

Development, Survival, and Reproduction of *Scymnus frontalis* (Coleoptera: Coccinellidae), an Imported Predator of Russian Wheat Aphid, at Four Fluctuating Temperatures

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ABSTRACT Development, survival, and reproduction of *Scymnus frontalis* (F.) were studied in the laboratory at four temperature regimes with means ranging from 15 to 30°C, with daily fluctuations of $\pm 5^\circ\text{C}$. *S. frontalis* has four instars and a distinct prepupal stage. Developmental times from egg to adult averaged 79.7, 45.3, 21.4, and 17.2 d at mean temperatures of 15, 18.7, 26.2, and 30°C, respectively. Calculated stage-specific developmental thresholds ranged from 10.1°C for first instars to 13.0°C for fourth instars. Development from egg to adult required an average of 312.2 degree-days above a base of 11.7°C. Survival was highest at the two intermediate temperatures and lowest at a mean temperature of 15°C with mortality being highest in eggs and first instars. Preoviposition periods ranged from 20.5 d at a mean temperature of 15°C to 7.7 d at 30°C. Daily oviposition rates per female during the first several weeks of reproductive life were highest at a mean temperature of 26.2°C (7.25 eggs per female per day). The proportion of females ovipositing was highest at 26.2°C (0.97) and lowest at 15°C (0.42). Compared with its prey, *Diuraphis noxia* (Mordvilko), the Russian wheat aphid, *S. frontalis* requires higher temperatures to complete development and reproduce.

KEY WORDS Insecta, *Diuraphis noxia*, life history, developmental thresholds

THE RUSSIAN WHEAT APHID, *Diuraphis noxia* (Mordvilko), is widely distributed throughout much of Asia, the Middle East, and parts of Africa, southern Europe, and South America. It has recently invaded the United States, where it poses a serious economic threat to several cereal crops, particularly wheat, barley, and triticale. *D. noxia* was first discovered in Texas in 1986 and has since spread throughout most of the west-central United States (Stoetzel 1987).

There is considerable interest in using classical biological control against *D. noxia* in the United States. A program to import parasitoids and predators is being cooperatively conducted by various state and federal institutions in the United States and Great Britain. *Scymnus frontalis* (F.) was imported into the United States during June 1988 as a potential biological control agent of *D. noxia*.

Relatively little is known of the biology of many species of the genus *Scymnus* including *S. frontalis*. Knowledge of the biology and ecology of *S. frontalis* is important in assessing its potential as a predator of *D. noxia* and its eventual establishment in the United States and elsewhere. Many factors will be important in determining the utility of this predator as a biological control agent including searching behavior, prey preference and consumption rates, dispersal and habitat selection behavior,

the impact of other natural control agents on populations of both aphids and predators, and the impact of environmental variables (Hagan et al. 1976).

Temperature is among the most important environmental factors influencing development and reproduction in insects. This article examines the development and survival of immatures and the reproductive biology of *S. frontalis* provided *D. noxia* as prey in relation to ranges of temperatures these predators are likely to encounter during the cereal growing season in the west-central United States. This study is intended to provide baseline biological data on this species and permit comparisons to the influence of temperature on its target prey, *D. noxia*. Because developmental rates and thresholds often differ when an insect species is subjected to constant versus fluctuating temperature regimes (see Hagstrum & Hagstrum 1970), this study was conducted using fluctuating temperatures. Such regimes are more characteristic of natural environments and are more likely to provide useful estimates of developmental parameters.

Materials and Methods

Insect Sources and Environmental Regimes. *S. frontalis* used in these studies were F4 beetles obtained from a laboratory colony established in fall 1988. The colony was founded from approximately 95 female and 45 male adult beetles that had emerged after one generation of quarantine at the USDA-ARS, Beneficial Insects Research Labora-

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tory, Newark, Del. *S. frontalis* was originally collected by the staff of the USDA-ARS, European Parasite Laboratory, Paris, France, from a barley field infested with *D. noxia* near Beypazari, Turkey. The colony was maintained at $23 \pm 2^\circ\text{C}$ and $70 \pm 15\%$ RH with a 15:9 (L:D) photoperiod. Water was provided on saturated dental wicks and a mixture of *D. noxia*, *Schizaphis graminum* (Rondoni), *Macrosiphum granarium* (Kirby), *Acyrtosiphon pisum* (Harris), and *Rhopalosiphum padi* (L.) was provided as food.

Studies were conducted under fluctuating temperature regimes in programmable environmental chambers (Puffer-Hubbard, Asheville, N.C., and Kysor-Sherer, Marshall, Mich.). Four temperature regimes were used with all regimes oscillating according to a sine-wave function with a 24-h period with the maximum and minimum temperatures at 1500 and 0300 hours, respectively. Temperature ranges were 10.0–20.0°C ($\bar{x} = 15.0^\circ\text{C}$), 13.7–23.7°C ($\bar{x} = 18.7^\circ\text{C}$), 21.2–31.2°C ($\bar{x} = 26.2^\circ\text{C}$), and 25.0–35.0°C ($\bar{x} = 30.0^\circ\text{C}$). These regimes approximate the daily and seasonal fluctuations that would be expected in a typical growing season in the northern plains of the United States. All temperatures were regulated within $\pm 0.3^\circ\text{C}$, and all environmental chambers were maintained at $60 \pm 10\%$ RH with a 14:10 (L:D) photoperiod.

Immature Development and Survival. Development studies were initiated with cohorts of newly laid eggs (<1 d old) deposited by colony females on 3 by 10 cm sections of rolled cloth. A piece of the oviposition substrate containing an individual egg was placed in a 10-dram vial with a vented, snap lid. A 5-mm² piece of moistened sponge was placed in each vial to increase humidity and reduce static electricity. Studies were initiated with 100 eggs for each temperature regime. At hatch, *D. noxia*, reared in the greenhouse on potted wheat plants, were provided in excess to larvae, along with several wheat seedling leaves. This helped keep the aphids fresh and provided a resting place for larvae. All insects were observed daily for development and mortality. Aphids were replenished as needed. At emergence, the weight and sex of adults were determined. Developmental thresholds (t_b) for each stage and for the period from oviposition to adult emergence were computed by regressing individual development rates (day⁻¹) on mean temperature and solving for the x intercept (see Campbell et al. 1974). Mean thermal constants for each stage were calculated by averaging $(t - t_b) \times (\text{days per stage})$ over all individuals at all temperatures, where t is the mean temperature of each fluctuating regime. Analysis of variance and t tests were used to compare adult weights as influenced by temperature and to test for differences in development rates between the sexes.

Reproduction. To examine reproduction, individual mated pairs of newly emerged colony adults were established in each of the four temperature regimes. Pairs were individually confined in plastic

boxes (11 by 11 by 3.5 cm deep) with vented lids. Adults were provisioned with an excess of *D. noxia*, several seedling wheat leaves, and water on a saturated dental wick. A rolled section (1 by 5 cm) of cloth was provided as an oviposition substrate. Occasionally, when the stock of *D. noxia* was low, beetles were given a mixture of *D. noxia*, *S. graminum*, and *A. pisum* at an approximate ratio of 60:35:5. Adults were observed daily for oviposition and mortality during the first 2–3 wk and two or three times per week thereafter. Food was replenished as needed. Due to time constraints and prey availability, adults were held for approximately 3–6 wk at the two higher and lower temperatures, respectively. Given preovipositional periods, this allowed beetles to oviposit approximately 2–3 wk at each temperature. For comparative purposes, the time from oviposition to the onset of reproduction was estimated by summing mean developmental times from egg to adult emergence and mean preovipositional times. Note that this is not the generation time as it is usually defined in demographic analysis.

Voucher specimens of *S. frontalis* have been deposited in the Cornell University Insect Collection under Lot 1179.

Results

Immature Development and Survival. *S. frontalis* had four instars and a distinct nonfeeding prepupal stage. Overall development from egg to adult averaged 79.7 d at a mean temperature of 15°C and declined to 17.2 d at a mean temperature of 30°C (Table 1). The egg and pupal stages required the longest development times, averaging 23 and 29%, respectively, of the total developmental time from egg to adult. On average, approximately 37% of total development time was occupied by the four instars. Of the four instars, the fourth stadium was the longest. There were significant differences ($t \geq 2.36$, $df > 37$, $P < 0.05$) in total immature development times between sexes, with females completing development 1.4, 0.6, and 0.4 d earlier at mean temperatures of 18.7, 26.2, and 30°C, respectively. The difference in total immature development times between sexes was not significant ($t = 1.45$, $P > 0.05$) at a mean temperature of 15°C.

In general, newly emerged females were slightly heavier than males. However, the difference was only significant ($t = 3.46$, $df = 55$, $P < 0.05$) at a mean temperature of 26.2°C (Table 1). Adult weights also differed significantly in relation to mean temperature ($F \geq 6.61$; $df \geq 3, 74$; $P < 0.01$) for both sexes. In comparison with the two medium temperature regimes (means of 18.7 and 26.2°C), adults weighed less at emergence when immatures were reared at the two extremes of temperature (means of 15 and 30°C).

Examination of residuals and lack-of-fit analysis (Drapper & Smith 1966) indicated that there were

Table 1. Developmental times and adult weights of *S. frontalis* reared on *D. noxia* at four fluctuating temperatures

Mean temperature, °C	Egg, days	Larval stadia, days				Prepupa, days	Pupa, days	Egg to adult, days	Adult weight, mg	
		I	II	III	IV				♀	♂
15.0										
\bar{x}	18.5	6.6	5.8	6.5	9.8	9.7	23.3	79.7	2.76	2.76
SE	0.2	0.2	0.3	0.3	0.4	0.3	0.4	0.6	0.10	0.31
n	70	45	36	32	27	26	26	26	19	6
18.7										
\bar{x}	10.1	3.5	3.3	3.3	7.0	5.1	13.2	45.3	3.60	3.51
SE	0.1	0.1	0.1	0.1	0.2	0.1	0.1	0.2	0.06	0.07
n	76	66	63	62	61	59	58	58	35	23
26.2										
\bar{x}	4.8	2.0	1.6	1.9	2.7	2.2	6.2	21.4	3.83	3.45
SE	0.1	0.03	0.1	0.05	0.1	0.05	0.1	0.1	0.07	0.09
n	78	69	63	59	58	57	57	57	26	31
30.0										
\bar{x}	4.0	1.6	1.4	1.2	2.3	1.8	4.9	17.2	3.36	3.15
SE	0.0	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.13	0.07
n	74	54	53	45	44	39	39	39	20	18

no significant deviations ($F \leq 0.20$; $df \geq 3, 176$; $P > 0.05$) from linearity in the relationship between developmental rates and mean temperature for any insect stage over the range of temperatures examined in this study. Therefore, the x intercept method should provide reasonable estimates of developmental thresholds. Regressions of individual developmental rates on mean temperatures indicated that calculated developmental thresholds for all stages were $>10^\circ\text{C}$. Because the 15°C regime subjected insects to temperatures below these thresholds for portions of the day, regressions were repeated using only data from regimes with means of 18.7 , 26.2 , and 30°C . Degree-day (DD) accumulations (thermal constants) for each stage were, however, calculated using data from all four temperature regimes. The Baskerville-Emin method (Baskerville & Emin 1969) was used to calculate DD accumulations for individuals from the 15°C regime.

Developmental thresholds ranged from 10.1°C for first instars to 13.0°C for fourth instars (Table 2). Total development from egg to adult required an average of 312.2 DD above a base of 11.7°C . There was relatively little variance in stage-specific thermal constants.

Survivorship varied with temperature (Table 3). Overall survival from egg to adult was lowest at a

mean of 15°C (26%) and highest at mean temperatures of 18.7 and 26.2°C (57–58%). With the exception of 15°C , most of the mortality occurred in the egg stage. This probably resulted from a combination of normal physiological mortality coupled with nonviability of eggs due to infertility. For the most part, stage-specific mortalities were highest at 15°C , especially for first instars which had the lowest survivorship of any stage and temperature. Overall survival of pupae was comparatively high.

Reproduction. Reproduction was dramatically affected by temperature (Table 4). Only 42 and 63% of the females oviposited at mean temperatures of 15 and 18.7°C , respectively. In contrast, in the two higher temperature regimes $>90\%$ of the females oviposited. The preoviposition period lasted an average of 20.5 d at a mean temperature of 15°C and declined to 7.7 d at a mean temperature of 30°C (Table 4). From observations, it appeared that mating preceded first oviposition by about 3–4 d at all temperatures. Because adults were maintained for only 3–6 wk, depending on temperature, females were allowed to oviposit for only 2–3 wk. Thus, while rates of oviposition could be only approximately estimated they should provide some useful information on temperature effects. Daily rates of oviposition were comparatively low at the two lower temperature regimes, averaging from

Table 2. Developmental thresholds (T_b) and thermal constants (DD) for immature *S. frontalis* reared on *D. noxia*

Variable	Egg	Larval stadia				Prepupa	Pupa	Egg to adult
		I	II	III	IV			
T_b ($^\circ\text{C}$)	10.9	10.1	11.2	12.2	13.0	12.5	11.8	11.7
SE	0.2	1.1	1.1	0.8	0.5	0.7	0.3	0.1
n	228	189	179	166	163	155	154	154
DD	76.8	31.5	25.0	23.5	36.4	31.2	89.1	312.2
SE	0.4	0.5	0.6	0.4	0.6	0.5	0.5	1.0
n	299	235	216	199	191	182	181	181

Table 3. Stage-specific survival rates for immature *S. frontalis* reared on *D. noxia* at four fluctuating temperatures

Mean temperature, °C	Egg	Larval stadia				Prepupa	Pupa	Egg to adult
		I	II	III	IV			
15.0	0.70	0.64	0.80	0.89	0.90	0.96	1.0	0.26
18.7	0.76	0.89	0.95	0.98	0.98	0.97	0.98	0.58
26.2	0.78	0.96	0.93	0.97	0.98	0.98	1.0	0.57
30.0	0.75	0.90	1.0	0.87	0.98	0.89	1.0	0.39

0.5 to 1.2 eggs per female per day, but increased considerably with an increase in temperature averaging 7.25 eggs per female per day at a mean temperature of 26.2°C (Table 4). On average, times from oviposition to the onset of reproduction were 100.2, 62.1, 29.7, and 24.9 d at mean temperatures of 15, 18.7, 26.2, and 30°C, respectively.

Discussion

Based on what little published information is available, members of the genus *Scymnus* are primarily aphidophagous (Davidson 1923, Gordon 1982, Aalbersberg et al. 1984). The primary prey of *S. frontalis* in the field is unknown, although they no doubt encounter *D. noxia* in their native homeland and readily accept and perform well when provided this species in the laboratory. Feeding by *D. noxia* causes a characteristic longitudinal rolling of the leaf, creating a sheltered environment for the aphids (Webster et al. 1987). Given the small size of *S. frontalis*, they should be capable of penetrating and attacking *D. noxia* within these refugia. In fact *S. frontalis* larvae and adults were often found inside curled wheat leaves in their rearing cages.

The *S. frontalis* colony from which the individuals in this study were obtained has been in continuous culture for nearly 8 mo at the Northern Grain Insects Research Laboratory with no signs of an interceding diapause between generations. Based on this and published data on several other members of the genus *Scymnus* (Hagan 1962), multivoltinism appears characteristic of the genus. Given spring and summer temperature regimes throughout much of the west-central United States and adequate prey, *S. frontalis* could probably complete several generations per year. In the laboratory the time from oviposition to the onset of reproduction (egg to egg) varied greatly as a function of temperature ranging from 24.9 to 100.2 d. This contrasts greatly from birth to the onset of reproduction in their targeted prey, *D. noxia*, at comparable temperatures. Kieckhefer & Elliott (1989) reported average times of 19.6, 10.0, and 7.0 d for alate *D. noxia* at mean temperatures of 12.0, 20.0, and 27.0°C, and even shorter times for apterae.

Diuraphis noxia, like many aphids, is tolerant of low temperatures. Estimates of immature developmental thresholds for *D. noxia* range from 0.54 to 5.0°C (Aalbersberg et al. 1987, Webster &

Starks 1987, Kieckhefer & Elliott 1989). Immature developmental thresholds for *S. frontalis* were considerably higher, ranging from 10.1 to 13.0°C for various developmental stages and an estimated 11.7°C for overall immature development. At the lowest mean temperature studied here (15°C), immature survival was comparatively low and only 42% of the adult females oviposited, and then at <1 egg per female per day during the first 2–3 weeks of reproductive life. Although temperature–rate relationships remained linear up to a mean of 30°C for immatures, there was a slight reduction in rate of oviposition at a mean of 30°C compared with that at a mean of 26.2°C. Based on the limited oviposition data presented here, temperatures fluctuating between 25 and 35°C may be somewhat detrimental to adults.

The discordant relationships between temperature, development, and reproduction between *S. frontalis* and *D. noxia* are characteristic of many coccinellide–aphid associations (Hagan et al. 1976), but its impact in the field is uncertain. Differences in temperature thresholds for activity between predators and their prey is cited as an important factor contributing to failure of biological control (Hagan et al. 1976). The low temperatures that prevail in the early part of the cereal-growing season, particularly in the northern United States, are suitable for *D. noxia* development and reproduction (Kieckhefer & Elliott 1989), but would likely be less suitable for development and reproduction of *S. frontalis*. Assessing the overall impact of temperature in the field will require further study.

The majority of developmental rate studies on insects are conducted at constant temperature; however, there is evidence that developmental rates

Table 4. Reproduction of *S. frontalis* at four fluctuating temperatures

Mean temperature, °C	Proportion of females ovipositing	Preovipositional period, days, $\bar{x} \pm SE$	Oviposition per female per day, ^a $\bar{x} \pm SE$	n
15.0	0.42	20.5 ± 1.1	0.53 ± 0.20	16
18.7	0.63	16.8 ± 1.1	1.21 ± 0.29	24
26.2	0.97	8.3 ± 0.5	7.25 ± 0.78	35
30.0	0.94	7.7 ± 0.5	6.55 ± 0.86	33

All experiments were initiated with 40 individual pairs of mating adults.

^a Based on oviposition during the first 2–3 weeks of reproductive life.

estimated in this way fail to predict development in the field where temperatures naturally fluctuate over the course of a day (e.g., Hagstrum & Hagstrum 1970, Gregg 1981). Studies here were conducted at temperatures that fluctuated daily by 10°C and, thus, more closely mimicked the thermal environment that *S. frontalis* will encounter in the field. An important point to note is that because calculated developmental thresholds and thermal constants are based on fluctuating temperatures, mean daily temperatures, and not typical minimum–maximum temperatures, should be sufficient to estimate development in the field. These data may be useful in the development of predictive models describing the population dynamics of this predator and its interaction with *D. noxia*.

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