# Contributions in Biology and Geology

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## In Northwestern Costa Rica

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*Abstract:* The annual peak emergence periods for the adults of several species of cicadas (Homoptera: Cicadidae) and their habitat associations are summarized for the lowland tropical dry forest region of northwestern Costa Rica. The basic observations involved repeated census of recently discarded nymphal skins (recognizable for each species) and visual and auditory searches for adults in forest or highly disturbed habitats (yards) at several localities in this region. Given the occurrence of a pronounced annual dry season lasting about six months and the availability of several distinctive habitats (forest patches, city yards, beachfront yards, secondary growth, etc.), as expected, different cidada species exhibit allochronic emergence periods and have different habitat associations, whatever selective mechanisms operate. Records were kept for the individual canopy-size trees having an abundance of nymphal skins at each study site. The cicadas studied included *Zammara smaragdula* Walker, *Fidicina mannifera* (Fabricius), *Diceroptocta* sp., and *Proarna* sp., with notes on others such as *F. pronoe* Walker, *F. amoena* Distant and *Pacarina* sp. The study sites covered a long transect from Puntarenas to Santa Rosa National Park near the Nicaraguan border, and studies were conducted from 1973-1980. As with previous studies of cicadas at wet or moist forest localities in other regions of Costa Rica, definite peak adult emergence periods, habitat associations, and clumping of nymphal skins around particular trees (especially Leguminosae) in both forest and yards were found for the tropical dry forest region. Three basic strategies of seasonal peak emergence were found: wet season cicadas, dry season cicadas, and transitional cicadas (from dry to wet seasons).

## INTRODUCTION

Two distinct ecological features of the northwestern lowlands of Costa Rica are (1) the annual occurrence of a pronounced dry season extending from December to May, and (2) the spatially very patchy distribution of adult-size primary forest trees generally limited to riparian forests (Fig. 1), steep hillside forests, scattered small patches of forest in grazed and regenerating pasturelands, and yards. This lowland tropi-

cal dry forest region of Costa Rica includes the major portion of the Guanacaste Province and the northern tip of Puntarenas Province. A large portion of the forest tree species of the region synchronize flowering with the dry season and also drop their leaves during this period (Janzen 1967). There are also substantial changes in the species composition and population structures of the insect communities between wet and dry seasons, with larger-bodied insects comprising the bulk of insect biomass during the dry season in several types of habitats (Janzen and Schoener 1968; Schoener and Janzen 1968). The present paper describes the seasonal adult emergence patterns for several species of cicadas (Homoptera: Cicadidae) thriving in different habitats within the lowland tropical dry forest zone of northwestern Costa Rica. Emphasis is placed on the determination of periods of peak adult activity for each of seven species, and the habitat associations of each species. These studies complement previous studies of cicada populations in other climatic regions of Costa Rica (Young 1972; 1975; 1980a, b) and one study of *Pacarina* cicadas in Guanacaste Province (Young 1974). The general conclusions of the present study are that some species exhibit peak emergence in the wet season and others in the dry season, and that each species is associated with a particular habitat, and sometimes with particular tree species.

## METHODS AND STUDY LOCALITIES

The basic method used in this field study was to examine the occurrence of various species of cicadas in different habitats within the lowland tropical dry forest region (lowland Guanacaste Province and portion of Puntarenas Province) of Costa Rica be censusing recently discarded nymphal skins of each species, and by noting dates of the year when adults of each species were heard chorusing in these habitats.

The general terrain encompassed by the localities visited consisted of flat plains and rolling hills; all study sites were well below 200 meters elevation (Fig. 2). The decision to limit censuses below 200 meters elevation was not entirely arbitrary, but based largely upon my observation that the lushness of the vegetation at many sites in this region of Costa Rica increases noticeably above this point during the dry season, thereby perhaps altering the patters of seasonal emergences of cicadas in the tropical dry forest lowlands. A separate paper will concern the distribution of cicada species on the western slopes of the Central Cordillera at sites above 200 meters elevation.

The studies extended from 1973 to 1980, with from one to several visits at one or more localities each year. Following an initial period of discovering localities and habitats where adult emergences of one or more cicada species were dense, specific census plots were established for repeated censuses over several years. Visits were made

to the various sites during both wet and dry seasons in order to determine seasonal patterns of emergence. In cases where gound plots, usually 5 x 6 meters, were beneath individual large trees in forests or yards, nymphal skins were collected from the tree itself as well as from the ground and lower vegetation within the plots. When larger plots were used, nymphal skins were always collected from all trees, other vegetation, and from the ground. The object was to make exhaustive collections of nymphal skins from the plots for each census date. My censuses were limited to fresh nymphal skins in all cases. These are nymphal skins belonging to the current year's emergence and excluding those from previous years. Old nymphal skins are easily detected, being discolored and often broken. Vouchers of adult cicadas were collected whenever possible along with samples of nymphal skins for further studies. Censuses of nymphal skins generate reliable data on periods of peak adult emergence, sex ratio trends, and other populational information (e.g., see Young 1972; 1974; 1975; 1980a, b for Costa Rican species). However, various sources of error may arise when censusing nymphal skins. In the present study, nymphal skins were censused in yards at some localities. Periodic raking of yards undoubtedly results in the removal of some skins, and strong rains and winds can bring into study plots nymphal skins from emergences outside, and such effects can also remove nymphal skins from plots. Every attempt was made to census nymphal skins in the same fashion for all plots at all localities, taking special care to check for nymphal skins in piles of raked leaves and debris.

Given the vast size of the lowland Guanacaste Province, my studies comprise only a very small portion of the cicada habitats found there. Yet the localities and habitats selected are fairly representative of the region. Rainfall data were not obtained for the years of study, although the general pattern for the region is very similar to that reported in Janzen (1967) for a several year period. A long and pronounced dry season occurs between December and May each year.

The following is a description of the localities and habitats where cicada populations were studied by censuses of nymphal skins, and where adult cicadas were heard chorusing.

**Puntarenas.** The Pacific port city of Puntarenas (9°30′N, 84°35′W; 50 m elev.), Puntarenas Province. The region is generally semi-decidious to fully deciduous tropical dry forest, heavily disturbed, with riparian and other pockets of forest remaining. Several species of canopy-size trees are found in yards and open pastures, generally scattered as isolated individuals. The region is a patchwork of open grasslands, yards with large trees, and scattered forest. Study sites were the following: (1) "inner city yards" — one yard, about 500 m² associated with a private residence; this yard containing 5 adult-size trees, including *Tabebuia* sp. (Bigno-

niaceae), *Tamarindus indica* L. (Leguminosae), and an unidentified species of Lecythidaceae. Second yard: about 600 m² and associated with a restaurant ("La Arenas") and containing several tree species including *T. indica*. This site was excavated as of February 1974 and replaced with a building. Yards at both sites were periodically raked. The ground cover is very sparse. (2) "city limits yard" —. a large (2400 m²) yard associated with a sprawling farm building and house complex about 5 km from downtown Puntarenas and along the left side of the main highway artery as you leave the city traveling east. The dominant feature of this site is a conspicuous row of adult-size *Chrysophyllum mexicanum* Brand ex Standl. (Sapotaceae) trees (known locally as "Caimito") bordering the roadside edge of the yard (Fig. 3). The yard also contains scattered adult-size Leguminosae (at least 7 other individuals) excluding *Enterolobium cyclocarpum* ("Guanacaste tree") (Fig. 3). Other legume trees including *Cassia moschata* H.B.K. scattered in adjacent pastures.

**Barranca Forest.** A large rectangular tract of lightly disturbed to undisturbed semi-deciduous tropical moist forest (roughly 700,000 m²; 50 m elev.) located along the Pan-American Highway, along the left side driving toward Cañas from San Jose to lowland Guanacaste Province. The locality is about 2 km north of the turnoff to Miramar and in the Puntarenas Province. A detailed description of the site is given in Orians (1969). From the standpoint of cicada biology, an interesting feature of the site is an area covered primarily by advanced secondary forest with patches of primary forest, and an expansive northern lower area of primary forest with a border of advanced secondary forest. In the upper area, a common tree is *Guazuma ulmifolia* Lam. (Sterculiaceae) while in the *Scheelea* palm-dominated lower area common trees are *Samanea saman* (Leg.) and *Enterolobium cyclocarpum* (Leg.). A year-round stream cuts through the flat lower area which resembles a sandy floodplain dominated by a palmaceous understory. Immediately north there is a strip of dense secondary forest with a border of trees such as *Ochroma* sp. (Bombacaceae). The whole forest is an island in a region dominated by rolling pastures with strips of riparian forest.

**Playas del Coco.** The pertinent area consists of beachfront yards and one short strip of trees immediately behind the beach and at the bottom of a hill (Figs. 4 and 5). The site is on the Pacific coast in northern Guanacaste Province, with an elevation of 2-6 m and about 20 km from Liberia (10°45′N, 85°40′W). The study sites consisted of several yards associated with summer homes along the beach. The common tree species in the yards and along the beachfront forest strip was *Tamarindus indica* L. (Leguminosae).

The above localities were the major study sites for cicada censuses,

being selected on the basis of discovering where nymphal skins were generally abundant. In addition, less regular observations were also made at localities in Guanacaste such as "Finca La Taboga" near Cañas, and Santa Rosa National Park north of Liberia (Fig. 2). For example, *Zammara smaragdula* was studied in a patch of dry forest on a hillside at Finca La Taboga.

The following is a summary of the census program for nymphal skins associated with trees or plots of vegetation at the three major study sites:

(1) **Puntarenas** — Census of nymphal skins of *Proarna* sp. and *Diceroprocta* sp. on or at the base of trees in each of the two "inner city yard" sites and the "city limit yard" site. Censuses taken as follows: (1) inner city yard ("Fernando's site"): 30 January, 2, 10, 28 February, 2 March, 14 April, 9, 31 May, 20 June, 28 July, and 20 August 1973; 12 July, 2, 17 August 1974; 20 January and 20 July 1976; 24 February 1977 (area destroyed prior to this date). (2) city limits yard: 21 June and 27 July 1973; 10 July and 2 August 1974; 10 April and 29 July 1976; 25 February and 27 August 1977; 20 February and 10 August 1978; 21 March 1979; 16 February 1980. Nymphal skins at the "city limit yard" site were collected from and beneath *Chrysophyllum mexicanum, Enterolobium cyclocarpum* and a few other legume trees, for a total of 16 trees (9 of which were *C. mexicanum* in single row) censused on each date. More than 90% of the nymphal skins of *Diceroprocta* sp. and *Proarna* sp. collected in this yard were from these trees. Most of the nymphal skins for both species were found attached to the tree trunks and very few on the ground.

(2) **Barranca Forest** — Census of nymphal skins of *Zammara smaragdula* and *Fidicina mannifera* within 5 x 6 meter plots beneath 6 large forest trees in primary forest area *(Samanea saman; Enterolobium cyclocarpum),* and within a 30 x 15 meter plot in the level secondary forest area north of the primary forest. Censuses were taken only during the wet season as follows: 29-30 July and 21 August 1973; 10 July, 3 and 18 August 1974; 30 July 1976.

(3) **Playas del Coco** — Censuses of *Diceroprocta* sp. (same species as that found in *Puntarenas)* and occasionally *Proarna* sp. and *Pacarina* sp. beneath and on a total of 35 *Tamarindus indica* trees in beachfront yards and at the juncture between beach and hillside forest. Twenty-one trees, with range of DBH of 15-30 cm, were located in several beachfront yards about 10-20 m from the high-tide shoreline. The remaining trees censused for *Diceroprocta* sp. nymphal skins were located along a stretch of isolated beachfront about 700 m from the yard trees. These forest beachfront trees were contained in a 12 x 4 m plot at the foot of a forested hill ending at the beach. See Figs. 7 and 8 for general views of these sites. Censuses taken on these dates: 29-30 April and 14 May 1975; 19 February, 8 April and 29 July 1976; 26 January 1977; 15 February 1980.

In addition, a census of nymphal skins of *Pacarina* "sp.-1" (see Young 1974 for a discussion of *Pacarina* species in the region) and a 4 x 3 meter ground plot of dried grasses was taken on each of two dates (8 April 1976, 26 January 1977) near the Historical House landmark at Santa Rosa National Park. Very limited observations on emergences and adults of *Fidicina amoena* and *F. pronoe* were made here. The area is a patchwork of grasslands and various kinds of forest habitats with dry forest predominating.

The census of nymphal skins generated adult emergence data for part of the year for the following species of cicadas: *Fidicina mannifera* (Fab.), *Zammara smaragdula* Walker, *Diceroprocta* sp.\*, *Proarna* sp.\*, and *Pacarina* sp. Clearly most censuses were taken in the dry season or early wet season thus giving a somewhat incomplete picture of emergences for wet season species. Because of this bias, the discussion is generally limited to those cicadas that emerge in the dry season or early wet season. The time intervals between censuses at each site were of sufficient length in most instances to allow the accumulation of nymphal skins. Nymphal skins remain more or less intact for several weeks or months, but are damaged more rapidly in the wet season. Intervals between censuses were on the order of weeks or months and each census was exhaustive; peak emergence periods were estimated without testing biases resulting from the periods of accumulation of nymphal skins. In addition to obtaining both nymphal skin abundance data and adult chorusing data for these five species, data on adults of two additional species, *Fidicina pronoe* (Walker) and *F. amoena* Distant, was obtained. All of these cicada species are shown in Fig. 6 along with their nymphal skins. As with previous studies (Young 1980a, b), species such as *F. mannifera* are considered as a "large-bodied" cicada, others such as *F. pronoe*, *F. amoena*, *Z. smaragdula* and *Diceroprocta* sp. as "medium-sized" species, and still others such as *Proarna* sp. and *Pacarina* sp. as "small-bodied" cicadas. The differences in size, profile, and color of the nymphal skins of various tropical species (Fig. 6) facilitate field identification, particularly when more than one species emerges in the same habitat. Although quantitative data on nymphal skins was obtained only on certain dates at each locality, each locality was visited at least once in each season and records taken of cicadas heard chorusing. Several such visits were made to the Barranca Forest in the dry season in particular, even though censuses of nymphal skins were not taken. The

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\*Both *Proarna* sp. and *Diceroprocta* sp. belong to complexes of very similar species extending from Mexico through much of Central America. It is difficult to assign precise species status to the material studied. Preliminary matching of voucher specimens from this work with previously determined specimens at The Museum of Zoology, University of Michigan, or with color transparencies of type material from European museums, suggests that the *Proarna* is close to *P. olivieri* Metcalf and the *Diceroprocta* close to *D. bicosta* (Walker).

identity of nymphal skins was taken as the evidence for a species being active at a particular time and place. A reference collection of nymphal skins identified by associating known eclosed adults with their nymphal skins was the basis for determining the cicada species emerging at a particular site and time. Although my studies of lowland species and habitats were conducted below 200 meters elevation, some observations on another large-bodied cicada, *Quesada gigas* (Olivier), taken at about 200 m on the western slopes of the Central Cordillera (along the road to the Monteverde Cloud Forest Preserve) in Guanacaste Province, are included. Another small cicada, a second species of *Pacarina*, is found in the region but not included in the present study (see Young 1974). The cicadas studied (Fig. 6) probably represent the majority of species found below 200 meters elevation in the region.

## RESULTS

**Seasonality and Peak Adult Emergence Periods.** The data suggest three basic strategies of seasonal peak emergence: wet season cicadas, dry season cicadas, and transitional cicadas (from dry to wet seasons). Although data for every month of the year are lacking, it appears that *Proarna* sp. emerges in both wet and dry seasons at Puntarenas (Fig. 7 and Table 1). My limited Puntarenas data suggest a peak period early in the wet season (July-August), and rather diffuse annual emergence curve. In sharp contrast is the narrow transitional emergence period for *Diceroprocta* sp. as seen at Puntarenas and Playas del Coco (Tables 2 and 3). *Diceroprocta* sp. exhibits a short emergence period during late April extending into June, with peak numbers (Fig. 8) probably emerging in May. This period is the transitional period between dry and wet seasons at both localities. When samples are small and variance is high, it is often useful to examine variance-mean ratios rather than standard deviations as measures of variation among study plots. The high variance-mean ratios for *Diceroprocta* and *Proarna* nymphal skins (Tables 2 and 3) indicate considerable variation in the numbers of nymphal skins among study plots. The observed higher abundance of female nymphal skins for both *Diceroprocta* and *Proarna* in the Puntarenas samples (Table 2) indicates that these censuses were made after the peak emergence period since female nymphal skins generally appear in greater numbers later in the emergence period in many tropical cicadas (Young 1972; 1975; 1980a, b). Such a pattern is not seen in the earlier censuses of *Diceroprocta* at Playas del Coco (Table 3) since these samples were taken at the peak emergence period. *Fidicina mannifera* and *Zammara smaragdula* emerge during the wet season at the Barranca Forest (Table 4), and adults of these species are conspicuously absent from this habitat during the dry season. The very high variance-mean ratios for both species (Table 4) indicates considerable variation in the size of the emergence associated with different plots in the forest habitat.

Of the two species of *Pacarina* known to occur in this region (Young 1974), one species exhibits emergence near the end of the dry season as indicated by the occurrence of 29 fresh nymphal skins (Fig. 9) in a grass patch (Fig. 10) near the "Historical House" at Santa Rosa National Park (9 April 1980). No skins were found in January samples from this site.

Based on the limited data on nymphal skins gathered over several years, and from records of adult males of each species heard chorusing (Table 5), generalized emergence curves for these species are proposed (Fig. 11). These hypothetical adult emergence curves also agree well with general observations of adult cicadas at other localities throughout Guanacaste Province. Included here are observations at Santa Rosa National Park on *Fidicina pronoe* and *F. amoena*. Based upon records of when males of these two species were heard singing, *F. pronoe* is predicted to emerge late (March-April) in the dry season, being preceded by *F. amoena* which emerges in the early portion of the dry season (Fig. 11). Above approximately the 200-meter elevation on the western slopes of the Central Cordillera, *Quesada gigas* also emerges in large numbers during the late dry season.

**Year-to-Year Evenness of the *Diceroprocta* Emergence.** The generalized emergence curves given in Fig. 11 also show estimates of peak densities of nymphal skins for each species, as an indication of relative abundance among the species. Although no field data on nymphal skins of *F. amoena* and *F. pronoe* are available from Guanacaste Province, my observations on the abundance of these species at other localities in Costa Rica (Young 1980a, b) is the basis for predicting their densities in the present study. The densities used for other species are generated as single means of means from all of the density data summarized in Table 6 and used here as standards for comparing species. These values are: *Diceroprocta*—1.14 nymphal skins/m², *Proarna*—0.26 nymphal skins/m², *Zammara smaragdula*—0.33 nymphal skins/m², and *Fidicina mannifera*—0.15 nymphal skins/m². These values are probably underestimates of true densities since my samples are discontinuous through time for all species and sites. However, they are useful in comparing relative levels of abundance among the species studied and therefore provide a basis for future studies aimed at elucidating the complete emergence patterns and abundance levels for these species in lowland Guanacaste Province. The highly stylized and hypothetical emergence curves shown (Fig. 11) are based on incomplete and discontinuous emergence data and suggest general trends in seasonal emergence for each species. Very likely there exists considerable variation in the total numbers and densities of individuals emerging in each year for each species (Table 6). An example might be *Proarna* sp. as studied in Puntarenas, where considerable variation in the number of nymphal skins, independent of number of censuses, was seen (Fig. 7). Sampling

error might have been introduced for this particular example since the yard site was raked frequently in different years and thee is no reason to assume that raking "error" was the same in different years. Raking removes fallen nymphal skins in the leaf litter. A similar situation for *Proarna* sp. is seen by examining the July-August samples for 1973 and 1974 in Table 2.

An approximation of year-to-year evenness in cicada emergences is shown by *Diceroprocta* at Puntarenas. The population data for the other species studied are too fragmentary to test for year to year evenness. For *Diceroprocta* I am assuming that the highest density figures from my data are, in fact, representative for the emergence period of each species. Any density figure, of course, depends upon the length of the census period and the time of year the censuses were taken. Judging from the condition of nymphal skins and census dates relative to the usual lengths of season at a particular site, I am reasonably sure that data on peak densities are representative for the populations. Therefore, these data can be used to estimate year-to-year evenness, or lack thereof, in emergences of cicadas. Under the null hypothesis that each mean value is equal to all other mean values, the emergence data for each species was examined. The Student-Newman-Keuls Test can be used to measure differences among means and test for significance (Sokal and Rohlf 1969). I applied this test to the observed mean nymphal skin abundances for *Diceroprocta* sp. at the "city limits yard" site near Puntarenas (Table 2). There is no difficulty with using the first samples of nymphal skins found at a particular site in a given year, since it is usually easy to distinguish the current year's emergence from nymphal skins associated with prior years. In the case of cicadas such as *Dicero-procta,* where the emergence is restricted to a relatively short period each year, any possible bias in the data from accumulations of nymphal skins from more than one year is highly remote. Even though it was not always possible to determine the precise beginning and end of an emergence period, because each site was visited several times it was feasible to estimate emergence periods, and certainly to determine periods of peak emergence. I compared the highest means for any census date for five different years (Table 2): (1) 21 June 1973 (11.87 $\pm$ 8.97), (2) 19 June 1974 (7.00 $\pm$ 9.04), (3) 29 July 1976 (7.31 $\pm$ 9.13), (4) 27 August 1977 (3.68 $\pm$ 9.35), and (5) 10 August 1978 (18.06 $\pm$ 34.83 and found **significant differences (P = 0.05 or P = 0.95)** since the maximal range difference was less than the Least Significant Range value of $LSR_5 =$ 16.93.

**Habitat and "Host Tree" Associations.** The census program for nymphal skins and adult cicadas included the examination of primary and secondary forest successional stages as well as highly disturbed yards. *Diceroprocta* sp. emerges in both yard and tropical dry forest habitats,

and exhibits an association with certain tree species. The greatest number of nymphal skins occurred immediately beneath *Tamarindus indica* trees at Playas del Coco, and beneath *Chrysophyllum mexicanum, Enterolobium cyclocarpum, Cassia moschata,* and a few other unidentified leguminous trees at Puntarenas. *Proarna* sp. emerges in the same habitats and also is associated with the same tree species. In addition, this cicada emerges in small yards where *T. indica* (and other leguminous trees) trees occur (Puntarenas) even though *Diceroprocta* sp. is seldom found in such a habitat. On the 14 April and 9 May 1973 censuses, a total of 38 fresh nymphal skins of *Diceroprocta* were collected in this yard, and one more several years later (20 July 1976). *Pacarina* cicadas emerge in clumps of grasses over much of lowland Guanacaste Province. *Pacarina* sp. is primarily a cicada of open grasslands where the nymphal skins are found in patches of tall grass (i.e., Santa Rosa National Park). *Fidicina mannifera* and *Zammara smaragdula* are clearly associated with primary forest leguminous tree species such as *Samanea saman* and *Enterolobium cyclocarpum* in the Barranca Forest, but there is also evidence that both species emerge in advanced secondary forest habitats. The few nymphal skins of *F. mannifera* found within the large study plot for *Z. smaragdula* in secondary forest at the Barranca Forest site were found beneath one *Ochroma* tree whereas the nymphal skins of *Z. smaragdula* were rather evenly distributed over the plot. *Fidicina amoena* and *F. pronoe* are associated with different kinds of forest habitats at Santa Rosa National Park. The former species has been heard in the "Bosque humedo" (humid forest) (see Janzen 1977) in the Park, and the other species has been heard in large numbers on the forested lowland flats. At Finca La Taboga, *Z. smaragdula* nymphal skins and adults have been found at the bottom of the secondary forested hills behind the living quarters for visitors. As with Santa Rosa National Park, a complete survey of the forest habitats at "La Taboga" has not been undertaken.

Most of the nymphal skins encountered on or beneath certain adult trees in this study were clinging to the plants, and not scattered on the ground as if blown in by wind or rain. Association of cicadas with particular tree species is also indicated by the observation that many individuals of a given tree species at a site had nymphal skins on or beneath them. For example, all ten adult *Chrysophyllum mexicanum* at the Puntarenas "city limits" site had nymphal skins of *Diceroprocta*, as did more than 50% of the *Tamarindus indica* trees at Playas del Coco. Neighboring trees had little or no nymphal skins. But the confirmation of cicada-tree associations requires further documentation, with large-scale surveys of all tree species in an area. An abundant tree species such as *T. indica* may have cicadas simply because it is very abundant, or because the cicadas prefer the species as a food plant. Further data are necessary to distinguish between these hypotheses.

## DISCUSSION

In both lowland and highland tropical wet forests of Costa Rica, there is some evidence that cicada species co-occuring in the same habitat or region undergo peak adult emergence at different times of the year (Young 1972; 1975; 1980a, b). In addition to such allochronic annual emergence patterns, different species are often found in different habitats at the same locality (e.g., Young 1980a). The lowland tropical dry forest region of northwestern Costa Rica has a much more intense and prolonged dry season than most other regions of the country (e.g., Janzen 1967), and the cicada species exhibited associated differences in the timing of estimated peak adult emergences each year. For example, forest-dwelling species such as *Fidicina mannifera* and *Zammara smaragdula* are wet season cicadas while others such as *Diceroprocta* sp. have a highly synchronized and short emergence at the very beginning of the wet season. *Fidicina amoena* and *F. pronoe* follow one another for peak adult emergences during the dry season, and others such as *Proarna* emerge during both seasons.

Of the seven cicada species studied, three *(F. mannifera, F. amoena, F. pronoe)* are also found in lowland tropical wet forest, and two others *(F. smaragdula, Proarna* sp.) have closely allied species in this region. *Fidicina amoena* and *F. pronoe* also occur in the highlands of central Costa Rica as does *Z. smaragdula* (Young 1976). In fact, *F. pronoe* is part of a complex of several closely related species extending over much of Central America (Moore 1962). In lowland tropical wet and central highland forest regions of Costa Rica *F. amoena* and *F. pronoe* also emerge during the dry season, and *Z. smaragdula* in the central highlands and *Z. smaragdina* (Walker) in the wet lowlands emerge during the wet season (Young 1980a, b). *Fidicina mannifera* emerges throughout most of the year in the wet lowlands (Young 1972; 1980b) in contrast to the population studied at the Barranca Forest where emergence occurs during the wet season. Other interesting differences in *F. mannifera* between the Barranca Forest site and the wet lowlands of northeastern Costa Rica concern morphological and behavioral features: males of *mannifera* sing primarily in a dawn-dusk pattern in the tropical wet forest region, they are larger in size and the thoracic area is primarily brown; males of *mannifera* in the Barranca Forest are smaller, and have a greenish thorax, and sing during the day. The northeastern wet lowlands are less seasonal than the tropical dry forest zone, and the dry season is generally short (January-March) and irregular. Furthermore, rainfall does not cease completely during the wet lowland dry season and the upper strata of the soil beneath forest litter does not dry out completely.

Assuming that mature tropical cicada nymphs time their seasonal emergences with changes in (1) soil moisture content with a "critical"

upper zone, and/or (2) seasonally-induced changes in the plant sap tapped as food from roots, the "triggering" of annual and highly seasonal peak emergences for a given species is expected to be more consistent annually in a highly seasonal region such as lowland Guanacaste and portions of Puntarenas Province, than in the apparently less seasonal wet lowland areas. Thus a cicada such as *F. mannifera* which emerges primarily under "wet conditions" may perceive the environment in lowland Guanacaste as more seasonal since the soils in forest habitats in this region are probably considerably drier than forest soils in the northeastern lowlands at the heights of the dry seasons at both localities. Dryness may inhibit emergence in a wet season species such as *F. mannifera* and *Z. smaragdula*. It is not unusual for hatches of grasshopper eggs to be synchronized with an annual pattern of seasonality in temperature and precipitation (Key 1942). Likewise, other species such as *F. amoena*, *F. pronoe*, and *Diceroprocta* sp. are perhaps inhibited to emerge by wet conditions and therefore emerge in the dry season. Cicada species that exhibit non-seasonal emergence patterns in the tropics may use very different environmental cues from those with strictly dry or wet season cycles, and the whole matter of how emergences are synchronized with certain features of the environment may indeed be very complex.

Very little is known about the proximal cues and underlying physiological mechanisms that result in seasonally-synchronized peak adult emergences in tropical cicadas of the type described in this paper. The strong correlation between emergences in many species and the annual cycle of wet and dry seasons in the lowland tropical dry forest zone suggests a causal relationship. The physiological tolerances to heat and dryness, and behavioral tactics used by adult cicadas under such potentially-stressful conditions (e.g., Heath and Wilkins 1970) must also be studied to account for seasonal patterns of peak adult activity. The effectiveness of transmission of the songs of different cicada species may vary in different seasons (Young 1980c). What forms of selection pressure result in allochronic and highly seasonal adult emergences of cicadas in the tropics are in need of elucidation. Most of the species studied possess distinctive songs and males often chorus in small (*Proarna* sp., *Pacarina* sp.) or large assemblages (*Z. smaragdula, Diceroprocta* sp.) in large trees. Whether or not such a structuring of chorusing groups establishes a potential for reducing mating efficiency if several species are active at the same time warrants study.

The observed differences in habitat associations for cicadas in the tropical dry forest zone is related to the associations of nymphs with particular tree species. From other studies of cicadas in Costa Rica (Young 1980a, b) it was suggested that the nymphs of particular species are associated with the root crowns of certain tree species, and that such specific relationships account for the observed patterns of habitat association. In both relatively undisturbed and some disturbed primary wet

or moist forest habitats in other climatic zones of Costa Rica, many cicada species are associated with various leguminous tree species (Young 1972; 1976; 1980a, b), although not exclusively. The association of *Diceroprocta* sp. and *Proarna* sp. with legumes such as *Tamarindus indica, Enterolobium cyclocarpum*, and *Cassia moschata*, and *Fidicina mannifera* and *Zammara smaragdula* with *Samanea saman* and *Enterolobium cyclocarpum* indicates that cicada-legume relationships are also found within forest environments in the lowland tropical dry forest zone of Costa Rica. All of these tree species are members of the original forest systems of this zone, with the exception of *Tamarindus indica* which originated in tropical Asia but today is "naturalized" in all tropical regions (Holdridge and Poveda 1975). Given the observation that cicada species in several different climatic zones of Costa Rica are associated with leguminous trees in primary forests, these trees might have been the original host plants for these insects throughout much of Central America. This is not to say that cicadas are not associated with other trees today. From the observations on *Z. smaragdula* and *F. mannifera* in the secondary forest habitat at the Barranca Forest, and previous observations for secondary forest habitats in wet forests (Young 1980b), the root crown associations of nymphs appears to be less clear than originally proposed since usually there are several small seedlings or shrubs present, rather than one or two canopy-size trees. The observed association of *Diceroprocta* nymphal skins with *Chrysophyllum mexicanum* trees at Puntarenas may indicate a nymphal feeding relationship with a non-leguminous tree, although these trees (av. dbh=40 cm) were in a single row with a very large *Enterolobium cyclocarpum* tree (dbh=2.0 m) located about four meters from the midpoint of the row.

In many instances, the clumping of nymphal skins beneath a certain tree may indicate a feeding relationship of nymphs with the root crown of that tree. Other factors, however, such as the proximity of understory plants suitable as emergence sites for nymphs, can distort any correspondence between nymphal skins and root crowns used for nymphal feeding. For example, if a species such as *Diceroprocta* exhibits a proneness to undergo adult emergence on a substrate other than the ground, and if the habitat consists of a closely cropped lawn dotted with large trees (such as "city limits yard" site at Puntarenas), nymphs possibly associated with the expansive outer portions of the root crown of the *Enterolobium* tree may encounter the *Chrysophyllum* trees as the closest suitable eclosion substrates. In a forest habitat, cicada nymphs associated with a particular root crown of a large forest tree probably encounter many suitable eclosion sites within the canopy shadow of the tree. My field experience with primarily large-bodied forest genera such as *Zammara* and *Fidicina* over the past eleven years in selected wet forest habitats in Costa Rica supports this view. The Leguminosae have been in past geological periods, and are today, a principal family of canopy-

size trees in tropical rain forests throughout the world (Flenley 1979). Whether or not tropical cicadas in general originally evolved root crown relationships with these trees cannot be ascertained.

The apparent annual stability in average abundance of nymphal skins for several species suggests that population structure may be similar in different years, barring sampling error introduced by small sample sizes. It appears that the annual seasonal cycle of the region contributes to the observed periods of peak abundances.

The densities of nymphal skins found in the various habitats are consistent with some densities estimated for cicadas in wet forest habitats. The density of nymphal skins of *Zammara smaragdina* beneath canopy-size *Pentaclethra macroloba* trees in northeastern lowland Costa Rica was about one per m² each year over several years (Young 1972; 1980b), a figure comparable to densities of the closely related *Z. smaragdula* beneath canopy-size trees in the Barranca Forest. In a paper on cicada emergences at "Finca Le Selva" (Young 1972), *Z. smaragdina* was incorrectly called *Z. smargdula*. *Fidicina mannifera* generally has low density emergences beneath forest legume trees in both wet and semi-dry forest habitats (i.e., the Barranca Forest), and nymphal skin abundances are seldom as great as for other species emerging in the same patches (e.g., *Fidicina sericans* Stal and *Zammara smaragdina* in primary forest habitats at "Finca La Selva" and "Finca La Tirimbina" — Young 1972; 1980b, and *Z. smaragdina* in the Barranca Forest — the present study). *Proarna* densities are also low (i.e., less than 0.40 nymphal skins per m²) in wet and dry forest habitats. For Costa Rican cicadas, a density of about one nymphal skin per m² for a given species at the peak of the adult emergence period is high. Such densities are usually realized for forest-dwelling *Zammara* species and certain species of *Fidicina*, and sometimes *Proarna* (e.g., Table 6).

Relatively high densities of emerging cicadas appear to be associated with individual canopy-size trees in both primary forests (Young 1972; 1980a, b, and the present study) and in forest remnants (Young 1980a), and even with individual trees surviving in yards following removal of the forest cover (the present study). Presumably such trees have larger root crowns capable of supporting large nymphal populations. Fecundated or ovipositing cicadas may locate trees with large root crowns by recognizing distinctive physical features (i.e., canopy crown shape, leaf shape — a substantial portion of the leguminous trees involved in cicada associations are species with pinnate leaves) and perhaps proximal attributes such as odor, bark texture, and suitability for adult-feeding. Such a tree may function as a feed and mating site, and the understory beneath it as an oviposition site, since several cicadas studied oviposit in the understory beneath individual trees where large accumulations of nymphal skins have been found (e.g., Young 1972; 1980b).

## ACKNOWLEDGMENTS

**Fig. 1.** Riparian primary growth tropical dry forest along the Rio Tempisque, near Liberia, Guanacaste Province, Costa Rica, during the dry season (February 1977).
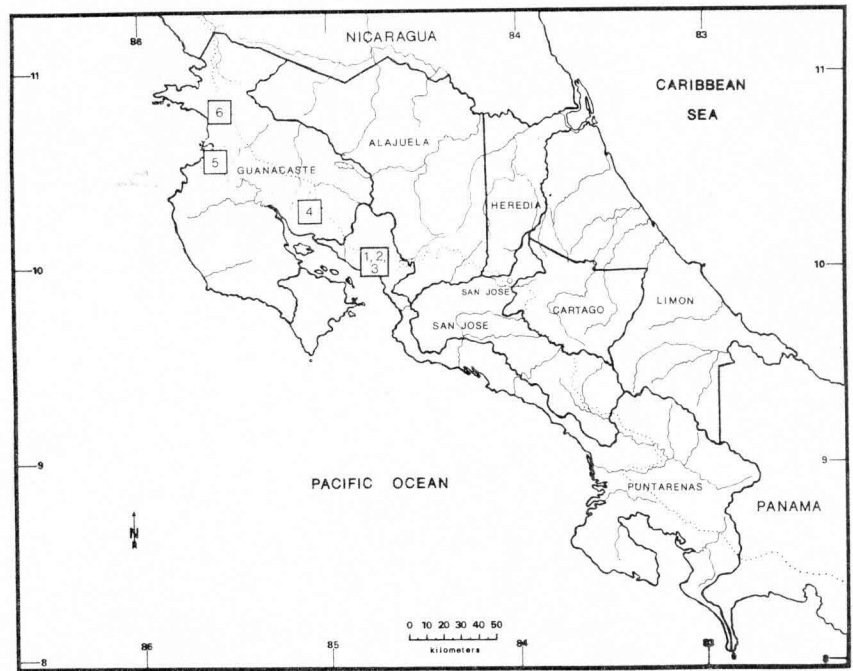
**Fig. 2.** The distribution of study sites in the lowland tropical dry forest region of Costa Rica. The boxes with numbers indicate the approximate locations of six study sites. Site 1: two "inner city yards" in the port city of Puntarenas; Site 2: "city limits yard" along with the highway connecting Puntarenas with the Pan-American Highway; Site 3: Barranca Forest along the Pan-American Highway and east Puntarenas; Site 4: "Finca La Toboga" near Canas; Site 5: Playas del Coco; Site 6: Santa Rosa National Park. The bulk of observations on cicada emergences was made at Sites 1, 2, 3 and 5. Sites 1-3 are in Puntarenas Province, sites 4-6 are in Guanacaste Province.
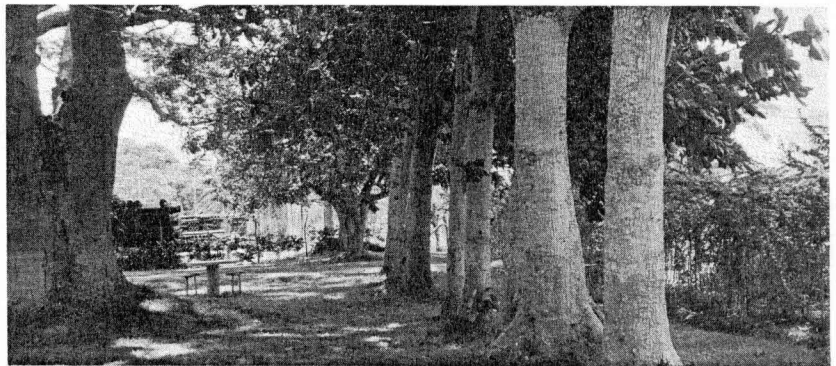


**Fig. 3.** The "city limits yard" site near Puntarenas. The row of *Chrysophyllum mexicanum* trees are seen to the right, and the single large adult *Enterolobium cyclocarpum* on the left.

**Fig. 4.** One of the yards at Playas del Coco where very large and dense emergences of *Diceroprocta* sp. occur. Note the *Tamarindus indica* tree to the right.



**Fig. 5.** *Tamarindus indica* and other trees behind the beach at Playas del Coco. Many nymphal skins of *Diceroprocta* sp. were found on the trunks of the trees in this particular section of beachfront forest.

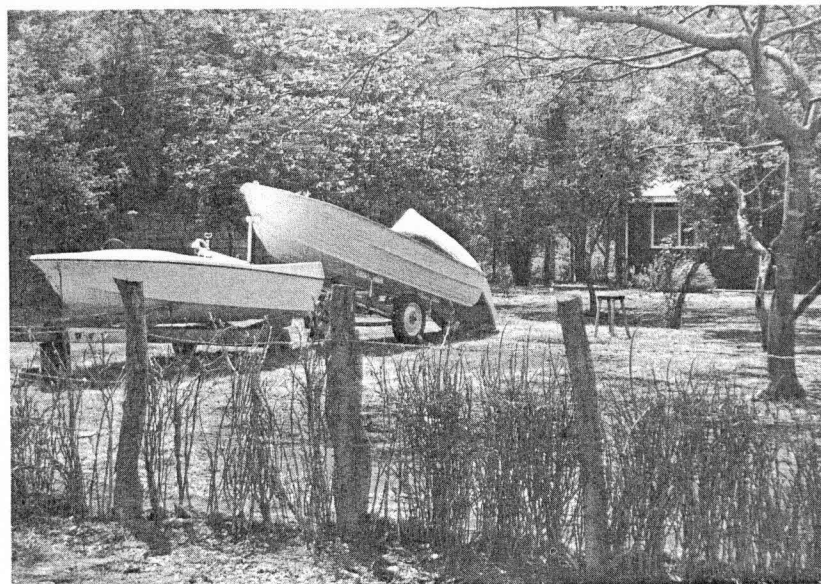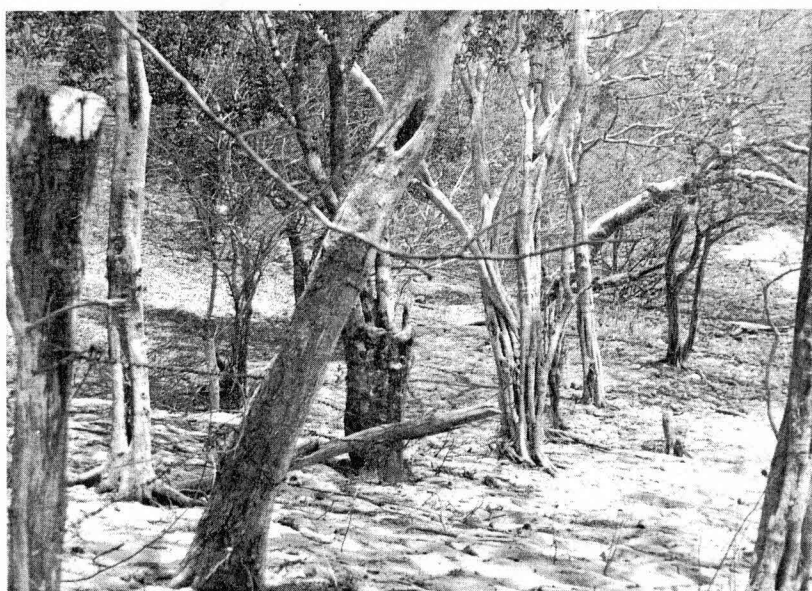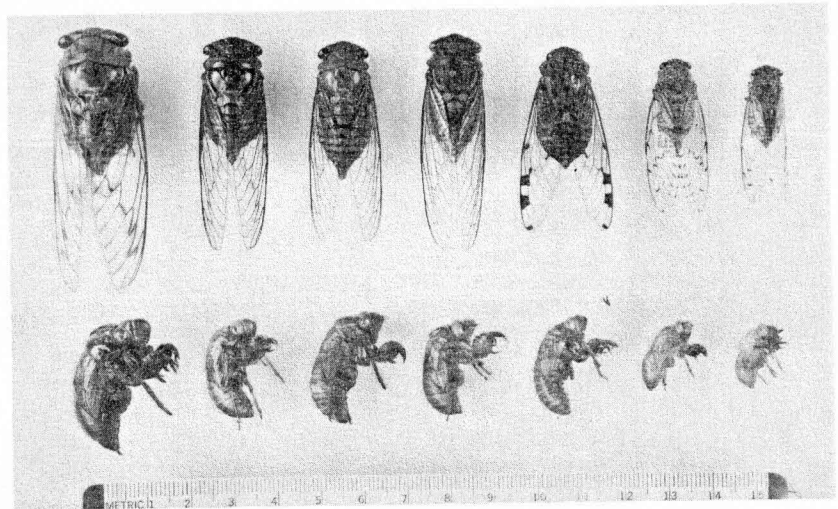**Fig. 6.** The adult cicadas and nymphal skins of species studied within the lowland tropical dry forest region of Costa Rica. From left to right: *Fidicina mannifera*, *F. pronoe*, *F. amoena*, *Diceroprocta* sp., *Zammara smaragdula*, *Proarna* sp., and *Pacarina* sp.
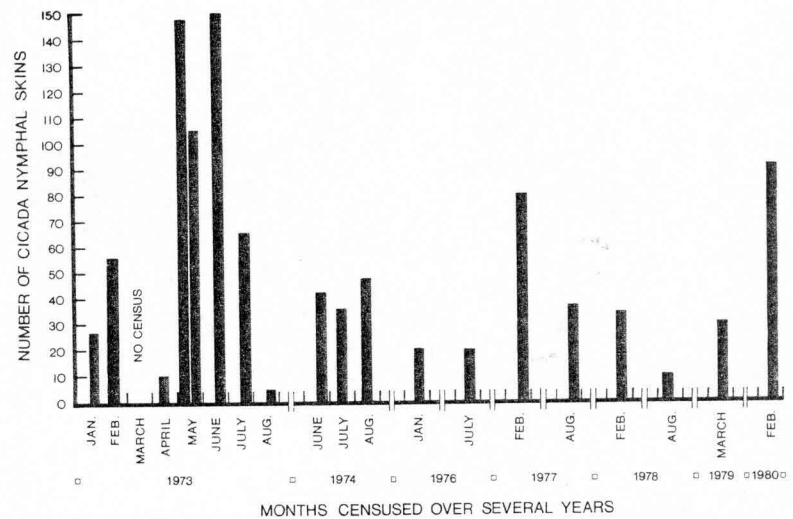


**Fig. 7.** The emergence pattern of *Proarna* sp. at one of the "inner city yard" sites ("Fernando's site") in Puntarenas, based on censuses of nymphal skins on and beneath trees. Although emergence data are available for multiple census dates during February 1973 and August 1974, these data are combined into one histogram bar for each of these months to make them comparable to the single census dates and emergence data for the other months and years. The single exception is the May 1973 emergence: the emergence data from each of the two census dates are shown separately for comparison and since otherwise the huge peak would run off the graph. See Table 2 for different but nearby data.
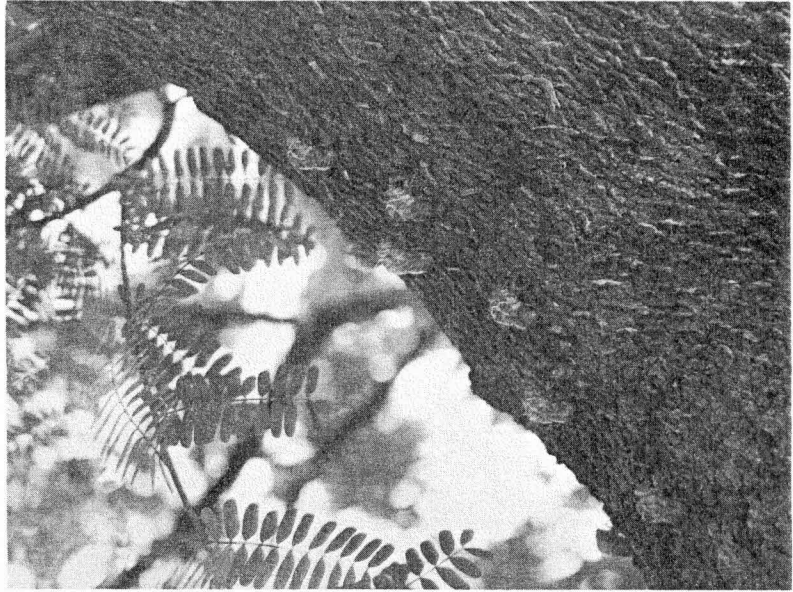
**Fig. 8.** Nymphal skins of *Diceroprocta* sp. on the trunk of a *Tamarindus indica* tree at Playas del Coco, at the peak of the emergence in late April 1975.
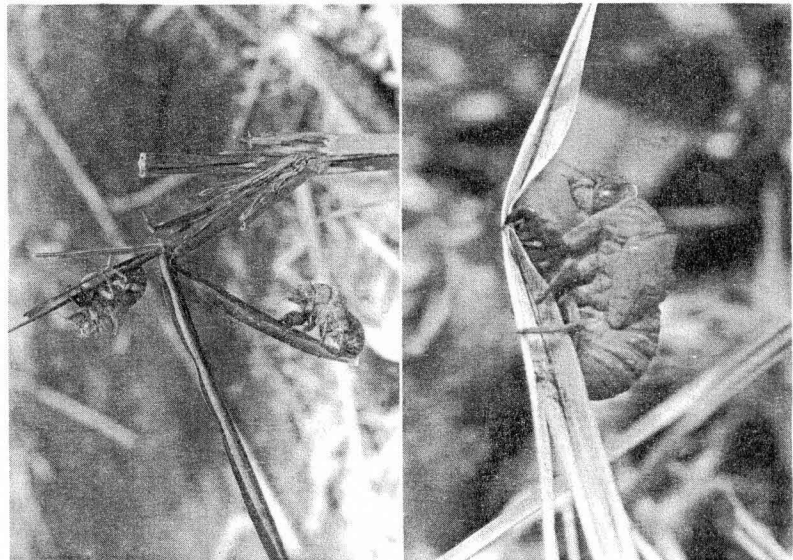


**Fig. 9.** Nymphal skins of *Pacarina* sp. clinging to dried grass stems and leaves in a grass patch along a foot path near the Historical House at Santa Rosa National Park.
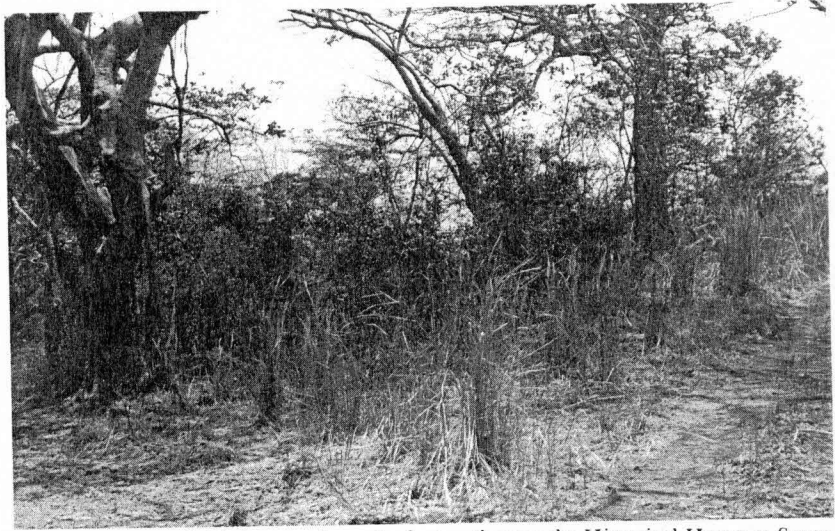
**Fig. 10.** A patch of dried grass along the foot path near the Historical House at Santa Rosa National Park, where many nymphal skins of *Pacarina* sp. were found.
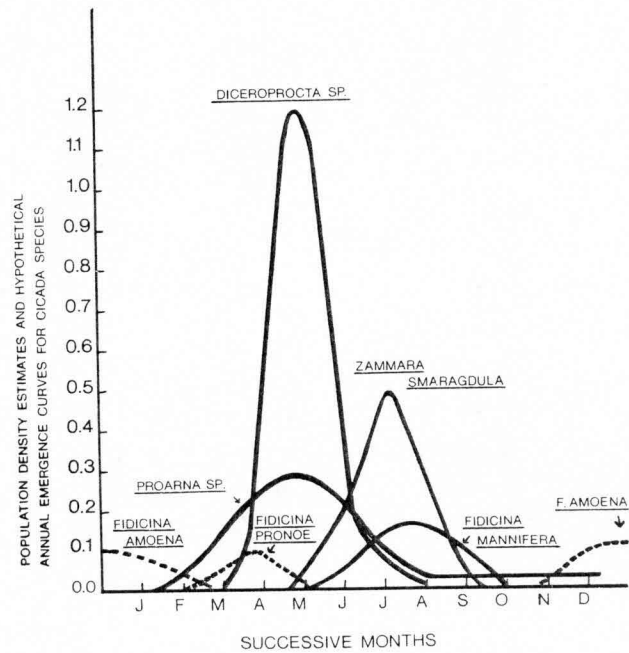


**Fig. 11.** Hypothetical densities and annual adult emergence periods for six species of cicadas in the lowland tropical dry forest region of northwestern Costa Rica. Means

of means/m² were calculated from the nymphal skin data in Table 6 and used as peak reference points for the hypothetical emergence curves shown. Dotted lines are used for *F. amoena* and *F. pronoe* since no data on nymphal skins was available from the region, and the curves are predicted from adult data and data on nymphal skins and adults elsewhere in Costa Rica (Young 1980a, b). Various emergence strategies are shown: species such as *F. amoena* and *F. pronoe* are dry season species while others such as *Diceroprocta* and *Proarna* emerge during the transition between dry and wet seasons, and still others such as *Zammara smaragdula* and *Fidicina mannifera* emerge during the wet season. It is emphasized that the smoothed and highly stylized emergence curves shown are expected to vary from site to site for a given cicada species.

**Table 1.** The abundance of nymphal skins of the cicada *Proarna* sp. in an "inner city yard" site at the Pacific port city of Puntarenas, Puntarenas Province, Costa Rica.*

| Census date | Number of nymphal skins | | |
| | Females | Males | Total |
|---|---|---|---|
| 10 February 1973 | 21 | 23 | 44 |
| 2 March | 3 | 9 | 12 |
| 14 April | 13 | 14 | 27 |
| 9 May | 10 | 10 | 20 |
| 31 May | 6 | 4 | 10 |
| 20 June | 64 | 58 | 122 |
| 28 July | 53 | 32 | 85 |
| 20 August | 11 | 9 | 20 |
| 12 July 1974 | 11 | 17 | 28 |
| 2 August | 9 | 8 | 17 |
| 17 August | 2 | 1 | 3 |
| 20 January 1976 | 7 | 10 | 17 |
| 20 July | 6 | 8 | 14 |
| 24 February 1977 | Habitat completely destroyed in construction project. | | |

* Nymphal skins were collected from trunks of various trees and bushes, and also from the ground. This yard was about 600 m² and contained a small restaurant called "Las Arenas". The whole area was cleared and plowed for a new construction project.

**Table 2.** The distribution and abundance of nymphal skins of the cicadas *Diceroprocta* sp. and *Proarna* sp. on 16 adult-size trees* in a yard** near Puntarenas, Puntarenas Province, Costa Rica. See Fig. 7 also for nearby *Proarna* sp. data.

| Census Date | *Diceroprocta* Nymphal Skins | | | | | | *Proarna* Nymphal Skins | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Females | Males | Total | Total range per tree | Mean | Variance/ Mean Ratios | Females | Males | Total | Total range per tree | Mean | Variance/ Mean Ratios |
| 21 June 1973 | 118 | 81 | 199 | 7-33 | 12.44 | 6.47 | 39 | 18 | 57 | 0-12 | 3.56 | 3.85 |
| 27 July | 1 | 1 | 2 | 0-1 | 0.12 | 0.96 | 4 | 1 | 5 | 0-1 | 0.31 | 0.71 |
| 19 June 1974 | 71 | 41 | 112 | 0-24 | 7.00 | 11.67 | 4 | 2 | 6 | 0-3 | 0.37 | 2.09 |
| 10 July*** | 7 | 7 | 14 | 0-1 | 0.87 | 3.17 | 5 | 5 | 10 | 0-3 | 0.62 | 1.03 |
| 2 August | 0 | 0 | 0 | — | — | | 0 | 0 | 0 | — | — | |
| 10 April 1976 | 2 | 6 | 8 | 0-1 | 0.50 | 1.58 | 9 | 8 | 17 | 0-1 | 1.06 | 2.07 |
| 29 July | 64 | 53 | 117 | 0-37 | 7.31 | 11.40 | 4 | 0 | 4 | 0-1 | 0.25 | 4.75 |
| 25 February 1977 | 0 | 0 | 0 | — | — | | 0 | 0 | 0 | — | — | |

| | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 27 August | 31 | 28 | 59 | 0-17 | 3.68 | 23.76 | 0 | 0 | 0 | — | — | |
| 20 February 1978 | 0 | 0 | 0 | — | — | | 0 | 0 | 0 | — | — | |
| 10 August | 171 | 118 | 289 | 0-38 | 18.06 | 67.17 | 20 | 6 | 26 | 0-6 | 1.62 | 3.18 |
| 21 March 1979 | 0 | 0 | 0 | — | — | | 0 | 2 | 2 | 0-1 | — | |
| 16 February 1980 | 0 | 0 | 0 | — | — | | 0 | 0 | 0 | — | — | |

\* There were nine adult-size individuals of the tree *Chrysophyllum mexicanum* (Sapotaceae) arranged in a row, and an additional 7 trees of various Leguminosae, including one *Enterolobium cyclocarpum*. The trees were in a large yard about 60 x 40 m. See Fig. 3. Sample size of N=16 trees used to calculate abundance statistics.

\*\* Located about 5 km from the city of Puntarenas and along the main highway artery; the locality is referred to in this paper as the "city limits yard" site.

\*\*\* Two very fresh nymphal skins of *Zammara smaragdina* were found on one *C. mexicanum* tree at the site on this date.

**Table 3.** The distribution and abundance of nymphal skins of the cicada *Diceroprocta* sp. on 35 adult-size *Tamarindus indica* trees along the beachfront at Playas del Coco, Guanacaste Province, Costa Rica.

| Census Date | Females | Males | Total | Total range (both sexes) per tree | Mean | Variance/ Mean Ratios |
|---|---|---|---|---|---|---|
| 29-30 April 1975 | 1,230 | 1,143 | 2,373 | 2-320 | 67.76 | 106.81 |
| 14 May 1975 | | 141 | 592 | 0-97 | 15.54 | 39.64 |
| 19 February 1976 | 0 | 0 | 0 | — | — | |
| 8 April** 1976 | 22 | 29 | 51 | 0-5 | 1.45 | 4.73 |
| 29 July** 1976 | 54 | 54 | 108 | 0-6 | 3.05 | 4.71 |
| 26 January 1977 | 0 | 0 | 0 | — | — | |
| 15 February 1980 | 0 | 0 | 0 | — | — | |

* 17 fresh nymphal skins of *Pacarina* sp. and one (male) of *Proarna* sp. were also found in one yard site on 8 April 1976.

** 10 fresh nymphal skins of the *Proarna* sp. were also found in another yard site on 29 July 1976.

**Table 4.** The abundance of nymphal skins of the cicadas *Zammara smaragdula* over several census dates during the period of peak adult emergence, in the "Barranca Site" forest*, Puntarenas, Puntarenas Province, Costa Rica.

| Annual Census Dates | *Zammara smaragdula* Total nymphal skins Females | Males | Total | Range per tree | Mean | Variance/ Mean Ratios | *Fidicina mannifera* Total nymphal skins Females | Males | Total | Range per tree | Mean | Variance/ Mean Ratios |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | **6 adult-size trees in primary forest** | | | | | | | | |
| 1973:30 July; 21 Aug. | 45 | 46 | 91 | 1-25 | 15.16 | 2.43 | 9 | 7 | 16 | 0-8 | 2.25 | 9.54 |
| 1974:10 July, 3 Aug.; 18 Aug. | 62 | 72 | 134 | 0-72 | 22.33 | 67.63 | 23 | 18 | 41 | 0-17 | 6.83 | 19.70 |
| 1973:30 July | 3 | 5 | 8 | 1-5 | 1.33 | 2.60 | 3 | 2 | 5 | 0-5 | 0.83 | 5.01 |
| | | | | **30 x 15m plot in advanced secondary forest** | | | | | | | | |
| 1973:3 & 21 Aug. | 67 | 73 | 140 | — | — | | 6 | 5 | 11 | — | — | |
| 1974:10 July, 3 & 18 Aug. | 84 | 52 | 136 | — | — | | 0 | 1 | 1 | — | — | |
| 1976:30 July | 0 | 1 | 1 | — | — | | 0 | 0 | 0 | — | — | |

* A good description of the area is given in Orians (1969). The forest patch is a mixture of both primary and advanced secondary habitats.

**Table 5.** Field Records of Chorusing for Cicadas (Homoptera: Cicadidae) at Various Localities and Habitats in Lowland Guanacaste Province, Costa Rica.

| Cicada Species | Dates Heard Chorusing | Season of Peak Chorusing | Localities | Habitats |
|---|---|---|---|---|
| *Zammara smaragdula* | 28 July-3 Aug. 1973; 21 Aug. 1973; 10 July, 3 & 18 Aug. 1974; 30 July 1976 | Mid-Wet | Barranca Forest; Finca La Taboga | Advanced secondary; Borders of primary forest |
| *Fidicina mannifera* | 28 July - 3 Aug. 1973; 21 Aug. 1973; 10 July, 3 & 18 Aug., 1974; 30 July 1976 | Mid-Wet | Barranca Forest | Primary forest |
| *F. amoena* | 8 April 1976; 26 Jan. 1977 | Dry | Santa Rosa National Park | Primary forest |
| *F. pronoe* | 8 April 1976 | Late dry | Santa Rosa National Park | |
| *Proarna* sp. | 16 & 30 Jan., 2, 10, 28 Feb.; 9 & 31 May; 20 June & 28 July 1973; 18 June, 12 July, 2 Aug. 1974; 20 Jan., 8-9 April; 20 July 1976; 24 Feb. 1977; 20 Feb. 1978; 16 Feb. 1980 | Dry and early wet | Puntarenas, Barranca Forest, Finca La Taboga, Canas, Liberia, Liberia, Playas del Coco, Playa Tamarinda, Cabo Velas, Santa Rosa National Park | Yards, secondary forest, primary forest· |
| *Diceroprocta* sp. | 29-30 April & 14 May 1975 | Early Wet | Playas del Coco | Yards |
| *Pacarina* sp-1 | 4-5 Jan. 1973; 12-15 Dec. 1974; 22-23 Jan. 1976; 26 Jan. 1977; 15 Feb. 1980 | Dry | Puntarenas, Canas, Liberia | Grasslands |

**Table 6.** Densities* of nymphal skins of four species of cicadas. All sites in the lowland tropical dry forest region of northwestern Costa Rica.

| Cicada species | Year | Maximal abundance data | | Description of study site (size in m, trees, etc.) | Area | Density of nymphal skins |
| | | No. of censuses | No. of nymphal skins | | | |
|---|---|---|---|---|---|---|
| *Diceroprocta* sp. | 1973 | 2 | 201 | 3x4 m plots beneath 16 trees in one yard (Puntarenas) | 192m² | 1.05/m² |
| | 1974 | 3 | 125 | same | same | 0.65/m² |
| | 1976 | 2 | 126 | same | same | 0.66/m² |
| | 1977 | 1 | 59 | same | same | 0.31/m² |
| | 1978 | 2 | 289 | same | same | 1.50/m² |
| | 1975 | 2 | 2,965 | 5x4 m plots beneath 35 trees in Playas del Coco | 1100m² | 2.70/m² |
| *Proarna* sp. | 1973 | 2 | 62 | 3x4 m plots beneath 16 trees in one yard (Puntarenas) | 192m² | 0.32/m² |
| | 1974 | 2 | 16 | same | same | 0.08/m² |
| | 1976 | 2 | 26 | same | same | 0.14/m² |
| | 1978 | 2 | 26 | same | same | 0.14/m² |
| | 1973 | 11 | 621 | same | 500m² | 1.24/m² |

| | | | | | | |
|---|---|---|---|---|---|---|
| | 1974 | 4 | 125 | same | same | 0.25/m² |
| | 1976 | 2 | 54 | same | same | 0.11/m² |
| | 1977 | 2 | 116 | same | same | 0.23/m² |
| | 1978 | 2 | 45 | same | same | 0.09/m² |
| | 1979 | 1 | 20 | same | same | 0.04/m² |
| | 1980 | 1 | 91 | same | same | 0.18/m² |
| *Zammara smaragdula* | 1973 | 2 | 91 | 5x5 m plots beneath Barranca Forest | 150m² | 0.61/m² |
| | 1974 | 2 | 134 | same | same | 0.89/m² |
| | 1976 | 1 | 8 | same | same | 0.05/m² |
| | 1973 | 2 | 140 | 30x15 m plot in secondary habitat at Barranca Forest | 450m² | 0.31/m² |
| | 1974 | 2 | 136 | same | same | 0.30/m² |
| | 1976 | 1 | 1 | same | same | 0.00/m² |
| | 1973 | 2 | 8 | same | same | 0.02/m² |
| *Fidicina mannifera* | 1974 | 2 | 41 | 5x5 m plots beneath six large trees in Barranca Forest | 150m² | 0.27/m² |
| | 1976 | 1 | 5 | same | same | 0.03/m² |

* These entries are the maximum abundances observed, and form the basis for much of the discussion.

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