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Daily Nest Opening and Closing of the Ant Pogonomyrmex Californicus

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DAILY NEST OPENING AND CLOSING OF THE ANT POGONOMYRMEX CALIFORNICUS

by

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Each person whose signature appears below certifies that he has read this thesis and that in his opinion it is adequate, in scope and quality, as a thesis for the degree of Master of Arts.

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Dedicated to my wife, Joan, whose support and loving encouragement made my graduate education possible.

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CHAPTER I

INTRODUCTION

There is little reported in the literature concerning the timing of activity of the worker caste of the common red harvester ant Pogonomyrmex californicus (Buckley, 1867). Michener (1942) observed a nest in his back yard in Pasadena, California, and for several years kept careful notes on all activity above the ground. The nest was opened in the morning and closed in the evening except during the winter months, when it remained closed.

Cole (1932) found that P. californicus in the Mojave Desert, rather than closing the nest in the evening, closed in the late morning and opened in the evening. Foraging was generally done in the late evening and early morning, continuing in some instances all night.

One nest of Pogonomyrmex badius (Latr.) in Florida was observed for several months by Van Pelt (1953). He found the closing activity to be more closely correlated with the temperature measured three inches below the surface of the ground than with the temperature at the surface or with humidity. He also believed that opening and closing activities were influenced by wind, rain, and the approach of daylight or darkness.

Ayre (1958) studied meteorological factors which affect the field foraging activity of Formica subnitens Creighton. Though he was mainly concerned with temperature, atmospheric pressure, and relative humidity in the field, he did find that light intensity in the

laboratory had a distinct influence on the level of activity, but extremes did not cause cessation of activity.

Worker activity was shown to have a diurnal rhythm in the leaf cutter ant Atta cephalotes L. These ants move to the entrance of the nest about an hour before dawn. When the light intensity reaches a level of about 0.3 foot candles foraging begins. Foraging could be initiated sooner if the ants were exposed to light as soon as they came near the nest opening, and foraging could be delayed if the nest openings were shaded from all light. The congregating of the workers at the nest opening before dawn seems to indicate an inherent diurnal rhythm, unrelated to the effects of light or any other variable operating outside the nest (Hodgson, 1955).

In laboratory studies the males and females of certain species of ants have been shown to have an endogenous "clock," producing a diurnal periodicity, i.e. a circadian rhythm in constant conditions of temperature and lighting (McCluskey, 1963 and 1967).

CHAPTER II

OBJECTIVE

Because the opening and closing of the nest by *P. californicus* workers is such a clear, discrete event, this research was undertaken to determine whether the workers were responding to an endogenous clock or whether their behavior was merely due to some environmental variable such as temperature. This objective is part of the larger aim of discovering what role biological clocks may play in a social group such as ants.

CHAPTER III

METHODS AND MATERIALS

Twelve nests of the common red harvester ant, Pogonomyrmex californicus Buckley (determined by A. C. Cole), about two miles west of Loma Linda, California, were studied. These nests were located in the middle of a dirt road running east and west. This road was of uniform light-colored, sandy soil and the nests in the middle of it were in a nearly straight line extending a distance of about one hundred yards; the surface throughout this distance was flat. The apparent uniformity of conditions was remarkable.

A nest was considered closed when it was completely covered over with no trace of an opening left, and was considered opened (always from the inside) when an opening was made and a worker had come out.

The opening and closing of the nests were observed during the months of July, August, and September, 1967. The time and temperature of opening and closing for each nest was recorded. The temperatures were taken at about one sixteenth of an inch above the surface of the ground and at three inches below the surface with a glass bulb mercury thermometer. Temperatures were recorded in degrees centigrade, and time was recorded as Pacific Standard Time.

Since most of the nests closed after the sun had set, observations made in the dark were done with a two cell flash light which had the lens covered with nine sheets of red cellophane. The assumption

was made that the ants would be little affected by red light, especially of very low intensity, consistent with observations made by McCluskey (1963) in studies of another species.

Observations of each nest were made every ten to fifteen minutes so that initiation as well as completion of the opening and closing process could be noted accurately.

In addition, the three following types of field experiments were done. In each case three nests were treated as experimental, and three other nests as controls. All those chosen were ones which had been seen to open and close consistently.

1. Nest areas were cooled with ice.
2. Nest openings were kept in darkness as the light intensity increased in the morning.
3. Nest openings, after closing, were kept under constant light until the light of dawn was as intense as the light of the sealed beam lamps being used.

The ice was used in two separate experiments to see if a lowering of the temperature would prevent the opening of the nests in the morning. Twenty-five pounds of ice were placed in six plastic bags and laid around the nest on aluminum foil which was placed so as to leave an opening around the entrance about six inches square. The bags of ice were then covered with several sheets of newspaper and a thin layer of soil for insulation. This procedure was carried out at about 2330. The ice was left in place until about 0800, or later in some cases, when it had almost all melted.

The temperature at the surface about one sixteenth inch above the nest opening was found to be maintained at 12 to 16 degrees centigrade. In order to take temperatures three inches directly beneath the ice packs without disturbing a nest by digging into it, ice was used as described above, but at a location where there was no nest (Table XVI, page 42).

The nests were darkened in the morning to see if opening could be delayed. A cardboard box, capable of keeping the light intensity down far below that following dawn, was put over the entrance of each nest about midnight and soil was put loosely around the base of the box to prevent light from entering. These boxes were left in place until the workers appeared outside of them.

"EVEREADY" sealed-beam lanterns (model 150) equipped with EVEREADY no. 520 alkaline batteries were used to illuminate nests in order to determine whether light could cause the workers to open the nests earlier than they ordinarily would. The light was placed in position one and an eighth inches directly above the nest entrance at 0230. It gave a light intensity of 11,000 lux at the surface of the nest opening (measured with a "Gossen LUNASIX, 2 Batt. Mallory PX 13" light meter). The lights were left in position until the daylight intensity was greater than that of the lanterns. The temperature measured on the surface of the ground directly beneath the light was about one degree warmer than the surface temperature elsewhere.

CHAPTER IV

RESULTS

The closing procedure began in most cases with one or two ants scratching vigorously with their two front legs in a somewhat random manner around the nest opening. Soon these would be joined by two or three other workers which would scratch and carry small pieces of soil into the nest opening; all the while other workers were coming and going through the opening. In most cases traffic through the nest opening diminished rapidly and the nest was closed, sometimes by only one or two workers on the outside which remained out all night and at other times by workers on the inside with none remaining out.

Nests A and B (Tables XVII and XVIII in the Appendix) were unusual in that neither of them was seen to close at night; in fact nest A was never seen to close at all, though above ground activity was reduced at night and no foraging took place then. One day nest B was observed in the morning about 0930 just as the workers were in the process of closing. It closed about 0930 or 1000 in the morning and opened up about 1630 or 1700 in the evening on days when it was observed; however, no records were kept of opening and closing times and temperatures. The foraging activities of this nest took place in the morning before closing and in the evening after opening, but no foraging activity was seen after dark.

The rest of the Results section is based on the other ten nests. Some of these failed to close on some nights, and were of necessity

omitted from the means on those days. All of the observations are given in Tables XVII and XVIII in the Appendix.

For the nests as a group the opening time was significantly later for each succeeding month (Table I and Figs. 1 and 2). But when the opening temperatures for each month, whether at the surface or three inches deep, were considered, only September was significantly different from the other two months, with the highest surface temperature and the lowest deep temperature.

The seasonal progression of mean opening times from month to month seen in Table I is also evident in Table II where all the days are compared with each other and shown to vary significantly. When Tukey's w-procedure is applied to the data in these tables the mean opening values for most of the days early in the season are shown to be significantly different from most of those late in the season. (When an analysis of variance has an F ratio which is significant, Tukey's w-procedure may be applied to determine between which values the differences lie (Steel and Torrie, 1960).)

Likewise, the daily mean opening temperatures at the surface and three inches deep are seen to differ (Tables III and IV). Tukey's w-procedure shows the differences to be generally between days in September and all other days.

Within the month of July there was a significant difference of mean opening time between days (Table II), and between nests (Table V), for August the difference was between nests (Table VI), but not between days (Table II), while for September there was a difference between

days (Table II). This is illustrated for July by Fig. 3 with a 70 percent confidence interval for each day and each nest.

Table III indicates no significant difference in mean opening surface temperatures between the days within any one of the three months. There was, however, a difference between nests for the month of July and for August (Tables V, VI, and VII). The 70 percent confidence intervals are shown for July in Fig. 3.

The mean opening temperature measured at three inches depth was different from day to day within the months of July and of August but not of September (Table IV). No difference is shown between nests for any of the months (Tables V, VI, and VII). The 70 percent confidence intervals for the July means are shown in Fig. 3.

It can be seen on Fig. 3 that July 15 has the latest mean opening time for that month (significantly later in three cases); it was chosen as a day against which to compare all other days in July (Fig. 5). It has already been shown in Table III that the mean opening temperatures at the surface of the ground are not significantly different from each other from day to day. As might be expected then, Fig. 5 shows that on July 15, when the temperature reached the usual opening level an hour late, the nests opened about an hour later, as compared with other days in the month.

Figure 6 plots opening time against opening temperature measured three inches below the surface of the ground and shows the same thing as Fig. 5, i.e., that on July days when the temperature was high at an early hour the nests were opened earlier than on cooler days.

The mean closing time for September was earlier than that for August and for July, but no significant temperature difference is indicated between the three months, whether measured at the surface or three inches deep (Table VIII). The monthly progression in closing times is clearly seen in Figs. 7 and 8.

When the mean closing times for all the days on which observations were made are compared (using Tukey's w-procedure), those for days early in the season generally are seen to be later than for those late in the season (Table IX). The mean closing surface temperatures compared in the same way (Table X) show no significant difference between days. While the mean closing temperatures measured three inches deep show the days to be significantly different from each other, no clear seasonal progression is evident (Table XI).

When the mean closing times for the days within any given month are compared with each other no significant difference is seen (Table IX); the same is true for the mean closing temperatures measured three inches below the surface of the ground (Table XI).

The mean closing surface temperature for the days within the month of July are different from each other (Table X). Using Tukey's w-procedure, July 21 is shown to differ from July 28 and July 20.

No significant difference is found between the nests with regard to the three closing variables measured (time, temperature at the surface, and temperature three inches below the surface) in July. For August and for September just the opposite is true, the nests are different from each other with respect to all three variables (Tables

XII, XIII, and XIV).

Figure 4 shows the mean 70 percent confidence intervals for closing time, closing surface temperature, and closing three inch deep temperature for July.

The results of the field experiments described in the Methods section are given below.

Table XV shows that on each of the two different days the nests which had ice packed around them were different than the controls in opening time.

In contrast to the ice experiment mentioned above, in which there was a marked difference between the control nests and the experimental nests, the three nests which were kept dark on September 16 all opened at the same time and temperature as the controls (Table XV).

The experiment done September 21, in which lights were used to illuminate three nests from midnight on, showed some variation in opening time, in temperature at the surface, and in temperature three inches deep, but the differences from the control nests were not significant. Days other than the experimental day were noted (Table XVII in the Appendix); on two days the mean opening time of the experimental nests was earlier than the controls and on two days it was later.

All experimental and control nests are marked on Table XVII in the Appendix.

CHAPTER V

DISCUSSION

A major result of this study is a quantitative description of the variation in opening and closing times of a group of nests. The amount of variation is striking, especially considering how close together the nests were, and how uniform the environment was. Perhaps the nests differed in size, age, or in arrangement of subsurface chambers.

Ten of the twelve nests opened in the morning and closed in the evening similar to the one Michener (1942) observed in his back yard. But most nights at least one of these would fail to close. Of the other two nests one was never seen to close; the other closed during the day rather than night, following a pattern similar to those in the Mojave Desert described by Cole (1932). If the temperature had been warm enough here during the day, would more nests have closed?

The rest of the discussion concerns the ten nests which usually closed at night. For these the standard deviation of opening time was less than a half hour on most of the days observed (Table II). When the ten nests are compared over a number of days of a month the mean opening times of the different nests are seen to be within an hour of each other (Tables V, VI, and VII).

The mean opening times for the different days within a month varied as much as an hour from each other (Table II) while the sunrise time for the observation days of a given month changed only five to ten minutes. The mean opening time for July was 0559, an hour after sunrise

(0448 on July 15 and 0458 on July 29). Opening time for August was 0634, about an hour and fifteen minutes after sunrise, and for September it was 0722, nearly two hours after sunrise.

The closing time was much more varied than the opening time (Fig. 3). This is reflected in the larger standard deviations of the mean closing time for July (Tables I and VIII). The smaller number of closing observations during August and September prevent a fair comparison of standard deviations then. The standard deviations for the mean closing times for individual nests and for individual days were also larger than those for opening, indicating a greater variation in closing times, with the means for nests and for days in several cases varying from each other by more than an hour in spite of the uniform environment (Tables IX, XII, XIII, and XIV). The mean closing time for July was 2050, about two hours after sundown (1906 on July 14 and 1900 on July 28). Closing time for August was 2027, about two hours after sundown also; for September it was 1906, only an hour after sundown, but with a large standard deviation. The mean closing times for these three months do show a seasonal progression which is more obvious in the scattergrams of Figs. 7 and 8.

Michener (1942) found that the span of daily activity became shorter and shorter in the fall until finally the nest failed to open at all and remained closed until spring. Since the mean opening times for the three months were progressively later after sunrise and earlier after sunset, this may support Michener's observations.

The regularity of opening time suggests the importance of the light cycle in the timing of the event. If temperature were the sole

timing factor, opening should occur any time after closing that the critical temperature was reached, but no nest was ever observed to open (once it was closed) at any other time except after sunrise. One nest of P. californicus (determined by A. C. Cole), located in my back yard, was heated with a 250 watt heat lamp for about six hours (from 2000 to 0200) very soon after it had closed for the night. The temperature three inches deep was raised to 40° C over this period of time yet the nest did not open until about an hour after sunrise. No other experiments were performed with this nest and no other data were collected.

A possible explanation for the greater variability in closing than in opening time might be that the temperature in the evening fell rather slowly while the increase in temperature in the morning was rapid.

Illuminating the area after the nest had closed had no effect on the opening time (Table XV), perhaps because the light intensity was not great enough to penetrate the dirt plug which appeared to be quite thick. Opening does not normally occur until some time after the surface is well lighted. However, this brief experiment was not sufficient to rule out the possibility of the more intense light of later morning penetrating the plug.

During the summer when these observations were made the days were very warm and there were no rainy days or days on which clouds covered the sky all day. On some mornings there were high clouds making a complete cover for an hour or two after sunrise but the light intensity was always greater than the intensity of the light used to

illuminate the nests (11,000 lux). On other mornings there was fog but it was quickly burned off soon after sunrise. The opening time never seemed to be affected by these mild weather conditions. The evenings were uniformly clear and warm.

When the nests were covered by boxes to keep the light intensity at a very low level (Table XV), they opened and the ants were active at the same time as the other nests. This is in contrast to the experiment done by Hodgson (1955) with the ant Atta cephalotes, in which the nest was covered to prevent the light of dawn from reaching it and the ants were delayed in forming their foraging columns. If the workers of P. californicus were responding directly to the light, the covering of the nests should have delayed activity unless temperature above a certain point is an overriding factor.

The mean opening temperature three inches deep was never significantly different from nest to nest for any of the three months. For the two months (July and August) in which the mean opening surface temperature between nests was different, only one nest in each month was significantly so; for July number 8 differed from all others, and for August number 4 differed from numbers 7 and 8. The difference between nests may be due to location of subsurface chambers, since the surface temperature would have to become higher for ants in chambers farther down to sense the increase; in addition, since the temperature below the surface rises rather slowly this may account for the fact there was no difference between nests when the opening temperatures three inches deep were compared (Tables V, VI, and IX). However, the

mean opening temperatures at three inches deep differed from each other from day to day.

Cooling by ice delayed the opening time significantly. At least three explanations may be given for this delay: (1) The ants were immobilized by the low temperature and came to the surface only when they were able to move after the ice was removed. (2) The temperature below the ground was lower than the normal threshold temperature for opening. (3) The cool area around the exit discourages the workers from leaving the warmer chambers. The first explanation may be borne out by the fact that in a few cases two or three workers were outside of the nest after closing and appeared unable to move until the ice pack was removed. Even though the two non-experimental nests which were dug up had chambers covering a wide area indicating that the ants probably were not confined to the spot directly beneath the ice pack, they may have been cooled below threshold on their way under it toward the exit.

The experiments did show that temperature can be a limiting factor in the opening of the nest.

The data collected failed to define temperature limits for opening and closing. No matter how warm the night at least seven nests closed; no mornings were observed when it was cool enough to prevent opening of any of the nests. It is interesting to note, however, that the temperature at which the ants opened their nests in the ice experiment (15^{o} C, measured three inches beneath the ice pack a half hour after it was removed, Table XVI) was similar to the temperature recorded for opening on November 4 (Table IV).

Figures 5 and 6, in which certain days in July are compared against other days in July, show that in most cases the days which had the earliest opening time also had the highest temperature at opening time, whether the temperatures were measured at the surface of the ground or three inches deep. If a "clock" is influencing opening activity it may be that the high temperatures of these mornings of early opening induce the ants to open at a lower point in their activity cycle than usual.

The factor causing closing of the nests is difficult to show since between months the only variable which is significantly different is September closing time (Table VIII), and between days only the day in November has a mean closing time and deep temperature significantly different from some of the other days (Tables IX and XI). When nests are considered none of the variables are significantly different between nests for the month of July (Table XII), but for the other two months all of the variables between nests differ (Tables XIII and XIV). This may indicate that none of the variables measured have any effect on closing; or that since the temperature was high enough the ants could remain active until some other stimulus, possibly an internal "clock," indicates that it is time to close the nest.

Though the above observations do not give direct evidence concerning an internal clock, the results are not inconsistent with the possibility of indirect clock control, with opening and closing occurring if a suitable temperature is reached within certain timed segments of the day. The whole light (or temperature) cycle might keep such a clock in phase, since the nests are still plugged at dawn.

CHAPTER VI

SUMMARY

Is the opening and closing of the nest by the harvester ant Pogonomyrmex californicus timed by an endogenous clock?

Twelve nests, in a remarkably uniform natural environment, were studied. Ten of the nests opened in the morning and closed in the evening, only one or two failing to close on any one night. However, of the remaining two nests, one was never seen to close and the other closed during the day and remained open all night.

The closing time was much more varied than the opening time; all of the nests were usually opened within the same hour, but it always took longer for all of the nests to close.

As the season progressed the opening time occurred later in the morning and closing occurred earlier in the evening. The nests also opened progressively later after sunrise and closed earlier after sunset.

In most cases days which had the earliest opening time also had the highest temperature at opening time, whether the temperatures were measured at the surface of the ground or three inches deep.

When the nests were illuminated soon after they had closed, they remained closed until the usual opening time. Cooling the nests with ice delayed the opening time significantly, possibly because the ants were immobilized by low temperatures or because the temperature below the surface was lower than the normal threshold temperature for

opening. Thus low temperatures can be a limiting factor in the opening of the nest.

The results are not inconsistent with the possibility of indirect clock control. The whole light (or temperature) cycle might keep such a clock in phase, since the nests are plugged at dawn.

TABLE I. Analysis of variance between the mean opening times, temperatures (C^{o}) measured at the surface of the ground, and temperatures measured 3" deep. Tabulated values of F in parentheses.

Months	No. of nest observations	Mean opening time ± 1 SD in mins.
July	78	0559 ± 30
August	24	0634 ± 35
September	42	0722 ± 36
	$F = 84.9$	$(F_{.05} = 3.1, F_{.01} = 4.8)$
		Mean opening surf. temp. ± 1 SD
July	78	19.3 ± 3.0
August	23	19.3 ± 3.4
September	32	23.8 ± 4.5
	$F = 19.98$	$(F_{.05} = 3.07, F_{.01} = 4.79)$
		Mean opening 3" deep temp. ± 1 SD
July	78	23.5 ± 1.9
August	23	22.9 ± 1.9
September	32	19.3 ± 1.8
	$F = 55.56$	$(F_{.05} = 3.07, F_{.01} = 4.79)$

FIG. 1. Opening surface temperatures (C^{o}) plotted against opening time.

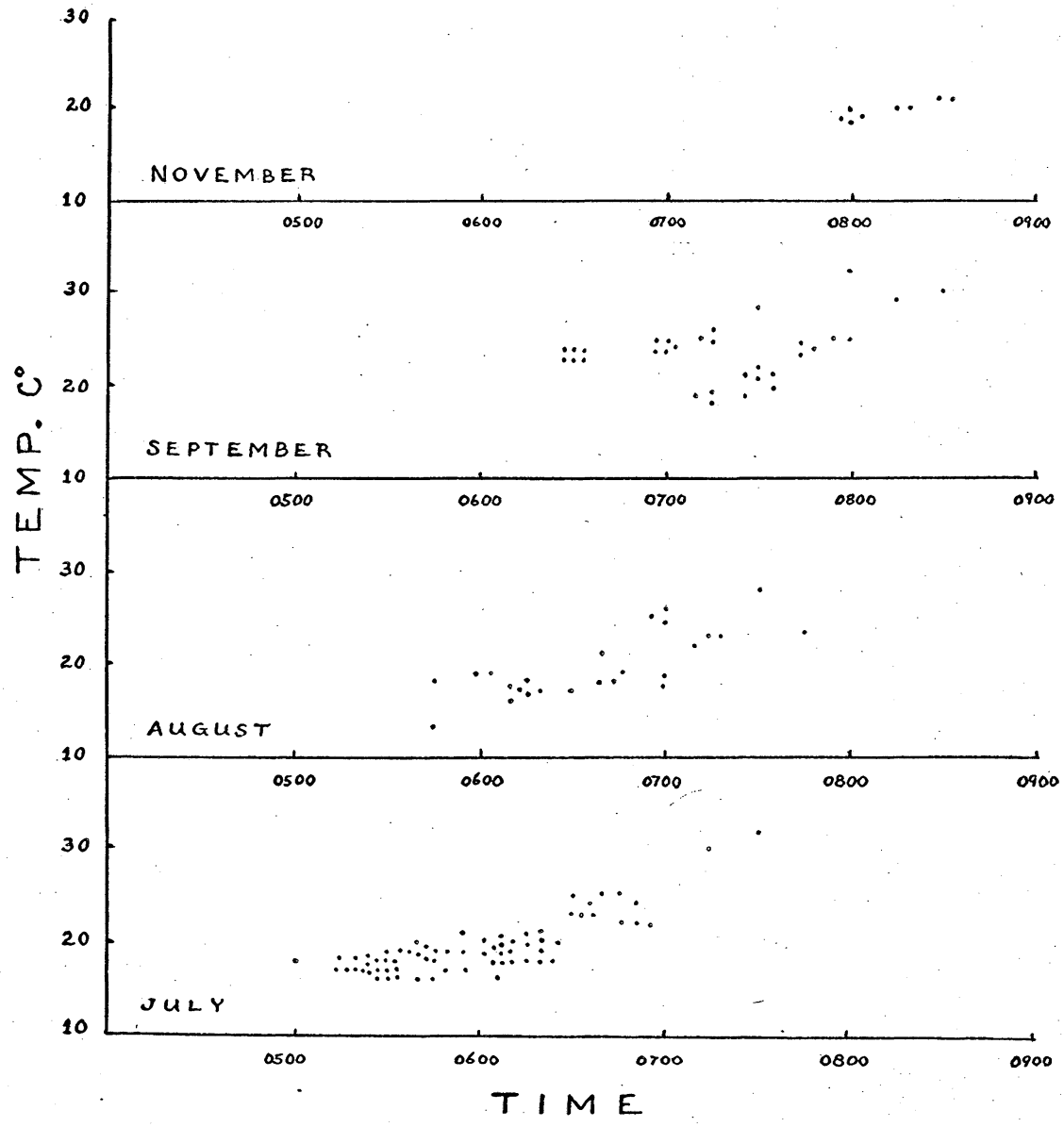


FIG. 2. Opening 3" deep temperatures (C°) plotted against opening time.

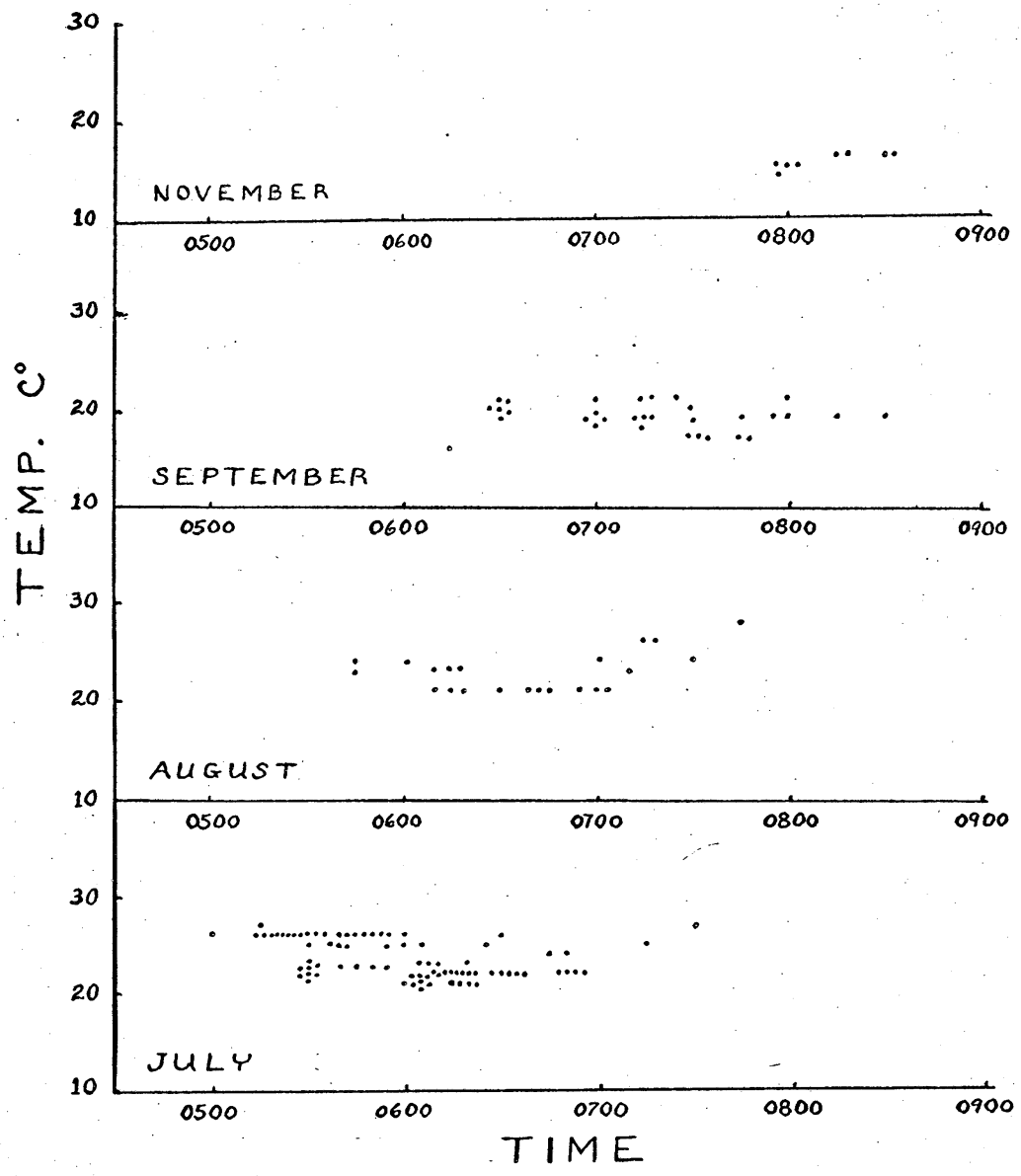


TABLE II. Analysis of variance between the mean opening times for all of the days on which observations were made.

D a y s	No. of nests which opened	Time ± 1 SD in mins.	F values, with tabulated values in parentheses
July 15	10	0631 ± 19	All days, July - November
July 17	10	0628 ± 16	$F = 26.3$ ($F_{.05} = 1.7$, $F_{.01} = 2.0$)
July 18	10	0617 ± 12	
July 20	10	0548 ± 37	
July 21	8	0603 ± 33	July days only
July 22	8	0531 ± 20	$F = 3.6$ ($F_{.05} = 2.0$, $F_{.01} = 2.7$)
July 25	7	0547 ± 20	
July 28	7	0524 ± 11	
July 29	8	0551 ± 17	August days only
Aug. 23	6	0702 ± 23	$F = 2.1$ ($F_{.10} = 2.4$, $F_{.05} = 3.1$)
Aug. 24	7	0633 ± 36	
Aug. 28	5	0622 ± 13	
Aug. 29	6	0617 ± 45	September days only
Sep. 13	8	0733 ± 06	$F = 6.8$ ($F_{.05} = 2.5$, $F_{.01} = 3.5$)
Sep. 14	9	0750 ± 52	
Sep. 15	9	0715 ± 19	
Sep. 16	6	0630 ± 00	
Sep. 21	6	0736 ± 19	
Sep. 22	4	0713 ± 10	
Nov. 4	8	0810 ± 13	

TABLE III. Analysis of variance between the mean opening temperatures (C°) measured at the surface of the ground for all days on which observations were made.

D a y s	No. of nests which opened	Surface temp. ± 1 SD	F values, with tabulated values in parentheses
July 15	10	19.5 ± 2.9	All days, July - November
July 17	10	21.4 ± 2.4	$F = 4.1$ ($F_{.05} = 1.7$, $F_{.01} = 2.0$)
July 18	10	20.4 ± 1.7	
July 20	10	18.7 ± 4.6	
July 21	8	18.5 ± 4.7	July days only
July 22	8	19.1 ± 1.5	$F = 1.6$ ($F_{.10} = 1.8$, $F_{.05} = 2.1$)
July 25	7	18.8 ± 2.7	
July 28	7	17.0 ± 0.0	
July 29	8	19.2 ± 0.4	August days only
Aug. 23	6	19.5 ± 2.3	$F = 0.9$ ($F_{.10} = 2.4$, $F_{.05} = 3.1$)
Aug. 24	7	20.0 ± 5.3	
Aug. 28	5	17.2 ± 1.1	
Aug. 29	5	20.4 ± 2.4	September days only
Sep. 13			$F = 2.2$ ($F_{.10} = 2.2$, $F_{.05} = 2.7$)
Sep. 14	9	24.7 ± 7.1	
Sep. 15	9	25.6 ± 2.6	
Sep. 16	6	23.0 ± 0.0	
Sep. 21	4	23.7 ± 1.8	
Sep. 22	4	18.5 ± 1.0	
Nov. 4	8	19.7 ± 0.8	

TABLE IV. Analysis of variance between the mean opening temperatures (C^{o}) measured 3" below surface of ground for all days on which observations were made.

D a y s	No. of nests which opened	3" deep temp. $\pm$ 1 SD	F values, with tabulated values in parentheses
July 15	10	21.5 $\pm$ 0.5	All days, July - November
July 17	10	22.1 $\pm$ 1.1	$F = 44.2$ ($F_{.05} = 1.7$, $F_{.01} = 2.0$)
July 18	10	21.7 $\pm$ 0.7	
July 20	10	22.7 $\pm$ 1.5	
July 21	8	23.2 $\pm$ 0.7	July days only
July 22	8	26.0 $\pm$ 0.0	$F = 53.3$ ($F_{.05} = 2.0$, $F_{.01} = 2.7$)
July 25	7	26.0 $\pm$ 0.0	
July 28	7	26.0 $\pm$ 0.0	
July 29	8	25.0 $\pm$ 0.0	August days only
Aug. 23	6	22.5 $\pm$ 2.8	$F = 5.4$ ($F_{.05} = 3.1$, $F_{.01} = 5.0$)
Aug. 24	7	23.4 $\pm$ 0.5	
Aug. 28	5	21.0 $\pm$ 0.0	
Aug. 29	5	24.8 $\pm$ 1.1	September days only
Sep. 13	0		$F = 2.0$ ($F_{.10} = 2.2$, $F_{.05} = 2.7$)
Sep. 14	9	18.3 $\pm$ 3.0	
Sep. 15	9	19.3 $\pm$ 0.7	
Sep. 16	6	20.0 $\pm$ 0.0	
Sep. 21	4	19.0 $\pm$ 0.0	
Sep. 22	4	21.0 $\pm$ 0.0	
Nov. 4	8	15.5 $\pm$ 0.5	

TABLE V. Analysis of variance of mean opening times, of temperatures (C°) measured at the surface of the ground, and of temperatures measured 3" below the surface for all of the ten nests which opened; July.

Nests	No. of days observed	Time ± 1 SD in mins.	Surface temp. ± 1 SD	3" deep temp. ± 1 SD
1	9	0600 ± 32	19.6 ± 2.9	24.0 ± 1.8
2	8	0542 ± 23	17.8 ± 1.1	23.1 ± 2.2
3	9	0550 ± 22	18.0 ± 1.7	23.7 ± 2.1
4	5	0548 ± 33	18.2 ± 0.8	22.2 ± 2.2
5	9	0546 ± 27	18.3 ± 2.0	23.6 ± 2.2
6	9	0555 ± 28	18.9 ± 1.8	23.9 ± 1.8
7	9	0607 ± 27	20.1 ± 2.6	23.9 ± 1.8
8	7	0650 ± 24	25.3 ± 4.3	24.4 ± 1.9
9	5	0657 ± 17	17.8 ± 2.2	22.0 ± 0.7
10	8	0659 ± 20	18.9 ± 1.5	23.8 ± 2.2
	F	3.6	6.6	0.9

(Tabulated values: $F_{.10} = 1.7$, $F_{.05} = 2.0$, $F_{.01} = 2.7$)

TABLE VI. As Table V, but for August. In second column the number in parentheses refers to temperatures only.

Nests	No. of days observed	Time ± 1 SD in mins.	Surface temp. ± 1 SD	3" deep temp. ± 1 SD
1	2	0606 ± 10	18.0 ± 1.4	22.5 ± 2.1
2	2 (1)	0552 ± 31	17.0	21.0
3	2	0607 ± 31	17.5 ± 0.7	22.5 ± 2.1
4	1	0545	13.0	23.0
5	2	0625 ± 21	17.5 ± 0.7	22.0 ± 1.4
6	2	0627 ± 30	17.5 ± 0.7	22.0 ± 1.4
7	2	0704 ± 07	23.0 ± 1.4	23.5 ± 0.7
8	3	0730 ± 15	24.7 ± 2.9	26.0 ± 2.0
9	4	0621 ± 26	17.5 ± 1.3	22.3 ± 1.5
10	4	0700 ± 12	21.0 ± 2.9	23.0 ± 2.4
	F	6.1	5.6	1.2

(Tabulated values: $F_{.10} = 2.1$, $F_{.05} = 2.6$, $F_{.01} = 3.9$)

TABLE VII. As Table V, but for September. In the second column the numbers in parentheses refer to temperatures.

Nests	No. of days observed	Time ± 1 SD in mins.	Surface temp. ± 1 SD	3" deep temp. ± 1 SD
1	2 (1)	0730 ± 21	25.0	19.0
2	4 (2)	0740 ± 76	31.0 ± 11.3	23.0 ± 4.2
3	3 (2)	0724 ± 22	24.0 ± 0.0	18.0 ± 1.4
4	4 (3)	0645 ± 27	20.3 ± 5.5	18.3 ± 2.1
5	3 (2)	0721 ± 18	22.5 ± 2.1	18.0 ± 1.4
6	4 (3)	0725 ± 44	25.7 ± 3.1	19.3 ± 0.6
7	6 (5)	0734 ± 40	25.6 ± 5.3	20.0 ± 1.0
8	5	0724 ± 34	23.8 ± 3.3	19.4 ± 1.5
9	6 (5)	0709 ± 24	21.2 ± 2.7	19.2 ± 1.5
10	5 (4)	0730 ± 14	22.5 ± 3.0	19.0 ± 1.6
	F	0.7	1.2	1.6

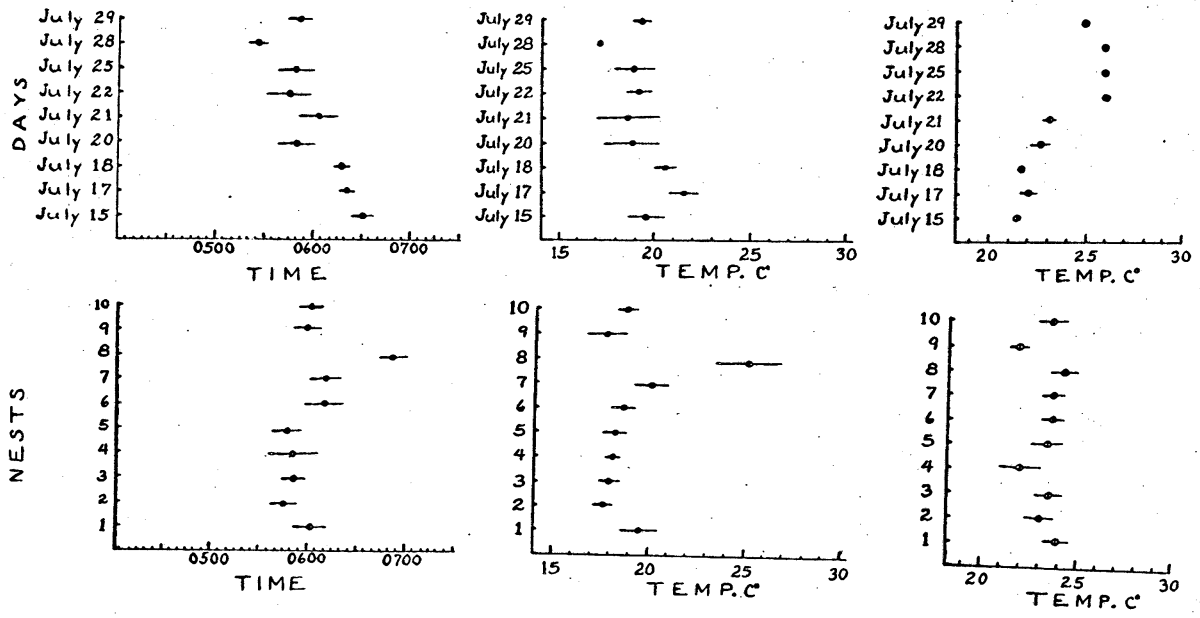
(Tabulated values: $F_{.10} = 1.9$, $F_{.05} = 2.3$)

FIG. 3. Mean opening times, surface temperatures, and 3" deep temperatures for July with 70 percent confidence intervals.

Days with nests as replicates.

Nests with days as replicates.

FIG. 4. The same as Fig. 3, but for closing.


DAYS
July 29
July 28
July 25
July 22
July 21
July 20
July 18
July 17
July 15
0500
0600
0700
TIME
15
20
25
30
TEMP. C°
NESTS
10
9
8
7
6
5
4
3
2
1

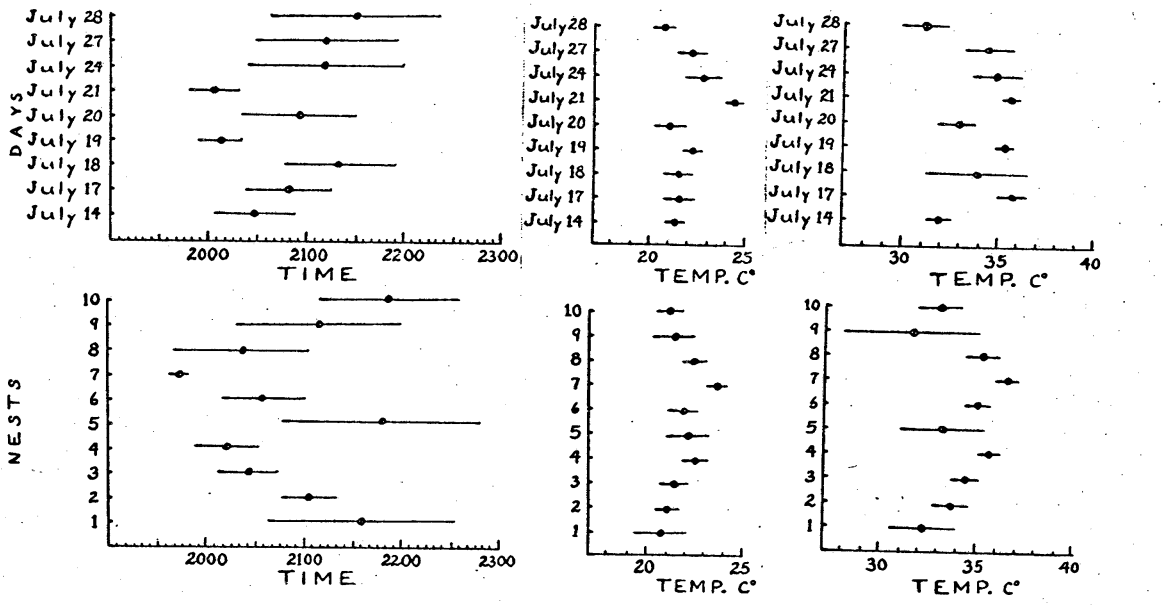

DAYS
July 28
July 27
July 24
July 21
July 20
July 19
July 18
July 17
July 14
2000
2100
2200
2300
TIME
20
25
30
35
40
TEMP. C°
NESTS
10
9
8
7
6
5
4
3
2
1

FIG. 5. An indication of the warmness or coolness of some mornings in July.

Air temperatures at the surface of the ground at the time of each nest opening, plotted against that time.

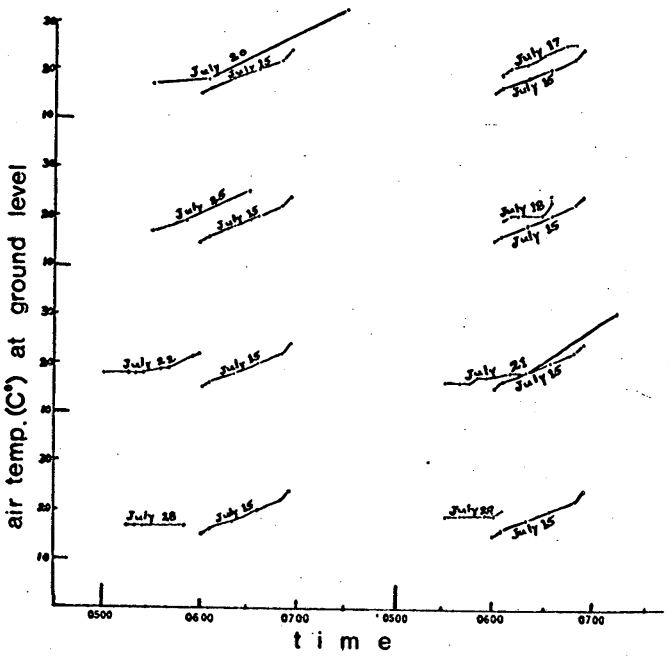


FIG. 6. The same as Fig. 5, but for 3" deep temperatures.

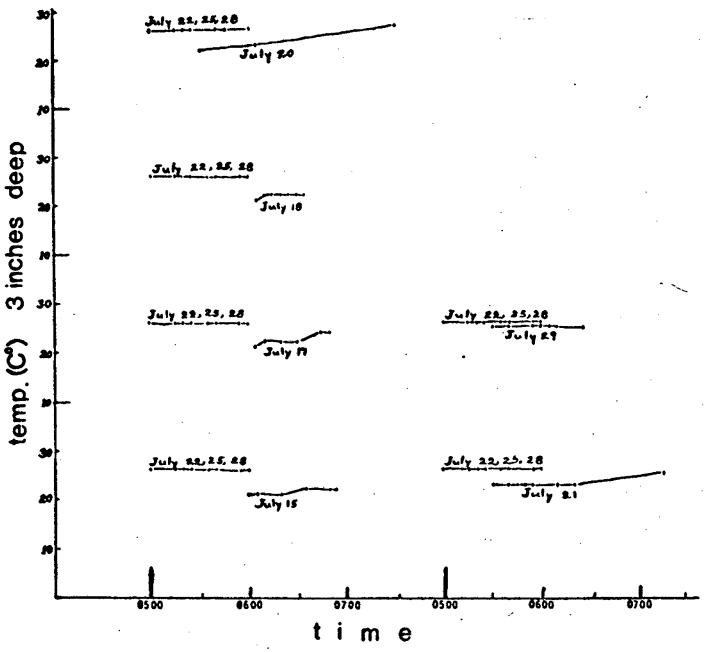


TABLE VIII. Analysis of variance between the mean closing times, temperatures (C^{o}) measured at the surface of the ground, and temperatures measured 3" below the surface. Tabulated values of F are in parentheses.

Month	No. of nest observations	Mean closing time ± 1 SD in mins.
July	73	2050 ± 90
August	15	2027 ± 120
September	19	1906 ± 144
	$F = 7.3$, ($F_{.05} = 3.1$, $F_{.01} = 4.8$)	
		Mean closing surface temp. ± 1 SD
July	73	21.9 ± 2.2
August	15	23.1 ± 2.3
September	19	21.3 ± 4.5
	$F = 1.8$, ($F_{.10} = 2.4$, $F_{.05} = 3.1$)	
		Mean closing 3" deep temp. ± 1 SD
July	73	34.2 ± 3.2
August	15	34.9 ± 2.7
September	19	32.9 ± 4.5
	$F = 1.5$, ($F_{.10} = 2.4$, $F_{.05} = 3.1$)	

FIG. 7. Closing surface temperatures (C^o) plotted against closing time.

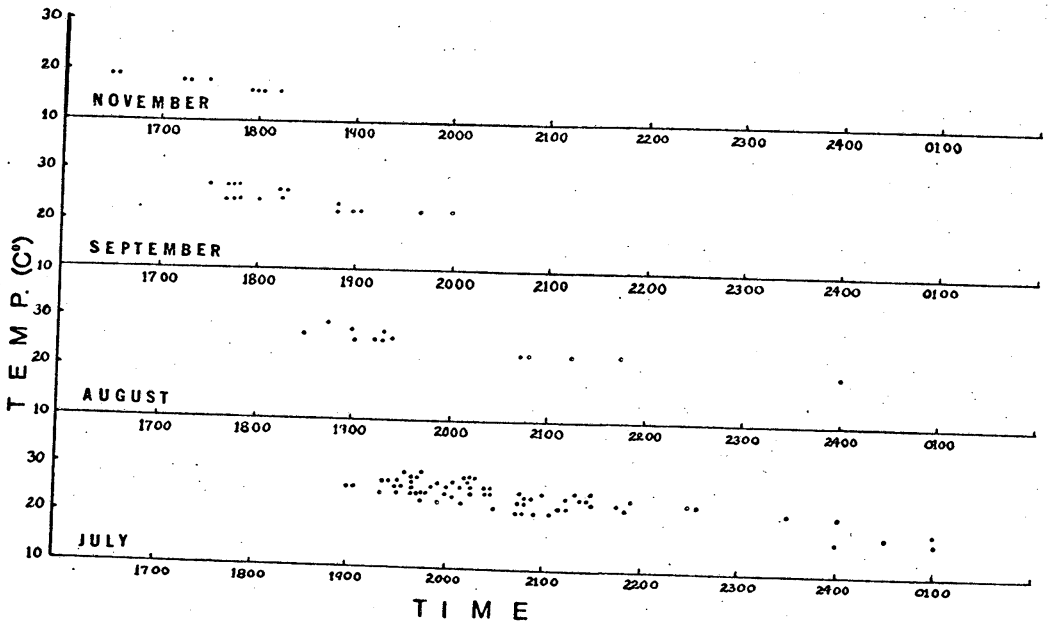


FIG. 8. Closing 3" deep temperatures (C^o) plotted against closing time.

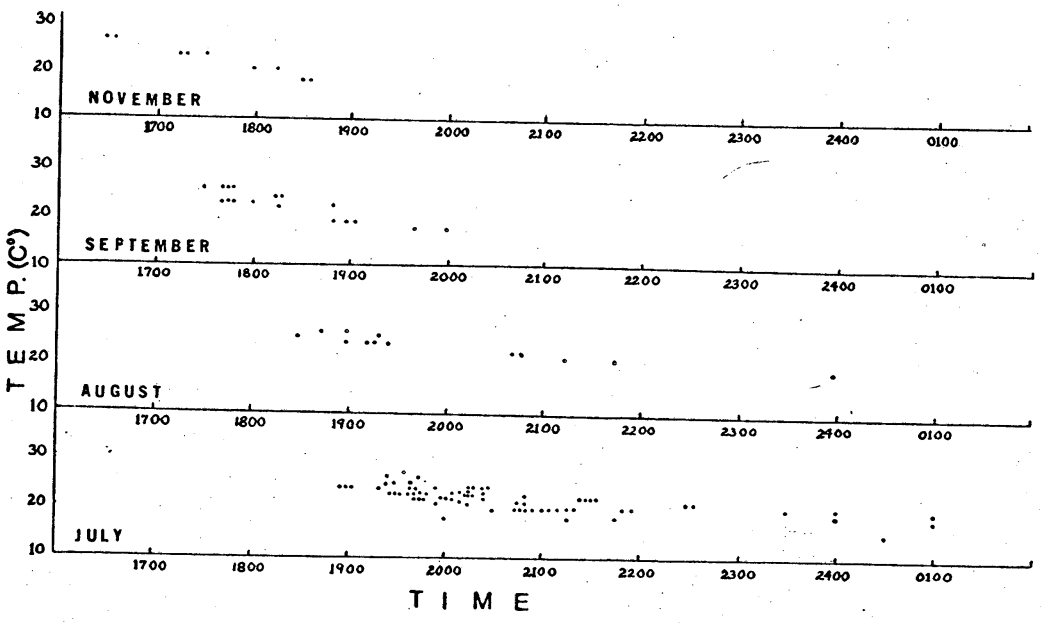


TABLE IX. Analysis of variance between the mean closing times for all of the days on which observations were made.

Days	No. of nests which closed	Time ± 1 SD in mins.	F values, with tabulated values in parentheses
July 14	10	2029 ± 75	
July 17	9	2050 ± 73	All days, July - November
July 18	7	2121 ± 81	$F = 3.7$ ($F_{.05} = 1.8$, $F_{.01} = 2.3$)
July 19	8	2007 ± 34	
July 20	8	2055 ± 94	
July 21	8	2004 ± 43	July days only
July 24	8	2113 ± 126	$F = 1.0$ ($F_{.10} = 1.8$, $F_{.05} = 2.1$)
July 27	7	2113 ± 105	
July 28	8	2131 ± 134	
Aug. 10	8	2113 ± 153	August days only
Aug. 23	7	1933 ± 53	$F = 0.6$ ($F_{.10} = 3.1$, $F_{.05} = 4.5$)
Sep. 13	9	1905 ± 147	
Sep. 14	10	1907 ± 143	
Nov. 3	9	1734 ± 46	September days only
			$F = 0.0$ ($F_{.10} = 3.0$, $F_{.05} = 4.5$)

TABLE X. Analysis of variance between the mean closing temperatures (C^{o}) measured at the surface of the ground for all days on which observations were made.

D a y s	No. of nests which closed	Surface temp. $\pm$ 1 SD	F values, with tabulated values in parentheses
July 14	10	21.3 $\pm$ 1.5	All days, July - November
July 17	9	21.5 $\pm$ 2.5	$F = 1.6$ ($F_{.10} = 1.6$, $F_{.05} = 1.8$)
July 18	7	21.6 $\pm$ 2.1	
July 19	8	22.2 $\pm$ 1.0	
July 20	8	21.0 $\pm$ 2.5	July days only
July 21	8	24.4 $\pm$ 1.2	$F = 2.6$ ($F_{.05} = 2.1$, $F_{.01} = 2.8$)
July 24	8	22.9 $\pm$ 2.7	
July 27	7	22.1 $\pm$ 2.0	
July 28	8	20.6 $\pm$ 1.7	August days only
Aug. 10	8	22.6 $\pm$ 3.0	$F = 0.0$
Aug. 23	7	23.6 $\pm$ 1.1	
Sep. 13	9	19.9 $\pm$ 4.8	
Sep. 14	10	22.6 $\pm$ 3.9	September days only
Nov. 3	9	21.9 $\pm$ 3.1	$F = 1.8$ ($F_{.10} = 3.0$, $F_{.05} = 4.5$)

TABLE XI. Analysis of variance between the mean closing temperatures (C^{o}) measured 3" below the surface of the ground for all days on which observations were made.

Days	No. of nests which closed	3" deep temp. ± 1 SD	F values, with tabulated values in parentheses
July 14	9	33.1 ± 2.1	All days, July - November
July 17	8	35.9 ± 1.8	$F = 4.4$ ($F_{.05} = 1.8$, $F_{.01} = 2.3$)
July 18	7	34.0 ± 6.4	
July 19	9	35.4 ± 0.9	
July 20	9	33.0 ± 2.9	July days only
July 21	8	35.8 ± 1.5	$F = 2.0$ ($F_{.05} = 2.1$, $F_{.01} = 2.8$)
July 24	8	35.0 ± 3.1	
July 27	7	34.6 ± 3.2	
July 28	8	31.3 ± 3.4	August days only
Aug. 10	8	34.5 ± 3.5	$F = 0.0$
Aug. 23	7	35.3 ± 1.6	
Sep. 13	9	31.8 ± 4.5	
Sep. 14	10	34.0 ± 4.4	September days only
Nov. 3	9	27.3 ± 1.3	$F = 1.2$ ($F_{.10} = 3.0$, $F_{.05} = 4.5$)

TABLE XII. Analysis of variance of mean closing times, of temperatures (C^{o}) measured at the surface of the ground, and of temperatures measured 3" below the surface for all of the ten nests which closed; July. In second column the numbers in parentheses refer to temperatures.

Nests	No. of days observed	Time ± 1 SD in mins.	Surface temp. ± 1 SD	3" deep temp. ± 1 SD
1	7	2135 ± 136	20.9 ± 3.7	32.3 ± 4.2
2	8	2103 ± 41	21.1 ± 1.6	33.9 ± 2.0
3	9	2027 ± 53	21.6 ± 2.2	34.4 ± 2.0
4	5	2013 ± 40	22.6 ± 1.1	35.6 ± 0.9
5	7 (5)	2147 ± 136	22.2 ± 2.4	33.2 ± 4.3
6	9	2035 ± 67	22.0 ± 2.3	35.0 ± 2.1
7	9	1944 ± 19	23.8 ± 1.4	36.6 ± 1.5
8	7	2022 ± 99	22.6 ± 1.5	35.3 ± 2.6
9	5	2110 ± 97	21.4 ± 2.3	31.6 ± 6.8
10	7 (9)	2151 ± 104	21.3 ± 1.5	33.0 ± 3.2
	F	1.9	1.4	1.8

(Tabulated values: $F_{.10} = 1.7$, $F_{.05} = 2.0$)

TABLE XIII. As Table XII, but for August.

Nests	No. of days observed	Time ± 1 SD in mins.	Surface temp. ± 1 SD	3" deep temp. ± 1 SD
1	2	2415 ± 21	18.0 ± 1.4	29.0 ± 1.4
2	1	1945	24.0	36.0
3	2	2252 ± 180	20.5 ± 2.1	31.5 ± 2.1
4	1	2045	22.0	33.0
5	2	2020 ± 77	22.5 ± 2.1	34.5 ± 2.1
6	2	2115 ± 42	21.5 ± 0.7	33.0 ± 0.0
7	2	1917 ± 03	24.5 ± 0.7	36.5 ± 0.7
8	2	1837 ± 10	25.5 ± 0.7	38.0 ± 1.4
9	2	1900 ± 00	25.0 ± 1.4	37.0 ± 1.4
10	1	1915	24.0	36.0
	F	5.0	5.0	6.7

(Tabulated values: $F_{.05} = 3.7$, $F_{.01} = 6.7$)

TABLE XIV. As Table XII, but for September.

Nests	No. of days observed	Time ± 1 SD in mins.	Surface temp. ± 1 SD	3" deep temp. ± 1 SD
1	1	1940	18.0	32.0
2	2	1737 ± 10	24.5 ± 2.1	35.5 ± 2.1
3	2	1850 ± 00	20.5 ± 2.1	32.5 ± 0.7
4	2	1930 ± 04	18.5 ± 0.7	32.0 ± 0.0
5	2	1752 ± 10	24.5 ± 2.1	35.5 ± 2.1
6	2	1745 ± 00	24.5 ± 2.1	35.5 ± 2.1
7	2	1745 ± 00	24.5 ± 2.1	35.5 ± 2.1
8	2	2430 ± 00	12.0 ± 5.7	21.5 ± 2.1
9	2	1815 ± 00	23.0 ± 1.4	35.0 ± 1.4
10	2	1837 ± 32	21.5 ± 3.5	34.0 ± 2.8
	F	117.6	4.2	9.9

(Tabulated values: $F_{.05} = 3.2$, $F_{.01} = 5.4$)

TABLE XV. Analysis of variance comparing three experimental nests with three control nests. Tabulated values of F in parentheses.

	Exper. nests opening time and approx. temp.	Means for control nests ± 1 SD	F values ($F_{.05} = 7.7$ $F_{.01} = 21.2$)
Ice, Aug. 23 (removed 0800)			
Time	0913 ± 42	0648 ± 14	19.5
Surface temp.	37 (Table XVI)	19.3 ± 2.3	
3" deep temp.	17 (Table XVI)	21.7 ± 1.2	
Ice, Aug. 28 (removed 0800)			
Time	0928 ± 28	0620 ± 08	126.9
Surface temp.	37 (Table XVI)	17.0 ± 0.0	
3" deep temp	17 (Table XVI)	21.0 ± 0.0	
Shade, Sept. 16			
Time	0630 ± 00	0630 ± 00	0.0
Surface temp.	23.0 ± 0.0	23.0 ± 0.0	0.0
3" deep temp.	20.0 ± 0.0	20.0 ± 0.0	0.0
Light, Sept. 21			
Time	0715 ± 12	0742 ± 10	6.3
Surface temp.	19.7 ± 0.9	23.3 ± 1.7	7.1
3" deep temp.	18.3 ± 0.5	19.0 ± 0.0	4.0

TABLE XVI. Control temperatures (C^{o}) for comparison with the ice experiments (Table XV). Aug. 24.

Time	Surface temp. (not near ice)	Temp. 1" below ice	Temp. 3" below ice	Temp. 3" deep (not near ice)
0530	13	11	14	23
0600	17	11	14	23
0630	20	11	14	23
0700	24	12	14	24
0730	28	12	14	24
0800	30	14	14	25
ice removed at 0800				
0830	33	17	15	26
0900	37	22	17	27

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LITERATURE CITED

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APPENDIX

TABLE XVII

Record of all observations. July (J); August (A); September (S); November (N). 1967.

The first row of values (OT) gives opening time.

The second row of values (OD) gives opening surface temperatures (C^{o}).

The third row of values (OD) gives opening temperatures (C^{o}) measured three inches below the surface.

Each column contains the values for one nest.

All experimental nests are marked +.

All control nests are marked x.

	1	A	2	3	B	4	5	6	7	8	9	10
J15 OT	0655		0620	0605		0620	0620	0650	0650	0650	0600	0635
J15 OD	24		18	16		18	18	22	22	22	15	20
J15 OD	22		21	21		21	21	22	22	22	21	22
J17 OT	0645		0605	0610		0605	0630	0620	0630	0650	0610	0605
J17 OD	25		19	20		19	23	21	23	25	20	19
J17 OD	24		21	22		21	22	22	22	24	22	21
J18 OT	0615		0605	0630		0605	0605	0610	0635	0635	0615	0620
J18 OD	20		19	20		19	19	20	24	23	20	20
J18 OD	22		21	22		21	21	22	22	22	22	22
J20 OT	0530		0530	0530		0530	0530	0605	0605	0730	0530	0530
J20 OD	17		17	17		17	17	18	18	32	17	17
J20 OD	22		22	22		22	22	23	23	27	22	22
J21 OT	0550		0530	0545			0540	0610	0620	0715	0555	
J21 OD	17		16	16			16	18	18	30	17	
J21 OD	23		23	23			23	23	23	25	23	
J22 OT	0540		0520	0535		0500	0515	0525	0600			0555
J22 OD	19		18	19		18	18	18	22			21
J22 OD	26		26	26		26	26	26	26			26
J25 OT	0550			0530			0545	0530	0545	0630		0545
J25 OD	19			17			18	17	18	25		18
J25 OD	26			26			26	26	26	26		26
J28 OT	0520		0515	0520			0515	0525	0525			0550
J28 OD	17		17	17			17	17	17			17
J28 OD	26		26	26			26	26	26			26
J29 OT	0555		0540	0605			0530	0540	0540	0625		0600
J29 OD	19		19	20			19	19	19	20		19
J29 OD	25		25	25			25	25	25	25		25
A23 OT	+0925		+0815	+1000			0640	0640	0710	0745	0700	0700
A23 OD	+37		+29	+40			×18	×18	×22	23	18	18
A23 OD	27		24	29			21	21	23	28	21	21
A24 OT	0640			0700		0545	0610	0615	0700	0730	0615	0700
A24 OD	21			24		13	17	17	24	28	17	24
A24 OD	23			24		23	23	23	24	24	23	24
A28 OT	0615		0615	0630			+0930	+0900	+0955		0610	0645
A28 OD	×17		×17	×17			+36	+33	+38		16	19
A28 OD	21		21	21			28	26	29		21	21
A29 OT	0600		0530	0545			0545	0530	0645	0715	0600	0715
A29 OD	19			18			18		20	23	19	23
A29 OD	24			24			24		25	26	24	26
S13 OT	0745		0730	0730			0730	0745	0730		0730	0730
S13 OD												
S13 OD												
S14 OT			0930	0745		0615	0735	0815	0830	0745	0730	0730
S14 OD			39	24		14	21	29	30	24	21	21
S14 OD			26	17		16	17	19	19	17	17	17
S15 OT	0715			0700		0700	0700	0715	0800	0730	0700	0715
S15 OD	25			24		24	24	25	32	28	24	25
S15 OD	19			19		19	19	19	21	20	19	19
S16 OT			0630	+0630		0630	+0630	0630	0630	0630	0630	+0630
S16 OD			23	+23		23	+23	×23	×23	23	×23	+23
S16 OD			20	20		20	20	20	20	20	20	20
S21 OT			0715	+0700		0715	+0715	+0730	0745	0800	0730	0755
S21 OD				+19			+19	+21	×24	25	×21	×25
S21 OD				18			18	19	19	19	19	19
S22 OT				0630			0630	0705	0715	0715	0700	0725
S22 OD				17			17	19	19	19	17	19
S22 OD				21			21	21	21	21	21	21
N4 OT			0800	0800		0830	0815	0830		0815	0800	0800
N4 OD			19	19		21	20	21		20	19	19
N4 OD			15	15		16	16	16		16	15	15

TABLE XVIII

Record of all observations. July (J); August (A); September (S); November (N). 1967.

The first row of values (CT) gives closing time.

The second row of values (CD) gives closing surface temperature (C^{o}).

The third row of values (CD) gives closing temperatures (C^{o}) measured three inches below the surface.

Each column contains the values for one nest.

	1	A	2	3	B	4	5	6	7	8	9	10
J14 CT	1955		2105	2055		1945	2330	1930	1945	1900	2045	2045
J14 CD	21		20	20		22		23	22	24	20	20
J14 CD	33		31	31		35		35	35	36	31	31
J17 CT			2100	2115		2005	2330	2145	1940	1940	2015	2025
J17 CD			20	18		23		18	24	24	23	22
J17 CD			35	34		37		33	38	38	36	36
J18 CT				2155		2120		2015	2015	2015	2000	2130
J18 CD				20		21		24	23	23	18	22
J18 CD				34		35		38	38	38	20	35
J19 CT	2050		2045	2000		1940		1930	1930	1950	2050	
J19 CD	21		21	22		23		23	23	23	21	
J19 CD	34		35	36		36		36	36	36	34	
J20 CT	2430		2115	2005			2045	2130	1945	1940	2000	
J20 CD	15		20	22			21	20	23	23	22	
J20 CD	26		32	34			33	32	35	35	35	
J21 CT	2130		2025	1940		2015	1925	1930	1925			2025
J21 CD	22		24	25		24	25	25	26			24
J21 CD	33		35	37		35	37	37	37			35
J24 CT	1935		2230	1900			1900	2230	1945	2400		2330
J24 CD	27		21	24			24	21	26	20		20
J24 CD	39		34	36			36	34	39	31		31
J27 CT	0100		2015	2025			2125	1955	2010			2125
J27 CD	18		23	23			22	24	23			22
J27 CD	28		37	36			34	37	36			34
J28 CT	1945		2110	2050			0100	2050	1920	2010		2400
J28 CD	22		20	20			19	20	24	21		19
J28 CD	33		32	32			26	33	35	33		26
A10 CT	0100		1945	2400			2115	2145	1920	1845	1900	
A10 CD	19		24	19			21	21	25	26	26	
A10 CD	30		36	30			33	33	37	39	38	
A23 CT	0130			2045		2045	1925	2045	1915	1830	1900	1915
A23 CD	17			22		22	24	22	24	25	24	24
A23 CD	28			33		33	36	33	36	37	36	36
S13 CT			1745	1850		1900	1800	1745	1745	0130	1815	1900
S13 CD			23	19		19	23	23	23	08	32	19
S13 CD			34	32		32	34	34	34	20	34	32
S14 CT	1940		1730	1850		2000	1745	1745	1745	0130	1815	1815
S14 CD	18		26	22		18	26	26	26	16	24	24
S14 CD	32		37	33		32	37	37	37	23	36	36
N4 CT			1815	1715		1730	1630	1630	1800	1715	1830	1830
N4 CD			20	23		23	26	26	20	23	18	18
N4 CD			26	28		28	29	29	26	28	26	26

LOMA LINDA UNIVERSITY

Graduate School

DAILY NEST OPENING AND CLOSING OF THE ANT POGONOMYRMEX CALIFORNICUS

by

Lynn R. Heath

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ABSTRACT

In a study of timing in this ant ten of the twelve nests which were observed opened synchronously in the morning and closed in the evening. However, one was never seen to close and another closed during the day and stayed open at night.

A seasonal progression was shown by later opening times and earlier closing times. Opening and closing temperatures at the surface of the ground and three inches deep showed no seasonal progression.

In most cases the days when the nests opened the earliest the temperatures at opening time were the highest.

Soon after nests had closed they were illuminated but remained closed until the usual opening time. When nests were cooled with ice their opening time was delayed significantly.

Possibly opening and closing are clock controlled, occurring if a suitable temperature is reached within certain timed segments of the day; such a clock might be kept in phase by the whole light (or temperature) cycle.