

Chapter 3

Temperature effects on reproductive life history of *Otiorhynchus sulcatus*

Introduction

The black vine weevil, *Otiorhynchus sulcatus* (Fabricius), is a serious insect pest of greenhouse and nursery ornamentals and small fruits in Europe, North America, Japan and Australia (Smith, 1932; Masaki et al., 1984). Adult weevils are all females and reproduce by thelytokous parthenogenesis (Smith, 1932), that is, unfertilized *O. sulcatus* eggs develop into females and daughters are genetically identical to mothers. Due to the parthenogenetic reproduction and long reproductive life span of adults, a single *O. sulcatus* female can establish a new population, which can reach a very high density in just a few generations. Damage by *O. sulcatus* in the United States was first reported in 1831 and this species spread throughout northern climes to 26 states and 6 Canadian provinces (Warner & Negley, 1976). Larval feeding on the roots causes serious damage to the host plant, which frequently results in plant death. Larval control with conventional insecticides is problematic due to the difficulties of detection and access (Nielsen & Boggs, 1985). Thus, the most suitable target for insecticide application is adult weevils after eclosion but before they begin to oviposit a few weeks later (Neiswander, 1953). During the preoviposition period, the weevils feed on the foliage of a wide array of host plant species. Insecticide application before adult emergence is ineffective, and application after oviposition has begun is too late to prevent the infestation from developing (Umble & Fisher, 2002). Ideally, insecticide applications should be timed so that no female survives to reach reproductive maturity (Hanula, 1990) and thus careful monitoring of adult activity is a prerequisite for optimum spray timing.

Insect reproduction is governed by interactions between intrinsic life history traits and extrinsic factors such as temperature, food, moisture, light intensity, chemicals, and pathogens (Danks, 1994). Of the many abiotic factors that may influence the reproduction of many insect species, temperature is usually the most important (Andrewartha, 1952; Tauber et al., 1986). Optimal temperature ranges for egg production vary greatly among insect species. Often these temperatures reflect what the species normally encounter during reproductive periods (Engelmann, 1970), which may act to regulate the timing of many life history events. Temperature also can act to limit the geographic distribution of a species (Krebs, 1994). Thus, documenting the effects of temperature on the reproductive life history of insects is fundamental to understanding their population dynamics and managing pest populations (Ims, 1990).

Despite the economic importance of *O. sulcatus*, significant gaps in the knowledge of its basic biology remain. Understanding the impact of temperature on reproduction is essential for predicting the timing of egg occurrence and explaining the annual phenology of *O. sulcatus*. Although several previous studies have assessed the impact of temperature on *O. sulcatus* reproduction, published data that describe these aspects are sparse and largely insufficient to describe the effect completely. Significant components to measure when evaluating the reproductive success of insects include total fecundity per female, preoviposition period, oviposition period, life duration, and egg viability. However, most quantitative investigations on *O. sulcatus* reproduction have been conducted exclusively on the preoviposition duration under a limited range of temperatures (Stenseth, 1979; Masaki & Ohto, 1995). Some of these studies were inconclusive because the weevils' ages were not standardized (Evenhuis, 1978) and others lacked sufficient replications to measure variation among individuals (Stenseth, 1979; Masaki & Ohto, 1995). Documenting the variation in reproductive success among individuals is critical to

understanding population dynamics and to using this information for pest management (Fincke, 1988; Lomnicki, 1988). Furthermore, there is no quantitative information on the age specific survivorship and fecundity of *O. sulcatus* under different temperature conditions although they are among the key population processes that influence the intrinsic rate of increase (Birch, 1948).

This is the first study to evaluate specifically the effect of temperature on the complete suite of reproductive life history traits of *O. sulcatus*. The goal of this study was to determine the effects of temperature on the reproductive potential of *O. sulcatus*. Toward this end, I compared the duration of the preoviposition period, oviposition period, life span, and fecundity under nine constant temperatures ranging between 11-36 °C. Using these data, I developed a reproduction model of *O. sulcatus* that combined temperature and adult age. This approach was accomplished by using simple mathematical models, which together can be used to predict the timing and intensity of egg occurrence and to develop an *O. sulcatus* population dynamics model.

Materials and Methods

Experimental protocol

Otiorynchus sulcatus larvae were obtained from nursery-grown *Astilbe* pots in April-June 2002, Blacksburg, Virginia, USA. Larvae were maintained in moist potting soil in a plastic container (20 cm x 20 cm, 7 cm height) and then pupated individuals were transferred to clear plastic rearing cups (30 ml) containing moist potting soil. The containers and rearing cups were held at 21-23°C and a photoperiod of L16: D8 h. Teneral adults (< 1 day old) were collected daily from the containers and allowed to tan for 1 day. Weevils were then weighed individually and placed in a clear plastic Petri dish (9.0 cm diameter, 3 cm height) provisioned with a moist filter paper (90 mm diameter, Whatman®) and a cotton square. Petri dishes were not sealed, which allowed

adequate ventilation. Fresh *Rhododendron* foliage (*Rhododendron caucasicum* x *ponticum* var. *album*) was used for adult food, based on preliminary tests showing that adults reproduced successfully with this food source. Foliage was changed before wilting to provide adults with constant access to high-quality diet. Petri dishes were maintained in environmental chambers to provide constant temperatures of 11, 15, 18, 21, 24, 27, 30, 33 or 36 (± 0.5) °C, and a photoperiod of L16: D8 h.

The following adult life-history traits were measured: preoviposition feeding period (i.e. the age in days at first deposition of eggs), oviposition period (days), longevity (days) and total number of eggs per female. Dishes were monitored every 1-2 days to record the first oviposition for each replicate weevil. Once oviposition commenced, eggs of each adult were collected every 1-2 weeks and surface-sterilized with 0.5% benzalkonium chloride. For calculation purposes, events were assumed to have occurred at the midpoint between two consecutive observations if a scheduled observation was not made (Roy et al., 2002). The eggs were maintained at the treatment temperature until they were melanized in approximately 1 week regardless of temperature. Egg viability was determined by calculating the proportion of eggs that turned from white to brown (Montgomery & Nielsen, 1979; Maier, 1981). All response variables were recorded for 37 weeks or until all weevils in a treatment were dead.

Data analysis

One weevil per Petri dish was considered as a replicate and each treatment had 25-30 replicates. All observations were checked for normality and constant variance before statistical analysis. Egg viability (%) was transformed by arcsine ($\arcsine \sqrt{p}$) and all the other variables were transformed by square-root ($\sqrt{x+0.5}$) to achieve normal distributions. Treatment means and

variations (as standard error of the mean) for response variables were presented unless otherwise indicated. Presence of treatment effects for each response variable was determined using analysis of variance (ANOVA) at 5% significance level (SAS Institute, 1995). Means were separated by the Student-Newman-Keuls (SNK) Test. Kaplan-Meier survival analysis was used to compare weevil death rates among temperature treatments.

Models for *O. sulcatus* reproduction

Nonlinear regression was used to estimate models for temperature effects on each life history trait measured. The estimates of parameters for the linear and nonlinear regression models were obtained using TableCurve 2D Automated Curve Fitting program (Jandel Scientific, 1996).

Reproductive maturation rate, the reciprocal of preoviposition period, was modeled as a function of temperature using a combination of the Briere model (Briere et al., 1999) and a degree-day model (Campbell et al., 1974). The expression of the Briere model is:

$$r(T) = nT(T - T_b)(T_L - T)^{1/m}$$

where $r(T)$ is the rate of development at temperature T ; T_L is the upper temperature developmental threshold, T_b is the lower temperature developmental threshold; n and m are empirical constants. The degree-day model is: $r(T) = a + bT$, where a and b are the model parameters; the lower developmental threshold is $-a/b$; the degree-day requirement above the lower developmental threshold is $1/b$ for mean emergence (Campbell et al., 1974).

The total number of eggs per female was obtained by summing the number of eggs collected during the adult life span. The relationship between mean *per capita* egg production and temperature was described by an extreme-value distribution function (Kim & Lee, 2003). The equation is:

$$f(T) = k \exp[1 + (T_{\max} - T) / \rho - e^{(T_{\max} - T) / \rho}]$$

where $f(T)$ is the total number of eggs produced by a female at temperature T ; k is the maximum reproductive capacity; T_{\max} is the temperature ($^{\circ}\text{C}$) at which maximum egg production occurs; ρ is a fitted constant. The percentage egg viability, $v(T)$, was also modeled as a function of temperature using the same equation.

The median life span of adults was estimated by the Kaplan-Meier survival analysis technique, which allows construction of a survivorship curve without complete mortality in the sample population. The relationship between median life span and temperature was analyzed by a linear regression. A single temperature-independent survival curve was produced versus the normalized age using a sigmoid equation, because the shape of the survival curve at different temperatures approximately coincided. Before fitting data, the survival rate distributions at different temperatures were normalized by dividing the adult age by the median longevity at each temperature. The equation of the survivorship curve is:

$$s(x) = \frac{1}{1 + \exp((\gamma - x) / \delta)}$$

where $s(x)$ is the percentage of live females at the normalized age (time/median longevity) x ; γ is the normalized age at 50% survival and δ is a fitted parameter.

The cumulative distribution of oviposition probability through normalized age, age divided by median longevity, was calculated in terms of percentiles for each temperature. The shape of oviposition distribution curves at different temperatures coincided and the two-parameter Weibull function (Cockfield et al., 1994), was used to describe the cumulative oviposition rate against the normalized age as an independent variable. The Weibull function is:

$$p(x) = 1 - \exp[-(x / \alpha)^{\beta}]$$

where $p(x)$ is the cumulative oviposition at normalized age x ; α and β are scale and shape parameters, respectively.

Reproduction for a cohort of insects has been described by combining three temperature-dependent components: the total reproductive capacity, the age-dependent fractional reproductive rate, and the survival probabilities (Curry & Feldman, 1987; Kim & Lee, 2003). Typically, egg production of insects varies from low numbers at both the high and low temperature extremes to relatively high numbers in the species-specific optimum temperature range. Age-dependent reproduction describes the proportion of the total lifetime reproductive potential that occurs during each age interval. Therefore, the cumulative egg production of a female from emergence day to the n^{th} day was simulated by combining four components: (1) temperature-dependent total egg production, $f(T)$; (2) egg viability, $v(T)$; (3) oviposition rate, $p(x)$; and (4) survival rate, $s(x)$. According to Kim & Lee (2003), the number of viable eggs produced during the age interval between x_i and x_{i+1} was calculated as:

$$v(T)f(T)[p(x_{i+1}) - p(x_i)] \frac{s(x_i) + s(x_{i+1})}{2}$$

Results

Preoviposition and oviposition periods

Adult feeding on *Rhododendron* leaves was observed at all temperatures between 11 and 33 °C and all adults at 36 °C died without feeding. The time to first feeding on foliage differed among temperatures ($F = 34.8$, $df = 7$, 180 ; $P < 0.0001$). The mean number of days from eclosion to first feeding was 11 days at 11 °C, 3 days at 30 °C, and 4-6 days at the other temperatures. At temperatures between 15 and 27 °C, the duration of oviposition period decreased as the

temperature increased. Once oviposition began, females continued egg production until their death. Weevils oviposited at all temperatures tested between 11 and 27 °C but no egg production was observed at 30 °C or above due to early mortality (Fig. 3.1). Temperature had a significant effect on the duration of the preoviposition period ($F = 75.54$; $df = 5, 103$; $P < 0.0001$) and oviposition ($F = 7.39$; $df = 5, 104$; $P < 0.0001$). The duration of the preoviposition period was significantly longer at 11 °C than at 15, 18, 21, 24, or 27 °C (Fig. 3.1). The duration of the oviposition period was significantly longer at 15, 18, and 21 °C than at 11 or 27 °C (Fig. 3.1). The longest preoviposition period (151.8 ± 16.2 days) and the shortest ovipositional period (106.1 ± 16.2 days) were observed at 11 °C. The shortest preoviposition period (34.6 ± 1.1 days) occurred at 24 °C and the longest oviposition period (199.2 ± 7.3 days) occurred at 15 °C. As a covariate, neither the weight of teneral adults nor life span had a significant relationship with the duration of the preoviposition period ($P > 0.05$).

Egg production and egg viability

Temperature affected both *per capita* total egg production ($F = 45.25$; $df = 5, 103$; $P < 0.0001$) and egg viability ($F = 83.02$; $df = 5, 103$, $P < 0.0001$) of *O. sulcatus* (Table 3.1). Both total number of eggs and egg viability were highest at 21 °C, although significant differences in egg production were not observed from 18-24 °C ($P > 0.05$). There was a significant reduction in egg production and egg viability per adult at extreme temperatures. The lowest egg production was 66.7 ± 13.0 eggs per adult at 11 °C, due to the delayed reproductive maturation combined with the brief duration of oviposition. Egg viability was lowest at 27 °C, with only $5.0 \pm 1.0\%$ of the eggs becoming melanized. The minimum and maximum egg production for an individual weevil occurred at 27 °C and 21 °C, with 2 and 1366 eggs, respectively. Mean daily egg

production, calculated by dividing total egg production by oviposition period, was influenced by temperature ($F = 41.95$; $df = 5, 103$; $P < 0.0001$). In the analysis of total egg production and egg viability, two covariates were analyzed: the weight of teneral adults and adult life span. Each was a significant covariate for total eggs per female ($P < 0.01$) but neither was significant for egg viability ($P > 0.01$). This suggests that heavier females may produce more eggs and that nutritional conditions during the larval stage might influence the reproductive potential of adults (Zhou, 2001).

Longevity

At 24 °C or above, no adults survived the entire 37-week duration of the experiment. All adults died within 3 days at 36 °C and within 17 days at 33 °C. However, many adults survived longer than the experimental duration at 11 and 15 °C. At the end of the experiment the median longevity could not be estimated for these temperatures, causing their exclusion from the regression analysis. Temperature influenced the longevity of the weevils ($F = 30.67$; $df = 8, 246$; $P < 0.0001$; Table 3.1) and death rates among temperature groups were significantly different ($\chi^2 = 175.4$, $df = 8$, $P < 0.0001$, Kaplan-Meier analysis). The median longevity of *O. sulcatus* adults was estimated in the temperature range of 18-36 °C: 189, 215, 144, 117, 21, 11 and 2 days at 18, 21, 24, 27, 30, 33, and 36 °C, respectively. If longevity was compared between ovipositing and non-ovipositing females, the former lived significantly longer than the latter at each temperature ($P < 0.05$, t-test).

Models for *O. sulcatus* reproduction

The Briere model (Briere et al., 1999) described the nonlinear relationship between the rates of reproductive maturation and temperature from 11-30 °C (Table 3.2; Fig. 3.2). The predicted low and high threshold temperatures for *O. sulcatus* reproductive development were 6.8 and 30.0 °C, respectively. The estimated optimum temperature was 22.7 °C, with the highest developmental rate (1/preoviposition period) of ≈ 0.0288 . The rate of reproductive maturation at temperatures 11-21 °C (the linear portion of the Briere model) was described by the degree-day model (Table 3.2; Fig. 3.2). This degree-day model estimated the developmental threshold to be 6.7 °C and the thermal constant to be 505.0 degree-days.

The effect of temperature on median life span was described by the linear regression equation: $y = 450.86 - 13.00x$, $r^2 = 0.9035$ (Fig. 3.3A). The overall survivorship curve was obtained by a sigmoid function versus normalized adult age, which was calculated by dividing the age-specific survival by the median longevity at each temperature (Table 3.3; Fig. 3.3B). Fifty percent mortality was estimated at the normalized age of 0.87, represented by the parameter γ in the model.

The relationship between temperature and total egg production was well described by the extreme value function (Table 3.3; Fig. 3.4A). In the egg production model, the optimum temperature (T_{\max}) was 21.8 °C with a theoretical maximum production of 1110.8 eggs (parameter k). The highest egg viability (96.0%) was estimated to occur at 19.8 °C (Table 3.3; Fig. 3.4B). By combining the two equations, the estimated number of viable eggs was highest (1014.6) at 20.9 °C. Cumulative age-specific egg production at different temperatures is shown in Fig. 3.5A. The cumulative oviposition rate curve against normalized adult age was fit to the two-parameter Weibull equation (Table 3.3; Fig. 3.5B).

In Fig. 3.6, the predicted reproductive density curve of female cohorts in relation to temperatures suggested that both egg production and the duration of the ovipositing periods decreased with increasing temperature above the optimum range (20-24 °C). Our simulation predicts that viable egg production of *O. sulcatus* is highly limited at extreme temperatures (< 10 or >30 °C).

Discussion

In the current study, we were able to make direct comparisons of all life history traits related to reproduction for *O. sulcatus* at a wide range of temperatures that includes high and low extremes. Temperatures encountered by *O. sulcatus* adults played a critical role in reproductive success. Significant differences were detected in preoviposition period, oviposition period, longevity, total fecundity, daily oviposition rate, and egg viability among cohorts of adult *O. sulcatus* tested at 9 temperatures. It is noteworthy that the upper lethal temperature for *O. sulcatus* adults is relatively low and the reproductive capacity of *O. sulcatus* at 27 °C or above is severely impaired due to the shortened life span and reduced production of viable eggs. It is evident that exposure to extreme temperatures would lead to a decrease in the intrinsic rate of increase for *O. sulcatus*.

In our study, the relationship between temperature and *O. sulcatus* reproductive maturation was first quantified by applying the nonlinear Briere model (Briere et al., 1999) over the full range of temperatures. The Briere model estimated that the optimum temperature for the rate of *O. sulcatus* reproductive maturation was 22.7 °C, and the lower and higher thresholds were 6.8 °C and 30.0 °C, respectively. Our results confirm that the rate of reproductive maturation during the preoviposition period increases up to 26 °C (Masaki & Ohto, 1995) and temperatures at 27 °C or above cause a delay in reproductive maturation (Stenseth, 1979).

Despite the consistency in the pattern of temperature-dependence of the preoviposition period, there are discrepancies in the duration of the preoviposition period. For example, at 12 °C, the long preoviposition period (61 days) reported by Stenseth (1979) was very different from that (258 days) of Masaki & Ohto (1995), even though strawberry leaves served as food in both studies.

It is important to note the differences in experimental methods between the present study and others. In the current study, I obtained data from weevils that were collected as mature larvae from the field. After eclosion, adults of the same age were caged individually in each treatment and the date of first egg production of each individual was recorded within 1-2 days. Therefore, we were able to document statistical significance among temperature treatments and variation among individuals for preoviposition periods for the first time. Stenseth (1979) collected data from 3 replicates of 10 adults each, and the time to first eggs laid by each batch (not each weevil) determined the preoviposition time. These data did not allow calculation of the mean preoviposition period from each treatment, based on individual weevils.

Masaki & Ohto (1995) estimated a lower developmental threshold of 8.4 °C and the thermal constant to be 571.1 DD. Using the same estimation procedure, we estimated the lower developmental threshold to be 6.7 °C and the thermal constant at 505.0 DD. These differences may be the result of variations in environmental conditions other than temperature, such as species of food plants or photoperiod (Garth & Shanks, 1978; Nielsen & Dunlap, 1981). In Masaki & Ohto (1995), the photoperiods in different temperature treatments were not controlled uniformly: natural light at 12 °C; 16 h light at 15, 18, 21, and 24 °C; complete dark at 26 °C. These uncontrolled photoperiods could cause significant confounding experimental variation, and is a limitation of their study.

The development threshold and thermal constant can be used to determine the onset of *O. sulcatus* reproduction in the field by adding the daily thermal units (degree-days) above the threshold 6.7 °C until the value 505.0 DD is reached, at which point reproductive maturation is complete. Accurate prediction of the duration of the preoviposition period is critical to determine the best timing of foliar insecticide sprays for adult control.

I calculated the reproductive life span by subtracting the duration of the preoviposition period from total longevity. Delayed reproduction of *O. sulcatus*, as observed at 12 °C and 27 °C, can result in a shortened reproductive life and reduction of total egg production per female. Our data agree with those collected by Maier (1981) that suggest the preoviposition period can serve as an important indicator of *O. sulcatus* reproductive success and it may be a relatively easy method to estimate the fecundity of this weevil for a limited experimental duration.

I determined that temperature influences the reproductive capacity of *O. sulcatus*. *Per capita* egg production and daily oviposition rate of *O. sulcatus* increased up to 21 °C but decreased sharply at 27 °C (Table 3.1). The *per capita* egg production and daily oviposition rate were significantly lower at 11 °C than at 15 °C, due to the delayed reproductive maturation and thus short reproductive life. At 11 °C, there was 89% reduction in *per capita* egg production and 69% reduction in daily oviposition rate, compared with those at 15 °C. The optimum temperature for *per capita* egg production was estimated to be 21.8 °C with a theoretical maximum production of 1110.8 eggs, using the extreme-value distribution function (Kim & Lee, 2003). Our findings provide crucial information in understanding the population dynamics of *O. sulcatus*, because in studies of population demography, reproduction is characterized as the *per capita* rate of offspring production in a given time period (Carey, 1993).

Published totals of egg production of individual weevils are extremely variable at 20-22 °C, ranging from 20 to > 2000 eggs (Stenseth, 1979; Nielsen & Dunlap, 1981), although values from 500-1200 are more typical (Cram, 1965; Penman and Scott, 1976; Moorhouse et al., 1992b). Differences may result from variable experimental conditions such as host plants (Penman and Scott, 1976; Maier, 1981) or photoperiod (Garth & Shanks, 1978). Evenhuis (1978) observed that field-collected adults in late September did not oviposit at constant temperatures < 11 °C or > 26 °C respectively, with optimum egg production (\approx 600 eggs) at 23 °C. However, we observed that egg production occurred at 27 °C, which is above the upper threshold temperature suggested by him. Zepp et al. (1979) recorded an average egg production per female of 624 at 28 °C, which is similar to the 421 eggs at 27 °C in our study. Evenhuis (1978) did not draw a general conclusion due to the unknown age of the weevils, the lack of replicates (i.e. 5 adults per treatment), and short period of observation. Stenseth (1979) observed egg production at 18, 21, and 24 °C over a period of 250 days but he did not determine the temperature effects on the *per capita* egg production or the variability among individuals due to the grouping of ten females as an experimental unit. Assuming that each adult lays 150 eggs and no immature mortality occurs, Feytaud (1918) estimated that a single weevil could result in 7.59×10^{10} offspring after 5 years.

The age specific oviposition pattern of *O. sulcatus*, quantified using the cumulative Weibull model (Cockfield et al., 1994), was similar at different temperatures. Stenseth (1979) proposed a cyclic pattern of *O. sulcatus* egg production, but this pattern is not evident in other studies including ours (Penman & Scott, 1976; Zepp et al., 1979; Nielsen & Dunlap, 1981). The pattern seems to result from varying host quality rather than inherent periodicity of age-specific oviposition (Moorhouse et al., 1992b). On the contrary, vigorous egg production early in the season by young adults was consistent in most reports. Because larvae that have not reached the

third instars do not withstand and survive the low temperature during the winter (Garth & Shanks, 1978; Moorhouse et al., 1992a), such early-season oviposition would increase overwintering survival of offspring. The larvae hatching from eggs laid late in the season would likely experience high winter mortality.

Relatively little research has focused on how egg viability is affected by the environmental conditions experienced by the adult that produces them. Tanaka & Tokihoro (1983) observed that the seasonal egg production and egg hatchability of *O. sulcatus* was greatly reduced during summer when temperatures exceeded 28 °C. In southwestern Virginia, *O. sulcatus* adults were observed in the field from early May to September, but their abundance declined throughout the summer, with peak occurrence in mid May (Son & Lewis, 2003). Temperatures increase in July and August, with many days where temperatures above 30 °C last for several hours. Under these conditions, temperature could contribute to adult mortality and few adults would continue to produce viable eggs during this period. In the present study, egg viability was significantly diminished by constant exposure of adults to both high and low temperature extremes (i.e. 11 and 27 °C, respectively). Based on these reports, it is evident that the high temperature during the summer months would limit the time window during which the eggs laid would survive to adulthood. Complementary to these data, the overwintering survival of larvae that have not reached at least the third instar is very low (Garth & Shanks, 1978; Moorhouse et al., 1992a). Just before the onset of winter, *O. sulcatus* adults were rarely found and late instar-larvae were most abundant (Son & Lewis, 2003). So, if eggs are produced in early fall, after the high-temperature season has ended, they cannot survive winter conditions. The combined effects of poor winter survival of early instars with poor viability of eggs laid in the summer could be hypothesized to cause limited age variation in the field.

Otiorhynchus sulcatus has a relatively long adult life span. Once preovipositional feeding and development is complete, *O. sulcatus* weevils produce eggs until their death. Published accounts of *O. sulcatus* longevity are highly variable, and range from 28 days to more than 1 year (Penman & Scott, 1976; Nielsen & Dunlap, 1981; Moorhouse et al., 1992b). Although some adults occasionally survive more than 1 year in suitable laboratory conditions (Penman & Scott, 1976), such a long life span is not likely to be achieved in field conditions due to winter mortality and lack of food (Nielsen & Dunlap, 1981). I have found that the life span of *O. sulcatus* adults increases linearly with decreasing temperatures. For example, only 18% mortality was observed at 11 °C in 259 days but 100% mortality occurred at 36 °C in 3 days. In the linear regression model of temperature-dependent longevity, it might be argued that the extrapolation method for *O. sulcatus* longevity below 18 °C overestimates the actual life span at lower temperatures.

The effect of temperature on reproductive traits of insects has been described by applying mathematical models (e.g. Jones et al., 1975; Greever & Georghiou, 1979; Curry & Feldman, 1987; Allen et al., 1995; Kim & Lee, 2003). The models developed in our study quantified the differential effects of temperature on life history traits in *O. sulcatus* reproduction. As with the invading red imported fire ant (e.g. Stoker et al., 1994; Killion & Grant, 1995), the temperature-dependent models for *O. sulcatus* reproduction enable the prediction of potential range limits created by a ‘reproductive border’ of *O. sulcatus*, based on climatic data. Stenseth (1987) suggested that the distribution of *O. sulcatus* was concentrated in areas having a mean air temperature above – 4 °C in January. I suggest that upper temperature limits would also restrict *O. sulcatus* distribution. In North America, this species is most commonly found in the northern United States and Canada (Warner & Negley, 1976). This species has not established in

Houston, Texas (Warner & Negley, 1976), where the mean number of days with maximum air temperature > 32 °C in May-September is 95 days in contrast to only 27 days in Blacksburg, Virginia (NOAA, 2003). Therefore, I can speculate that despite its wide host range and the frequent shipment of infested plant material to new locations, establishment and population growth of *O. sulcatus* would be substantially limited in geographic areas that experience very hot summers.

In conclusion, I showed that temperature is a key factor regulating the reproduction of *O. sulcatus* and that temperature plays an important role in regulating the phenology, seasonal abundance and geographical distribution of populations. Future studies should include the evaluation of effects of daily temperature cycles on *O. sulcatus* reproduction because short-term exposure to high or low temperatures may change mortality or reproductive success beyond predictions based on constant temperature studies (Beck, 1983). Collectively, the current and suggested future studies will contribute to improve the decision support systems for *O. sulcatus* management by providing better prediction to pest managers.

Table 3.1. Longevity, egg production, egg viability, and daily egg production (mean \pm SEM) of *O. sulcatus* females at constant temperatures.

Temp, (°C)	N	Longevity (in days)	Adults with oviposition			
			n	No. eggs per female	Viability (%)	No. eggs per female per day ^a
11	28	223.9 \pm 15.4a	16	66.7 \pm 13.0d	48.2 \pm 6.2b	0.9 \pm 0.3d
15	29	208.2 \pm 17.6a	23	599.0 \pm 44.2b	82.3 \pm 2.2a	2.9 \pm 0.2c
18	27	174.1 \pm 20.3ab	18	851.6 \pm 67.2a	89.1 \pm 1.8a	4.3 \pm 0.3b
21	26	129.2 \pm 23.3bc	14	1094.1 \pm 78.1a	90.1 \pm 1.5a	5.8 \pm 0.3a
24	28	146.2 \pm 20.7bc	19	915.1 \pm 76.2a	84.5 \pm 2.5a	5.6 \pm 0.3a
27	25	106.2 \pm 18.8c	14	420.8 \pm 66.5c	5.0 \pm 1.0c	3.2 \pm 0.3c
30	28	19.8 \pm 1.6d	0	–	–	–
33	28	9.0 \pm 1.0d	0	–	–	–
36	28	2.1 \pm 0.1d	0	–	–	–

N, numbers of tested weevils. n, number of ovipositing adults. ^a Daily egg production during oviposition periods. Means followed by the same letter within a column are not significantly different ($P > 0.05$, Student-Newman-Keuls Test).

Table 3.2. Parameter estimates for the rate of reproductive maturation (1/ preoviposition period) for *O. sulcatus*.

Models	Parameters	Estimates	SEM	r ²
Briere et al. (1999)	<i>n</i>	0.00001709	0.00000226	0.987
	<i>T_b</i>	6.7786	1.5405	
	<i>T_L</i>	30.0001	0.0226	
	<i>m</i>	1.2905	0.1560	
Degree-day	<i>a</i>	-0.01320	0.00643	0.929
	<i>b</i>	0.001980	0.000386	

Table 3.3. Parameter estimates for temperature-dependent models of *O. sulcatus* reproduction.

Model type	Parameters	Estimates	SEM	r^2
Fecundity model	k	1110.8443	63.3248	0.974
	T_{\max}	21.8153	0.2961	
	ρ	-4.3689	0.3260	
Viability model	k	95.9987	10.1326	0.909
	T_{\max}	19.5522	0.8311	
	ρ	-5.7906	0.9599	
Oviposition rate model	α	0.7750	0.0084	0.896
	β	2.1271	0.0647	
Survival rate model	γ	0.8744	0.0344	0.808
	δ	-0.5192	0.0349	

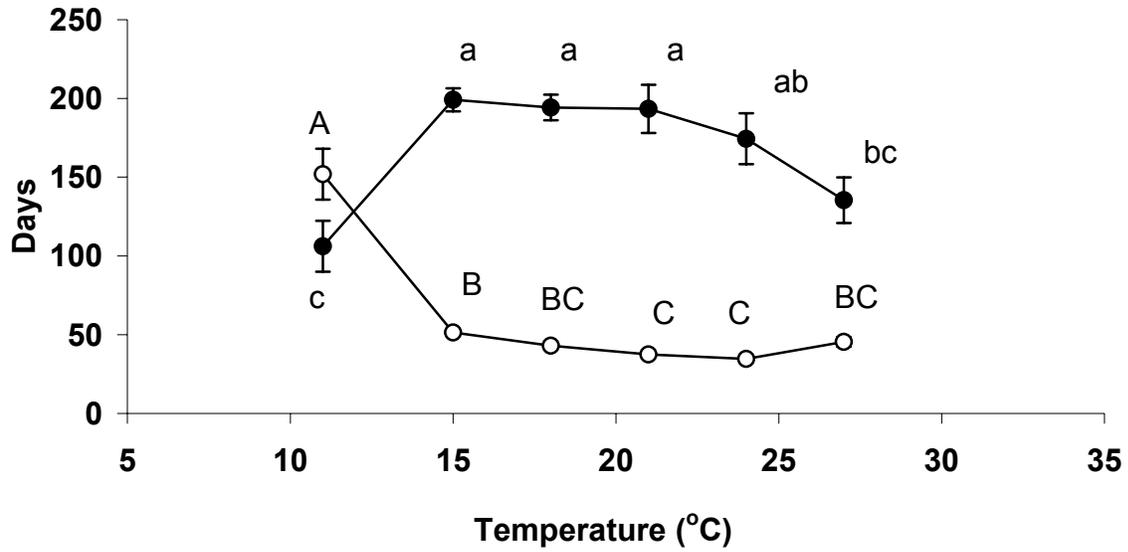


Fig. 3.1. Length of preoviposition period (○) and oviposition period (●) (mean ± SEM) for *O. sulcatus* adults under constant temperatures. Values followed by different characters differ significantly ($P < 0.05$, Student-Newman-Keuls Test).

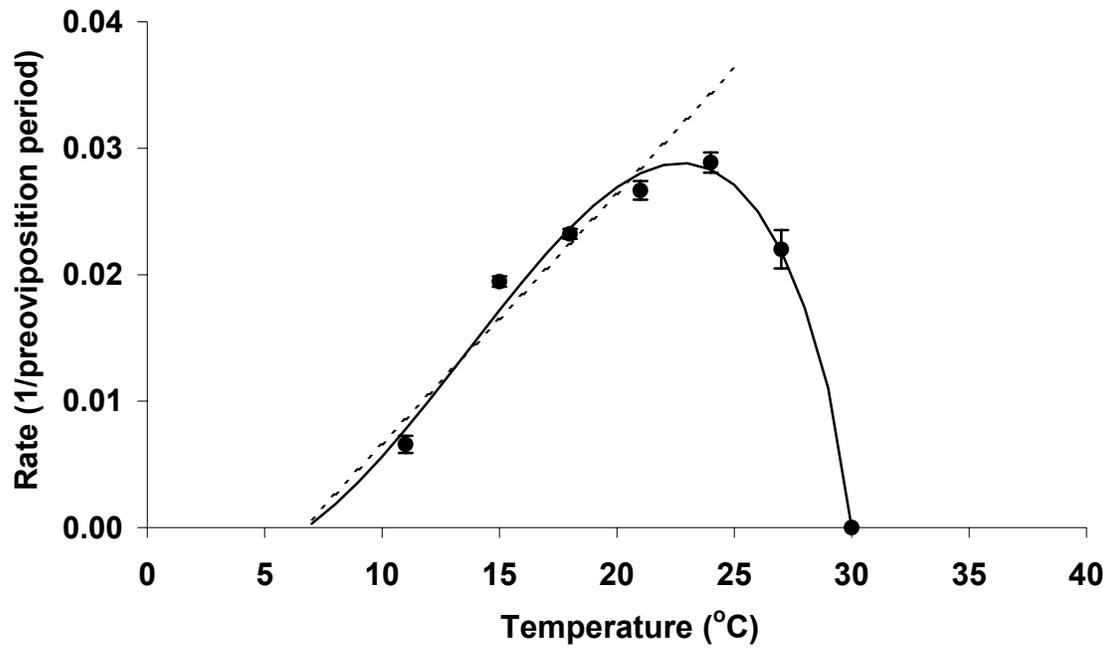


Fig. 3.2. Temperature-dependent rate (mean \pm SEM) of reproductive maturation (1/preoviposition period) of *O. sulcatus*: Observed data (●) fitted to Briere model (solid line) and degree-day model (dotted line).

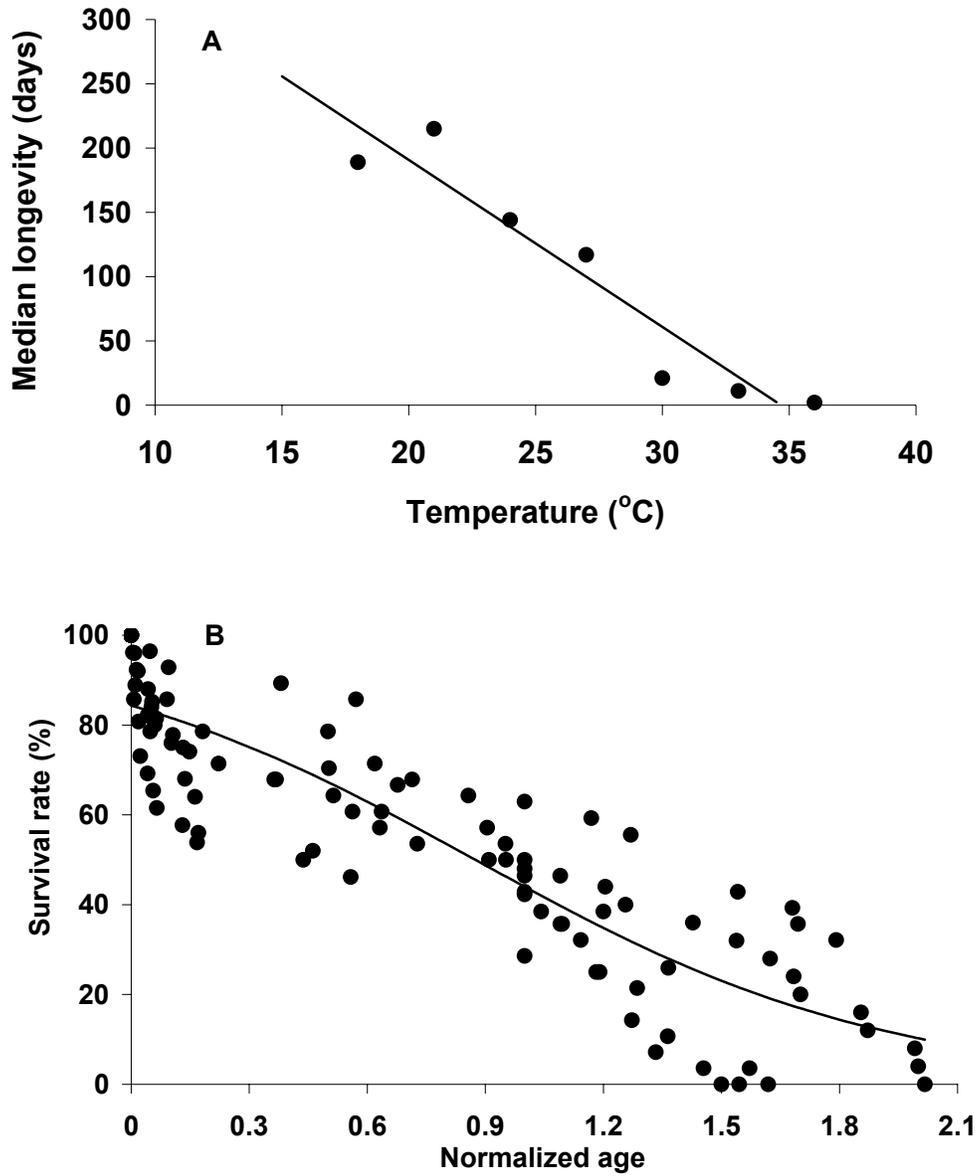


Fig. 3.3. Temperature-dependent median longevity (A) and age-specific survivorship curve (B) of *O. sulcatus* adults in relation to normalized age (age/median longevity). Observed data (●) fitted to linear regression model (solid line, A) and a sigmoid function (solid line, B)

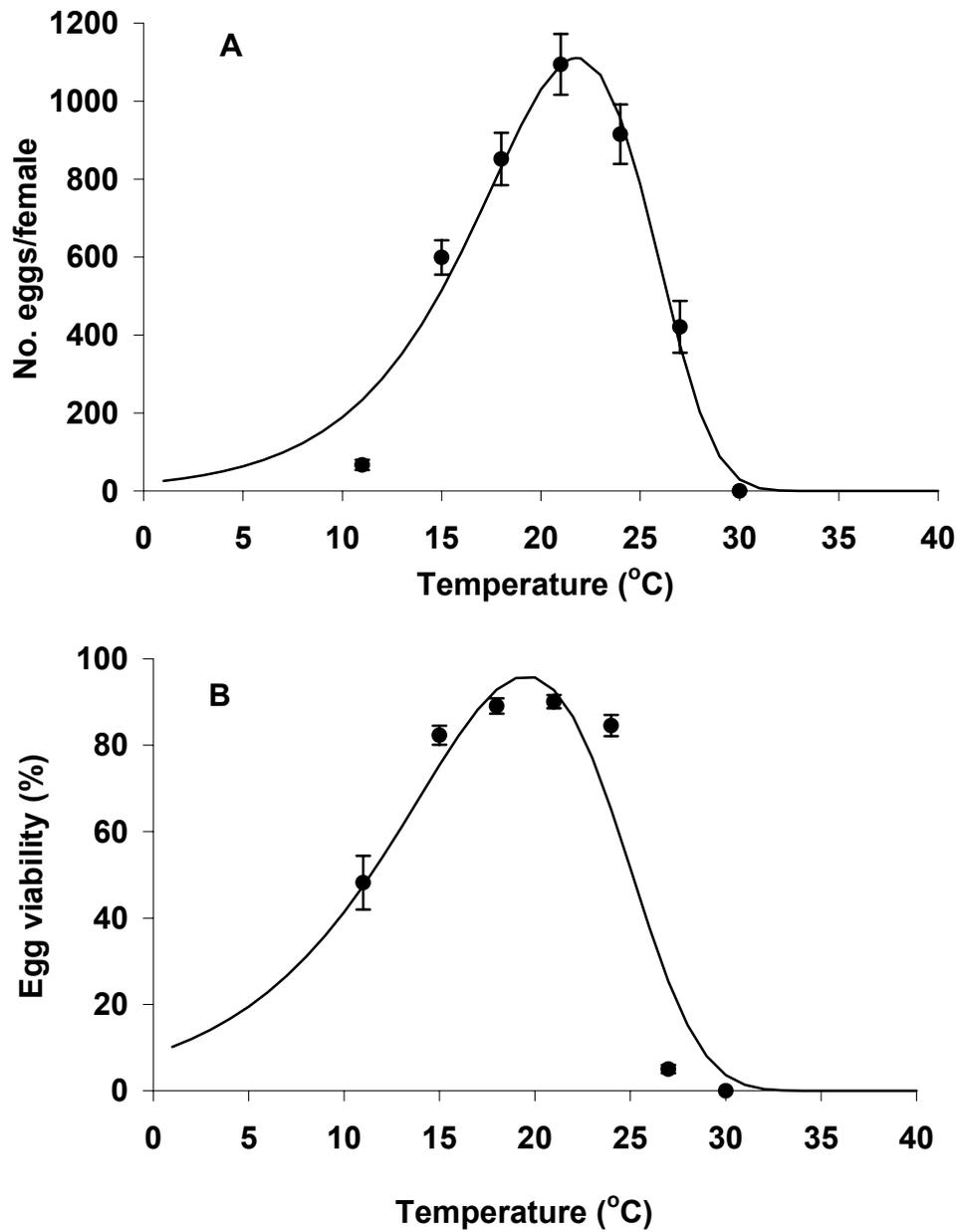


Fig. 3.4. Temperature-dependent egg production (A) and egg viability (B) per female (mean \pm SEM): observed data (\bullet) fitted to extreme value function (solid line).

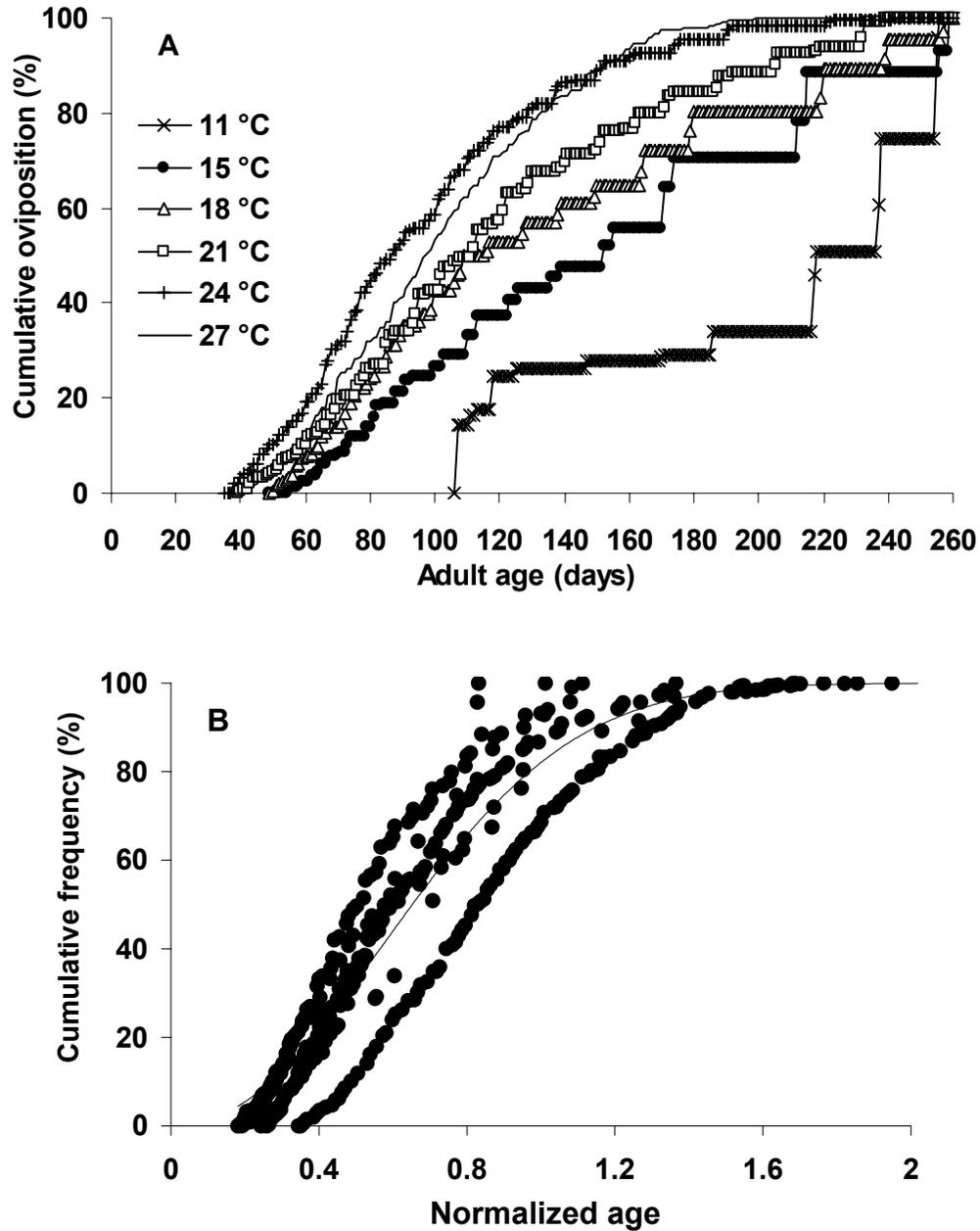


Fig. 3.5. Cumulative reproduction curve of *O. sulcatus*: (A) Age expressed as chronological time (days) post adult emergence. (B) Age expressed as normalized age (age/median longevity). Observed data (●) fitted to two-parameter Weibull function (solid line, B).

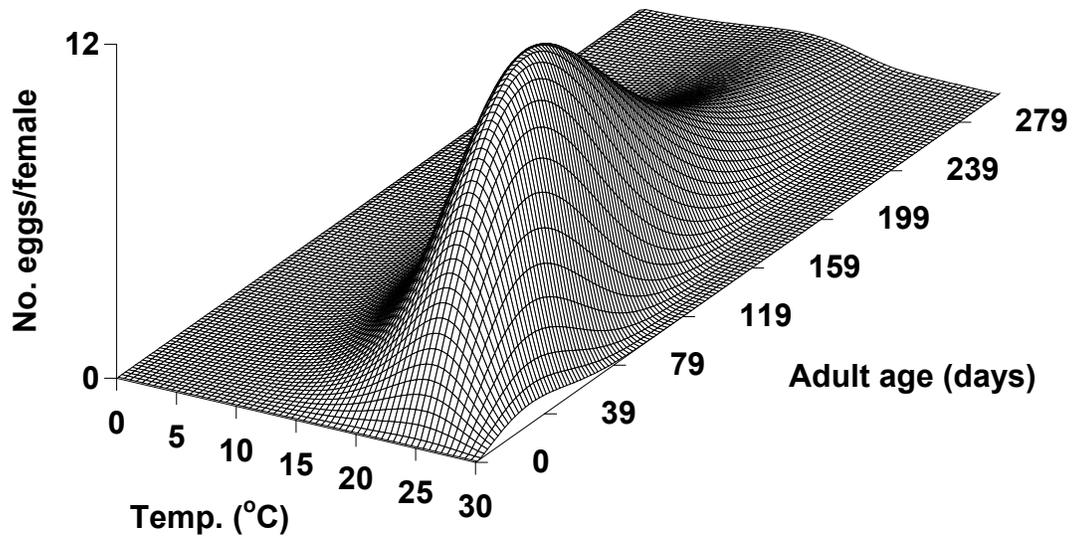


Fig. 3.6. Predicted density curves of viable egg production of *O. sulcatus* adults in relation to adult age and temperature.

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