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Effects of Meteorological Variation on Mortality in Populations of the Spittlebug *Deois flavopicta* (Homoptera: Cercopidae)

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ABSTRACT We found that variation in temperature and humidity significantly affected mortality rates and population dynamics of the spittlebug *Deois flavopicta* Stål by monitoring cohorts of diapausing eggs and nymphs for three generations. Cohorts of quiescent eggs, when exposed to increasing periods of high moisture (free water), produced higher proportions of eggs resuming embryonic development in laboratory experiments. The accumulated number of eggs resuming development as a function of days of exposure to moist conditions was modeled using a β distribution. Periods of drought and high temperatures after the beginning of postdiapause development increased embryonic and nymphal mortality. Mortality was modeled with a linear function, and in combination with the development model allowed the simulation of varying mortality rates in the newly emerged nymphal population. Comparisons with field data demonstrated a close fit to the observed and expected proportion of nymphs hatching daily. By accurately simulating natural mortality, hatching distribution and population dynamics, the model promises to be useful for managing the spittlebug in the field.

KEY WORDS *Deois flavopicta*, population dynamics, survivorship, seasonality, climatic factors

THE SPITTLEBUG *Deois flavopicta* Stål is the main pest of cultivated grass pastures in tropical central Brazil (Botelho and Reis 1980, Cosenza and Naves 1980). The insect's life history strategy includes survival over the dry season (May–August) as diapausing eggs, and risk distribution (bet-hedging) in which females vary both the proportion of diapausing eggs and the duration of the dormancy in its progeny (Fontes et al. 1995). Other characteristics such as oviposition in protected places (e.g., soil and pasture straw), spittle that protects nymphs against desiccation and natural enemies, along with the capacity to colonize several species of grass (mainly *Brachiaria*), allow for frequent outbreaks of this insect.

In central Brazil, *D. flavopicta* generally has three non-overlapping generations per year throughout the rainy season (September–April). After the dry season, postdiapause eggs remain quiescent waiting for favorable conditions to hatch (Pires et al. 2000a). The occurrence of high densities of *D. flavopicta* has been related to various factors such as precipitation, temperature, and evapotranspiration (Reis et al. 1980, Ribeiro et al. 1980, Milanez et al. 1981, Melo et al. 1984, Sujii et al. 1995, Pires et al. 2000a). Although many studies show how patterns of climatic variation can influence insect population abundance in the tropics (e.g., Wolda 1988, Medeiros and Vasconcellos-Neto 1994, Pires et al. 2000a), there is a lack of data to explain how variations in weather that occur during the transition between dry and rainy seasons affect mortality rates and population dynamics of spittlebug in pastures habitats. The occurrence of sparse and irregular rainfalls, alternating with periods of elevated evapotranspiration, produce a prominent water deficit that appears to control the annual abundance of *D. flavopicta* (Pires et al. 2000a). It is possible that sudden weather variation after the beginning of the rainy season may play an important role in the survivorship of first-generation nymphs and thus the size of subsequent population peaks.

In this work we evaluated mortality rates during three distinct stages of spittlebug development: diapausing eggs during the dry season; postdiapause eggs prior the establishment of first instars on the plant; and nymphs until the emergence of teneral adults. Our goal was to understand how mortality rates vary during *D. flavopicta*s life cycle and how variation in weather conditions affects the insect's annual abundance.

Materials and Methods

Dry Season and the Viability of Diapausing Eggs. During the months of April and May in 1990 and 1991 (end of the third population peak), *D. flavopicta* adults

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were captured weekly from pastures of *Brachiaria decumbens* Stapf, located ≈40 km north of Brasilia, DF (15° 35′ S, 47° 42′ W; 1,000 m of altitude). Approximately 150 pairs were placed in each of 12 cages randomly distributed over the same pasture from which they were captured. Cages consisted of cylindrical iron frames (0.80 m high by 0.30 m diameter) covered with a white nylon screen. The cages did not have bottoms and were placed directly over the pasture to allow access to grass for feeding and to soil for oviposition. After the death of the insects (≈14 d), the cages were removed and their location marked with wooden stakes for future identification and egg sampling throughout the dry season.

At the beginning of each month, from June to September, the soil under three cages was collected to a depth of 2 cm. Eggs were recovered using soil filtration, flotation in a saturated solution of NaCl (400 WV) and a supernatant wash with distilled water (Sujii 1994). All recovered eggs, even those with alterations in color or form, suggesting that they were dead, were included in the sample. Empty chorions were excluded. Cohorts of 50 eggs were placed in a 10-cm-diameter petri dish containing a layer of cotton covered with moist filter paper. Petri dishes, five replicates in 1990 and four replicates in 1991, were kept in environmental chambers at 28 ± 1°C and a photoperiod of 12:12 (L:D) h until the emergence of nymphs. Egg hatching was monitored every other day until the emergence or death of all eggs in each replicate. Eggs that did not hatch and became flat and black were considered dead for the mortality evaluation. Monthly mortality rates within a given year were compared using analysis of variance (ANOVA) and Tukey test, after arcsine transformation.

Moisture and Postdiapause Embryonic Development. The proportion of postdiapause eggs that starts final embryonic development was tested in the laboratory by varying the periods of an initial high moisture condition (direct exposure to free water). This experiment simulated the occurrence of low precipitation (<30 mm) followed by periods of drought longer than 7 d at the beginning of the rainy season, so that the soil is moist for only a few days. Diapausing eggs, obtained from adults collected in the field in April and May, were maintained in Petri dishes at ambient conditions (≈20 ± 6°C and a photoperiod of 12:12 [L:D] h) in the laboratory from May to August (Sujii et al. 1995). At the beginning of September, when the eggs naturally enter the postdiapause or quiescence without any token stimuli (Pires et al. 2000a), 15 randomly selected eggs were placed on filter paper and then in Petri dishes lined on the bottom with absorbent cotton. Four replicates of these eggs, forming each treatment, were then exposed to moisture (direct exposure to free water) for 6 and 12 h and 1, 2, 4, 6, 8, and 15 d at 28 ± 1°C and a photoperiod of 12:12 (L:D) h (condition 1) in an environmental chamber. Moisture was provided by adding water ad libitum to the cotton underneath the filter paper. For the treatments longer than 2 d, this layer was moistened every other day to ensure continuous contact between water and eggs.

After exposure to varying periods of moisture, eggs were transferred to Petri dishes lined with dry filter paper and kept without moisture (25–50% RH), at 28°C (condition 2) for a 14-d period to kill any embryos that had resumed development. Preliminary studies showed that 100% of nondiapausing eggs died when exposed to this drought treatment (see also Pires et al. 2000b). Following this dry period, eggs were again transferred to moist conditions (condition 3), as described above for condition 1, until hatching of quiescent eggs or death of all individuals. Nymphs that emerged under condition 1 were considered representative of the group that started final embryonic development and then died under condition 2, and did not emerge under condition 3. Nymphs trapped inside eggs after 60 d were considered dead. With this procedure, it was possible to distinguish the proportion of eggs that resumed final embryonic development in response to different periods of exposure to moisture (condition 1) from those that were naturally infertile.

To estimate the average proportion of natural infertility in the population and the time of exposure to moist conditions required for postdiapause eggs to resume embryonic development, a group of four Petri dishes with 15 eggs each was kept under moist conditions until hatching or death of all eggs. The time of exposure to moist conditions required for each egg to resume final embryonic development was calculated by subtracting the average time of 12 d, equivalent to the thermal constant of 168 degree-days at 28°C (Sujii et al. 1995), from hatching time of each egg in the experiment. The last egg hatching in this group allowed the estimation of the time necessary under moist conditions to induce all eggs of a population to start final embryonic development.

Egg hatching was monitored every other day throughout the experiment. For each period of moisture exposure, hatching time and egg mortality rates were calculated. Because egg mortality was due to either low moisture (lack of contact with free water) or infertility, the average rate of infertility in the control (11.7%) was subtracted from the total mortality rate in each treatment to give an estimate of moisture-related mortality or the corresponding proportion of embryos that resumed postdiapause development.

To model the proportion of eggs resuming embryonic development as a function of moisture exposure time, a graph of the accumulated proportion of embryos that resumed development was constructed. An empirical function that approximated a bounded β distribution (Stinner et al. 1975) was used to model the daily proportion P of eggs resuming development as a function of time (t) under moist conditions:

$$P(t) = (1 - Z)^{hZ^k} \qquad 0 \leq Z \leq 1 \qquad [1]$$

where $Z = (B\text{-}t)\ (B\text{-}A)^{-1}$, A is the day in which the first embryo resumed development, B the day in which the last embryo resumed development, and t is a given time between A and B. The parameter k was given a value of 2, which has been used to describe the cumulative emergence of several insect species (Stinner et al. 1975). The value of h was estimated from comparisons of model predictions (equation 1) with the frequency distribution observed in the experiment. Modeled and observed curves of hatching proportion were compared using the Kolmogorov-Smirnov test (Wilkinson 1990).

The average time for egg hatching was calculated by subtracting the time spent in conditions 1+2 in each treatment. Comparing the means among the treatments, using the Kruskal-Wallis ANOVA, we tested if initial exposure to moisture (condition 1) could be initiating embryonic development in some eggs that then wait for condition 3 to resume embryonic development. If so, these eggs would hatch early reducing the average time in some treatments.

Mortality of Postdiapause Eggs and Newly Emerged Nymphs. Eggs recovered from soil samples brought from the field (as above) were incubated in Petri dishes lined with a layer of cotton covered with moist filter paper, and kept in incubators at 28 ± 1°C and a photoperiod of 12:12 (L:D) h until the eggs reached the final stage of embryonic development, following the description of Koller et al. (1987). Groups of 20 eggs with fully developed embryos were chosen randomly and placed at the base of potted plants of *B. ruziziensis* in a greenhouse. These pots had been watered to saturation 24 h before the experiment. After initial watering, pots were kept without water for periods of 4, 8, 12, and 16 d (treatments). Pots were then watered daily using overhead sprinklers. Each treatment had eight replications. A control set of eight pots was kept under daily irrigation throughout the experiment. The plants were observed three times weekly, and examined for the presence of first instars. Newly emerged first instars of spittlebug move directly to the nearest suitable plant and establish themselves at the base of stems and exposed roots, where they immediately start feeding and producing spittle (Pires et al. 2000c). First instars usually feed gregariously in the same spittle, and all nymphs that died were removed with a small paintbrush. Observations stopped when all surviving nymphs reached the second instar. The relationship between period of water deficit and mortality of eggs and newly emerged nymphs was described by linear regressions.

Mortality Acting on Nymphs in the Field. Cohorts with variable numbers (7–108) of *D. flavopicta* first instars in a *Brachiaria* pasture were observed beginning when first instars established on grass stems until the emergence of teneral adults. Each cohort was protected from predators by cages consisting of a wooden frame (0.5 m long by 0.5 m wide by 0.7 m high) covered with a nylon organdy screen (mesh 0.25 mm). The base of the cage was buried 10 cm deep to impede the entrance of soil insects from beneath. Ten cohorts were observed during the three annual generations of 1995/1996, and five were observed during the second generation of 1996/1997.

To determine the movement and survivorship of each individual during the nymphal stage, the position of each nymph within cages was marked with a small numbered wooden stake. Records about the position and development stage of nymphs were made every 1–3 d following Sujii (1998). Proportional mortalities for each instar were compared among the different generations to evaluate the effects of seasonal weather variation. Nymphal density in each cage was recorded and correlated with mortality estimates. Weather data were obtained from a weather station installed ≈5 km N of the field.

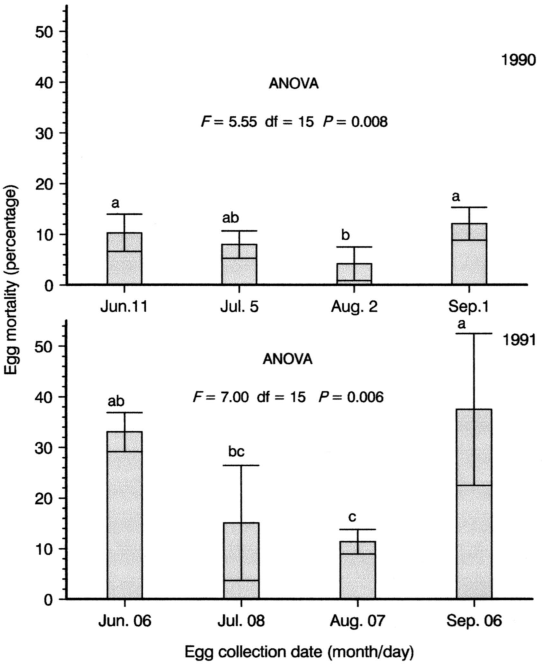

Fig. 1. Mean ± SE percent mortality of diapausing eggs of *D. flavopicta* collected in different months of the dry season from the field and incubated in the laboratory at 28°C under moist conditions. Same letters above the bars within a year indicate nonsignificant difference among the means (Tukey test $P = 0.05$).

Results

Dry Season and the Viability of Diapausing Eggs. Monthly mortality of diapausing eggs collected during the dry season (June–September) over 2 yr varied from 4.2 to 37.5%, and presented a general pattern of decreasing mortality from June to August followed by an increase in September (Fig. 1). Mortality rates in July–August in the two different years did not differ significantly (ANOVA, $F = 2.85$, df = 17, $P > 0.05$), revealing that the average rate of mortality of 9.7 ± 2.69% can be attributed to direct and indirect effects of the dry (monthly precipitation < 15 mm) and warm (average temperature 21°C) conditions during this time of year.

Moisture and Postdiapause Embryonic Development. The proportion of postdiapause eggs starting final embryonic development increased as a consequence of exposure to increasing periods of moisture

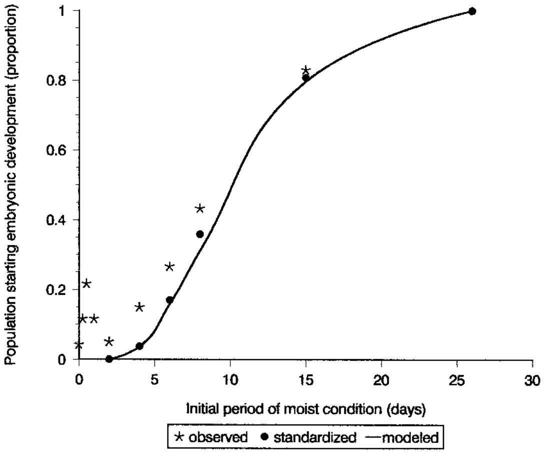

Fig. 2. Postdiapause eggs of the spittlebug resuming embryonic development after exposure to moist conditions for different periods. Natural infertility of eggs (0.117) was subtracted from the observed data to standardize them. Curve is a β distribution; parameters $h = 1.13$ and $k = 2$ (see text for details). Simulated and standardized data were not significantly different (Kolmogorov-Smirnov test, $D = 0.167$, $P > 0.999$, $N = 6$).

in condition 1 (Fig. 2). The proportion of these that died from the hydric stress of condition 2 was detected under condition 3. The group of eggs kept continuously in moist conditions revealed a natural infertility rate (mean ± SD) of 11.7 ± 8.53%. This rate of natural infertility was subtracted from all moisture-exposed treatments to better estimate the proportion of eggs starting final embryonic development (Fig. 2). The last hatching, in this group of eggs continuously exposed to moisture, occurred after 38 d. Thus, postdiapause eggs need 26 d of moisture to ensure initiation of embryonic development in all individuals of a population.

The β distribution described the accumulated proportion of eggs resuming embryonic development as a function of time of exposure to moist conditions. The first postdiapause eggs resuming embryonic development, parameter A (equation 1), were observed after 4 d of exposure to moist conditions, and the last diapausing egg resuming embryonic development, parameter B (equation 1), was observed after 26 d. The value $h = 1.13$ provided the best fit between observed and simulated values (Fig. 2). The average time for egg hatch in all treatments (Fig. 3) did not differ significantly ($H = 11.24$, df = 7, $P = 0.13$), supporting the assumption that all hatched eggs began the final embryonic development simultaneously during condition 3.

Mortality of Postdiapause Eggs and Newly Emerged Nymphs. Increasing exposure to low moisture progressively raised mortality rates of newly emerged nymphs and embryos (Fig. 4). Linear regression analysis showed that there is a positive relationship between days of hydric stress (*HS*) and both the average proportional mortality (*PM*) of eggs in the final stage of development and newly emerged nymphs ($PM = 0.534 + 0.029\ HS$; $r^2 = 0.89$, $F = 25.12$, $P = 0.015$, $N = 5$). This result suggests that even in the absence of hydric stress ($HS = 0$), only half of postdiapause eggs become established as nymphs on the potted plants. Plants under field conditions may provide better or worse conditions for nymphs survivorship because at microclimate or root size, and additional tests in the field are warranted.

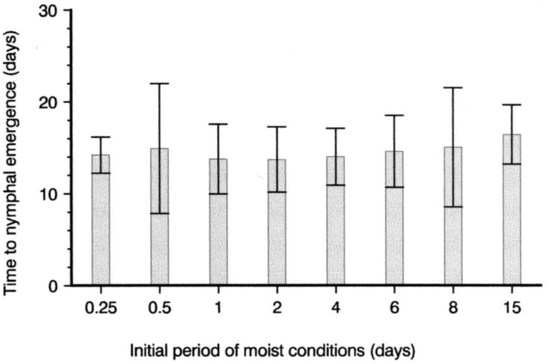

Fig. 3. Time taken for eggs of *D. flavopicta* to hatch (mean ± SD) after 0.25, 0.5, 1, 2, 4, 6, 8, and 16 d of exposure to moist conditions (treatments 1–8, condition 1) followed for a period of 14 d of drought (condition 2), and a return to moist conditions until egg hatch (condition 3). Bars represent only the time spent in condition 3.

Convolving the β distribution of embryonic development with the proportion of egg mortality, obtained from the above equation, generated a curve of total mortality expected for each combination of moisture exposure time followed by a period of low moisture (Fig. 5). An absence of hydric stress (<4 d without rain) maximizes nymphal survivorship. At the other

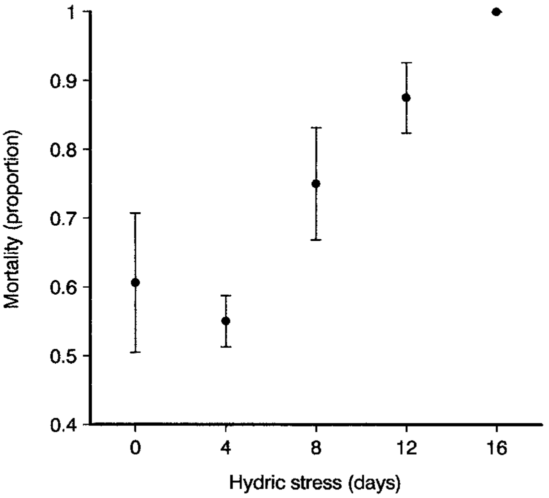

Fig. 4. Mortality (mean ± SE, $N = 8$) of eggs in final stage of embryonic development and of newly emerged nymphs of *D. flavopicta* exposed for different periods of drought (ANOVA, $F = 10.39$, df = 39, $P < 0.001$).

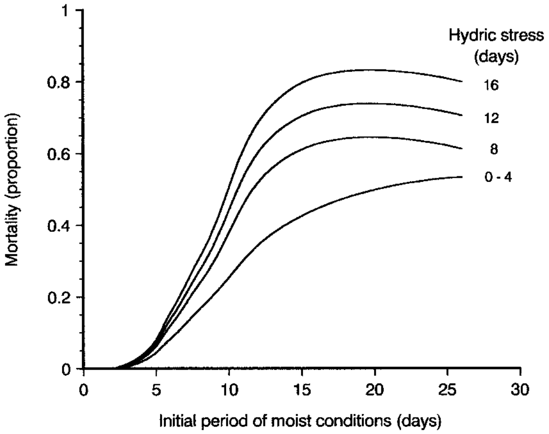

Fig. 5. Predicted mortality of eggs in final stage of embryonic development and of newly emerged nymphs of *D. flavopicta,* after a combination of an initial period of moist conditions followed by hydric stress, simulating lack of rain.

extreme, 16 d of drought after initial intense and frequent rain (keeping the soil moist for 14 d) maximize mortality in local populations of *D. flavopicta.*

Nymph Mortality After Establishment on the Host Plant. Mortality of nymphs in abscense of predators and parasites, in 1995/1996 and 1996/1997 was low and did not differ significantly across generations (Table 1). Differences in mortality between nymphal stages were not detected (Kruskal-Wallis, $H = 15.710$, df = 11, $P = 0.152$; Fig. 6), and there was no correlation between the insect density inside the cages and the resultant mortalities (Pearson, $r = 0.20$, $P = 0.29$, $N = 30$; Fig. 7).

The number of nymphs that moved from the initial plant was positively correlated with the number of first instars within the same spittle mass (Pearson, $r = 0.899$, $P = 0.006$, $N = 21$). In 80% of observations, first instars that were aggregated in the same spittle mass (2–12 nymphs/spittle) moved out to new isolated spittle, where they became teneral adults.

Discussion

Diapausing *D. flavopicta* eggs are well adapted to resist drought. The low mortality rates of eggs observed during the middle of the dry season (July and August) indicate that lack of moisture and warm soil do not preclude outbreaks of *D. flavopicta* populations. Although mortality rates varied from 4.2 to 37.5% through the dry season (Fig. 1), higher mortality early in the dry season (June) was probably due to the

Table 1. Nymphal mortality in cohorts of *D. flavopicta* nymphs during 1995/1996 and 1996/1997 in pastures of *B. ruziziensis* located in Federal District, Brazil

Population generation	Mortality of caged nymphs mean ± SD (*N*)
1st/1995/1996	0.134 ± 0.156 (10)
2nd/1995/1996	0.308 ± 0.152 (10)
3rd/1995/1996	0.157 ± 0.252 (09)
2nd/1996/1997	0.138 ± 0.105 (05)

ANOVA $F = 1.897$, df = 33, $P = 0.15$; Data arcsine transformed for analysis.

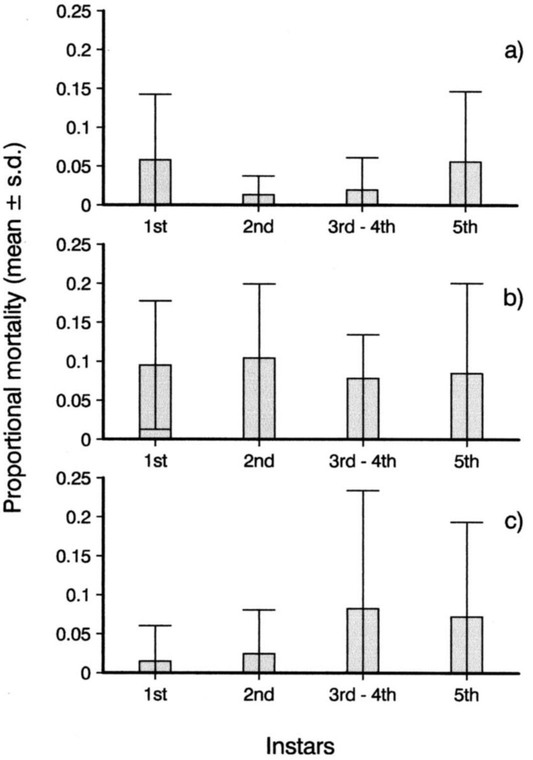

Fig. 6. Proportional mortality of the spittlebug, *D. flavopicta,* in *B. ruziziensis* pastures in 1995/1996. There is no difference in the mortality among instars of the same generation. (a) first generation (Kruskal-Wallis, $H = 1.489$, df = 3, $P = 0.685$), (b) second generation (Kruskal-Wallis, $H = 0.542$, df = 3, $P = 0.910$), and (c) third generation (Kruskal-Wallis, $H = 1.356$, df = 3, $P = 0.716$).

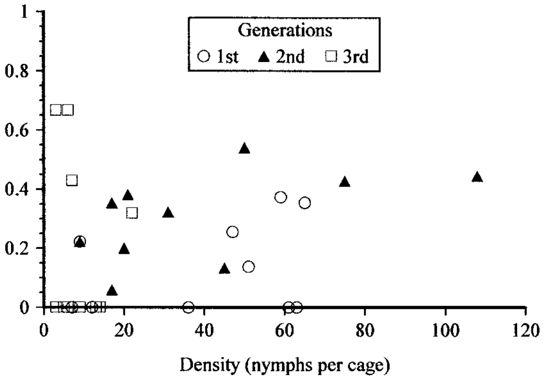

Fig. 7. Relationship between nymphal density and the mortality observed in the same cage during the immature phase of the spittlebug *D. flavopicta* in *B. ruziziensis* pastures in 1995/1996.

presence of nondiapausing eggs laid by third generation females in April/May, as observed by Sujii et al. (1995) and Fontes et al. (1995). Such eggs die when faced with drought conditions, but they were still found in the June–July soil samples. By July, these eggs had decomposed and the chorions were excluded from the samples. The termination of diapause at the beginning of the rainy season, when the frequency of rain is unpredictable, probably caused the increase of egg mortality in September. The mortality rate of around 9.7%, observed in the middry season (July–August), is probably the best estimate of diapausing egg mortality caused by the adverse conditions of the dry season. Although Hewitt (1986) observed that only 8.5% of spittlebug eggs survived the dry season in the state of Mato Grosso, Brazil, 73% of the mortality was attributed to predation. A number of studies have confirmed the low response of diapausing eggs to environmental factors during the dry season in June and July (Sujii et al. 1995, Pires et al. 2000a), and the impact of precipitation and humidity at the beginning of the rainy season on postdormancy population size (Oomen 1975, Melo et al. 1984, Sujii et al. 1995, Pires et al. 2000a).

The interplay among diapause and rainfall distribution at the beginning of the rainy season results in a variable pattern of population dynamics from year to year. In the current study, we propose a model that explains how different combinations of precipitation and drought periods at the beginning of the rainy season can influence the mortality of eggs in the final embryonic stage and of newly emerged nymphs. Based on our results we hypothesize that after the beginning of the rainy season, continued rain for >14 d promotes embryonic development of a high proportion of postdiapause eggs, and synchronizes nymphal occurrence in the field. In contrast, sparse rainfall keeps postdiapause eggs quiescent, and hatching occurs asynchronously over a long period of weeks in accordance with the distribution of precipitation. Other species of spittlebugs, *Aeneolamia occidentalis* (Walker) and *Prosapia simulans* (Walker), show the same pattern of occurrence in Mexico (Oomen 1975), suggesting that this mechanism of risk distribution related to rain frequency may be common for this subgroup of the family Cercopidae. Newly emerged nymphs desiccate quickly and die if they do not find a host plant, or if a drought period with high temperature occurs at this nymphal stage (Pires et al. 2000c). Eggs in the final stage of embryonic development are also susceptible to desiccation. Our experiments and field observations indicate that in years when the rains start in late August or September and are frequent (periods of interruption no longer than 4 d), survival of postdiapause eggs and newly emerged nymphs is maximized, and the chances of population outbreaks are increased (Fig. 5). However, the occurrence of sparse and less frequent rainfall (6–16 d of dampened soil followed by more than 16 d of drought), following the second half of August, drastically increases mortality and reduces the chances of economically important population densities developing (see also Pires et al. 2000a).

Our results show that climatic factors, such as drought stress and high temperature, had little influence on the mortality of diapausing eggs and nymphs of *D. flavopicta* established on plants. We observed only a constant and low rate of mortality in different years. This could explain why several authors (Milanez et al. 1981, Melo et al. 1984) were unsuccessful in relating climatic factors such as temperature, soil humidity, and precipitation to the population dynamics of spittlebugs and its outbreaks. Although further field studies are necessary, quantifying mortality rates of postdiapause eggs and newly emerged nymphs, before their establishment on plants, can serve as the basis for understanding *D. flavopicta* outbreaks and developing new management approaches.

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