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TEMPERATURE EFFECTS ON DEVELOPMENT IN
APHELINUS ALBIPODUS (HYMENOPTERA: APHELINIDAE)
FROM TWO GEOGRAPHIC REGIONS

Jang-Hoon Lee^{1,2} and Norman C. Elliott¹

ABSTRACT

Aphelinus albipodus Hayat & Fatima was imported to the United States for classical biological control of the Russian wheat aphid, *Diuraphis noxia* (Mordvilko). Temperature effects on development of *A. albipodus* from two geographic regions (hereafter referred to as strains) were measured using the Russian wheat aphid as host. Temperature thresholds for egg to mummy, mummy to adult, and egg to adult development were 8.9, 10.9, and 9.7°C for *A. albipodus* collected near Pingluo, China, and were 8.5, 10.3, and 9.6°C for *A. albipodus* collected near Urumqi, China. The time required to develop from egg to adult did not differ among strains. However, when total immature development was partitioned into egg to mummy and mummy to adult, the time required for development through these two periods differed among strains. The Urumqi strain developed faster than the Pingluo strain from egg to mummy, while the Pingluo strain developed faster from mummy to adult. Degree-day requirements for egg to mummy development were 135 and 104 for the Pingluo and Urumqi strains, respectively. Corresponding requirements for mummy to adult development were 70 and 101 degree-days. The ability to vary immature development rate in response to climate or other factors could have adaptive significance because it would permit the parasitoid to exploit environments over a broad geographic range.

The Russian wheat aphid, *Diuraphis noxia* (Mordvilko), is a recently introduced pest in North America (Stoetzel 1987). The aphid spread rapidly throughout the western cereal growing regions of United States and Canada (Jones et al. 1989) where it is now a serious pest of wheat and barley. *Aphelinus albipodus* Hayat & Fatima is one of several exotic parasitoid species imported into the United States from several regions including Europe and Asia for classical biological control of the Russian wheat aphid (Tanigoshi et al. 1995). Recoveries of *A. albipodus* were recently reported from Colorado (Elliott et al. 1995a) and Washington State (Tanigoshi et al. 1995), indicating that the ecological requisites are present for the parasitoid to establish reproducing populations in these areas. The parasitoid is sometimes abundant in the field.

Developmental response to temperature is one of several biological characteristics that can influence the ability of a parasitoid to survive and be-

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come an effective biological control agent in a new region. The development threshold and degree-day requirements are two parameters for describing developmental response of insects to temperature. The developmental threshold is defined as the temperature below which no measurable development occurs, and the development time in degree-days is defined as the amount of heat above the developmental threshold required to complete development through a particular life stage (Campbell et al. 1974). The timing of appearance of insect populations in the field is largely determined by their developmental responses to temperature, which can be summarized in terms of the developmental threshold and degree-day requirements for development (Frazer & Gilbert 1976, Gilbert et al. 1976).

The appearance of natural enemy populations early in the growing season, when aphid populations are low is thought to be particularly important in aphid biological control. A high ratio of natural enemies to aphids at that time may allow the natural enemies to suppress the aphid population early in the growing season before the period of rapid aphid population growth (van Emden 1988). Knowledge of the developmental threshold and degree-day requirements for development can yield insight as to whether a parasitoid to be used as a prospective biological control agent will exhibit early appearance and activity in the field.

Morris (1971) and Morris and Fulton (1970) were among the first to observe that insect populations in different geographic areas sometimes exhibit different developmental responses to temperature in laboratory studies. They found a difference in the degree-day requirements for development, but not the developmental threshold, of fall webworm populations, *Hyphantria cunea* (Drury) (Lepidoptera), from New Brunswick and Nova Scotia. Geographic populations of parasitoids are sometimes differently adapted to climate, due to natural selection in their region of origin (Messenger 1971). As a result, inherent differences sometimes exist among strains in their response to temperature or other climatic variables that influence their ability to establish in a region where they are released. Furthermore, if they do establish, these differences can influence the ability of a strain to control the target pest in the region (Messenger 1971, Messenger and van den Bosch 1971).

This study was conducted on *A. albipodus* obtained from two geographic regions (hereafter referred to as strains). Our objectives were to determine if differences existed among the *A. albipodus* strains in the effects of temperature on immature development that might foretell differences in climatic adaptation among the strains. The information obtained may be useful for assessing whether strain-specific differences in biology exist that might be exploited in developing release strategies for *A. albipodus*, and in assessing the likelihood that the parasitoid will be effective as a biological control agent of the Russian wheat aphid.

MATERIALS AND METHODS

The *A. albipodus* laboratory colonies used in this study were obtained from the USDA, ARS European Biocontrol Laboratory, Montpellier, France. The parasitoid strains were collected from Russian wheat aphid hosts in wheat fields near Pingluo (38° 5'N, 106° 30'E) and Urumqi (43° 45'N, 87° 45'W) China in the spring of 1992. From 100 to 200 individuals of each strain were received as founder colonies in the summer of 1992 and were maintained on Russian wheat aphids for 5–6 generations prior to initiating the study. Laboratory colonies were maintained in a plant growth chamber at 16L:8D, 22±0.5°C, and 55±5% relative humidity.

To establish an experiment, 50 1st-3rd instar Russian wheat aphid nymphs were placed on each of 5-7 barley (*Hordeum vulgare* L.) seedlings growing in 10-cm diameter plastic pots (one seedling per pot) using an artist's brush. Each potted plant was then covered with a vented clear plastic cylindrical cage (10-cm diameter ~ 30-cm height). After allowing the aphids to settle for 4 h, 10 active female parasitoids were randomly taken from a stock colony using an aspirator and introduced into the cage. After 4 h exposure, the parasitoids were removed from the cage and the caged plant was placed in a growth chamber maintained at a constant temperature of 14, 18, 22, or 26°C (all $\pm 0.5^\circ\text{C}$), 16L:8D, and $55\pm 5\%$ relative humidity. The plants were checked daily, and mummies that formed were removed from plants, placed in a plastic petri dish (5-cm diameter ~ 1.4-cm height), and returned to the plant growth chamber. Petri dishes were shaded from direct light in order to minimize heat build-up. Mummies were examined daily for adult emergence. The number of days required for development from egg to mummy formation and the number of days for development from mummy formation to adult emergence from the mummy were recorded for each mummy that formed. Developmental threshold temperatures and development times in degree-days for the period from egg to mummy, mummy to adult, and egg to adult were estimated by least squares regression [PROC REG (SAS Institute 1988)]. Average development rate (1/development time in days) for each temperature was calculated based on all individuals that developed to a particular stage at that temperature. The developmental threshold and degree-day requirements for development from egg to adult emergence were estimated from a linear regression of development rate (Y) against temperature (X):

$$Y = a + bX$$

The developmental threshold is the intercept of the X-axis ($-a/b$) and development time in degree-days is the reciprocal of the regression coefficient ($1/b$) (Campbell et al. 1974). Standard errors of the estimates of the developmental threshold and degree-day requirement were calculated using formulae presented in (Campbell et al. 1974). Tests of the statistical hypotheses that developmental thresholds and degree-day requirements did not differ among strains were made using t-tests (Campbell et al. 1974). Developmental times were compared among strains using ANOVA and the LSD test [PROC GLM (SAS Institute 1988)].

RESULTS

The number of days required for development from egg to mummy, mummy to adult, and egg to adult for the two *A. albipodus* strains are listed in Table 1. Development times for the three developmental periods decreased as temperature increased for both strains. The two strains showed similar developmental responses to temperature for the egg to adult period. For example, the Pingluo strain required 41.8 d (SE = 0.27) to complete development at 14°C, whereas the Urumqi strain required 42.8 d (SE = 0.28). At 26°C both strains required 12.2 d to develop from egg to adult. When egg to adult development time was partitioned into times from egg to mummy and mummy to adult, differences in developmental times were evident among strains. The Urumqi strain developed faster from egg to mummy at all temperatures than did the Pingluo strain, with the difference averaging 9.5, 3.7, 1.6, and 2.2 d at 14, 18, 22, and 26°C, respectively. Conversely, the Pingluo

Table 1. Average number of days for three developmental periods for *Aphelinus albipodus* at four temperatures. Standard errors are enclosed in parentheses.

Place of Origin/Life Stage	Temperature (°C)			
	14	18	22	26
Pingluo, China				
sample size	46	53	64	51
egg-mummy formation	27.0* (0.23)	15.0* (0.11)	10.0* (0.10)	8.00* (0.07)
mummy formation-adult	14.8* (0.27)	11.1* (0.18)	7.6* (0.18)	4.2* (0.08)
egg-adult	41.8 (0.27)	26.1 (0.18)	17.6 (0.19)	12.2 (0.08)
Urumqi, China				
sample size	51	55	56	49
egg-mummy formation	17.5* (0.27)	11.3* (0.15)	8.4* (0.15)	5.8* (0.08)
mummy formation-adult	25.3* (0.23)	14.1* (0.23)	8.8* (0.13)	6.4* (0.08)
egg-adult	42.8 (0.28)	25.4 (0.24)	17.2 (0.17)	12.2 (0.09)

Mean developmental time for a particular stage differs significantly ($P < 0.01$) among strains if followed by an asterisk.

strain developed faster from mummy to adult than the Urumqi strain at all temperatures. In this case, 10.4, 3.0, 1.2, and 2.2 fewer days were required by the Pingluo strain to complete mummy to adult development at 14, 18, 22, and 26°C, respectively.

The Pingluo strain had a lower developmental threshold than the Urumqi strain for all three developmental periods, although the difference was not statistically significant for any period (Table 2). Both strains required 205 degree-days above their respective developmental thresholds to complete development from egg to adult (Table 2). However, a greater number of degree-days were required by the Pingluo strain to complete egg to mummy development (135 degree-day, SE = 0.6) than the Urumqi strain (104 degree-days, SE = 2.5). The Pingluo strain required fewer degree-days to complete mummy to adult development (70 degree-days, SE = 2.2) than the Urumqi strain (101 degree-days, SE = 1.7).

DISCUSSION

Degree-day requirements for egg to mummy and mummy to adult development differed significantly among strains in this study. More time was spent developing from egg to mummy and less from mummy to adult by the Pingluo strain when compared with the more northern Urumqi strain. Bernal and González (1995) suggested that the living host and the mummy may afford different levels of buffering to developing parasitoids against ambient temperature as an explanation of why developmental thresholds, degree-day requirements, or both parameters might vary for pre-mummy and post-mummy immature development of a parasitoid.

We can speculate that developmental rate is inversely related to the degree of protection from high temperatures afforded during the particular developmental period. For example, the Pingluo strain originated from a slightly warmer climate than the Urumqi strain and spends a smaller proportion of its total immature development period inside the mummy than the Urumqi strain. This could be because the developing parasitoid is not often

Table 2. Developmental thresholds (SE) and degree-day requirements (SE) for two strains of *Aphelinus albipodus*. Also listed are regression equations relating developmental rate to temperature were calculated from mean developmental rate at the four temperatures (n = 4).

Place of Origin/Life Stage	Thermal threshold	Degree-days	Regression equation	r ²
Pingluo, China				
egg-mummy formation	8.9 (0.05)	135* (0.6)	Y = -0.066+0.0074X	0.99
mummy formation-adult	10.9 (0.32)	70* (2.2)	Y = -0.156+0.0143X	0.83
egg-adult	9.7 (0.15)	205 (2.8)	Y = -0.048+0.0049X	0.96
Urumqi, China				
egg-mummy formation	8.5 (0.29)	104* (2.5)	Y = -0.082+0.0096X	0.89
mummy formation-adult	10.3 (0.17)	101* (1.7)	Y = -0.101+0.0099X	0.94
egg-adult	9.6 (0.13)	205 (2.4)	Y = -0.047+0.0049X	0.97

Developmental thresholds and degree-days requirements differ significantly (P<0.05) among strains if followed by an asterisk.

exposed to extreme temperatures while inside the mummy in the cooler climate, whereas extreme temperatures are more frequently encountered at Pingluo. Thus, the Pingluo strain may have adapted to minimize the time spent in this exposed state.

Historical records indicate that the climate at Pingluo is slightly warmer than at Urumqi. For example, average maximum daily temperature during March-May is 17.7°C at Pingluo versus 14.1°C at Urumqi; while average maximum temperatures during June-August are about 1°C higher (29.3°C) at Pingluo than at Urumqi (Hoare 1998). Factors other than climate, for example reducing exposure time for parasitism by conspecific or other parasitoid species or by hyperparasitoids, could also be responsible for the variable development times of different life stages of these strains.

The ecological significance of the variation in developmental threshold and degree-day requirements during portions of the immature development period is unknown to us. However, we can speculate that it is an adaptation by the parasitoid to minimize the time spent in life stages with potentially high mortality subject to constraints on the total time required to complete immature development. In this case the parasitoid would minimize mortality over a fixed generation time, in the respective climates, and as a result increase its fitness. The ability to vary immature development rate in response to climate in new environments could have adaptive significance because it would permit the parasitoid to exploit environments over a broad geographic range.

Estimates of developmental thresholds reported for total immature development of *A. albipodus* were 9.7 and 9.6°C for two geographic regions in China (this study) and 8.2°C for a strain from Tacheng, China (Bernal and González 1996). These estimates are substantially greater than those for species of Aphidiidae that parasitize the Russian wheat aphid. For example, estimates of the developmental threshold for *Aphidius matricariae* Haliday were 1.4°C for a Czechoslovakian strain (Miller and Gerth 1994) and 4.5°C for a strain from Iraq (Bernal and González 1993). For *D. rapae*, Bernal and González (1993) estimated the developmental threshold at 2.1°C for a Pakistani strain, and Elliott et al. (1994) estimated it at 3.5°C for a Syrian strain. Elliott et al. (1995a) observed a developmental threshold of 2.8°C for

an Argentinean strain of *Aphidius colemani* Viereck. Although the developmental threshold differs among aphidiid species and among geographic strains of the same species, all reported values for aphidiids are 1.9°C or more lower than the lowest estimate reported for *A. albipodus*.

The developmental threshold for *A. albipodus* is several C higher than that of the Russian wheat aphid (Michels and Behle 1988, Kieckhefer and Elliott 1989). This indicates that development of *A. albipodus* populations would lag substantially behind those of the Russian wheat aphid. However, the existence of geographic variation in developmental parameters of *A. albipodus* suggests that the degree of difference in developmental response to temperature between the host and parasitoid varies regionally. For example, in geographical areas where the temperature transition from cold to warm occurs over a short time interval in the early spring, the time lag between Russian wheat aphid and *A. albipodus* development would be reduced. Therefore, the comparison of developmental thresholds and degree-day requirements for immature development do not necessarily provide an accurate picture of the degree of synchrony between the parasitoid and host.

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