

Comparison of Developmental and Reproductive Rates of *Nabis americanoferus*, *N. roseipennis*, and *N. rufusculus* (Hemiptera: Nabidae)

S. K. BRAMAN AND K. V. YEARGAN

Department of Entomology, University of Kentucky,
Lexington, Kentucky 40546

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ABSTRACT Developmental and survival rates were determined under seven constant temperatures for *Nabis rufusculus* and under two alternating temperature regimes for *N. americanoferus*, *N. roseipennis*, and *N. rufusculus*. Reproductive rates were determined for all three species under two constant and one alternating temperature regimes. *N. rufusculus* completed development at temperatures between 18 and 33°C. Successful development did not occur at 15°C. Time required to complete development from egg to adult ranged from 82.8 d (18°C) to 27.1 d (33°C) and was similar for males and females. Nymphal survival was highest at 27°C (84.1%) and lowest at 33°C (38.9%). An alternating temperature regime of 21 and 33°C (mean, 27°C) resulted in slower development than that which occurred at constant 27°C because the upper limit of the alternating regime (33°C) was a detrimental temperature. Development under an alternating regime of 12 and 24°C (mean, 18°C), however, was accelerated compared to that under a constant 18°C regime. Developmental thresholds calculated for egg, nymphal, and total development for *N. rufusculus* were 13.1, 11.6, and 11.9°C, respectively. *N. rufusculus* develops at a rate similar to that of *N. roseipennis* and more slowly than *N. americanoferus*. Total egg production was similar for all three species at an optimal temperature (27°C), but *N. americanoferus* deposited eggs over a shorter period of time than did the other two species. Egg production was lower at 21°C than at 27°C for all species, but especially so for *N. rufusculus*. Egg production was often, though not always, lowered when green bean pods rather than soybean seedlings were used as the ovipositional substrate.

KEY WORDS Insecta, predators, damsel bugs, biology

NABIDS, the predaceous damsel bugs, are abundant predators in many agricultural habitats including cotton, alfalfa, and soybean (Dinkins et al. 1970, Pimentel & Wheeler 1973, Shepard et al. 1974, Benedict & Cothran 1975, Pitre et al. 1978, Irwin & Shepard 1980). Nabids often are predominant predator species numerically at some point during the growing season, and their contribution as predators against a variety of pest insects has been suggested (e.g., Tamaki & Weeks 1972, Irwin et al. 1973, Rancy & Yeargan 1977). At present the potential importance of predators as control agents is largely ignored in the derivation of economic thresholds. Ostlie & Pedigo (1987) have, however, proposed a method whereby natural mortality estimates can be incorporated into economic threshold calculations. The ability to predict population phenology, as well as predator impact, is necessary to incorporate mortality that is the result of predation by nabids into economic injury assessments. Possible manipulation of these predators and future inclusion in pest management strategies require an understanding of their biology and behavior.

Earlier studies under controlled laboratory conditions determined developmental times in relation to temperature or reproductive biologies for several *Nabis* species (Perkins & Watson 1972, Hornmchan

et al. 1976, Guppy 1986, Nadgauda & Pitre 1986). Our studies were undertaken to compare the effects of constant and alternating temperature regimes on the survival, development, and reproductive potential of three *Nabis* species that co-occur in alfalfa and soybean fields in central Kentucky. The effects of constant temperatures on the survival and development of *N. americanoferus* (Carayon) and *N. roseipennis* Reuter were reported previously by Braman et al. (1984). The data here describe the effects of constant temperatures on the survival and development of the immature stages of *N. rufusculus* Reuter and on reproduction by all three species. Development, survival, and reproductive potential of the three species under two alternating temperature regimes also are presented.

Materials and Methods

Developmental Biology. Colonies started with field-collected insects were maintained in the laboratory under a 15:9 (L:D) photoperiod and at room temperature (23-26°C) in a manner similar to that of Sloderbeck & Yeargan (1983). Adults and nymphs were fed eggs of the tobacco budworm, *Heliothis virescens* (F.), from a colony maintained by methods similar to those used by Ignoffo (1965). De-

developmental rates and survival by stage were examined for *N. rufusculus* at 15, 18, 21, 24, 27, 30, and $33 \pm 1^\circ\text{C}$. These temperatures were the same as those used in examining developmental rates for *N. americanoferus* and *N. roseipennis* (Braman et al. 1984). Development under the fluctuating temperature regimes 33/21 (mean 27°C) and 24/12 (mean 18°C) was compared among the three *Nabis* species. A 15:9 photoperiod and 12:12 thermoperiod were maintained throughout all experiments and relative humidities fluctuated between 70 and 90%.

Reproductively mature females were confined to a soybean seedling, *Glycine max* (L.) Merrill var. 'Williams,' and allowed to lay eggs during a 12-h period at the experimental temperature. Seedlings containing eggs were placed at the experimental temperature in 0.9-liter cardboard cartons with a plastic wrap lid. The eggs were monitored twice daily for hatching. Upon emergence, nymphs were housed individually in 32-ml, ventilated plastic cups and provided with a moistened cotton dental roll to serve as a source of free water. Nabids were fed daily with an excess of tobacco budworm eggs and monitored twice daily for the presence of exuviae. The date and time of each egg hatch or nymphal molt was estimated as the midpoint of the time period (i.e., between observations) during which the event occurred. Duration of development was compared between males and females at each temperature using the least significant difference test (LSD) following a significant analysis of variance.

Reproductive Biology. Fifth-instar nabids from the colonies were isolated and observed twice daily for the final molt. Upon emergence as adults, females were paired with males in 0.9-liter cardboard containers and were placed in environmental chambers. Female nabids were supplied daily with living soybean seedlings ('Williams') or green bean pods as an ovipositional substrate. Nabids were supplied only one kind of plant material during the course of their lifetimes. Nabids were provided an excess of tobacco budworm eggs and supplied with a moistened cotton dental roll. Plant material was searched daily for eggs. Males that died were replaced throughout the life of the female. Data collected at each of two constant and one fluctuating temperature regimes (21, 27, and $27/21^\circ\text{C}$) included length of the preoviposition period, the number of eggs oviposited per female per day, the total number of eggs oviposited per female, the longevity of the female, and male longevity. Comparisons were made among the three species at each of the temperature regimes (ANOVA followed by LSD if significant) and between the two different ovipositional substrates (Student's *t* test). Voucher specimens of *N. americanoferus*, *N. roseipennis*, and *N. rufusculus* have been deposited in the insect museum in the Department of Entomology at the University of Kentucky, Lexington, Ky.

Results and Discussion

Developmental Biology. *Nabis rufusculus* completed development at temperatures between 18 and 33°C , but not at 15°C (Table 1). Eye spots were present in eggs that were dissected from plant tissue indicating that some development within the egg had occurred at 15°C , yet eclosion from the egg was not observed. Time required to complete development ranged from 82.8 d (18°C) to 27.1 d (33°C).

Survivorship during the egg stage ranged from 36% at 24°C to 71% at 30°C and averaged 53.5%. Nymphal survivorship was highest at 27°C (84.1%) and lowest at 33°C (38.9%). Males and females required the same amount of time to develop ($P > 0.05$).

Comparison with *N. americanoferus* and *N. roseipennis* (Table 1) reveals that *N. rufusculus* developed at a rate similar to that of *N. roseipennis*, and *N. americanoferus* developed most rapidly. Development at lower temperatures required longer for *N. rufusculus* than for *N. roseipennis*. The highest temperature (33°C) was less detrimental to *N. rufusculus* than to *N. roseipennis*, as indicated by improved survivorship of the former, although developmental times were similarly prolonged for the two species at that temperature. When developmental rates of *N. roseipennis* and *N. rufusculus* were compared under summer field conditions in New York, average nymphal durations were similar, 50.1 and 51.5 d, respectively (Mundinger 1922).

Extrapolation of the temperature development curves for *N. rufusculus* (Fig. 1, $18\text{--}30^\circ\text{C}$) allowed estimation of the developmental thresholds for egg, nymphal, and total development. These threshold temperatures were 13.1° (egg), 11.6° (nymphal), and 11.9°C (total development). Developmental thresholds previously determined for egg, nymphal, and total developmental stages of *N. americanoferus* and *N. roseipennis* were 11.9° , 10.8° , and 11.3°C for *N. americanoferus* and 11.2° , 10.7° , and 11.0°C for *N. roseipennis* (Braman et al. 1984). The slightly higher threshold for development of the egg stage of *N. rufusculus* than for the eggs of the other two species suggests that this species may require a longer period to establish the first generation in the spring after overwintering in the adult stage.

Developmental periods of the three *Nabis* species under the alternating temperature regime with a mean of 27°C were slightly longer when compared with those that occurred at constant 27°C (Tables 1 and 2). This might be expected because the upper temperature of the alternating regime (33°C) was shown to have detrimental effects (increased mortality and lengthened developmental times) under constant exposure. Development under an alternating regime with a mean of 18°C , however, resulted in accelerated development compared with that which occurred at constant 18°C . Thermal unit accumulation above the threshold temperature

Table 1. Duration in days of immature stages under constant temperatures

Temp (°C)	Stage	<i>N. americanoferus</i> ^a $\bar{x} \pm SE (n)$	<i>N. roseipennis</i> ^a $\bar{x} \pm SE (n)$	<i>N. rufusculus</i> $\bar{x} \pm SE (n)$
18	Egg	20.9 ± 0.1a (126)	26.7 ± 0.1b (82)	26.7 ± 0.1b (83)
	1st instar			10.2 ± 0.2 (70)
	2nd instar			8.0 ± 0.2 (66)
	3rd instar			8.8 ± 0.2 (64)
	4th instar			10.6 ± 0.3 (62)
	5th instar			19.1 ± 0.4 (54)
	Total			
	Nymphal period	49.1 ± 1.0a (35)	49.3 ± 0.3b (36)	56.0 ± 0.7c (54)
	Developmental period	70.0 ± 1.0a (18 ♂♂, 17 ♀♀)	75.9 ± 0.3b (20 ♂♂, 16 ♀♀)	82.7 ± 0.7c (27 ♂♂, 27 ♀♀)
21	Egg	13.1 ± 0.1b (59)	16.2 ± 0.1b (60)	16.5 ± 0.2b (101)
	1st instar			5.6 ± 0.1 (90)
	2nd instar			4.8 ± 0.1 (88)
	3rd instar			4.9 ± 0.1 (85)
	4th instar			5.9 ± 0.2 (83)
	5th instar			8.5 ± 0.2 (73)
	Total			
	Nymphal period	25.2 ± 0.1a (40)	29.2 ± 0.3b (38)	29.3 ± 0.3b (73)
	Developmental period	38.3 ± 0.3a (17 ♂♂, 23 ♀♀)	45.3 ± 0.3b (22 ♂♂, 16 ♀♀)	45.5 ± 0.3b (33 ♂♂, 40 ♀♀)
24	Egg	10.0 ± 0.1a (49)	12.8 ± 0.1b (40)	11.6 ± 0.1c (55)
	1st instar			5.7 ± 0.1 (54)
	2nd instar			4.7 ± 0.2 (51)
	3rd instar			5.5 ± 0.4 (49)
	4th instar			5.6 ± 0.2 (48)
	5th instar			7.8 ± 0.2 (45)
	Total			
	Nymphal period	19.7 ± 0.2a (39)	24.0 ± 0.3b (27)	29.0 ± 0.4c (45)
	Developmental period	29.6 ± 0.2a (17 ♂♂, 22 ♀♀)	36.8 ± 0.2b (11 ♂♂, 16 ♀♀)	40.5 ± 0.4c (23 ♂♂, 22 ♀♀)
27	Egg	7.3 ± 0.1a (101)	10.1 ± 0.0b (116)	9.5 ± 0.1c (82)
	1st instar			4.5 ± 0.1 (82)
	2nd instar			3.3 ± 0.1 (77)
	3rd instar			3.4 ± 0.1 (74)
	4th instar			4.5 ± 0.1 (71)
	5th instar			6.2 ± 0.2 (69)
	Total			
	Nymphal period	16.8 ± 0.3a (68)	21.0 ± 0.3b (83)	21.9 ± 0.3b (69)
	Developmental period	24.0 ± 0.3a (30 ♂♂, 38 ♀♀)	30.7 ± 0.4b (41 ♂♂, 42 ♀♀)	31.3 ± 0.3b (34 ♂♂, 35 ♀♀)
30	Egg	5.7 ± 0.4a (164)	8.3 ± 0.1b (115)	7.7 ± 0.1c (84)
	1st instar			4.2 ± 0.1 (63)
	2nd instar			2.4 ± 0.1 (58)
	3rd instar			3.1 ± 0.1 (55)
	4th instar			3.2 ± 0.1 (55)
	5th instar			4.8 ± 0.1 (52)
	Total			
	Nymphal period	16.9 ± 0.3a (57)	16.4 ± 0.1a (97)	18.0 ± 0.3b (52)
	Developmental period	22.4 ± 0.2a (37 ♂♂, 20 ♀♀)	24.6 ± 0.2b (61 ♂♂, 36 ♀♀)	25.4 ± 0.3b (23 ♂♂, 29 ♀♀)
33	Egg	5.8 ± 0.1a (237)	8.5 ± 0.1b (173)	9.4 ± 0.1c (95)
	1st instar			4.0 ± 0.2 (53)
	2nd instar			2.5 ± 0.1 (46)
	3rd instar			2.7 ± 0.1 (45)
	4th instar			3.4 ± 0.1 (42)
	5th instar			5.1 ± 0.2 (37)
	Total			
	Nymphal period	13.2 ± 0.2a (52)	16.8 ± 3.1b (4)	17.6 ± 0.4b (37)
	Developmental period	18.6 ± 0.3a (30 ♂♂, 22 ♀♀)	27.8 ± 1.1b (3 ♂♂, 1 ♀)	27.0 ± 0.4b (18 ♂♂, 19 ♀♀)

Means within a row, followed by the same letter are not significantly different ($P > 0.05$, least significant difference test).

^a Braman et al. (1984).

should be the same for both the constant and the alternating temperature regimes. Duration of development would therefore be expected to be similar.

When insects are reared under constant temperatures, their developmental rates tend to be directly proportional to the temperatures selected providing those temperatures represent the mid-

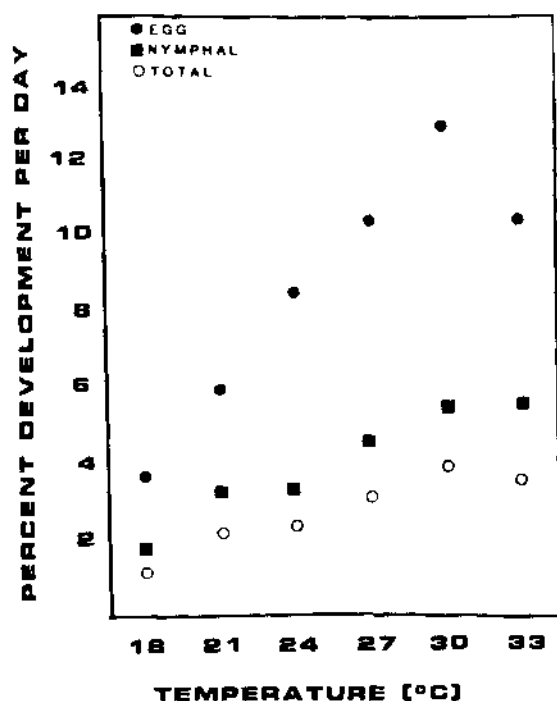


Fig. 1. Relationship between temperature and rate of development for *N. rufusculus*.

range of temperatures usually experienced in a species-typical range (Morris & Fulton 1970, Beck 1983). Species reared under fluctuating temperatures have been reported to develop more rapidly, at the same rate, or more slowly than under the constant temperatures that represent the mean of the fluctuating temperature regime. These different effects may depend on the nature of the temperature regime employed (either phase of the thermoperiod may be beyond a developmental

threshold), as well as on the particular species or method of growth measurement (Beck 1983).

Development under an alternating regime may differ from that under a constant temperature regime because rate-limiting, enzyme-mediated reactions essential for development may be affected differently under the two regimes. Availability of substrate and enzymes may be altered by fluctuating temperatures with resultant changes in rates of reactions and subsequent development (Howe 1967, Beck 1983, Higley et al. 1986). Degree-day requirements therefore may be influenced by fluctuating temperatures and thus affect the accuracy with which we predict phenology in the field.

Reproductive Biology. Ovipositional substrate often, though not consistently, affected various aspects of the reproductive potential of the three *Nabis* species (Table 3). Total egg production was significantly ($P < 0.05$) reduced when using green bean as an ovipositional substrate for *N. americanoferus* at 21 and 27/21°C, but not at 27°C. *N. roseipennis* tended to deposit fewer eggs in green beans at 21° and 27°C, although not significantly fewer ($P > 0.05$). *N. rufusculus* had a similar tendency at 27/21 and 27°C. Green bean pods are used routinely in insect rearing, especially for Hemiptera, as an ovipositional substrate or moisture source, or both. Estimates of reproductive capabilities derived under conditions where green beans are the ovipositional substrate may underestimate true reproductive potential. Kiman & Yeargan (1985) suggested possible negative effects of using green beans either because of inherent properties of the fruit or pesticide residues, and our data concur with those previously reported effects.

Egg production was somewhat depressed for all three species at 21°C when compared with that which occurred at 27°C (Table 3). This was especially true for *N. rufusculus*; only 9 of 25 (36%) females oviposited, compared with 69 and 67%

Table 2. Duration in days of immature stages under alternating temperature regimes

Temp (°C)	Stage	<i>N. americanoferus</i> $\bar{x} \pm SE$ (n)	<i>N. roseipennis</i> $\bar{x} \pm SE$ (n)	<i>N. rufusculus</i> $\bar{x} \pm SE$ (n)
24-12 $\bar{x} = 18$	Egg	18.6 ± 0.2a (65)	22.1 ± 0.1b (58)	20.4 ± 0.1c (53)
	1st instar	8.2 ± 0.4a (33)	8.8 ± 0.4ab (47)	9.5 ± 0.4b (35)
	2nd instar	5.9 ± 0.4a (27)	6.3 ± 0.3a (45)	6.7 ± 0.4a (34)
	3rd instar	5.3 ± 0.3a (26)	7.0 ± 0.5b (37)	6.6 ± 0.5b (32)
	4th instar	6.4 ± 0.3a (25)	7.0 ± 0.5a (33)	6.5 ± 0.4a (31)
	5th instar	11.6 ± 0.6a (22)	10.3 ± 0.4b (31)	11.3 ± 0.4a (29)
	Total			
	Nymphal period	36.6 ± 0.6a (22)	38.7 ± 0.6b (31)	40.8 ± 0.4c (29)
	Developmental period	55.0 ± 0.8a (22)	60.7 ± 0.5b (31)	61.2 ± 0.4b (29)
33-21 $\bar{x} = 27$	Egg	7.7 ± 0.1a (70)	11.0 ± 0.1b (62)	10.5 ± 0.1c (68)
	1st instar	3.6 ± 0.2a (46)	4.6 ± 0.2b (39)	5.7 ± 0.3c (47)
	2nd instar	3.4 ± 0.3a (41)	3.8 ± 0.3a (33)	3.9 ± 0.2a (38)
	3rd instar	2.7 ± 0.1a (35)	3.2 ± 0.2a (30)	3.1 ± 0.2a (38)
	4th instar	3.1 ± 0.2a (33)	3.6 ± 0.3a (28)	3.7 ± 0.3a (36)
	5th instar	4.9 ± 0.2a (31)	6.4 ± 0.1b (25)	6.1 ± 0.3b (32)
	Total			
	Nymphal period	17.5 ± 0.3a (31)	22.0 ± 0.4b (25)	22.2 ± 0.4b (32)
	Developmental period	25.2 ± 0.3a (31)	32.9 ± 0.5b (25)	33.3 ± 0.5b (32)

Means followed by the same letter within a row are not significantly different ($P > 0.05$; least significant difference test).

ovipositional success by *N. roseipennis* and *N. americanoferus*, respectively, at that temperature. Ovipositional success at 27 and 27/21°C, respectively, for the three species was 86% (*N. americanoferus*), 79% (*N. roseipennis*), 75% (*N. rufusculus*), and 90% (*N. americanoferus*), 74% (*N. roseipennis*), and 84% (*N. rufusculus*). *N. rufusculus* produced the expected intermediate number of eggs at 27/21°C (\bar{x} = 24°C), but reduced fecundity was observed for *N. americanoferus* under this alternating temperature regime. When soybean was the ovipositional substrate, *N. roseipennis* produced similar numbers of eggs at 21 and 27/21°C.

At 27°C (a temperature that was favorable for development), all three species produced similar numbers of eggs (Table 3). *N. americanoferus*, however, deposited eggs during a shorter period than the other two species. Under optimal temperatures, *N. americanoferus* developed more rapidly and deposited eggs at a faster rate than did *N. roseipennis* and *N. rufusculus*, although comparable numbers of eggs are produced.

In laboratory studies at 23°C, *N. americanoferus* reared on a diet of pea aphids had a 7–10-d preoviposition period and deposited an average of 157 eggs in pea seedlings during a 19-d oviposition period (Guppy 1986). Similar total fecundities were observed for *N. americanoferus* during our study at 27°C (171 eggs on soybean and 143 eggs on green bean). Nadgauda & Pitre (1986) observed lower fecundity by *N. roseipennis* at 20°C compared with a more favorable temperature, 24°C, and suggested that extended feeding periods allowed females less time for oviposition. Different diets, *H. virescens* larvae compared with *Lygus lineolaris* (Palisot de Beauvois) nymphs did not affect fecundity, but high temperature (30°C) reduced total egg production. Mean total number of eggs per female per lifetime in their study ranged from 22 to 66 eggs per female depending on temperature and diet. Those figures are generally lower than observed during our study and might, in part, be explained by the use of green beans as an ovipositional substrate, or reflect differences in diet. However, *N. alternatus* Parshley, fed salt marsh caterpillars and ovipositing in green bean sections, produced comparatively large numbers of eggs (\bar{x} = 281 eggs/female per lifetime, Perkins & Watson 1972). *N. capstiformis* (Cermar), another species closely related to those in this study, deposited an average of 105 eggs/female per lifetime in sweet corn seedlings when fed primarily *L. lineolaris* (Hornmchan et al. 1976).

Laboratory developmental, survival, and reproductive rate data collected at 27°C with a photoperiod of 15:9 were used to prepare complete laboratory life tables for *N. americanoferus*, *N. roseipennis*, and *N. rufusculus* (Braman 1987), and net reproductive rates (R_0), generation times (T), and intrinsic rates of increase (r) were calculated for the three *Nabis* species. As expected from previous examination of developmental and repro-

ductive data, *N. americanoferus* showed the greatest potential for population increase under the optimal conditions provided in the laboratory (r = 0.72 as compared with 0.50 and 0.44 for *N. roseipennis* and *N. rufusculus*). This larger r value resulted from a larger net reproductive rate and a shorter generation time relative to the other two species. Net reproductive rates were 41.7, 35.9, and 32.0 for *N. americanoferus*, *N. roseipennis*, and *N. rufusculus*, respectively. Generation times were 5.12, 7.13, and 7.74 weeks for those three species, respectively. During three years of sampling for seasonal phenology and relative abundance of the three *Nabis* species in alfalfa (unpublished data), *N. americanoferus* was always the most abundant nabid, corroborating predictions made on the basis of laboratory life table data.

Mean thermal unit requirements were calculated for total developmental and preovipositional periods (with soybean as the ovipositional substrate) for the range of temperatures over which development was linear using the above reported developmental thresholds. Requirements for *N. americanoferus* (18–33°C), *N. roseipennis* (18–30°C), and *N. rufusculus* (18–30°C) were 497.4, 610.4, and 597.7 Celsius degree-days, respectively. The range over a 3-yr period of degree-day accumulations above the respective threshold temperatures that regularly occur in central Kentucky (1844–2047, *N. americanoferus*, 1900–2100 *N. roseipennis*, and 1892–1933 *N. rufusculus*) suggest that all three species are capable of producing three generations per year. Predictions of seasonal phenology based on developmental rate data have been confirmed with field sampling for *N. americanoferus* (unpublished data).

Developmental rates, thresholds, and thermal unit requirements characteristic of local populations of a species may illustrate a degree of adaptation to the climatic conditions prevalent in that particular geographical area. Differences in geographical location of populations of widely distributed species can be reflected in differences in developmental thresholds or thermal unit requirements or both, serving to synchronize the species' development with local environmental conditions or prey-host availability (Tauber & Tauber 1978, Obrycki & Tauber 1982, Braman et al. 1985). Thermal unit requirements calculated for nymphal development of a population of *N. americanoferus* originating in eastern Ontario, for example, were almost 20% greater than for a Kentucky population of the same species, although thermal unit requirements for the egg stages were similar (Braman et al. 1984, Guppy 1986). Direct comparison in this case is difficult because different nymphal diets were used during rearing and may have influenced duration of development. However, we note that thermal unit requirements allow exactly the completion of two generations of the Ontario population (Guppy 1986), while the extended season and different thermal unit requirements in Kentucky permit three

Table 3. Mean \pm SE (*n*) reproductive potential of three *Nabis* species under two constant and one alternating temperature regimes, when supplied with one of two different ovipositional substrates

Substrate	Temp 21°C		
	<i>N. americanoferus</i>	<i>N. roseipennis</i>	<i>N. rufusculus</i>
	Total egg production		
Soybean	101.5 \pm 15.5a (21)	102.5 \pm 14.9a (19)	25.6 \pm 17.6b (5)
Greenbean	58.6 \pm 9.5a (19) <i>P</i> = 0.02	71.6 \pm 11.9a (20) <i>P</i> = 0.11	33.8 \pm 12.9a (4) <i>P</i> = 0.73
	Eggs/♀/d		
Soybean	2.5 \pm 0.3a (21)	2.0 \pm 0.2a (19)	0.7 \pm 0.4b (5)
Greenbean	1.8 \pm 0.2a (19) <i>P</i> = 0.07	1.9 \pm 0.2a (20) <i>P</i> = 0.74	0.8 \pm 0.3b (4) <i>P</i> = 0.80
	Preoviposition period (d)		
Soybean	10.9 \pm 0.8a (21)	11.2 \pm 0.6a (19)	17.2 \pm 4.2b (5)
Greenbean	12.3 \pm 1.1a (19) <i>P</i> = 0.31	13.0 \pm 1.1ab (20) <i>P</i> = 0.17	17.5 \pm 1.5b (4) <i>P</i> = 0.95
	Female longevity (d)		
Soybean	37.3 \pm 4.1ab (21)	45.4 \pm 5.2b (19)	28.7 \pm 3.4a (12)
Greenbean	30.4 \pm 2.8a (10) <i>P</i> = 0.18	34.6 \pm 3.8a (20) <i>P</i> = 0.10	27.6 \pm 3.7a (12) <i>P</i> = 0.83
	Male longevity (d)		
Soybean	18.4 \pm 3.2a (10)	22.9 \pm 5.3ab (12)	32.9 \pm 2.6b (9)
Greenbean	22.8 \pm 3.2ab (10) <i>P</i> = 0.34	18.4 \pm 4.6b (11) <i>P</i> = 0.52	33.1 \pm 4.6a (9) <i>P</i> = 0.97
	Temp 27/21°C (\bar{x} = 24°C)		
	Total egg production		
Soybean	68.2 \pm 13.6a (17)	93.2 \pm 23.2a (10)	147.2 \pm 16.1b (9)
Greenbean	32.7 \pm 7.4a (15) <i>P</i> = 0.03	98.6 \pm 19.8b (16) <i>P</i> = 0.86	99.5 \pm 16.2b (17) <i>P</i> = 0.07
	Eggs/♀/d		
Soybean	2.4 \pm 0.3a (17)	2.9 \pm 0.5a (10)	3.5 \pm 0.3a (9)
Greenbean	1.7 \pm 0.3a (15) <i>P</i> = 0.09	2.9 \pm 0.4b (16) <i>P</i> = 0.99	2.6 \pm 0.3b (17) <i>P</i> = 0.03
	Preoviposition period (d)		
Soybean	6.9 \pm 0.4a (17)	11.5 \pm 0.7b (10)	10.5 \pm 0.3b (9)
Greenbean	7.8 \pm 0.5a (15) <i>P</i> = 0.10	10.2 \pm 0.6b (16) <i>P</i> = 0.16	9.8 \pm 0.5b (17) <i>P</i> = 0.38
	Female longevity (d)		
Soybean	25.1 \pm 2.1a (17)	28.2 \pm 3.1a (10)	42.9 \pm 3.0b (9)
Greenbean	18.5 \pm 1.9a (15) <i>P</i> = 0.03	30.7 \pm 2.5b (16) <i>P</i> = 0.54	37.7 \pm 4.6b (17) <i>P</i> = 0.45
	Male longevity (d)		
Soybean	18.2 \pm 1.9a (17)	22.6 \pm 2.5a (9)	21.2 \pm 4.0a (6)
Greenbean	10.0 \pm 0.8a (15) <i>P</i> = 0.0008	30.4 \pm 3.9b (16) <i>P</i> = 0.18	19.4 \pm 2.4c (10) <i>P</i> = 0.69
	Temp 27°C		
	Total egg production		
Soybean	171.2 \pm 31.2a (9)	190.0 \pm 30.3a (6)	181.0 \pm 37.1a (9)
Greenbean	142.7 \pm 32.6a (10) <i>P</i> = 0.53	120.0 \pm 24.5a (9) <i>P</i> = 0.09	140.5 \pm 31.3a (12) <i>P</i> = 0.52
	Eggs/♀/d		
Soybean	5.8 \pm 1.4a (9)	4.2 \pm 0.4b (6)	4.4 \pm 0.6b (9)
Greenbean	4.9 \pm 0.7a (10) <i>P</i> = 0.40	3.4 \pm 0.6a (9) <i>P</i> = 0.32	3.9 \pm 0.7a (12) <i>P</i> = 0.63
	Preoviposition period (d)		
Soybean	5.8 \pm 1.4a (9)	7.3 \pm 0.6a (6)	7.0 \pm 0.5a (9)
Greenbean	4.7 \pm 0.3a (10) <i>P</i> = 0.45	6.9 \pm 0.5ab (9) <i>P</i> = 0.57	10.2 \pm 1.9b (12) <i>P</i> = 0.19
	Female longevity (d)		
Soybean	30.3 \pm 3a (9)	43.5 \pm 3.8b (6)	38.5 \pm 4.4ab (9)
Greenbean	23.8 \pm 3.2a (10) <i>P</i> = 0.16	35.1 \pm 3.9a (9) <i>P</i> = 0.17	35.1 \pm 5.3a (12) <i>P</i> = 0.63

Table 3. Continued

Substrate	Temp 21°C		
	<i>N. americanoferus</i>	<i>N. roseipennis</i>	<i>N. rufusculus</i>
	Male longevity (d)		
Soybean	32.3 ± 5.1a (9)	35.2 ± 6.5a (6)	27.2 ± 5.7a (5)
Greenbean	32.0 ± 7.3a (8)	35.2 ± 5.0a (9)	45.7 ± 4.8a (12)
	<i>P</i> = 0.97	<i>P</i> = 0.99	<i>P</i> = 0.04

Means within a row followed by the same letter are not significantly different ($P > 0.05$; least significant difference test). Comparisons between substrate are denoted by *P* value.

generations per year (Braman et al. 1984, unpublished data). Average degree-day accumulation at Ottawa was 1085 DDC (degree days centigrade) corresponding with thermal requirements of 1072 DDC to complete two generations including a preovipositional period for the first generation. A lengthened nymphal period may prevent the production of a partial generation at the end of the season in Ontario. *N. americanoferus* adults overwinter in reproductive diapause (Harris 1928) and thermal unit requirements specific to different geographical populations of the species may serve to synchronize this aspect of their phenology with local average degree day accumulations.

Finally, studies such as we report here help to make it possible to predict seasonal growth, development, and reproduction in the field. Understanding these aspects of population dynamics of beneficial, as well as pest species, is useful in developing successful integrated pest management strategies.

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