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Population fluctuations of mosquitoes in the non-seasonal tropics

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ABSTRACT. 1. Seasonal and annual fluctuations in abundance of a number of species of mosquitoes were studied in a relatively non-seasonal climate near Almirante, Panama.

2. The fluctuations observed were large, but did not have a period of 1 year and should be classified as non-seasonal.

3. At each site the various species were not synchronous in their fluctuation pattern, but the fluctuations of each species were synchronous over an area of at least 4 km long, in spite of large differences in habitat.

4. Changes in abundance from year to year observed in these mosquitoes are large compared with those of insects, including mosquitoes, in other areas of Panama.

5. The importance of such large and unpredictable fluctuations in abundance for planning control measures is discussed.

Introduction

The control of any insect species is made the easier the more predictable the fluctuations in abundance of that species, e.g. because of predictable seasonal changes in the environment. There is ample evidence that seasonal fluctuations in abundance are commonplace in the tropics (for references see Wolda, 1978a, 1979a). However, almost all of the available data from the tropics are from areas where distinct dry and wet seasons alternate and very few studies are available from relatively non-seasonal areas. Really non-seasonal climates may not exist, but the weather pattern is some part of Panama approaches that situation rather closely. Studies in one such area, Fortuna (Wolda, 1980a; unpublished data), show that there is a clearcut tendency towards fluctuation patterns which are less seasonal than in parts of the tropics where predictable dry seasons do occur. This is hardly surprising. However, in spite of the apparent lack of seasonality in the weather pattern, several species of insects, in various orders, are highly seasonal in their presence as active adults.

The seasonality of tropical mosquitoes is strongly affected by the availability of suitable breeding sites, which in most localities is correlated with the rainfall pattern (Standfast & Barrow, 1968; Page, 1967; Grjebine *et al.*, 1977; Galindo *et al.*, 1956). In areas, therefore, where precipitation does not vary appreciably throughout the year, one might expect seasonal fluctuations in mosquitoes to be absent. Some data point in this direction. The same species which occur virtually only during the rainy season at Cerro La Victoria in Central Panama (Galindo *et al.*, 1956), occur throughout the year in Almirante, in NW Panama, where distinct dry seasons do not occur (Trapido & Galindo, 1957).

In the present paper we analyse collections of mosquitoes made near Almirante from early 1966 through early 1969 and demonstrate that several species fluctuate widely in

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abundance in the relatively non-seasonal climate, but that the fluctuations are mostly non-seasonal in character.

Materials and Methods

The study area

Almirante, at 82° 24′ W; 9° 17′ N, is a coastal town in the Panamanian province of Bocas del Toro, with an annual rainfall of 2500 mm and no predictable dry season. There are no rainfall records from Almirante for the study period, but there are from Changuinola, also in the lowlands, some 20 km NW of Almirante, and these are presented in Fig. 1. Annual maxima in rainfall tend to occur around April and December and minima around February and September. The latter months, however, are far from dry.

In the lowlands near Almirante the annual variation in mean temperature is small. It ranges from 24°C in December to 26–27°C in May (Caballero, 1979). Mean maximum and minimum temperatures are some 4 or 5 degrees above and below these values respectively and show the same annual variation.

Samples of mosquitoes were taken in various places around Almirante. The Filo del Riscó is a ridge South of Almirante. The other localities are in the lowlands within 3 miles NW of Almirante. Patoistown is a waterfront section of the town of Almirante itself. Tucan is in a swamp forest, a brackish water association consisting mostly of 'orey' trees (*Campnosperma panamensis*). Weatherborn is in a swampy palm forest which occurs landward of the 'orey'-swamp. Bambu is in a young second growth situation and Campamento is in an area where the forest has been cut extensively.

Mosquito collections

Following an outbreak of yellow fever near Almirante in 1951, a long-term project was started to monitor mosquitoes and arboviruses in that area. For details of the mosquito species occurring in the area see Trapido & Galindo (1957) and Galindo *et al.* (1966). Collections were made in several localities, at various occasions, using various techniques. The data selected for analysis here are the longest series available. These were all made on human bait and, with the exception of Patoistown, in the canopy of trees. In Patoistown the collections cover all of 1966 and last well into 1968 with only a short interruption in early 1967. In the other localities, Tucan, Weatherborn, Bambu and Campamento, the series of collections also started at the beginning of 1966 but continued until April 1969 with only occasional interruptions.

The number of collections per unit of time was far from constant so that the data had to be standardized. It was decided to take periods of 4 weeks as a time unit, there being thirteen such units per year. The average number of collections per 4-week period was about 10, so that for each period the number of individuals caught for each species was con-

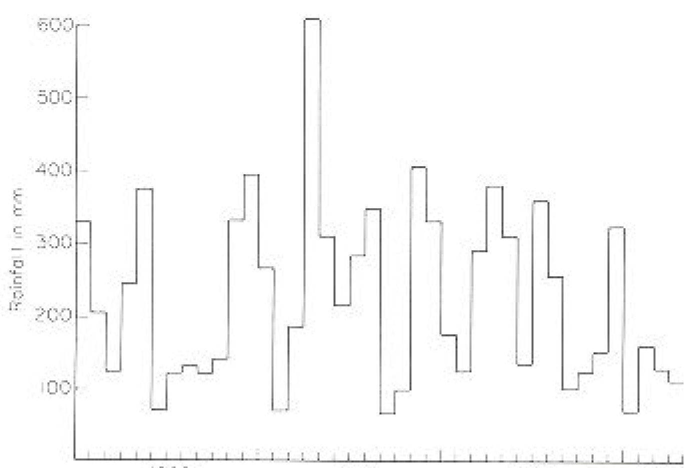

FIG. 1. Rainfall in mm per month in Changuinola, 20 km NW of Almirante, province of Bocas del Toro, Panama.

verted to the number per ten collections. All specific names are according to Knight (1977).

Annual variability

When discussing fluctuations in abundance it is usually profitable to distinguish between seasonal fluctuations, those which occur predictably within a year, and annual fluctuations, those occurring from year to year. A useful way to analyse annual fluctuations is by calculating the Annual Variability (AV) parameter (Wolda, 1978b) for each set of data.

The number of specimens of species i caught in year 1 is called N_{1i} and in year 2 it is N_{2i}. The change in abundance, the net reproduction, of this species is the ratio $N_{2i}/N_{1i} = R_i$. It is advisable to use logarithms, log R_i. In a sample of n species, a total n values of log R_i are obtained which give a frequency distribution. That distribution is usually roughly normal and can be characterized by its mean and variance. The mean gives information about the tendency for all species together to increase or decrease in abundance during the years concerned. The variance, called Annual Variability (AV) reflects differences between the species. If all species changed more or less in the same way, the value for AV would be small, whereas if some species increased a great deal while others decreased, AV would be large. AV, therefore, can be considered as a measure of stability of the group of species concerned. For further details and problems associated with AV see Wolda (1978b).

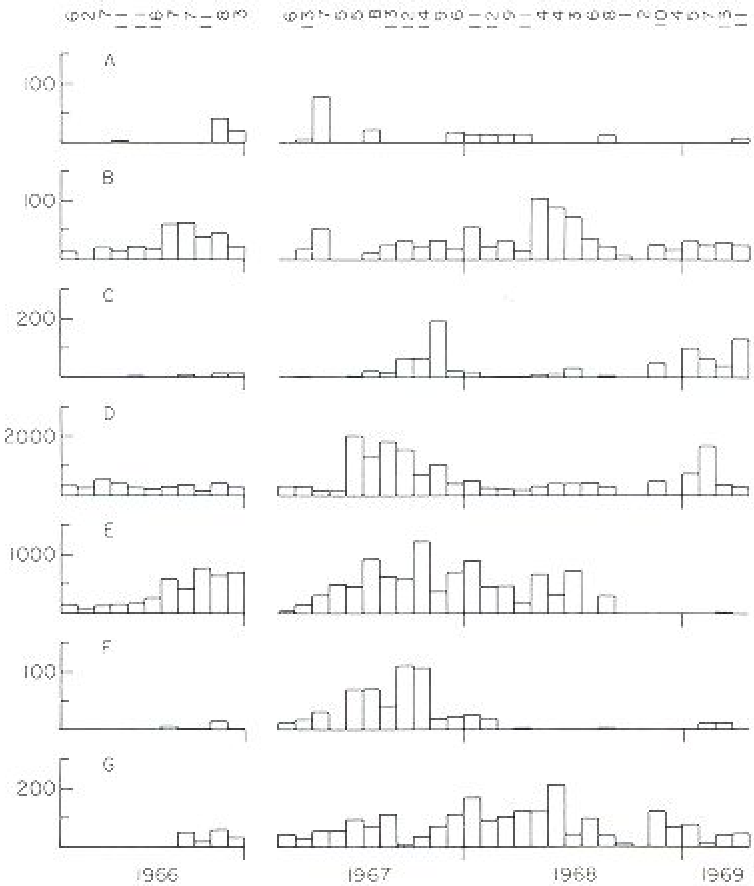

FIG. 2. Number of individual mosquitoes collected on human bait in the canopy of a wet palm forest in Weatherborn, Almirante, Panama. The numbers in each species are given per ten collections in each period of 4 weeks. The actual number of collections for each period is given at the top of the figure. A = *Aedes angustivittatus* Dyar & Knab., B = *Culex epanastasis* Dyar, C = *Culex taeniopus* Dyar & Knab., D = *Culex vomerifer* Komp., E = *Coquillettidia venezuelensis* (Theobald), F = *Coquillettidia arribalzagae* (Theobald), G = *Psorophora cingulata* (Fabricius).

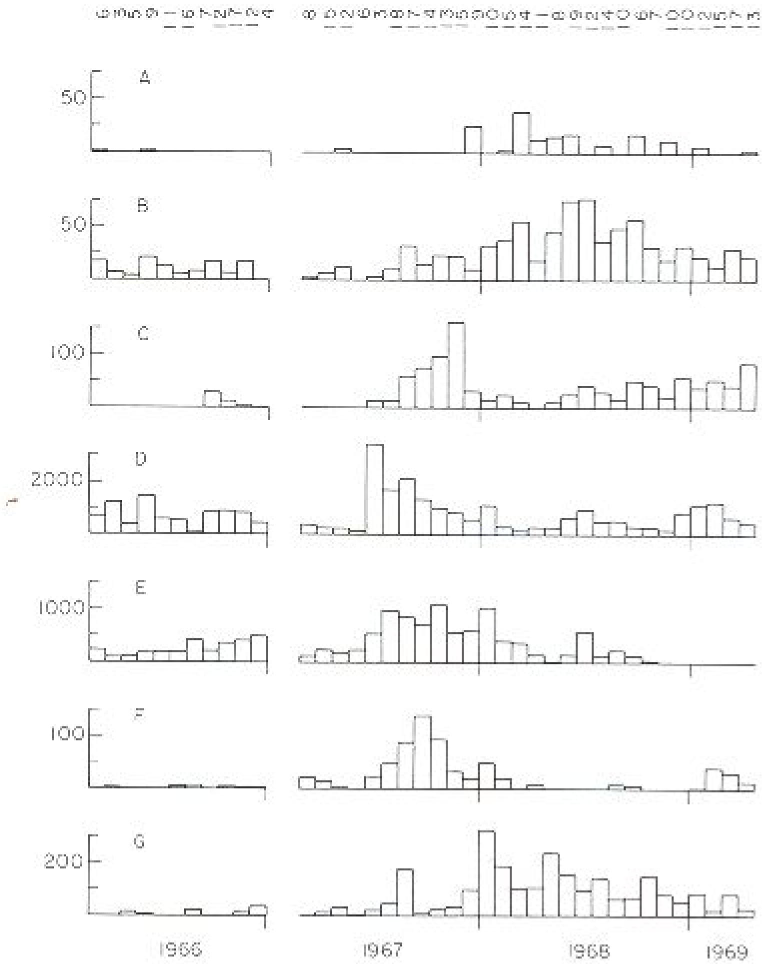

FIG. 3. Number of individual mosquitoes collected on human bait in the canopy at Bambu, near Almirante, Panama. For explanation see Fig. 2.

Results

The data for the more common species taken in the palm forest at Weatherborn are presented in Fig. 2. Similar data from Bambu, an area strongly affected by man about 1.5 km north of Weatherborn, are given in Fig. 3. Because of the variable number of collections per period of 4 weeks, the reliability of the data varies between periods. Above each of the two figures numbers indicate the actual number of collections on which the data in each period are based.

One of the most salient features of Figs. 2 and 3 is that all species fluctuate widely in abundance, fluctuations which cannot be explained on the basis of a variable reliability of the data. Species that are absent, or nearly so, during some part of the study period are abundant or very abundant at some other time. The period of these fluctuations, however, is not 1 year and the fluctuations, therefore, are non-seasonal. At any one locality the various species are not synchronous so that a change in abundance in one species has little or no predictive value for changes which might occur in other species.

The same species are represented in Figs. 2 and 3 and those two figures are remarkably similar in the fluctuation patterns shown. In fact all five localities studied here show fluctuations which, for most of the species, are highly synchronous. In order to demonstrate this, correlation coefficients were calculated for each species between the five sites in the number of individuals per period

TABLE 1. Correlations between five localities in and around Almirante in the number of individuals per 4 weeks for each of seven species of mosquitoes. The localities are Weatherborn (W), Tucan (T), Bambu (B), Campamento (C) and Patoistown (P). Data first transformed to logarithms.

Species	W × T	W × B	W × C	W × P	T × B	T × C	T × P	B × C	B × P	C × P
Aedes angustivittatus	0.444	0.196	0.191	0.044	0.199	0.397	0.191	0.425	−0.008	0.558
Culex epanastasis	0.438	0.530	0.658	0.416	0.591	0.598	0.295	0.323	0.143	0.730
Culex taeniopus	0.688	0.646	0.772	0.845	0.573	0.609	0.666	0.672	0.810	0.696
Culex vomerifer	0.748	0.659	0.470	0.515	0.560	0.428	0.552	0.529	0.715	0.700
Coquillettidia venezuelensis	0.464	0.576	0.557	0.645	0.567	0.110	0.212	0.625	0.594	0.700
Coquillettidia arribalzagale	0.659	0.876	0.739	0.749	0.666	0.716	0.671	0.735	0.801	0.604
Psorophora cingulata	0.848	0.675	0.706	0.856	0.611	0.631	0.734	0.858	0.753	0.694

of 4 weeks, after logarithmic transformation of the data. The results are given in Table 1, showing very little correlation between sites for *Aedes angustivittatus*, but strong to very strong correlations for the other species. This is especially striking considering the sources of error, such as the sometimes low number of collections, in this kind of data. Had the logarithmic transformation not been applied the results would have been more striking still. The average correlation coefficient would be higher by 0.1, and twenty-nine of the seventy coefficients are then over 0.8, with twelve even over 0.9. The apparent exception to this rule of strong synchrony between the sites, *Aedes angustivittatus*, could be interesting, but could also be related to the fact that this is the least abundant of the seven most abundant species selected for this analysis and at lower numbers the correlation coefficient becomes less reliable.

The changes in abundance from year to year, as expressed by the mean and variance (= AV) of log R_i for all sets of data on mosquitoes near Almirante are given in Table 2. Only those species which in both of the two successive years are represented by at least five individuals are included in the calculations (for a discussion of the problems involved see Wolda, 1978b). The means are mostly positive indicating a general increase in abundance of the mosquito species concerned in the study years, with some exceptions. The values of AV range from 0.105 to 0.525 and tend to be high relative to values found elsewhere (Wolda, 1978b, 1979b). In some twenty-seven other sets of data on insects from various places in Panama, including some on mosquitoes (mostly unpublished), the values of AV range from 0.019 to 0.185 and the difference between those data and the ones on the mosquitoes from Almirante is highly significant. The early Almirante data (top three lines in Table 2) fall well within this 'normal' range, albeit in its upper reaches. The data for 1966/67 are well above this, ranging from 0.192 to 0.346 and the ones for 1967/68 are significantly higher again.

Discussion

The climate in Almirante is much less seasonal than that in most parts of Panama, but does have recognizable seasonal features, both in rainfall and in temperature. Many organisms could, and probably do, use seasonal clues to determine the time for reproduction, emergence, flowering, leaf production, etc. However, for some organisms the environment could be effectively non-seasonal. In fact, even in parts of Panama where there is a pronounced dry season of some 4 months duration, there are some insect species which do not show any seasonal changes in abundance at all (Wolda, 1980b, c). In an area

TABLE 2. Variation in abundance from year to year as measured by the Annual Variability (AV) for mosquitoes near Almirante, Panama. All samples are taken on human bait except the one labelled 'Almirante' which comes from a light-trap. K = degrees of freedom. For further explanation see text.

Locality	Years	*K*	Mean log *R*	Var log *R* = AV
Filo del Riscó	1951/53	15	0.152	0.177
Almirante	1959/60	6	0.134	0.105
Campamento	1962/63	16	−0.098	0.140
Campamento canopy	1966/67	16	−0.191	0.215
Bambu ground	1966/67	13	0.304	0.222
Bambu canopy	1966/67	19	0.318	0.232
Weatherborn ground	1966/67	11	0.335	0.192
Weatherborn canopy	1966/67	16	0.390	0.346
Tucan canopy	1966/67	13	0.424	0.295
Patoistown	1966/67	13	0.449	0.311
Campamento canopy	1967/68	16	−0.170	0.349
Bambu canopy	1967/68	15	−0.274	0.261
Weatherborn canopy	1967/68	15	0.045	0.525
Tucan canopy	1967/68	13	0.137	0.435

near Fortuna, where the climate is much less seasonal even than in Almirante, insect species which show little or no seasonal changes in abundance are more common (Wolda, 1980a; unpublished data). However, in the majority of these cases the alternative to seasonal changes is gradual change or constancy. The mosquitoes discussed here demonstrate another alternative, that of rapid, large, unpredictable variation. A detailed knowledge of the fluctuation pattern for one year has little or no predictive value for the pattern next year.

The causes of these fluctuations in abundance and of the differences between the species are not known. One should keep in mind that the data presented refer to adult insects only, while it seems probable that the events in the aquatic environment of the larvae are of paramount importance in determining numerical fluctuations. We have no information on adult dispersal in these mosquito species. If they would tend to stay near the site of emergence the synchrony of the fluctuations over an area at least 4 km long would be difficult to explain. One would have to assume that the same factors affect the mosquito populations in the urban environment of Patoistown as in the forests of Weatherborn and Tucan and the rural environments of Campamento and Bambu. It seems much more likely that the synchrony of the fluctuations of the adults over a relatively large area is caused by adult dispersal, similar to the suggestion by Disney (1975) for blackflies in Cameroon.

The most likely candidate for an environmental factor involved in the determination of the variations in abundance is some feature of the weather, especially rainfall. The data on rainfall per month (Fig. 1) do not seem to provide a clue, but these monthly totals could be very misleading about the actual weather in those months. Rainfall is very erratic in this area and the entire monthly total may fall in one 24 h period or it may be evenly distributed over the month. The actual pattern could be significant, but we lack the data to test this idea. Whatever the cause of these large fluctuations, it produced especially large changes in abundance from 1966 to 1967 and, again, from 1967 to 1968, as is shown by the unusually large values of AV (Table 2).

In order to plan control measures against the mosquitoes in an area like the one near Almirante one cannot rely on data obtained in previous years, because the occurrences in one year have little or no predictive value for those in the next year. One has to have a continuous monitoring programme for the mosquitoes in order to be aware of increases and decreases in abundance of the important species. However, one only needs to set up a monitoring station in one locality in order to predict changes in abundance over a fairly large area.

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