Variable Population Growth of *Varroa destructor* (Mesostigmata: Varroidae) in Colonies of Honey Bees (Hymenoptera: Apidae) During a 10-Year Period

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ABSTRACT We measured significant variation in the instantaneous growth rates for varroa mites, *Varroa destructor* (Anderson & Trueman) from 1993 to 2002 in Baton Rouge, LA. Mite population growth was monitored in colonies of honey bees, *Apis mellifera* L., with queens from miscellaneous U.S. sources that had not been selectively bred for varroa resistance. Mite populations were measured at the beginning and end of short field tests that started in the late spring of each year. Analyses of multiple regression showed that only the first two of the following regressors were linear predictors of *r*, the instantaneous growth rate: 1) percentage of reproducing female mites, 2) proportion of total mites in capped brood, 3) mortality of mites in brood cells, 4) growth of the bee population, 5) capped brood area at the end of a test, and 6) duration of the test. Analysis of commonality indicated that the percentage of reproducing female mites explained ≈26% of the total variation in *r*, and the proportion of total mites in capped brood explained 6%. The joint expression of both variables accounted for another 4%. Thus, residual error reflected most of the total variation in *r*, which suggested possible climatic or environmental effects on mite growth. The lowest growth rates occurred in three consecutive years of drought in Louisiana. Measures of ambient temperature and relative humidity correlated to growth of mite populations among different years. Reduced growth rates were probably the result of diminished reproductive rates by varroa mites during periods of hot and dry weather.

KEY WORDS varroa mites, growth rate, exponential growth, honey bees

Varroa destructor (ANDERSON and Trueman) is an ectoparasitic mite of the Asian hive bee, *Apis cerana* F., and the honey bee, *Apis mellifera* L. The adult females feed on the hemolymph of immature and adult bees, whereas nymphs and adult males feed only on immature bees. *V. destructor* does not significantly harm colonies of *A. cerana*, but this mite normally kills colonies of *A. mellifera.*

Varroa destructor has a reproductive cycle of ≈19 d in *A. mellifera*, if only worker brood is available for invasion. Female mites enter worker brood cells to reproduce ≈1 d before cell capping. This reproductive period lasts 12.5 d and coincides with the capped period during which a worker bee completes metamorphic development from the last larval stage through the pupal stage to the adult stage. A typical female varroa mite produces one male and three to four female progeny in a worker brood cell, and usually the male and one or two females reach maturity by the end of the capped period (Martin 1994, Ifantidis et al. 1999). Adult male and immature female mites die soon after the host bee emerges from its brood cell. Only adult females survive outside the brood cell, and they average ≈7 d of phoresy on adult bees before repeating the reproductive cycle (Otten 1991, Fries et al. 1994). A typical mite attempts two to three reproductive cycles during her life (Martin and Kemp 1997).

Growth of varroa mite populations is exponential during short periods and when mite populations are relatively low (Fries et al. 1994, Calatayud and Verdu 1995, Kraus and Page 1995, Marcangeli et al. 1995, Harbo 1996, Harbo and Harris 1999a). Logistic growth equations more adequately describe changes in varroa populations over longer periods when density-dependent factors influence population growth (Sumpter and Broomhead 2001). Generations of female mites overlap, and although reproduction by mites may be age-dependent (de Ruijter 1987), a stable age distribution of mites probably becomes established in colonies when brood production by bees is maintained at a high level.

The instantaneous growth rate for varroa mites can be determined by monitoring the exponential growth of mite populations through time (Kraus and Page 1995, Branco et al. 1999). The instantaneous growth rate (r) is defined as the net per capita change in mite population, or as the difference between the per capita birth rate (b) and the per capita death rate (d) (Dublin and Lotka 1925). The birth rate for varroa mites is determined by various aspects of reproduction. These include the proportion of total mites at-

tempting to reproduce per unit time, the percentage of reproductive mites per unit time (fertility), the number of offspring produced per reproductive female mite per unit time (fecundity) and the total number of reproductive attempts per mite during her life (Fries et al. 1994). The overall death rate of adult female mites is the result of mortality of mites during reproduction in capped brood cells and during phoresy on adult bees (Fries et al. 1994). Mortality of mites in brood cells can be estimated by examining foundress mites in brood, but the mortality of mites during phoresy is difficult to measure directly (Fries et al. 1994, Fries and Perez-Escala 2001).

Many factors affect growth of mite populations. High temperature (Le Conte et al. 1990, Kraus et al. 1998) and extremes in relative humidity (Kraus and Velthuis 1997) reduce reproduction by varroa mites. Genetics of the host bee (Harbo and Harris 1999b, Rinderer et al. 2001) and genetics of the infesting mite (de Guzman et al. 1999, Anderson and Trueman 2000) also influence the growth rate. Several of these factors may simultaneously affect growth of mite populations. For example, mite populations in colonies of Africanized and European honey bees (De Jong and Soares 1997) grow much slower in Brazil than in the United States. The lower growth has been attributed to the tropical climate (Ritter and De Jong 1984, Ritter 1988), resistance traits in the Africanized bees (Camazine 1986, Moretto et al. 1993, Guzman-Novoa et al. 1996, Corrêa-Marques and De Jong 1998, Medina and Martin 1999, Vandame et al. 2000), and genetically less pernicious mites (Anderson 1994, 2000; Anderson and Fuchs 1998, Anderson and Trueman 2000, Vandame et al. 2000).

The usual consequence of varroa infestation of *A. mellifera* in Europe and the United States is death of a colony of bees within 1–2 yr of initial infestation. The severe effects of varroa mites on the honey bee probably reflect the relative newness of this host–parasite relationship, and adaptive processes that will likely moderate the interaction have begun only relatively recently (Oldroyd 1999, Fries and Camazine 2001). However, there have been reports of changing dynamics between varroa mites and host bees. For example, infestations of varroa mites in colonies of Africanized honey bees significantly decreased in Brazil from 1986 to 1993 (Moretto et al. 1995). In addition, the frequency of swarms from feral colonies of bees decreased during the first 2–7 yr after varroa mites were introduced into southern Italy, but the frequency began to increase within 10–12 yr of the this first exposure to varroa mites (Monaco 1997). Presumably, the increased swarming frequency reflects a change in compatibility between the parasite and host.

The purpose of this study was to document changes in the rate of growth of varroa mite populations in our area (south Louisiana.). One goal was to see whether some of the variables related to populations of varroa mites and honey bees that we had measured could be correlated to changes in the growth rate through time. Additionally, we looked at the relationship between climatic data and the variation in growth rates of mite populations.

Materials and Methods

As part of a selective honey bee breeding program, we monitored populations of varroa mites in nonresistant colonies of bees during short field trials. Starting with small mite populations and allowing growth for only short periods kept mite populations low and minimized density-dependent effects on reproduction of mites. Although varroa mites prefer drone cells to worker cells (Fuchs 1990), we simplified the growth model by using only combs with worker-sized cells.

Colonies of Bees. Uniform colonies of bees were established in each apiary in late spring (April–June) of each year of this study (1993–2002). The methods used to make colonies have been described previously (Harbo 1996; Harbo and Hoopingarner 1997; Harbo and Harris 1999a, b). The process began by collecting 30 kg of mite-infested bees into a large cage and then subdividing the bees to form ≈1-kg test colonies that were given a test queen and four to five empty brood combs at the start. The mite-infested bees were taken from source colonies with queen bees that were not selectively bred for varroa resistance. Between 11 and 29 colonies of bees were monitored each year.

Growth Rate. The instantaneous growth rate for a population of mites was calculated from the exponential growth equation $P_2 = P_1 e^{rn}$ (Branco et al. 1999). Variables include the final mite population (P_2) after n number of weeks, the initial mite population (P_1), and the growth rate (r) for time expressed in units of weeks (week^{-1}), and e is the base of the natural logarithm. This model assumes overlap of generations of female mites and that the average reproductive and mortality rates per female are not age-dependent. Requirement of age independence can be relaxed if a stable-age distribution of mites exists in the population. Colonies within apiaries were arranged to minimize drifting of bees, and the chance for movement of mites between colonies through drift or robbing was assumed equally likely for all colonies. A study by Neumann et al. (2000) indicated that low drift of workers (5%) and high drift of drones (50%) between 30 colonies in a test apiary did not significantly affect populations of varroa mites within colonies.

Initial Mite Population. The initial mite populations (P_1) for colonies in an experiment were estimated from four to five samples, each with ≈150 g bees, taken from the large cage of mite-infested bees as it was being subdivided. The bees in each sample were weighed before the mites were washed through a sieve to count the number of mites (mites per kilogram of bees). The initial mite load for colonies was found by multiplying the average adult bee infestation for all samples by the average weight of bees (kilograms) in all colonies at the start of the test. This method assigned the average mite load as P_1 for all colonies in an apiary. This procedure does not measure variation for P_1 in a group of colonies. Any such variation would be included in experimental error. We have estimated

the standard deviations for P_1 to be no greater than ± 25% of the mean.

Final Mite Population and Proportion of Mites in Capped Brood. The final adult mite population (P_2) was found in each colony at the end of 9–19 wk by summing the total mites on adult bees with the total number of foundress female mites living in capped brood cells. First, the total weight of bees (kilograms) in each colony was determined by weighing hives with and without bees. The infestation rate of mites on adult bees (mites per kilogram of bees) was determined for each colony by washing a weighed sample of ≈150 g bees taken after all bees were shaken from the combs into an empty box. Total mites on adult bees were calculated from total bee weight, the number of mites in the sample, and sample weight.

Total capped worker brood area (square centimeters) was measured by using a 2.54 by 2.54-cm wire grid, and brood area was converted to total numbers of capped worker cells (brood area × 3.7 worker cells per square centimeter). The infestation rate of foundress mites in capped worker brood cells was obtained by opening 200 capped worker cells from two brood combs. The total number of foundress mites in brood was found by multiplying the total number of capped cells by the infestation rate. The proportion of mites in capped brood was the ratio of total mites in capped brood divided by the total mites in the colony of bees.

Percentage Reproductive Mites. Fertility of varroa mites was measured as the percentage of reproductive mites at the end of each experiment (9–19 wk) in all years except 2001. This measurement was made once and may not reflect the fertility of mites throughout the entire experimental period. Usually, 75–92% of all foundress mites are reproductive when bees are actively rearing brood (Martin et al. 1997). Mite fertility may remain constant over periods of 2 mo or more during the summer in Louisiana (Harris and Harbo 1999). The percentage of reproductive mites may decrease from 85 to 92% in late spring to summer to 60–70% during autumn in temperate (Otten and Fuchs 1990) and tropical climates (Eguaras et al. 1994) and to 34% during the winter in temperate climates (Martin 2001).

The percentage of reproductive mites was measured by examining 11–35 foundress mites from singly infested capped brood cells in each colony (3,521 total mites examined). Brood cells were examined using a dissecting microscope. Only foundress mites from brood cells that were 260–270 h postcapping were considered when determining the percentage of reproductive mites. A foundress mite was considered nonreproductive if she had produced 1) no progeny, 2) only a son, or 3) female progeny too late in the 12.5-d period to permit maturation of the oldest daughter.

Mortality of Mites in Brood Cells. Mortality of mites in brood cells was estimated by examining 14–58 foundress mites from singly infested brood cells in each colony (4,306 total mites examined). Only foundress mites from brood cells that were 260–270 h postcapping were used to estimate the percentage of dead foundress mites. This measurement is probably an underestimate, but the mortality of mites in capped brood cells is usually very low (Fries at al. 1994, Medina and Martin 1999). Mortality in capped brood was not measured in 1994, 2001, and 2002.

Statistical Analyses. Comparison of variables among years was made using a hierarchical analysis of variance (ANOVA). The mixed model included 1) year as a fixed effect, 2) apiary location within year [location (year)] as a random effect, 3) source of queen within location within year [source (location year)] as a random effect, and 4) the random error term (PROC MIXED; SAS Institute 2000). The factor year had 7–10 levels, depending on the variable analyzed. The location (year) factor accounted for variation related to 1–3 different apiaries within a single year. The source (location year) factor modeled variation attributed to 1–13 different queen sources within locations within year. Degrees of freedom were adjusted using the Kenward–Roger estimation. Mean comparisons among the different years were made using Tukey's mean separation test.

Multivariate linear regression was used to identify variables that significantly predicted the growth rate (r). The mixed model included year, location (year), source (location year), and the random error term as random factors. Six independent variables were used as predictors in the model. These variables were 1) percentage of reproductive mites, 2) proportion of total mites in capped brood, 3) mortality of mites in capped brood cells, 4) duration of a test in weeks, 5) percentage change in the adult bee population, and 6) capped brood area measured at the end of the experiment. Nonsignificant independent variables were removed by a backward stepwise regression analysis ($F\alpha_{withdraw} = 0.15$).

Multivariate regression analysis indicated that two variables (percentage of reproducing mites and the proportion of total mites in capped brood) significantly predicted the r. Analysis of commonality was used to partition the corrected total sum of squares for r into unique components for each regressor and a common component that accounted for variation uniquely related to the joint expression of the two-regressor combination (Kempthorne 1957, Emigh 1984). All regression models used in the analysis of commonality included the random terms associated with year, location (year), source (location year), and the random error term. The residual error term from the analysis of commonality was further partitioned into variance components related to each random term in the mixed model (PROC MIXED; SAS Institute 2000).

The effects of climate on r were examined using correlation analysis. The growth rates for experiments were averaged over each year and compared with similar annual means of variables related to temperature, relative humidity, and rainfall. Climate data were collected from a weather station located <8 km from our experimental sites (Louisiana Office of State Climatology, Baton Rouge, LA). Measurements of climate variables were restricted to periods that corre-

Table 1. Growth rates (mean ± SD) for populations of varroa mites from 15 different apiaries during a 10-yr period in Baton Rouge, LA

Year	Apiary	No. colonies	No. queen sources	Duration (wk)	Initial population, P_1	Final population, P_2	Instantaneous growth rate, r (wk^{-1})
1993	1	15	1	9.3	140	1,079 ± 367	0.214 ± 0.04
1994	1	24	1	10.9	87	491 ± 219	0.150 ± 0.05
1995	1	10	1	9.0	289	1,030 ± 486	0.131 ± 0.05
	2	12	1	10.0	289	757 ± 396	0.083 ± 0.05
1996	1	15	9	11.0	363	1,838 ± 830	0.139 ± 0.04
1997	1	22	13	13.0	193	1,419 ± 486	0.150 ± 0.02
1998	1	11	1	15.7	444	432 ± 225	−0.008 ± 0.03
1999	1	11	3	11	741	1,130 ± 402	0.033 ± 0.03
	2	6	4	10.6	862	1,124 ± 218	0.023 ± 0.02
2000	1	4	2	16.4	717	949 ± 321	0.015 ± 0.02
	2	7	4	16.4	487	666 ± 532	−0.003 ± 0.06
	3	6	3	16.4	732	1,394 ± 1124	0.024 ± 0.05
2001	1	22	2	16.0	111	349 ± 273	0.047 ± 0.06
2002	1	9	5	19.4	129	2,966 ± 822	0.159 ± 0.02
	2	20	2	15.1	221	871 ± 457	0.095 ± 0.06

sponded to each field test in a particular year. The climatic variables were the average daily maximum temperature, the percentage of days with ambient temperature ≥35.0°C, the average daily relative humidity (RH %), the percentage of days with relative humidity ≤70%, the average daily rainfall, and the percentage of days with no rainfall.

Results

The r for varroa mite populations varied significantly ($F = 8.88$; df = 9, 4.6; $P < 0.02$) among years (Table 1; Fig. 1). The growth rate was highest in 1993, which was the first year that varroa mites were found at our laboratory. Growth rates were lowest from 1998 to 2001. Of the other variables measured from colonies, only the mortality of foundress mites in capped brood varied significantly among different years ($F = 2.91$; df = 6, 15.6; $P < 0.05$) (Table 2). No significant differences among years were found for the percentage of reproducing mites ($F = 2.28$; df = 8, 3.6; $P > 0.2$), proportion of total mites in capped brood cells ($F = 1.74$; df = 8, 1; $P > 0.5$), percentage increase of the bee population ($F = 0.03$; df = 1, 143; $P > 0.8$), and final capped brood area ($F = 0.35$; df = 1, 146; $P > 0.5$) (Table 2).

Multiple regression analysis of r from individual colonies indicated that only the percentage of reproducing mites ($F = 20.49$; df = 1, 145; $P < 0.0001$) and the proportion of total mites within capped brood ($F = 15.54$; df = 1, 143; $P = 0.0001$) were significant linear predictors of the growth rate. The duration of the test ($F = 0.37$; df = 1, 5.8; $P > 0.5$), mortality of mites in capped brood ($F = 0.22$; df = 1, 110; $P > 0.6$), growth of the bee population ($F = 0.03$; df = 1, 143; $P > 0.8$), and final capped brood area ($F = 0.35$; df = 1, 146; $P > 0.5$) did not predict the growth of mite populations.

Analysis of commonality showed that ≈35% of the total variation in the growth rate (r) was explained by the percentage of reproducing mites (25.5%), the proportion of total mites within capped brood (6.1%), and the joint expression of both variables (3.6%). Thus, ≈65% of the total variation in r was related to residual error. This residual error was subdivided into variance components for each random term in the mixed model. Variation related to year contributed the high-

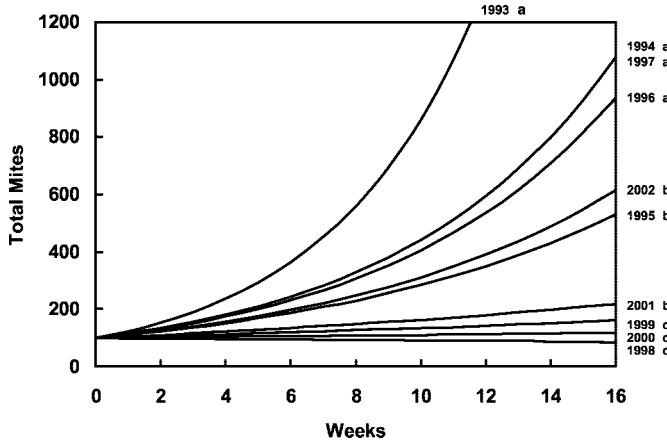

Fig. 1. Standardized growth curves for populations of varroa mites for each year of this study. Curves were generated from the mean growth rates for each year and by assuming an initial mite population $P_1 = 100$ mites at time = 0. Growth rates for years with the same letter are not significantly different as determined by the least significant difference (LSD).

Table 2. Variables related to populations of varroa mites and honey bees during a 10-yr period in Baton Rouge, LA

Year	Varroa mites[a]			Honey bees		
	Percentage reproductive	% in capped brood	Mortality in brood cells[b]	Initial population (kg)	Final population (kg)	Final capped brood area (cm^2)
1993	87 ± 7	60 ± 9	0.023 ± 0.02ab	1.02 ± 0.01	0.89 ± 0.12	539 ± 193
1994	84 ± 18	—	—	0.38 ± 0.03	1.21 ± 0.38	—
1995	74 ± 27	65 ± 11	0.035 ± 0.05ab	0.99 ± 0.01	2.00 ± 0.35	1,758 ± 506
1996	86 ± 9	64 ± 10	0.015 ± 0.02bc	0.92 ± 0.03	1.76 ± 0.46	2,061 ± 807
1997	70 ± 14	69 ± 13	0.012 ± 0.01bc	1.01 ± 0.01	1.47 ± 0.57	1,052 ± 515
1998	53 ± 14	69 ± 10	0.052 ± 0.02a	0.82 ± 0.01	1.03 ± 0.45	1,171 ± 434
1999	63 ± 18	70 ± 10	0.042 ± 0.05a	0.93 ± 0.01	0.93 ± 0.35	1,146 ± 562
2000	67 ± 13	74 ± 7	0.009 ± 0.01c	0.90 ± 0.09	3.44 ± 1.21	1,184 ± 425
2001	—	63 ± 14	—	0.85 ± 0.03	2.28 ± 0.83	1,803 ± 970
2002	68 ± 13	66 ± 10	—	1.07 ± 0.27	2.16 ± 0.60	2,115 ± 771

Data (mean ± SD) were averaged over apiaries within each year.
[a] Variables were measured at the end of each experimental period.
[b] Means with the same letter are not significantly different as determined by the least significant difference.

est percentage (44%) of the total variation in *r*, whereas location (year), source (location year), and the random error term explained smaller percentages (5.4, 0.0, and 15.0%, respectively). Because year accounted for a substantial amount of variation in *r*, it seemed reasonable to investigate weather parameters associated with years having slow growth of mite populations.

Variables related to climate and the growth rates were averaged for each year, and correlation analysis was performed to identify possible significant relationships. Generally, mean measurements of temperature and relative humidity were correlated to the mean growth rate. The growth rate for each year was inversely correlated to the percentage of days in an experiment in which the maximal temperature was ≥35.0°C (Fig. 2A) and, to a lesser extent, the average daily maximum temperature (Fig. 2B). Similarly, the mean growth rate for each year was inversely correlated to the percentage of days in which the average daily relative humidity was ≤70% (Fig. 2C) and to the average daily RH % (Fig. 2D). Neither the percentage of days with no rainfall (Fig. 2E) nor the average daily rainfall (Fig. 2F) correlated to the growth rate. Average annual rainfall had a range of 97–142 cm for 1998–2000 and 155–191 cm for the remaining 7 yr in this study.

Discussion

The major finding was that *r* for varroa mites varied significantly among years during a 10-yr period. The annual average *r* values for most years in this study ($r = 0.105–0.214\ wk^{-1}$) were similar to the values from other studies ($r = 0.108–0.236\ wk^{-1}$) (Thrybom and Fries 1991; Calatayud and Verdu 1993, 1995; Kraus and Page 1995; Marcangeli et al. 1995; Branco et al. 1999; Vandame et al. 2000; Lodesani et al. 2002). However, the three lowest values ($r = -0.008–0.047\ wk^{-1}$) were well below the lowest growth rates reported elsewhere, and they occurred during a period (1998–2000) of below normal rainfall in Louisiana. At least one other study has noted differences in growth of mite populations among years in the same location (Lodesani et al. 2002).

About one-fourth of the variation in growth rate between colonies among the different years was directly related to the percentage of reproducing mites. Hence, the effect of climate on *r* can be partially explained by the effects of temperature and relative humidity (RH %) on reproduction by varroa mites. In considering the effects of climatic factors on the growth of mite populations, we acknowledge that changes in ambient temperature and ambient RH % may not reflect changes within the broodnest of colonies of bees in our study. Without actually measuring temperature and RH % within the broodnest, we cannot be sure that either factor directly influenced the growth rates for varroa mites. However, our best hypothesis is consistent with the results of other studies in which temperature and relative humidity of the broodnest influenced reproduction by varroa mites.

The direct effects of temperature and RH % on reproduction by varroa mites are known from studies in which mites inside brood cells were maintained under controlled conditions (Le Conte et al. 1990, Bruce et al. 1997, Kraus and Velthuis 1997). The actions of temperature and RH % on reproduction and mortality of varroa mites probably relate to different rates of desiccation of mites under different environmental conditions (Bruce et al. 1997). Optimal reproduction by varroa mites occurs in the temperature range of 32.5–33.4°C (Le Conte et al. 1990, Kraus et al. 1998), which falls within the range of the typical broodnest temperature of 31.0–36.0°C (Levin and Collison 1990) reported for honey bee nests in various climates (Rosenkranz 1988). Reproductive rates are reduced at temperatures above 36.0°C (Le Conte et al. 1990, Kraus et al. 1998). Reproductive rates are also higher at 70 RH % than at 40 RH % (Le Conte et al. 1990), but mites stop reproducing when relative humidity in the broodnest exceeds 80 RH % (Kraus and Velthuis 1997). The normal RH % found in the honey bee broodnest in temperate climates is ≈40 RH %, and it rarely exceeds 70 RH % (Wohlgemuth 1957).

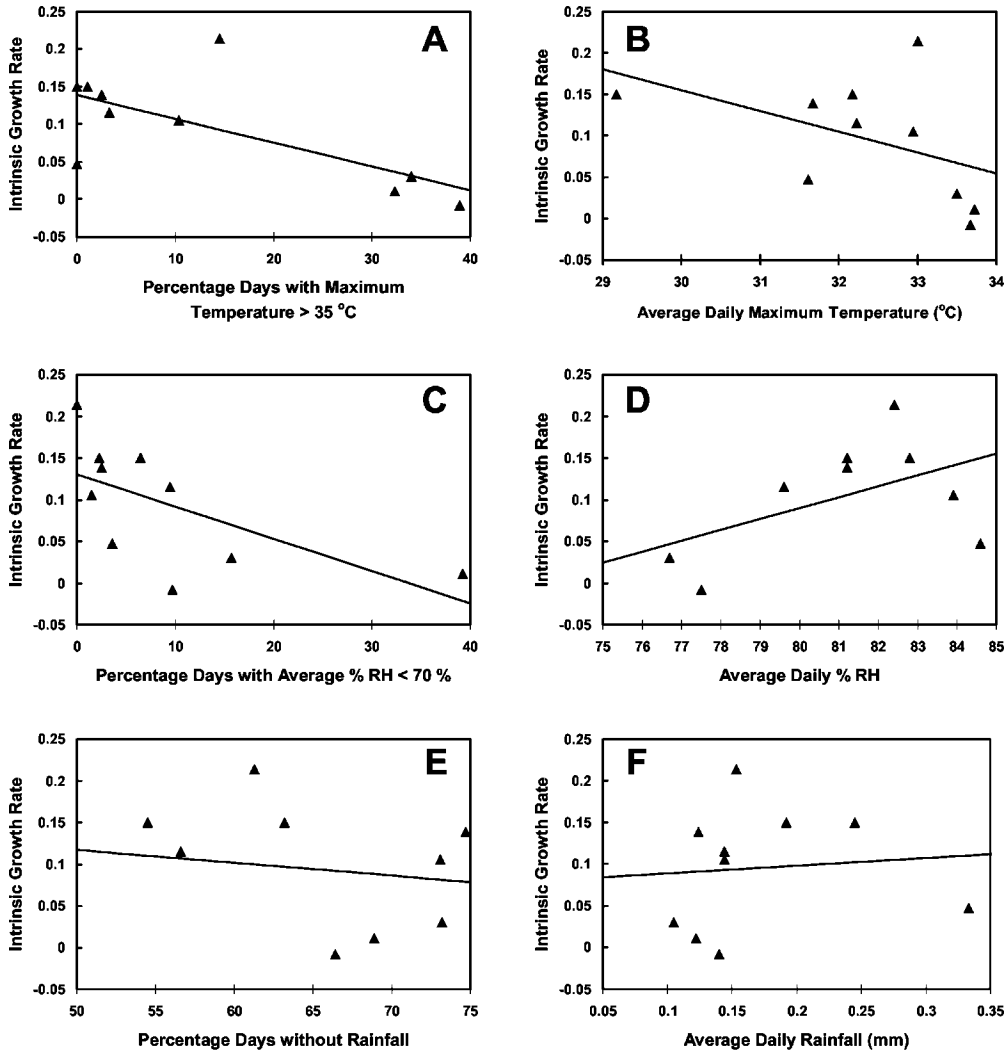

Fig. 2. Correlation between some climatic variables and the average growth rate for varroa mites ($n = 10$ yr). Correlation data (Pearson's correlation coefficient and probability are listed for each plot: (A) −0.68; $P = 0.03$; (B) −0.48; $P = 0.16$; (C) −0.62; $P = 0.05$; (D) 0.61; $P = 0.06$; (E) −0.18; $P = 0.61$; and (F) 0.09; $P = 0.81$.

The usual summertime climate for Louisiana is more tropical than Mediterranean, and the temperature and RH % within the broodnest are favorable for reproduction by varroa mites. The decrease in mite reproduction during 1998–2000 may reflect inadequate cooling of the broodnest during relatively hot and dry periods. Either the broodnest temperature exceeded the optimal range for varroa, which would reduce mite reproduction (Le Conte et al. 1990), and/or the relative humidity within the nest fell to levels significantly below 70 RH %, which would also decrease the reproductive rate of mites (Le Conte et al. 1990). Alternatively, the influence of climate on growth rate may extend beyond direct effects on mite fertility. Changes in climate may have affected the number of female offspring produced per female by increasing the mortality of the immature offspring (Le Conte et al. 1990, Ifantidis et al. 1999). If mortality of male mites had increased, the percentage of fertile mites could have decreased over time as the result of increased numbers of unmated female mites that cannot lay eggs (Martin et al. 1997, Martin 2001). Climate may have also influenced the distribution of adult female mites within a colony of bees. If the proportion of total mites infesting brood cells is reduced for long periods, the average number of reproductive cycles attempted per female during a lifetime could be reduced, and the growth of the mite population would be reduced.

Climate also influences the overall death rate for adult female mites (Le Conte et al. 1990, Kraus and Velthuis 1997). Varroa mites begin to die when temperatures exceed 38.0°C (Le Conte et al. 1990). Mites may die within brood cells or during the phoretic period when they live on adult bees. Although mor-

tality of mites in brood cells was significantly higher from 1998 to 2001, the death rates in brood cells were low and comparable with other studies (Fries at al. 1994, Medina and Martin 1999). If the death rate of adult female mites had substantially increased in some years, it must have occurred during the phoretic period.

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