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ECOLOGY OF SANDFLIES (DIPTERA: PSYCHODIDAE) IN A RESTRICTED FOCUS OF CUTANEOUS LEISHMANIASIS IN NORTHERN VENEZUELA. III. SEASONAL FLUCTUATION

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A one year-long study (March 1979-March 1980) was carried out at San Esteban, an endemic focus of cutaneous leishmaniasis in Northern Venezuela, with the aim of observing the seasonal fluctuation of the local phlebotomine sandflies species. The influence of climatic factors (temperature, relative humidity and rainfall) on population dynamics was analyzed in three collecting sites – a house, a peridomestic area and a sylvatic region.

Among anthropophilic species, L. panamensis *behaved as a wetseason species, the mean minimun relative humidity being the critical factor influencing the total number of individuals. When the population density of this fly decreased, it was successfully replaced by* L. ovallesi, *a dry-season species. On the other hand, seasonal variations of* L. gomezi *were more strongly affected by the temperature.*

Key words: ecology of sandflies – cutaneous leishmaniasis – northern Venezuela – seasonal fluctuation

Ecological studies on phlebotomine sandflies (Diptera: Psychodidae) were initiated at San Esteban, which is an endemic focus of cutaneous leishmaniasis in Northern Venezuela.

The species composition of the natural vectors was analyzed in relation to habitats, catching methods and hour of catching in the hope that such information would help elucidate the natural transmission dynamics of the disease. Twelve species of *Lutzomyia* and one species of *Brumptomyia* were detected. On the base of their abundance and occurrence, they were classified in two groups: common species, i.e., *L. panamensis, L. gomezi, L. ovallesi L. shannoni, L. o. bicolor, L. atroclavata, L. cayennensis* and *L. trinidadensis* and rare species, i.e., *L. dubitans, L. rangeliana, L. punctigeniculata* and *L. evansi.* Additionally, *L. panamensis, L. gomezi* and *L. ovallesi* were found to be strongly antropophilic while *L. shannoni* and *L. o. bicolor* only accidentally bit man (Feliciangeli, 1987 a, b).

The present paper gives results of a one year-long study of the seasonal fluctuations undergone by the common species adult populations in three habitats (a house, a peridomestic area and a sylvatic area), which were analyzed in relation to the metereological variations.

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MATERIALS AND METHODS

Study area – San Esteban, is a small village of Carabobo State, Venezuela, which is situated at 10°26′ North, 68°01′ West, 85 m of altitude a.s.l. and about 17 km from Puerto Cabello, an important port of the Caribbean Sea. Secondary forest and agricultural settlements have been replacing the original vegetation, a moist tropical forest. Main features of the remnant primary forest are the presence of trees with large trunks and buttresses, sparse ground cover and numerous epiphytes. There are few species of deciduous trees, but the forest remains evergreen all year.

Climate records – From March 1979 to March 1980 records of the temperature (T) and relative humidity (RH) were made with three thermohygrographs placed at three collecting stations: a house in the village, a periodomestic area (about 20 m from the same house) and a sylvatic area (about 200 m from the outmost house in the village). A pluviometer, available from August 1979 to August 1980, was sited at the sylvatic station. Four daily readings were taken from the continuous records at 02h, 08h, 14h, and 20h and the means for T and RH were calculated.

Sandflies collections – Catching and handling methods have been described in full in a previous publication (Feliciangeli, 1987a). Results from the six methods used over the first 12 months without omission are presented and analyzed here, i.e., collection in resting places: walls of the houses, trees in peridomestic and sylvatic areas and collection from humans in the three habitats described. Both day and night catches were included. Additionally, the nightly collection from the Shannon light trap was also analyzed. This gave the most complete information on seasonal variation. It was used both to chart the month by month variation and also to measure the correlation between monthly catches and metereological data.

Statistical methods – The analysis of the counts of sandflies was carried out using Genstat, a statistical package developed at Rothampstead Experimental Station (Alvey et al., 1977). Advantages of the analysis of Deviance in opposition to a standard analysis of Variance has been explained in a previous paper (Feliciangeli, 1987b). In this section, at first, the factors Method and Month were fitted and the significance of the monthly changes, assessed. Then, the various metereological measures were used in turn to predict the sandflies catches. This permitted to see which metereological variate was the best predictor of sandflies number.

RESULTS

Metereological observations – Temperature decreased from the house ($\bar{x}$ = 26.8 ± 1.04) through the periodomestic area ($\bar{x}$ = 24.5 ± 0.73) to the field ($\bar{x}$ = 23.01 ± 0.90). The mean relative humidity was similar in all there stations (house: $\bar{x}$ = 75.26 ± 2.65; peridomestic station: $\bar{x}$ = 77.08 ± 4.15; field station: $\bar{x}$ = 76.6 ± 3.86). Although differences in average RH were negligible, values for minimum RH were significantly different for the three habitats. During the dry season (January-April) the values for minimum RH in the house and in the peridomestic site quickly reached 60% and stayed at about this level until July. In the sylvatic area, the minimum humidity was less than 60% until September when it slowly increased to 70% until December, but, later on, dramatically decreased during the dry season (Min. RH = 48.1%).

The rainfall ranged from a monthly minimum of 0.5 mm to a maximum of 144.4 mm, the total annual precipitation was 773.20. The resultant climatogram (Fig. 1) built, following Walter & Lieth's method (1967), reveals a four month dry season (January to April) and an eight month wet season (May to December). The wet season had two peaks of rainfall, one around June-July and the other at the end of the year. The driest month was March and the wettest, December.

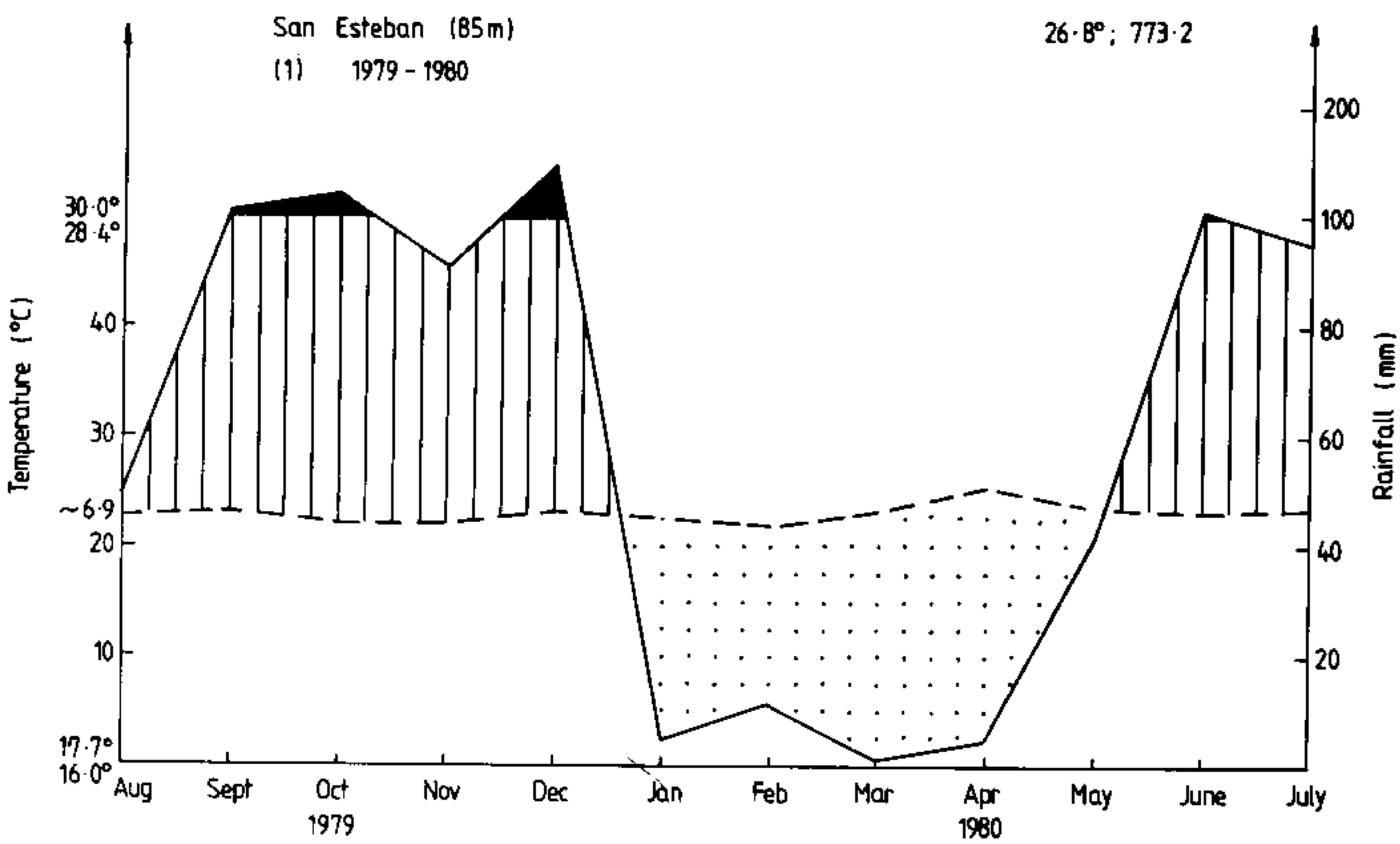


Fig. 1: Climatogramme at San Esteban, Venezuela (1979-1980).

Seasonal fluctuation – Fluctuation in total sandfly population at San Esteban and its correlation with the metereological condition has not been analysed in the present study. This is due to the bias created by fluctuation in *L. panamensis* which formed most of the collection. All species have, therefore, been treated separately and results will be presented in the same manner.

Table I shows the values of significance of the female monthly variation of common species collected at San Esteban. Since observations of the weight of the climatic factors on the numbers of sandflies collected, shows that they are to a great extent correlated (i.e. humidity is closely correlated to the rainfall), there seems to be little point in presenting the full results of this analysis and only the most important factor is identified.

For each species, graphs of seasonal trends of the most abundant collections deserving special comments are presented (Fig. 2 to 8).

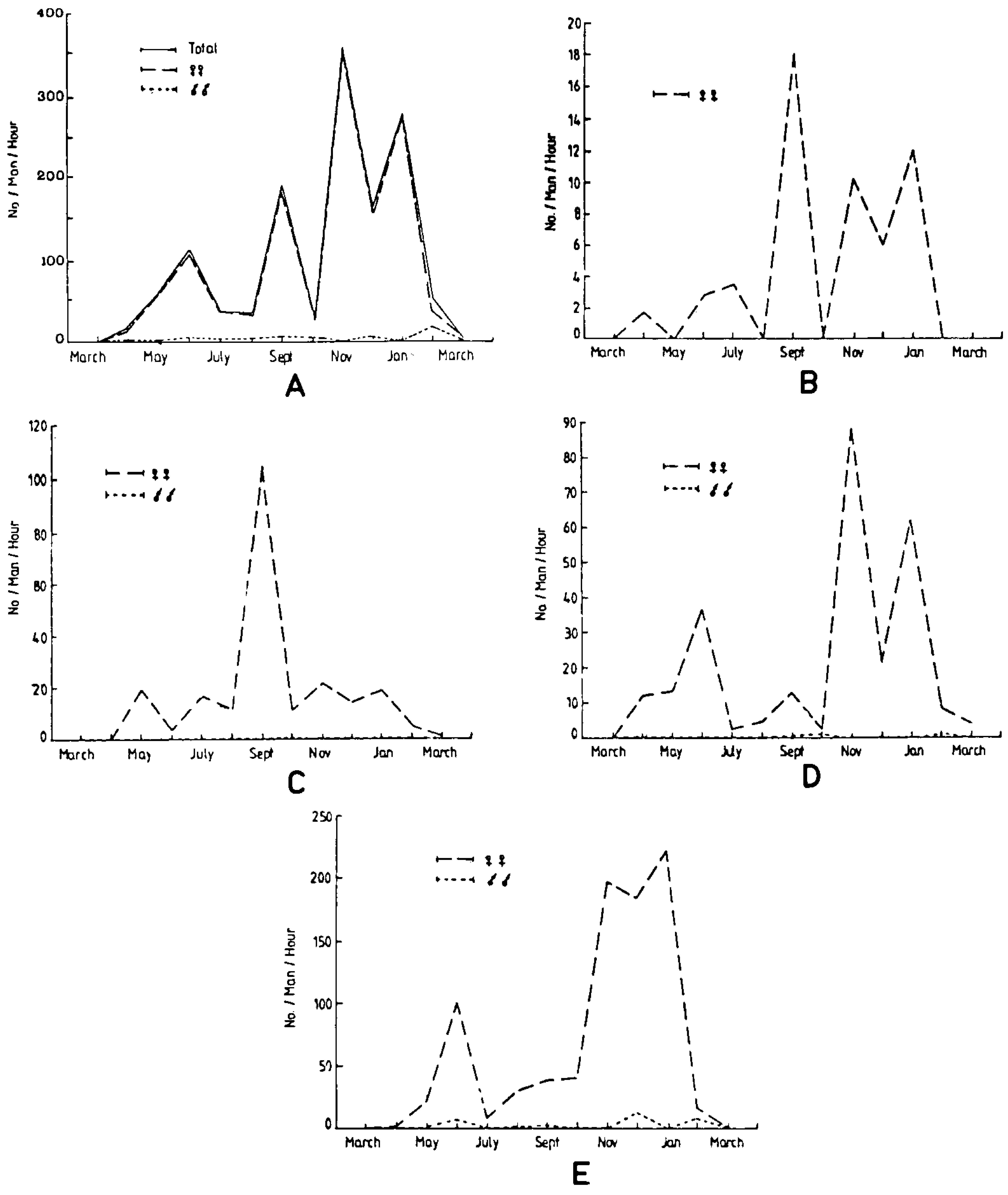


Fig. 2: *L. panamensis* – Seasonal fluctuation of the total population (A). Monthly collection at night: biting man in the house (B), biting man in peridomestic habitat (C), biting man in sylvatic habitat (D), with Shannon trap (E), (San Esteban, Venezuela, March 1979-1980).

Anthropophilic species

L. panamensis – For *L. panamensis* females, monthly variation (Fig. 2A) was highly significant (χ^2 = 3618 with 11df.) and the most significant factor was the mean minimun value of relative humidity recorded each day. With a χ^2 of 1969 (1 df.) this measure explained 54% of the total monthly variation.

Fig. 2B, C, D, show the results of collections biting man at night in the three habitats. Although flies were more frequently found resting on walls than feeding on bait, the highest density was observed in those biting man, reaching a maximum of 18 females/man/hour in September. This high level of biting activity in September coincided with an increase in abundance of sandflies in the periodomestic habitat where the peak was represented by more than 100 sandflies/man/hour. In the field site, the greatest density was comparatively lower (80 females/man/hour) and was seen in November (Fig. 2D). The Shannon trap caught a large number of sandflies, November and January being the months with the highest density. (Fig. 2E). The sex ratio, in all captures through the year, showed and overwhelming preponderance of females.

L. gomezi showed a different pattern from that of *L. panamensis* (Fig. 3). The size of the population was extremely low from March to August and increased abruptly in September, particularly on human bait in the peridomestic habitat (Fig. 3B). In the next three months (Oct.-Dec.), the population fell and there was a slight increase towards February of the next year. The critical climatic factor on the population dynamics of *L. gomezi* was the mean minimum temperature. The number of *L. gomezi* attracted by light trap was much lower than that of *L. panamensis*.

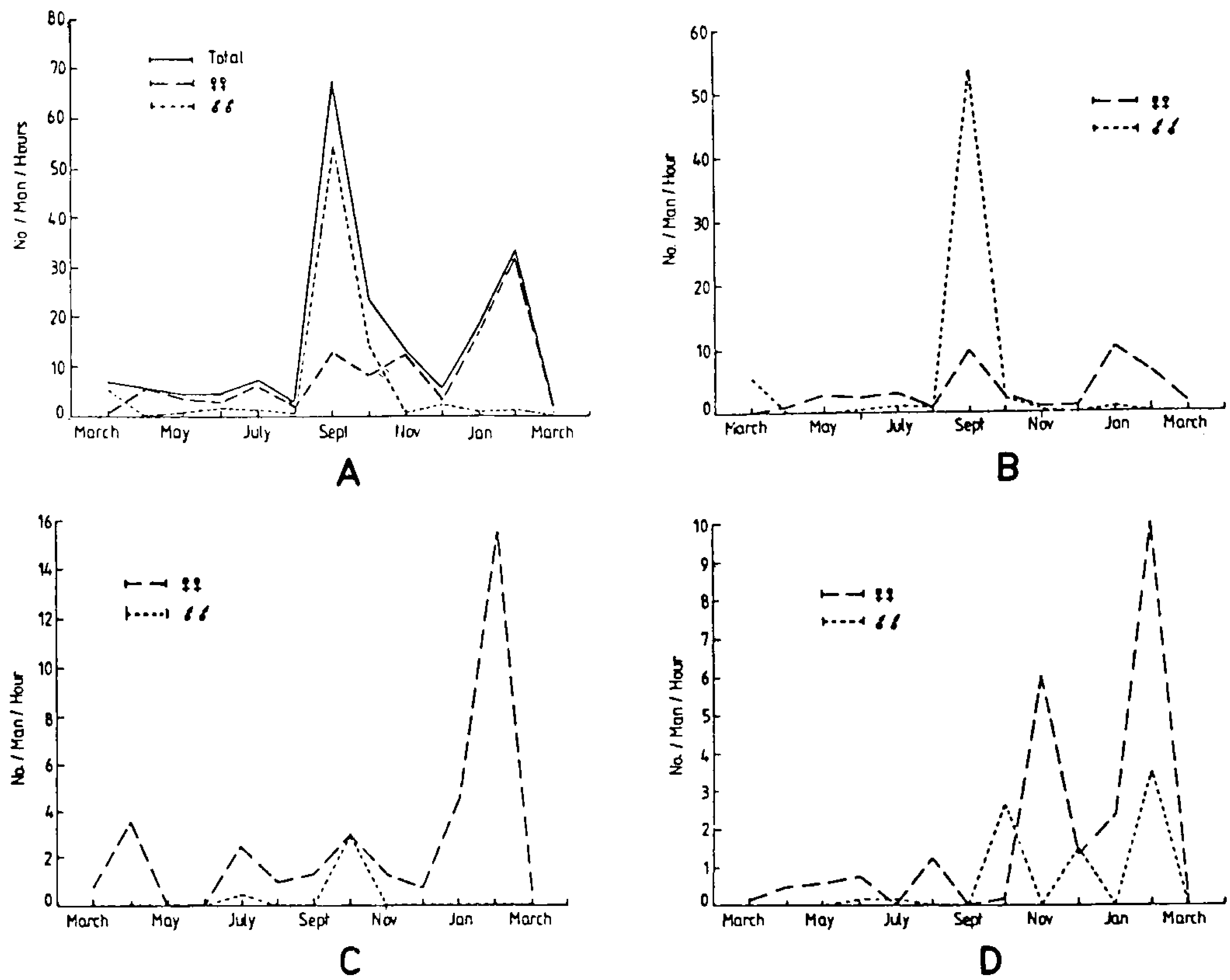
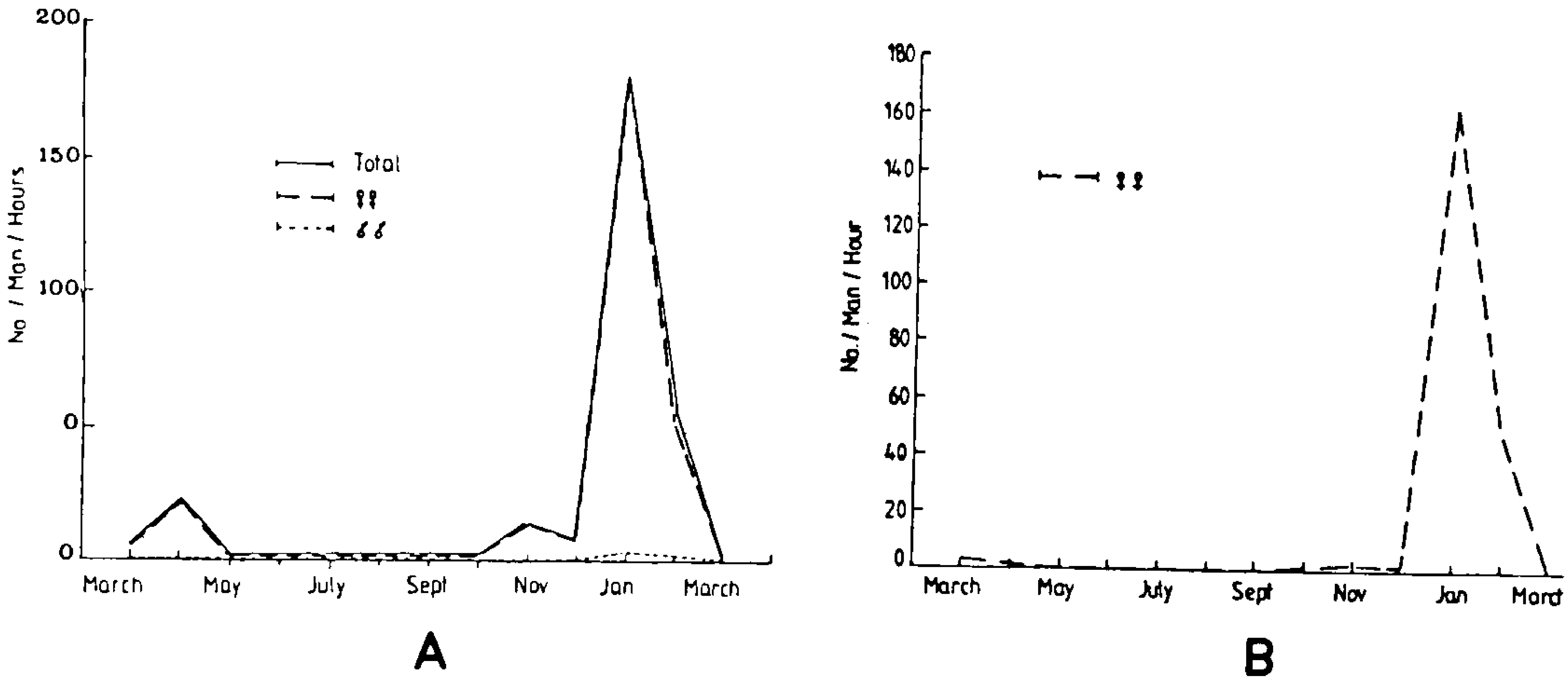


Fig. 3: *L. gomezi* – Seasonal fluctuation of the total population (A). Monthly collection at night: biting man in peridomestic habitat (B), biting man in sylvatic habitat (C), with Shannon trap (D) (San Esteban, Venezuela, March 1979-1980).

L. ovallesi – The seasonal changes in the *L. ovallesi* population are shown in Fig. 4A. Total rainfall appeared to be the major variable responsible for the population size variation (Table I). Though detected every month, there was a sudden "explosion" at the beginning of the year. Although this fly occasionally entered houses and was found in the peridomestic habitat, it occurred in these places at very low densities. Only catches in the field habitat are shown. The number of sandflies which attacked man in the field (Fig. 4B) was very high, exceeding the highest densities of *L. panamensis* (Fig. 2D). This catching constituted the greatest part of the total population. Very few specimens were caught in Shannon trap (Fig. 4D).



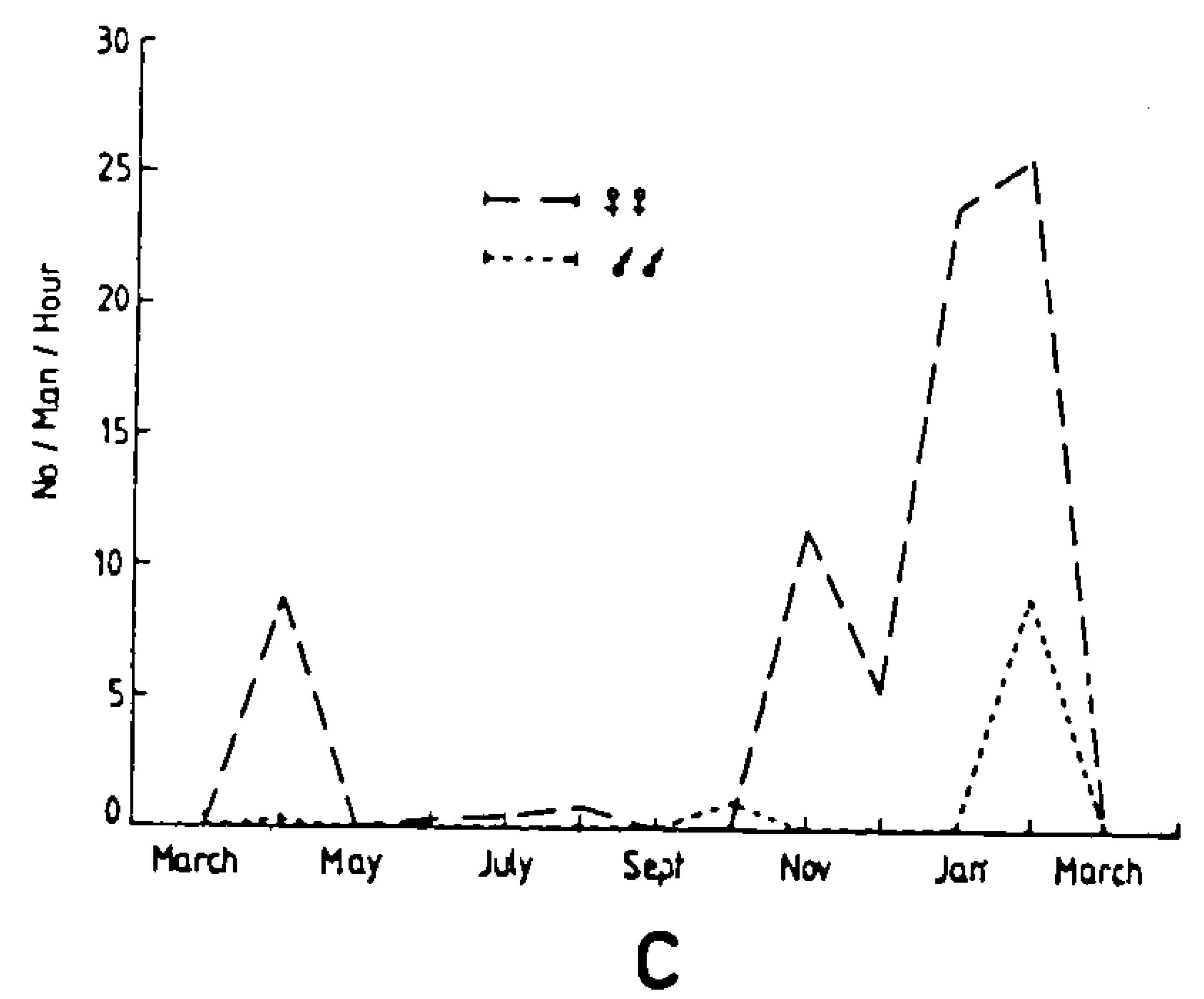


Fig. 4: *L. ovallesi* – Seasonal fluctuation of the total population (A). Monthly collection at night: biting man in sylvatic habitat (B); with Shannon trap (C) (San Esteban, Venezuela, March 1979-1930).

TABLE I

Analysis of Deviance: Degrees of freedom, deviance, mean deviance and significance levels for "common species" of sandflies which bite man at San Esteban, Venezuela

Factor		*L. panamensis*		*L. ovallesi*		*L. gomezi*		*L. o. bicolor*		*L. shannoni*	
	DF	Dev.	Mean Dev.	Dev.	Mean Dev.	Dev.	Mean Dev.	Dev.	Mean Dev.	Dev.	Mean Dev.
Month	11	3618.00	328.91***	1629.00	148.09***	183.00	16.64***	27.10	2.46**	34.67	3:15**
Climatic Factor	1	Mean Min RH 1969.00***		Total Rainfall 728.00***		Mean Min. Temp. 85.00**		Mean Min. RH 11.80**		Mean Fainfall 49.34***	

***P <0.001 **P <0.01 *P <0.05 – No significant

L. shannoni (Fig. 5A) and *L. olmeca bicolor* (Fig. 5B) – These two species were caught in very low numbers. It seemed that the size of the population of *L. shannoni* was highest in the early wet season, and that of *L. o. bicolor* was highest during the late wet season.

Non-anthropophilic species

L. trinidadensis population dynamics showed two peaks in fly density in May and November (Fig. 6A). The mean minimun RH appeared to play some role on the variation of population size. Samples from the peridomestic habitat during the day and at night were similar in size and in sex composition with predominance of males (Figs. 6B, C). In contrast, the number of sandflies caught in the field at night was relatively small and the proportion of females relatively high compared with day catches (Figs. 6D, E).

The majority of *L. atroclavata* (Fig. 7) and *L. cayennensis* (Fig. 8) were caught in the morning. Though in low densities, they were present throughout the year and in all habitats. The highest density of *L. atroclavata* was reached in March and of *L. cayennensis*, in December.

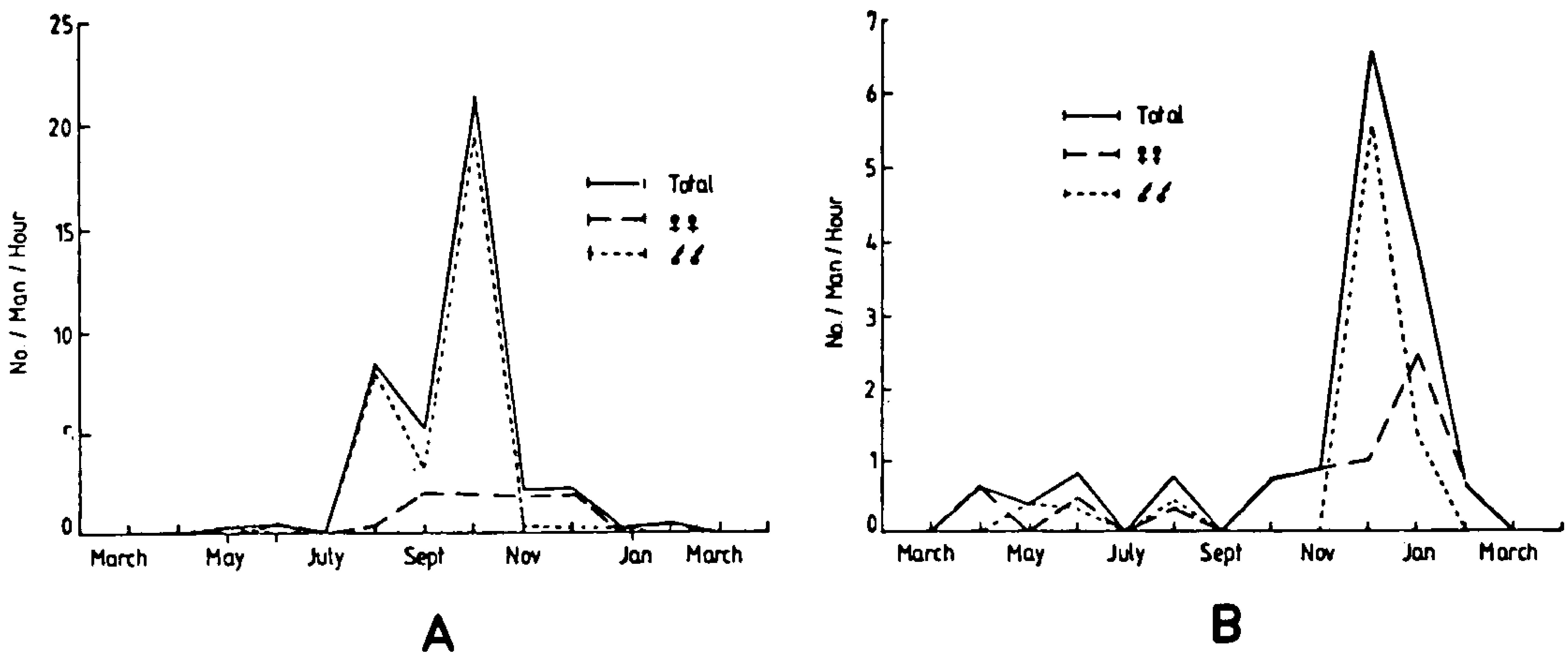


Fig. 5: Seasonal fluctuation of *L. shannoni* (A) and *L. olmeca bicolor* (B) at San Esteban, Venezuela (March 1979-1980).

TABLE II

Analysis of Deviance. Degrees of freedom, deviance, mean deviance and significance levels for "common" non-antrhopophilic species at San Esteban, Venezuela

Factor		*L. trinidadensis*		*L. atroclavata*		*L. cayennensis*	
	DF	Dev.	Mean Dev.	Dev.	Mean Dev.	Dev.	Mean Dev.
Month	11	36.00	3.27**	10.12	0.92 –	31.10	2.83**
Climatic Factor	1	Mean Min. RH 12.00**		Max. Rainfall 1.44 –		Max. Rainfall 6.40*	

***P <0.001 **P <0.01 *P <0.05 – No significant

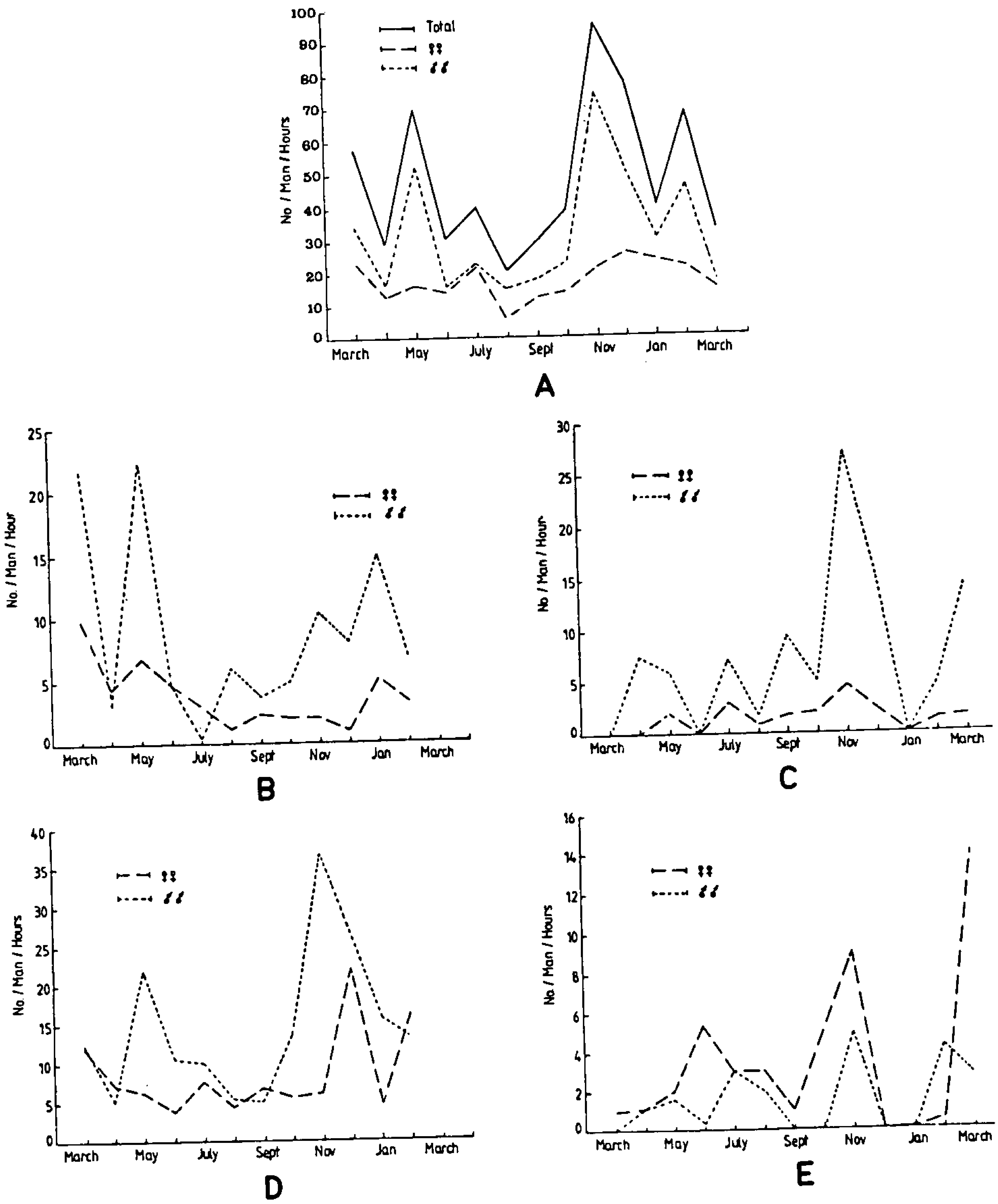


Fig. 6: *L. trinidadensis* – Seasonal fluctuation of the total population (A). Monthly collection in peridomestic habitat: during the day (B), at night (C); monthly collection in sylvatic habitat: during the day (D), at night (E).

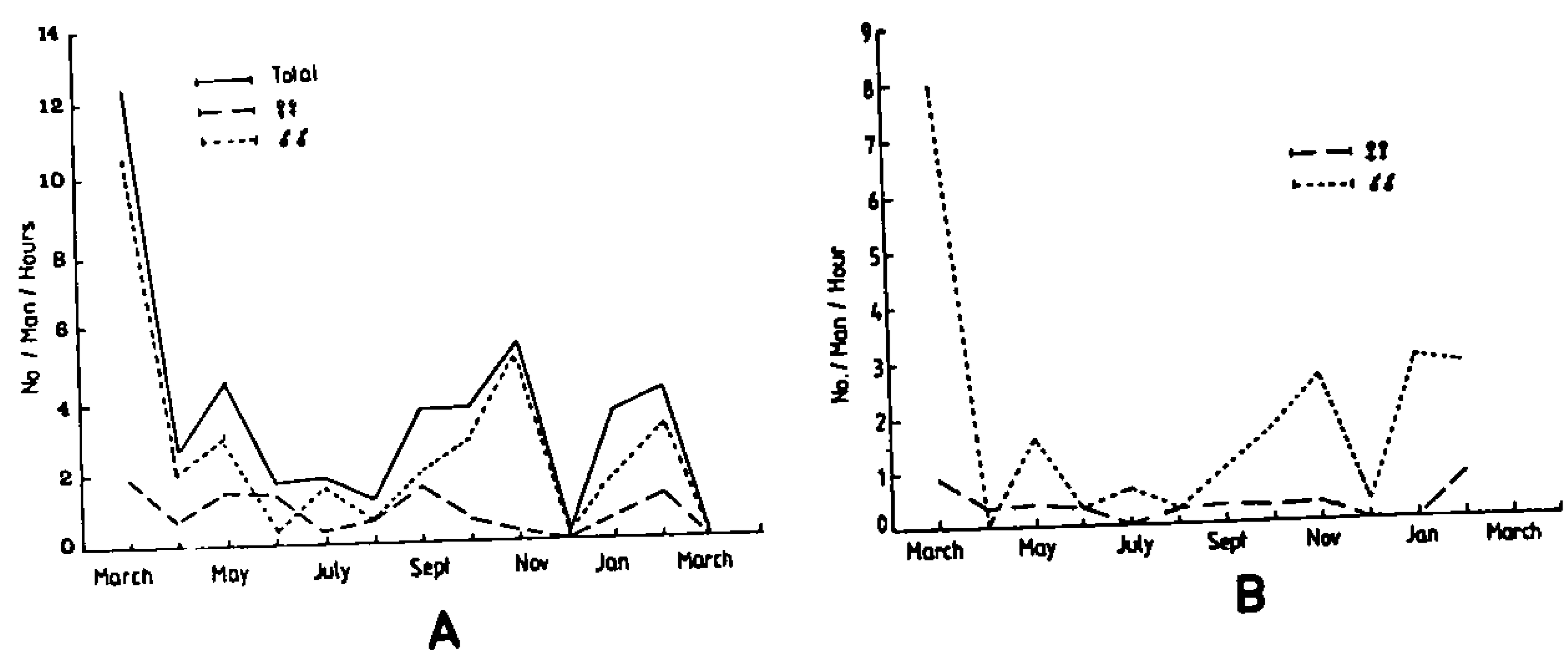


Fig. 7: *L. atroclavata* – Seasonal fluctuation of the total population (A). Monthly collection in trees at day-time (B).

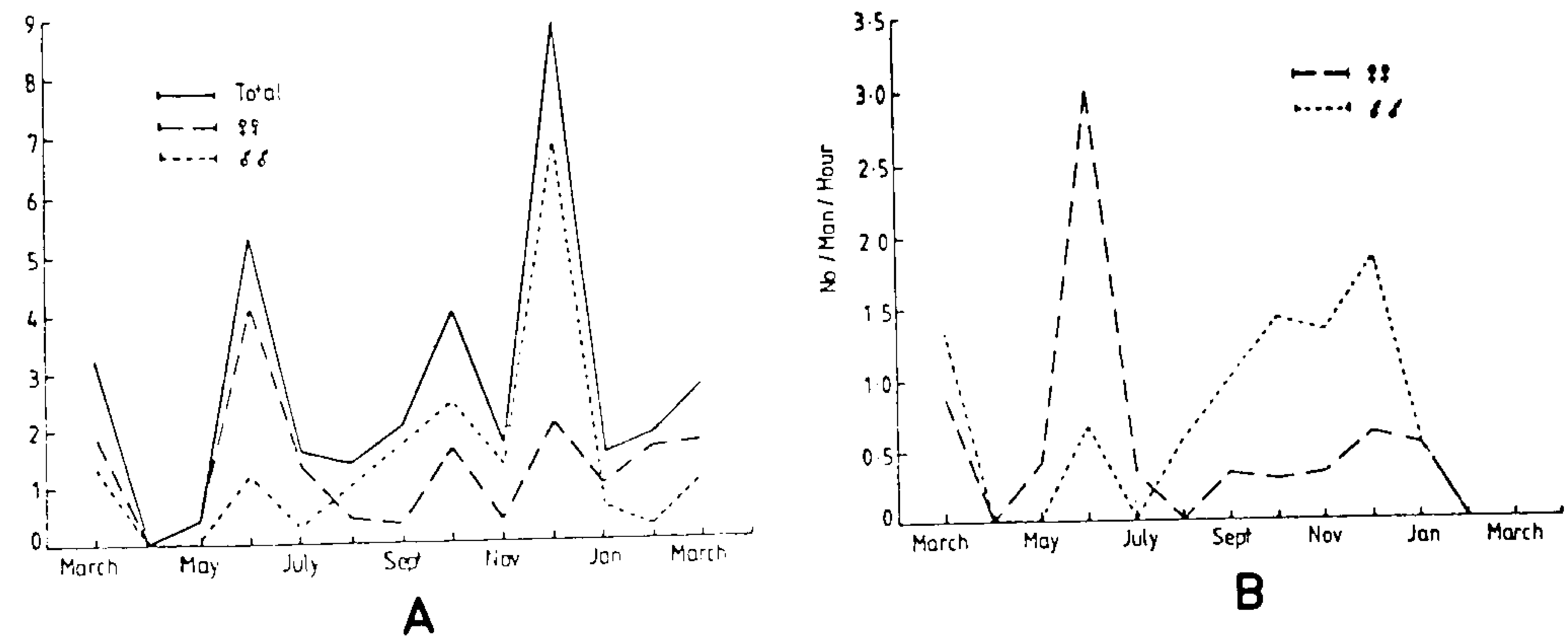


Fig. 8: *L. cayennensis* – Seasonal fluctuation of the total population (A). Monthly collection in trees at day-time (B).

DISCUSSION

Long-term studies on the population dynamics of a vector species are of inestimable value in planning a control strategy and for determining the most effective time to plan out an attack (Killick-Kendrick, 1978). Seasonal fluctuation in population density which results from the changing metereological patterns in different geographical regions has been widely studied. In the Neotropics, mean daily temperatures may differ by only two or three degrees throughout the year and, therefore, have little effect on sandfly populations. In this part of the world, rainfall and the consequent levels of humidity appear to be the most important determinants of the seasonal density of many species of sandflies. It has been observed that the pattern of seasonal variation of a fly population differs from that of the area studied. Such variation may be the result of local metereological fluctuation and differences in the biotic and abiotic characteristics of each region. Occasionally, very severe or very mild weather may also cause unusual troughs or peaks in a sandfly population. In spite of all these variables, a general pattern predominates in the Neotropics, i.e., an increase in population density during the wet season followed by a decrease in the dry season (Barretto, 1943; Pifano et al., 1960; Scorza et al., 1968; Chaniotis et al., 1971). This pattern exists for all but a few species which show increases in the dry season. The behaviour of each species varies so little over successive years or areas that the terms "wet season species" or "dry season species" have often been used to describe a fly (Chaniotis et al., 1971; Rutledge et al., 1976).

Anthropophilic species

L. panamensis – This species, considered primarily as a wet season species in Mexico, Panamá and Colombia (Biagi & Biagi, 1953; Chaniotis et al., 1971; Rutledge et al., 1976; Christensen & Herrer, 1980; Porter & De Foliart, 1981) showed the same tendency at San Esteban (Venezuela). The population density was lowest from February to May. This coincided with the dry weather when the normal habitats available for sandfly breeding would be unsuitable for that purpose. Sandfly eggs, larvae and pupae are known to be highly susceptible to extreme conditions of dryness. The wetting of the forest ground improves breeding conditions substantially and an increase in the population size is evident after the first rain. However, once the rainfall exceeded 100mm the adult population size decreased. A similar pattern has been observed and discussed in other places and with other species. In Panamá, Chaniotis et al. (1971) indicated that excessive dampness and immersion in water kill the immature stages of sandflies. When Rutledge & Ellenwood (1975a) studied the production of phlebotomine sandflies on the open forest floor in Panamá, they obtained the smallest collection of *L. panamensis* during the rainy season. Frequent erosion of breeding sites is known to occur (Rutledge & Mosser, 1972; Rutledge & Ellenwood, 1975b).

The man-biting activity of *L. panamensis* reached a maximum in the domestic and peridomestic habitats two months earlier than in the sylvatic habitat. By the time biting activity had peaked in the sylvatic site, late in the wet season, the activity in the two other places was falling. This result suggests that there are two separate populations, experiencing different biotic and abiotic conditions. There is probably a stable peridomestic population and all *L. panamensis* approaching houses at dusk do not, therefore, come from sylvatic resting places (Pifano et al., 1960). Doubt is, therefore, cast on the value of "clearing, development of the land and thinning of trees" which Rutledge et al. (1976) suggested as a method of control for this species. Low relative humidity appears to influence strongly the fly population. Humidity is different between the sylvatic and peridomestic habitat, becoming quite humid (60% minimum) some months earlier than the other. Breeding sites may be more easily damaged by heavy rain pools around houses than in sylvatic habitats where the natural processes of absortion, percolation and seepage are not disturbed.

L. gomezi – This species was considered as a "dry season species" at Gamboa, Canal Zone, Panamá (Chaniotis et al., 1971), at Sasardi, Panamá (Christensen et al., 1972) and on the Pacific coast of Panamá (Christensen & Herrer, 1980) but behaved as a typical wet season species elsewere in the Panamá Canal Zone (Rutledge et al., 1976). The population dynamics of adult populations of *L. gomezi* at San Esteban seemed to reflect two different situations in the peridomestic and in the field habitats, as seen in *L. panamensis.* For six months from the late dry season to the early wet season (March to August), the fly density was very low. A population explosion, mostly of male flies, occurred in the peridomestic habitat in the second half of the wet season. The population then began to fall with further rainfall but a second peak was later observed at the beginning of the dry season. In contrast, in the sylvatic habitat, the maximum population density was reached in February; thus, in that area *L. gomezi* behaved as a typical dry season species. Local factors, might in part explain this variability which may not be "an aberration" as defined by Rutledge et al. (1976). These same authors pointed out that breeding populations of *L. gomezi* are more strongly affected by local and seasonal factors of the environment than those of *L. panamensis.*

L. ovallesi seasonal fluctuation at San Esteban shows that this species is a true "dry season species" as was observed also in Panamá (Christensen & Herrer, 1980). The sudden population explosion of this species after a long period of virtual absence and its equally sudden disappearance a short time later, constitutes a peculiar feature. The temporal distribution of adult population of *L. ovallesi* and *L. panamensis* in this area seem to be remarkable: *L. ovallesi* arrives just when the *L. panamensis* population is declining and replaces it very successfully as a manbiter.

The virtual absence of *L. ovallesi* during the long period of heavy rains is probably a result of either asthenobiosis or diapause of an immature stage which allows this species to survive in the adverse conditions. The phenomenon of asthenobiosis has been suggested by Scorza et al., (1968) to explain sharp rises in the size of sandfly populations immediately after the first rains. This involves the arrested development of an immature stage which is "reactivated" as soon as moisture levels rise. The dormancy induced and terminated immediately by changes in temperature or moisture has also been used to explain quiescence of sandfly larvae in laboratory conditions (e.g. Killick-Kendrick, 1978). A true diapause involves a prolonged and predetermined period of arrested development of an insect, which is not immediately reversible and which is the result of intrinsic rather than extrinsic factors (Ready & Croset, 1980). Diapause, which was well studied in larvae of some Paleartic sandflies (Ready & Croset, 1980), has also been observed in eggs of the Neotropical sandfly *L. lainsoni* (Fraiha & Ward, 1974) by Ward & Killick-Kendrick (1974) and in fourth-instar larvae of *L. whitmani* (Antunes & Coutinho, 1930) by Barretto (1941). However, no observations of diapause or quiescence have been reported for *L. ovallesi.* Further studies in laboratory conditions will help to explain the ecological patterns of this anthropophilic species.

Non-anthropophilic species

L. trinidadensis – Because of its abundance, this species deserves some comments. The three peaks in the size of the adult population at San Esteban, suggest a direct correlation with the rainfall. Some of the concepts expressed above seem also to be applicable to this species. Excessive rainfall in the late wet period seems to affect population density. No clear differences were observed in the dynamics of peridomestic and sylvatic populations.

RESUMO

Ecologia dos flebótomos em um foco restrito de leishmaniose cutânea no norte da Venezuela – III. Flutuação sazonal – Foi feito durante um ano (março de 1979 a março de 1980) um estudo em um foco endêmico de leishmaniose tegumentar na Venezuela Setentrional a fim de observar a flutuação estacional das espécies de flebotomíneos. Foi analisada a influência dos fatores climáticos (temperatura, umidade relativa e índice pluviométrico) em três sítios de coleta – uma casa, uma área peridomiciliar e uma área selvática – sobre a dinâmica populacional dos flebotomíneos.

Entre as espécies antropofílicas, a *L. panamensis* comportou-se como uma espécie de estação úmida sendo a umidade relativa mínima média o fator crítico que influenciou o número total de indivíduos. Quando diminuia a densidade populacional dessa espécie, era ela substituída com sucesso pela *L. ovallesi*, uma espécie de

estação seca. De outro lado a variação estacional de *L. gomezi* era mais fortemente influenciada pela temperatura.

Palavras-chave: ecologia de flebótomos – leishmaniose tegumentar – norte da Venezuela – flutuação estacional

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