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Effect of temperature on growth, reproductive activity, and survival of the invasive bromeliad-eating weevil *Metamasius callizona* (Coleoptera: Curculionidae)

Teresa M. Cooper* and Ronald D. Cave

Abstract

Growth, oviposition, and survival rates of the bromeliad-eating weevil *Metamasius callizona* (Chevrolat) (Coleoptera: Curculionidae) were measured at a range of temperatures to determine optimal temperature range, lower and upper development thresholds, and degree-days needed for development of immature stages. Optimal temperature range for growth was 25 to 30 °C and for oviposition 22 to 33 °C. The lower development threshold was 13 °C and upper threshold about 35 °C. Development of the egg and larval stages required 518 degree-days, and from pupation to adult 140 degree-days. Adult weevils suffered higher mortality at 35 °C than at 25 or 16 °C. Typical winter conditions likely have at most a minimal effect on weevil populations in central Florida and no effect in southern Florida. As well, high summer temperatures could potentially cause weevil mortality due to heat stupor but, as with winter temperatures, the effects would be minimal. Extremely cold winters and extremely high summer temperatures may cause high weevil mortality, particularly in central Florida. Sea breezes on the east coast of Florida may create cooler habitats during the summer and therefore ameliorate mortality due to summer temperatures.

Key Words: Florida; *Tillandsia*; optimal temperature range; development threshold; degree day

Resumen

Se midieron las tasas de crecimiento, oviposición y sobrevivencia del picudo *Metamasius callizona* (Chevrolat) (Coleoptera: Curculionidae) a un rango de temperaturas para determinar el rango de temperaturas óptimas, umbrales inferior y superior para desarrollo y los días-grados que se requieren para el desarrollo de los estados inmaduros. El rango de temperaturas óptimas para crecimiento fue 25-30 °C and para oviposición 22-33 °C. El umbral inferior para desarrollo fue 13 °C y el umbral superior fue aproximadamente 35 °C. Se requieren 518 días-grados para cumplir el desarrollo del huevo + larva y 140 días-grados para cumplir la etapa de pupa. Picudos adultos sufrieron mayor mortalidad a 35 °C que a 25 o 16 °C. Condiciones típicas durante el invierno probablemente tienen a lo más un efecto mínimo las poblaciones del picudo en Florida central solamente y ningún efecto en el sur de Florida. Asimismo, las altas temperaturas de verano potencialmente pueden causar mortalidad debido a estupor de calor pero, como las temperaturas en invierno, los efectos serían mínimos. Inviernos extremadamente fríos y temperaturas extremadamente altas en verano podrían causar mayores tasas de mortalidad de picudos, especialmente en Florida central. Brisas marinas en la costa oriental de Florida posiblemente crean habitats más frescos durante el verano y por lo tanto aliviar la mortalidad debido a temperaturas de verano.

Palabras Clave: Florida; *Tillandsia*; rango optimal de temperatura; umbral de desarrollo; día-grado

Metamasius callizona (Chevrolat) (Coleoptera: Curculionidae) is an invasive bromeliad-eating weevil destroying native bromeliad populations in Florida. Florida has 16 native bromeliad species (Luther & Benzing 2009), and 12 are attacked by the weevil (Frank & Cave 2005). These 12 bromeliad species are frost intolerant and limited to central and southern Florida, where the climate is subtropical to tropical (Luther & Benzing 2009). The weevil has become established throughout central and southern Florida (Frank 1996), where it is active throughout the year (Frank 1996; Cooper 2008). The northern boundary of the weevil's range is approximately a straight line running from Volusia County on the east coast to Hillsborough County on the west coast, which corresponds with the northern boundary of the range of the weevil's host bromeliads, suggesting that the range of the host bromeliads, not cold temperatures, is what limits the weevil's northern expansion in Florida.

Insects have an optimal temperature range in which they develop and reproduce (Block 1990; Chapman 1998). Below this optimal range,

cold temperatures slow insect growth and reproductive rates, and below the lower threshold, these processes will cease. If temperatures are sufficiently and persistently cold, they may be lethal. Above the optimal range, heat stupor may increase mortality quickly. Central and southern Florida usually have mild winters and hot, wet summers (Chen & Gerber 1990). Central Florida has lower average and minimum temperatures than southern Florida during the winter months and may experience freezing or sub-freezing temperatures a few to several times each year, whereas southern Florida rarely experiences temperatures at or below freezing (SERCC 1989; FAWN 1997). Differences in winter conditions between central and southern Florida may cause differences in weevil abundance in these areas of the state. In addition, Florida can experience high temperatures (30–35 °C or higher) in Jun to Aug (SERCC 1989; FAWN 1997). Hot temperatures, like cold temperatures, have the potential to modify an organism's demographic patterns (Block 1990; Chapman 1998).

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During the winter of 2009–2010, the southeastern region of the United States suffered very cold and persistently low temperatures (NOAA 2010). Snow flurries fell as far south as central Florida and records of lowest daily temperatures and duration of those temperatures were repeatedly broken from Daytona to Key West. Jan to Mar 2010 was the coldest Jan to Mar period experienced in Florida in the 116 yr period of record keeping. During the midst of this record-breaking winter, those concerned with bromeliad conservation wondered if such extreme weather conditions could have an adverse effect on the Mexican bromeliad weevil population, perhaps to the extent of diminishing the damage to the bromeliads by the weevil. This paper attempts to answer this question, as well as provide basic temperature data for an invasive insect species, which will help in designing and implementing conservation and management efforts as well as provide greater understanding of the dynamics that exist between the weevil and its host bromeliads.

Materials and Methods

WEEVILS

Weevils used in the experiments were taken from a laboratory colony maintained at the Hayslip Biological Control Research and Containment Laboratory at the Indian River Research and Education Center, University of Florida, Ft. Pierce, Florida. Pineapple leaves were used to feed weevil larvae and adults and as an oviposition substrate for gravid females. The leaves were taken from fresh pineapple tops, and each piece was approximately 4 cm in length, cut from the base of the leaf. Outermost leaves on the pineapple tops were not used because they are too small and tough, and central leaves were not used because they are too thin and soft. Eggs, larvae, and pupae were kept individually in 20 × 60 mm clear plastic Petri dishes, and adults were kept individually in 18.5 mL clear plastic vials with white, plastic, tightly capped, slit snap caps. To maintain moisture, Petri dishes with eggs and pupae had moistened paper towels cut in squares approximately 7 × 7 cm that were folded and pressed against the side of the Petri dish.

For cold and heat tolerance, development time, and survival research, eggs were collected from the colony's egg-laying population. Every 24 h, the egg-laying weevils were given a fresh piece of pineapple leaf, and the old leaf was removed. The old leaves were checked for eggs, and those leaves with a single egg were placed individually in Petri dishes with a piece of moistened paper towel and used directly for experimentation or reared to the life stage needed for experimentation. To rear to later life stages, larvae that emerged from the eggs remained in their Petri dishes and were provided a fresh pineapple leaf twice a week by slipping it underneath the old pineapple leaf. Third instars were used for experimentation (the pineapple leaves remained in the Petri dish, and the larvae were regularly fed during the experiments) or were continually reared until they pupated. Pupae were removed from the pineapple leaves and their pupal chambers and placed individually in clean Petri dishes with moistened paper towel and used for experimentation or held until adult emergence. Emergent adults were placed in vials (described above) with a pineapple leaf (provided twice a week, with the old leaf removed and the new leaf added) and used for experimentation when needed.

Adults that were used to study the weevil's oviposition rate were taken from the weevil colony's egg-laying population and were approximately 4 mo old as adults. They were kept in the vials (described above) and were provided fresh pineapple leaves twice a week.

COLD AND HEAT TOLERANCE

All experiments were done in environmentally controlled chambers with 65% RH and a photoperiod of 12:12 h L:D. Weevils used in experiments were maintained at 25 °C and held at that temperature until they reached the proper life stage and age for exposure. Weevil eggs, 3rd instars, pupae, and adults were exposed to constant -2, 0, 5, 10, 16, 22, 25, 28, 32, or 35 °C. Specimens were stepped down or up to the next experimental temperature every 24 h until they reached their assigned temperature. Specimens remained at their assigned temperature for 1, 2, or 4 d and were then returned to 25 °C where larvae, pupae, and adults were kept for 24 h, at which time the numbers of living and dead individuals were recorded. A specimen was considered dead if it did not move when poked with a finger. Eggs were held at 25 °C for 2 wk after exposure and monitored for larval emergence; at the end of 2 wk, eggs from which larvae did not emerge were considered dead.

Proportions and confidence intervals were calculated for each stage's survival for each temperature–time exposure. Confidence intervals ($\alpha = 0.05$) were calculated using Wilson score intervals (Wilson 1927). Differences in survival were inferred by comparing the confidence intervals.

DEVELOPMENT TIME

Portions of pineapple leaves each containing a single egg were collected and placed in individual plastic Petri dishes with moistened paper towel (previously described), and were assigned to a temperature. Based on the results of cold tolerance exposure, we studied weevil development time at the following temperatures: 15, 18, 20, 22, 25, 28, 30, 33, and 35 °C. Larvae were fed a fresh pineapple leaf twice a week until pupation. Pupae were monitored daily for adult emergence. Development time was measured from time of egg collection to pupation and from pupation to adult emergence. The development time of each instar was not measured because, based on previous experience, checking for molting disturbs the larvae and results in very high mortality.

Average development times from egg collection to pupation and from pupation to adult emergence were calculated for each temperature and compared for differences among temperatures using analysis of variance and Tukey's method of multiple comparisons, with $\alpha = 0.05$. Linear regression was used to determine the regression equations for development times from egg collection to pupation and from pupation to adult emergence (Equation 1; $y = \text{rate of development}$; $a = \text{intercept}$; $b = \text{slope}$; $T = \text{temperature } [^{\circ}\text{C}]$). Degree-days (Equation 2) and lower development thresholds (Equation 3) were calculated from the regression equations.

$$\text{Equation (1): Regression equation: } y = a + bT$$

$$\text{Equation (2): Degree days} = 1/b$$

$$\text{Equation (3): Lower threshold } (^{\circ}\text{C}) = -a/b$$

OVIPOSITION RATE

Mated females from the weevil colony's egg-laying population were placed in 18.5 mL plastic vials (previously described) with a piece of pineapple leaf and assigned to 1 of 7 temperatures from 15 to 35 °C. Every 24 h for 14 d, the pineapple leaves were removed from the vials and replaced with a fresh piece of leaf. The leaves that were removed were checked for eggs. The inside walls of the vials were also checked for eggs (which, if present, were removed). The number of eggs oviposited by each female was recorded daily, and the average number of eggs laid per female per day was calculated for each temperature.

Analysis of variance and Tukey's method of multiple comparisons ($\alpha = 0.05$) were used to detect significant differences among the experimental temperatures.

ADULT SURVIVAL CURVES AT THREE TEMPERATURES

Newly emerged weevil adults were collected, placed individually in 18.5 mL plastic vials (previously described), and held in environmentally controlled chambers set at 16, 25, or 35 °C. They were fed pineapple leaves twice a week and checked daily for survival for 40 d. Right censored, non-parametric survival analysis using Kaplan–Meier estimators (Kaplan & Meier 1958) was used to create survival curves with confidence intervals for the 3 temperatures and to test for statistical similarity ($\alpha = 0.05$).

Results

COLD AND HEAT TOLERANCE

Egg survival rates at 0 °C for 1 and 2 d, 5 to 28 °C for all time exposures, and 32 and 35 °C for 1 and 2 d ranged from 20 to 75% (Fig. 1A). No eggs survived exposure at -2 °C for 1, 2, and 4 d, at 0 °C for 4 d, and at 32 and 35 °C for 4 d. Larval survival rates ranged from 89 to 100% for most temperatures, with the lowest survival rates at -2 °C for 2 and 4 d (Fig. 1B). Pupal survival rates at 5 to 32 °C for all time exposures and at 35 °C for 1 and 2 d ranged from 62 to 92% (Fig. 1C). No pupae survived at 0 and -2 °C for any exposure period and at 35 °C for 4 d. Adult survival rates at all temperatures and time exposures ranged from 95 to 100% (Fig. 1D). Adults were also tested at 0 °C for 6 and 8 d, and the survival rates were 95 and 56%, respectively (Fig. 1E); confidence intervals for 0 °C at 8 d were clearly separated from the confidence intervals of the other survival rates.

DEVELOPMENT TIME

Weevils developed from egg to adult at 6 of the 9 temperatures tested (Table 1). Development times were significantly shorter at temperatures >25 °C than at temperatures ≤ 25 °C. Development times below 25 °C were significantly lengthened with each successive 2 °C decrease in temperature. The pupal stage was significantly shorter at 28 and 30 °C compared with temperatures ≤ 25 °C. The pupal stage was significantly lengthened with each successive 2 to 3 °C decrease in temperature below 28 °C. At 33 °C, no larvae pupated, and at 35 °C no larvae hatched from eggs. At 15 °C, larvae lived for up to 12 wk but never developed beyond 2nd instar.

Regression lines and equations for development times from egg collection to pupation and from pupation to adult emergence are given in Fig. 2. Calculated degree-days and lower thresholds were: egg collection to pupation: degree-days = 518; lower development threshold = 12.7 °C; pupation to adult emergence: degree-days = 140; lower development threshold = 12.3 °C.

OVIPOSITION RATE

Metamasius callizona females had statistically similar oviposition rates at temperatures from 22 to 33 °C (Fig. 3). At these temperatures, the overall mean oviposition rate was 0.40 eggs per female per day, with 4 eggs being the most laid by 1 female in 1 d. Oviposition rates at 35, 18, and 15 °C were significantly lower, although the oviposition rate at 35 was not significantly different from the rate at 22 °C. The overall mean oviposition rate at the lowest 2 temperatures was about 0.05 eggs per female per day, with 2 eggs being the most laid by 1 female in 1 d. All females oviposited in the pineapple leaf except those at 35 °C; at this temperature, 78% of the eggs were laid outside of the pineapple leaf, either on the leaf surface or the inner wall of the vial.

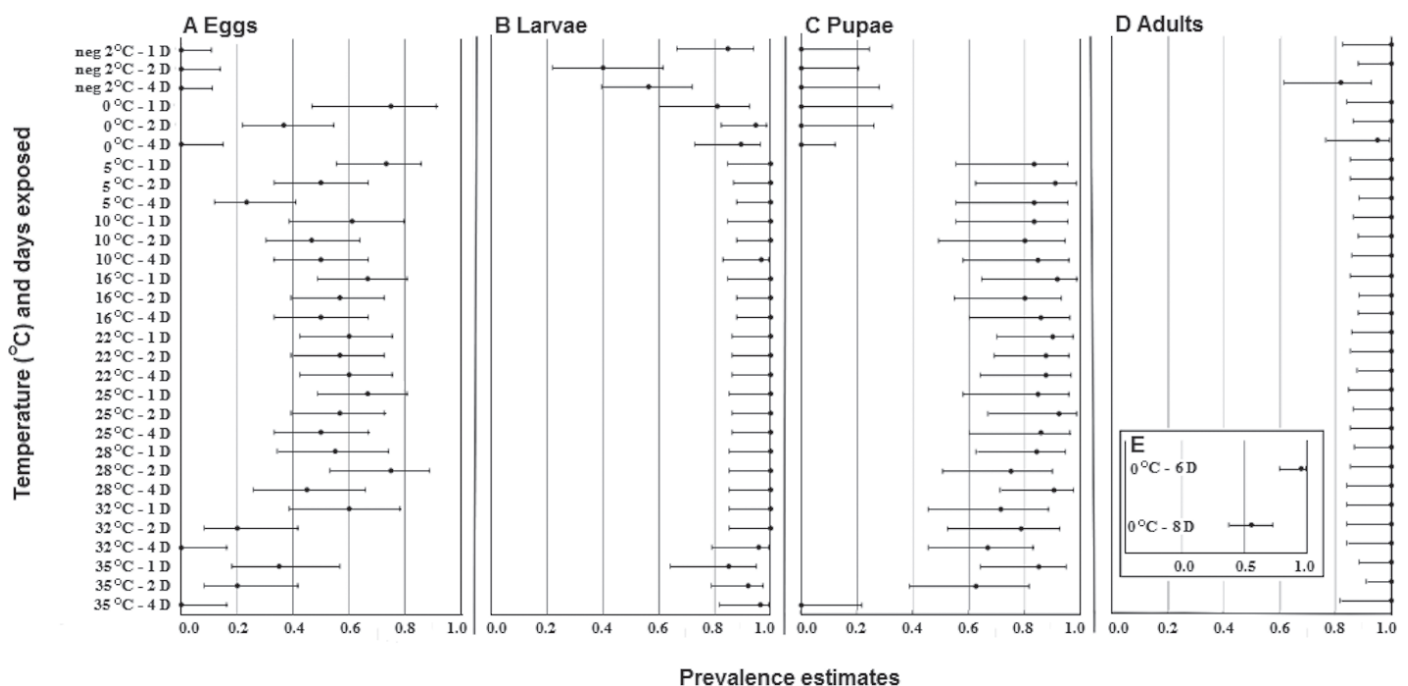


Fig. 1. Proportion and 95% confidence intervals of A) eggs, B) larvae, C) pupae, and D) adults surviving after exposure to 1 of 7 temperatures for 1, 2, or 4 d, and E) adult survival rate after exposure to 0 °C for 6 and 8 d. Confidence intervals were calculated using Wilson score intervals ($\alpha = 0.05$; Wilson 1927). For each life stage, the average number and range of replicates per the temperatures and days to which they were exposed were: eggs, average 25, range 12 to 32; larvae, average 25, range 20 to 37; pupae, average 15, range 10 to 28; adults, average 23, range 17 to 38.

Table 1. Average development time ± SE for *Metamasius callizona* at 9 temperatures. Measurements were made from egg collection to pupation and from pupation to adult emergence. Means within rows with the same letter are statistically similar (ANOVA and Tukey's method of multiple comparisons, α = 0.05).

Temperature:	15 °C	18 °C	20 °C	22 °C	25 °C	28 °C	30 °C	33 °C	35 °C
Days from egg to pupa:	— ^a	107.33 ± 8.66 a n = 15	71.15 ± 6.77 b n = 27	51.62 ± 4.23 c n = 13	43.39 ± 3.51 d n = 28	43.89 ± 6.27 d n = 36	45.34 ± 5.17 d n = 32	No pupation	No egg hatch
Days from pupa to adult:		26.57 ± 1.13 a n = 7	17.56 ± 1.44 b n = 23	15.71 ± 1.11 c n = 7	11.09 ± 1.15 d n = 22	9.29 ± 1.61 e n = 28	8.65 ± 1.37 e n = 29		

^aNo development past 2nd instar.

ADULT SURVIVAL CURVES AT THREE TEMPERATURES

All survival curves were significantly different (df = 2, P < 0.001; Fig. 4). For adults at 35 °C, the first 3 deaths occurred on day 12 and the final death occurred on day 24, resulting in a survival curve with a sharp decline. The LT50 (median lethal time) at 35 °C was between 18 and 19 d. The survival curves for 16 and 25 °C are similar in shape, with a slightly lower survival rate for 25 °C. At 40 d, the LT50 was not reached for either 16 or 25 °C.

Discussion

In central Florida, the average winter temperature is 16 °C (SERCC 1989; FAWN 1997), which is below the weevil's optimal range (25–30 °C; Table 1; Fig. 3) but above the weevil's lower threshold (13 °C). Therefore, at temperatures near the winter average, weevil growth and oviposition might slow but not likely halt. The average minimum temperature (9 °C) is below the weevil's lower threshold (13 °C) but

above temperatures that cause mortality (Table 1; Fig. 1). Therefore, growth and oviposition would be halted as the average minimum temperature is reached, but with the return of warmer temperatures, the weevils would revive and growth and oviposition would resume. Central Florida has on average 3 to 5 d at or below 0 °C (SERCC 1989; FAWN 1997), so there is potential for weevil mortality during these events, particularly for the eggs and pupae (Fig. 1). But these events are rare and of short duration, usually lasting for a few hours during the night and warming up during the day (SERCC 1989; Chen & Gerber 1990; FAWN 1997), often to temperatures within the weevil's operational and optimal ranges because central Florida's average maximum winter temperature is 21 °C and high temperatures can reach up to 32 °C (SERCC 1989; FAWN 1997).

In southern Florida, the mean overall winter (21 °C), mean minimum (18 °C), and mean maximum (24 °C) temperatures (SERCC 1989; FAWN 1997) are within the weevil's developmental range, with the maximum near the optimal range. Events ≤ 0 °C are rarer in southern Florida (0.1–1.4 d/yr) than in central Florida and of shorter duration. The mild conditions of a typical winter in southern Florida might slow or even halt weevil growth and oviposition for short, intermittent periods, but would likely not cause significant reduction of weevil populations. Warm winter temperatures in central and southern Florida would allow the weevil to be active year-round, and this is consistent with field observations (Frank 1996; Cooper 2008).

Southern Florida might experience temperatures as low as -5 °C during abnormally cold winters, but these conditions persist less than a day. Central Florida, on the other hand, may experience nighttime temperatures as low as -10 °C that may occur on consecutive nights for a week (SERCC 1989; Chen & Gerber 1990; FAWN 1997). The winter of 2009–2010 in Florida was one of the coldest winters on record

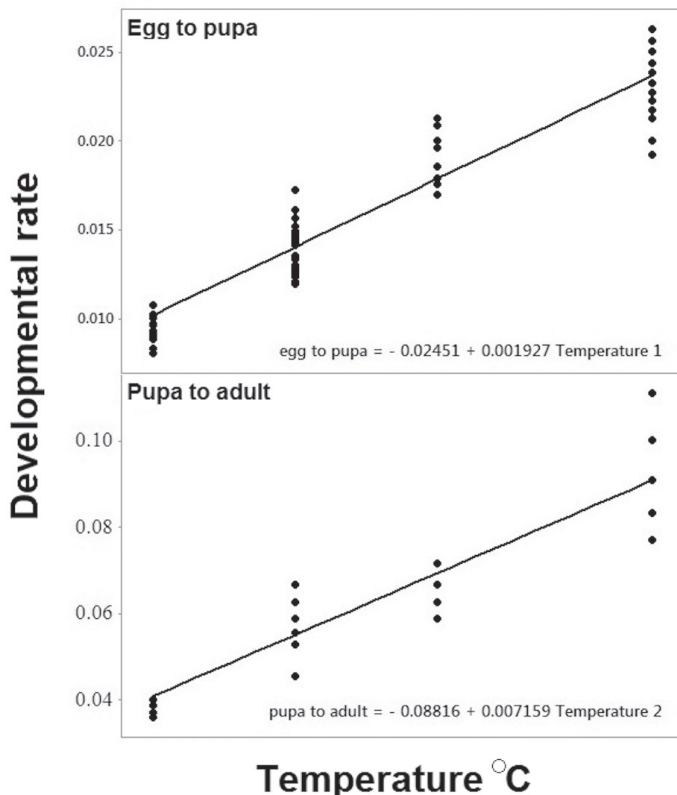


Fig. 2. Development rate of *Metamasius callizona* from A) egg collection to pupation and from B) pupation to adult emergence at 4 temperatures in the weevil's operational range.

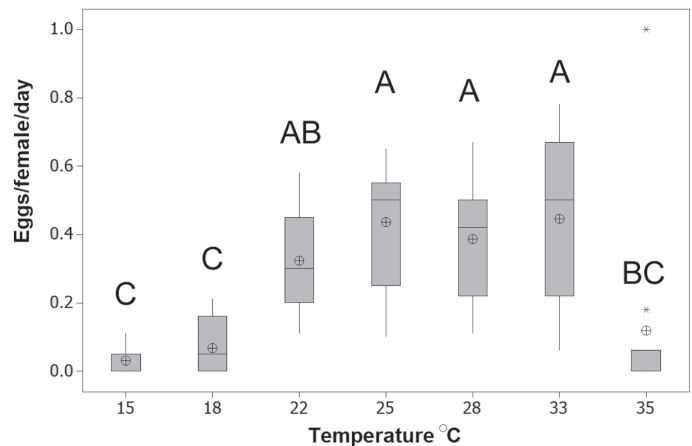


Fig. 3. Oviposition rate of *Metamasius callizona* at 7 temperatures. Results with the same letter are statistically similar; determined using analysis of variance and Tukey's method of multiple comparisons; α = 0.05; data collected daily from 10 females ovipositing for 14 d.

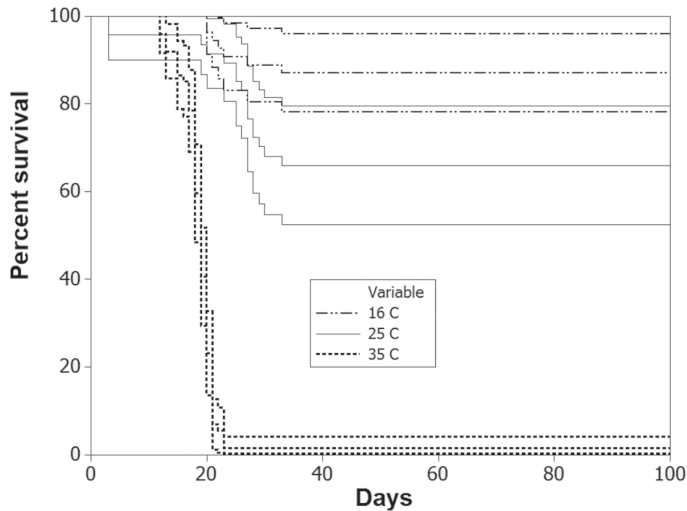


Fig. 4. Survival curves with 95% confidence intervals for *Metamasius callizona* adults at 3 temperatures. Numbers of individuals at time zero were: 16 °C, $n = 54$; 25 °C, $n = 47$; and 35 °C, $n = 74$.

(NOAA 2010), and it is possible that weevil populations suffered high mortality that year, particularly in central Florida where temperatures were colder and more persistent. As eggs and pupae are the stages most susceptible to cold temperatures, they may have suffered high mortality during the winter of 2009–2010, but some portion of the adults and larvae, which survived at all temperatures and time exposures tested, will survive the coldest Florida winters. Field observations since 2010 have not indicated any reduction in damage caused to bromeliad populations by the weevil, even in the most northern part of the bromeliads' range.

Central Florida has lower average and minimum temperatures than southern Florida (SERCC 1989; Chen & Gerber 1990; FAWN 1997). Also, for any given year, central Florida suffers more and longer freezing and sub-freezing events, as well as temperatures below the weevil's optimal and operational ranges, than southern Florida. For these reasons, cold temperature effects on the weevil may be more pronounced in central Florida. However, the differences are not likely enough to cause lower rates of destruction to bromeliad populations in central Florida compared with populations in southern Florida. Bromeliad populations in central Florida have been destroyed by the weevil as rapidly and as thoroughly as in southern Florida (Frank & Thomas 1994; Frank 1996; Frank & Cave 2005; Cooper 2006; Cooper et al. 2014), with the exception of host bromeliads growing in Miami-Dade County, where large, healthy bromeliad populations can still be found. The weevil was observed in Miami-Dade County before Hurricane Andrew in 1992, but has not since been seen in that area (Frank 1996). Because summer temperatures in Miami-Dade County are similar to other areas in central and southern Florida where the weevil is able to thrive, it is unlikely that high summer temperatures keep the weevil out of the Miami-Dade area, especially along coastal habitats that are cooled by ocean breezes (Chen & Gerber 1990).

Summer temperatures in central and southern Florida are less variable than winter temperatures (Chen & Gerber 1990), and therefore the effect of summer temperatures on weevil populations should be similar across central and southern Florida (except, perhaps, along the eastern coast, which is cooled by ocean breezes). During Jun to Aug,

temperatures average 30 to 35 °C during the daytime and can reach 40 °C (SERCC 1989; FAWN 1997). Such high temperatures, especially if persisting for several days, could interrupt biological activity due to heat stupor and cause increased mortality in weevil populations (Figs. 1–3). However, because summer temperatures are usually above 35 °C for short durations during afternoon hours, with subsequent cooling in the evening and nighttime hours (average summer low temperatures range from 23 to 25 °C; SERCC 1989; FAWN 1997), the weevils are subjected to adverse high temperatures for only short periods. When tested for heat tolerance, the weevil adults and larvae had high survival rates at ≤ 35 °C for all time exposures, whereas eggs and pupae suffered 100% mortality at 35 °C for 4 d (Fig. 1). This indicates that although eggs and pupae might die due to summer heat, adults and larvae will survive short-term exposure to high temperatures.

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