1-1975

# Comparison of Laboratory Rhythms in Several Species and Genera of Ants

Siu-Ming A. Soong

Abstract

COMPARISON OF LABORATORY RHYTHMS IN SEVERAL SPECIES AND GENERA OF ANTS

by Siu-Ming A. Soong

Few simultaneous comparative studies of functional diversity have been made at the genus level. Four genera (Pogonomyrmex, Veromessor, Formica, Myrmecocystus) of ants were compared, two of them represented by two species each. Under controlled temperatures, in alternating light and dark, there was more difference in phase of rhythm among than within genera. This evidence adds to previous field evidence for a taxonomic explanation of such diversity in ants.

LOMA LINDA UNIVERSITY

Graduate School

---

# COMPARISON OF LABORATORY RHYTHMS IN SEVERAL SPECIES AND GENERA OF ANTS

by

Siu-Ming A. Soong

---

A Thesis in Partial Fulfillment

of the Requirement for the Degree

Master of Arts in the Field of Biology

---

January 1975

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

Elwood S. McCluskey, Chairman
Elwood S. McCluskey, Assistant Professor of Physiology

Leonard R. Brand, Associate Professor of Biology

Conrad D. Clausen, Assistant Professor of Biology

ACKNOWLEDGEMENTS

I wish to express my sincere appreciation to Dr. Elwood S. McCluskey for his guidance and patience in this study, and to Drs. Leonard R. Brand and Conrad D. Clausen for their counsel and suggestions. I thank Dr. D. Zimmerman for help with statistical analysis, and him and G. McCluskey for aid with programing, Dr. A. Francoeur for determining F. pilicornis and Dr. R. Snelling, M. mimicus.

Computer time for the project was supported in part by NIH, Division of Research Resources, Grant RR-00276. For the analysis of variance, UCLA Health Sciences Computing Facility made its BMDX General Linear Hypothesis program available; this was run at the Loma Linda University Data Processing Facility.

TABLE OF CONTENTS

# LIST OF TABLES

LIST OF FIGURES

## INTRODUCTION

Various species of ants are active during different parts of the 24 hours (Talbot, 1946). The species within a genus are often more alike in field timing than species of different genera (McCluskey, 1973, 1974). Would the same be true in the laboratory, in the relative absence of cyclic or other field variables? McCluskey (1965) compared the rhythms of five species of male ants in constant temperature, but these were mostly not simultaneous comparisons, and there was only one species per genus. At the genus level, there has been little analysis of physiological or behavioral diversity in other animals.

The object of this laboratory study was to compare the workers of more than one genus simultaneously, two of the genera being represented by more than one species.

## MATERIAL AND METHODS

The species observed were: Pogonomyrmex californicus (Buckley), Pogonomyrmex rugosus Emery, Veromessor andrei (Mayr), Veromessor pergandei (Mayr), Formica pilicornis Emery, and Myrmecocystus mimicus Wheeler. The ants were all collected May 24 and 25, 1973, near Loma Linda or Colton, San Bernardino County, California, at an elevation of about 350 m.

Each group of ants was placed in a clear plastic refrigerator dish 9 cm in diameter by 3 cm deep. Constant moisture was provided by a wick of dental cotton projecting up from water in a like dish nested underneath. Sugar water was provided by a cotton-plugged tube hanging down

through the lid of each nest. A clear plastic (Tygon) tube 8 cm long led to a dish of the same type to serve as a dry arena. The nest dish was totally covered by heavy black paper, while the tube and arena were fully exposed to the light.

There were 5 of these nest units per species (except only one for Myrmecocystus), and 30 ants per nest unit. The 26 arenas were lined up side by side, the first replicate of each species, then the second of each, etc. Heating tape was stretched alongside the whole row of arenas so that it was about 1 cm from one side of each arena; it provided constant heat throughout the experiment.

The ants were kept in a constant temperature room. The nests averaged 24.3°C ± 0.5. The hot side of the arenas was kept at least 10° (± 1°) hotter than this, but the ants (except Pogonomyrmex) rarely came to the hot side of the arenas, and so the temperature varied according to their position in the arena. Twelve hr of fluorescent light (2000 lux) was alternated with 12 hr of darkness [the last two nights there was dim incandescent light (15 lux) to permit observations].

The ants were installed May 25 and observations began May 27. Each hour during the light periods of May 27-31, and also during the two nights beginning May 30 and 31, the number out in the arena and in the Tygon tube were counted by eye. In addition, the total number active (moving) in tube and arena were counted.

For each hour, Figs. 1 and 2 show the total (tube plus arena) number of ants out as well as the number just in the arena. The points in Fig. 1 are averaged from the first three days and in Fig. 2 from the last two days. Figure 3 is based on the same data as Fig. 1, but before

calculating the mean each count was converted to the percentage of the day's total count for that replicate nest. This was done so that each replicate would contribute an equal amount of timing information to the mean (otherwise, a replicate with unusually high counts could bias the results).

## RESULTS

The number of ants out for both Pogonomyrmex species rose in early midday and remained high through the afternoon (Figs. 1 and 3). For the other species the rise was not until the afternoon but continued until observations ceased at the end of the light period. Veromessor andrei (and possibly Formica pilicornis) counts were high at the beginning of the light period also, soon falling to the midday low.

The activity level (plotted above the number out in Fig. 1) was highly rhythmic in both species of Veromessor, with late afternoon highs; and here there may possibly be an early morning high in V. pergandei as well as in V. andrei. The activity records for the rest of the species were but feebly rhythmic, if at all.

In F. pilicornis and V. pergandei, few ants ever came out as far as the arena; the rhythmic count was made up largely of those in the tube leading to the arena (i.e., the difference between the arena curve and the total curve), as shown in Figs. 1 and 2. Many V. andrei were in the arenas, but there were many in the tubes as well near the last of the light period. See Table 1 for a summary of the above comparisons.

The most direct comparisons of the species or genera are afforded by the percentage graphs of Fig. 3. The hours of the curve above the average for the day are shaded. This shows the contrast between the early rise of the two Pogonomyrmex species, and the late rise of the two Veromessor species.

Table 2 shows the hour at which the number out for each replicate passed up through its mean for the day. Analysis of variance indicates the difference between genera to be highly significant.

The counts were analyzed in another way by cosine curve fitting (Halberg et al., 1972). The computed hour of maximum for each replicate is shown in Table 3. Again the genera are seen to differ significantly.

After three days counts were made at night also (Fig. 2). It was now six days after collection from the field, and some of the ants were dead or else came out into the tubes or arenas less frequently. But the patterns for the "day" part of the cycle were similar to before. And now it can be seen that the numbers out at night were often even higher than in the day.

## DISCUSSION AND CONCLUSIONS

The laboratory conditions were radically different from those in the field (constant high temperature, no queen, only 30 workers in each unit, no soil, etc.). With these severe limitations in mind, the laboratory timing will be compared with that in the field.

Veromessor andrei and pergandei forage in the morning and evening in summer (Creighton, 1953; McCluskey, 1963). This fits the laboratory timing for these species, especially V. andrei (Fig. 3).

The Pogonomyrmex species were the only species to rise in numbers in the arenas at midday in this laboratory study. While Bernstein (1971) and Cole (1932) mention morning and afternoon peaks in the field for both species, Whitford (1973) noted that P. californicus were out even in the intense heat of midday.

In the field, Myrmecocystus mimicus are strictly diurnal. Cazier and Statham (1961) saw them out only between 9 a.m. and 4:30 p.m. in the summer. In the laboratory (based on only one group), the number out did not increase until toward the end of the day (Fig. 3).

There are no records of field timing for F. pilicornis.

According to Bernstein (1971), P. californicus in the field are usually out during the hottest hours, P. rugosus less hot, and V. pergandei the least hot. Therefore it might be predicted that in a high temperature laboratory, P. californicus would be out the most time, P. rugosus less, and V. pergandei the least. This is what was observed (see Fig. 3).

All six species were prominently out in the arenas during the night (Fig. 2). That this might be explained by the constant high temperature

is suggested by field observations. Tevis (1958) found that night foraging of V. pergandei is rare, but could occur if temperatures are higher than normal. McCluskey (1963) reported foraging in V. andrei on warm nights. Also the activity pattern in his laboratory, -- high evening, night, and morning, -- was similar to mine. P. californicus sometimes works at night (Cole, 1932), and P. rugosus does so when warm (Whitford, 1973).

McCluskey (1973, 1974) compared the field worker rhythms of many species and genera (including the genera studied here), and found more difference in phase of rhythm among than within genera. In my laboratory study, the same was true. Not all factors were controlled as was temperature. But the advantage of the laboratory conditions was that the 'habitats' of the various species were made identical so that differences in rhythm itself might stand out. Although the samples are small, this strengthens the conclusion of McCluskey (1974) that generic diversity of phase of rhythm has a truly taxonomic basis, as distinguished from a strictly geographical or ecological basis.

## LITERATURE CITED


Batschelet, E. 1965. Statistical methods for the analysis of problems in animal orientation and certain biological rhythms, p. 13. American Institute of Biological Sciences.

Bernstein, R. 1971. The ecology of ants in the Mojave Desert: their interspecific relationships, resource utilization and diversity. Ph.D. dissertation, Univ. of Calif. at Los Angeles.

Cazier, M.A., and Statham, M. 1962. The behavior and habits of the myrmecophilous scarab Cremastocheilus stathamae Cazier with notes on other species (Coleoptera: Scarabaeidae). J.N.Y. Entomol. Soc. 70:125-149.

Cole, A.C. 1932. Notes on the ant Pogonomyrmex californicus, Buckley (Hym.: Formicidae). Entomol. News 43:113-115.

Creighton, W.S. 1953. New data on the habits of the ants of the genus Veromessor. Amer. Mus. Novit. 1612:1-18.

Halberg, F., Johnson, E.A., Nelson, W., Runge, W., and Sothern, R. 1972. Physiology Teacher 1 (4):1-11.

McCluskey, E.S. 1963. Rhythms and clocks in harvester and Argentine ants. Physiol. Zoology 36:273-292.

_____. 1965. Circadian rhythms in male ants of five diverse species. Science 150:1037-1039.

_____. 1973. Generic diversity in phase of rhythm in formicine ants. Psyche 80:295-304.

_____. 1974. Generic diversity in phase of rhythm in myrmicine ants. J.N.Y. Entomol. Soc. 82:93-102.

Talbot, M. 1946. Daily fluctuations in aboveground activity of three species of ants. Ecology 27:65-70.

Tevis, L. 1958. Interrelations between the harvester ant Veromessor pergandei (Mayr) and some desert ephemerals. Ecology 39:695-704.

Whitford, W.G. 1973. Demography and bioenergetics of herbivorous ants in a desert ecosystem as functions of vegetation, soil type and weather variables. US/IBP Desert Biome Research Memorandum RM 73-29.

TABLE 1

Comparison of the rhythms of the 6 species, based on inspection of Figs. 1 and 3. Each X represents the presence of a feature and each _____ represents the absence of a feature.

| Species | Hour of rising above mean of day | Morning high | Prominent tube rhythm | Prominent arena rhythm | Prominent rhythm in % active |
|---|---|---|---|---|---|
| P. californicus | 12.3 | ___ | ___ | X | ___ |
| P. rugosus | 13.6 | ___ | ___ | X | ___ |
| V. andrei | 16.6 | X | X | X | X |
| V. pergandei | 15.4 | ? | X | ___ | X |
| F. pilicornis | 15.4 | ? | X | ___ | ___ |
| M. mimicus | 13.9 | ___ | ___ | X | ___ |

Table 2. Hour of rise in number out, based on same data as Fig. 1. For each replicate is shown the hour the count (total in tube and arena) passed up through the mean count for the light period (the hour was averaged from the hours of passing through the mean, the mean X 0.9, and the mean X 1.1). Hours are expressed in decimal form.

Analysis of Variance Based on the Data Below

| Source of variation | DF | MS | F | P |
|---|---|---|---|---|
| Genera | 3 | 16.8 | 24.4 | < .001 |
| Days | 3 | 1.9 | 2.7 | |
| Sampling Error | 17 | 0.7 | | |

The replicates within each genus-day of the ANOVA were the species averages - two each for *Pogonomyrmex* and *Veromessor* and one each for *Formica* and *Myrmecocystus*.

TABLE 2 contd

| Date | Repl. | P. cal. | P. rug. | V. and. | V. per. | F. pil. | M. mim. |
|---|---|---|---|---|---|---|---|
| M 27 | 1 | 9.9 | 10.7 | 16.3 | 16.2 | 12.5 | 12.7 |
| | 2 | 12.3 | 12.5 | 16.1 | 17.4 | 14.9 | |
| | 3 | 12.1 | 12.6 | 18.1 | 15.4 | 15.8 | |
| | 4 | 10.2 | 11.3 | 15.7 | 16.9 | 11.7 | |
| | 5 | 12.3 | 10.2 | 15.8 | 14.4 | 15.4 | ____ |
| | avg: | 11.4 | 11.5 | 16.4 | 16.1 | 14.1 | 12.7 |
| M 28 | 1 | 11.2 | 12.6 | 16.7 | 15.5 | 16.6 | 14.8 |
| | 2 | 12.7 | 14.0 | 16.5 | 16.8 | 14.8 | |
| | 3 | 12.8 | 13.6 | 17.5 | 15.1 | 14.6 | |
| | 4 | 11.5 | 14.2 | 17.4 | 15.6 | 16.5 | |
| | 5 | 12.0 | 11.4 | 15.2 | 15.1 | 14.4 | ____ |
| | avg: | 12.0 | 13.2 | 16.7 | 15.6 | 15.4 | 14.8 |
| M 29 | 1 | 12.4 | 13.4 | 15.8 | 17.5 | 17.6 | 14.2 |
| | 2 | 12.6 | 13.9 | 17.8 | [a] | 17.3 | |
| | 3 | 13.5 | 13.7 | 18.2 | 14.4 | 14.7 | |
| | 4 | 10.1 | 15.7 | 16.6 | 15.3 | 16.7 | |
| | 5 | 13.3 | 11.8 | 15.6 | 14.7 | 16.0 | ____ |
| | avg: | 12.4 | 13.7 | 16.8 | 15.5 | 16.5 | 14.2 |
| M 30 | 1 | 10.7 | 15.2 | 15.4 | 15.1 | 15.9 | 15.7 |
| | 2 | 12.7 | 14.4 | 16.6 | [a] | 16.6 | |
| | 3 | 14.9 | 14.6 | 14.4 | 16.0 | 16.4 | |
| | 4 | 12.8 | 15.1 | 17.4 | 16.4 | 15.1 | |
| | 5 | 11.9 | 11.8 | 14.2 | 14.2 | 15.5 | ____ |
| | avg: | 12.6 | 14.2 | 15.6 | 15.4 | 15.9 | 15.7 |
| 4-day avg: | | 12.1 | 13.2 | 16.4 | 15.7 | 15.5 | 14.4 |

[a]In these two cases there was no meaningful rise time.

Table 3. Hour of maximum count (total in tube and arena) computed by fitting to 24-hour cosine curve; based on counts during light period only and on same data as Table 2, but from 1000-0900 (so as to start and end the 24 hours near the daily minima for all the species). Averages were computed by a circular distribution method (Batschelet, 1965).

Analysis of Variance Based on the Data Below

| Source of variation | DF | MS | F | P |
|---|---|---|---|---|
| Genera | 3 | 45.3 | 26.8 | < .001 |
| Days | 2 | 2.5 | 1.5 | |
| Sampling error | 12 | 1.7 | | |

Table 3 contd.

| Date | Repl. | P. cal. | P. rug. | V. and. | V. per. | F. pil. | M. mim. |
|---|---|---|---|---|---|---|---|
| M 27-28 | 1 | 13.1 | 14.9 | .2 | 23.5 | .2 | 21.3 |
| | 2 | 17.4 | 15.4 | 23.4 | 23.7 | .1 | |
| | 3 | 16.3 | 16.6 | 1.1[a] | 22.5 | 1.2 | |
| | 4 | 12.7 | 16.6 | .3 | 23.5 | 17.6 | |
| | 5 | 16.6 | 13.1 | 23.0 | 19.4 | 19.1 | ____ |
| | avg: | 15.2 | 15.4 | 23.7 | 22.6 | 22.3 | 21.3 |
| M 28-29 | 1 | 14.6 | 17.9 | .0 | 22.4 | .8 | 22.9 |
| | 2 | 17.7 | 21.0 | .6 | 23.2 | 22.9 | |
| | 3 | 15.7 | 19.3 | 1.5 | 22.4 | 21.8 | |
| | 4 | 14.1 | 20.2 | 1.8 | 22.7 | 21.2 | |
| | 5 | 17.8 | 14.3 | 22.7 | 21.7 | 21.6 | ____ |
| | avg: | 16.0 | 18.7 | 24.5 | 22.5 | 22.4 | 22.9 |
| M 29-30 | 1 | 15.8 | 20.6 | 22.5 | .7 | 20.1 | 21.2 |
| | 2 | 17.4 | 21.1 | 23.8 | 22.9 | 1.1 | |
| | 3 | 19.3 | 20.0 | 3.0 | 20.8 | 23.1 | |
| | 4 | 14.2 | 22.0 | 11.6[a] | 22.6 | 23.6 | |
| | 5 | 16.7 | 15.4 | 22.1 | 19.4 | .8 | ____ |
| | avg: | 16.7 | 20.0 | 23.8 | 22.3 | 23.4 | 21.2 |
| 3-day avg: | | 16.0 | 18.0 | 24.0 | 22.5 | 22.7 | 21.8 |

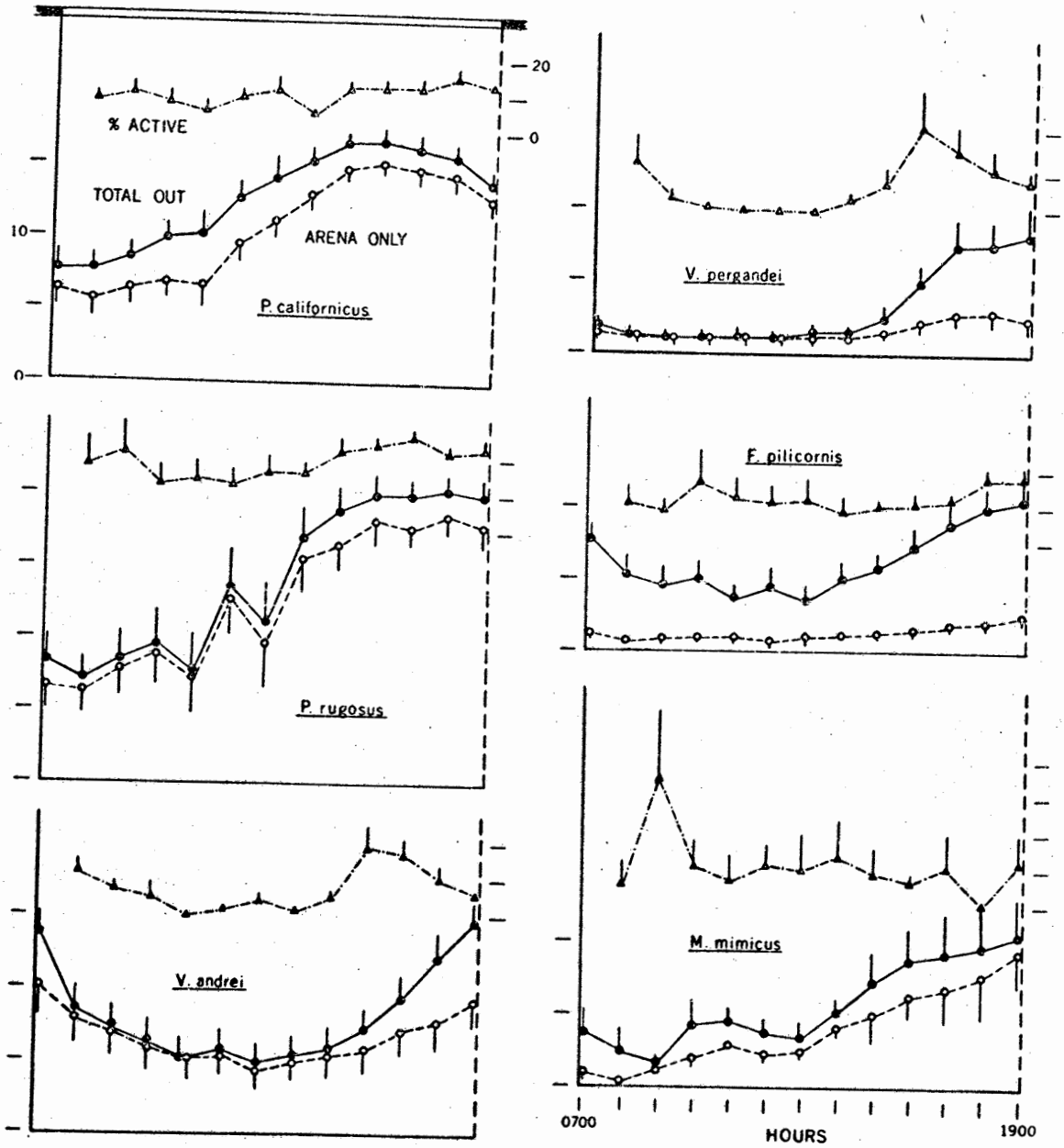
[a]In some cases the records were too limited to locate a meaningful maximum; the two replicates where a test for rhythm sinusoidality (Halberg et al, 1972) gave P > .50 were left out in computing the averages and the ANOVA.

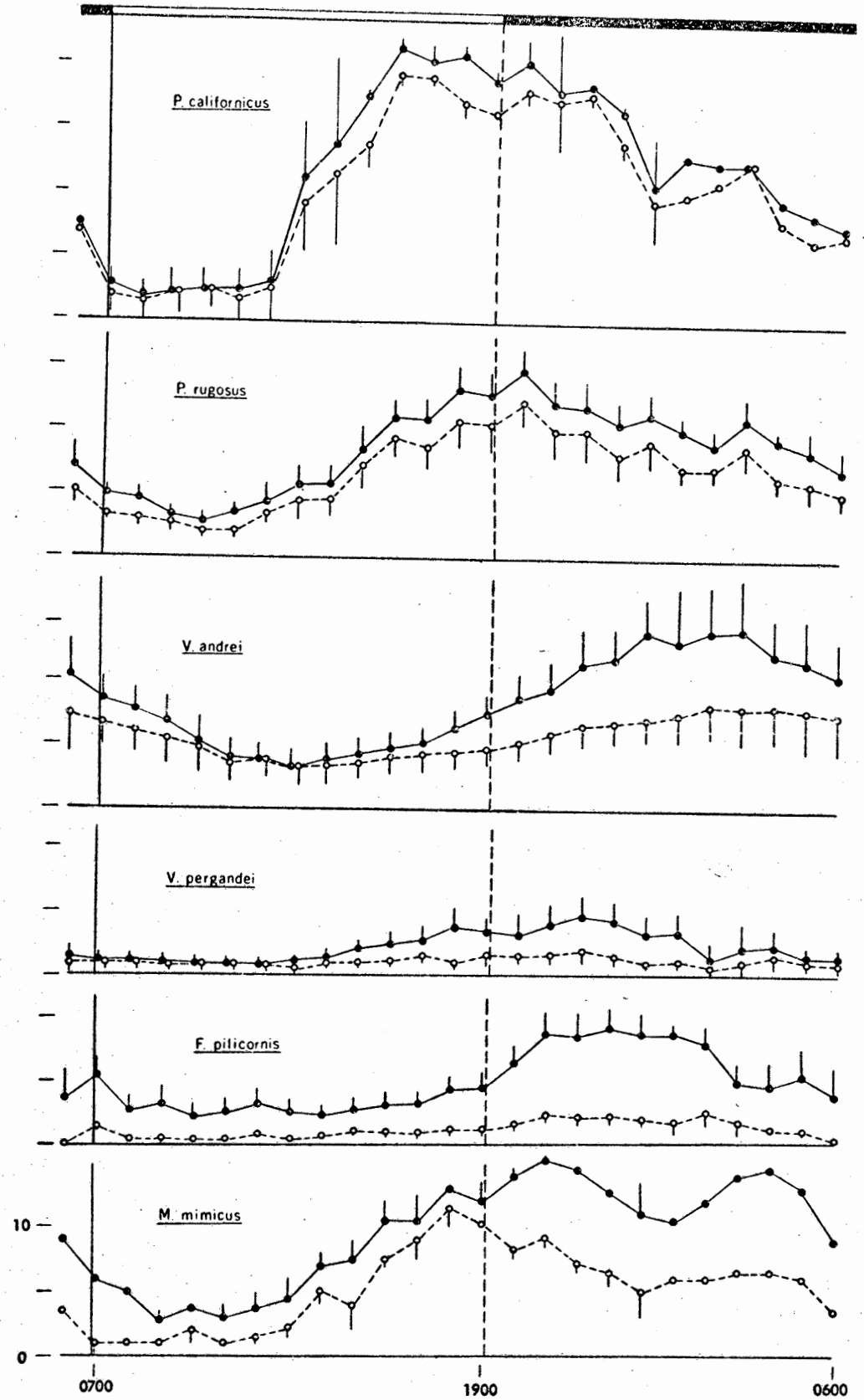
## LEGENDS

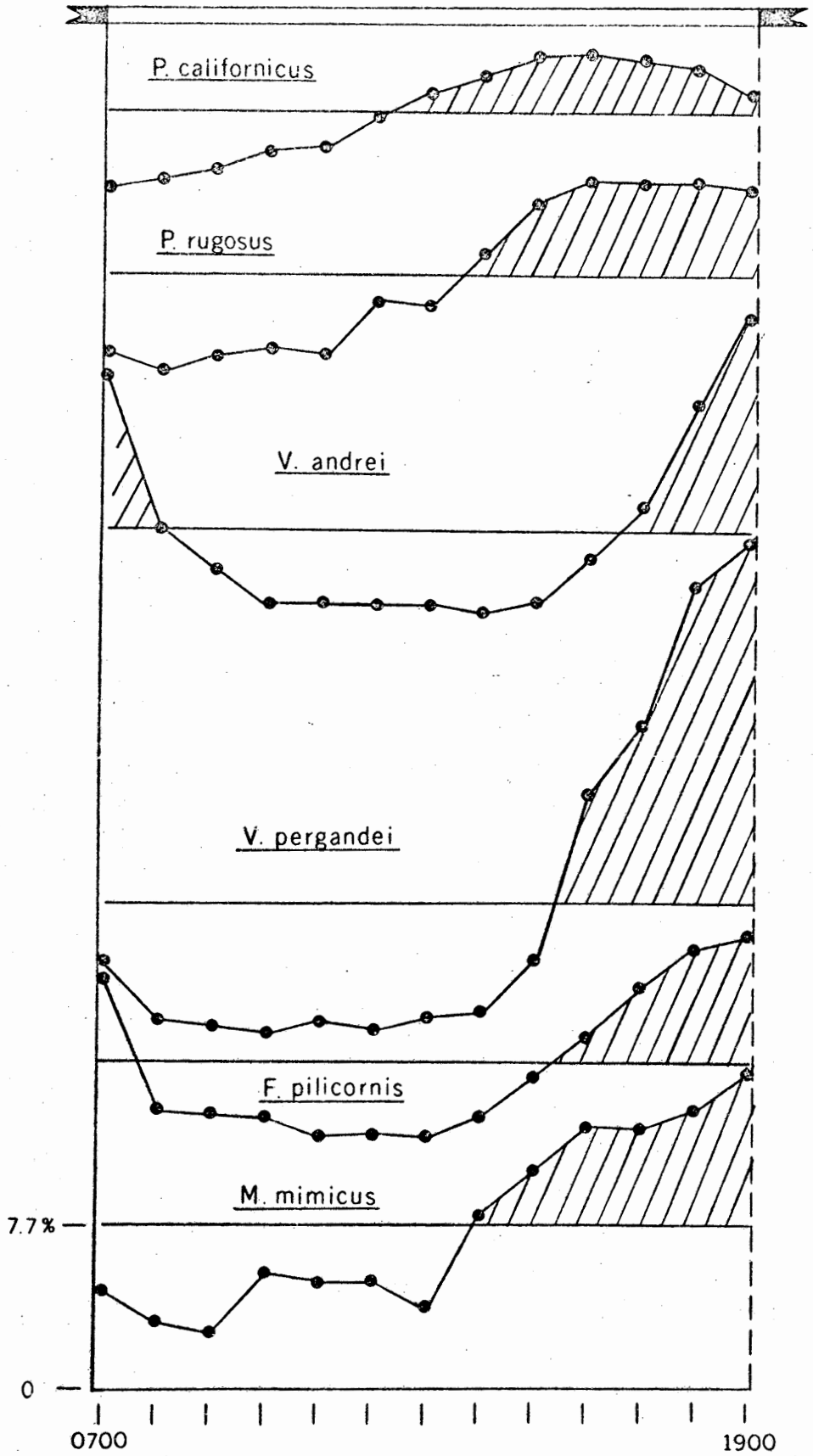
Fig. 1 The number of ants out during the light period. Each hourly mean and SE is based on the 5 replicate nests (1 for *M. mimicus*) for 3 replicate days of observation (May 27-29). In some cases, SE is too small to show. The activity level (% of the total which were active) is also shown.

Fig. 2 The number of ants out during both light and dark periods. Five replicate nests (1 for *P. californicus* and 1 for *M. mimicus*) for nearly 2 replicate days (May 30-31). The 0600 reading is duplicated at the end.

Fig. 3 Percentage of the total of the 13 hourly counts, based on the same replicate nests and days as Fig. 1. The horizontal line indicates the daily avg per hour (100/13 = 7.7%). A zero line is shown for the bottom species only; the vertical scale is the same for all 6 species. Shaded area represents the hours that are above the average.


% ACTIVE
TOTAL OUT
ARENA ONLY
P. californicus
20
0
10
0
V. pergandei
F. pilicornis
P. rugosus
V. andrei
M. mimicus
0700
HOURS
1900


P. californicus
P. rugosus
V. andrei
V. pergandei
F. pilicornis
M. mimicus
10
0
0700
1900
0600


P. californicus
P. rugosus
V. andrei
V. pergandei
F. pilicornis
M. mimicus
7.7%
0
0700
1900