Hoffman, Christopher John

THE EFFECT OF PHOTOPERIOD AND TEMPERATURE UPON ADULT ECLOSION OF THE SWEETPOTATO WHITEFLY, BEMISIA TABACI (GENNADIUS)

The University of Arizona M.S. 1985

THE EFFECT OF PHOTOPERIOD AND TEMPERATURE UPON ADULT ECLOSION OF THE SWEETPOTATO WHITEFLY, BEMISIA TABACI (GENNADIUS)

by

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A Thesis Submitted to the Faculty of the

DEPARTMENT OF ENTOMOLOGY

In Partial Fulfillment of the Requirements
For the Degree of

MASTER OF SCIENCE

In the Graduate College

The UNIVERSITY OF ARIZONA

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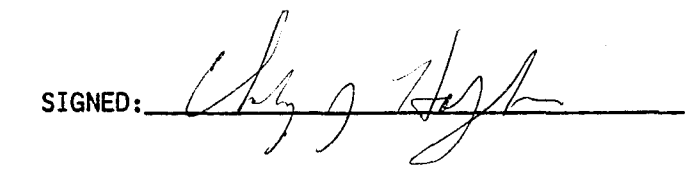
SIGNED: 

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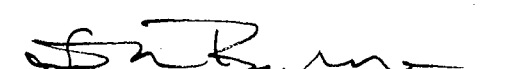

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Professor of Entomology

DATE

ACKNOWLEDGEMENTS

I would like to express my sincere thanks to Dr. David N. Byrne for his support and encouragement while serving as my major professor and to Drs. Merrit R. Nelson and Robert L. Smith for serving as my committee members.

I would also like to thank Dr. Judy K. Brown for her help with rearing and maintenance of insect colonies and for her continual support and guidance.

Finally, I would like to express my appreciation to the faculty, staff, and students of the Department of Entomology for their assistance in making my stay at the University of Arizona an enjoyable as well as an educational experience.

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ABSTRACT

To develop a greater understanding of the life history of the sweetpotato whitefly, Bemisia tabaci (Gennadius), a series of experiments were conducted to characterize patterns of adult eclosion and determine how they are influenced by environmental parameters. Under constant temperature (29.5°C) and a 14:10 LD photoperiod, 90% of the adults emerged between lights-on (0600 hours) and 0930 hours. The majority of adult emergence was delayed when temperatures were regulated to mimic the temperature fluctuations present under field conditions. Under a variety of constant temperature regimes, a significant inverse correlation ($p < 0.001$) was found between the time of median emergence and temperature. No emergence was observed at temperatures below 17°C. Emergence patterns persisted under conditions of continuous light and continuous darkness suggesting the presence of a circadian system. A circadian system focusing upon early morning emergence may increase the survival of B. tabaci by avoiding harsh environmental conditions at this vulnerable developmental stage.

INTRODUCTION

The sweetpotato whitefly, Bemisia tabaci (Gennadius), is a major agricultural pest in many areas of the world. It is responsible for significant crop losses in more than 33 countries (CIBC 1981) and is found on at least 315 plant species belonging to more than 60 families (Russel 1957, Gerling 1967, Gameel 1972, Mound and Halsey 1978, and Brown 1984). Rainfall and/or high relative humidity are essential for the population increase of B. tabaci (Vetten and Allen 1983) thus limiting their distribution to tropical and sub-tropical regions, and to temperate climates proximal to such areas.

Heavy infestations of this insect can cause significant damage to crops as a result of feeding and honeydew production. More importantly, B. tabaci has been implicated in the transmission of more than 50 disease-causing pathogens of economic importance (Costa 1976, Bird and Maramorosch 1978, Duffus and Flock 1982, and Brown 1984). Most of these pathogens are suspected to be viral in nature (Muniyappa 1980).

Viruses associated with whiteflies are adapted to tropical conditions and require high light intensity for propagation (Bird and Maromorosch 1978). Among the most serious of these pathogens are cassava mosaic virus in India and Africa; tobacco leaf curl virus in Indonesia, Africa, and the Americas; cotton leaf curl virus in Africa;

and viruses associated with bean diseases in the tropics (Bird and Maromorosch 1978).

The recent increase of whitefly population levels and the increased severity of diseases resulting from its vectored pathogens world-wide has been attributed to several factors. Large outbreaks of whiteflies have occurred since the 1940's following the development and use of broad spectrum insecticides such as DDT, suggesting that natural enemies played an important part in population regulation (CIBC 1981). Increases in whitefly numbers can also be attributed to increases in the acreage devoted to crops which serve as alternate hosts of the insect and its vectored pathogens (Bird and Maromorosch 1978). Weed species provide another primary reservoir for economically important viruses and it is believed that viral transmission may be more efficient in some of these weeds than in the crop itself (Costa 1976).

B. tabaci in the Southwestern United States

B. tabaci was first reported in the desert areas of the southwestern United States in 1926 near Gila Bend, Arizona on cotton and in 1928 near Calipatria, California (Russel 1957) on the same host. Twenty years after the discovery of B.tabaci in Arizona and California, viral diseases associated with this insect began to appear.

The first pathogen associated with B. tabaci in the southwest was cotton leaf crumple virus (CLCV), discovered in California in 1948 (Duffus and Flock 1982), and in Arizona in 1958 (Allen, Tucker,

and Nelson 1960). A geminivirus was found to be responsible for the disease by Brown and Nelson (1984). Yield losses in some years were significant, as evidenced by reports of losses as high as 71% in California, and of approximately 24% in Arizona as a result of the presence of CLCV (Allen et al. 1960). In artificially infected fields near Brawley, California, yield losses ranged from 23-81%, primarily depending upon the host growth stage at the time of infection. In 1981, an estimated loss of $4 million was attributed to the presence of B. tabaci on cotton in the Imperial Valley of California (Zalom, Natwick, and Toscano 1985). This loss is thought to result from reduced boll-set by plants infected at an early growth stage and is perhaps an indirect effect of a reduced flowering rate (van Schaik, Erwin, and Garber 1962). Others have attributed reduced yield to a general physiological shock to infected plants induced by the pathogen (Allen et al. 1960).

Concerning the epidemiology of the pathogen, it appears the increased incidence of CLC in 1958 in Arizona was associated with an increase in acreage of ratooned cotton which provided a continual reservoir for the virus and a host for the vector (Allen et al. 1960). Weed species such as cheeseweed, Malva parviflora L., have also been implicated as a reservoir for CLCV (Brown and Nelson 1984).

In 1977, squash leaf curl virus (SLCV) was observed in melons in California and B. tabaci was implicated as its vector (Duffus and Flock 1982). In 1977 and 1978 as a result of this geminivirus, yield was reduced drastically (Flock and Mahew 1981). It was later

suggested, however, that a complex of distinct pathogens may have produced the observed symptoms (Cohen et al. 1983). Brown (1984) suggests the presence of two distinct viruses affecting Arizona cucurbits: one affecting only squash and pumpkin (SLCV) and the other (watermelon curly mottle virus) affecting those crops as well as cantaloupe and watermelon. Both of these agents are capable of being transmitted by B. tabaci. Additionally, the SLCV present in Arizona may be distinct from those examined in California based on differences in transmission characteristics and symptomologies on common hosts (Brown 1984).

Perhaps the most economically important viral pathogen transmitted by B. tabaci in the southwest is lettuce infectious yellows virus (LIYV). This filamentous pathogen has been classified as a closterovirus (Brown 1984) and is quite distinct morphologically from the paired dimer form of the CLC and SLC geminiviruses. LIYV was reported in 1981 in Yuma county, Arizona and Imperial County, California. The presence of LIYV was associated with abnormally high populations of B. tabaci in both areas and was responsible for significant losses to lettuce and nearby sugarbeets in many desert agricultural areas in both states (Duffus and Flock 1982). Symptoms were observed in over 60% of Arizona lettuce fields in the spring, summer, and fall of 1982 (Brown 1984). Since lettuce is the most economically significant vegetable produced in Arizona, with a typical annual production value in excess of $100 million (AAS 1983), the presence of this disease is of great concern.

Conditions in the southwestern United States can create an environment highly conducive to an outbreak such as the one seen in the 1981-82 growing season. These include the increasing use of pyrethroid insecticides, the spacial and temporal array of suitable hosts for the whitefly vector (melons, squash, sugarbeets, cotton, and a number of weed species), and the mild winter and early build-up of heat units.

Life History of B. tabaci

Members of the family Aleyrodidae share a unique life history. Eggs of B. tabaci are most commonly laid on the underside of the host plant leaf. Cemented into a slit made by the ovipositor, they maintain their water balance osmotically in association with surrounding plant cells (Gameel 1974). A vagile first instar emerges from the egg and attaches itself to the leaf where it begins to feed. Legs and antennae are lost and the insect becomes sessile for three additional nymphal stages. Although metamorphosis is considered gradual, the last nymphal instar (IV) is a quiescent stage often designated a pupa. These immature forms are transparent and scale-like in appearance. Following stage IV, a mobile, winged adult emerges, which is quite different in appearance from immature forms. Adults are yellow-green in color, about 2 mm in length, with two pairs of membranous wings covered with a white powdery wax. Adults emerge from their pupal cases primarily between 0600 and noon (Hussain and Trehan 1933, Azab, Megahed, and El-Mirsawi 1971, and Butler, Henneberry, and Clayton 1983). Development from egg to adult can take anywhere from 16 to 65

days depending upon temperature (Butler et al. 1983). Adult longevity is also temperature-dependent and ranges from two to 17 days for males and from eight to 60 days for females, depending upon the season (Azab et al. 1971). Copulation takes place within one to two days of eclosion, with a pre-oviposition period of one to six days followed by an oviposition period between four and 42 days (Azab et al. 1971). Eggs are laid primarily in afternoon hours (Butler et al. 1983) and the number of eggs per female can vary seasonally from 28 to 394 (Hussain and Trehan 1933, Avidov 1956, and Azab et al. 1971). Male offspring are produced parthenogenetically when females are prevented from mating (Hussain and Trehan 1933). Male to female sex ratios vary seasonally from 1:1.1 to 1:5.75 (Azab et al. 1971). B. tabaci is reported to overwinter in nymphal (Azab et al. 1971) or adult (Gerling 1967) stages on available crop or weed hosts.

Circadian Rhythms and Adult Eclosion

Rhythmic patterns of behavior and physiological responses with a period of 24 hours are quite common in nature (Bunning 1973, Saunders 1977 and 1982, and Brady 1979). Prior to the last 30 years, these diel rhythms were commonly attributed to a reaction by the organisms to some exogenous cue such as a sunrise or temperature change. More recently, when many of these rhythmic behaviors were studied under constant environmental conditions, the rhythmicity was often found to persist. These rhythms are said to be circadian in nature and are characterized as being driven by some endogenous factor or clock. The period at which these rhythms free-run (τ or tau) is

rarely exactly 24 hours, but is often within the range of 22-28 hours per cycle (Brady 1979). The rhythm appears as 24 hours in nature due to its entrainment by an environmental cue(s) or zeitgeber. This zeitgeber (usually a light-dark or dark-light transition) serves to reset the internal clock daily, so that the event occurs at the same time each day. If the rhythm persists as exactly 24 hours following introduction into continuous light (LL) or continuous darkness (DD), then the existence of a zeitgeiber other than light or darkness is assumed (Smith 1970).

The presence of endogenous circadian rhythms has been demonstrated in a number of plant and animal species from relatively simple fungi and unicellular algae (Palmer 1976) to complex human rhythms (Still 1972). Whether or not these rhythms exists in most organisms is unknown, but there is thought to be some kind of physiological periodicity in all eukaryotes (Saunders 1982).

The first description of a true circadian rhythm was made in 1729 by the French astronomer DeMairan who observed daily leaf movements of the plant Mimosa in constant darkness (Pittendrigh 1976). In the early 1930's, Bremer described the possibility of external factors governing rhythms and suggested an additional endogenous component (see Scott 1936). In the early 1960's, two principal theories arose to explain observed rhythms. F.A. Brown (1960) held that the rhythms were in response to "...subtle geophysical forces..." which were not adequately accounted for in laboratory experiments. This point of view has lost popularity as a result of additional evidence presented

by Hamner et al. (1962) from experiments conducted at the south pole. They placed several species of plants and animals thought to possess endogenously controlled rhythms on a turntable with a counter-clockwise rotation of 24 hours at the south pole. This largely ruled out the effects of geophysical forces. The rhythms were found to persist under constant conditions, thus confirming the presence of an internal controlling mechanism.

Much of what we know concerning the underlying mechanisms responsible for the periodicity observed in organisms comes from the eclosion experiments of C.S. Pittendrigh and his co-workers. Using two species of Drosophila he developed an intricate model of a photoperiodic clock which free-runs in total darkness after taking a cue from a previous lights-on zeitgeber (Pittendrigh 1954,1966; Pittendrigh and Minis 1964). He found that adult eclosion of D. photobscura reared in darkness from the egg stage to be arhythmic. A single pulse of light, as short as .002 seconds, exposed to larvae or pupae initiated a rhythm of eclosion (τ = 24.5 hours) which persisted for several days (Pittendrigh, 1954).

The neural-hormonal relationships of eclosion were investigated by Truman and Riddiford (1970). They found a species-specific period of time of eclosion, termed a gate, in three species of giant silkmoth. The eclosion behavior of each species remained when all nervous connections were severed. If a brain from one species was transplanted into either of the other two species, the timing of eclosion was characteristic of the species donating the brain. Raabe

(1982) described the eclosion hormone of Schistocerca gregaria, secreted by the pars intercerebralis, and stored in the corpora cardiaca, which acts upon the central nervous system to initiate a species-specific rhythm. In Manduca sexta eclosion hormone is released from the corpora cardiaca in a 20 minute burst 2.5 to 3 hours before eclosion (Mordue 1982). This eclosion hormone may be responsible for all ecdysis in insects and has shown activity in several other insect orders (Truman et al. 1981).

Another area of interest is the location of the ultimate controlling mechanism governing these processes. Konopka and Benzer (1971) have found three "clock mutants" in D. melanogaster. When mutations were mapped and subjected to a series of genetic crossings and surgical manipulations the results suggested that the clock lies in the brain of the fly. The optic lobe is suggested as the clock location governing periodic activity of Periplaneta americana (Roberts 1974) and the cricket Teleogryllus commodus (Loher 1972). Activity patterns of several insects, including flight of Schistocerca gregaria, may ultimately be controlled through the pars intercerabralis (Raabe 1982).

Adult eclosion of whiteflies has been given little detailed attention. Under field conditions, Khidir (1972) found a sharp peak of emergence of the cabbage whitefly, Aleyrodes brassicae, between 0600 and 1000 hours. Studies with B. tabaci, however, have been confined to laboratory situations. Hussain and Trehan (1933) found most emergence between 0800 and 1100 hours; this corresponds to Azab

et al. (1971) who observed a peak between 0800 and 1200 hours and to a lesser extent with Butler et al. (1983), who found a peak between 0600 and 0900 hours. Observed diel rhythms such as these make this species a likely candidate for the possession of a circadian system.

The experiments presented here were designed to characterize in detail patterns of emergence observed in B. tabaci, and to learn to what extent these patterns are influenced by environmental parameters. It is hoped that a better understanding of factors responsible for emergence in this species may aid in understanding general patterns of activity observed under field conditions.

MATERIALS AND METHODS

Potted cotton plants (Delta-Pine 70) at the 4-6 node growth stage were used in the rearing of whiteflies. One colony was maintained in a greenhouse with evaporative cooling and ambient summer photoperiod from 14.0:10.0 to 13.5:10.5 (LD). Night temperature was kept at 26°C, while day temperatures varied seasonally from 26-32°C. A second colony was reared indoors in a plexiglass chamber measuring 2.3 by 1 by 1 m., with controlled temperature (30°C), and photoperiod (14:10). Whiteflies collected from commercial cotton fields in Pima and Maricopa Counties, Arizona, were periodically introduced into this second colony. The light source consisted of eight 150 watt incandescent floodlamps illuminating the upper cotton leaf surface with approximately 18,900 lux. Light intensity was measured with a Sekonic model L-398 selenium cell-based light meter.

Leaves bearing mixed ages of whiteflies were obtained from either the greenhouse- or laboratory-reared colonies. Each leaf was placed singly upon a piece of filter paper in a 10 cm petri dish. Each petri dish had a hole in the center, into which a cotton wick was placed and kept in a shallow water bath to provide a constant moisture source for the leaves. A total of 10 leaves were examined during each experimental period. The 10 petri dishes were covered with a fine mesh cloth to prevent escape of adult whiteflies. Newly emerged adults were counted at 30- or 60-minute intervals and removed with an

aspirator. During simulated daylight, whiteflies were exposed to an incandesent light source which provided an illumination of 600 lux at the leaf surface. This intensity is within the range received by the lower surfaces of cotton leaves within the canopy under field conditions. Counts in darkness were made under a 25 watt safelight through a Kodak # 1AV red filter. All experiments were performed in a room with controlled temperature and photoperiod.

In Experiment #1, temperature was held at a constant 29.5°C for the purpose of determining any periodicity in emergence patterns. In Experiment #2, the temperature was fluctuated to mimic natural environmental variations to learn what effect this may have upon the timing of eclosion. The insects were exposed to 19°C during the period of darkness and 29°C during the subjective day. The rate of rise in temperature was 6.7°C per hour beginning at 0600 hours in one trial, and 2°C per hour for a second trial. In Experiment #3, whiteflies were exposed to 24-hour periods of constant temperatures ranging from 17-35°C to learn what effect these temperatures had on emergence and to determine temperature thresholds for adult emergence. In Experiment #4, the insects were exposed to 72 hours of continuous light (LL) and 72 hours of continuous darkness (DD), with all other parameters remaining constant. These conditions were intended to expose any endogenous circadian rhythms controlling the timing of emergence.

Mathematical interpretation of the data included a non-parametric median test (Dixon and Massey 1957) to confirm observed differences in emergence patterns.

RESULTS

Under conditions of a constant 29.5°C and a 14:10 photoperiod, a peak of emergence (33% of the total) occurred between 30 and 60 minutes following lights-on at 0600 hours (Fig. 1). Fifty percent of the total number of adults emerged by 0700 hours; 90% emerged by 0930 hours. This characteristic pattern of emergence was observed within a wide range of leaf population densities (60-2000) and did not significantly differ whether the insects were reared in the laboratory, in the greenhouse, or collected on leaves from commercial cotton fields ($p < 0.05$). Data from five replications under these conditions revealed an average of 6.3% of the adults emerging in darkness between 0500 and 0600 hours, and less than 1% of whitefly adults emerging between 1400 and 0500 hours.

In reaction to fluctuating temperatures (20:29°C, dark:light) emergence peaked at a time later in the day; the extent depended upon the rate of temperature increase following lights-on (Figs, 2,3). Slowing the rate of rise in temperature further delayed the emergence. With a sharp rise in temperature (1.5 hours), 50% emergence (the emergence median) occurred at 0930 hours (Fig. 2); with an increased delay of maximal temperature (5 hours), the median was delayed to 1030 hours (Fig. 3).

Emergence patterns varied markedly when observed under a variety of constant temperature regimes. Figures 4, 5, and 6

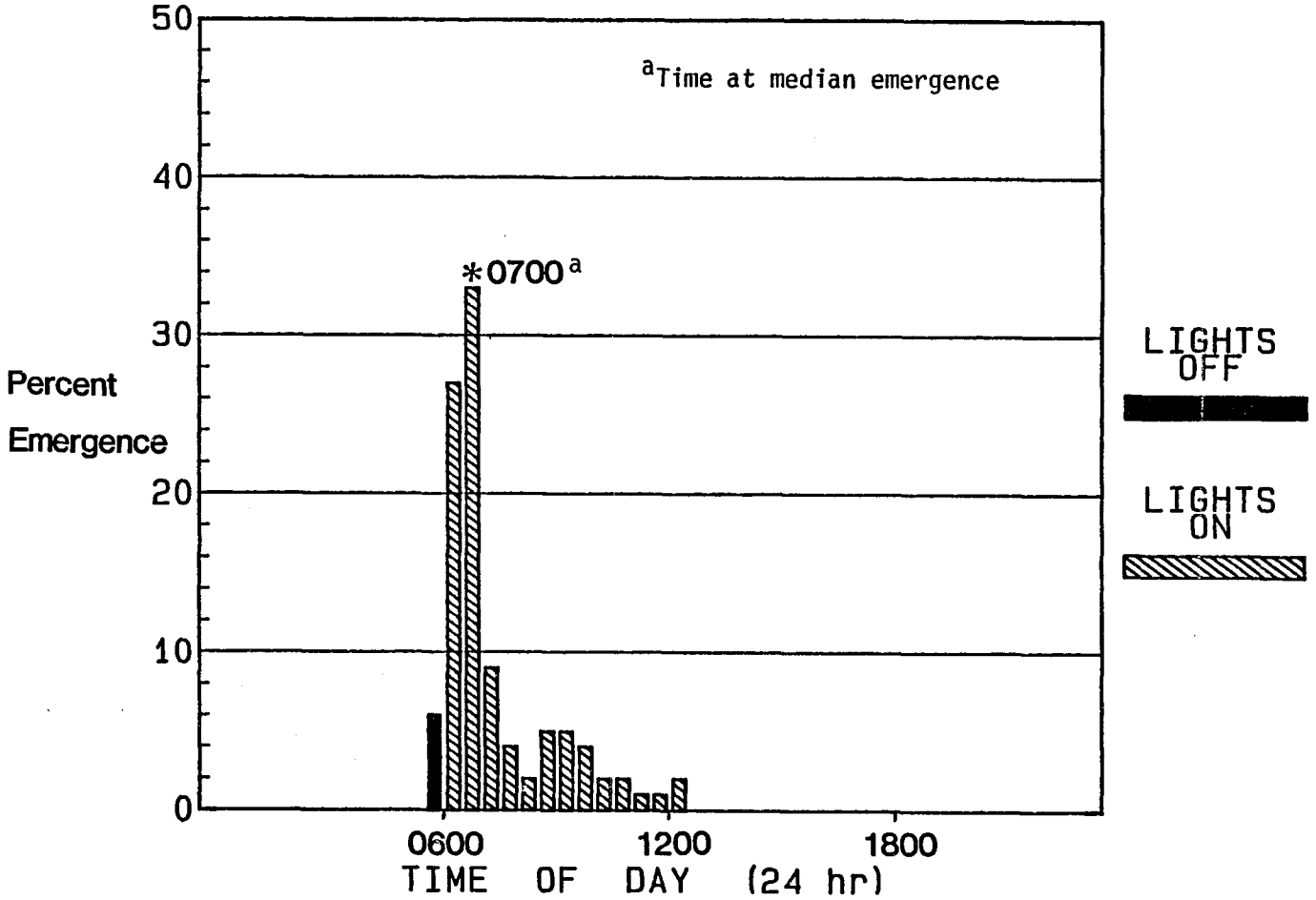

Figure 1. Percent of the total individuals of Bemisia tabaci emerging at 30-minute intervals under conditions of constant temperature (29.5 °C) and 14:10 photoperiod with lights-on at 0600 hours. N = 134.

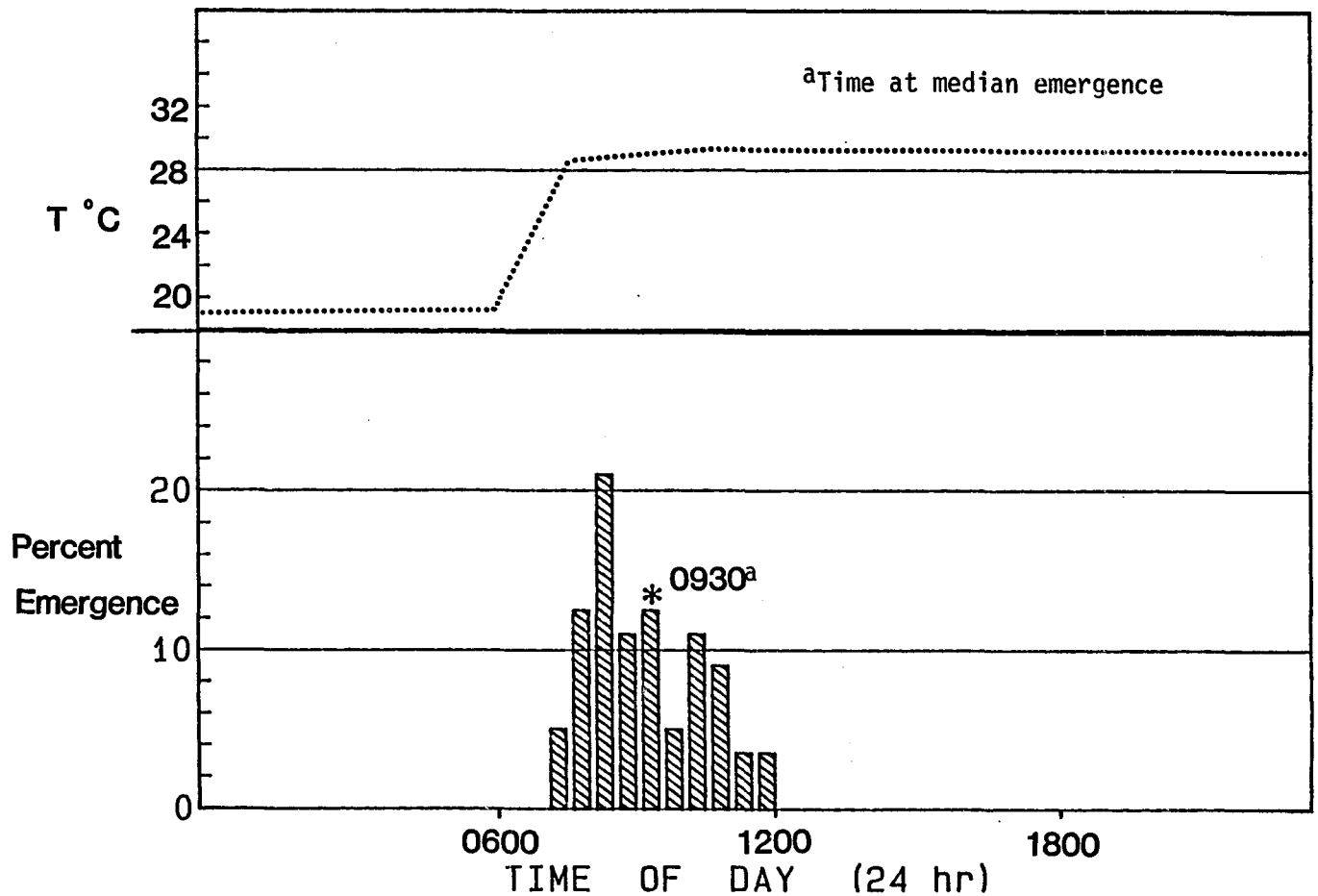

Figure 2. Percent of the total individuals of Bemisia tabaci emerging at 30-minute intervals under conditions of fluctuating temperature (19-29 °C) and 14:10 photoperiod with lights-on at 0600 hours. The rate of rise in temperature is 6.7° per hour. N = 56.

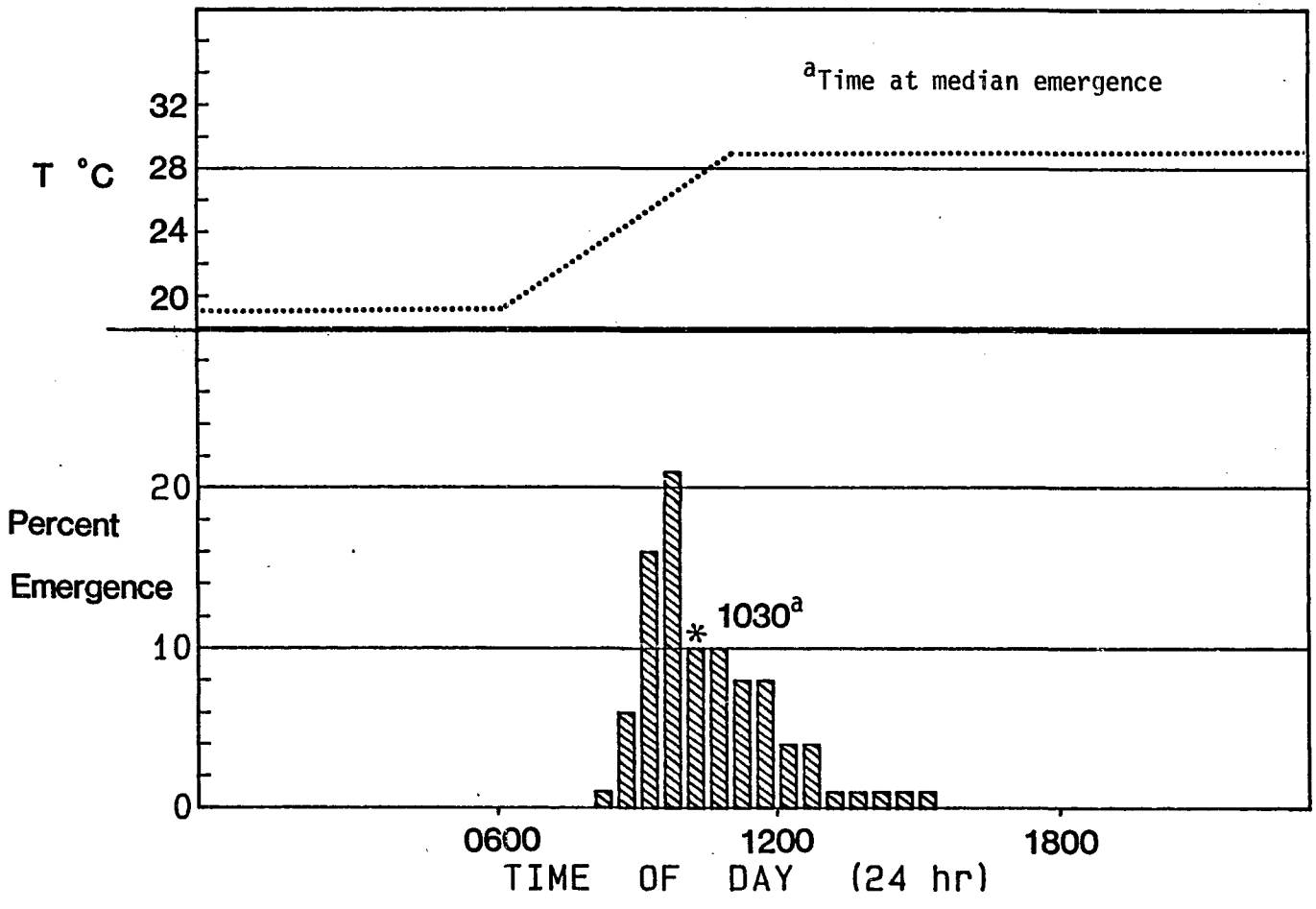

Figure 3. Percent of the total individuals of Bemisia tabaci emerging at 30-minute intervals under conditions of fluctuating temperature (19-29 °C) and 14:10 photoperiod with lights-on at 0600 hours. The rate of rise in temperature is 2.0° per hour. N = 77.

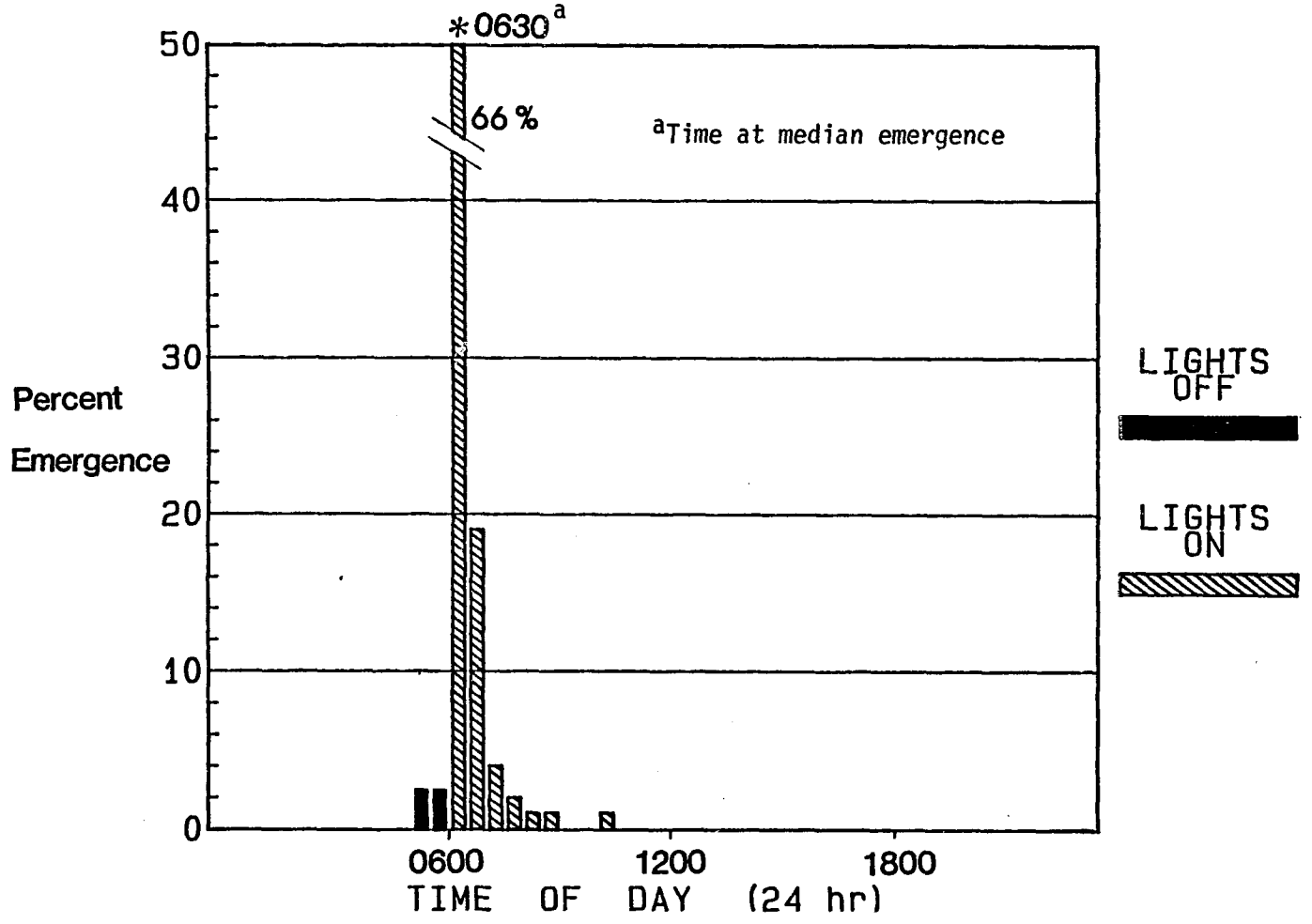

Figure 4. Percent of the total individuals of Bemisia tabaci emerging at 30-minute intervals under conditions of constant temperature (31.5 °C) and 14:10 photoperiod with lights-on at 0600 hours. N = 172.

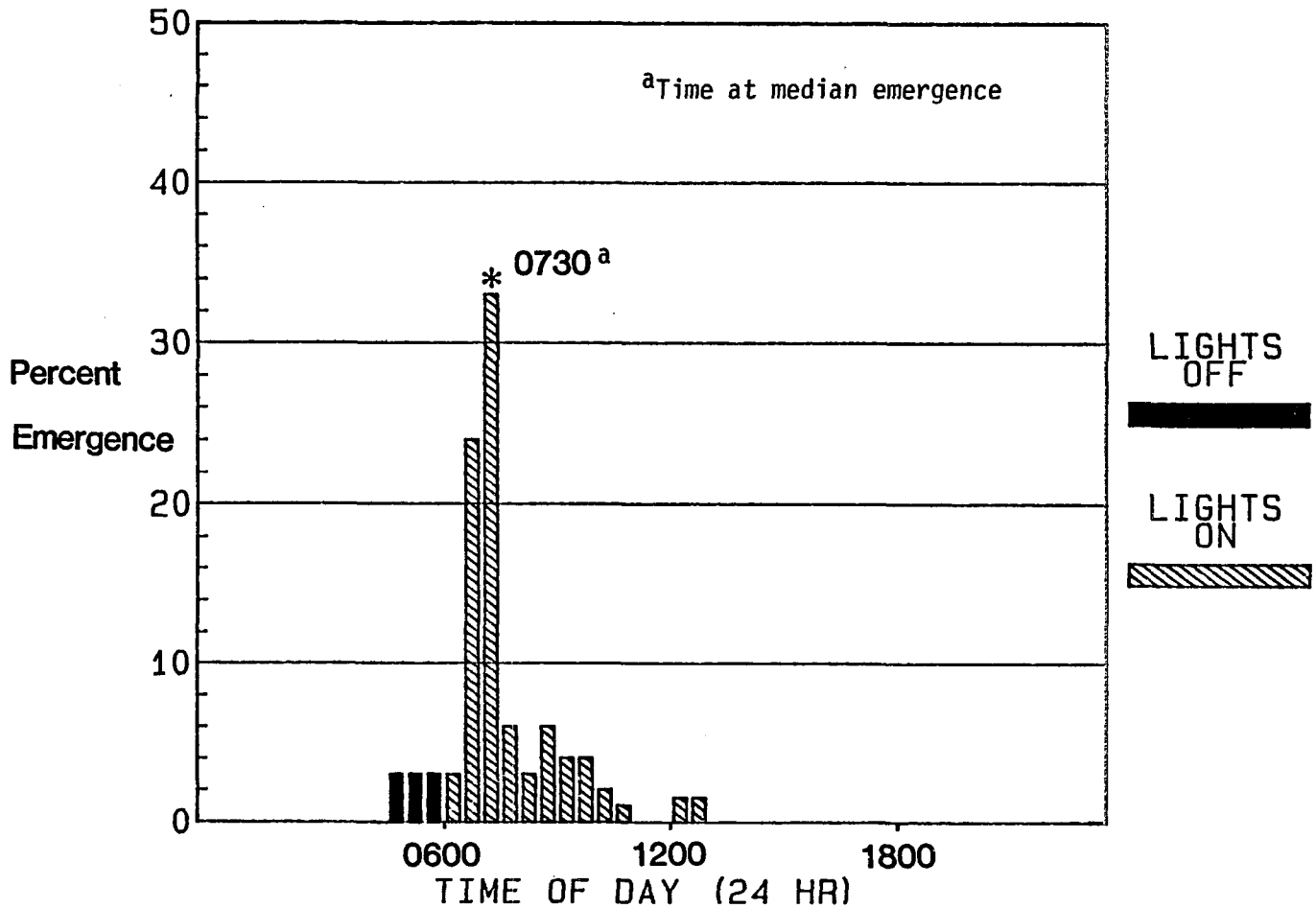

Figure 5. Percent of the total individuals of Bemisia tabaci emerging at 30-minute intervals under conditions of constant temperature (25.6 °C) and 14:10 photoperiod with lights-on at 0600 hours. N = 33.

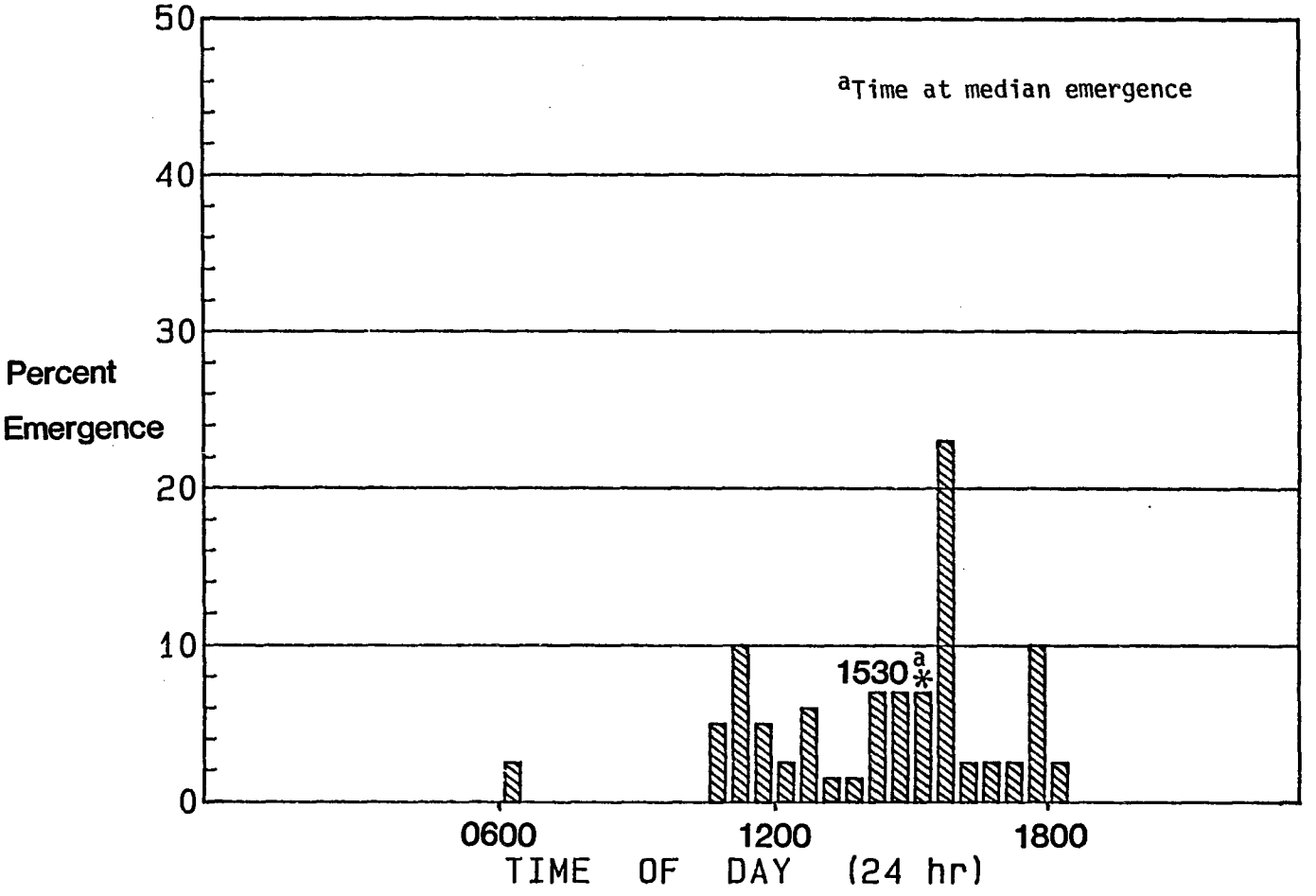

Figure 6. Percent of the total individuals of Bemisia tabaci emerging at 30-minute intervals under conditions of constant temperature (19 °C) and 14:10 photoperiod with lights-on at 0600. N = 40.

represent observations at 31.5, 26.5, and 19°C respectively. At 31.5°C, median emergence occurred at 0630 hours and was very pronounced. More than 90% of the adults emerged in the two-hour period following lights-on. In contrast, at 19°C the peak was more diffuse, and median emergence occurred at 1030 hours. In this cooler temperature, 90% of the adults emerged during an eight-hour period from 1030 to 1830 hours.

The relationship between temperature and time of median emergence is illustrated in Fig. 7. These data suggest a significant exponential relationship between these two parameters ($r = 0.7209$). In addition, emergence medians calculated at different temperatures were all found to be significantly different ($p < 0.001$). The data also indicate a lower temperature threshold (17°C), at which eclosion was not observed.

Under conditions of constant light, following an initial baseline peak, a peak of emergence was present during the second 24-hour period following lights-on (Figs. 8,9). Peak emergence occurred between 0500 and 0630 hours and was not as pronounced as the initial peak observed under a 14:10 photoperiod. Here, 50% emergence occurred at 0530 hours, which is only 23 hours after the previous median. After 48 hours no distinct patterns of emergence could be detected, although the pattern was still non-random (Fig. 10). Following a return to a 14:10 LD regime, a pattern was seen similar to that of the baseline day (Fig. 11). The patterns observed in these four successive days were all significantly different ($p < 0.001$).

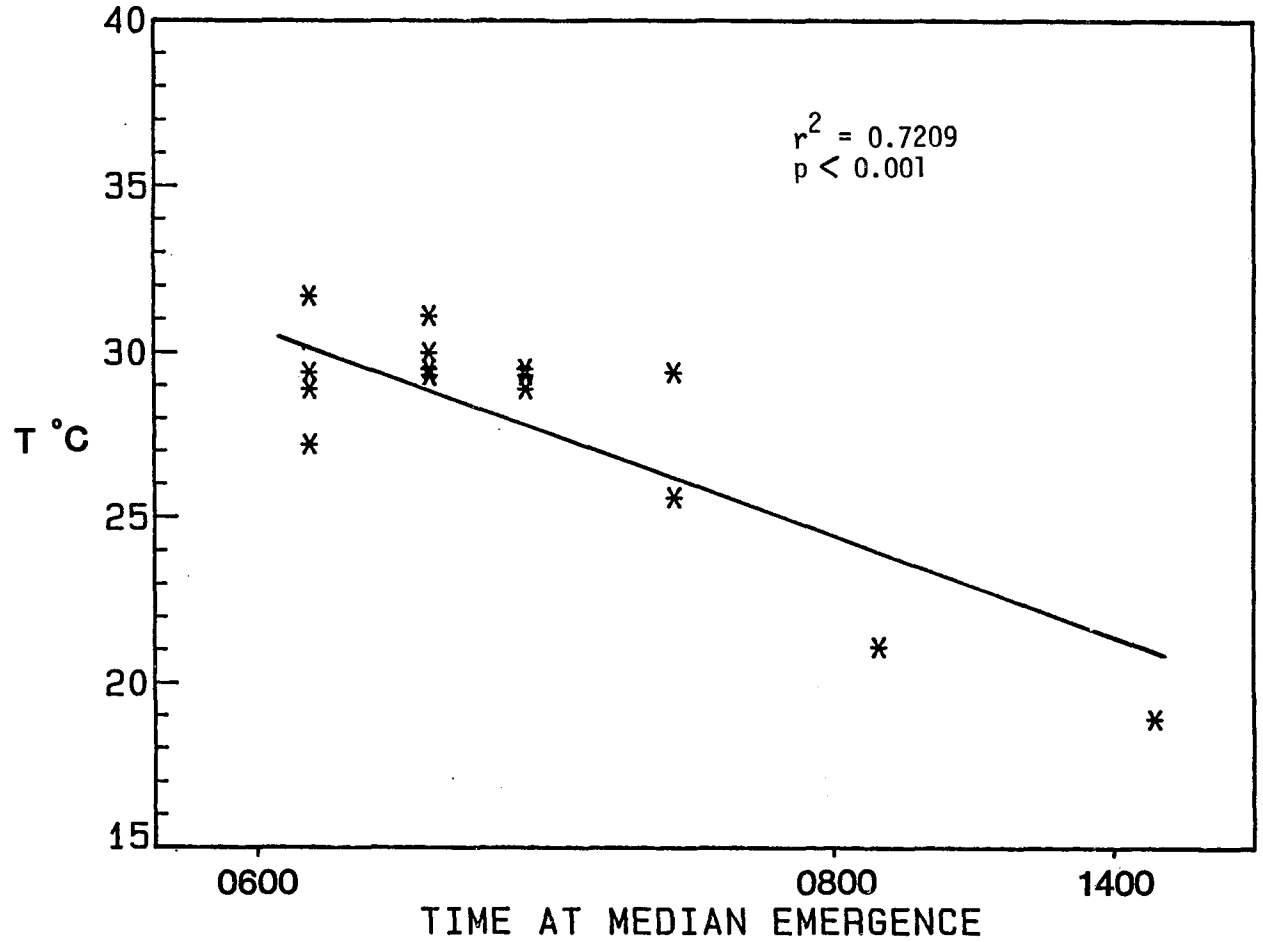

Figure 7. Exponential relationship between the time of median emergence of Bemisia tabaci adults (plotted on a log scale) and temperature. N = 15.

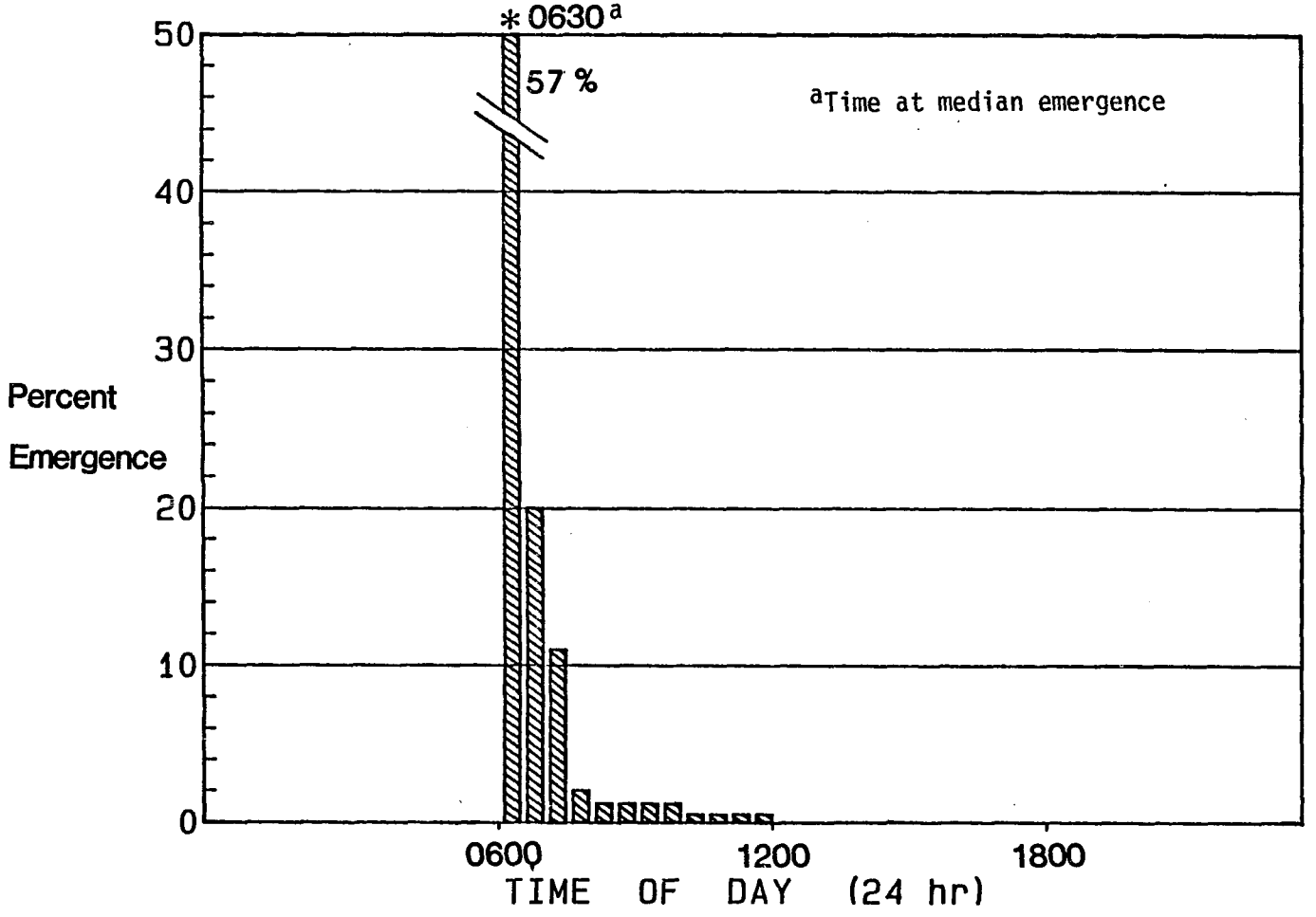

Figure 8. Percent of the total individuals of Bemisia tabaci emerging at 30-minute intervals: Day 1 of exposure to conditions of continuous light (lights-on at 0600 hours) at 30.5°C. N = 202.

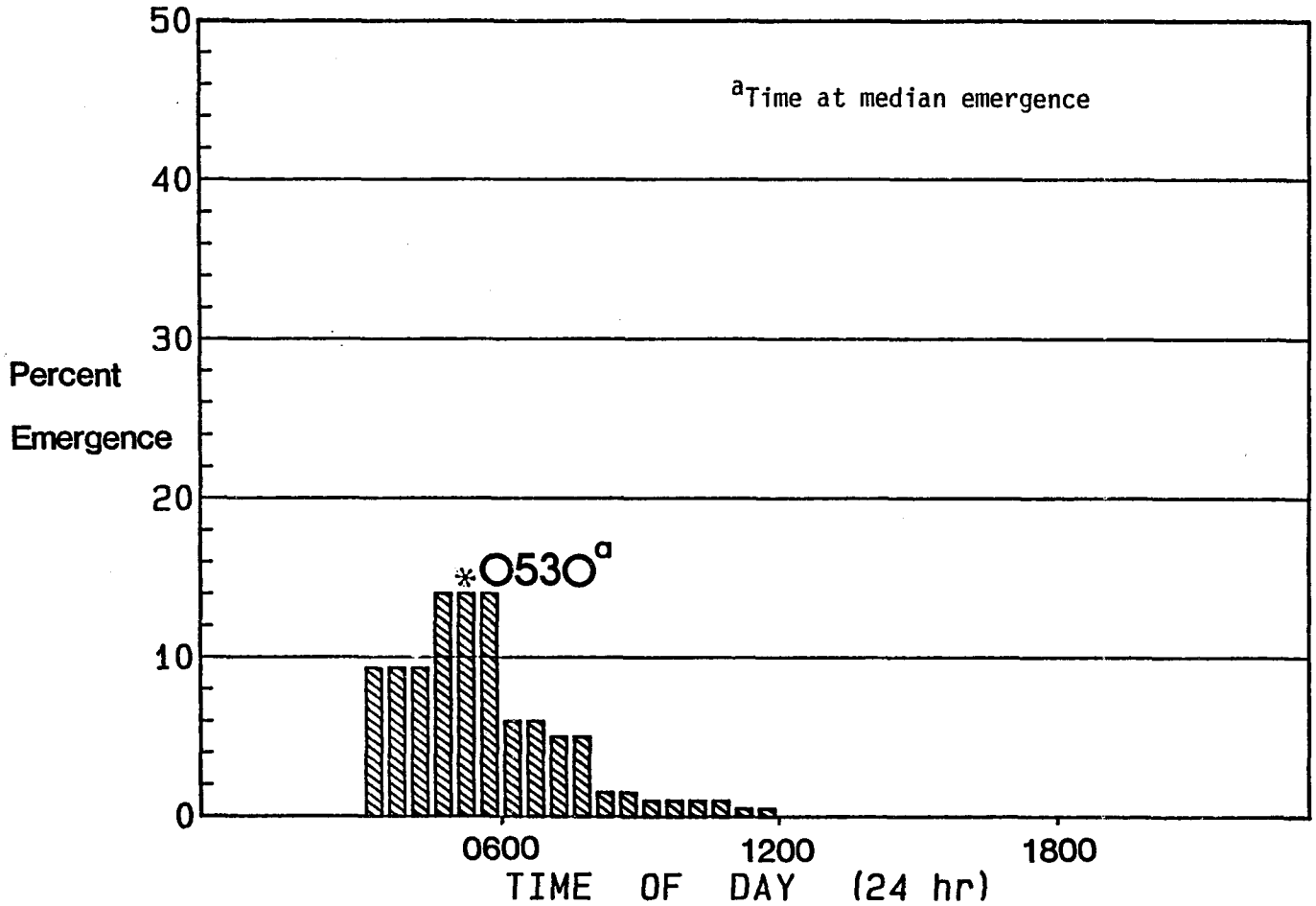

Figure 9. Percent of the total individuals of Bemisia tabaci emerging at 30-minute intervals: Day 2 of exposure to conditions of continuous light at 30.5° C. N = 177.

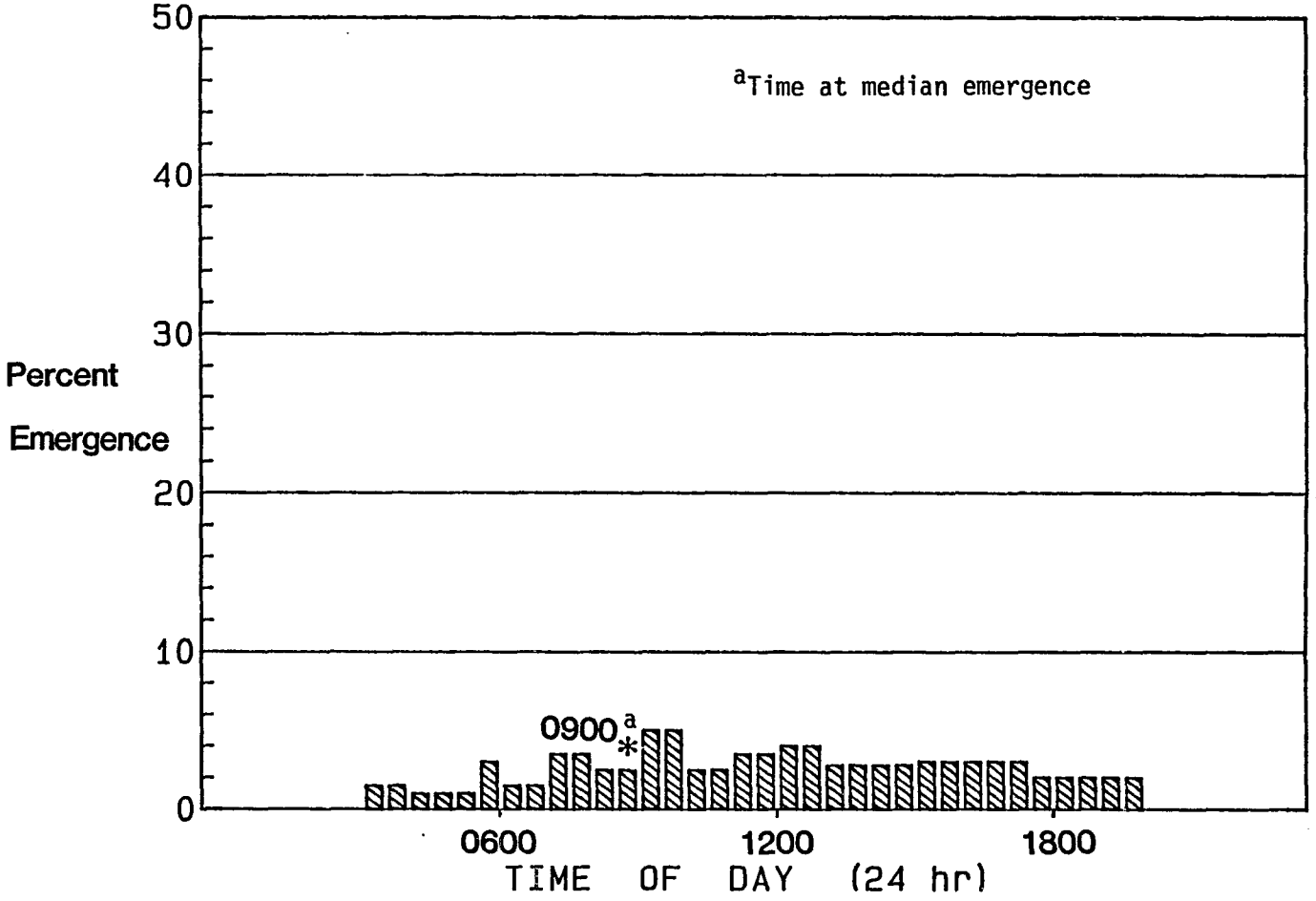

Figure 10. Percent of the total individuals of Bemisia tabaci emerging at 30-minute intervals: Day 3 of exposure to conditions of continuous light at 30.5 °C. N = 149.

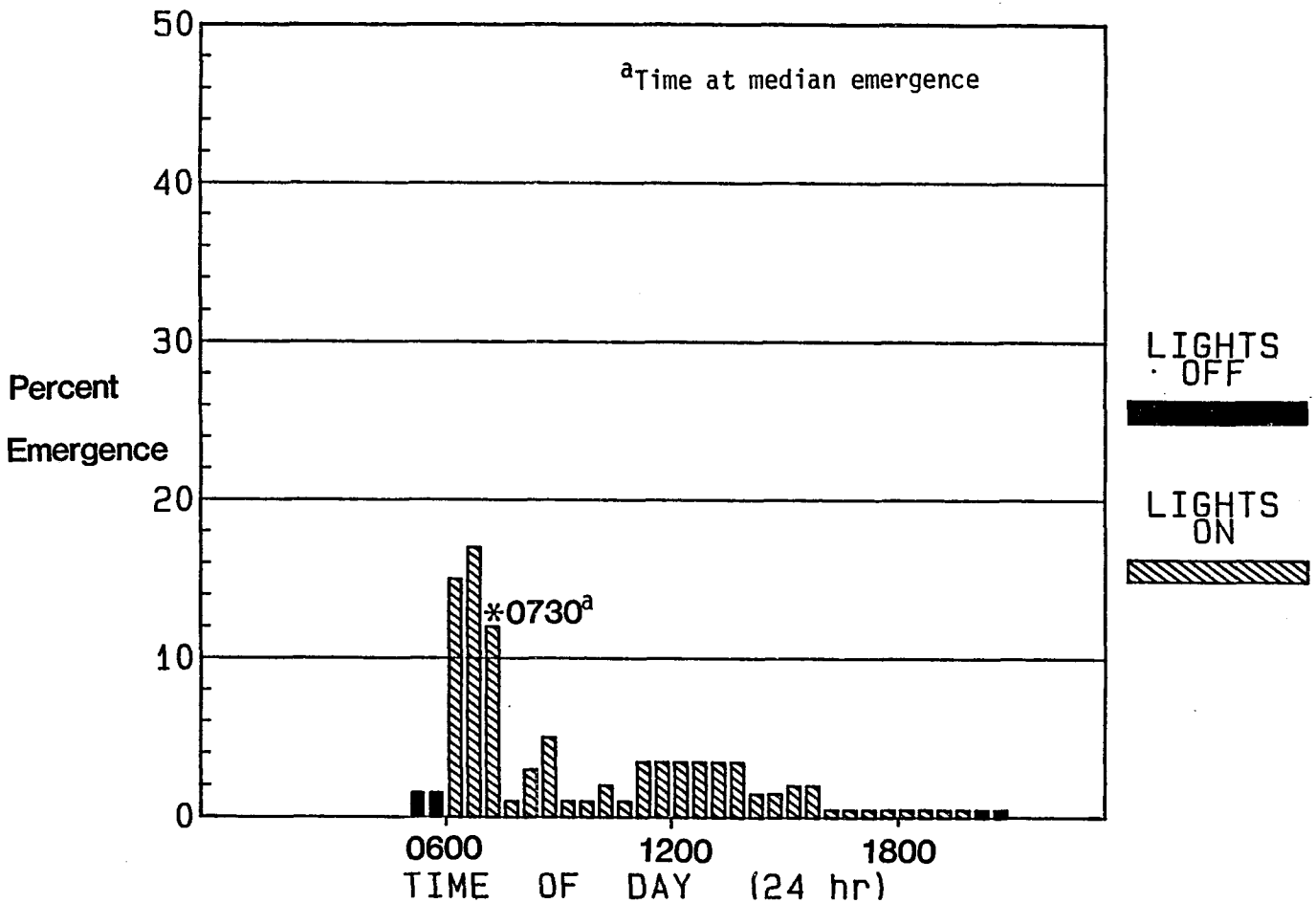

Figure 11. Percent of the total individuals of Bemisia tabaci emerging at 30-minute intervals upon return to a 14:10 photoperiod at 30.5 °C. N = 137.

Under conditions of constant darkness, the majority of emergence was markedly delayed during the second 24-hour period of the experiment (Figs. 12,13). In this case, 50% emergence occurred at 1030 hours, 27.5 hours after the previous median. The peak was more diffuse after 48 hours; at which time 50% of the adults had emerged at 1800 hours (Fig. 14). Seventy-two hours after the initial peak, following lights on (0600 hours), a small increase in the rate of emergence was observed (Fig. 15). Aside from this, no distinct pattern of emergence was seen although the distribution was still non-random.

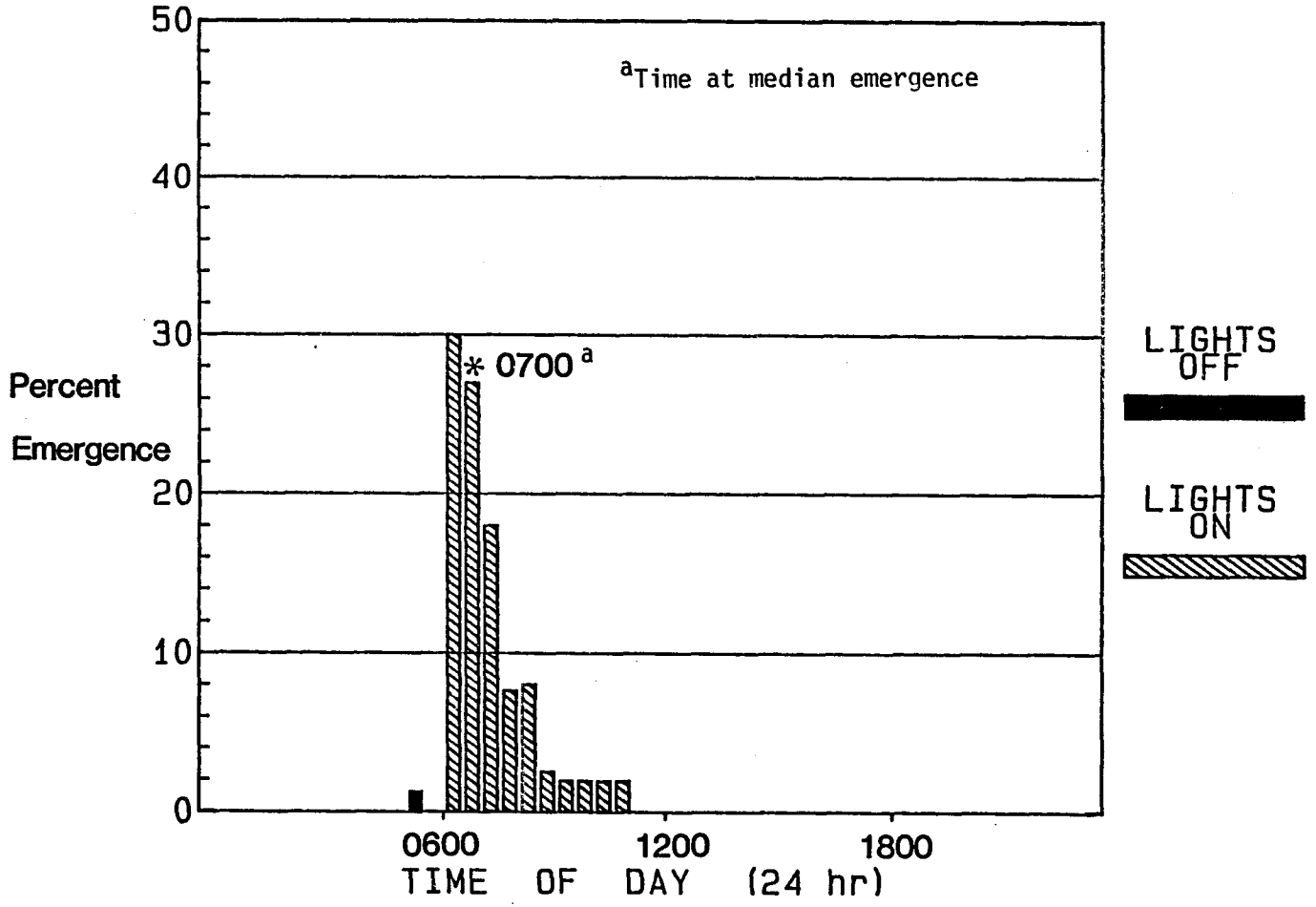

Figure 12. Percent of the total individuals of Bemisia tabaci emerging at 30-minute intervals under conditions of constant temperature (29.5 °C) and 14:10 photoperiod: Baseline day of exposure to continuous darkness (lights-off at 2000 hours). N = 156.

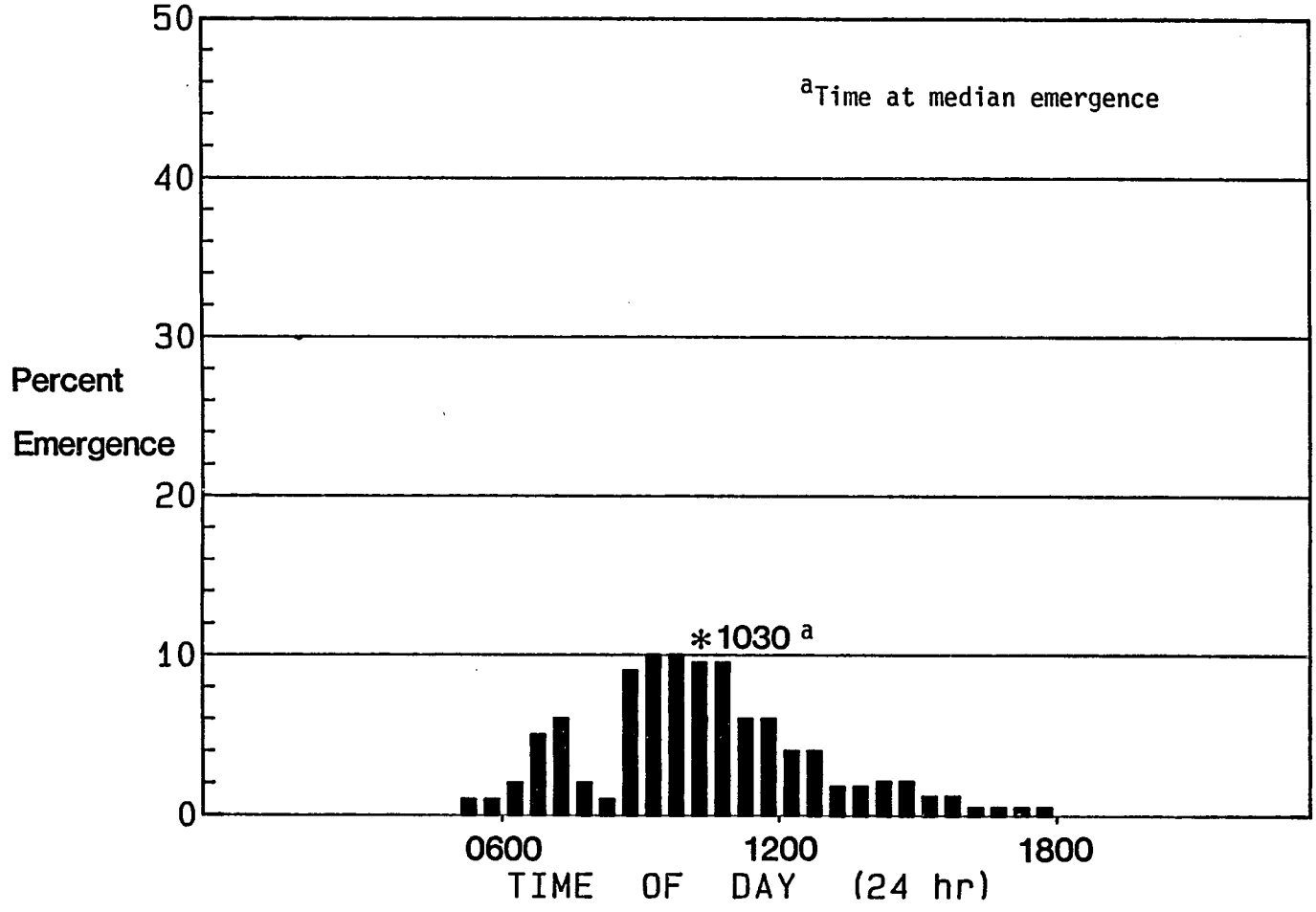

Figure 13. Percent of the total individuals of Bemisia tabaci emerging at 30-minute intervals: Day 1 of exposure to conditions of continuous darkness at 29.5 °C. N = 162.

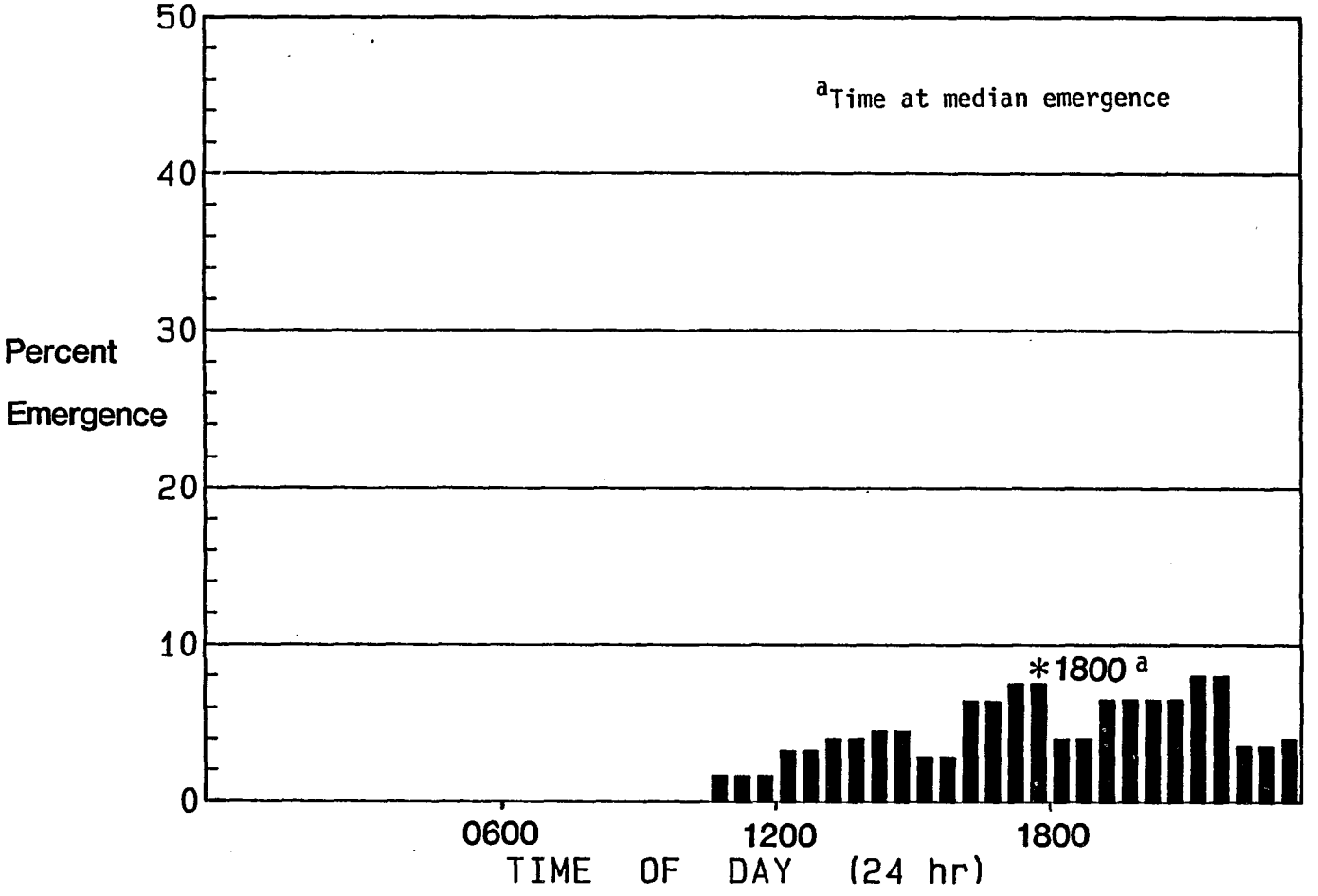

Figure 14. Percent of the total individuals of Bemisia tabaci emerging at 30-minute intervals: Day 2 of exposure to conditions of continuous darkness at 29.5 °C. N = 180.

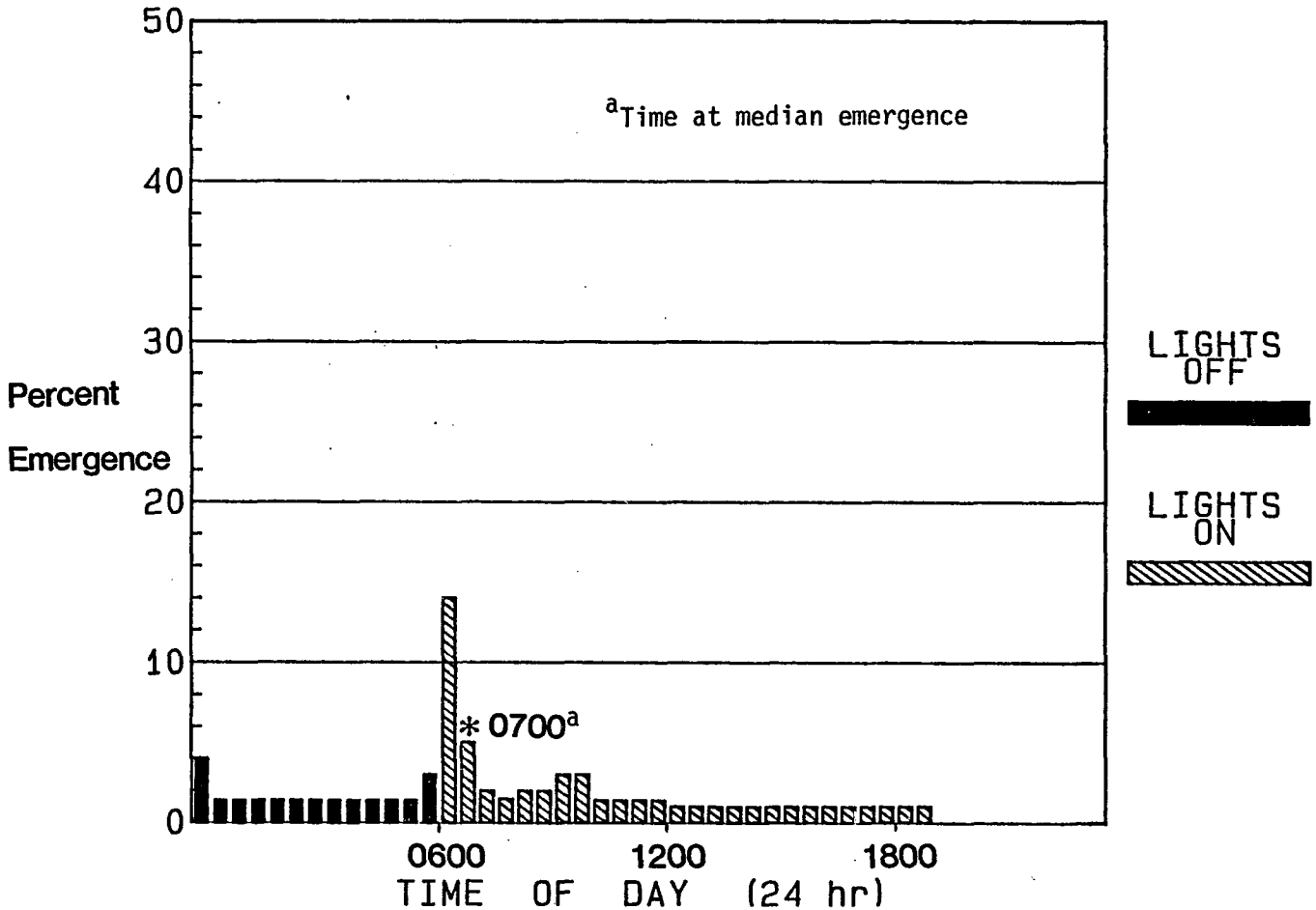

Figure 15. Percent of the total individuals of Bemisia tabaci emerging at 30-minute intervals upon return to a 14:10 photoperiod at 29.5 °C. N = 100.

DISCUSSION

Emergence of B. tabaci adults characterized in this study agree with the general pattern reported by Butler et al. (1983), in which 76% of adults emerged between the hours of 0600 and 0900 at 26.7°C. An experiment run at 25.6°C in the present study (Fig. 5) revealed a 75% emergence during this same time period. Other findings do not agree as closely with this work. Hussain and Trehan (1933) described a major emergence between 0800 and 1100 hours, and Azab et al. (1971) observed a major emergence between 0800 and 1200 hours. This discrepancy may in part be due to the effect of fluctuating temperatures and seasonal photoperiodic changes upon emergence as demonstrated in the present study. Detailed descriptions of these environmental factors were not included in the work of Hussain and Trehan or Azab et al.

Temperature had a marked effect upon the time of adult eclosion in the present experiments. As temperature was decreased, emergence was delayed to a time later in the day, culminating with a lower temperature threshold of emergence of 17°C, at or below which emergence did not occur or was severely inhibited. Emergence was also delayed when temperatures fluctuated. These data suggest the presence of temperature-dependent developmental processes preceeding actual emergence.

Temperature-dependent eclosion has been described by Willard (1972) who observed the emergence patterns of first instar nymphs of California red scale, Aonidiella aurantii. Willard's observation that the major period of eclosion occurred closer to lights-on as the temperature was increased was similar to that of the present experiments. These data disagree with Khidir (1972), however, who reported no association between the periodicity of emergence and temperature in his observations of the cabbage whitefly, A. brassicae, in the field.

Emergence during the early morning hours may be of selective advantage to B. tabaci. The success of eclosion is greatest when temperatures are mild and relative humidity is high (Saunders 1982) a common condition of early morning hours. Teneral individuals of Drosophila sp. lose water at double the rate of mature adults and fail to expand their wings when the humidity is too low (Pittendrigh 1954). The severe daylight temperatures experienced in the southwestern deserts of the United States (often exceeding 40°C) may markedly affect the mortality of a newly emerged adult whitefly.

The diel patterns of emergence observed in these studies may relate to other behavioral or physiological processes. The peak period of flight activity has been related to eclosion and teneral periodicity in a number of insect species (Johnson, Taylor, and Haine 1957, Johnson, Haine, Cockbain, and Taylor 1957, Lewis and Taylor 1964). A. brassicae needs 150 minutes to develop the ability to fly at 20°C (Iheagwam 1975). Daily rhythms of flight activity have been

suggested for B. tabaci (Byrne 1985) which may be related to, or result from, the timing of these processes or activities. Whiteflies are capable of copulation shortly after emergence (Gameel 1974), and this synchronization of eclosion may also increase mating success.

Diel patterns of adult eclosion by whitefly species observed in the field and laboratory by several investigators suggest the possibility of an underlying circadian rhythm which may ultimately govern the eclosion process. As stated, the rhythm of emergence observed in the present experiments persists following transfer into continual darkness. The peak becomes diffuse after 48 hours but a non-random pattern still exists. This fits the definition of circadian rhythm by Harker (1961) who describes a rhythm as being circadian when it persists for at least two days in constant conditions. The collapse of rhythms under LL or DD conditions does not necessarily indicate a collapse of the underlying rhythmicity. It may mean that overt processes are so disturbed by the abnormal conditions that the influence of the clock can no longer be dominating (Bunning 1973). The presence of a circadian rhythm is also supported by Aschoff's rule (see Saunders 1977). He maintains that diurnal animals will have a shorter τ in LL than in DD conditions. The periods of 23 hours under LL and 27.5 hours under DD observed in the present experiments agree with this contention.

Pittendrigh (1954) defined a circadian system as one which is temperature-independent, stating that, "A temperature-dependent clock will guarantee only mis-timing". Even though temperature has a marked

effect upon the time of major emergence, a circadian clock may still exist in B. tabaci. The clock may still be running at τ = 24 hours but the physiological process of eclosion may be influenced by temperature (Brady 1979).

The circadian system postulated in this case is not as pronounced as those observed in species of Drosophila which Pittendrigh used to develop his models of endogenous behaviors. The aleyrodids are considered phylogenetically primitive when compared to dipterans and the rhythms observed in B. tabaci may represent an evolutionary step toward the development of a strong circadian system.

B. tabaci appears to have adapted a successful eclosion behavior aimed at morning emergence. It follows that the development of a system of periodic, entrainable emergence patterns would be advantagous. Perhaps the most fundamental selective advantage of a circadian rhythm is that of preparation or anticipation (Saunders 1977). An insect can be physiologically prepared for the eclosion event prior to sunrise to take maximal advantage of the ecological situation. To facilitate the efficiency of behaviors such as flight, mating, feeding, and the escape from environmental severity, the preparation for and the timing of emergence is very important in this species.

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