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Effects of abiotic factors on the population of an acridid grasshopper, *Diabolocatantops pinguis* (Orthoptera: Acrididae) at two sites in southern India: a three-year study

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Abstract

Population dynamics of an acridid grasshopper, *Diabolocatantops pinguis*, were monitored for 3 y, from October 1990 to September 1993, at two sites in Tamil Nadu, a southern state of India. The fluctuations in the population at the two sites were related to abiotic factors, such as maximum and minimum temperatures, rainfall and relative humidity, using Kendall's correlation coefficient test. We tested a hypothesis that the effects of each abiotic factor may be varying, *i.e.*, from immediate to delayed. These analyses involved several correlation coefficient tests. Hence we also performed a sequential Bonferroni test to eliminate levels of significance that emerged due to sheer chance. Maximum temperature imposed a significant delayed negative effect on the population of this species that was prolonged 2-3 mo. Minimum temperature had a significant negative lag effect of about 2 mo. at Tambaram. Rainfall had a significant positive effect on the population immediately at Tambaram or with a lag (~ 1 mo.) at Chinglepet. Relative humidity had a significant positive lag effect of about a month at Chinglepet only. The trends in the immediate effects of abiotic factors on the population of *D. pinguis* in both the study sites were comparable.

Key Words

Population dynamics, physical factors, immediate and delayed effects, temperature, rainfall, relative humidity, lag correlation

Introduction

The family Acrididae is comprised of short-horned, nonmigratory grasshoppers and highly destructive, migratory locusts (Davies 1988). The damage caused by migratory locusts and by sudden outbreaks of populations of some nonmigratory grasshopper species are well known. Environment, both biotic and abiotic factors, is a major selective force, influencing the insects to evolve certain characters by which they adapt to environmental changes. These adaptations, expressed in the insects' behavior, physiology and/or genetic variability, enable them to survive and achieve their optimal life history performance (Slansky & Scriber 1985).

Population studies gain importance as, in most cases, a species' survivability is reflected in its numbers. Reports of the extensive damage to agroecosystems (COPR 1982) and rangeland ecosystems (Hewitt & Onsager 1983) caused by acridids, attest to their pest status. Rangeland grasshopper populations are well documented (Capinera *et al*. 1983; Kemp 1990, 1992) in contrast to grasshoppers found in agroecosystems.

Long-term data on rangeland grasshopper populations have demonstrated periods of great abundance interspersed with periods of rarity (Kemp 1992) and such fluctuations were correlated with weather (Capinera & Thompson 1987). Using correlation and multiple regression analyses, Capinera & Horton (1989) analyzed the population data of grasshoppers for 53 y in the short-grass prairie regions of Montana, Wyoming, Colorado and New Mexico, in relation to weather data on temperature, precipitation and monthly heat/precipitation ratio (H/P) or drought index.

Population dynamics of a nonmigratory acridid of the subfamily Catantopinae, *Diabolocatantops pinguis* (Walker), were studied for a 3-y period from 1990 to 1993, at two agroecosystem sites (described elsewhere). This species is widely distributed in the Indian subcontinent, Thailand and Kampuchea and is one of the commonest species of grasshopper in India. It is observed to attack many economically important crops like cotton, tea, lablab and teak and is considered an occasional minor pest (COPR 1982, Vedham & Muralirangan 2000). Population fluctuations during a 3-y period were compared with three main abiotic factors, *viz.*, temperature (maximum and minimum), rainfall and relative humidity. The study presented here tests the presence (or absence) of immediate and delayed (lag) effects of abiotic factors on populations of *D. pinguis*, which have not been explored thus far in any orthopteran species. The influence of biotic factors was not studied, as food resources were not a limiting factor during any part of the year, chiefly due to the wider host breadth of *D. pinguis* (Vedham & Muralirangan 2000). In addition, our earlier studies (Vedham & Muralirangan 1999, 2000) have shown that *D. pinguis* grow and reproduce optimally on hosts like *Arachis hypogaea* and *Phaseolus aureus*, which are grown in the study sites almost throughout the year.

Materials and Methods

Sampling technique.—D. pinguis, a multivoltine species, feeds on several dicotyledonous and a few monocotyledonous plants (Vedham & Muralirangan 2000). The adults are brownish, while the nymphs are bright green, the females being larger than the males. In Tamil Nadu, a state in southern India, their distribution ranges from agroecosystems to forest floors and dry grasslands.

Populations of *D. pinguis* were monitored for a 3-y period (October 1990 to September 1993) in the agroecosystems at Tambaram (lat12°56′N, long 80° 08′E) and Chinglepet (lat12° 42′N, long 80° 01′E). Tambaram, a southern suburb of Chennai, and Chinglepet are 20 km apart (Fig. 1). Fields that grow dicotyledonous crops like

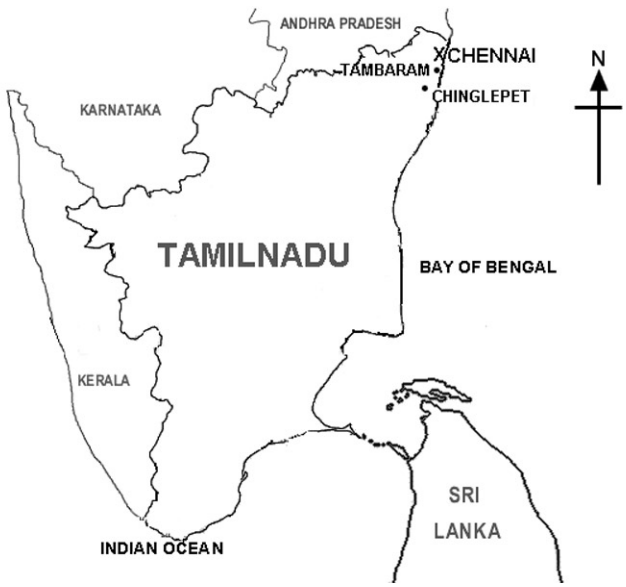

Fig. 1. Map of Tamil Nadu, a southern state in India depicting the location of the two study sites; **X** indicates the capital city of the state, Chennai.

A. hypogaea and other crops of the Fabaceae family for the larger part of the year were selected in both the study sites.

Five plots were randomly selected in a farmer's field at each study site. Sampling was conducted once every week between 0700 and 0900 h. A 30-cm diameter sweep net was used to sample the population. Sweeps were made covering a marked area of 10 m², thus with the 5 plots, sampling a total area of 50 m². Grasshoppers caught were released in the original sampled plot after the counts were made in all the plots.

Data analysis.—The weekly population data of *D. pinguis* from Tambaram and Chinglepet were converted to monthly means for analysis. Monthly means of abiotic factors, *viz.*, maximum and minimum temperature, rainfall and relative humidity, were obtained from the Regional Meteorological Station, Madras. This weather station is about 8 and 28 km from Tambaram and Chinglepet respectively. Population dynamics of *D. pinguis* at Tambaram and Chinglepet were examined for correlation with the abiotic factors.

All data — population and abiotic factors — were transformed to normal variates:

$$z = (X - \mu) / \sigma$$

where z is the standard normal deviation from the mean $(X - \mu)$ of the sample data, measured in units of standard deviations. This transformation was done to bring the values of abiotic factors and the population data to a comparable scale for plotting the histogram and also for further analyses. A nonparametric Kendall's correlation coefficient test (STATISTICA for Windows 1999) was done to compute the correlation between the monthly population of *D. pinguis* and the corresponding month's abiotic factors.

A further hypothesis tested is whether the effects of each abiotic factor are reflected varyingly in the population over time, *i.e.*, the effect may be imposed on the population within a short time period (here, within 1 mo.) or with a lag in time (1-3 mo.). The hypothesis, however, excludes effects of extreme conditions like drought, fire, flood and overgrazing by larger herbivores on the grasshopper population. The abiotic factors of a month were compared with monthly populations of the following one, two and three months; for example, correlation coefficients were computed between the abiotic factors of January 1991 and the population of *D. pinguis* in February, March and April 1991. Kendall's correlation coefficients are denoted as τ_0, τ_1,τ_2 and τ_3, *i.e.*, without lag, with lag of one, two and three months respectively. The lag correlations were done to verify the presence of prolonged, long-term effects of abiotic factors on the population dynamics of *D. pinguis*.

Thirty-two correlation coefficient values were obtained from these analyses. Nonparametric sequential Bonferroni tests (Rice 1989) were performed to eliminate significant correlations that emerged due to chance alone. The levels of significance obtained from correlation tests were compared with the α/k values of the sequential Bonferroni tests (α is the significance level of the table statistic, *i.e.*, 0.05, and k is the number of correlations subjected to sequential Bonferroni tests). Correlation values between the insect population without lag and all four abiotic factors are provided in the figures. Only the most significant correlation values are provided in Figs 2-4, those that remained significant after subjection to sequential Bonferroni tests, for each abiotic factor with the lag of one, two or three mo.

Results

Tambaram.—At Tambaram, crops like *A. hypogaea, P. aureus, Abelmoschus esculentus, Solanum melongena, Oryza sativa* and *Zea mays* are commonly cultivated. These agricultural fields are well irrigated and fertilizers and insecticides used extensively.

With high average temperatures, particularly between the months of March and July, the population decreased. The population was on the increase between October and January, when average temperatures were low. Correlation coefficient data show that the maximum and minimum temperatures had a significant immediate negative effect on the population (τ_0 = -0.269 at p = 0.023 and τ_0 = -0.237 at p = 0.047, respectively). However, these significance levels were higher than the α/k value (0.013) of the sequential Bonferroni test and hence have to be ignored. The delayed (lag) effects occurred after about 2 mo (Fig. 2a, b; maximum temperature: τ_2 = -0.401 at p = 0.001; minimum temperature: τ_2 = -0.414 at p = 0.0008). These probability levels of significance were lower than 0.013 (sequential Bonferroni test) and hence these abiotic factors do have negative delayed effects on the population.

Relative humidity had no significant immediate or delayed effects on the population of *D. pinguis*(Fig. 3a). As for the influence of rainfall, it usually supported a high population and so, soon after the monsoon (September – November), a significant population increase was always observed. Rainfall had a significant positive correlation with population within a short period (τ_0 = 0.304 at p = 0.012). This immediate positive effect is biologically real, as the level of significance was lower than the α/k value (0.013) of the sequential Bonferroni test. No significant prolonged effect of rainfall was exerted on the population at Tambaram, and hence only the effect without lag is provided in Fig. 3b. Interestingly, as observed at this site, rainfall could encourage an increase in population in a very short time.

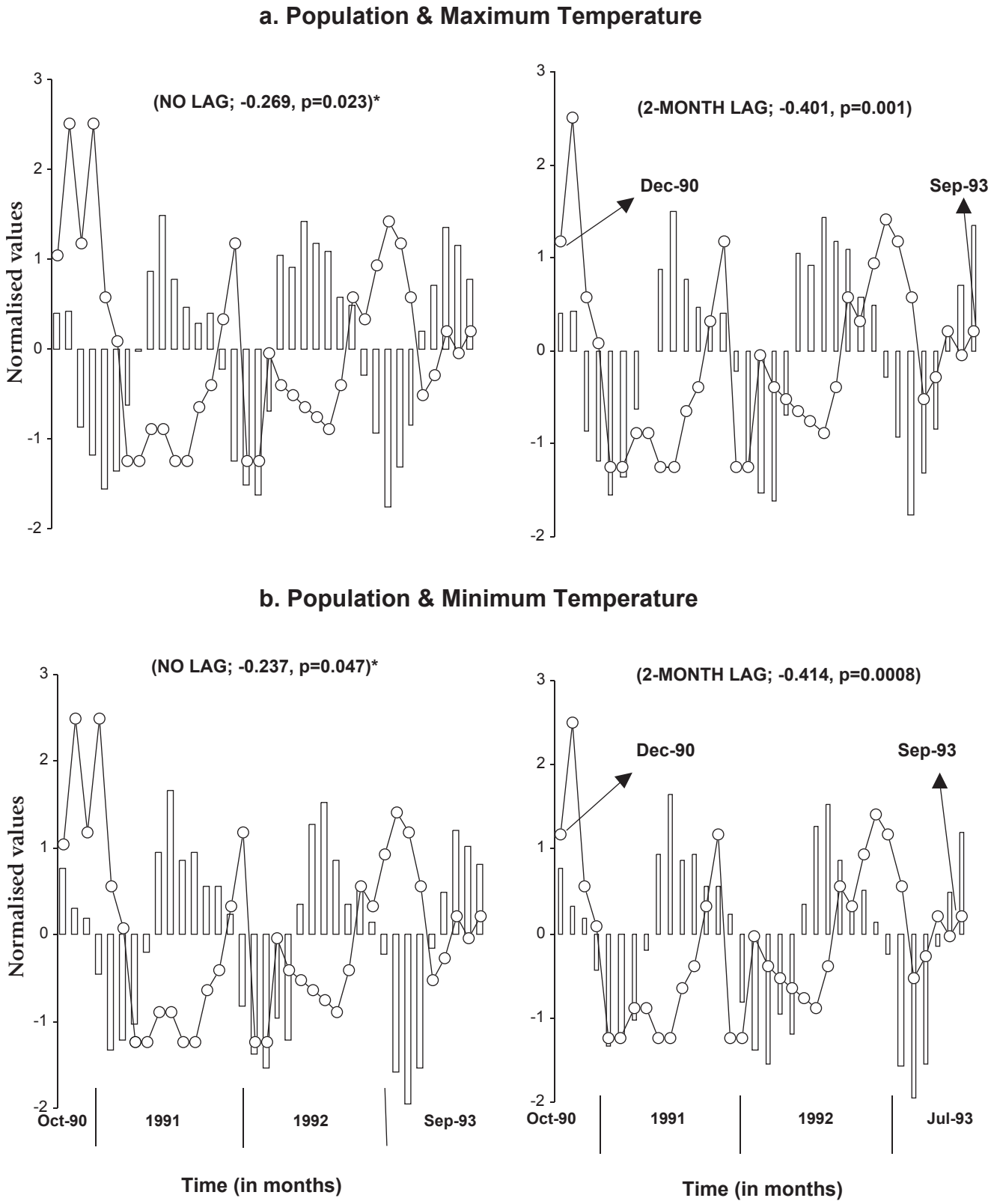

Fig. 2. Immediate and lag effects of maximum temperature (a) and minimum temperature (b) on the population of *D. pinguis* at Tambaram. Abiotic factors are represented as bars and population as lines. Values are normalized. Correlation coefficient values with significance levels are given within parentheses. * refers to p level as insignificant after subjection to a sequential Bonferroni test. The 'month-year' indicated on the x-axis refers to the beginning and end of abiotic factor data, with vertical lines marking the beginning of each year. The 'month-year' indicated beside the arrow pointer refers to the beginning and end of the population data with lag and with respect to the corresponding abiotic factor.

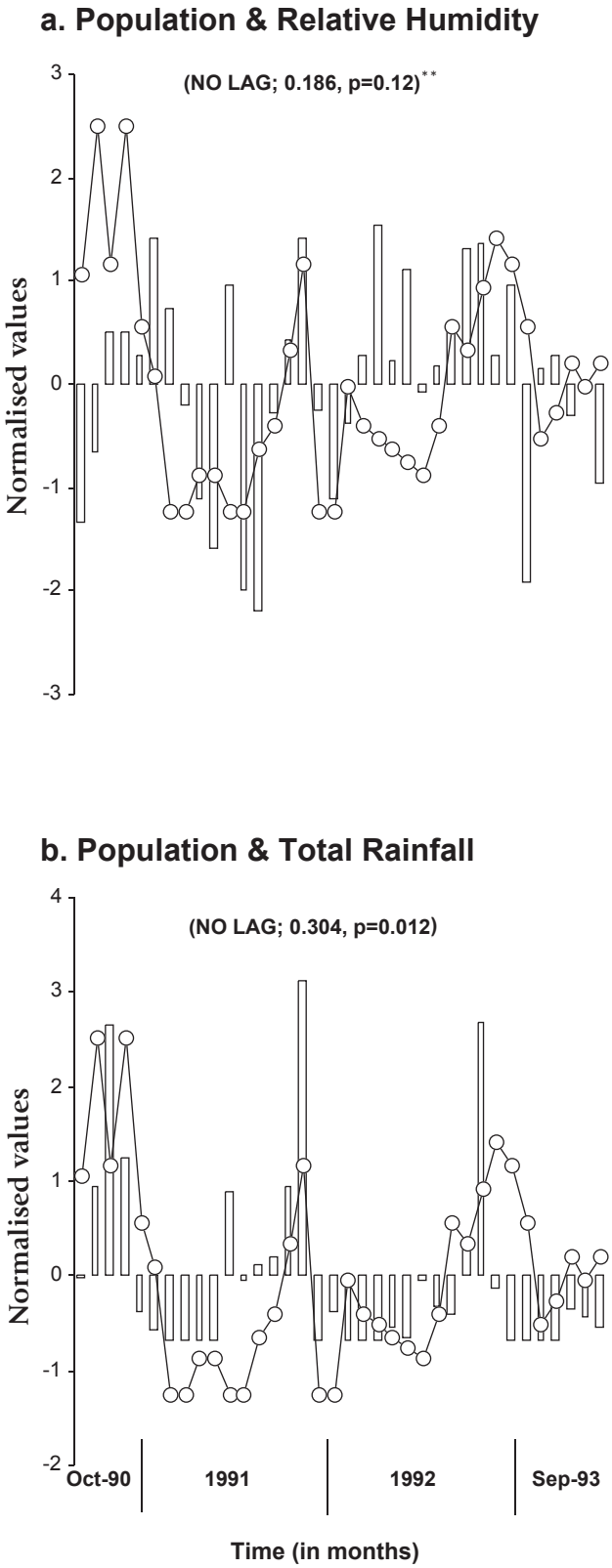

Fig. 3. Immediate effects of relative humidity (a) and total rainfall (b) on the population of *D. pinguis* at Tambaram. None of the lag correlation analyses were statistically significant for effect of total rainfall and relative humidity on the population, and hence only the correlation coefficient results without lag are provided.

** refers to nonsignificance even before subjection to sequential Bonferroni tests. Graph format as in Fig. 2.

Chinglepet.—The agricultural lands are well irrigated and crops like *A. hypogaea, Sesamum indicum, A. esculentus, O. sativa* and *Sorghum vulgare* are cultivated. The cropping pattern is less diverse compared to that at Tambaram.

Maximum and minimum temperatures during this period were inversely related to the population numbers in general. Maximum temperature had no short-term effect on the population at Chinglepet. However, this abiotic factor had a significant negative effect on the population with a 3-mo delay, as the level of significance was lower than the α/k value (0.013) of the sequential Bonferroni test (Fig. 4a, maximum temperature $\tau_3 = -0.326$ at $p = 0.01$). Minimum temperature had no significant immediate or delayed effects on the population (Fig 4b).

Relative humidity had a positive prolonged effect (1-mo lag) on the population and no short-term effect (Fig. 5a, $\tau_1 = 0.421$, at $p = 0.0007$). Similarly, no short-term effect of rainfall was observed on the population of *D. pinguis*, but a significant positive effect was imposed in about a month (Fig. 5b, $\tau_1 = 0.33$ at $p = 0.008$). The levels of significance observed for the effects of relative humidity and rainfall on the population of *D. pinguis* existed after the data were subjected to the sequential Bonferroni test.

Discussion

D. pinguis is widely distributed in Tamil Nadu (Vedham 1994) and studies on the distribution and density of acridids in the state report this species as a core species (Muralirangan *et al.* 1993). The relationship between grasshopper population dynamics and the biotic and abiotic factors is so complex that a holistic understanding of this relationship is still lacking. Abiotic factors like temperature, rainfall and relative humidity, and associated biotic factors such as availability of food, mates and the density of predators and parasites influence the biology of grasshoppers, which in turn affects the overall population. Tamil Nadu, with its typical subtropical climate, is an ideal region for the successful survival of *D. pinguis* and so this study on their population dynamics gains in importance.

Riegert (1972) suggested that correlation between climatic conditions and population changes are often weak and nonexistent. However, Gage & Mukerji (1977) observed that warm weather favors growth, survival and reproduction. A positive correlation was reported between grasshopper abundance and hot dry weather in temperate latitudes at high elevations and with seasonal rainfall in tropical and arid regions (Capinera 1987, Capinera & Thompson 1987).

In our study, the correlation coefficient tests revealed the short-term and prolonged effects of each abiotic factor on the populations of *D. pinguis*. Maximum temperature had a significant negative lag effect on the population of *D. pinguis* at both the localities, these effects lasting up to 2 or 3 mo. Minimum temperature had a significant negative lag effect on the population in about 2 mo at Tambaram but no significant immediate or delayed effects at Chinglepet. This trend suggests that maximum temperature, and not minimum temperature, is more likely to be a limiting factor for population growth in our study sites, due to a long summer and the absence of a pronounced winter. Rainfall had either immediate (as at Tambaram) or delayed (at about a month, as at Chinglepet) positive effects on the population. Relative humidity had a delayed positive effect, *i.e.*, at about a month, on the population of *D. pinguis* at Chinglepet, but no immediate effects were observed. None of

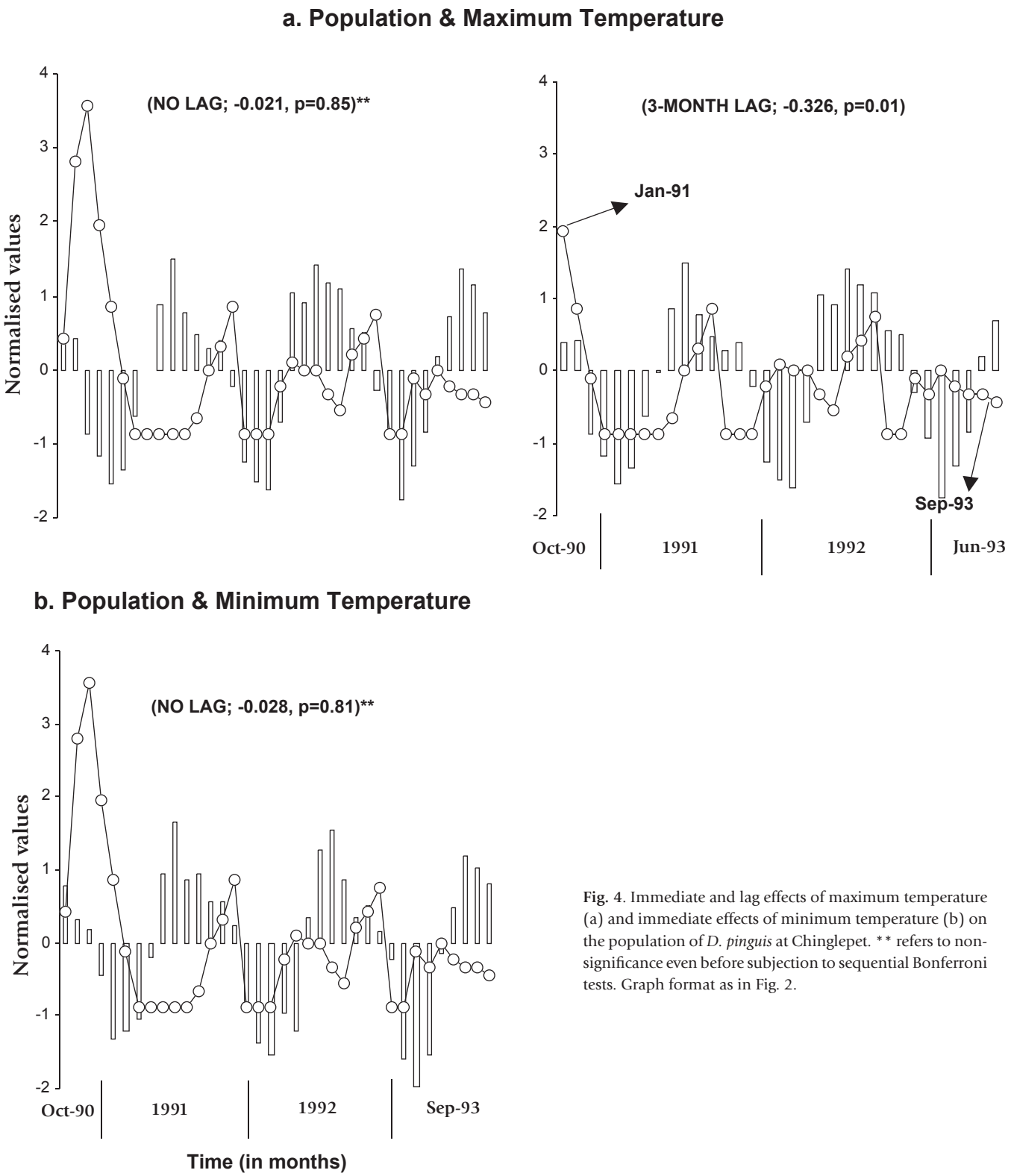

Fig. 4. Immediate and lag effects of maximum temperature (a) and immediate effects of minimum temperature (b) on the population of *D. pinguis* at Chinglepet. ** refers to non-significance even before subjection to sequential Bonferroni tests. Graph format as in Fig. 2.

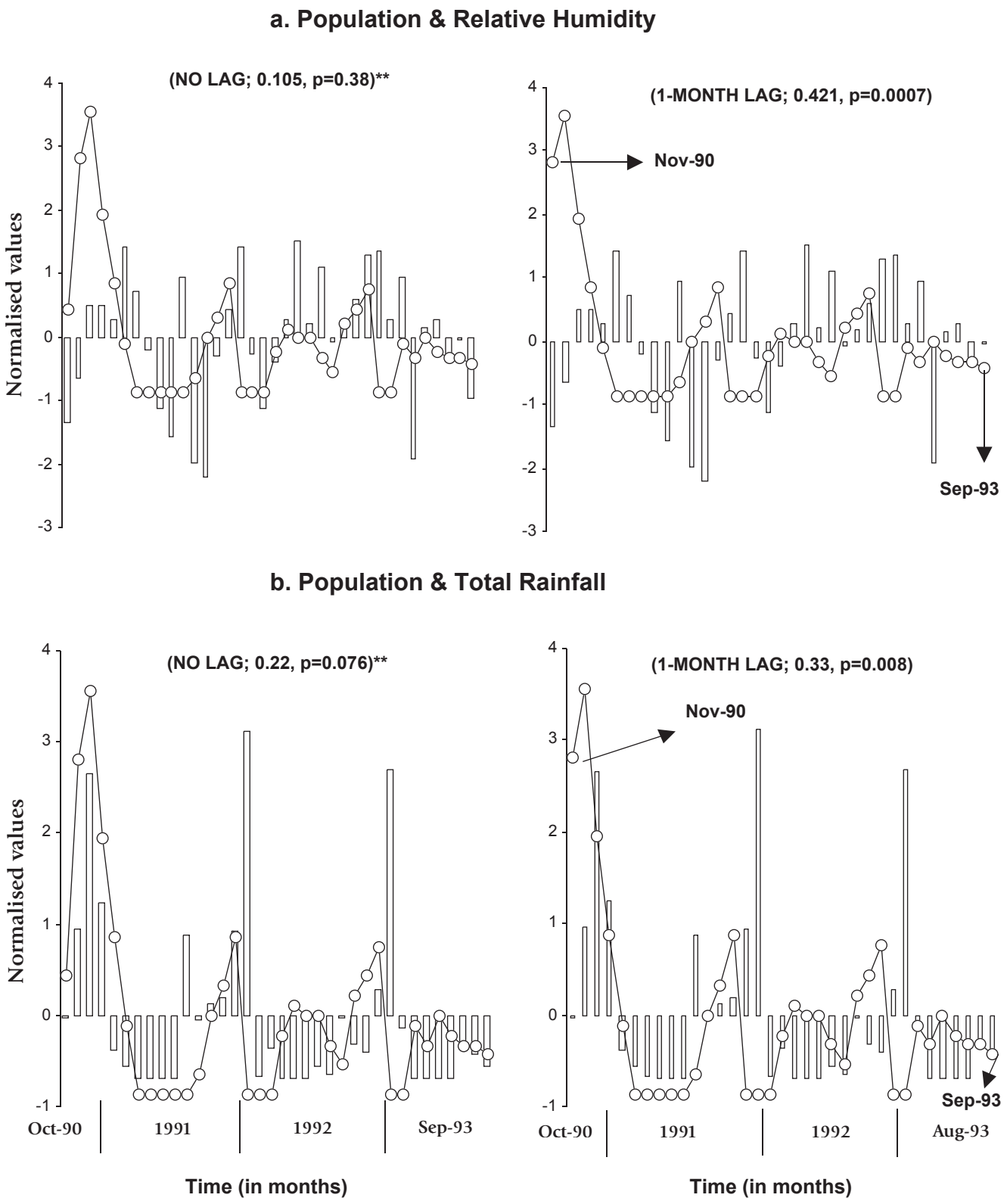

Fig. 5. Immediate and lag effects of relative humidity (a) and total rainfall (b) on the population of *D. pinguis* at Chinglepet. ** refers to non-significance even before subjection to sequential Bonferroni tests. Graph format as in Fig. 2.

the abiotic factors had immediate effects on the population of *D. pinguis* at Tambaram and Chinglepet, with the lone exception of rainfall at Tambaram.

Gage & Mukerji (1977) and Kemp (1990, 1992) have reported positive effects of precipitation and moisture on populations of grasshoppers. In contrast, in Argentina, autumn to spring precipitation was considered an important factor effecting population change through a decrease in fecundity and fertility of the females and the survival of eggs in *Laplatacris dispar* (Sanchez & Liljesthrom 1986). A high negative correlation was observed between the accumulated precipitation during the autumn-to-spring period and the total number of hatchlings. Similarly, Suresh (1993) observed a negative correlation between rainfall and the population of *A. exaltata* in a 3-y study at two sites. These variable effects of rainfall on the population of different species indicate that optimal levels of rainfall (and moisture) may encourage the population to increase to a certain level;2 and beyond threshold levels, rainfall may have adverse effects on the populations. Similarly, phenological relationships of grasshopper ecology are temperature-dependent and favorable temperature can encourage population buildup (Begon 1983, Kemp & Onsager 1986).

Capinera (1987) considered the regional variations to be a key factor in addition to the abiotic and biotic factors considered quantitatively. In addition, Fielding & Brunsven (1990) reported that the biotic factors might have some impact on the grasshopper populations through cropping patterns and irrigation practices. However, the local variations between Tambaram and Chinglepet (20 km apart) were not so significant as to influence the populations of *D. pinguis*: the populations of these two sites had comparable trends throughout the study period (data not shown).

In this study, among the biotic factors, parasites and predators were not observed to impose any significant effect on populations of *D. pinguis*. Laboratory studies have indicated that crops like *A. hypogaea* and *P. aureus* favor optimal growth and development of *D. pinguis* (Vedham & Muralirangan 1999, 2000) and in addition, many other plant species are also preferentially consumed at varying levels (Vedham & Muralirangan 2000). Several of these crops are grown seasonally in the two study sites. *A. hypogaea* is grown almost throughout the year, except for 2-3 mo; *P. aureus* and *H. annuus* are cultivated between February and April. When the most preferred crops are unavailable in the agroecosystems, populations of low density survived on alternate hosts like *A. esculentus*, *Z. mays*, *S. vulgare, Crotalaria verrucosa* (a weed) and many other species belonging to the family Fabaceae (pers. obs.). Due to the continuous availability of most preferred hosts and the wider host breadth, food was never a limiting factor for *D. pinguis* at Tambaram and Chinglepet.

It can be concluded that different abiotic factors imposed delayed effects of varying durations on the populations of *D. pinguis*. Rainfall alone had an immediate positive effect on the population at Tambaram. Minimum temperature and relative humidity had no effects at all on the populations of *D. pinguis* at Chinglepet and Tambaram, respectively. Most importantly, this study has demonstrated a method by which such differential effects of weather on insect population can be analyzed.

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