COLONIZING FLIGHTS AND ASSOCIATED ACTIVITIES OF TERMITES.
I. THE DESERT DAMP-WOOD TERMITE *PARANEOTERMES SIMPLICICORNIS* (KALOTERMITIDAE)[1]

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INTRODUCTION. — The swarming period provides the only occasion when observations can be made undisturbed on many species of termites. Flights involving large numbers of alates, apparently synchronized with particular seasons, are a conspicuous phenomenon in many parts of the world and well known to local inhabitants. Yet only the most limited information is available on the flights of a small percentage of the commoner species, *i.e.,* the months and time of day during which flights are staged, and perhaps an association with rainfall. Not until recent years have many real efforts been made to correlate the dispersal flights of termites (Snyder, '61) or the nuptial flights of ants (Kannowski, '59; Talbot, '56; '64) — which appear to be similarly related to definite weather patterns — with even the most obvious environmental factors. The difficulties involved in gathering more detailed intelligence, however, become apparent after a season or two of field study.

The following account is the result of an increasingly successful series of observations made on one of twelve different species in a single area over a period of seven years. It summarizes field notes on 78 separate flights together with a preliminary analysis of accompanying weather data. The ultimate objective of such a study should be the elucidation of the physical and physiological factors which trigger the flights of a species, both seasonally and daily, over its entire range. At present the bulk of the data is climatological and far outweighs that on the behavior of the termite itself; the study is thus perforce largely descriptive. Succeeding papers in this series should gain in significance from data being gathered concomitantly on additional species in the families Kalotermitidae, Hodotermitidae, Rhinotermitidae and Termitidae. Although the actual flight stimuli may eventually prove very different from those which suggest themselves from time to time, this descriptive state should provide a starting point for other more profitable approaches to the subject.

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[1]Arizona Agricultural Experiment Station Journal Article No. 1112.
Manuscript received by the editor February 25, 1966

Paraneotermes simplicicornis is apparently unique among the drywood termites (Kalotermitidae) for, although the reproductive center has never been found, it is fundamentally subterranean in habit. Over its known range in the deserts from southern California and northern Baja California to southern Nevada, southwestern Texas and northern Sinaloa, Mexico, it typically attacks moist wood in or on the ground in washes and canyons. Small living trees are even cut off just beneath the soil on occasion. A detailed account of the biology, distribution and taxonomic relations of this most interesting termite was published by Light in 1937. At that time swarming had never been observed, nor has it been reported since.

STUDY AREA AND METHODS. — Nearly all the flights were observed within an area of less than an acre in north-central Tucson, Arizona, at an altitude of 2400 ft. This part of the valley floor is now about equally divided between creosote bush desert *(Larrea tridentata)* and small residential developments. Three to four feet of fine-textured alluvium overlies a narrow zone of friable caliche or hardpan. The mean annual precipitation of 10.9 inches is almost equally divided between a summer (July-Sept.) and a winter (Dec.-March) rainy season, characteristic for most of the Sonoran Desert. Although the mean annual temperature is 19.6°C, it is of little significance unless it is realized that daily fluctuations of 15° are common and of 21°C not unusual. In 62 years the highest recorded temperature was 44.4° (July, 1953, and several other dates), the lowest −14.4°C (Jan., 1913) (Sellers, '60).

Considering our scant knowledge of the types of sense organs with which the various castes of termites are equipped, much less the information which they are collecting, it is still far from clear what environmental factors should be measured, to say nothing of the necessary degrees of accuracy. Hence, many of the methods used here are admittedly exploratory and probably crude. Certain refinements have already been made and others are continually suggesting themselves. For example, it would probably be desirable to measure many microclimatic parameters; however, their usefulness will depend upon a much greater knowledge of the termites and their preflight activities within and near the nest than is now available.

Starting in January, 1960, continuous records of air temperature and relative humidity have been made in the study area with a Bendix-Friez Hygrothermograph, Mod. 594 (maintained to an accuracy within approximately ±1°C from −12 to +43°C and ±5% from 0 to 100% RH). The instrument is sheltered six feet above the ground. Weekly mean temperatures and relative humidities were figured from the hygrothermograph records with the aid of a planimeter (Cutright, '27). Evaporation data are available (U. S. Department of Commerce, '62; '63) from measurements made daily at 5:00 PM on the campus of the University of Arizona, Tucson, 2.5 mi. SSW of the study area. Saturation deficit was calculated for time of sunset plus 15 minutes at Tucson, and for certain other times, on the basis of hygrothermograph records. Rainfall was measured daily with a simple plastic collecting gauge near the center of the area from midnight to midnight. Illumination at the zenith was measured several different times with a Weston photographic exposure meter (Master II, Mod. 735). During 1962 barometric pressure was continuously recorded on a temperature-compensated Taylor recording barometer. Some observations were made on flights from a laboratory colony in an 8×8-foot walk-in refrigerator which was equipped with a Partlow recording temperature program control (Mod. RCS) capable of providing any desired daily or weekly temperature pattern. All times are Mountain Standard and based on the 24-hour clock.

Development of alates and pre-flight behavior. — Light ('37) termed the large aggregations of nymphs and soldiers of this species "temporary outposts" or "foraging subcolonies"; no reproductives of any form, eggs or small nymphs have yet been found in them. Samples from 19 subcolonies collected in or within 25 miles of Tucson have revealed subimaginal nymphs (with large wing pads) to be present between August 30 (1962) and May 20 (1961). On the latter date an entire subcolony was removed from a large timber beneath the steps of a farm building and set up in a laboratory observation nest. It contained 39 soldiers and 760 nymphs, many of them pre-alates. Between June 2 and 15, all of these had developed into 130 alates at laboratory temperatures only slightly less variable than, and averaging a few degrees below, those outside. By a most fortunate coincidence another subcolony was found on June 14, 1961, in the roots of a dead palo verde tree *(Cercidium microphyllum)*. It contained 104 soldiers, at least 1100 nymphs (no pre-alates) and 190 alates. No flights were observed in the Tucson area in 1961 until July 5, although it is likely that this was not the first flight of the season. The above evidence shows an abrupt and rapid mass development of alates within three weeks, probably less, of the first flight. Although no local soil temperature records are available it seems reasonable to assume that this maturation is a direct result of the intense heating of the soil which occurs during the very clear, dry months of May and June. Monthly mean air temperatures increase rapidly from 18.1°C in April to 22.4° in May, 27.6° in June and 30.1° in July (Sellers, '60).

Light ('37) reported alates in colonies in California from late October into November and in Nevada during May. Snyder ('54) noted that alates were taken from a colony in Texas in mid-April. In the absence of flight records from these regions speculation is unprofitable, although flight schedules are probably shifted in conformity with local weather patterns which result from altitudinal and latitudinal differences over its entire range.

Once alates are present in a colony, the influence of biological factors on the initiation of flights must also be considered. Although the behavioral interactions among the members of a colony have only begun to be fathomed, the feverish activity exhibited within a colony at the onset of conditions favoring flight has probably been noted many times *(e.g.,* in *Kalotermes* [=*Incisitermes*] *minor* Hagen by Harvey, '34, p. 221). In this connection some early attempts were made to induce flights from a large sub-colony which had been in the laboratory for about a month. It was confined in an observation nest of seven plastic petri dishes interconnected with polyethylene

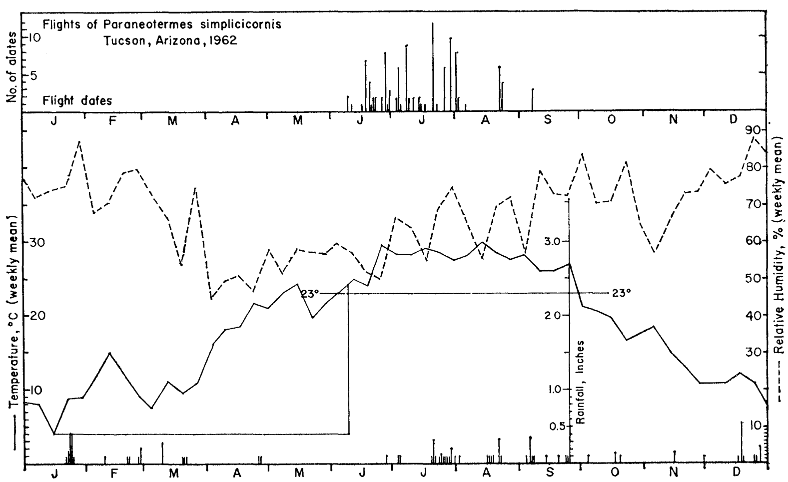

Figure 1. Flight season of *Paraneotermes simplicicornis* in relation to rainfall, weekly mean temperature and relative humidity at Tucson, Arizona, in 1962. Dates showing 0.1″ actually indicate amounts from a trace to 0.1″ of rain. Flights began when mean temperature remained above about 23°C. The upper section shows the numbers of alates observed on each date during the flight season from June 9 to Sept. 7.

tubing and placed on a large tray of moist soil. (*Paraneotermes* has been maintained for more than a year in this type of nest with the petri dishes containing a layer of 4% agar and thin slices of wood.) The colony was held in the dark, walk-in refrigerator for about a week at 27°C and 30% RH prior to a brief, simulated flight season. Observations were made with the program control set to duplicate the temperature cycle of five consecutive days of typical summer weather. Daily temperatures varied between 22° and 43°C, relative humidities between 28 and 78%. Temperature peaks occurred between 1500 and 1600 each day. During the middle of these days the temperature sometimes rose at a rate of about 3.3°C per hour and fell later by as much as 9°C per hour for short periods. No measurements were made within the nest, although it is certain that the relative humidity was continuously at or close to saturation. Most of the observations were made under a red light.

Under such conditions and below about 34°C, activity in the colony appeared to be normal, with the alates remaining almost motionless in one or more tightly packed clusters. As the temperature rose between about 34° and 36°C, the general activity gradually increased; the alates began to run about and the clusters broke up. Above about 36°C the entire colony became more and more agitated and the alates leaped and fluttered their wings in frenzied excitement. As the temperature dropped this behavioral sequence was reversed. In the range from 38° to 36°C, the alates again became gregarious — in one instance within 15 minutes from their peak of activity.

On three days, small numbers of these excited alates (15, 13, 2) actually emerged from the nest through a small hole drilled in the cover of one petri dish as well as from under the edge of the cover. In the latter case two soldiers were obviously and attentively stationed near the point of emergence although they did not appear to be regulating the exit of the alates as suggested for *Kalotermes (=Incisitermes) minor* by Harvey *(loc. cit.)*. The emerging alates rapidly gained high points on the soil and small stones in the tray, then took flight after much moving of heads from side to side and waving of antennae. The door of the chamber was opened and observations were terminated after the alates had made rapid, erratic flights into the day-lighted room outside.

These limited observations show that the phases of flight activity, even within the colony, are amenable to laboratory study. Although the preceding manipulations did not duplicate the environmental conditions under which this essentially subterranean termite stages its flights, they do suggest that high temperature (probably reached later in the day near the soil surface) may provide an important cue for the initiation of daily flight periods. As more data become available further refinements in this type of experimentation are planned with several other species of termites in Arizona.

FLIGHT SEASON. — According to legend in the Sonoran Desert, the summer rainy season begins on San Juan's Day, June 24. The rains are also believed to initiate the swarming season of the termites in this region; indeed, in many Latin American localities with a similar weather pattern, the swarming alates are called "Palomitas de San Juan" (Light, '34). Legend and meager published information led to some early and rather casual observations which resulted in one flight record for *Paraneotermes* on August 12, 1956; three in 1957, on July 10, 14 and 16; and one on July 17, 1959. More persistent observation, still within the rainy season, yielded 11 flights from July 5 through 29, 1961. Guided by experience of previous seasons and new knowledge that alate production may begin in early June, intensive observations were made from mid-May to mid-September in 1962 and, with the exception of six weeks of June and July, again in 1963. Thirty-one flights were thus recorded from June 9 through Sept. 7, 1962 (fig. 1), while the first and last flights in 1963 were recorded on June 15 and August 19 (fig. 2). These records spanning 91 and 66 days attest to a considerably protracted flight season for this species, beginning well in advance of the rainy season. A flight on May 29, 1965, further expands the cumulative seasonal record to 102 days within five consecutive months. T. E. Snyder has informed me ('64, *in litt.*) that the U. S. National Museum contains alates caught by light trap on July 6 and August 15, 1947, at Blythe, Riverside Co., California.

INFLUENCE OF ENVIRONMENTAL FACTORS ON TIME OF FLIGHT. — The flights of termites are considered to provide for the foundation of new colonies and hence the maintenance and dispersal of the species. Extensive observations on the termite fauna in Mexico and the southwestern United States have led the writer to conclude that matings between sexes from different colonies, in synchronous flights over limited areas, are presumably usual. The idea that sibling matings are the rule has been advanced by several authors (Weesner, '60, p. 161) although, admittedly, either position would be equally difficult to prove. Since alates of *Paraneotermes* have never been observed emerging from a nest in nature, the following factors actually describe the conditions under which flights are known to have occurred. A more refined analysis does not yet seem warranted on the basis of such data, limited as they are to only two seasons. A

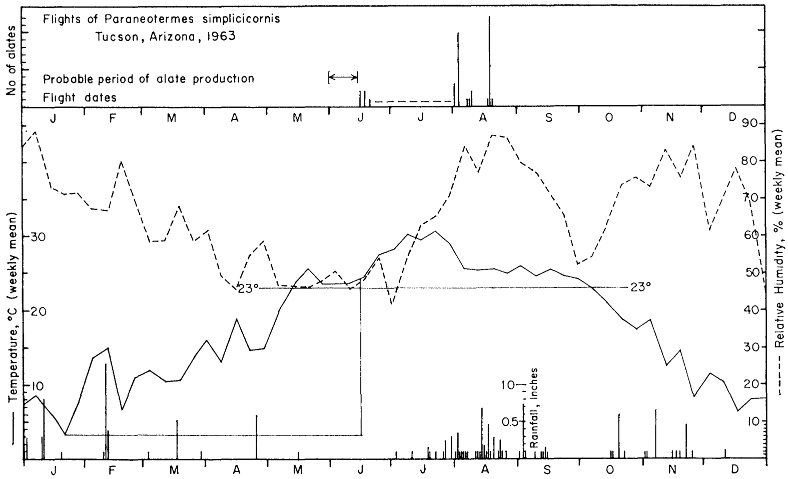

Figure 2. Flight season of *Paraneotermes simplicicornis* in relation to rainfall, weekly mean temperature and relative humidity at Tucson, Arizona, in 1963. Dates showing 0.1″ actually indicate amounts from a trace to 0.1″ of rain. Flights began when mean temperature remained above about 23°C. The upper section shows the numbers of alates observed on each date during the flight season from June 15 to Aug. 19. No observations were made between June 24 and August 1. Data on the maturation of alates were obtained from two colonies, one in the laboratory and one in the field.

few simple correlations are apparent, however, and may provide a basis for determining the cues which are actually used by *Paraneotermes* for initiating both its annual flight season and daily flight periods.

Temperature

The timing of the flight season in relation to weekly mean temperature and relative humidity for two years is plotted in figures 1 and 2. Flights began when the weekly mean temperature remained consistently above about 23°C, while later in the season means reached as high as 29.9° ('62) and 30.6°C ('63). The seasons ended during weekly means of 25.9° ('62) and 25.4°C ('63), leaving three and seven weeks in these years before falling to 23°C. At this point it might be mentioned that the areas under the curves for the two years studied — taken arbitrarily from the lowest weekly mean of the winter to the date of the first flight (figs. 1 and 2) — are very close as measured with a planimeter. This has suggested that it might eventually be profitable to explore modifications of the temperature-summation method in connection with alate development both in nature and in controlled environments, and then to relate results to the initiation of the flight season. However, the list of unknowns concerning this species is so great — location and environment of the nest, favorable temperature ranges for the development of any caste, etc. — that meaningful calculations are hardly possible at present. The simplest and perhaps most plausible explanation for the termination of the flight season might lie in the fact that all alates had flown.

Figure 3 shows the flight periods in relation to the following daily temperatures during the season in 1962; minimum, maximum and temperature 15 minutes after sunset. Daily flight periods (29 in 1962, 11 in 1963) occurred on days with a mean minimal temperature of 20.1° (range, 12.0 — 24.8) in 1962, and 19.0° (range, 13.7 — 22.0) in 1963. The mean maximal temperature for the same days was 33.3° (range, 26.9 — 37.6) in 1962, and 32.3° (range, 29.5 — 36.7) in 1963. Flights began each day at approximately 15 minutes after sunset; the mean temperature for this time, on the days when flights occurred, was 28.2° (range, 23.4 — 32) in 1962, and 26.0° (range, 23.7 — 29) in 1963. Within these limits there is no readily apparent relation to daily temperature patterns.

The temperature cycle of a "typical day," together with curves

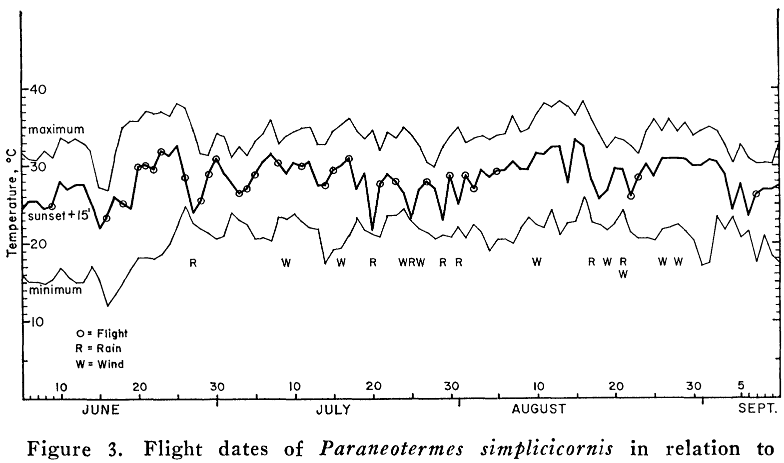

Figure 3. Flight dates of *Paraneotermes simplicicornis* in relation to daily temperature fluctuations in Tucson, Arizona, in 1962. Flights began at approximately 15 min. after sunset. Rain or wind may have prevented flights on at least 15 evenings.

for relative humidity and saturation deficit, is presented in figure 4. The combinations of temperature and relative humidity at the time of sunset plus 15 minutes are plotted in figure 6. Daily flights almost always begin while temperature is falling steadily and generally near or shortly after the low in humidity for the day.

Moisture

Rainfall and Soil Moisture. — The relation of the flight season and the daily flights to rainfall for 1962 and '63 is shown in figures 1 and 2. For these years, where the first and last flights were established with reasonable certainty, the flight season began well in advance of the summer rains. In 1962 the first flight was staged 81 days after the last measurable rain of 0.09″ was recorded on March 20. Eight flights had occurred before the next measurable rain (0.02″) had fallen 99 days later. The next year, 51 days elapsed between the last measurable rain of 0.58″ on April 25 and the first flight, with at least three flights occurring before the first measurable rain (0.01″) in 69 days. In 1965 the first flight took place 17 days after 0.01″ was measured on May 12. These records established beyond any doubt that *Paraneotermes* does not begin swarming in response to seasonal rainfall. This is apparently the case with many dry-wood termites, such as *Cryptotermes* (Weesner, '60, p. 160).

Although a few of the larger flights have taken place on days following substantial rains, the general pattern seems to be one in which rain is actually avoided (figs. 1 and 2). Of 29 flights observed in the study area during 1962, only eight occurred on rainy days, and on each of these days only 0.05″ or less was measured. Further, flights did not take place if any rain occurred within an hour before or after flight time. A similar pattern is evident for other years, although the data are much less complete.

No measurements of soil moisture have been made in connection with the flights of this termite. It is certain, however, that the general floor of the desert is hard-packed and that the soil is extremely dry to a depth of many feet during the early part of the season. The matter of the selection of nesting site is briefly covered under *Post-Flight Behavior.*

Relative Humidity. — Figures 1 and 2 show the relation of the total flight season to the weekly mean relative humidity for two years. The seasons took place within means of 50.1 and 79.1% ('62) and 40.6 and 86.9% relative humidity ('63). These ranges include very nearly the extremes for each year, and cover the summer trend from very low to high mean humidities.

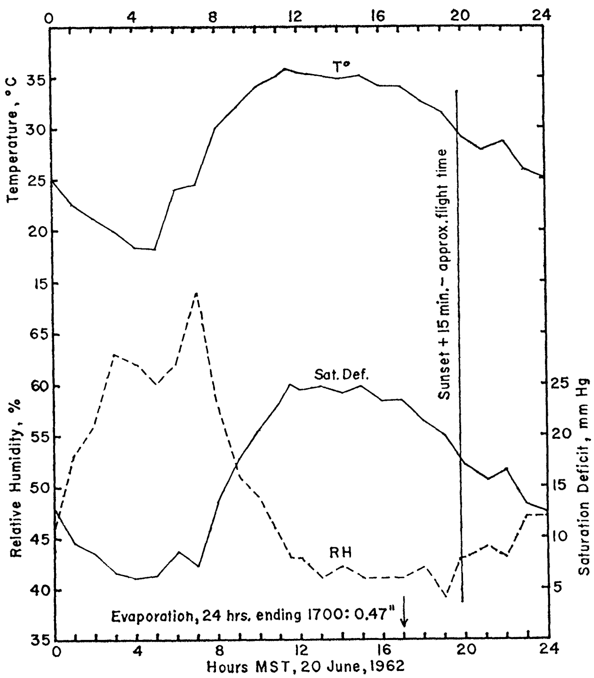

Figure 4. Relationship between approximate flight time (sunset plus 15 min.) of *Paraneotermes simplicicornis* and temperature, relative humidity, saturation deficit and evaporation. June 20 was taken as a typical day during the 1962 flight season in Tucson, Arizona.

In relation to daily fluctuations of relative humidity, individual flight periods (29 in 1962, 11 in 1963) occurred as follows: on days with a mean minimum humidity of 45.8% (range, 37 — 65) in 1962, and 47.4% (range, 30 — 65) in 1963; on days with a mean maximum humidity of 85.9% (range, 62 — 100) in 1962, and 91.4% (range, 65 — 100) in 1963. Mean humidity at flight time (sunset plus 15 minutes) was 56.8% (range, 38 — 92) in 1962, and 71.3% (range, 36 — 100) in 1963.

When the rains begin, usually in July, fluctuations in relative humidity vary widely during each day as well as from day to day. There were several days during the two years studied when the relative humidity at the time of sunset was at or close to 100%. Daily flights of *Paraneotermes* almost never occurred on such days; indeed, probably as a result of its avoidance of rain, it rarely flew when the relative humidity was as high as 80 or 90%. It is hardly necessary to point out that the relative humidity at the time of flight, generally well below 60%, is closely correlated with the high temperatures during afternoon and evening (fig. 4).

Evaporation and Saturation Deficit. — Since evaporation was measured 2.5 miles from the study area, the following figures are included only as a general indication of the evaporative power of the atmosphere in a region occupied by *Paraneotermes*. Figure 5 shows that flights occur during the season with the highest evaporation rate of the entire year. The mean daily evaporation rate for 29 flight days in 1962 and 11 in 1963 was 0.36″ (range, 0.10 — 0.51) in 1962, and 0.30″ (range, 0.10 — 0.56) in 1963 (U. S. Department of Commerce, '62; '63). The overriding influence of high temperature at this time of year insures a high level of evaporation in spite of the moderating effect of the rains which are, at best, sporadic and only infrequently heavy.

The saturation deficit at the study site provides another measure of the dryness of the atmosphere which the alates encounter during their brief period of actual flight. Also closely dependent on temperature, this factor varies about a very high level during the flight season. The weekly mean saturation deficit for the approximate time of flight (sunset plus 15 minutes) is plotted in figure 5. In 1962 the 29 daily flights began at a mean saturation deficit of 12.8 mm. Hg (range, 2.1 — 20.7 mm. Hg). The typically wide daily variation in saturation deficit is shown in figure 4. Although this information may be of little value at present, laboratory experiments might be designed to determine whether the alates respond to differences in relative humidity or in evaporation (or saturation deficit), and thus provide a means for evaluating the effect of these factors on flight behavior. For example, perhaps the contrast between a relatively dry atmosphere and the higher moisture levels in microclimates at the level of the soil provides gradients which are used by the alates, first in leaving the colony and later in seeking out suitable nesting sites.

Light

The rather consistent appearance of alates at lights in the early evening for several seasons suggested that light intensity might be a cue for the initiation of daily flight periods. The times of "first sightings" of alates during 1962 are shown in relation to time of sunset for Tucson in figure 7. Starting in 1963, measurements of light intensity at the zenith have been made with a photographic light meter on a number of evenings during each flight season. *Paraneotermes* has never been observed in flight until the light intensity has thus registered approximately 0.5 lumen per square foot (foot candles) or less. As with *Neotermes tectonae* Damm. (Kalshoven, '30) and probably other evening fliers, a few observations have shown that flight time is earlier on cloudy evenings. Considering the handicap of unknown nesting sites, the correlation between the beginning of the flight period and the time of sunset, or light intensity, is close. Whatever other advantages there may be, it is certain that many predators must be avoided by swarming at dusk.

These few notes indicate the desirability of continuous and more sensitive measurements of light intensity in the vicinity of the emergence holes, whenever they can be found. The subject of rhythms and other aspects of behavior in the alates, nymphs and soldiers should also be studied in laboratory colonies under controlled illumination. Indeed, a most encouraging find has been made in this connection with certain species of ants. McCluskey ('65) has shown that endogenous activity rhythms of the males correspond to the timing of mating flight in the field.

FLIGHT BEHAVIOR. — Considering the relative scarcity of evidence for *Paraneotermes* in the vicinity of Tucson and the numbers of alates appearing at lights, it is probable that there were no more than one or two colonies in or near the study area. On any basis, the number of alates involved in each daily flight would be very small. Assuming that most of the alates in 71 flights were from a single colony and visited the lights (front and back of house), the average

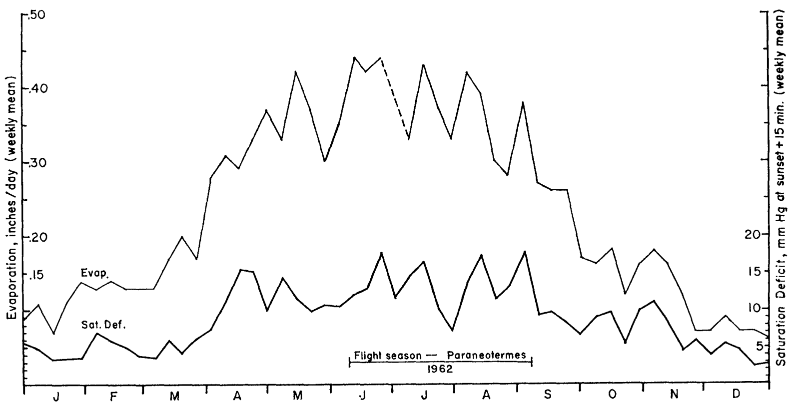

Figure 5. Relationship between flight season of *Paraneotermes simplicicornis* and evaporation rate and saturation deficit in Tucson, Arizona, 1962.

number per flight was approximately five. The usual number seen during a flight was between one and 12, but on three occasions in seven years, the numbers were 23, 48 and 57. Both sexes have been taken in single flights, although no record of the distribution was made. Concurrent flights have been recorded five times: At 1.8, 2.6, 2.8, 12 and 13 miles from the study area.

Paraneotermes was observed in natural flight only as it flew in rapidly, between two and six feet above the ground, to lighted areas. After alighting on walls or pavement, individuals frequently leaped and flew about very erratically. Light ('37) and Light and Weesner ('48) briefly described flights under what were probably abnormal conditions, and Light termed the species a strong and rapid flier. Although in a dry container alates will die in less than a day after capture, presumably of desiccation, they have been held for as long as two weeks in petri dishes containing 4% agar. Alates have been noted to remain in the vicinity of lights up to 80 minutes after their arrival.

Post-flight behavior. — Alates of this species were observed to lose their wings much more readily than many other members of

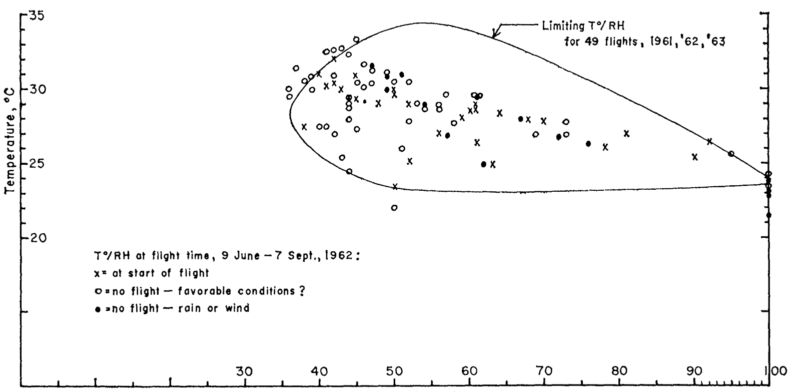

Figure 6. Combinations of temperature and relative humidity at approximate flight time (sunset plus 15 min.) for *Paraneotermes simplicicornis* at Tucson, Arizona. The limits of these conditions for 49 flights are shown by the closed curve. Conditions for the 91 evenings in the 1962 flight season are plotted as follows: x, at the start of 29 flights; solid circles, at flight time on 15 evenings when flights may have been prevented by rain or wind; open circles, at flight time on 47 evenings when no flights were observed. In the latter case these conditions could have been limiting on 13 evenings where they fell outside the curve.

the Family Kalotermitidae. However, it is strongly suspected that the environment under which the following observations were made (residential area with irrigated plantings) is far more suitable for the rapid entrainment of normal post-flight behavior than for that of other local, but strictly dry-wood species such as *Incisitermes (=Procryptotermes) hubbardi.* The de-alation of many adults around lights usually occurs within a few minutes to a half hour of their first appearance. This is accomplished through the usual bodily contortions and, frequently, by lunging forward and backward and rubbing the wings against the edges of cracks or protrusions. Similar behavior was also observed by Light ('37). Using several groups of alates of both sexes taken at lights, it was found that alates would eventually die in possession of their wings when confined in a dry environment. In contrast, and even after such confinement for several hours, alates rid themselves of their wings within one to five minutes upon being released in a petri dish containing agar and decaying wood. Further, both sexes were observed to lose their wings within as little as 30 seconds after being placed in a dish containing de-alated individuals. (In similar manipulations with *Amitermes emersoni* [*Termitidae*], alates lost their wings on an agar surface which had recently been occupied by de-alated individuals.) The readiness with which these alates divested themselves of their wings in the presence of others, albeit in a suitable environment, suggests that a pheromone may be released by the de-alated forms which provokes, or at least facilitates, de-alation. Since a strict accounting of the sexes was not kept, it is possible that the female odor (either in calling or shortly before) may also stimulate this behavior in the males, or even in both sexes.

Female alates frequently assumed the calling attitude soon after alighting on vertical or horizontal surfaces. The abdomen is typically raised at an angle of about 25° from the horizontal with the tip slightly downturned and thus roughly parallel with the surface. Under the artificial conditions provided in a petri dish containing agar and wood, a single, de-alated female assumed the calling attitude many times during three days' confinement. On the third evening a winged male responded to her presence by dropping his wings and following her within one minute. These disconnected observations on *Paraneotermes* are strongly suggestive of the post-flight behavior of *Neotermes tectonae* described by Kalshoven ('30): either sex may locate a suitable nesting site where it then survives, apparently capable of attracting a mate, for some weeks or months. In species such as these where small numbers fly rather frequently over a long season,

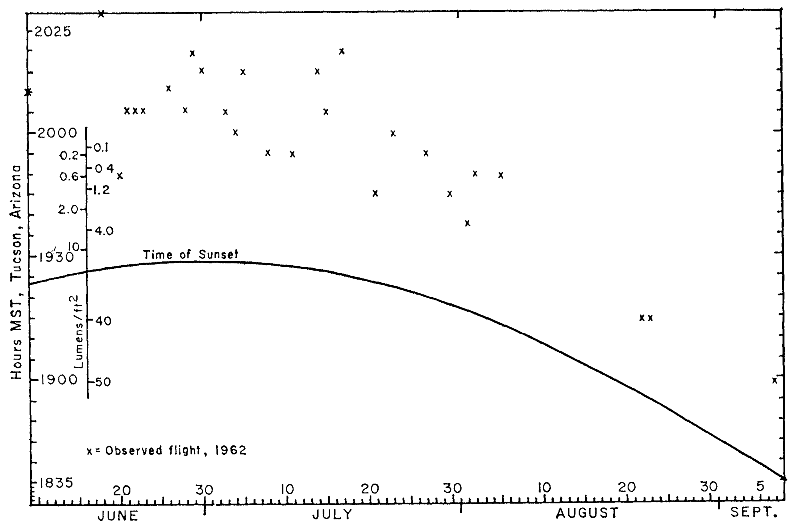

Figure 7. Relationship between observed time of flight of *Paraneotermes simplicicornis* and time of sunset in Tucson, Arizona, in 1962. Inset scale gives approximate light intensity (in lumens per square foot) in the study area on a cloudless evening early in the flight season. No flights have ever been observed earlier than 15 min. after sunset or at a light intensity greater than approximately 0.5 lumen per square foot.

the ability to survive and to attract a mate from succeeding flight periods is an obvious asset.

Alates often formed tandem pairs on walls and on pavement shortly after their arrival at lights. In situations involving several members of both sexes, de-alated pairs were soon formed and these generally left the lighted area within a half hour. This movement appeared to result from the unsuitability of the featureless pavement in the vicinity of the lights, and perhaps from a preference for more humid areas of soil nearby, for they seemed to be completely indifferent to light.

Light ('37, pp. 431 - 4) showed that colonizing pairs were able to dig into fine, damp soil, and did so in preference to wood, although they frequently dug in close to pieces of wood. In the present study, pairs isolated in petri dishes (containing 4% agar and a piece of decayed wood) readily dug into the agar and formed small cells partly in the agar and partly in the wood. These attempts to set colonies from primary pairs have been generally unsuccessful. All pairs started in dishes of agar and wood died within two months without producing any eggs. On the other hand, pairs of replacement reproductives have appeared in large laboratory subcolonies of 1000 - 2000 individuals, and these have produced dozens of eggs which hatched successfully over the course of a year or more. Colonizing pairs have been found a few hours after flights under pieces of dead wood in the study area. In the desert where the soil is hard and dry during much of the flight season, pairs may find points suitable for digging in next to, or beneath, dead wood. The sequence of post-flight behavior thus appears to bear certain similarities to that of many subterranean termites.

PREDATORS. — It has been assumed that most of the diurnal reptiles would find no opportunity for feeding on *Paraneotermes*. It was, therefore, a surprise when Asplund ('64) found 24 alates in one, and 10 in another, stomach of the tree lizard, *Urosaurus ornatus*. Such numbers suggest that the alates may have been taken at their emergence holes.

Observations in the study area and surrounding desert have established that most of the common birds have ceased their feeding activities and final vocal chorus shortly before the daily flight periods of *Paraneotermes* begin. Both Nighthawks and bats have been seen patrolling the area as early as five minutes before sunset and until no longer visible, approximately 25 minutes after sunset. Although no stomachs from any birds in the area have been examined, many stomachs of several species of bats have been carefully studied. Undetermined fragments of termite wings were found in the stomachs of three specimens of the Hoary Bat, *Lasiurus cinereus*, taken either in southern Arizona or New Mexico (Ross, '64).

DISCUSSION. — In the preceding presentation a variety of problems have arisen and possible approaches to their solutions have been suggested by the evidence at hand. A few additional questions of a more general nature are included here. During the long flight season of *Paraneotermes* there are many evenings when no flights are staged. In 1962 flights were recorded on only 29 out of 91 evenings between the inclusive dates July 9 — Sept. 7. On at least 15 of these evenings rain or moderate to strong winds occurred which are probably valid deterrents to flight. In this connection it should be worth determining the temperature limits within which the alates are capable of sustained flight. For example, on 13 evenings, the combinations of temperature and relative humidity (at sunset plus 15 minutes) were outside the range determined for a total of 49 flights in the study area (fig. 6). Allowing for a few flights which may have been missed, this still leaves 34 evenings, or over one-third of the total, when no flights took place. There are no other environmental factors which might obviously have prevented flights on these days. The most reasonable explanation which can be advanced at present — and which would also explain the long flight season characteristic of many termites — is a progressive production of alates. Evidence from the two subcolonies taken in 1961 does not support this idea, for large numbers of alates were produced within a short time, just prior to the flight season. It is still possible, however, that the pre-alates develop deep within the colony and migrate to the more superficial out posts to complete their development as the season progresses. Herfs ('51) found that *Reticulitermes lucifugus* (Rossi) (maintained in 13 large groups under constant conditions) produced alates over a period varying from 0.25 to 3.5 months.

During their flight season, and not always at the time of flight, one or more castes of the following genera in Arizona have been noticed at emergence ("observation"?) holes: *Incisitermes, Zootermopsis, Heterotermes, Amitermes* and *Gnathamitermes*. This habit, which has probably been noted by many other observers, has led to the suspicion that termites may not be so much the "dwellers in darkness" as generally believed. It further suggests that many termites may thus have considerable, and perhaps rather continuous, information on the photoperiod and other external environmental factors, either through actual openings to the outside or through the walls of superficial galleries in wood or soil. The behavior of alates, or of an entire colony, might then be readily imagined to be adjusted to the approximate frequency of one or more points in the daily photoperiod. Data on the flight behavior of *Paraneotermes* strongly suggest that the alates are initially stimulated by high temperatures, but that the daily flights may be finally triggered in response to a definite level of diminishing light intensity on otherwise favorable evenings. The flights of many termites and of several other insects have been shown to be closely correlated with dusk or to decreased light intensity (*e.g.,* Myers, '52; Bates, '49).

Field studies in progress on a variety of other termites in Arizona and Mexico are aimed at providing a basis for the comparative study of termite flight behavior. Thus far, limited experience has shown that it may be possible to resolve certain behavioral problems by the manipulation of captive colonies in the laboratory. It is anticipated that a balanced combination of field and laboratory studies may eventually permit the forecasting of both flight seasons and daily flight periods of the species within limited geographic areas.

SUMMARY. — Weather data have been collected and studied in

conjunction with field observations on 78 flights of the desert dampwood termite, *Paraneotermes simplicicornis*, in southern Arizona. Its flight behavior is characterized by a large number of generally small flights occurring over a prolonged season and over a rather wide range of environmental conditions. Alates appear in the colonies about three weeks in advance of the flight season. As many as 31 flights have been observed in one season which may extend from late May into early September. Flights begin when weekly mean temperatures remain consistently above 23°C. They are staged during evening twilight and begin at a mean temperature of 27.6°C. (range, 23.4 — 32) and a mean relative humidity of 60.8% (range, 36 — 100). Mean saturation deficit at the start of 29 flights in one season measured 12.8 mm. Hg and ranged between 2.1 and 20.7 mm. Records clearly indicate that this termite does not begin swarming, nor stage its daily flights, in response to rainfall. Since the summer rains occur in the form of sporadic thunderstorms, the mean daily evaporation rate remains high: 0.36 inches (0.10 to 0.51) for the flight days in 1962. The sequence of post-flight behavior is described and bears certain similarities to that of subterranean termites.

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