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ARTICLE

Winter Biology of *Aedes albifasciatus* (Diptera: Culicidae) from Córdoba, Argentina

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ABSTRACT Host-seeking females of *Aedes albifasciatus* (Macquart) were collected from April to September 1997, kept under seminatural conditions, and offered sugar solution and blood. Daily survival of females ranged from 0.91 to 0.96, with blood fed females living longer than sugar fed females. Overall, 43% of engorged females completed a gonotrophic cycle, and 15% of them refed and completed a second gonotrophic cycle. The life expectancy of females emerging at the end of summer was longer than those that emerged during winter. Immature developmental time and the developmental threshold were estimated by regression. Embryo development was recorded during autumn, winter, and spring, with a duration of 5–9 d. The developmental threshold for eggs was estimated to be 2.28°C. Egg mortality varied from 0.51 to 0.74. The development time for larva and pupa was between 16 and 29 d and was significantly correlated with temperature. The developmental threshold for larvae and pupae was estimated to be 4.75°C. A greater proportion of females than males emerged when temperatures averaged ≤18°C. Larval and pupal mortality was high at temperatures below the developmental threshold. *Aedes albifasciatus* females remained gonotrophically active and immature development continued during winter in Córdoba (10°C isotherm).

KEY WORDS *Aedes albifasciatus*, winter biology, female survival, gonotrophic cycles, basic population parameters

THE FLOOD-WATER MOSQUITO *Aedes albifasciatus* (Macquart) is distributed widely in Argentina (Prosen et al. 1960, Forattini 1965, Brewer et al. 1991), where it is an important pest of humans and livestock. Dairy production is affected in the NE of Córdoba Province (southern coast of March Chiquita Lake) where *Ae. albifasciatus* is the most abundant species (Raña et al. 1971; Ludueña Almeida and Gorla 1995a, 1995b). *Aedes albifasciatus* is a principal vector of western equine encephalomyelitis virus (Avilés et al. 1992, Sabattini et al. 1998) and probably of other arboviruses in Argentina (Bianchini et al. 1968, Sabattini et al. 1985, Mitchell et al. 1987).

Survival and peaks of host-seeking activity of *Ae. albifasciatus* females during the warm season in Córdoba Province as well as immature development time and mortality rates were reported previously (Ludueña Almeida and Gorla 1995a, 1995b); however, little is known of the winter biology of this species. Larvae and females were collected throughout the year in Córdoba Province, with peaks of abundance during summer and early autumn (Almirón and Brewer 1994, 1995; Ludueña Almeida and Gorla 1995a, 1995b; Gleiser and Gorla 1997; Gleiser et al. 1997, 1999; Almirón et al. 2000). The discovery of *Ae. albifasciatus* larvae and pupae in the field during the autumn–winter period in Córdoba Province indicated that immature development continues through these seasons (Almirón and Brewer 1994). Based on the examination of the primary and secondary follicles of *Ae. albifasciatus* females collected during the cold, dry period, Almirón et al. (2000) suggested that females remained gonotrophically active during winter; i.e., an overwintering strategy of considerable epidemiological importance for arbovirus persistence at this latitude. The overall objective of the current research in Córdoba Province was to confirm and extend our earlier findings that females remain gonotrophically active during the autumn–winter period. In addition, female survival and immature developmental time and mortality rates were estimated to understand the winter population dynamics of this species.

Materials and Methods

Sampling. During the autumn–winter period of 1997, females were collected at La Para town (30° 91′ S, 63° W) on the southwestern coast of Mar Chiquita Lake (NE of Córdoba Province) in central Argentina. Sampling methodology and features of the study area were described by Almirón et al. (2000). Biweekly females landing on two collectors were captured with mechanical aspirators during three 20-min periods. The abundance of adult females was expressed as the daily relative density (DRD) or the estimated number of females that would be captured during 24 h, taking into account the daily pattern of female flight activity (Ludueña Almeida and Gorla 1995b).

Survival of Field Females. The daily rate of survival (*Sd*) was estimated as $Sd = (N_{(i+t)}/N_i)^{1/t}$, where *Ni* is

the DRD in an *ith* sample, and *t* is the time between samples (Andis and Meek 1985, Focks et al. 1988). From these data, previously arcsine transformed, the mean rate of daily survival was calculated. Estimates of Sd only were possible for five successive sampling periods with decreases in the DRD; i.e., no increases due to emergence or immigration. Gleiser and Gorla (1997) found a negative relationship between *Ae. albifasciatus* abundance at the southern edge of Mar Chiquita Lake and distance from larval habitats, and we therefore assumed that losses due to emigration were minimal in our calculations.

Survival and Gonotrophic Cycles of Captive Females. Mosquitoes captured at La Para town were taken to Córdoba city (31° 5′ S, 64° 2′ W) and kept under seminatural conditions at a farm. Climatologically, Córdoba city and La Para town belong to the same mesothermal region, and semidry flat land biome (Capitanelli 1979). A cubicle 1.5 m on a side was constructed of wire mesh and positioned between *Morus nigra* L. trees, inside of which mosquito cages (30 by 30 by 30 cm) were placed. All captured females were fed 10% sugar solution from a cotton wick in a 70-ml flask that was changed twice per week and after that blood meals offered three times per week. A restrained hamster was placed into each cage during 2 h in the morning or in the afternoon. If no females took blood, a human hand was introduced into the cage for a subsequent 10-min period. Females that did not ingest blood were kept with sugar solution and their survival compared with those that ingested sugar solution and blood. For each cohort, approximately equal numbers of females were maintained under each feeding treatment. Living and dead individuals were enumerated every 48 h.

Engorged females were removed from the cohort cages and maintained individually in 70-ml plastic flasks containing moist cotton covered with filter paper on the bottom as oviposition substrate. Each flask was covered with netting and a piece of cotton soaked with sugar solution. Blood ingestion and oviposition dates, and the number of eggs deposited by each female were recorded. Because Ludueña Almeida and Gorla (1995a) reported that *Ae. albifasciatus* females laid eggs a 8 ± 4 d after blood feeding (spring and summer temperature), females in the current study were given 10–14 d for oviposition, after which they were offered a second blood meal by placing a human finger on the netting that covered the flask.

Egg Developmental Time and Mortality. To estimate development time, 23 egg batches (mean 49.6 eggs/batch) were kept under seminatural conditions and 5–10 eggs from each batch were checked daily by bleaching to observe embryonation. An embryo was scored as viable and mature if the hatching spine was darkly sclerotized, and the eyes were developed and pigmented (Trpis 1970). Egg batches were grouped by mean temperature during embryonic development. Development time in degree days was estimated by regressing the development rate (1/development time) as a function of mean temperature (Begon et al. 1990, Clements 1992, Mogi 1992). The developmental threshold temperature was estimated from the intersect of the regression function at the x-axis. Temperature data were obtained from the National Service of Meteorology of Córdoba Province.

Table 1. Values of daily relative density (DRD) used to estimate the survival of *Aedes albifasciatus* females

Sampling date	DRD
14 April	1,568
30 April	885
8 May	530
22 May	160
9 June	55
—	
29 July	510
14 August	369

—, The DRD increased after precipitation.

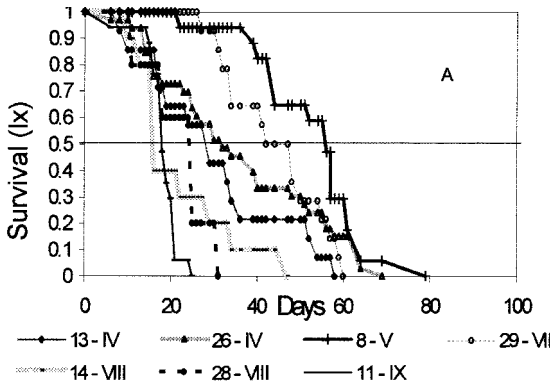
To estimate the mortality of eggs during autumn, winter and spring, 59 batches of eggs (more than seven batches per sample) were obtained from females. Mortality was expressed as the number of collapsed eggs over the initial number oviposited. Eggs were flooded three times, with two interceding dry periods of 16 and 49 d, respectively. Percentages were transformed by arcsine and compared by one-factor (sampling date) analysis of variance (ANOVA); results were back-transformed and reported as percentages. Significant differences were detected by the Tukey test (Sokal and Rohlf 1979, Steel and Torrie 1987).

Larval and Pupal Development Time and Mortality. The time and development threshold for larva and pupa were estimated from horizontal life tables for cohorts of 25–30 larvae kept under seminatural conditions. Cohorts obtained between July and November were pooled by temperature into the following three groups: (1) 28 cohorts between 14 July and 2 August; (2) seven cohorts between 27 and 30 August, and (3) 17 cohorts between 29 October and 7 November. Each cohort was kept in a 500-ml flask containing 300 ml of dechlorinated tap water. The number of living and dead individuals in each instar was recorded every 48 h, and the larvae fed powder liver (10 mg per cohort). Larvae in first and second instars were pooled because it was difficult to distinguish between them in the field. Pupae from each cohort were transferred to netting-covered flasks, and the number of emerging males and females recorded.

Larval and pupal mortality was calculated as the number of individuals dying within an age-class divided by the number at the beginning of that age-class. Mortality for the same stage or instar was compared among groups by ANOVA. Temperature relationships for 35 cohorts that completed development were calculated as described above for eggs.

Results

Survival of Adult Females. DRD values used to estimate survival are summarized in Table 1. Estimated survival rates ranged between 0.91 and 0.96, with a mean of 0.95 and a mean daily loss rate of 0.04.



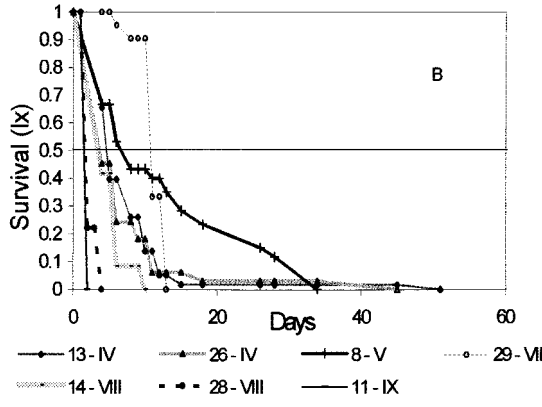


Fig. 1. Survival of *Aedes albifasciatus* females by sampling date. (A) Females that ingested both sugar solution and blood ($n = 352$). (B) Females that ingested only sugar solution ($n = 467$).

Population losses included death and to a lesser extent emigration and removal sampling.

Survival and Gonotrophic Cycles of Captive Females. A total of 819 females was collected, of which 467 took only sugar solution and 352 took both sugar solution and blood. The longest average survival among females that ingested blood was 56 d for those captured on 8 May and the shortest was 16 d for females collected on 14 August (Fig. 1). Blood engorged females remained alive longer than those only fed sugar-water. Among the latter, the longest average survival was 11 d for females captured on 11 July and the shortest was 2 d for those captured on 11 September.

Of the 352 females that fed on blood (Table 2), 15% refed, with >10 d between blood ingestion and oviposition (maximum = 53 d in the first ingestion). The percentage of females that laid eggs and the average number of eggs per female was greater after the first than after the second blood meal. Greatest fecundity was recorded for females captured in the first half of April, decreasing gradually until June (Fig. 2). A noticeable increase in fecundity was seen in July, with a peak among females captured in the second half of July that was maintained until the first half of August. Fecundity subsequently decreased among females captured during the following months.

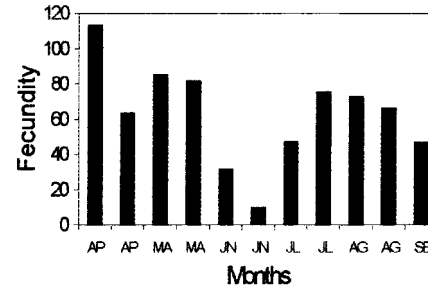


Fig. 2. Mean fecundity (eggs per female) of captive *Aedes albifasciatus* kept under seminatural conditions during the autumn–winter period of 1997.

Egg Developmental Time and Mortality. Egg development time (t) was 9.07 ± 2.25 d at 12.05 ± 1.18°C and 5.48 ± 1.41 d at 18.49 ± 0.84°C. The correlation between the development time and temperature was significant ($r = 0.95$, df = 17, $P < 0.05$; $n = 19$). The regression between the rate of development ($1/t$) and average temperature in °C (T) yielded the following equation: $1/t = 0.012\ T - 0.0274$ ($R^2 = 0.44$, df = 20, $P < 0.01$), with development threshold estimated as 2.28°C (95% CI = −1.53°C; 8.55°C; Fig. 3).

Lowest mortality (57%) was recorded for eggs from females captured in the first half of April, increasing slowly (59 and 63%) during the following months to a maximum in July (74%) and then decreasing noticeably for females collected in September (66%). Mortality rates did not vary significantly among batches throughout the sample period ($F = 0.3$; df = 4, 54; $P > 0.05$).

Larval and Pupal Development Time and Mortality. The developmental time of larval instars 1+2 and 3 and pupae decreased as temperature increased (Table 3). This reduction differed significantly ($F = 8.7$; df = 2, 32; $P < 0.05$) between instars 1+2 of groups I and II; the latter showed no significant differences with the time of development of the same instars of group III. A similar trend was observed for third instars, with significant differences ($F = 6.6$; df = 2, 32;

Table 2. Ingestion of blood and oviposition by *Aedes albifasciatus* females ($n = 352$) kept in captivity under seminatural conditions during the autumn-winter period of 1997

Blood ingestion	Engorged females	Time between ingestion of blood and oviposition, days	Females that laid eggs, %	Mean number of eggs/batch
First	151	17.87 ± 10.20	60	62.65 ± 38.62
Second	22	14.58 ± 8.26	54	42.42 ± 50.96

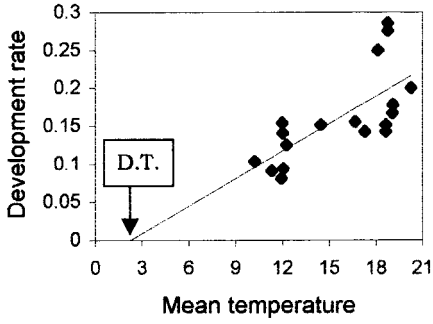


Fig. 3. Developmental threshold (DT) estimated by regression for *Aedes albifasciatus* egg development rate as a function of mean temperature.

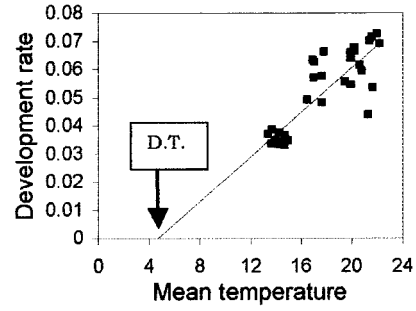


Fig. 4. Developmental threshold (DT) estimated by regression for *Aedes albifasciatus* larval and pupal development rates as a function of mean temperature.

$P < 0.05$) between groups I and III. Fourth instars showed no significant differences among groups ($F = 1.9$; df = 2, 32; $P > 0.05$) (Table 3). Pupal developmental times differed significantly ($F = 68.6$; df = 2, 32; $P < 0.05$) among groups. Total immature development time (larval plus pupal stages) of groups II and III showed no significant differences, but these groups were different from group I ($F = 128.9$; df = 2, 32; $P < 0.05$).

The correlation between the larval and pupal developmental time and temperature was significant ($r = -0.86$, df = 33, $P < 0.01$). Developmental rate increased significantly as a function of mean temperature: $1/t = 0.004\,T - 0.0187$ ($R^2 = 0.72$, df = 33, $P < 0.05$). Development threshold was calculated to be 4.71°C (95% CI = 0.76°C; 8.67°C) (Fig. 4). The mean developmental time was estimated to be 244 degree-days (standard error = 44; coefficient of variation = 0.18).

Mortality in instars 1+2 and pupa decreased as the temperature increased (Table 4). Mortality of instars 1+2 of groups II and III was significantly different ($F = 18.7$; df = 2, 49; $P < 0.05$) from group I. Mortality in third and fourth instars did not show a definite trend in relation to changes in temperature. Nonetheless, mortality in third instars showed significant differences ($F = 3.5$; df = 2, 48; $P < 0.05$) between groups I and II, whereas in fourth instars no significant differences were seen ($F = 2.5$; df = 2, 44; $P > 0.05$) among groups (Table 4). In the pupal stage, mortality was significantly different ($F = 4.04$; df = 2, 35; $P < 0.05$) between groups I and III.

Comparing the sex ratio within and between groups, the proportion of males emerging from groups I (29%) ($F = 8.2$; df = 1, 22; $P < 0.05$) and II (32%) ($F = 11.6$; df = 1, 12; $P < 0.05$) was significantly lower than females. This did not occur in group III, in which the differences between the proportion of sexes emerging (43% of males) was not significant ($F = 2.8$; df = 1, 30; $P > 0.05$). Above 18°C, males and females emerged in the same proportion. The proportion of males increased from group I to III, matching the increases in the temperature, but these differences were not significant ($F = 1.4$; df = 2, 32; $P > 0.05$).

Discussion

Ludueña Almeida (1994) reported that the density of adults of *Ae. albifasciatus* decreased by an average rate of 0.15 per day, without specifying if this estimate varied throughout the year. In the current study, car-

Table 3. Mean development time of *Aedes albifasciatus* larva and pupa under semi-natural conditions (winter and spring of 1997)

Stage/instar	Group	Temp, °C	Mean temp, °C	Time in days
1 + 2	I	14.33–17.74	16.03	6.70 ± 3.53a
	II	16.68–24.58	20.63	2.22 ± 1.03b
	III	16.45–19.69	18.07	4.60 ± 1.22ab
3	I	12.60–18.70	15.65	5.19 ± 3.71a
	II	16.67–18.22	17.44	4.15 ± 1.46ab
	III	20.88–22.48	21.68	2.06 ± 0.59b
4	I	12.41–14.82	13.61	8.08 ± 4.21
	II	16.22–16.84	16.53	5.61 ± 1.73
	III	21.78–22.33	22.05	6.20 ± 2.34
Pupa	I	12.59–14.67	13.63	8.75 ± 1.12a
	II	15.55–16.74	16.15	5.56 ± 1.82b
	III	20.84–21.46	21.15	3.63 ± 0.75c
Larva + pupa	I	13.84–14.46	14.15	28.73 ± 1.51a
	II	16.82–17.60	17.21	17.55 ± 2.20b
	III	19.83–20.96	20.39	16.49 ± 2.38b

Comparisons were between groups for each stage/instar. Means followed by no letter or the same letter were not significantly different ($P > 0.05$).

Table 4. Relative mortality of *Aedes albifasciatus* larva and pupa under seminatural conditions (winter and spring of 1997)

Stage/instar	Group	Temp, °C	Mean temp, °C	Relative mortality
1 + 2	I	15.67–18.26	16.97	0.56 ± 0.29a
	II	17.19–23.18	20.19	0.17 ± 0.15b
	III	16.50–20.02	18.26	0.13 ± 0.14b
3	I	12.08–15.05	13.56	0.52 ± 0.30a
	II	15.77–20.82	18.30	0.21 ± 0.15b
	III	21.47–21.95	21.71	0.40 ± 0.22ab
4	I	12.19–14.25	13.22	0.67 ± 0.30
	II	16.42–16.85	16.64	0.41 ± 0.14
	III	21.72–22.67	22.20	0.56 ± 0.23
Pupa	I	12.65–14.62	13.64	0.38 ± 0.39a
	II	15.57–16.78	16.17	0.19 ± 0.21ab
	III	20.62–21.44	21.03	0.09 ± 0.16b

Comparisons were between groups for each stage/instar. Means followed by no letter or the same letter were not significantly different ($P > 0.05$).

ried out during autumn and winter seasons, the average rate at which abundance decreased was much lower.

The survival of female *Psorophora columbiae* (Dyar & Knab) was affected strongly by taking blood (Horsfall 1955, Nayar and Sauerman 1977). O'Meara (1987) pointed out that in mosquitoes, excess nutrients from feeding on blood that was not used for the production of eggs may increase reserves of glycogen and fat. Our results indicated that females that fed on sugar-water and blood had a greater life span than females that fed only on sugar. The ingestion of blood in some way enhanced the survival of the females during the autumn–winter period.

Survival of captive females fed on blood did not show an expected pattern, bearing in mind the date of capture. Survival was lower for females captured on 13 April than on 26 April and on 8 May. According to our results, females that emerged at the end of summer survived longer than those that emerged during winter.

Female *Ae. albifasciatus* continued taking blood meals even during the autumn–winter period, as indicated by the degree of development of the primary follicles in host-seeking individuals (Almirón et al. 2000). This supposition was confirmed in the current study, because females that blood fed frequently laid eggs. The time between the intake of blood and the beginning of oviposition was >10 d, maximum of 53 d, a period markedly longer than the 3 d observed by Ludueña Almeida (1994) for females captured in Córdoba mostly during spring, summer, and fall.

The greater fecundity recorded for females captured in April could be due to their spending a relatively prolonged period of life in captivity. During May and June, when there was no emergence of adults, field-collected females possibly had completed some gonotrophic cycle(s), which could explain the reduction in their fecundity recorded during those months. The increase in fecundity observed for females captured in July and the first half of August most likely corresponded to the incorporation of young females after the rains recorded in June and July. In August and September, fecundity decreased again, even for recently emerged females, possibly because of their short survival.

Winter temperatures of Córdoba were not sufficiently low to preclude embryogenesis. *Aedes albifasciatus* required 4 d to complete embryogenesis at 20–22°C (Ludueña Almeida 1994), a period that extended to 9 d when the temperature decreased to ≈12°C.

Winter temperatures (average maximum and minimum of 15 and 6.3°C, respectively) and variation in the water level at larval habitats did not allow the hatching of *Ae. albifasciatus* eggs in the subtropical forest of Buenos Aires Province (Maciá et al. 1995). In temperate Córdoba Province, larvae of mixed ages were collected during the autumn–winter period of 1997 (April, June, August, September), indicating that eggs hatched even during the cold season (Almirón et al. 2000). During the current study in Córdoba, *Ae. albifasciatus* eggs hatched when the minimum temperatures were as low as −0.5°C, and therefore temperature did not appear to maintain egg diapause.

In the current study, there was a significant inverse relationship between development time and temperature for larval instars 1+2, 3, and pupa, but not larval instar 4. Although in group I, developmental time for instars 1+2, 3, and pupa was practically similar to that of the fourth instar because they were exposed to temperatures below the development threshold temperature. Development was slowed, so that this species could develop during the autumn–winter up to the latitude of Córdoba city, where the average normal temperatures in July and August (10.4 and 12°C, respectively) were higher than the estimated threshold and the average minimum temperature (3.5 and 4.7°C, respectively) are near the threshold.

Physiological developmental time in degree-days (DD) reported for other aedine species in forest and tundra pools ranged from 220 DD for *Ae. hexodontus* Dyar to 440 DD for *Ae. excrucians* (Walker) (Clements 1992). As expected, the estimated thermal constant for *Ae. albifasciatus* in temperate Córdoba Province was closer to that of *Ae. hexodontus.*

Ludueña Almeida (1994) found that *Ae. albifasciatus* sex ratio was 1:1, without specifying if this varied throughout the year. In the current study, the pro-

portion of females was greatest when temperatures averaged <18°C. We have no explanation to support these results. In general the warmer the temperature, the lower the mortality figures recorded both for larvae and pupae during the current study. Elevated mortality for larvae and pupae in group I may be due to their being exposed to absolute minimum temperatures below the estimated development threshold temperature, although other factors also may have been significant. According to our current and previous results, peaks of abundance of *Ae. albifasciatus* females occurred during summer and fall in Córdoba Province. Females remained active throughout the year and did not diapause. During the dry, cold seasons, abundance decreased considerably. Although females that emerged at the end of summer–beginning of autumn were able to survive for most of the autumn–winter period, they did not manage to reach the next warm and rainy seasons. Considering female abundance and longevity during the dry, cold seasons, they most likely would not be a mechanism for the overwintering virus. Egg diapause was the mechanism for *Ae. albifasciatus* overwintering, with rainfall being the factor that terminated diapause. Immature development continued during the autumn–winter period in Córdoba Province, and based on the estimated development threshold temperature may continue in other provinces south of Córdoba.

Acknowledgments

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