

Understanding Long-Term Fruit Fly (Diptera: Tephritidae) Population Dynamics: Implications for Areawide Management

MARTÍN ALUJA,^{1,2} MARIANO ORDANO,^{1,3} LARISSA GUILLÉN,¹ AND JUAN RULL¹

J. Econ. Entomol. 105(3): 823–836 (2012); DOI: <http://dx.doi.org/10.1603/EC11353>

ABSTRACT Fruit flies (Diptera: Tephritidae) are devastating agricultural pests worldwide but studies on their long-term population dynamics are sparse. Our aim was to determine the mechanisms driving long-term population dynamics as a prerequisite for ecologically based areawide pest management. The population density of three pestiferous *Anastrepha* species [*Anastrepha ludens* (Loew), *Anastrepha obliqua* (Macquart), and *Anastrepha serpentina* (Wiedemann)] was determined in grapefruit (*Citrus × paradisi* Macfad.), mango (*Mangifera indica* L.), and sapodilla [*Manilkara zapota* (L.) P. Royen] orchards in central Veracruz, México, on a weekly basis over an 11-yr period. Fly populations exhibited relatively stable dynamics over time. Population dynamics were mainly driven by a direct density-dependent effect and a seasonal feedback process. We discovered direct and delayed influences that were correlated with both local (rainfall and air temperature) and global climatic variation (El Niño Southern Oscillation [ENSO] and North Atlantic Oscillation [NAO]), and detected differences among species and location of orchards with respect to the magnitude and nature (linear or nonlinear) of the observed effects, suggesting that highly mobile pest outbreaks become uncertain in response to significant climatic events at both global and local levels. That both NAO and ENSO affected *Anastrepha* population dynamics, coupled with the high mobility of *Anastrepha* adults and the discovery that when measured as rate of population change, local population fluctuations exhibited stable dynamics over time, suggests potential management scenarios for the species studied lie beyond the local scale and should be approached from an areawide perspective. Localized efforts, from individual growers will probably prove ineffective, and unsustainable.

KEY WORDS population dynamics, climate, time series analysis, *Anastrepha*, areawide pest management

The environmental and socioeconomic impacts of controlling pests are so wide and potentially deleterious (Lewis et al. 1997, Thomas 1999) that solving the problem has become an issue of national interest in many countries (Miliczky et al. 2000) or entire geographic regions (Allen et al. 2001). Despite that trillions of dollars are being spent worldwide on an annual basis “controlling” pests (Pimentel et al. 2000), pest-related problems have not only increased (Gould 1991) but also, due to globalization, now impinge on society in ways never envisioned previously. Although pest control success stories exist (Prokopy et al. 1990, Kogan 1998, Aluja et al. 2009), with few exceptions, they were achieved by means of intensive intervention and high cost to the environment and human health (Paoletti and Pimentel 2000). As a result, there is a worldwide trend toward areawide, ecologically based pest management schemes that are less environmentally disruptive and that handle uncertainty in a more proactive way than previous schemes (Lewis

et al. 1997; Kogan 1998, Verkerk et al. 1998, Lindquist 2000; Klassen 2000, 2005; Shea et al. 2000; Kogan and Shenk, 2002; Koul et al. 2008).

At the core of the problem of lack of widespread success in pest control lies a lack of thorough understanding of pest biology, long-term population dynamics and the relationships of the latter to the local environment (i.e., agroecosystem) and global climatic patterns (Stenseth et al. 2002, Parmesan and Yohe 2003). Such interactions, and their applications, have been analyzed in fish (Tolimieri and Levin 2005), small mammals (Lima et al. 2002), large ungulates (Fritz and Duncan 1994), and arthropods (Ruohomäki et al. 2000, Barlow et al. 2002, McLaughlin et al. 2002, Jaramillo et al. 2009, de Valpine et al. 2010).

Fruit flies (Diptera: Tephritidae) include pest species of global importance (Aluja and Mangan 2008), yet only a handful of publications have seriously examined their long-term population dynamics (Bateman 1972, Drew and Hooper 1983, Hennessey 1994, Celedonio-Hurtado et al. 1995, Carey 1996, Aluja et al. 1996, Papadopoulos et al. 2001, Yonow et al. 2004, Ye and Liu 2005). Given that the latter is a fundamental prerequisite for ecologically based pest management, particularly integrative schemes encompassing entire

¹ Instituto de Ecología A.C., 91070 Xalapa, Veracruz, México.

² Corresponding author, e-mail: martin.aluja@inecol.edu.mx.

³ Fundación Miguel Lillo, Miguel Lillo 251, T4000JFE, San Miguel de Tucumán, Tucumán, Argentina, and Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET, Argentina).

regions (i.e., areawide pest management [Lindquist 2000, Klassen 2000, 2005]), here we set out to explore the possible role of global climatic patterns such as El Niño Southern Oscillation (ENSO) and the North Atlantic Oscillation (NAO) on *Anastrepha* populations within a defined region.

Fruit flies of the genus *Anastrepha* are distributed from southern Florida to northern Argentina, including most of the Caribbean Islands (Hernández-Ortiz and Aluja 1993). Of the ≈ 200 species described so far, eight are considered serious pests throughout their distribution range: *Anastrepha fraterculus* (Wiedemann), *Anastrepha grandis* (Macquart), *Anastrepha ludens* (Loew), *Anastrepha obliqua* (Macquart), *Anastrepha serpentina* (Wiedemann), *Anastrepha sororcula* Zucchi, *Anastrepha striata* Schiner, and *Anastrepha suspensa* (Loew) (Aluja, 1994, Malavasi and Zucchi 2000). All the latter species are either oligophagous or polyphagous, with some being able to infest fruit in >20 plant families (Aluja et al. 2000). Parasitoid wasps are among the most important biotic mortality factors (Ovruksi et al. 2000), with predatory ants (Aluja et al. 2005) and pathogens (Lezama-Gutiérrez et al. 2000) contributing to tephritid population regulation. In contrast, the role of abiotic factors, specifically rainfall and temperature play in tephritid outbreaks is poorly understood (Celedonio-Hurtado et al. 1995, Aluja et al. 1996).

Because of their economic importance, fruit flies represent an ideal system to apply ecological theory in solving problems of applied nature in agricultural settings. Our broad objective here was therefore to provide policy makers, program managers, and researchers with novel information to aid decision-making processes in both the arenas of pest management, particularly areawide approaches, and long-term funding of research. With this in mind, our specific aims were as follows: 1) characterize the long-term adult *Anastrepha* population fluctuations in three different commercial orchards [grapefruit (*Citrus* \times *paradisi* Macfad.), mango (*Mangifera indica* L.), and sapodilla [*Manilkara zapota* (L.) P.Royen] located in central Veracruz, México; 2) determine whether long-term population dynamics are driven by direct or delayed density-dependent (endogenous) and density-independent (exogenous) factors such as local (e.g., rainfall, air temperature) and global climatic variation (i.e., El Niño Southern Oscillation [ENSO] and North Atlantic Oscillation [NAO]); 3) determine possible differences between species with respect to the order of influence and the shape of linear or nonlinear effects; and 4) determine how patterns of local (i.e., single orchard), population dynamics, could impinge on management decisions at the regional level.

Materials and Methods

Study Sites. This work was carried out between January 1994 and December 2004 in a commercial grapefruit orchard located in Martínez de la Torre (20° 04' N, 97° 04' W; 80 m) and commercial, contiguous

mango and sapodilla orchards located in Apazapan (19° 19' N, 96° 43' W; 293 m), Veracruz, México. In Martínez de la Torre, native vegetation (tropical evergreen forest) has been replaced by citrus (*Citrus* spp.) groves, banana (*Musa* spp.) plantations, cattle pasture, and cultivated fields. The climate in this area is warm and humid (mean \pm 1 SE monthly temperature, $21.05 \pm 0.01^\circ\text{C}$; mean annual rainfall, 1677.4 ± 11.7 mm [1960–2004]), strongly influenced by seasonal monsoons. In Apazapan, isolated patches of native vegetation (tropical subdeciduous forest) can still be found on steep mountain slopes and river creeks, but much of the landscape is dominated by patches of native vegetation intermixed with commercial orchards (mango and sapodilla) and maize (*Zea mays* L.) fields. The climate in this area is warm and sub-humid (mean \pm 1 SE monthly temperature, $19.42 \pm 0.01^\circ\text{C}$; mean annual rainfall, $1,100.1 \pm 4.3$ mm [1960–2004]). All three orchards are located in proximity to the Gulf of México; therefore, local climate is greatly influenced by broad weather patterns originating in that area and elsewhere.

The orchard in Martínez de la Torre is a 25-ha monocrop of the 'Ruby Red' grapefruit. It is surrounded on all sides by citrus groves ('Valencia' orange, 'Marsh' and Ruby Red grapefruit). Trees are planted at a density of 204 trees per ha, totaling 3,265 trees. They range in age from 38 to 40 yr, and are all >6–13 m in height (canopy diameter, ≈ 10 m). The main flowering period of trees is during February to March. Trees bear commercial sized fruit from September until February, but harvest occurs between November and mid-January, because any fruit left on the tree after that date are usually heavily infested with *A. ludens* larvae. This grove is subjected to intensive management. Calendar bait sprays for fruit flies are applied from July to September.

The two orchards in Apazapan, are poorly managed. The mango orchard (4 ha) contains 'Manila' trees interspersed (haphazardly) with local 'Papaya', 'Manillilla', 'Tocotín', and 'Petacón' mangoes. The orchard is partially surrounded by trees of *Spondias purpurea* L. (Anacardiaceae; as are mangoes), a preferred host of *A. obliqua*. Trees are planted at a density of 51 trees per ha, totaling 204 trees. They range in age from 33 to 40 yr, and are all >14–16 m in height (canopy diameter, ≈ 20 m). Manila trees flower during late January and early February and bear commercial-sized fruit from May to July. Management is restricted to occasional irrigation and control of ants by means of insecticides. The sapodilla orchard (1.5 ha) contains trees from two cultivars, 'Morena' and 'Yoyo', grafted into native *M. zapota* (Sapotaceae) trees. Trees are planted at a density of 400 trees per ha, totaling 560 trees. They range in age from 25 to 30 yr, and are all >12–15 m in height (canopy diameter, ≈ 7 m). Flowering occurs during June, and trees bear commercial-sized fruit from November to December. Fruit in this orchard are usually heavily infested by *A. serpentina* (up to 100% infestation has been observed). As is the case with mango trees, management is restricted to occasional irrigation during the peak of the dry season

(April–June). As far as we know, nothing is done to control fruit flies.

Measurement of Adult Fly Population Fluctuations. Twelve McPhail traps were deployed in the grapefruit orchard in Martínez de la Torre. In Apazapan, 16 traps each were deployed in both the mango and sapodilla orchards. Traps were placed as uniformly as possible in each orchard (no corner left uncovered). Each glass trap was baited with 10 ml of hydrolyzed protein (Captor Plus, Agroquímica Tridente, México City, México) and 5 g of borax (granular borax pentahydrate) mixed with 250 ml of water and hung in a tree between 3 and 4 m above the ground (McPhail 1939). Traps were serviced every 7 d throughout the study. All captured tephritid flies were transferred into glass vials filled with 70% alcohol that were transported to the laboratory for fly identification.

Every *Anastrepha* adult was sexed and identified to species. As noted by Aluja et al. (1996) “even though a large number of *Anastrepha* species are present in commercial fruit orchards, one or two species account for >90% of all flies captured in traps.” Based on the latter, populations of *A. ludens* alone were analyzed in the grapefruit orchard (representing 95.3% of all flies captured in grapefruit trees), whereas *A. obliqua* and *A. serpentina* were analyzed in mango and sapodilla orchards, respectively (representing 42.3 and 80.0% of all flies captured in mango and sapodilla trees, respectively). Weekly trap captures were converted to flies per trap per day (FTD) values by using the formula total number of flies / (number of traps × days of trap exposure) (IAEA 2003). This way, variability in trap number or capture periods was standardized.

Weather Data. We used four variables as proxy of climatic conditions. At a local level, rainfall and air temperature data were obtained from the Comisión Nacional del Agua (www.cna.gob.mx) and Comisión Federal de Electricidad (www.cfe.gob.mx). These data originated from two weather stations at Martínez de la Torre (20° 04' N, 97° 02' W; 50 m) and Jalcomulco (19° 20' N, 96° 46' W; 330 m). Rainfall (millimeters) was reported as accumulated monthly precipitation. Temperature data (Celsius) correspond to daily values recorded at 0800 hours and were averaged over each month.

On a global scale we used the North Atlantic Oscillation Index (NAOI) and Southern Oscillation Index (SOI), both which are widely used in ecological studies (Stenseth et al. 2003). NAOI is the most robust pattern of recurrent atmospheric oscillations in the North Atlantic region that are most marked during November and April. A positive NAOI value is related to the magnitude of change in storm activity in the north. In our analyses, we used a monthly averaged and standardized NAOI calculated from data obtained at <http://www.cpc.ncep.noaa.gov/data/teledoc/teleindcalc.shtml>. SOI is one of the indices used to estimate the magnitude and direction of the “El Niño Southern Oscillation” (ENSO) and is calculated as the difference in weather conditions between Tahiti and Darwin, two tropical localities in the Pacific Ocean. Persistent negative SOI values correspond to “El Niño”

events, whereas positive SOI values correspond to “La Niña” events (Stenseth et al. 2003). In our analyses, we used a monthly averaged and standardized SOI calculated from data obtained at <http://www.cpc.ncep.noaa.gov/data/indices/soi>. We note that both ENSO and NAO significantly influence weather patterns in areas near the Gulf of México (Giannini et al. 2001a,b), which is where our study sites were located.

Data Analysis. Population estimates (i.e., FTD values) of *A. ludens* were based on the 12 traps hung in the grapefruit orchard. In the neighboring mango and sapodilla orchards, we considered the total number of traps (32 [16 per orchard]) because capture series of the two dominant species, *A. obliqua* and *A. serpentina*, were strongly correlated (Spearman correlation, *A. obliqua*, $r_s = 0.89$; *A. serpentina*, $r_s = 0.92$; $P < 0.0001$, $N = 132$ in both cases). We chose to work with monthly FTD values (i.e., averaged over 4 wk, considering that all three *Anastrepha* species considered for analysis are multivoltine, exhibiting a mean generation time of 45 d (Celedonio-Hurtado et al. 1988), coupled with the rainfall and air temperature data that were calculated as monthly averages. FTD values were transformed to $\log_{10}(X + x_{\min})$, where x_{\min} represents the minimum number of flies that can be captured in a trapping session ($x_{\min} = 1/12$ for *A. ludens*, $x_{\min} = 1/32$ for *A. obliqua* and *A. serpentina*). Missing values (i.e., lack of captures due to loss of traps) were interpolated from adjacent points. The logarithmic transformation stabilized variance and allowed us to run population dynamics models. Replacing zeros (by x_{\min}) and missing values allowed us to work with uninterrupted time series.

The temporal tendency of every series was determined by means of simple linear regression between the series differentiated at time lag 1 of the FTD-transformed data and the trapping date (McCrimmon et al. 1997). Seasonality, tendency, and stationarity of the trapping series also were explored by means of autocorrelation functions (ACFs) to build correlograms. These analyses were run in STATISTICA 7.0 (StatSoft, Inc. 2004). The shape of the ACF in the correlogram is an indicator of seasonality and periodicity in the time series (Royama 1992). To determine the dominant density dependent order, we used partial rate correlation functions (PRCFs; Berryman and Turchin 2001) run on the FTD-transformed series.

To model the population dynamics of the three *Anastrepha* species under study, we used two approximations. First, we applied a second order autoregressive linear model [AR(2)] to examine density-dependent patterns (Royama 1992). By defining the rate of population change (or rate of per capita growth) as $R_t = \log(N_t) - \log(N_{t-1})$, where N is the population density (Royama 1992), the AR(2) model can be expressed as follows:

$$R_t = \beta_0 + (1 + \beta_1) X_{t-1} + \beta_2 X_{t-2} + \varepsilon_t \quad [1]$$

where β_i ($i = 1$ and 2) are the parameters of an ordinary autoregressive model representing the strength of the first and second orders on R_t , in which population density is $X_{t-i} = \log(N_{t-i})$ and ε_t is a

Gaussian error. Population dynamics analyses also can be evaluated by means of a model that ties the first (direct density dependence) and second (delayed density dependence, Royama, 1992) order parameters. The AR(2) was run in STATISTICA 7.0 (StatSoft, Inc. 2004).

Second, we modeled nonlinear dynamics and the possible influence of climatic variation by applying generalized additive models (GAMs, Hastie and Tibshirani 1990). If we define R_t as in the previous AR(2) model, the weather and stochastic factors that possibly drive the population dynamics can be integrated in a general function (Bjørnstad et al. 1998, Murúa et al. 2003) in which

$$R_t = b + \sum f_i(N_{t-d}) + \sum g_j(C_i) + s(D_N) + p(SBC_t) + \varepsilon_t \quad [2]$$

with b being an intercept, $f_i(N_{t-d})$ representing a population density function at a certain time lag (i.e., the density dependent effect), $g_j(C_i)$ representing a function of a climatic variable, $s(D_N)$ representing a seasonality function, $p(SBC_t)$ representing a function of the sex bias in capture (SBC), and ε_t representing an error term. On top of allowing the inclusion of terms related to exogenous terms, this model differs from the AR(2) in the sense that the relationship between variables is represented by a family of functions by means of a GAM. Such statistical approximation allows one to evaluate the density dependent structure as well as the possible influence of climatic factors on the rate of population change.

To be able to identify proximate relationships with climatic variation (as opposed to ultimate causes), we subtracted the historical monthly mean ($n = 11$ yr) from every one of the climatic data points. As a result, we obtained variables that represented the deviation with respect to the historical monthly mean (Lewellen and Vessey 1998) as follows:

$$C_x = C_{t-1} - \hat{C}_m \quad [3]$$

where C_{t-1} is the measure of climatic variable the month preceding the rate of population change, and \hat{C}_m is the historical mean of that same month. The seasonal and delayed influence on the rate of population change was evaluated as follows:

$$C_d = (\sum C_{t-k}/12) - \hat{C} \quad [4]$$

where C_{t-k} represent the observations of the climatic variable of the 12 preceding months of C_{t-1} and \hat{C} is the monthly historical mean. C_x in equation 3 represents the direct influence of climatic variation on the rate of population change, whereas C_d in equation 4 represents the seasonal and delayed influences of climatic variation on the rate of population change. We note that all climatic proxys (C_x and C_d) were calculated for each of the four climatic variables (Supp Table 1 [online only]).

Because they are baited with a feeding attractant, McPhail traps tend to capture more females than males (Houston 1981). Given that during exploratory data analysis we found that this SBC varies over time,

we incorporated the SBC into the model to examine its possible effect on the estimated rate of population change. The SBC was calculated as a proportion p (number of captured males divided by the total number of flies captured in a trap in a week). When no flies were captured ($N = 0$), the missing values were interpolated from adjacent points to be able to work with a continuous series. We preferred to consider the effect of the variation over time of the SBC, to the option of only using a time series based on females, to render the model more robust. Furthermore, given that we detected a strong seasonal component in the temporal structure of the FTD time series during exploratory data analysis, we incorporated a differentiation of annual order where $D_N = \log(N_{t-1}) - \log(N_{t-13})$. The latter represents a rate of population change of seasonal annual order and can be interpreted as the variation caused by host availability or the delayed effect of parasitism. Extending equation 2, the complete initial model we ran was as follows:

$$R_t = b + f_1(N_{t-1}) + f_2(N_{t-2}) + f_3(N_{t-3}) + g_1(C_{x-rainfall}) + g_2(C_{x-temperature}) + g_3(C_{x-SOI}) + g_4(C_{x-NAOI}) + g_5(C_{d-rainfall}) + g_6(C_{d-temperature}) + g_7(C_{d-SOI}) + g_8(C_{d-NAOI}) + s(D_N) + p(SBC_t) + \varepsilon_t \quad [5]$$

where *rainfall* represents accumulated monthly precipitation, *temperature* represents air temperature averaged over a monthly period, and *SOI* and *NAOI* represent the global weather indexes described in Materials and Methods. The decision to include population densities with a time lag of 3 mo (i.e., $t-3$) was intended to cover the possible influence of two previous generations on R_t .

The best model was selected by running a stepwise generalized additive regression in S-PLUS 2000 (Mathsoft, Inc. 1999, Hastie 1993) and applying the Akaike Information Criterion (AIC; Burnham and Anderson 2002), with the lowest AIC values and information differences between models (Δ AIC) to identify the most parsimonious models.

Results

In total, 10,359 *A. ludens*, 7,572 *A. obliqua*, and 26,525 *A. serpentina* were captured in 578 weekly samples at Martínez de la Torre and 574 weekly samples at Apazapan. Time series data for the three species are given in Supp Table 1 ([online only]), and the corresponding descriptive statistics are shown in Table 1.

Temporal Variability in SBCs. McPhail trap SBCs fluctuated over the 11 yr of the study for the three fruit fly species. *A. ludens* series exhibited a stronger bias toward female capture than *A. obliqua* and *A. serpentina* series (Table 1). No temporal pattern in the first SBC difference series (for arcsine square root of p -transformed data) was detected for *A. ludens* (mean \pm 1 SE = 0.00001 \pm 0.0238), *A. obliqua* (0.0011 \pm 0.0026), or *A. serpentina* (-0.0066 ± 0.003) (adjusted $R^2 \approx$

Table 1. Descriptive statistics of the three time series of fruit fly captures in three orchards of central Veracruz, México, from January 1994 to December 2004

Variable	N	Mean	Median	Max.	SD
<i>A. ludens</i>					
Mean FTD	132	0.22	0.07	2.78	0.41
Mean SBC	113	0.31	0.32	1.00	0.20
No. of females	132	52.79	18	584	94.26
No. of males	132	25.69	8	329	49.82
Mean FTD of females	132	0.15	0.05	1.74	0.27
Mean FTD of males	132	0.07	0.02	0.98	0.14
<i>A. obliqua</i>					
Mean FTD	132	0.12	0.01	1.70	0.27
Mean SBC	103	0.44	0.43	1.00	0.24
No. of females	132	35.62	4	696	94.25
No. of males	132	21.74	3	321	47.32
Mean FTD of females	132	0.07	0.01	1.24	0.18
Mean FTD of males	132	0.04	0.01	0.57	0.09
<i>A. serpentina</i>					
Mean FTD	132	0.41	0.02	6.37	1.03
Mean SBC	99	0.40	0.35	1.00	0.25
No. of females	132	136.38	4	2457	364.64
No. of males	132	64.57	3	849	150.52
Mean FTD of females	132	0.28	0.01	4.71	0.74
Mean FTD of males	132	0.13	0.01	1.66	0.30

Means were calculated for each month from weekly captures. FTD = flies per trap \times day index. SBC = no. of males/total no. of captures.

-0.007, $P > 0.75$, $N = 131$ for data on the three species), indicating that SBC is constant through time for all three species (e.g., means are not different from zero). SBC variation was higher from August to January, the seasonal period of lowest captures (Fig. 1). SBC values contained significant autocorrelations on several lags beyond zero, with a dominant autocorre-

lation of first order (*A. ludens*, $r = 0.41 \pm 0.09$, $P < 0.0001$; *A. obliqua*, $r = 0.39 \pm 0.09$, $P < 0.00001$; *A. serpentina*, $r = 0.27 \pm 0.09$, $P = 0.017$) by Box-Ljung Q test.

Temporal Variability in Rate of Population Change and Population Density. Population density, estimated through FTD index displayed annual peaks during the 11-yr observational period (Fig. 2). Seasonal increases between March and June were recorded for *A. ludens*, May and June for *A. obliqua*, and May and August for *A. serpentina* (Fig. 3). Fluctuations in the rate of population change (R_t) were relatively scarce across the eleven years of study for the three fruit fly species (Fig. 2). No temporal pattern was detected for any of the three species (mean ± 1 SE, *A. ludens* = -0.003 ± 0.026 ; *A. obliqua* = -0.0025 ± 0.003 ; *A. serpentina* = 0.0008 ± 0.004 (adjusted $R^2 \approx -0.008$, >0.75 , $N = 131$ for all cases). The mean R_t value over time was not significantly different from zero for any species, indicating that populations were stable during the study period.

Yearly variation patterns revealed a negative tendency in R_t between July and September for the three species that tended to become positive and greater at the end of winter and spring. *A. ludens* displayed smaller within-year R_t variation than the other species, although seasonal patterns were overall similar (Fig. 3).

Endogenous Dynamics. Autocorrelation functions revealed for the three species a series of transformed FTD characterized by a seasonal process of annual order (assuming a seasonal process). The apparent lack of tendency exhibited by a balanced distribution of positive and negative correlations among delays (Fig. 4) provides support for results of a simple regression of R_t and the transformed FTD series. PRCFs revealed for the three species a strong direct density dependent effect on R_t as well as a delayed second order density-dependent effect (Fig. 4). That is, the intrinsic population change rate was strongly dependent on the previous generation population size.

The combination of autoregressive parameters of the AR(2) model allowed us to determine that populations of all three fruit fly species exhibited stable dynamics (Fig. 5). Points outside of the triangle can be interpreted as populations moving toward extinction. Above the semicircle and to the left, populations exhibit strong direct density dependence. To the right of the vertical line, populations are stable. Under the semicircle, populations exhibit a multiannual cycle (Royama 1992, Krüger et al. 2002). As shown in Fig. 5, the deseasonalized series (differenced at lag 12 because otherwise the model was inadequate) for the three species were located above the semicircle to the right of the vertical line, indicating that the three populations under study were stable and could be characterized by logistic dynamics when exogenous variables such as weather were not incorporated in the model.

Nonlinear Dynamics and Climatic Effects on Rate of Population Change. Best models revealed that R_t for the three species was a decreasing function of first order population density, linear for *A. ludens* and *A.*

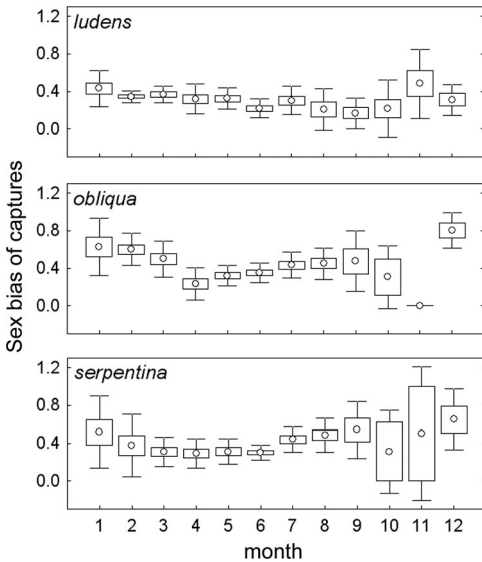


Fig. 1. Monthly variation in mean sex ratio (number of males/total number) in weekly captures of *A. ludens*, *A. obliqua*, and *A. serpentina* from January 1994 to December 2004 in orchards of central Veracruz, México. Points represent the mean, boxes represent ± 1 SE, and whiskers represent ± 1 SD ($n = 11$ yr).

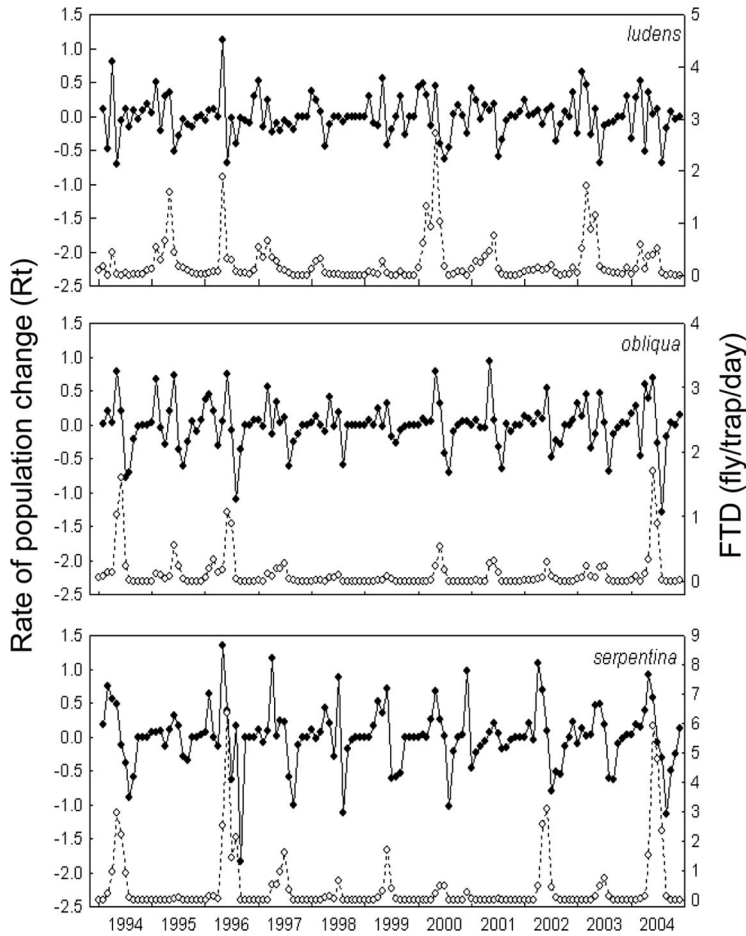


Fig. 2. Monthly variation in the rate of population change (closed boxes), and mean FTD (open boxes) in weekly captures of *A. ludens*, *A. obliqua*, and *A. serpentina* from January 1994 to December 2004 in orchards of central Veracruz, México.

obliqua, and nonlinear for *A. serpentina* (Table 2; Figs. 6–8). For *A. obliqua* (Fig. 7) and *A. serpentina* (Fig. 8), R_t was also a decreasing nonlinear function of density-dependent delays, corresponding to two previous generations. Along with endogenous dynamics, formulation of the most parsimonious best fit models included seasonal variation, sex bias in captures and amount of rainfall from the previous year as common factors influencing population dynamics of the three species (Table 2; Figs. 6–8). For all three species the changes in R_t values of greatest magnitude were driven by direct density dependence and delayed density dependence of annual order.

Both global and local scale climatic variation affected population dynamics of the three species chiefly in a nonlinear, nonmonotonic manner (Table 2; Figs. 6–8). For *A. ludens*, NAO affected R_t in direct and delayed manner (Fig. 6d and e), whereas rainfall and air temperature had a delayed effect on R_t (Fig. 6b and c). By contrast, both rainfall and air temperature had both direct and delayed effects on the R_t values of *A. obliqua* populations (Fig. 7c–f), and ENSO had a direct effect (Fig. 7g). For *A. serpentina*, both

monthly NAO and ENSO had a direct effect on R_t (Table 2; Fig. 8d–e). For rainfall, temperature, and NAO, extreme values characterized the nonlinear structure of their effects on R_t , whereas ENSO exhibited patterns of linear influence.

Discussion

Lack of consistent success in pest control can often be explained by a scant understanding of the factors that drive the long-term population dynamics of a particular pest or pest complex. Here, we studied representatives of a group of devastating agricultural pests (Aluja and Mangan 2008) that illustrate the problem well. To our knowledge, this study represents the first demonstration on the influence of both local and global climatic variation on fruit fly population dynamics and provides critical data to support the notion that these types of pests can only be successfully controlled through large-scale, areawide schemes that incorporate all the growers in a particular region (Lindquist 2000, Klassen 2005). Our study also supports the notion that studying the effect of

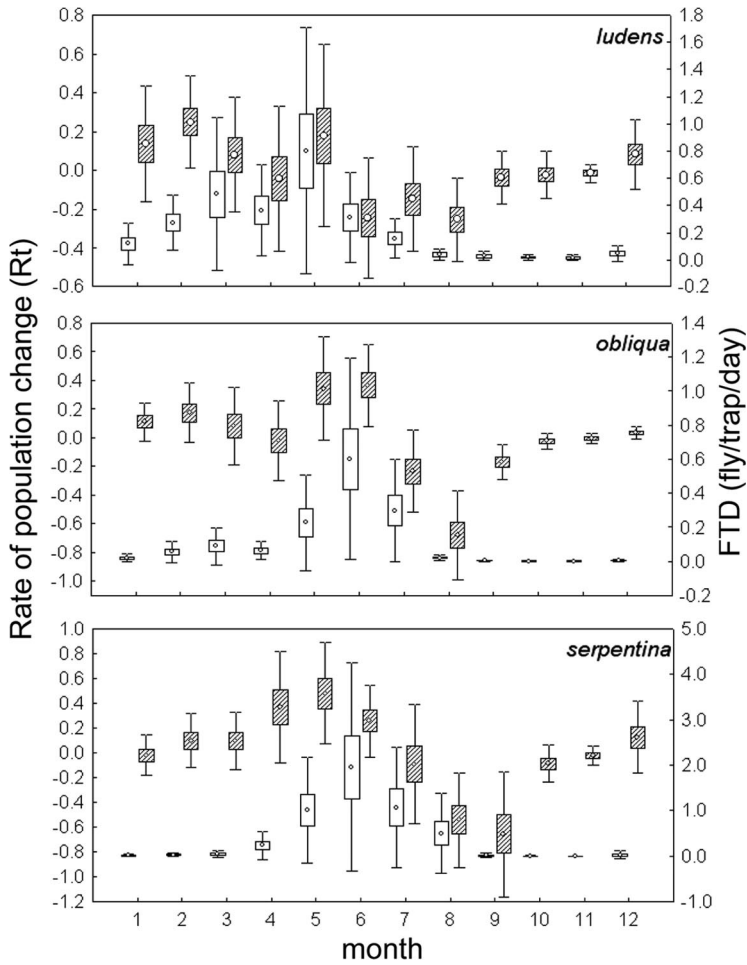


Fig. 3. Monthly variation in the rate of population change (closed boxes), and mean FTD (open boxes) in weekly captures of *A. ludens*, *A. obliqua*, and *A. serpentina* from January 1994 to December 2004 in three orchards of central Veracruz, México. Points represent the mean, boxes represent ± 1 SE, and whiskers represent ± 1 SD ($n = 11$ yr).

global climatic patterns on particular study organisms can provide significant insight into the critical factors that drive the ecology of insect populations at a local level (Stenseth et al. 2002, 2003; Parmesan and Yohe 2003). Specifically, we observed that fruit fly population dynamics were mainly driven by a direct density-dependent effect and a seasonal feedback structure of annual order. We also detected important direct and delayed influences of both local (rainfall, air temperature) and global climatic variation (ENSO and NAO), and detected differences among species and location of orchards with respect to the order of influence and the shape of these effects. Given the enormous economic impact of fruit flies worldwide and the urgent need to develop more environmentally friendly management schemes (Aluja et al. 2009), we center the discussion of our results on their practical applications, particularly in the realm of areawide pest management (Klassen 2000, 2005; Lindquist 2000).

In terms of magnitude, the greatest changes in R_t for the three species were driven by extreme differences in climatic variation. Climatic unpredictability has re-

cently been shown to have a strong negative impact on the ability of insect natural enemies to track their hosts (Stireman et al. 2005). Our models predicted that when rainfall seasonal difference is maximal, the rate of population change should diminish for the three species. The same occurs for *A. obliqua* when direct effects of temperature and rainfall are considered. For applied purposes, these results suggest that independently of any other factor, fruit fly managers should count on greater expected population size uncertainty, in *A. ludens*, *A. obliqua*, and *A. serpentina*, when interannual climatic changes are forecasted, and for *A. obliqua* also when intra-annual changes in rainfall and temperature are expected. Seasonal variation in rainfall and most importantly climatic abnormalities, can be influenced by events related to ENSO (Montecinos and Aceituno 2003), suggesting that global climatic patterns are an additional important factor for prediction of fruit fly population abundance when effect of local climatic variation on the population change rate have been detected.

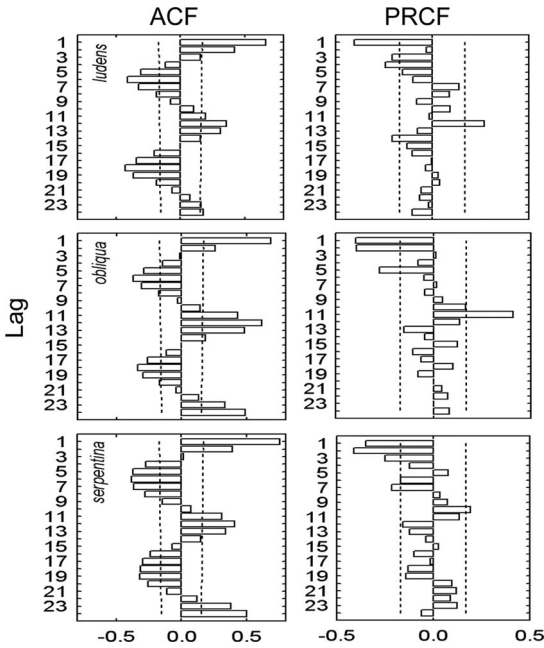


Fig. 4. ACF and PRCF plots for the rate of population change based on mean FTD data (with log transformation of N) from captures of *A. ludens*, *A. obliqua*, and *A. serpentina*. Pointed lines indicate 95% confidence bands for autocorrelations. Note the strong seasonal pattern revealed by ACF and PRCF.

NAO and ENSO directly affected the rate of population change. NAO seems to be the most important climatic factor in directing *A. ludens* dynamics. This

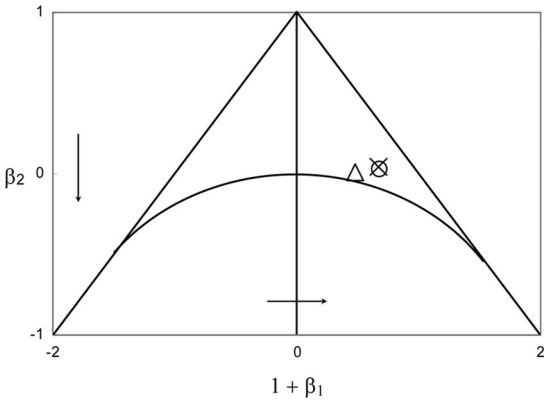


Fig. 5. Dynamics of the second order linear autoregressive model (equation 1 based on the values of parameters β_1 and β_2 of the three fruit fly species. The symbols indicate the parameter values for the second order model (equation 1 fitted to the deseasonalized (at lag 12) time series of the populations of *A. ludens* (cross), *A. obliqua* (triangle), and *A. serpentina* (circle). The short-to-long periodicity gradients is indicated by the arrows, when β_2 decrease and $1 + \beta_1$ increase, population dynamics is dominated by periodic fluctuations. The combination of the values of the parameters shows that the three species are situated above the semicircle and under the triangle, suggesting that the three fruit fly species are characterized by stable dynamics.

could be explained by the geographical situation of the grapefruit orchard where *A. ludens* was studied, as in Martínez de la Torre the influence of monsoons from the Gulf of México (area of greatest NAO influence) is greater than in Apazapan, where *A. obliqua* and *A. serpentina* were studied. The influence in NAO variation the year preceding measurement of population density, was the only significant delayed effect of global scale climatic variation acting on *A. ludens* population rate of change. By contrast, ENSO had direct negative effects on *A. obliqua* and *A. serpentina* population dynamics.

We next attempt to integrate the above-mentioned results with other relevant information to build a package of the “biologically based criteria” needed to implement a successful regional fruit fly management scheme. But before focusing on details, we highlight some additional results of our long-term study that we consider noteworthy and will hopefully help design effective approaches at lowering pestiferous fruit fly populations with minimal impact on the environment. Importantly, we found that when measured as the rate of population change, population fluctuations exhibited relatively stable dynamics over time (Figs. 1 and 3). The autoregressive second order linear model revealed that, in the absence of a seasonal effect and exogenous factors such as climate, long-term dynamics for the three species are apparently stable. The combination of parameter values that represent direct and delayed density-dependent effects, displayed a stable periodic component for the three populations, corresponding to the magnitude of change in direct density dependence. This finding is particularly relevant in the case of the grapefruit grove in Martínez de la Torre, located in the middle of a large citrus-growing region (>250,000 ha). Over the 11-yr study period, we learned that insecticide applications were frequent and in the peak fruiting season, involved high application rates. We now know that such intensive use of toxic agrochemicals had no significant impact on the long-term rate of population change in the case of *A. ludens* (Fig. 1). This provides an opportunity to convince the local grower association to join a regional control program (discussed below). Why did intensive insecticide spraying have little impact on the local *A. ludens* population? We believe that the most important element is the high degree of mobility exhibited by *A. ludens* adults that have been shown to fly over several kilometers (Aluja et al. 2000, Thomas 2001) and have the tendency to move in and out from orchards in search of food or alternative hosts (Aluja et al. 1996). In our case, a local population in the grapefruit orchard may be decimated by insecticide applications and then quickly replaced by individuals flying into the grove from neighboring groves or native vegetation. So, unless control measures are applied on an areawide scale to lower overall fruit fly populations, any local effort will be ineffective and prone to foster insecticide resistance.

In addition to the effect of global weather patterns on fruit fly population dynamics, time series analyzed in this study revealed that *A. ludens*, *A. obliqua*, and *A.*

Table 2. Selected models using AIC after stepwise generalized additive regressions, in the analysis of rate of population change of the three fruit flies *Anastrepha* species

Species	Model
<i>A. ludens</i>	$R_t = b + N_{t-1} + g_5(C_{d-rainfall}) + C_{d-temp} + g_4(C_{x-NAOI}) + C_{d-NAOI} + s(D_N) + p(SBC_t) + \epsilon_t$
<i>A. obliqua</i>	$R_t = b + N_{t-1} + f_2(N_{t-2}) + g_1(C_{x-rainfall}) + g_5(C_{d-rainfall}) + g_2(C_{x-temp}) + g_6(C_{d-temp}) + C_{x-SOI} + s(D_N) + p(SBC_t) + \epsilon_t$
<i>A. serpentina</i>	$R_t = b + f_1(N_{t-1}) + f_3(N_{t-3}) + g_5(C_{d-rainfall}) + C_{x-SOI} + g_4(C_{x-NAOI}) + s(D_N) + p(SBC_t) + \epsilon_t$

R_t is rate of population change; b is intercept; N_{t-d} is fruit fly population density at lags 1, 2, and 3; C_x and C_d represent, respectively, the direct and delayed effects of corresponding climatic variables (precipitation, air temperature, SOI, and NAOI); D_N is seasonal difference of fruit fly population density (annual lag); SBC_t is sexual bias of captures; and ϵ_t is error. Letters g , p , and s depict functions. See Data Analysis for the initial model (equation 5 and detailed explanation of model parameters and functions).

serpentina population dynamics are characterized by a strong seasonal effect of annual order and a primarily direct density-dependent effect, with annual peaks roughly corresponding to the fruiting phenology of each species respective primary host. This finding corroborates previous reports primarily linking local population fluctuations to annually driven factors such as the fruiting phenology and host availability of the main host plants, timing of prewinter fruit infestation, para-

sitoid activity, and natural sources of food (Celedonio-Hurtado et al. 1995, Aluja et al. 1996, Eber and Brandl 1996, Israely et al. 1997, Rull and Prokopy 2000, Papadopoulos et al. 2001). Thus, one can conclude that endogenous population dynamics of multivoltine fruit fly species exhibiting annual peaks are similar to those exhibited by univoltine species, for which the population change rate is regulated by interannual changes.

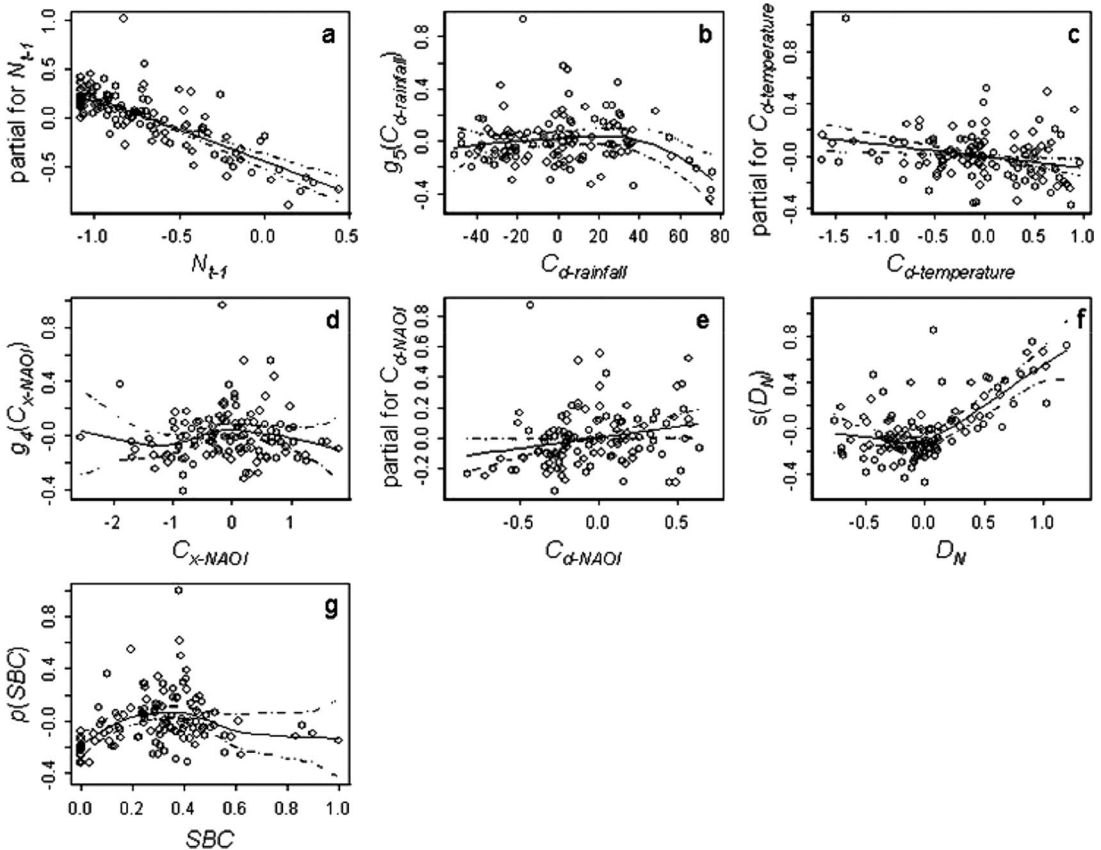


Fig. 6. Estimated parametric and nonparametric regression lines with residuals (points) and SEs (broken bands) for the generalized additive model (see Table 2) for the *A. ludens* population. N_{t-1} is fruit fly population density at lag 1; C_x and C_d represent respectively the direct and delayed effects of corresponding climatic variables (rainfall, air temperature, SOI, and NAOI); D_N is seasonal difference of fruit fly population density (annual lag); SBC_t is sexual bias of capture. Note the strong linear endogenous dependence of the previous generation (a); the relatively weak nonlinear effects of rainfall, temperature, and NAOI (b-e); the nonlinear endogenous dependence of previous year (f); and SBC (g). Compare with *A. obliqua* and *A. serpentina*. See Data Analysis for the initial model (equation 5 and detailed explanation of model parameters and functions).

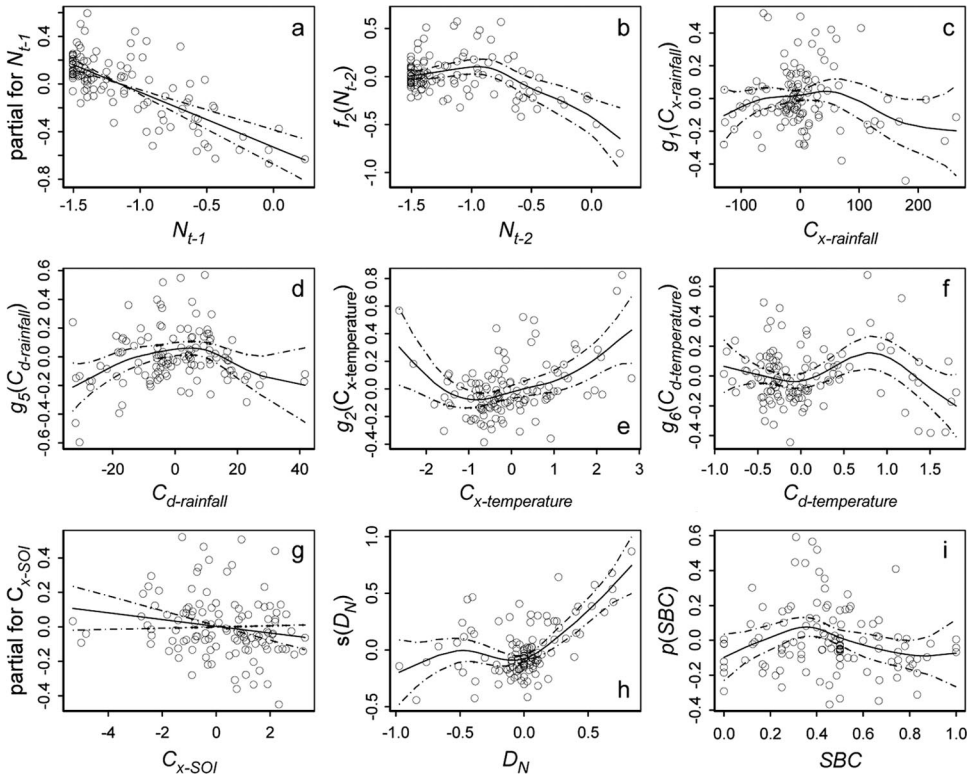


Fig. 7. Estimated parametric and nonparametric regression lines with residuals (points) and SEs (broken bands) for the generalized additive model (see Table 2) for the *A. obliqua* population. N_{t-1} and N_{t-2} are fruit fly population density at lags 1 and 2, respectively; C_x and C_d represent respectively the direct and delayed effects of corresponding climatic variables (rainfall, air temperature, SOI, and NAOI); D_N is seasonal difference of fruit fly population density (annual lag); and SBC_t is sexual bias of capture. Note the strong endogenous dependence of the previous generation (a); the two previous generations (b); the nonlinear strong effects of rainfall, temperature, and SOI (c-g); the nonlinear endogenous dependence of previous year (f); and SBC (i). See Data Analysis for the initial model (equation 5 and detailed explanation of model parameters and functions).

That both NAO and ENSO affected *Anastrepha* population dynamics, coupled with the discovery that when measured as rate of population change, local population fluctuations exhibited relatively stable dynamics over time, clearly suggests that potential management scenarios for the species under study here lie beyond the local scale and should be approached from an areawide perspective. Our findings suggest that conventional, within orchard pest control measures, have at best a localized temporal impact on mobile pest populations of species such as *A. ludens*, and that prevention of fruit infestation will require constant insecticide applications if traditional pest control schemes continue to govern fruit production. An alternative to this environmentally unfriendly scheme is represented by an areawide scheme.

To address this, we envision an areawide fruit fly management program that uses the predictive ability of our models to gauge the magnitude of the yearly areawide intervention. A successful program hinges on the ability of local plant protection officials to garner the support of the majority of growers as it has been shown that if <80% of growers participate (Reichelderfer et al. 1984), no measurable success can

be achieved. Once a well organized base of growers is in place, then areawide releases of sterile flies and parasitoids (Sivinski et al. 1996, Klassen 2005) coupled with a manipulation of fruit resistance using plant hormone analogs (Aluja and Mangan 2008) could lower pestiferous populations to manageable levels. Replacing attractive susceptible or tolerant cultivars in the orchard with resistant cultivars could mitigate fruit fly damage and perhaps pest movement into large orchard blocks. All the latter could be reinforced by occasional aerial sprays if population levels are too high for suppression by use of the sterile insect technique. But overall, the frequency and quantities of insecticides used for tephritid control could be dramatically reduced achieving the ultimate goal of areawide approaches: mitigate damage to the environment.

Despite that we did not generate time series for all factors that could possibly influence fruit fly population dynamics (e.g., host availability, parasitoid incidence and prevalence, orchard management measures, and agrochemical spraying), this work identified fundamental factors that should be considered when designing areawide, biorational fruit fly man-

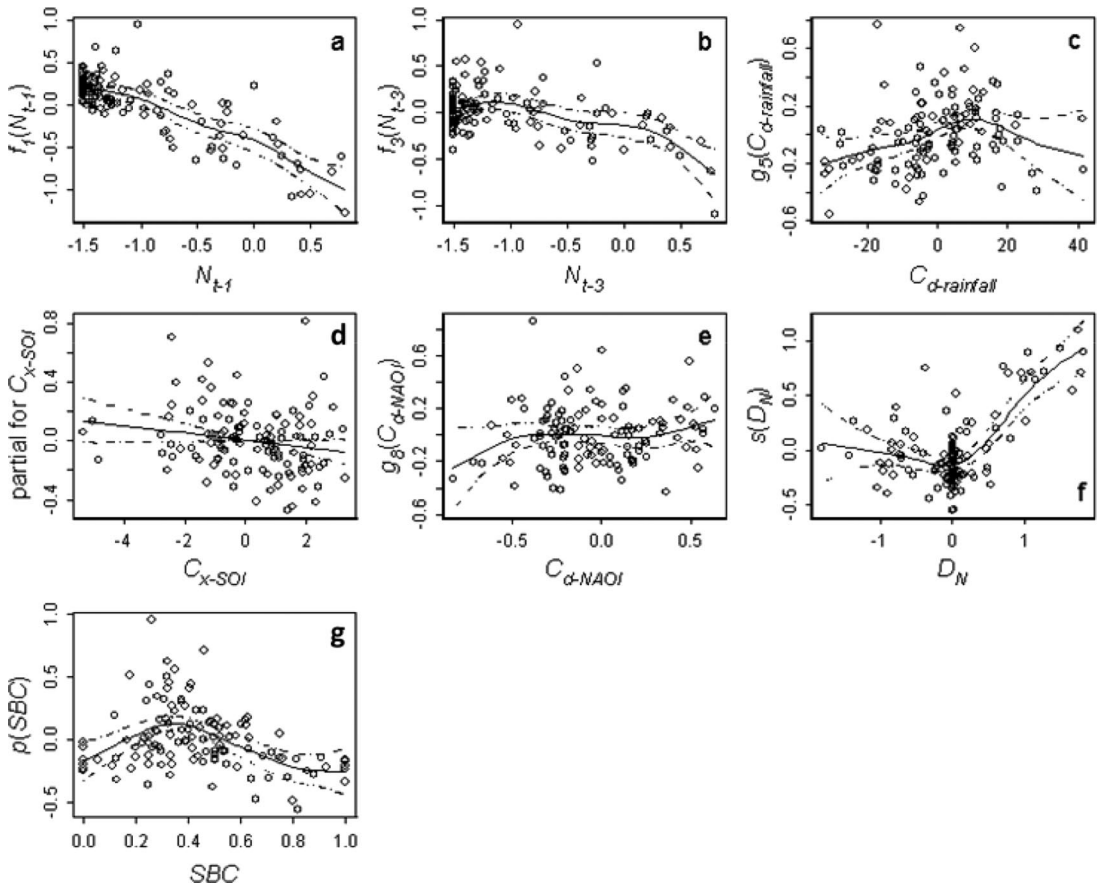


Fig. 8. Estimated parametric and nonparametric regression lines with residuals (points) and SEs (broken bands) for the generalized additive model (see Table 2) for the *A. serpentina* population. N_{t-1} and N_{t-3} are fruit fly population density at lags 1 and 3, respectively; C_x and C_d represent respectively the direct and delayed effects of corresponding climatic variables (rainfall, air temperature, SOI, and NAOI); D_N is seasonal difference of fruit fly population density (annual lag); and SBC_t is sexual bias of capture. Note the strong endogenous dependence of the previous generation (a); the three previous generations (b); the nonlinear effects of rainfall, SOI, and NAOI (c-e); the nonlinear endogenous dependence of previous year (f); and SBC (g). See Data Analysis for the initial model (equation 5 and detailed explanation of model parameters and functions).

agement schemes. This includes knowledge on the effects of intra- and interspecific interactions under uncertain scenarios encompassed within climatic variation in NAO and ENSO. Furthermore, for the three species under study, annual seasonal effects on population density influenced, in a nonmonotonic positive manner, the monthly rate of population change, suggesting that a good year in fruit production will favor fruit fly populations outbreaks if populations are not managed from an areawide perspective. We believe that temporally and spatially extended fruit fly monitoring is needed in a greater variety of host taxa (e.g., Lundberg et al. 2000), to corroborate whether the fairly stable dynamics with annual outbreaks observed in the grapefruit, sapodilla, and mango orchards studied here, are expressed in a similar manner in other regions (i.e., Moran effect, Peltonen et al. 2002) and to determine whether global weather patterns, impinging in similar ways on the population dynamics of highly mobile insects such as pestiferous fruit flies.

Furthermore, our study, coupled with classical studies on insect species exhibiting periodic outbreaks of great regional economic and social impact, such as locusts (Todd et al. 2002), gypsy moth, *Lymantria dispar* (L.) (Liebhold et al. 1992), and other forest pests (Logan et al. 2003, Dukes et al. 2009), highlight the need to fund long-term population studies that incorporate global climate phenomena (Parmesan and Yohe 2003, Stireman et al. 2005) as an additional variable when trying to understand what drives the population dynamics of pestiferous insect species over time.

Acknowledgments

We dedicate this paper to the late Robert R. Heath, a pioneer in fruit fly chemical ecology, who developed insect traps and attractants that are now used globally and that represent seminal contributions to the study of fruit fly biology and control. We acknowledge the Bigurra-Armida fam-

ily and Doña Leticia Lagunes Rivera for access to orchards. We thank Andrea Birke-Biewendt, Gemma Quintero, Isabel Jácome, and Jaime Piñero technical support. José Llanos Arias and Jesús García Morales (Comisión Nacional del Agua, Xalapa) and Efraín Cámara Archivero and Armando Hernández Trujillo (Comisión Federal de Electricidad, Xalapa) provided access to weather data. Víctor Pavón, Oscar Palafox, Darío García, Martín Pale, and Emilio Acosta serviced traps. We thank Derik Castillo, Roberto Munguía, and Andrea Cruz Angón for statistical advice. We thank Trevor Williams and two anonymous reviewers for critically reviewing an earlier version of this manuscript. This study was funded by the Mexican Campaña Nacional Contra Moscas de la Fruta (DGSV-SAGARPA-IICA), the Mexican Consejo Nacional de Ciencia y Tecnología (CONACyT grants D111-903537 [1990–1991], 0436P-N9506 [1996–1998], and 46846-Q [2004–2008]), the International Foundation for Science (IFS grant C/1741-1), Mexican Comisión para el Conocimiento y Uso de la Biodiversidad (CONABIO project H-296), the Sistema de Investigación Regional del Golfo de México (SIGOLFO-CONACyT project 96-01-003-V). M.A. acknowledges support from CONACyT through a Sabbatical Year Fellowship (ref. 79449) and thanks Benno Graf and Jörg Samietz (Forschungsanstalt Agroscope Changins-Wädenswil ACW, Switzerland) for providing ideal working conditions to finish this paper.

References Cited

- Allen, W., O. Bosch, M. Kilvington, J. Oliver, and M. Gilber. 2001. Benefits of collaborative learning for environmental management: applying the integrated systems for knowledge management approach to support animal pest control. *Environ. Manag.* 27: 215–223.
- Aluja, M. 1994. Bionomics and management of *Anastrepha*. *Annu. Rev. Entomol.* 39: 151–174.
- Aluja, M., and R. L. Mangan. 2008. Fruit fly (Diptera: Tephritidae) host status determination: critical conceptual, methodological, and regulatory considerations. *Annu. Rev. Entomol.* 53: 473–502.
- Aluja, M., H. Celedonio-Hurtado, P. Liedo, M. Cabrera, F. Castillo, J. Guillén, and E. Ríos. 1996. Seasonal population fluctuations and ecological implications for management of *Anastrepha* fruit flies (Diptera: Tephritidae) in commercial mango orchards in southern Mexico. *J. Econ. Entomol.* 89: 654–667.
- Aluja, M., J. Piñero, I. Jácome, F. Díaz-Fleischer, and J. Sivinski. 2000. Behavior of flies in the genus *Anastrepha* (Trypetinae: Toxotrypanini), pp. 375–406. In M. Aluja and A. Norrbom (eds.), *Fruit flies (Diptera: Tephritidae): phylogeny and evolution of behavior*. CRC, Boca Raton, FL.
- Aluja, M., J. Sivinski, J. Rull, and P. J. Hodgson. 2005. Behavior and predation of fruit fly larvae (*Anastrepha* spp.) (Diptera: Tephritidae) after exiting fruit in four types of habitats in tropical Veracruz, Mexico. *Environ. Entomol.* 34: 1507–1515.
- Aluja, M., T. Leskey, and C. Vincent (eds.). 2009. *Biorational tree fruit pest management*. CAB International, Wallingford, United Kingdom.
- Barlow, N. D., J. R. Beggs, and M. C. Barron. 2002. Dynamics of common wasps in New Zealand beech forests: a model with density dependence and weather. *J. Anim. Ecol.* 71: 663–671.
- Bateman, M. A. 1972. The ecology of fruit flies. *Annu. Rev. Entomol.* 17: 493–518.
- Berryman, A., and P. Turchin. 2001. Identifying the density-dependent structure underlying ecological time series. *Oikos* 92: 265–270.
- Bjørnstad, O. N., M. Begon, N. C. Stenseth, W. Falck, S. M. Sait, and D. Thompson. 1998. Population dynamics of the Indian meal moth: demographic stochasticity and delayed regulatory mechanisms. *J. Anim. Ecol.* 67: 110–126.
- Burnham, K. P., and D. R. Anderson. 2002. *Model selection and multimodel inference: a practical information-theoretic approach*. Springer, New York.
- Carey, J. R. 1996. The incipient Mediterranean fruit fly population in California: implication for invasion biology. *Ecology* 77: 1690–1697.
- Celedonio-Hurtado, H., P. Liedo, M. Aluja, and J. Guillén. 1988. Demography of *Anastrepha ludens*, *A. obliqua* and *A. serpentina* (Diptera: Tephritidae) in Mexico. *Fla. Entomol.* 71: 111–120.
- Celedonio-Hurtado, H., M. Aluja, and P. Liedo. 1995. Adult population fluctuations of *Anastrepha* species (Diptera: Tephritidae) in tropical orchard habitats of Chiapas, Mexico. *Environ. Entomol.* 24: 861–869.
- de Valpine, P., K. Scranton, and C. P. Ohmart. 2010. Synchrony of population dynamics of two vineyard arthropods occurs at multiple spatial and temporal scales. *Ecol. Appl.* 20: 1926–1935.
- Drew, R.A.I., and G.H.S. Hooper. 1983. Population studies of fruit flies (Diptera: Tephritidae) in south-east Queensland. *Oecologia* 56: 153–159.
- Dukes, J. S., J. Pontius, D. Orwig, J. R. Garnas, V. L. Rodgers, N. Brazeel, B. Cooke, K. A. Theoharides, E. E. Stange, R. Harrington, et al. 2009. Responses of insect pests, pathogens, and invasive plant species to climate change in the forests of northeastern North America: what can we predict? *Can. J. For. Res.* 39: 231–248.
- Eber, S., and R. Brandl. 1996. Metapopulation dynamics of the tephritid fly *Urophora cardui*: an evaluation of incidence-function model assumptions with field data. *J. Anim. Ecol.* 65: 621–630.
- Fritz, H., and P. Duncan. 1994. On the carrying-capacity for large ungulates of African savanna ecosystems. *Proc. R. Soc. Lond. B* 256: 77–82.
- Giannini, A., M. A. Cane, and Y. Kushnir. 2001a. Interdecadal changes in the ENSO teleconnection to the Caribbean region and the North Atlantic Oscillation. *J. Clim.* 14: 2867–2879.
- Giannini, A., J.C.H. Chiang, M. A. Cane, Y. Kushnir, and R. Seager. 2001b. The ENSO teleconnection to the Tropical Atlantic Ocean: contributions of the remote and local SSTs to rainfall variability in the Tropical Americas. *J. Clim.* 14: 4530–4544.
- Gould, F. 1991. The evolutionary potential of crop pests. *Am. Sci.* 79: 496–507.
- Hastie, T. J. 1993. Generalized additive models, pp. 249–307. In J. M. Chambers and T. J. Hastie (eds.), *Statistical models in R*. Chapman & Hall, New York.
- Hastie, T. J., and R. J. Tibshirani. 1990. *Generalized additive models*. Chapman & Hall/CRC, Boca Raton, FL.
- Hennessey, M. K. 1994. Analysis of Caribbean fruit fly (Diptera: Tephritidae) trapping data, Dade County, Florida, 1987–1991. *Fla. Entomol.* 77: 126–135.
- Hernández-Ortiz, V., and M. Aluja. 1993. Listado de especies del género Neotropical *Anastrepha* (Diptera: Tephritidae) con notas sobre su distribución y plantas hospederas. *Folia Entomol. Mex.* 88: 89–105.
- Houston, W.W.K. 1981. Fluctuations in numbers and the significance of the sex ratio of the Mexican fruit fly,

- Anastrepha ludens* caught in McPhail traps. Entomol. Exp. Appl. 30: 140–150.
- [IAEA] International Atomic Energy Agency. 2003. Trapping guidelines for areawide fruit fly programmes. Insect Pest Control Section, International Atomic Energy Agency, Vienna, Austria.
- Israely, N., B. Yuval, U. Kitron, and D. Nestel. 1997. Population fluctuations of adult Mediterranean fruit flies (Diptera: Tephritidae) in a Mediterranean heterogeneous agricultural region. Environ. Entomol. 26: 1263–1269.
- Jaramillo, J., A. Chabi-Olaye, C. Kamonjo, A. Jaramillo, F. E. Vega, H. M. Poehling, and C. Borgemeister. 2009. Thermal tolerance of the coffee berry borer *Hypothenemus hampei*: predictions of climate change impact on a tropical insect pest. PLoS ONE 4(8): e6487. doi:10.1371/journal.pone.0006487.
- Klassen, W. 2000. Area-wide approaches to insect pest management: history and lessons, pp. 21–38. In K. H. Tan (eds.), Area-wide control of fruit flies and other insect pests. Penerbit University Sains Malaysia, Penang.
- Klassen, W. 2005. Area-wide integrated pest management and the sterile insect technique, pp. 39–68. In V. A. Dycck, J. Hendrichs, and A. S. Robinson (eds.), Sterile insect technique. Principles and practice in area-wide integrated pest management. Springer, Dordrecht, The Netherlands.
- Kogan, M. 1998. Integrated pest management: historical perspectives and contemporary developments. Annu. Rev. Entomol. 43: 243–270.
- Kogan, M., and M. Shenk. 2002. Conceptualización del manejo integrado de plagas en escalas espaciales y niveles de integración más amplios. Manejo Integrado de Plagas y Agroecología (Costa Rica) 65: 34–42.
- Koul, O., G. W. Cuperus, and N. C. Elliot (eds.). 2008. Area-wide pest management: theory and implementation. CAB International, Wallingford, United Kingdom.
- Krüger, O., R. Liversidge, and J. Lindstrom. 2002. Statistical modelling of the population dynamics of a raptor community in a semi-desert environment. J. Anim. Ecol. 71: 603–613.
- Lewellen, R. H., and S. H. Vessey. 1998. The effect of density dependence and weather on population size of a polyvoltine species. Ecol. Monogr. 68: 571–594.
- Lewis, W. J., J. C. van Lenteren, S. C. Phatak, and J. H. Tumlinson III. 1997. A total system approach to sustainable pest management. Proc. Natl. Acad. Sci. U.S.A. 94: 12243–12248.
- Lezama-Gutiérrez, R., A. Trujillo-de-la-Cruz, J. Molina-Ochoa, O. Rebollo-Domínguez, A. R. Pescador, M. López-Edwards, and M. Aluja. 2000. Virulence of *Metarhizium anisopliae* (Deuteromycotina: Hyphomycetes) on *Anastrepha ludens* (Diptera: Tephritidae): laboratory and field trials. J. Econ. Entomol. 93: 1080–1084.
- Liebold, A. M., J. A. Halverson, and G. A. Elmes. 1992. Gypsy moth invasion in North America: a quantitative analysis. J. Biogeogr. 19: 513–520.
- Lima, M., N. C. Stenseth, and F. M. Jaksic. 2002. Food web structure and climate effects on the dynamics of small mammals and owls in semi-arid Chile. Ecol. Lett. 5: 273–284.
- Lindquist, D. A. 2000. Pest management strategies: area-wide and conventional, pp. 13–19. In K. H. Tan (ed.), Area-wide control of fruit flies and other insect pests. Penerbit University Sains Malaysia, Penang.
- Logan, J. A., J. Régnière, and J. A. Powell. 2003. Assessing the impacts of global warming on forest pest dynamics. Front. Ecol. Environ. 1: 130–137.
- Lundberg, P., E. Ranta, J. Ripa, and V. Kaitala. 2000. Population variability in space and time. Trends Ecol. Evol. 15: 460–464.
- McPhail, M. 1939. Protein lures for fruit flies. J. Econ. Entomol. 32: 758–761.
- Malavasi, A., and R. A. Zucchi (eds.). 2000. Moscas-das-frutas de importância econômica no Brasil. Conhecimento Básico e Aplicado. Holos Editora, Ribeirão Preto, Brazil.
- Mathsoft, Inc. 1999. S-Plus 2000 user's guide. MathSoft, Inc., Seattle, WA.
- McCrimmon, D. A., Jr., S. T. Fryska, J. C. Ogden, and G. S. Butcher. 1997. Nonlinear population dynamics of six species of Florida Ciconiiformes assessed by Christmas bird counts. Ecol. Appl. 7: 581–592.
- McLaughlin, J. F., J. J. Hellmann, C. L. Boggs, and P. L. Ehrlich. 2002. Climate change hastens population extinctions. Proc. Natl. Acad. Sci. U.S.A. 99: 6070–6074.
- Miliczky, E. R., C. O. Calkins, and D. R. Horton. 2000. Spider abundance and diversity in apple orchards under three insect pest management programmes in Washington state, U.S.A. Agric. For. Entomol. 2: 203–215.
- Montecinos, A., and P. Aceituno. 2003. Seasonality of the ENSO-related rainfall variability in central Chile and associated circulation anomalies. J. Clim. 16: 281–296.
- Murúa, R., L. A. González, and M. Lima. 2003. Second-order feedback and climatic effects determine the dynamics of a small rodent population in a temperate forest of South America. Pop. Ecol. 45: 19–24.
- Ovruski, S., M. Aluja, J. Sivinski, and R. Wharton. 2000. Hymenopteran parasitoids on fruit-infesting Tephritidae (Diptera) in Latin America and the southern United States: diversity, distribution, taxonomic status and their use in fruit fly biological control. Int. Pest Manag. Rev. 5: 81–107.
- Paoletti, M. G., and D. Pimentel. 2000. Environmental risks of pesticides versus genetic engineering for agricultural pest control. J. Agric. Environ. Ethics 12: 279–303.
- Papadopoulos, N. T., B. I. Katsoyannos, J. R. Carey, and N. A. Kouloussis. 2001. Seasonal and annual occurrence of the Mediterranean fruit fly (Diptera: Tephritidae) in northern Greece. Ann. Entomol. Soc. Am. 94: 41–50.
- Parmesan, C., and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature 421: 37–42.
- Peltonen, M., A. M. Liebhold, O. N. Bjornstad, and D. W. Williams. 2002. Spatial synchrony in forest insect outbreaks: roles of regional stochasticity and dispersal. Ecology 83: 3120–3129.
- Pimentel, D., L. Lach, R. Zuniga, and D. Morrison. 2000. Environmental and economic costs of nonindigenous species in the United States. Bioscience 50: 53–65.
- Prokopy, R. J., S. A. Johnson, and M. T. O'Brien. 1990. Second-stage integrated management of apple arthropod pests. Entomol. Exp. Appl. 54: 9–19.
- Royama, T. 1992. Analytical population dynamics. Chapman & Hall, London, United Kingdom.
- Reichelderfer, K. H., Carlson, and G. A. Norton. 1984. Economic guidelines for crop pest control. Food and Agriculture Organization of the United Nations, Rome, Italy.
- Rull, J., and R. J. Prokopy. 2000. Attraction of apple maggot flies, *Rhagoletis pomonella* (Diptera: Tephritidae) of different physiological states to odour-baited traps in the presence and absence of food. Bull. Entomol. Res. 90: 77–88.
- Ruohomäki, K., M. Tanhuanpää, M. P. Ayres, P. Kaitaniemi, T. Tammaru, and E. Haukioja. 2000. Causes of cyclicity

- of *Epirrita autumnata* (Lepidoptera, Geometridae): grandiose theory and tedious practice. *Pop. Ecol.* 42: 211–223.
- Shea, K., P. H. Thrall, and J. J. Burdon. 2000. An integrated approach to management in epidemiology and pest control. *Ecol. Lett.* 3: 150–158.
- Sivinski, J. M., C. O. Calkins, R. Baranowski, D. Harris, J. Brambila, J. Diaz, R. F. Burns, T. Holler, and G. Dodson. 1996. Suppression of a Caribbean fruit fly (*Anastrepha suspense* (Loew) Diptera: Tephritidae) population through augmented releases of the parasitoid *Diachasmimorpha longicaudata* (Ashmead) (Hymenoptera: Braconidae). *Biol. Control* 6: 177–185.
- StatSoft, Inc. 2004. STATISTICA (data analysis software system), version 7. StatSoft, Inc., Tulsa, OK. (www.statsoft.com).
- Stenseth, N. C., A. Mysterud, G. Ottersen, J. W. Wurrell, K. S. Chan, and M. Lima. 2002. Ecological effects of climate fluctuations. *Science* 297: 1292–1296.
- Stenseth, N. C., G. Ottersen, J. W. Hurrell, A. Mysterud, M. Lima, K. S. Chan, N. G. Yoccoz, and B. Adlandsvik. 2003. Studying climate effects on ecology through the use of climate indices: the North Atlantic Oscillation, El Niño Southern Oscillation and beyond. *Proc. R. Soc. Lond. B* 270: 2087–2096.
- Stireman, J. O., L. A. Dyer, D. H. Janzen, M. S. Singer, J. T. Lill, R. J. Marquis, R. E. Ricklefs, G. L. Gentry, W. Hallwacks, P. D. Coley, et al. 2005. Climatic unpredictability and parasitism of caterpillars: implications of global warming. *Proc. Natl. Acad. Sci. U.S.A.* 102: 17384–17387.
- Thomas, M. B. 1999. Ecological approaches and the development of “truly integrated” pest management. *Proc. Natl. Acad. Sci. U.S.A.* 96: 5944–5951.
- Thomas, M. B. 2001. Reproductive phenology of the Mexican fruit fly, *Anastrepha ludens* (Loew) (Diptera: Tephritidae) in the Sierra Madre Oriental, northern Mexico. *Neotrop. Entomol.* 32: 385–397.
- Todd, M. C., R. Washington, R. A. Cheke, and D. Kniveton. 2002. Brown locust outbreaks and climate variability in southern Africa. *J. Appl. Ecol.* 39: 31–42.
- Tolimieri, N., and P. S. Levin. 2005. The roles of fishing and climate in the population dynamics of bocaccio rockfish. *Ecol. Appl.* 15: 458–468.
- Verkerk, R.H.J., S. R. Leather, and D. J. Wright. 1998. The potential for manipulating crop-pest-natural enemy interactions for improved insect pest management. *Bull. Entomol. Res.* 88: 493–501.
- Ye, H., and J.-H. Liu. 2005. Population dynamics of the oriental fruit fly, *Bactrocera dorsalis* (Diptera: Tephritidae) in the Kunming area, southwestern China. *Insect Sci.* 12: 387–392.
- Yonow, T., M. P. Zalucki, R. W. Sutherst, B. C. Dominiak, G. F. Maywald, D. A. Maelzer, and D. J. Kriticos. 2004. Modelling the population dynamics of the Queensland fruit fly, *Bactrocera (Dacus) tryoni*: a cohort-based approach incorporating the effects of weather. *Ecol. Model.* 173: 9–30.

Received 18 October 2011; accepted 23 January 2012.