to North America from Asia (McClure 1987). Since the mid-1980s, *A. tsugae* has been recognized as a serious pest of the eastern hemlocks *Tsuga canadensis* (L.) and *T. caroliniana* Engelm. The vulnerability of eastern hemlocks to *A. tsugae* is probably due to a lack of natural enemies and an intolerance to adelgid feeding (McClure 1987). Adelgid populations can build rapidly after infesting a tree and cause marked change in tree health within 4 yr (McClure 1991).

Biological controls of *A. tsugae* are being sought in Japan and China. A coccinellid beetle and an oribatid mite have been introduced into the United States from Japan (McClure 1995, McClure and Cheah 1998). The life history and biology of the Japanese coccinellid, *Pseudoscymnus tsugae* Sasaji & McClure, have been studied (Cheah and McClure 1998). A diverse guild of insect natural enemies of *A. tsugae* occurs in south-

western China (Wang et al. 1997). Coccinellids of the tribe Scymnini are particularly abundant and speciose. More than 20 *Scymnus* and five *Pseudoscymnus* species have been found associated with adelgid-infested hemlocks in Sichuan and Yunnan Provinces; many of these are new (Wang et al. 1997, Yu et al. 1997, Yu et al. 2000). *Scymnus* (*Neopullus*) *sinuanodulus* Yu et Yao is one of these newly described species and its host range is restricted to adelgids (Montgomery et al. 1997).

We present the results of a 2-yr study on the biology of *S. sinuanodulus*. Our objective was to obtain information to facilitate mass-rearing and field establishment of this beetle for possible biological control of *A. tsugae* in North America. We were particularly interested in oviposition, development on different adelgid stages, responses to temperatures, and whether laboratory rearing would change the biology or viability of *S. sinuanodulus*. We also compared our information to that on other members in the tribe Scymnini that have been used for biological control of conifer-feeding insects.

Materials and Methods

Adult *S. sinuanodulus* were field-collected from *T. dumosa* (D. Don) Eichler and *T. forrestii* Downie in Lijiang County and Heyuan County, Yunnan Prov-

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ince, at an altitude of 2,500–2,900 m, on both hemlocks and five-needle pines infested with adelgids, on 6–17 October 1996, 18 April–3 May 1997, and 9–10 September 1997. We received three shipments at the Forest Service quarantine laboratory, Ansonia, CT, in November 1996, May 1997, and September 1997, respectively. No parasitoids emerged from any of the shipments. We designated all these beetles as field-collected even though some were in the laboratory for >2 yr. First-generation progeny of field-collected beetles reared in the laboratory were designated G₁ and second-generation progeny of laboratory-reared G₁ beetles were designated G₂. Voucher specimens of *S. sinuanodulus* are deposited in Yale Peabody Museum and the U.S. National Museum of Natural History.

Adelgid-infested foliage of *T. canadensis* was collected directly from the field; some from November to June was stored at 5°C with the cut end in water. We moved the foliage to higher temperatures as needed to have a continuous supply of viable adelgid eggs and other active stages. For example, foliage infested with adelgid nymphs collected in June provided viable eggs until November if moved to 10 or 15°C 2 wk before use. We conducted oviposition experiments in 450-ml paperboard cups with translucent plastic lids. Foliage infested with overlapping stages of adelgid eggs, adults, and nymphs was inserted in the side of the cup and held in a water tube. We changed the foliage weekly to ensure continuous and excess presence of adelgid eggs. In addition, we conducted immature development and larval and adult feeding experiments with single individuals in 5 × 0.7 cm petri dishes containing foliage with overlapping stages of adelgid eggs, adults, and nymphs. The dishes were tight-lidded to prevent foliage from desiccation and preserve adelgid viability at least for 1 wk. We monitored these individuals and changed foliage daily to ensure excess presence of adelgid eggs. Overwintering conditions were 5°C and a photoperiod of 10:14 (L:D) h. Otherwise, conditions were as specified in each experiment. For each comparable test, we kept adelgids intact on foliage, provided excess prey, used the same source of foliage, and changed foliage at the same time to reduce variation in prey quality and quantity. We used SYSTAT 7.0 (SPSS 1997) for all statistical analyses.

Oviposition and Fecundity. In 1998, we transferred five groups of beetles at different times to 15°C and 12:12 (L:D) h. All the beetles had been stored in overwintering conditions since 2 December 1997 before the experiments. We changed beetle density after the February exposure to reduce the workload. We monitored oviposition and changed foliage weekly for all five groups until 2 July. We contrasted fecundity (cumulative weekly oviposition per year) between (1) the February (16 females per 16 cups) and April (20 females per 8 cups) groups of the third shipment; (2) the parental (second shipment, 13 females per 5 cups in April) and offspring (G₁, 16 females per 4 cups in March) generations; and (3) the 2-yr-old beetles (first shipment, 8 females per 4 cups in April) and 1-yr-old beetles (same as the April group of the third shipment) in the laboratory, using separate one-way

analyses of variance (ANOVA). We had far fewer males than females but were able to add males to about half the cups of beetles from the April group, the parental group, and its offspring group. To test whether continuous male presence affected oviposition, we used a two-way ANOVA with the groups treated as blocks to compare fecundity between cups with and without males.

Immature Development and Temperature. We compared development and survival of egg, larval, and pupal stages at 15, 20, and 25°C and 12:12 (L:D) h between G₁ and G₂ generations in March 1998. A total of 30, 87, and 23 G₁ eggs were observed at 15, 20, and 25°C, respectively, to record daily the number of hatchlings. Development of 18 G₂ eggs was also simultaneously compared with that of 32 G₁ eggs at 20°C.

In addition, we assigned an equal number ($n = 21$) of neonate larvae from each generation to each temperature simultaneously and monitored daily development and prey supply. We used a two-way ANOVA with temperature nested within generation to examine differences in development time between generations and among temperatures. Cumulative survival from larva to adult was also compared between generations and among temperatures using Pearson χ^2 tests.

Preoviposition and Environmental Factors. We examined whether prolonged adelgid egg presence with different photoperiods and temperatures affected beetle preoviposition. In 1997 we held 50 newly emerged G₁ females (10/cup) from 29 May until 23 September at 20°C and 14:10 (L:D) h (spring/summer-like conditions), then changed to 15°C and 10:14 (L:D) h through November (fall-like conditions). We provided foliage infested with overlapping adelgid stages during both periods to contrast the seasons. In 1998, we repeated the 1997 experiment, but changed the photoperiod to 12:12 (L:D) h to contrast with that of the first period in 1997, from 15 April through 4 August. We used ≈ 500 newly emerged G₁ females (50/cup) in 10 paperboard 3.8-liter cups with screen lids. Keeping the same photoperiod, we then changed the temperature to either 5 or 10°C and provided foliage infested only with aestivating and/or developing first instar nymphs from 4 August through November to see whether an early exposure to cold temperature would induce beetle oviposition. We exposed the beetles to room temperature for 4–6 h at 3-wk intervals to change foliage. We checked at least three foliage branches from each cup for beetle eggs or evidence of cannibalism. The remaining foliage was held for 10 d at room temperature and checked for beetle larvae.

Between 14–21 December 1998, we moved 56 beetles from each beetle group at 5 or 10°C to eight cups (5 females and 2 males/cup) at 20°C for 48 h with overlapping adelgid-infested foliage, and repeated this with different beetles five times (total 20 cups and 100 females per temperature). We recorded whether oviposition occurred in each cup and used a Pearson χ^2

test to contrast the number of cups with beetle eggs between 5 and 10°C exposures.

Adult Feeding and Prey Suitability. We first examined beetle feeding after removal from overwintering conditions. In 1997, we provided overlapping adelgid-infested foliage to 11 beetles (first shipment) at 20°C and on 19 March. We repeated the test twice at 15°C and 12:12 h (L:D) on 19 February and 2 March 1998, using 19 field-collected beetles and 18 laboratory-reared beetles, respectively. We recorded what was consumed or attacked and the percentage of beetles feeding in each group within 1, 2, and 7 d or longer. We also kept track of whether the beetles that fed were among those that oviposited within 1 wk of exposure to the warm temperatures in both years.

To see whether beetle adults fed on aestivating first instar nymphs, we then tested nine field-collected beetles (starved for 12–24 h at 15°C before test) at a time and repeated the test three times with different beetles during the first half of October 1998 at 20°C and 12:12 (L:D) h. We provided each beetle with 10 aestivating nymphs, excess adelgid-free foliage as shelter, and recorded the number of nymphs consumed in 24 h. We also compared two groups of seven beetles feeding on either 10 adelgid eggs placed on hemlock foliage free of adelgids or 10 aestivating nymphs intact on foliage for 24 h.

To evaluate whether feeding on different adelgid stages affected beetle oviposition, we moved 20 beetles from overwintering conditions to 15°C and 12:12 (L:D) h on 10 February 1999. Each 10 individuals were confined to two types of adelgid-infested foliage (eggs, adults, and nymphs or only nymphs). We recorded the percentage of beetles feeding and consumption on all adelgid stages available in 24 h, and checked oviposition per female at 2-wk intervals for 6 wk. To compare the differences in oviposition between beetles feeding on foliage with overlapping adelgid stages ($n = 8$) or with nymphs only ($n = 7$), we used t -tests on the square root transformed data for each biweekly period and the 6-wk total.

Larval Feeding and Prey Suitability. To compare the suitability of adelgid eggs and nymphs to support development of *S. sinuanodulus* larvae, we conducted two feeding trials on 19 and 27 March 1998 at 20°C and 12:12 (L:D) h, using neonates of the third shipment. We fed the larvae either a mixture of two-thirds nymphs older than the second instar and one-third adults bearing an average of 25 eggs per ovisac (simulating early spring foliage infested with mainly older adelgid nymphs), or a mixture of ovipositing adults bearing an average of 40 eggs per ovisac and < 10% older nymphs (simulating late spring foliage infested with mainly adelgid eggs and adults). We monitored daily at least 34 individuals for each type of adelgid-infested foliage. We used survival to adult and development time of each instar, prepupal, and pupal stage to indicate host suitability. A two-way ANOVA with trials treated as blocks was used to compare development of each instar, prepupal, and pupal stage between the two prey types (block effects were significant but not reported). Pearson χ^2 was used to

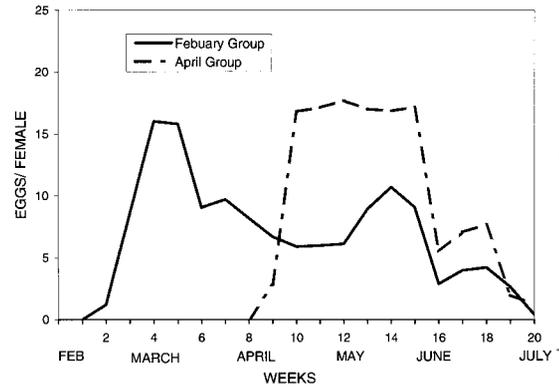


Fig. 1. Weekly oviposition by *S. sinuanodulus* at 15°C after transferal from overwintering conditions on 19 February ($n = 16$) and 9 April ($n = 8$) 1998.

analyze survival to adult and sex ratios of the newly emerged adults between the prey types.

To examine whether beetle larvae could develop on adelgid nymphs alone, we confined 64 neonates of the second shipment individually to foliage infested with second to third instar nymphs at 20°C from December 1998 to January 1999, and recorded daily survival and development time of larval and pupal stages.

Results

Oviposition and Fecundity. In 1998 at 15°C, regardless of transferal date from overwintering conditions and beetle density, all five groups of beetles started to lay eggs within 1 wk and stopped ovipositing in early July, although peak oviposition varied. For example, both the February and April groups of the third shipment started to lay eggs within 1 wk and peaked in 4 or 3 wk, respectively (Fig. 1). Oviposition duration was longer and oviposition peak was lower for the February group than the April group. Weekly oviposition by both beetle groups declined markedly at the end of May; by 2 July, they were laying < 2 eggs/wk (Fig. 1). For the February group, 16% laid eggs in 3 d and 53% within 1 wk; 80% laid >100 eggs and one laid < 30 eggs.

Differences in fecundity (eggs \pm SE, maximum) were all insignificant between (1) the February (121.99 ± 9.90 , > 160) and April groups (121.30 ± 15.51 , > 160), (2) the parental (139.91 ± 43.12 , > 200) and offspring (116.53 ± 15.53 , > 135) generations, and (3) the 1-yr old (as the April group) and 2-yr old (153.88 ± 5.81 , > 160) beetles in the laboratory. We observed mating frequently, but the presence of males did not affect fecundity ($F = 0.0068$; $df = 1, 13$; $P = 0.9356$; without males 125.68 ± 14.14 eggs versus with males 125.62 ± 12.49 eggs, block effect was not significant).

Immature Development and Temperature. G_1 eggs required 17.30 ± 0.17 , 10.21 ± 0.06 , and 8.00 ± 0.00 d to hatch at 15, 20, and 25°C, respectively. At 20°C, G_2 eggs required 10.11 ± 0.08 d to hatch.

Table 1. Larval and pupal development time (d ± SE) of *S. sinuanodulus* neonates of the first (G₁) and second (G₂) laboratory-reared generations in spring 1998 at different temperatures

Temp. °C	Generation	Instar				Pupa	Larva to adult
		1	2	3	4		
15	G ₁	6.29 ± 0.45	4.75 ± 0.27	5.78 ± 0.17	21.63 ± 0.97	19.20 ± 0.28	56.73 ± 4.28
	(21)	(21)	(20)	(18)	(16)	(15)	(15)
	G ₂	5.25 ± 0.39	5.39 ± 0.83	5.41 ± 0.23	20.14 ± 0.48	19.46 ± 0.31	54.46 ± 3.36
	(21)	(20)	(18)	(17)	(14)	(13)	(13)
20	G ₁	3.47 ± 0.19	2.53 ± 0.13	3.21 ± 0.54	12.08 ± 0.62	10.64 ± 0.31	31.64 ± 4.41
	(21)	(17)	(15)	(14)	(13)	(11)	(11)
	G ₂	2.71 ± 0.25	2.55 ± 0.17	2.75 ± 0.19	11.00 ± 0.36	10.59 ± 0.27	28.82 ± 1.42
	(23)	(21)	(20)	(20)	(20)	(17)	(17)
25	G ₁	2.58 ± 0.11	2.13 ± 0.08	2.07 ± 0.07	8.75 ± 0.25	10.50 ± 0.50	26.50 ± 0.71
	(21)	(19)	(16)	(15)	(4)	(2)	(1)
	G ₂	2.48 ± 0.19	2.22 ± 0.17	2.07 ± 0.07	8.00 ± 0.00		
	(21) ^a	(21)	(18)	(14)	(1)		
	F generation	6.65*	0.64	1.84	1.20	0.13	7.54**
	df	1, 113	1, 101	1, 92	1, 62	1, 52	1, 51
	F temperature	34.73**	17.71**	56.01**	68.02**	436.33**	354.72**
	(generation)						
	df	4, 113	4, 101	4, 92	4, 62	2, 52	2, 51

Sample size (in parentheses) also indicates cumulative survival. * and **, significant difference at $\alpha = 0.011$ and 0.001 , respectively. ^a 25°C values omitted in analysis of pupal and total development from larva to adult due to lack of data.

Larval and pupal development differed little between the laboratory generations, but was significantly affected by temperature (Table 1). G₂ grew faster than G₁ only in the first instar. The effect of temperature was highly significant for each stadium. Development at 15°C was slower than at 20°C. The difference between 20 and 25°C was not as great, except in the fourth instar. Development time of the second and third stadia was about equal, but the first instar required slightly more time than the second and third instars, and the fourth stadium (fourth instar and prepupa combined) was longer than all three previous stadia combined. Pupal development accounted for ≈one-third of the total development time from first instar to adult.

Survival to adult (Table 1) was not significantly different between G₁ (44% of 63) and G₂ (46% of 65) generations ($\chi^2 = 0.04$, df = 1, $P = 0.846$), but was significantly affected at 25°C (67%, 64%, 5%, respectively for 15, 20, and 25°C). Survival was extremely low at 25°C and only two pupae eclosed and one of them died (25 versus 20°C, $\chi^2 = 32.79$, df = 1, $P = 0.0005$; 25 versus 15°C, $\chi^2 = 35.50$, df = 1, $P = 0.0000$). Most mortality at 25°C occurred in the fourth instar (Table 1). There was no significant difference in survival between 15 and 20°C ($\chi^2 = 0.09$, df = 1, $P = 0.768$).

Preoviposition and Environmental Factors. Although provided continuously with adelgid eggs as food, newly emerged beetles remained preovipositional in both periods of 1997 and the first period of 1998, regardless of photoperiods. However, at the second 3-wkly foliage change, we found beetle eggs laid following 1.5 mo of early exposure to 5 or 10°C (since August 1998).

After more than 4 mo chilling at either 5 or 10°C and five foliage changes, most of the beetles (75 and 85% of 20, respectively) laid eggs within 48 h at 20°C. The percentage of cups with beetle eggs was not significantly different between 5 and 10°C ($\chi^2 = 0.625$, df =

1, $P = 0.429$), indicating either temperature satisfactorily induced oviposition.

Adult Feeding and Prey Suitability. In spring 1997, the field-collected beetles began feeding within 1 d (64%) or 2 d (91%) after transferal from overwintering conditions. In spring 1998, 63% of the field-collected beetles and 32% of the laboratory-reared beetles were feeding in 24 h; 84% and 50% in 48 h, respectively. Within 1 wk, 100% of the beetles in both groups were feeding. In both years 100% of the beetles that oviposited within 1 wk were among those that fed within 48 h; >90% (42/46) of the beetles preyed on both adelgid eggs and adults/nymphs.

In fall 1998, only 37% of the adult beetles (10/27) fed on aestivating first instar nymphs and each beetle that fed consumed only 1.8 ± 0.34 nymphs in 24 h. In another test, beetles consumed 5.28 ± 0.75 adelgid eggs (placed on foliage) and only 1.57 ± 1.75 aestivating first instar nymphs (intact on foliage) in 24 h; each group with 57% adults feeding. Both results indicated a relatively low percentage of beetles feeding in the fall and a feeding preference for adelgid eggs over aestivating nymphs.

In spring 1999, 100% of the beetles fed in 24 h whether given foliage infested with overlapping adelgid stages, or with only nymphs. Among those given overlapping adelgid stages, 80% fed on both eggs and adults/nymphs, consuming an average of 9.2 ± 1.03 individuals in 24 h; beetles given only nymphs consumed 6.9 ± 0.77 individuals. Feeding on different adelgid stages significantly affected the onset of beetle oviposition (Table 2). During wk 1–2, beetles given adelgid eggs laid significantly more eggs than those given only nymphs. The difference was less pronounced during wk 3–4. By wk 5–6 beetles feeding on only nymphs laid as many eggs as those given adelgid eggs. However, the total number of eggs laid during the total 6 wk was not significantly different between the prey types (Table 2).

Table 2. Oviposition (eggs per female \pm SE) by *S. sinuanodulus* feeding on adelgid eggs, adults, and nymphs ($n = 8$) or only nymphs ($n = 7$) after transferal from overwintering conditions in February 1999

Adelgid stage	Weeks 1-2	Weeks 3-4	Weeks 5-6	Total
Egg, adult, and nymph	6.44 \pm 2.68	11.44 \pm 5.27	12.78 \pm 5.56	30.67 \pm 11.30
Nymph	0.50 \pm 0.38	8.13 \pm 2.73	18.75 \pm 4.39	27.38 \pm 6.67
<i>t</i>	2.1551	0.0899	0.9619	0.0479
<i>P</i>	0.0478	0.9295	0.3513	0.9624

Data were square-root transformed for each *t*-test, all *df* = 15.

Larval Feeding and Prey Suitability. Survival of neonate larvae reared on early spring foliage infested with mainly nymphs and few eggs was significantly lower than neonates reared on late spring foliage with mainly eggs and few nymphs (61% of 36 and 85% of 34, respectively; $\chi^2 = 10.921$, *df* = 1, *P* = 0.001). The difference in survival was greatest in the prepupal stadium (Fig. 2A). Growth of beetle larvae on early spring foliage was slower than on late spring foliage (Fig. 2B). Development time of the first instar ($F = 61.10$; *df* = 1, 59; *P* = 0.0001), third instar ($F = 5.88$; *df* = 1, 54; *P* = 0.0187), and fourth instar ($F = 21.60$; *df* = 1, 48; *P* = 0.0001) was significantly longer when feeding on early spring foliage than on late spring foliage, but was not significantly different for the second instar ($F = 0.06$; *df* = 1, 57; *P* = 0.8113), prepupa

($F = 0.94$; *df* = 1, 48; *P* = 0.3374), and pupa ($F = 0.28$; *df* = 1, 48; *P* = 0.5970). Development time from first instar to adult emergence was significantly longer for early (31.00 ± 0.44) than for late (27.79 ± 0.20) spring foliage ($F = 49.33$; *df* = 1, 48; *P* = 0.0001). A higher percentage of females developed from larvae feeding on late spring foliage (18/29) than on early spring foliage (10/19), but the difference was not significant ($\chi^2 = 0.421$ *df* = 1, *P* = 0.517).

Larvae given only second-instar adelgids had 75% mortality in the first instar, and only 2/64 survived to pupate. The two survivors took >30 d to pupate and failed to emerge as adults, indicating that the larvae could not complete development on nymphs alone, but could live for some time.

Discussion

Many aphid-feeding coccinellids display partial synchrony with their prey, producing their offspring in the spring in response to increased prey abundance (Hagen 1962). Oviposition by *S. sinuanodulus* in the spring when adelgid eggs are most abundant (Fig. 1) and a long reproductive dormancy of newly emerged beetles conform to this pattern. Therefore, *S. sinuanodulus* is univoltine. Although many *Scymnus* species that feed on aphids are multivoltine (Hagen 1962), multivoltinism is not necessarily characteristic of the genus (*contra* Naranjo et al. 1990). *Scymnus (Pullus) impexus* (Mulsant), introduced to North America from Europe for biological control of the balsam woolly adelgid (Delucchi 1954), *S. (Scymnus) nigrinus* Kugelann, which feeds on pine aphids and adelgids (Vohland 1996), *S. (Pullus) suturalis* Thunberg, a European species that feeds on pine and hemlock adelgids (Montgomery and Lyon 1996), *S. (Neopullus) camptodromus* Yu et Liu, which feeds on *A. tsugae* (Lu and Montgomery 1999), are all univoltine. Univoltinism thus appears to be common in *Scymnus* feeding on Adelgidae.

Coccinellid adults often spend unfavorable periods relative to food and climatic conditions in a dormant state to allow synchronization of the active stages with prey supply (Hodek and Honek 1996). We did not observe diapause in *S. sinuanodulus* but rather long preoviposition in newly emerged beetles. Some coccinellid adults reach reproductive maturity only after they have fed on host prey or are exposed to a short photoperiod (Hagen 1962). Preoviposition of *P. tsugae* was shortened when given developing adelgid nymphs and a long photoperiod (Cheah and McClure

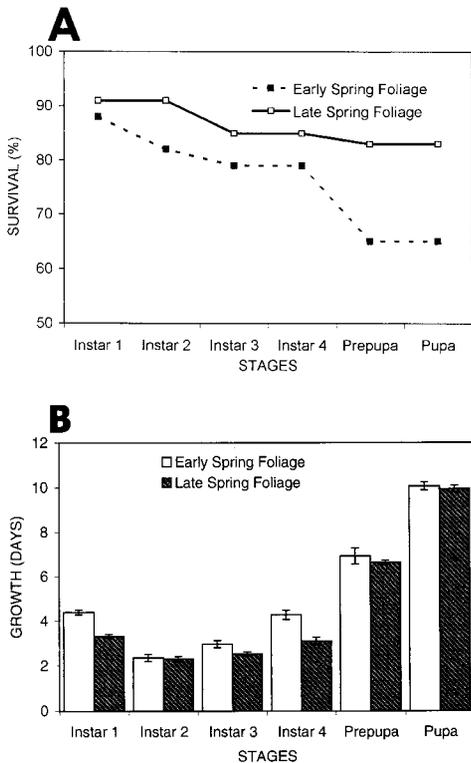


Fig. 2. Survival (A) and development time (B) ($d \pm$ SE) of *S. sinuanodulus* neonates reared on early spring foliage with mainly adelgid nymphs ($n = 34$) and late spring foliage infested with mainly adelgid eggs and adults ($n = 35$) at 20°C, March 1998.

1998). However, only exposure to cold temperatures shortened preoviposition of *S. sinuanodulus*, as has been reported in other coccinellids (Hagen 1962, Hodek and Honek 1996). This may be useful in mass rearing of the beetles in the laboratory. Viability varies little between field-collected and laboratory-reared immatures and adults. Adults lay about the same number of eggs regardless of their laboratory age, exposure date to spring warmth, and adelgid stage available. All this indicates great flexibility for mass rearing.

Adults of *S. sinuanodulus* feed on all stages of *A. tsugae*, but feeding rate and feeding preference may vary seasonally. Results from both years indicate that adults have no feeding preference for adelgid eggs or nymphs in the spring, but prefer adelgid eggs to nymphs in the fall. Newly emerged adults feed voraciously in the spring and less in the summer (Montgomery et al. 1997). There appears to be a positive correlation between feeding and oviposition: only those that fed immediately after removal from overwintering oviposited within the first week, and more eggs were laid when adelgid eggs were present than when absent in the first 2 wk (Table 2). Indeed, *S. sinuanodulus* may delay oviposition initiation in the spring if adelgid eggs are absent. The initial differences in oviposition may be behavioral rather than nutritional because of the eventual oviposition in the absence of adelgid eggs (Table 2). Immediate feeding and ovipositional responses of *S. sinuanodulus* to warming temperature and presence of adelgid eggs allow this small lady beetle to synchronize well with the spring egg production of *A. tsugae*.

Fecundity of *S. sinuanodulus* is comparable to *S. impexus* feeding on *A. piceae* (Ratzeburg) (Delucchi 1954), but is about half that of *P. tsugae* feeding on *A. tsugae* (Cheah and McClure 1998). Prolific species tend to lay eggs openly in clusters, whereas less fecund species usually lay eggs singly in areas protected from natural enemies and close to prey (Kawauchi 1991). All three species, *S. sinuanodulus*, *S. impexus*, and *P. tsugae*, lay their eggs singly in concealed areas close to prey. Therefore, the difference in fecundity between *S. sinuanodulus* and *P. tsugae* may not be behavioral, but may be related to host specificity: better larval growth on adelgid eggs than on nymphs (Fig. 2) and immediate oviposition in the presence of adelgid eggs (Table 2) in *S. sinuanodulus*. Larvae of *S. impexus* also specialize on eggs (Delucchi 1954), but *P. tsugae* may develop on either eggs or nymphs (Cheah and McClure 1998). Mortality and slow development of *S. sinuanodulus* feeding on nymphs alone indicate that adelgid eggs are critical in early stages.

Development of *S. sinuanodulus* larvae at 20°C is similar to *P. tsugae* (Cheah and McClure 1998). Each immature stage of *S. impexus* at 17°C (Delucchi 1954) spends the same proportion of time as does *S. sinuanodulus* at 15°C. Because of high larval survival at 15°C and capability to develop for some days at 25°C (Table 1), it is likely that *S. sinuanodulus* could survive the few hours of temperatures exceeding 25°C and its immature development may extend to early summer in the field during the eastern U.S. spring and early

summer when the adelgid is a serious problem. This suggests that oviposition and subsequent immature development of *S. sinuanodulus* occur concordantly with production of adelgid eggs by both the overwintering and spring generations, further evidence for adaptation of *S. sinuanodulus* to close synchrony with *A. tsugae*.

In nature, coccinellid species with a long period of inactivity usually live ≈ 1 yr (Hodek and Honek 1996). We monitored 17 beetles of the first shipment from receipt in November 1996; 41% survived through June 1999. The laboratory longevity of *S. sinuanodulus* seems to be longer than *P. tsugae* (Cheah and McClure 1998). Although the fecundity of *S. sinuanodulus* is relatively low, its behavior of laying eggs singly suggests that it can reproduce well even at low prey density, whereas its univoltinism and multi-year life span may be adaptations to summer scarcity of adelgid eggs. These attributes may enhance survival of both adult and immature *S. sinuanodulus* in the field when there are not only larvae but also old and newly emerged adults feeding in early summer.

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