THE REGULATION OF CYCLIC REPRODUCTIVE AND FEEDING ACTIVITY IN THE MILKWEED BUG ONCOPELTUS BY TEMPERATURE AND PHOTOPERIOD

ROY L. CALDWELL AND HUGH DINGLE

Department of Zoology, University of Iowa, Iowa City, Iowa 52240

Of the environmental stimuli which have been studied with respect to their effects on insect development and behavior, photoperiod and temperature have received the most attention. Much of this work deals with the effects of these stimuli on polymorphism, growth, diapause, reproduction and general activity (reviews in these areas are given by Lees, 1955; Danilevskii, 1965; de Wilde, 1962; and Birukow, 1966). In recent years, these stimuli have also been considered with reference to their effects on cyclic activities (Williams, 1935; Pittendrigh, 1960; Cloudsley-Thompson, 1961; Harker, 1964; Lewis and Taylor, 1965; and Corbet, 1966); most of these studies deal with either general locomotor activity, flight, or eclosion. Relatively few reports on cyclic reproduction, feeding, or other activities have appeared, exceptions to this being mating and oviposition studies in noctuid moths (Williams, 1936; Larsen, 1943; Shorey, 1964) and oviposition and feeding studies in mosquitoes (Haddow, 1945 *et seq.;* and Gillett, 1962).

Most of the work on cyclic activities in insects has been either purely descriptive or concerned with the analysis of the mechanisms involved, comparatively little attention having been paid to their adaptiveness. Studies where the adaptive value of cyclic activities has been considered are reviewed by Cloudsley-Thompson (1961). Also, there have been few reports where the interaction between two or more cyclic activities has been analyzed. Again, the work on the noctuid moths and mosquitoes represents some progress in this direction, as does, for example, the work of Parker (1962) who described several cyclic behaviors in *Musca domestica.*

This study presents some initial observations on several cyclic activities observed in the large milkweed bug, *Oncopeltus fasciatus,* primary consideration being given to this insect's responses to photoperiod and temperature. A description of the life history of *Oncopeltus* is given elsewhere (Dingle, 1967a, 1967b). An attempt is made to correlate these various cycles and also to assess their possible adaptive significance. This work is part of a continuing program in this laboratory to investigate the behavioral and ecological responses of *Oncopeltus* to its environment as well as the underlying mechanisms involved.

Materials and Methods

The insects used in this study were all descended from a culture of *Oncopeltus fasciatus* maintained in the Zoology Department at the University of Iowa. Experimental animals were kept at one of four temperature-photoperiod regimens: 12 hours Light-12 hours Dark, 23° C. (12L-12D 23° C.); 12 hours Light-12 hours

Dark, 27° C. (12L-12D 27° C.); 16 hours Light-8 hours Dark, 23° C. (16L-8D 23° C.); and 16 hours Light-8 hours Dark, 27° C. (16L-8D 27° C.). These animals were descendants of at least two generations maintained at the same temperature-photoperiod regimens. In all cases 20 males and 20 females were maintained together in 17 cm. × 12 cm. × 6 cm. plastic refrigerator boxes with cheese cloth covers and a layer of sand in the bottom. Animals were given dried milkweed seeds for food and had access to water from soaked cotton wool. Loose cotton wool was also supplied for oviposition, and all eggs oviposited were removed prior to hatching. Observations were made with respect to cyclic mating, feeding, and ovipositional activity, and also on cultures placed in continuous light or dark to determine if these activities were free running.

To examine periodic mating activity, 40 imaginal females and 40 imaginal males were collected at eclosion over a 48-hr. period from stocks maintained at the appropriate temperature-photoperiod regimens. Twenty pairs were placed in each of two boxes for each of the four conditions and mating activity was observed for at least 32 days. Any individuals which died during this time were replaced with animals of the same age and sex and which had been maintained under similar conditions. Every two hours, from light on to light off, the number of copulating pairs was recorded; from this the per cent of the total possible pairs mating was computed. After 32 days, the cultures were observed at two-hour intervals during the dark phase of the photoperiod, as well as during the light phase. This was done to determine to what extent mating activity continued in the dark. Observations made during the dark phase lasted approximately one to two minutes and were made under dim red illumination. No effect on activity during the observations was noted and the periodic fluctuations in mating activity during the light phase of the photoperiod remained similar to activity prior to the observations made in the dark phase. Thus it is assumed that these low-intensity, short-duration exposures to light had little or no effect on the mating cycles.

Fluctuations of feeding were recorded from 40 pairs of *Oncopeltus*, 20 pairs per container, in each of the four temperature-photoperiod regimens. In all cases, insects which had reached asymptotic mating frequencies were used. The number of insects feeding at any one observation was determined by simply counting the number of individuals with their proboscises inserted into milkweed seeds. Observations were made every two hours during the light phase of the daily cycle for 10 days and the number of individuals feeding per observation plotted. In the case of the two 12L-12D conditions, an additional observation was added four hours after light off at a time corresponding to that of light off in the 16L-8D photoperiod. These observations were made on the 10 days following the initial observations. A few milkweed seeds were added to the containers after each observation to eliminate possible bias from periodic feeding.

Oviposition cycles were recorded for each condition by removing and counting the number of egg clutches at two-hour intervals during the light phase of the daily cycle. Females in the act of oviposition were not disturbed but were allowed to continue ovipositing and the eggs collected at the next observation. The number of ovipositions per female per hour for each observational period was then calculated. Since oviposition rarely occurred at night, observations were not made in the dark; the number of clutches present at light on was divided to give the average oviposition rate per hour per female during the dark phase. Observations were made and averaged over a ten-day period.

To investigate the possibility of an endogenous control of periodic fluctuations in mating, feeding, and ovipositional behavior in *Oncopeltus,* 60 pairs of insects which had been reared at 16L-8D 23° C. and had reached asymptotic mating levels were transferred to continuous light at the same temperature for five days, and mating, feeding, and ovipositional activity recorded at three-hour intervals. At the end of this period, they were returned to 16L-8D 23° C. and the observations continued for two days. A similar group of 60 pairs was placed in continuous dark for four days and then returned to 16L-8D 23° C., observations being made at three-hour intervals under dim red illumination.

Results

Mating

Mating activity in cultures of sexually mature bugs maintained under the four temperature-photoperiod regimens was cyclic in nature. In all conditions mating activity was at its lowest level of the 24-hour cycle 8 hours after light off. In 12L-12D photoperiods the minimum mating level was maintained during the 4 hours

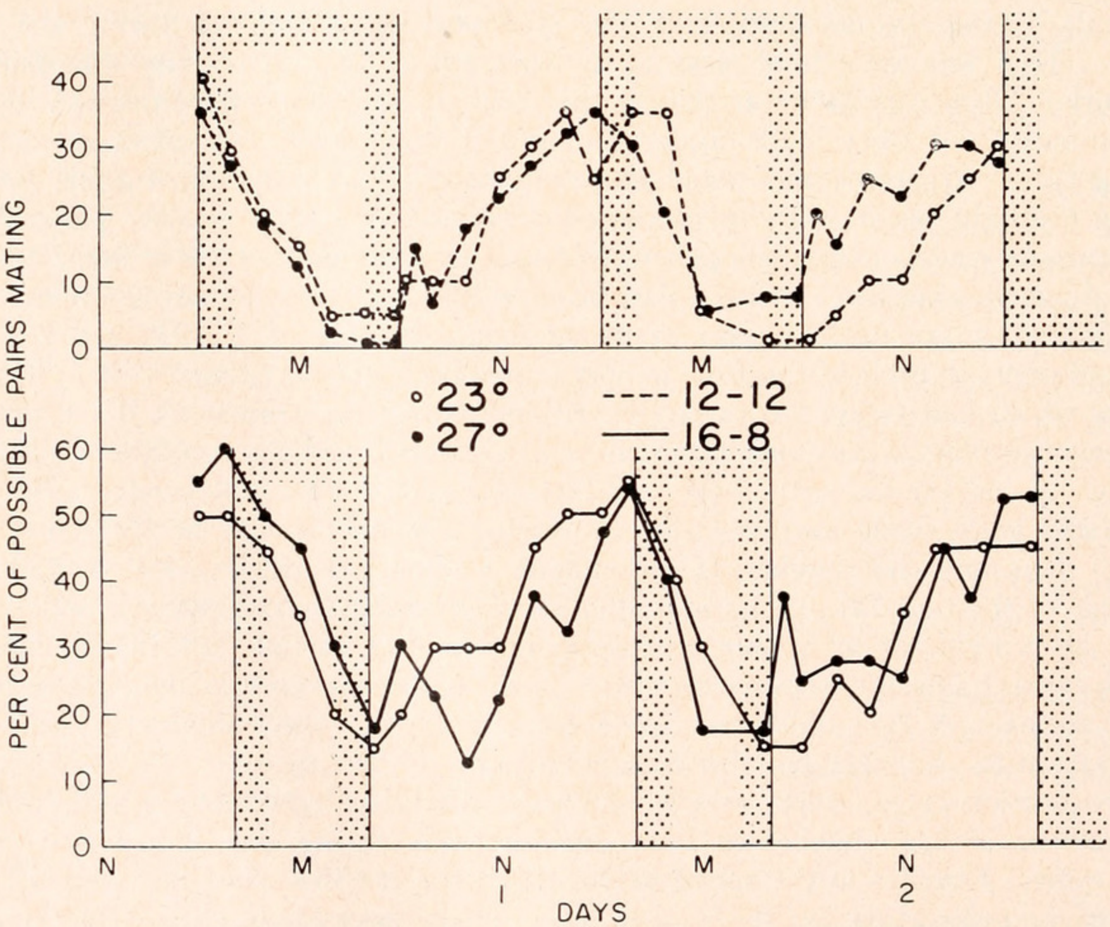

FIGURE 1. Mating activity of 4 cultures of *Oncopeltus fasciatus* reared under 4 different temperature-photoperiod regimens. Activity was plotted over an interval of 2 days. The shaded areas represent dark and the clear areas light phases of the photoperiod. Each culture contained 40 possible mating pairs which were sexually mature.

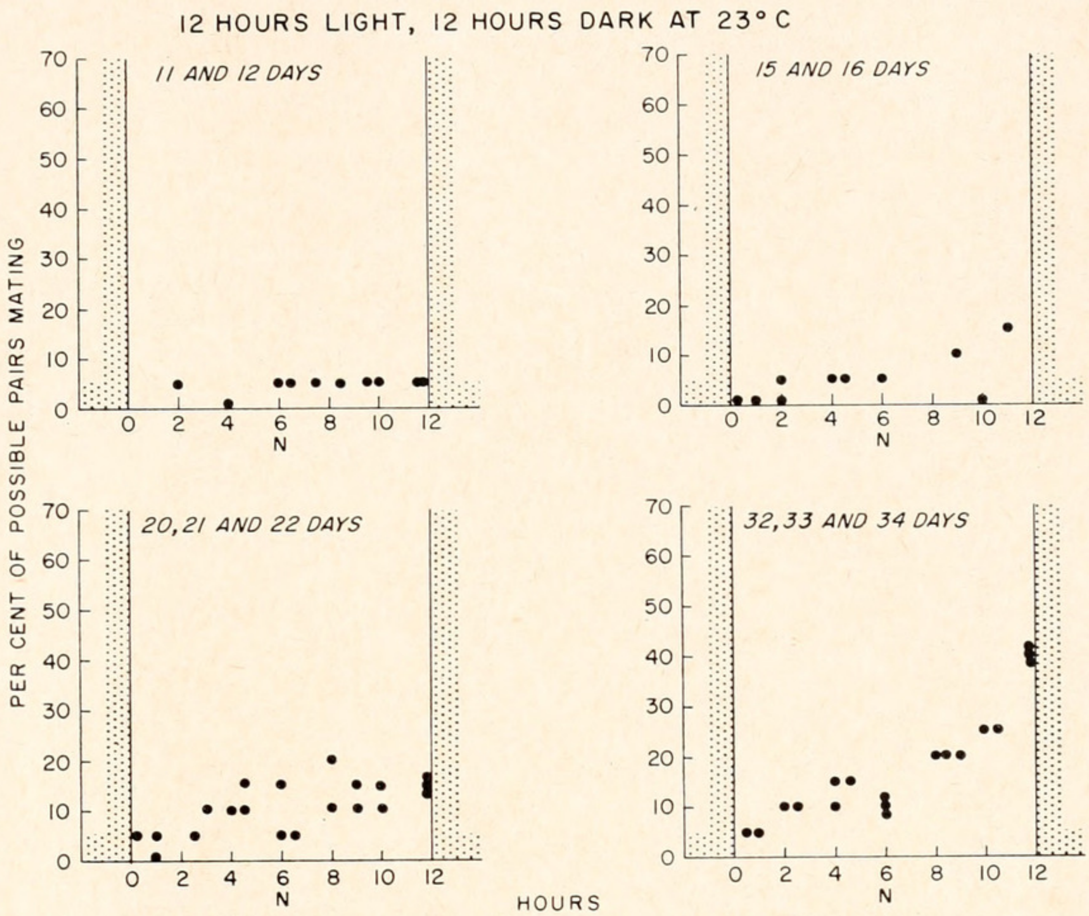

FIGURE 2. The development of the mating cycle in 40 possible mating pairs of *Oncopeltus* maintained at 12L–12D 23° C. First copulation occurred 11 days after adult eclosion, and some cyclic activity is evident after 15–16 days. Asymptotic mating activity had occurred by 32–34 days.

remaining until light on. At light on mating activity began to increase under all regimens, maximum levels being reached at light off, followed by a gradual decrease in mating activity during the dark phase of the photoperiod (Fig. 1).

First copulations were observed from 4 to 11 days following adult eclosion depending on conditions. Under high temperature and long photoperiod, 16L-8D 27° C., first matings occurred at 4 days. Under low temperature and short photoperiod, 12L-12D 23° C., first matings were delayed until 11 days after adult eclosion. In cultures reared under high temperature and short photoperiod or low temperature and long photoperiod the time to first mating was of intermediate duration, 8 and 9 days, respectively (Figs. 2–6).

Temperature and photoperiod also determined the maximum mating levels reached under a given regimen and how quickly these asymptotic mating levels were achieved. Photoperiod alone determined the asymptotic mating levels reached within a regimen. In 16L-8D, at both 23° C. and 27° C. a maximum of 65–70% of the possible pairs was observed mating. In 12L-12D, at either 23° or 27° C. a maximum of only 40% of the possible pairs was observed mating. Observations made on older cultures of *Oncopeltus* confirmed that maximum mating levels achieved during the first 30 days under these conditions were indeed asymptotic. There was no overlap between photoperiods.

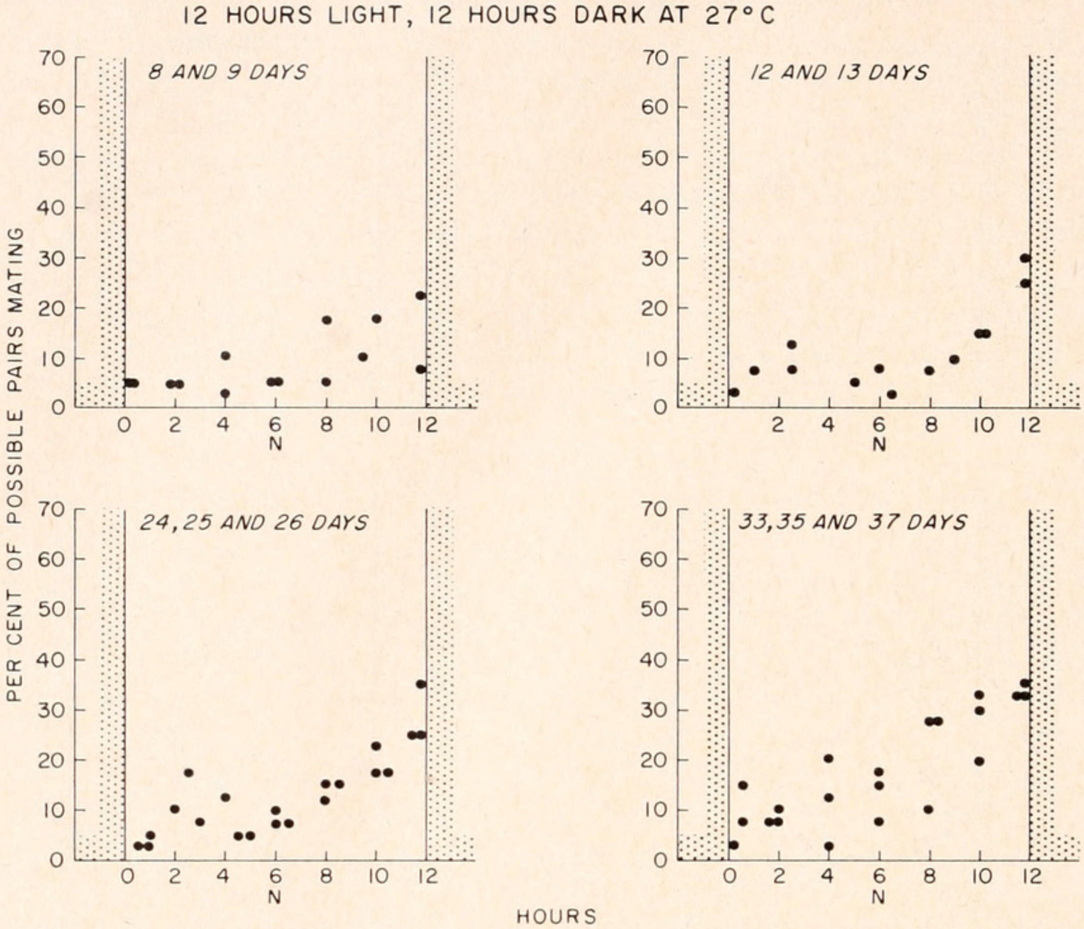

FIGURE 3. The development of the mating cycle in 40 possible mating pairs of *Oncopeltus* maintained at 12L–12D 27° C. First copulations occurred 8 days after adult eclosion at which time some cyclic activity was apparent. Asymptotic mating levels had already been achieved by days 24–26.

Temperature, as well as photoperiod, did appear to affect the rate at which asymptotic mating levels were achieved. At 16L-8D 27° it took only four days to reach asymptote once mating was begun and at 12L-12D 27° C. 75% of the asymptotic mating level was achieved three days from the onset of mating and full asymptote after 12 days. At 23° C., on the other hand, asymptotic mating levels were reached more slowly, taking 16 days from onset of mating under a 16L-8D photoperiod and 21 days under a 12L-12D photoperiod. Figures 2–5 illustrate the development of mating cycles under the four regimens used. Figure 6 summarizes the development of mating activity under the four regimens, giving the maximum percentage of the possible pairs mating on a given day following adult eclosion. In all cases the maxima so plotted occurred not more than 2 hours prior to light off.

Feeding and oviposition

A striking similarity is noted between the curves derived for periodic mating and feeding. Feeding was at a low level at light on, with perhaps a small increase in activity shortly thereafter. It declined to minimum levels eight hours after light on and then increased rapidly to reach maximum values at light off. This was

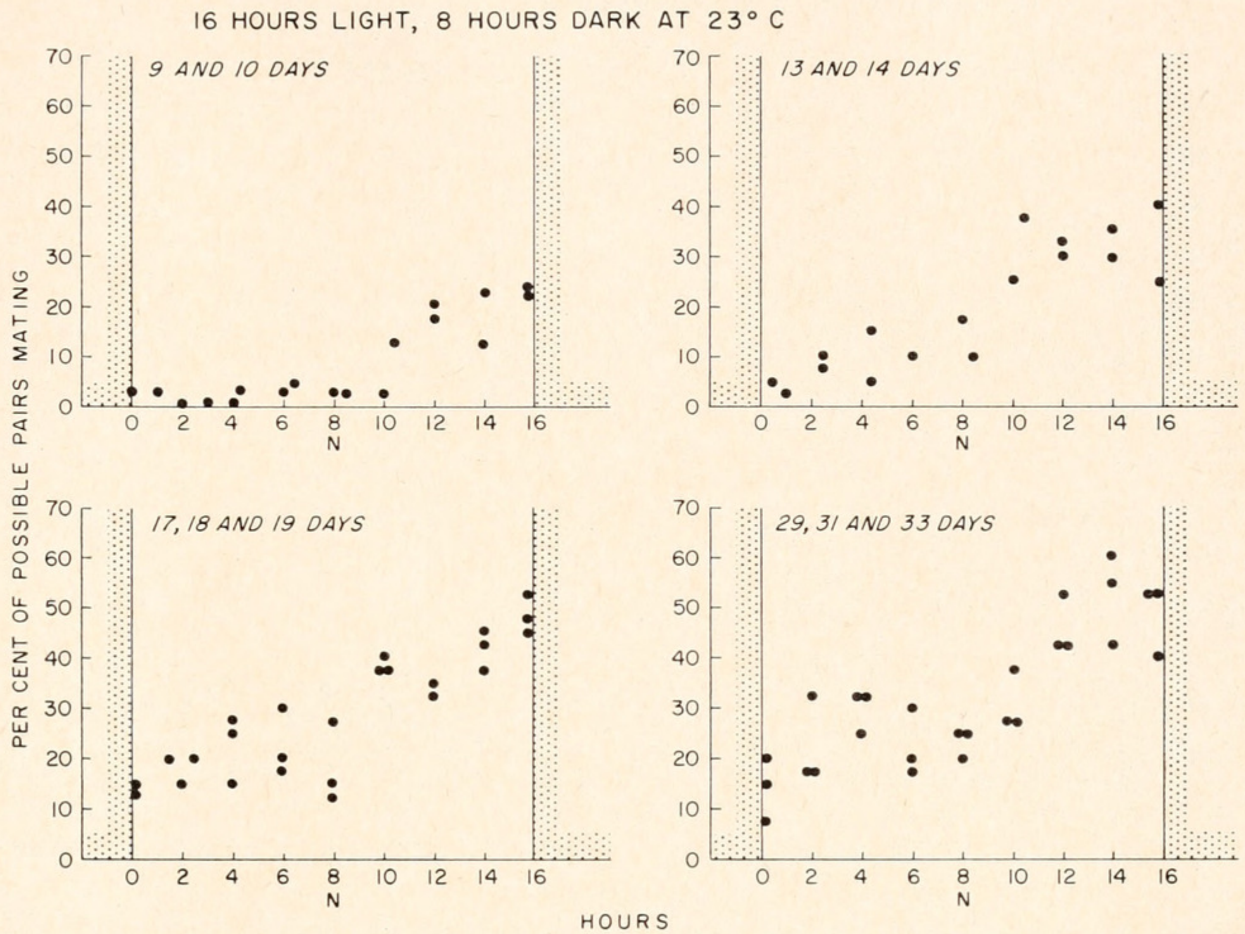

FIGURE 4. The development of the mating cycle in 40 possible mating pairs of *Oncopeltus* maintained at 16L-8D 23° C. First copulations occurred 9 days after adult eclosion at which time cyclic activity was evident. Asymptotic mating levels had been achieved by days 29–33.

true for all four conditions. At both temperatures the 16L-8D bugs achieved a higher percentage of feeding than did those at 12L-12D. In the 12L-12D regimens, however, feeding was maintained at maximum levels for at least four hours following light off (Fig. 7A). Females on 12L-12D or 16L-8D almost always oviposit during the light phase of the photoperiod, with little or no egg-laying occurring after light off. Under 16L-8D 23° C., 16L-8D 27° C., and 12L-12D 27° C. regimens oviposition reached a peak 8 hours after light on with values from 0.06 to 0.075 ovipositions per female per hour. Although the rate of oviposition was much lower at 12L-12D 23° C., reaching a maximum value of 0.02 ovipositions per female per hour, the peak activity still occurred 8 hours after light on (Fig. 7B).

Free running rhythms

When *Oncopeltus* maintained at 16L-8D 23° C. and at asymptotic mating activity were placed in continuous light for five days, mating did not begin to decline as usual 16 hours after light onset, but was maintained at high levels for the next six hours before a slight dip in activity was noted. During the next five days of continuous light, mating activity did not fall to normal minima. The first three cycles in constant light had a period of mating activity of 21 hours; a

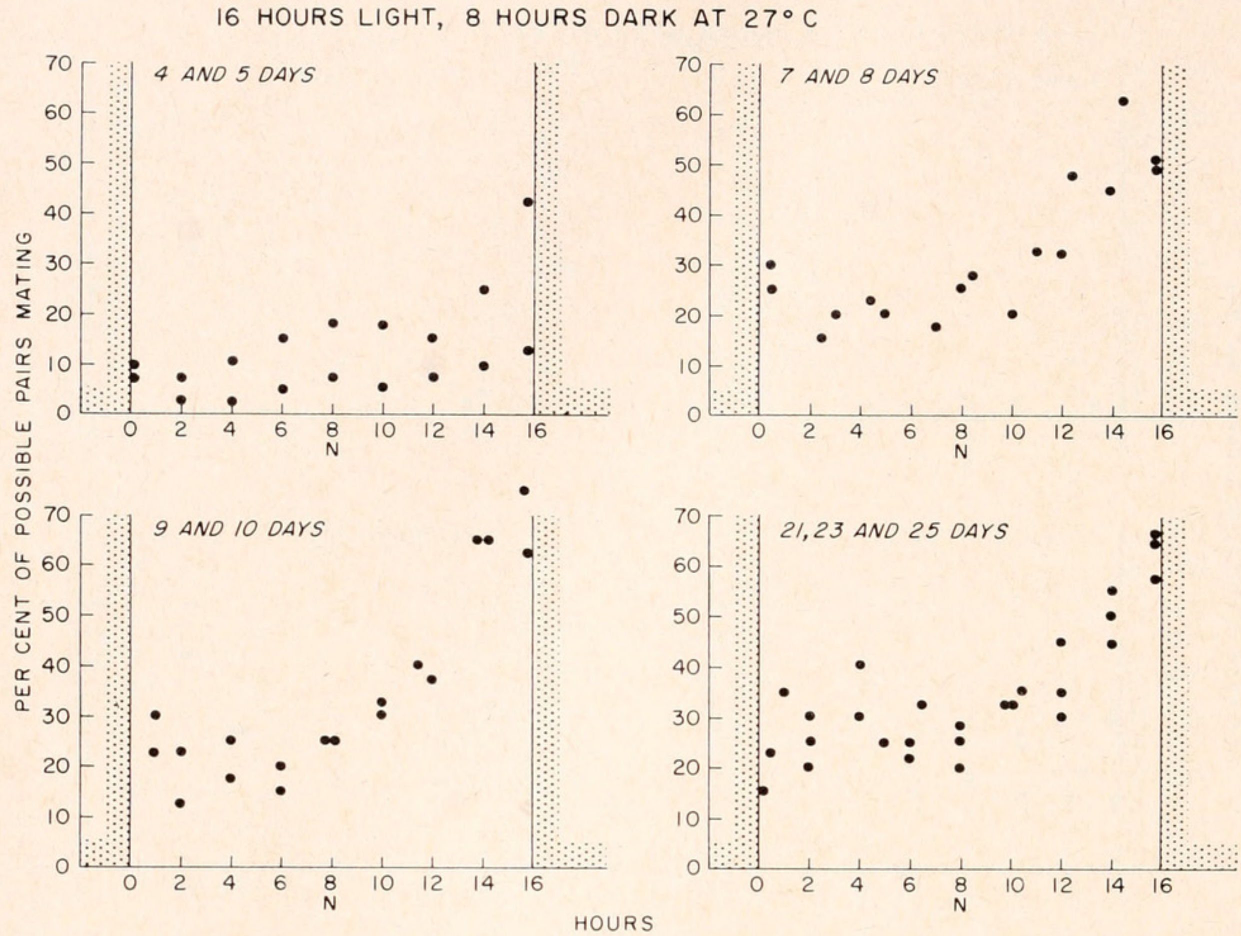

FIGURE 5. The development of the mating cycle in 40 possible mating pairs of *Oncopeltus* maintained at 16L–8D 27° C. First copulations occurred 4 days after adult eclosion at which time cyclic activity was present. Near asymptotic mating levels were achieved by 7–8 days and full asymptote by days 9–10.

fourth cycle had a period of 27 hours. When a similar group of 60 pairs was placed in continuous dark for four days, mating activity was depressed during the entire four days. There did, however, appear three peaks of mating activity, the first two cycles having a period of 21 hours and the third cycle a period of 24 hours. After three to four days in either continuous light or dark, mating activity became aperiodic (Fig. 8A).

Feeding, in general, was maintained at a slightly higher level under continuous light than under continuous dark. One difference noted between mating and feeding activity under continuous light was that feeding activity fell from maximum levels reached 16 hours after light onset to minimum values 8 hours later. One cycle of feeding activity under continuous light was recorded, having a period of 21 hours, after which cyclic activity apparently broke down. In continuous dark, no cyclic feeding was observed, although upon return to 16L-8D a peak of activity was reached 9 hours after light onset and at the normal time of 16 hours after light onset during the second 24-hour cycle (Fig. 8B).

Oviposition cycles were the most persistent of the three measured activities under both constant light and dark. Under continuous light there were periodic fluctuations in oviposition during the entire five-day period. The periods of the

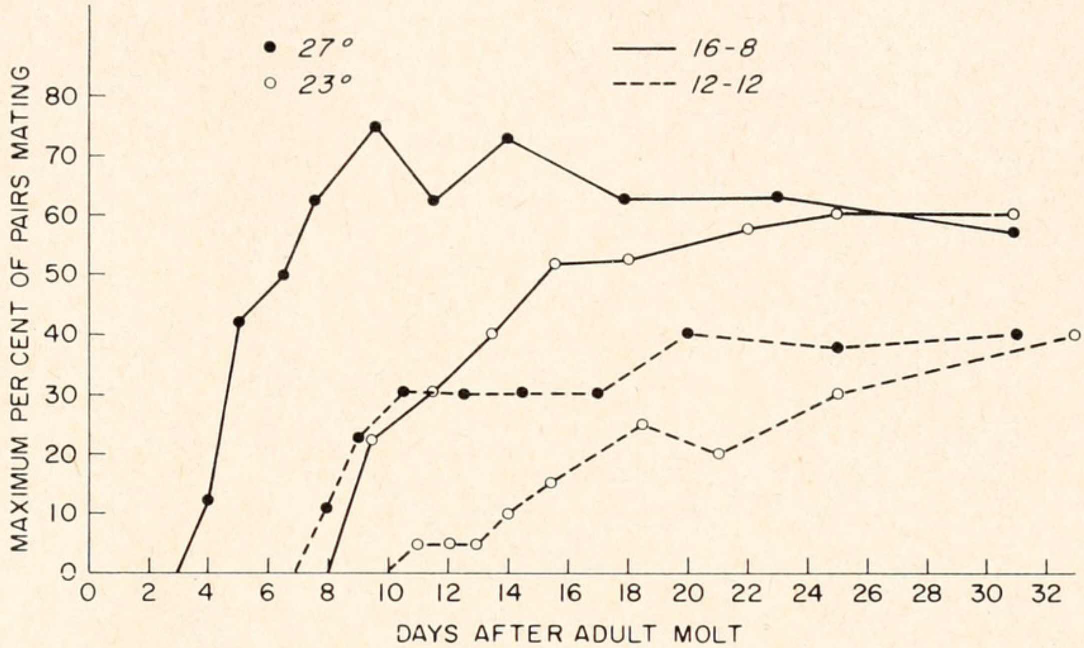

FIGURE 6. Maximum mating levels achieved by 4 groups of *Oncopeltus fasciatus* reared under 4 different temperature-photoperiod regimens. The maximum per cent possible pairs mating on a given day following the adult molt was plotted for each group and in every case the maximum occurred within 2 hours of light off. Note that photoperiod alone determines the maximum level of mating achieved within a regimen while both photoperiod and temperature determine the time to first mating and also the time to asymptotic mating levels.

five cycles were in order, 18, 21, 21, 24, and 27 hours. In continuous dark, the first peak of egg-laying came 21 hours after the preceding one, the remaining three cycles which occurred being somewhat variable, having periods of 21 to 27 hours. Under both conditions the amplitude of the fluctuations in oviposition were depressed, although no change in the overall number of clutches oviposited per 24 hours occurred (Fig. 8C).

DISCUSSION

In the laboratory, feeding and reproductive activities of *Oncopeltus fasciatus* occurred in daily cycles governed by the environmental regimens under which the animals were maintained. In these experiments only temperature and photoperiod were varied systematically, and within each regimen photoperiod alone provided possible "clues" (Cloudsley-Thompson, 1952) or "Zeitgeber" (Aschoff, 1954) which could synchronize endogenous rhythms or determine cycles exogenously. The results indicate that photoperiod can control cyclic mating, feeding, and oviposition in *Oncopeltus*.

The patterns of these activities are summarized in Figure 9. Note first that oviposition cycles are distinctly out of phase with mating and feeding. In both 12L-12D and 16L-8D egg-laying activity reached a peak 8 hours after light on while in the case of the latter two functions a peak was not attained until at least 12 hours. The fact that oviposition remains fixed with respect to light on indicates that this is the Zeitgeber that triggers or synchronizes egg-laying.

Feeding cycles under both photoperiods were identical for the first 12 hours after light on; at light on, feeding was at near minimal levels, but then showed a

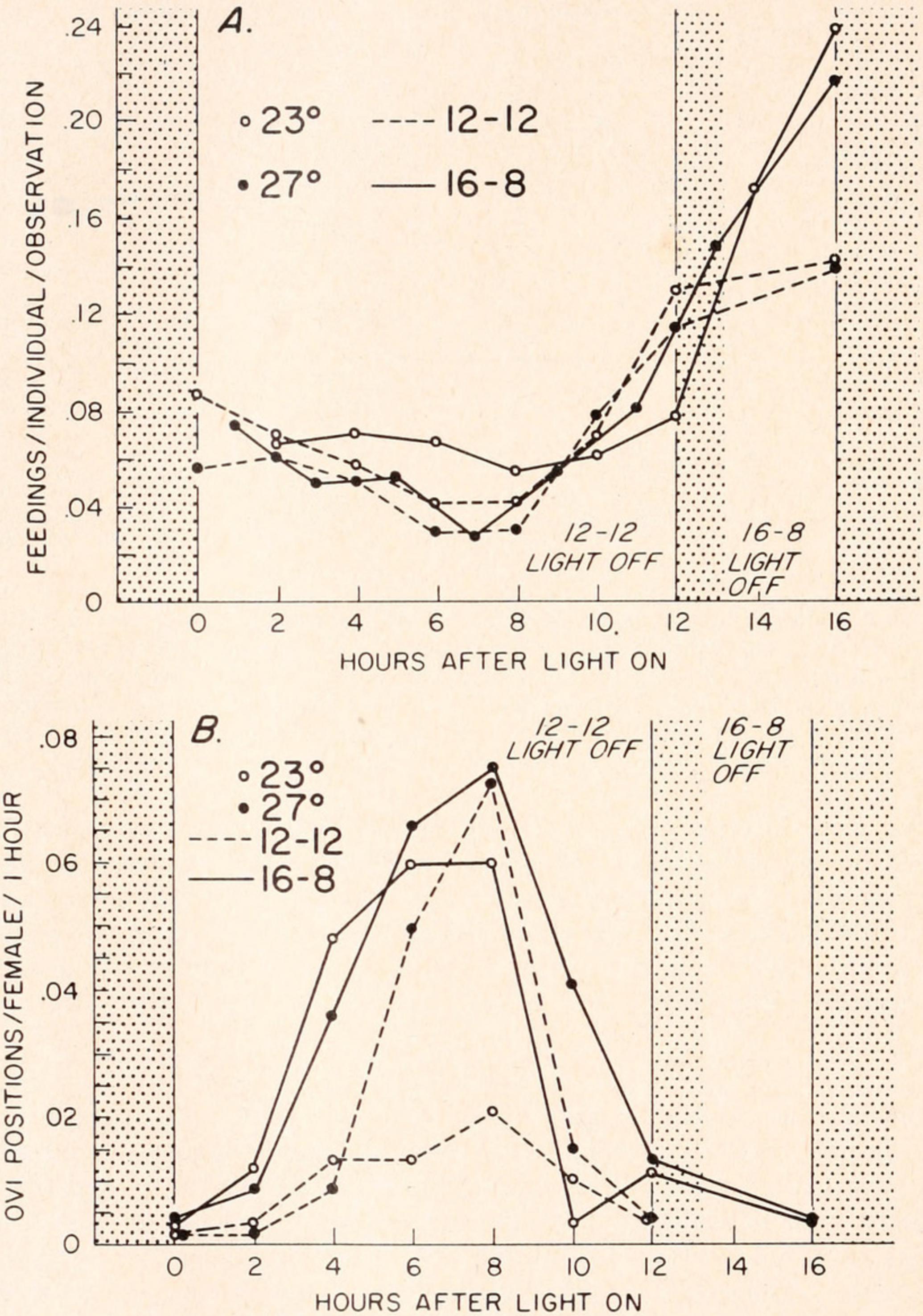

FIGURE 7. A. Feeding. B. Oviposition. Feeding and oviposition activity observed under 4 temperature-photoperiod regimens in 40 pairs of *Oncopeltus* per condition. Points represent the means of values taken over a 10-day period. Note that in all groups oviposition reached maximum 8 hours after light on while feeding reached maximum 16 hours after light on (4 hours after light off for 12L–12D regimens).

small transitory rise lasting about two hours. This brief early burst is presumably associated with an increase in locomotor activity immediately following light on (Caldwell and Dingle, unpublished observations) and the resulting increased probability of locating food. Eight hours after light on feeding fell to the lowest

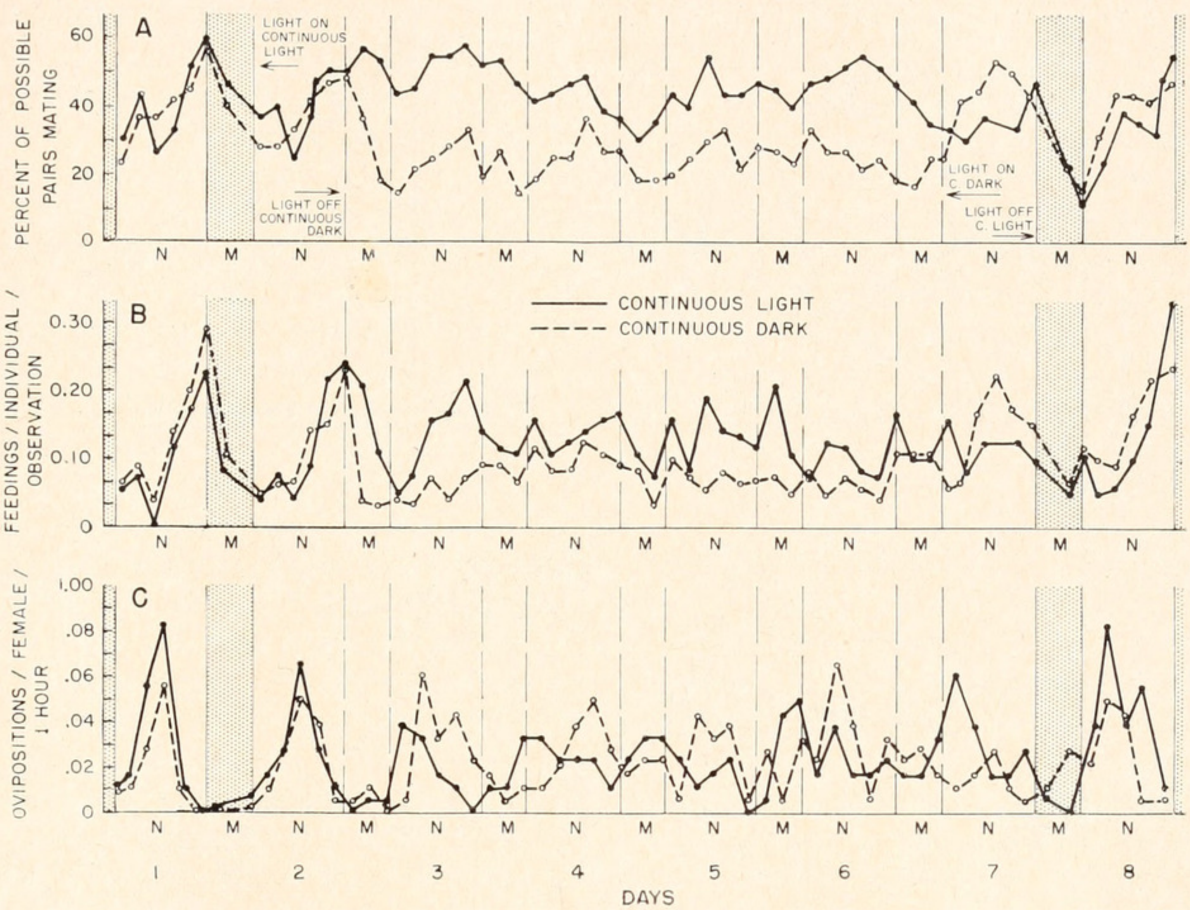

FIGURE 8. Activities observed in continuous light and dark. A. Mating. B. Feeding. C. Oviposition. Animals placed in constant light or dark at 23° C. were reared at 16L–8D 23° C. Broken vertical lines represent times that light on and off would have normally occurred. Note that in all cases (except Feeding, constant dark) at least one cycle of activity is observed after the onset of constant conditions.

levels recorded during the cycle, and then climbed rapidly until light off. During the four hours following light off, feeding in the 12L-12D cultures remained at or slightly increased above the levels reached at light off (Fig. 7A), whereas it began to fall at light off under 16L-8D (Fig. 8B). The difference in the maxima of the cycles under the two photoperiods is apparently due to the time at which light off occurs; in either case the onset of darkness damps further increases. This results in more feeding under 16L-8D than 12L-12D photoperiods. While growth, maturation, and reproduction could be affected indirectly *via* varying food intake as a result of differing photoperiods, feeding activity does not necessarily reflect nutrient intake (Feir and Beck, 1963).

Mating cycles under the two photoperiods were not in phase; in either condition, however, they were at minimum levels at light on. The initial increase in activity may be due to increased locomotion as in the feeding cycle, leading, in this case, to an enhanced probability of finding a mate. In the 16L-8D photoperiod, mating declined to minimal levels six hours after light on. Under 12L-12D, on the other hand, there was only a reduced rate of increase for a short period in the possible pairs mating. By six hours after light on, mating was the same under both photoperiods and continued to rise until light off. At light off, it began to decline and

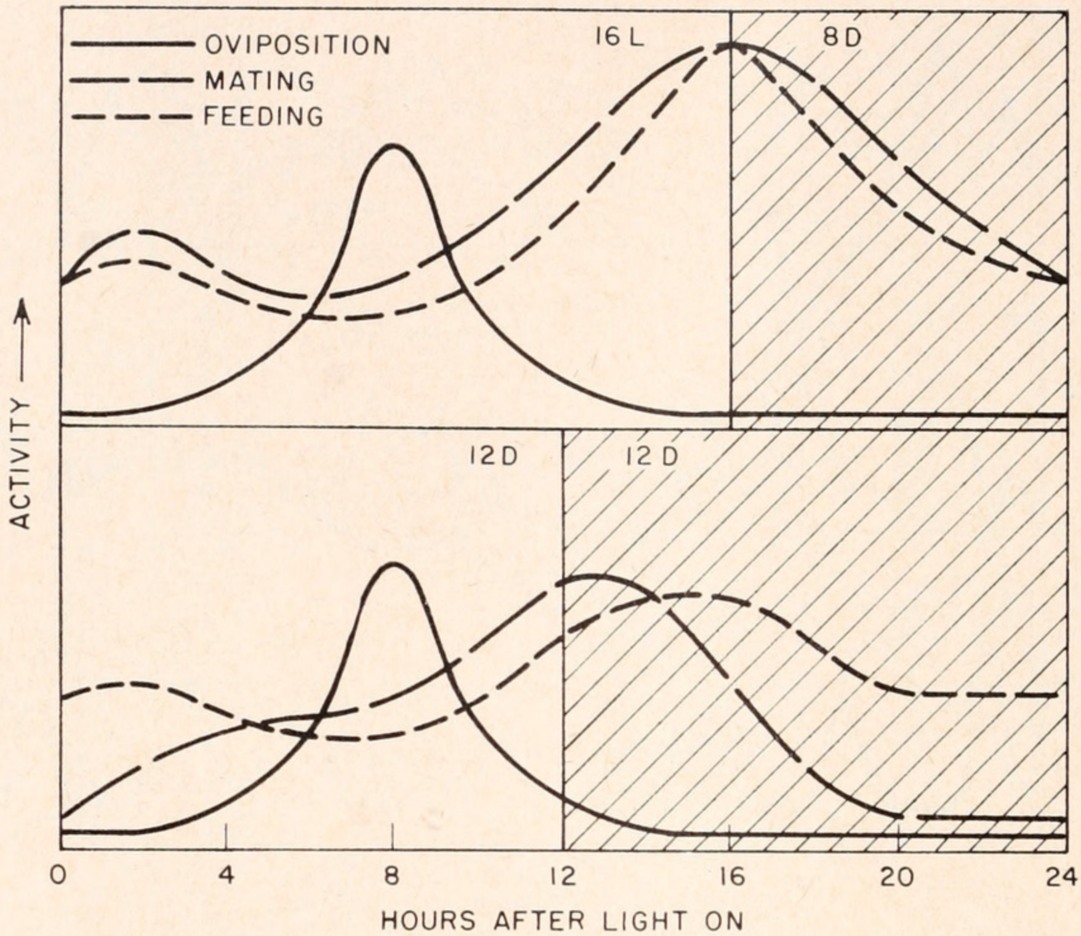

FIGURE 9. Interaction of mating, feeding, and oviposition cycles in *Oncopeltus fasciatus* under 12L–12D and 16L–8D photoperiods. Activity is represented in arbitrary units. Curves were constructed from data taken from cultures of sexually mature insects at both 23° and 27° C. (temperature has no effect on these cyclic activities over this range). Note that under both photoperiods all three activity cycles appear to be similar for the first 12 hours after light on and that dark suppresses further increases in mating and feeding.

reached minimal levels eight hours later. It appears that the duration of the light period determines the level of maximum activity, long days producing high levels, while the duration of the dark period determines the minima, long nights producing low levels. Light off shuts down mating and on a short day does so before it has reached its peak; the relatively short 8-hour night phase following a 16-hour day prevents a fall to near zero. Direct control by photoperiod is probably an oversimplification, however, for the cycles of animals reared in 16L-8D do not fall below normal minima, approximately 20% of possible pairs mating, even when the cultures are placed in continuous dark (Fig. 8A), nor is there much overshoot when in continuous light. Maximum amplitude thus seems to be reached on a 16-hour day. Factors other than direct stimulation by light or inhibition by dark therefore probably also affect mating activity.

In addition, continuous light or dark influenced the expression of all three activities measured (Fig. 8). In each instance, both in continuous light and continuous dark (except continuous dark, feeding) one cycle of activity was observed during the first 21 to 24 hours of constant conditions; further cyclic activity persisted in some cases, *e.g.*, oviposition, during the entire five-day period.

In general, the free running rhythms had initial periods of approximately 21 hours in continuous light. (Since observations were made at three-hour intervals, it is not possible to make a more precise statement as to the actual period length.) In the case of both mating and oviposition, the period was observed to lengthen after three days to 24 hours. In continuous dark, the free running rhythms were less persistent, although the first cycle also had a period of 21 hours. The periods of later cycles were more erratic, but in general were 24 hours or longer. Beck *et al.* (1958) and Feir and Beck (1963) observed the occurrence of a feeding rhythm in *Oncopeltus* fifth instar numphs under constant conditions (continuous dark interrupted one second each minute by a flash of light), indicating that an endogenous feeding rhythm is present even before the imaginal molt. Experiments are presently underway to define more precisely the free running rhythms found in *Oncopeltus* and to determine the role they may play in the activity cycles reported here.

There is in any case integration of the three cycles. Towards the end of the daylight hours, both feeding and mating reach a peak, but these two activities are not in conflict since *Oncopeltus* is able to mate and feed simultaneously. During the early afternoon hours, females oviposit; feeding and mating have not yet begun to increase so no conflict occurs. It may also be of interest to note that a review of the data from *Oncopeltus* flight tests made to determine the potential for migration (see Dingle, 1965 for a summary of procedures) indicates that significantly more bugs flew ("migrated") in the early afternoon, the same time that oviposition is at a peak. Migration, however, generally occurs pre-reproductively in *Oncopeltus* (Dingle, 1965 *et seq.*) and therefore would not interfere with either oviposition which has not yet begun or feeding which occurs in the evening. Some mating may occur at the same age as peak flight activity, but again would not be in conflict with flight since it also occurs mostly in the evening.

A causal relationship between the various cyclic activities can not at this time be specified. Activity cycles may be due to one underlying factor or an interaction of several discrete physiological events. Feeding cycles occur during the first few days after the imaginal molt and may be present during juvenile stages (Feir and Beck, 1963), while mating is initiated 4 to 10 days and oviposition 8 to 15 days following adult eclosion. This would seem to indicate that feeding and mating cycles are independent of the oviposition cycle, although again, the same ultimate physiological mechanism may underlie all three activities.

Although they were not investigated in this study, general locomotor activity and a possible cyclic pheromone production may influence feeding, mating and oviposition. Cyclic locomotor activity was not quantified, but general differences in levels of activity were noted. The bugs were more active in light than dark and also showed a marked increase in activity at light on. As mentioned above, such an increase in locomotion at light on could be related to corresponding bursts in feeding and mating. Experiments are now in progress to analyze the relationship between general activity and the cyclic behaviors described above.

Pheromonal control of mating is suggested by the observation that males attempt to copulate with females of already mating pairs and that introduction of a copulating pair into a culture triggers a burst of mating. Cyclic pheromonal production similar to that postulated in several Lepidoptera (Ouye *et al.*, 1965;

Shorey and Gaston, 1965) could exert control over cyclic mating in *Oncopeltus* and experiments are also in progress to explore this possibility.

The adaptive significance of cyclic activities in insects is difficult to assess and relatively few attempts have been made to determine their ecological importance. With respect to *Oncopeltus,* studies made in August, 1966, indicate that, as in the laboratory, a mating cycle exists in the field with maximum activity occurring in the early evening. Furthermore, a majority of the mating pairs were found on the seed pods of milkweed plants (the major source of food for *Oncopeltus* during this time of year) and many of these animals were feeding. Localization of feeding sites and the ability to mate while feeding may serve to bring pairs together, especially if a peak of activity occurs during one part of the day. Such a mechanism might be particularly adaptive in the early summer when population densities are low and feeding sites relatively scarce. Why mating and feeding should occur primarily in the early evening remains obscure except as a result of possible interactions with other activities. As mentioned above, flight occurs principally in the early afternoon. This corresponds with maximum daily temperatures and may be advantageous since high temperatures lower the threshold for flight. Suppression of mating and feeding during this period would assure maximum opportunity for flight to occur. A similar situation seems to occur in *Leptohylimyia coarctata,* a wheat bulb fly, in which an endogenous oviposition rhythm occurs with maximum activity two hours before dark while flight occurs in the early morning and later evening (Long, 1958). As noted, however, oviposition and migration flights generally do not overlap in the life-cycle of *Oncopeltus* females so that the occurrence of oviposition in the early afternoon would appear not to be related to flight activity. Environmental conditions, however, may promote oviposition at this time. For whatever reason, there seems to be some selective advantage in laying eggs in the afternoon since several other Hemiptera occupying somewhat similar niches, *e.g., Anasa tristis* (Beard, 1940), *Nysius huttoni* (Eyles, 1963) and *Euschistus conspersus* (Hunter and Leigh, 1965), have been reported to have oviposition cycles with peak activity occurring at that time.

Aside from determining the timing and amplitude of the various activity cycles in *Oncopeltus,* photoperiod, in combination with temperature, determines the time to onset of reproduction. Andre (1934) noted decreased time from the imaginal molt to first reproduction in *Oncopeltus* with an increase in temperature. Similar results were observed over the temperature range used in this study. But in addition, lengthened photoperiod also shortens the time to first copulation. Thus higher temperatures and longer photoperiods caused a rapid onset of reproductive activity while lower temperatures and shorter photoperiods delay reproduction. Such responses may be adaptive for a migrant such as *Oncopeltus* since delays in reproduction allow time for more migratory flights to occur (Dingle, 1967b). Thus in the early spring or late fall with short photoperiods and lower temperatures, there will be time for migratory flights; in the summer under longer photoperiods and higher temperatures reproduction will begin earlier with fewer and shorter flights occurring. The dependence of the prereproductive period on the photoperiod as well as temperature affords some protection from short periods of unseasonably high or low temperature, assuring that migration will occur in the spring and fall while reproduction continues during the summer. Also, early reproduction leads to more rapid population growth (Cole, 1954), an advantage for a migrant colonizer invading an empty habitat as *Oncopeltus* does in the late spring or early summer in the central and northern United States (Dingle, 1967b).

Blatchley (1926) reported that *Oncopeltus* may spend the winter in the southwestern United States in a state of quiescence, becoming active only on warm days and evidently not reproducing. It would be easy to extrapolate the photoperiodic-temperature response of *Oncopeltus* (Fig. 6) to a point where at short photoperiod and low temperature little or no reproductive development would occur and the adult would enter a non-reproductive period as occurs, for example, in *Plutella maculipennis* (Harcourt and Cass, 1966) and *Lygus hesperus* (Leigh, 1966). Such a delay in reproduction in response to short photoperiod and low temperature, as is found in *Oncopeltus,* probably represents an incipient diapause and an intermediate step in the evolution of adult reproductive diapause (Harcourt and Cass, 1966; Dingle, 1967b).

This paper has presented some initial observations on the responses of *Oncopeltus fasciatus* to two environmental stimuli, photoperiod and temperature. It is hoped that by accumulating a more complete knowledge of the repertoire of responses by *Oncopeltus* to the environment, such as possible locomotor activity cycles, reproductive responses to wider ranges of environmental conditions, social interactions, etc., a more integrated view of the behavior and ecology of *Oncopeltus* may be achieved, including some insight into the basic mechanisms underlying cyclic activities (Pittendrigh and Minis, 1964; Adkisson, 1966; Lees, 1966).

We thank Jean B. Haskell for invaluable assistance in the maintenance of the cultures and the data recording, John C. Naughten who first noticed that *Oncopeltus* cycled, and Dr. R. V. Bovbjerg for comments on the manuscript. Supported by a NSF Predoctoral Fellowship to R. L. C. and NSF Grant GB-2949 to H. D.

Summary

1. Mating, feeding, and oviposition cycles were observed in the large milkweed bug, *Oncopeltus fasciatus,* under four regimens of varying temperatures and 24-hour photoperiods.

2. Mating and feeding activity reached maximum at the end of the light phase while oviposition occurred 8 hours after light on.

3. When placed in continuous light or dark, cyclic activity of all three behaviors persisted for at least one cycle and in the case of oviposition for five cycles. In general, the period of the first one or two cycles for all three activities, in both continuous light and dark, was approximately 21 hours; subsequent cycles, if present, had periods of 24 hours or longer.

4. Photoperiod was found to affect the maximum mating and feeding activity which occurred during the day. Long photoperiods promoted higher levels of mating and feeding than did short photoperiods.

5. The time from eclosion to first mating was photoperiod- as well as temperature-dependent; longer photoperiods and higher temperatures shortened the time to first mating.

6. The interaction of the various cyclic activities was discussed in reference to the ecology of *Oncopeltus.* The hypothesis was proposed that the occurrence of

most mating and feeding in the early evening would allow maximum opportunity for oviposition or migratory flight, which reach peak activity earlier in the day, to occur.

LITERATURE CITED

ADKISSON, P. L., 1966. Internal clocks and insect diapause. *Science*, **154**: 234–241.

ANDRE, F., 1934. Notes on the biology of *Oncopeltus fasciatus* (Dallas). *Iowa State Coll. J. Sci.*, **9**: 73–87.

ASCHOFF, J., 1954. Zeitgeber der tierischen Tagesperiodik. *Naturwiss.*, **3**: 49–56.

BEARD, R. L., 1940. The biology of *Anasa tristis* De Geer with particular reference to the tachinid parasite *Trichopeda pennipes* Fabr. *Conn. Agric. Exp. Sta. Bull.*, **440**: 597–679.

BECK, S. D., C. A. EDWARDS AND J. T. MEDLER, 1958. Feeding and nutrition of the Milkweed Bug, *Oncopeltus fasciatus* (Dallas). *Ann. Ent. Soc. Amer.*, **51**: 283–288.

BIRUKOW, G., 1966. Orientation behavior in insects and factors which influence it. *Symp. Roy. Ent. Soc.*, **3**: 2–12.

BLATCHLEY, W. S., 1926. Heteroptera of Eastern North America. Indianapolis, The Nature Publishing Co.

CLOUDSLEY-THOMPSON, J. L., 1952. Diurnal rhythms. *Trans. IX Int. Cong. Ent., Amsterdam 1951*, **1**: 305–310.

CLOUDSLEY-THOMPSON, J. L., 1961. Rhythmic Activity in Animal Physiology and Behavior. New York, Academic Press.

COLE, L. C., 1954. The population consequences of life history phenomena. *Quart. Rev. Biol.*, **29**: 103–137.

CORBET, P. S., 1966. The role of rhythms in insect behavior. *Symp. Roy. Ent. Soc.*, **3**: 13–28.

DANILEVSKII, A. S., 1965. Photoperiodism and Seasonal Development of Insects. London, Oliver and Boyd.

DE WILDE, J., 1962. Photoperiodism in insects and mites. *Ann. Rev. Ent.*, **7**: 1–26.

DINGLE, H., 1965. The relation between age and flight activity in the milkweed bug, *Oncopeltus*. *J. Exp. Biol.*, **42**: 269–283.

DINGLE, H., 1966. Some factors affecting flight activity in individual milkweed bugs (*Oncopeltus*). *J. Exp. Biol.*, **44**: 335–343.

DINGLE, H., 1967a. A probable interaction between behavioral and meteorological events in the migration and distribution of the milkweed bug (*Oncopeltus*). *Proc. Fourth Int. Cong. Biometeorol., New Brunswick, N. J. 1966*, (In press).

DINGLE, H., 1967b. Life history and population consequences of density, photoperiod, and temperature in a migrant insect, the milkweed bug *Oncopeltus*. *Amer. Natur.* (In press).

EYLES, A. C., 1963. Fecundity and oviposition rhythms in *Nysius huttoni* White (Heteroptera: Lygaeidae). *New Zealand J. Sci.*, **6**: 186–207.

FEIR, D., AND S. D. BECK, 1963. Feeding behavior of the large milkweed bug, *Oncopeltus fasciatus*. *Ann. Ent. Soc. Amer.*, **56**: 224–229.

GILLETT, J. D., 1962. Contributions to the oviposition-cycle by the individual mosquito in a population. *J. Insect Physiol.*, **8**: 665–689.

HADDOW, A. J., 1945. The mosquitoes of Bwanba County, Uganda. II. Biting activity with special reference to the influence of microclimate. *Bull. Ent. Res.*, **36**: 33–73.

HADDOW, A. J., 1956. Rhythmic biting activity of certain East African mosquitoes. *Nature*, **177**: 531–532.

HARCOURT, D. C., AND L. M. CASS, 1966. Photoperiodism and fecundity in *Plutella maculipennis* (Curt.). *Nature*, **210**: 217–218.

HARKER, J. E., 1964. The Physiology of Diurnal Rhythms. London, Cambridge University Press.

HUNTER, R. E, AND T. F. LEIGH, 1965. A laboratory life history of the consperse stinkbug, *Euschistus conspersus* (Hemiptera: Pentatomidae). *Ann. Ent. Soc. Amer.*, **58**: 648–649.

LARSEN, E. B., 1943. The importance of master factors for the activity of noctuids. *Entomol. Meddelelser*, **23**: 352–374.

LEES, A. D., 1955. The Physiology of Diapause in Arthropods. London, Cambridge University Press.

LEES, A. D., 1966. Photoperiodic timing mechanisms in insects. *Nature*, **210**: 986–989.

LEIGH, T. F., 1966. A reproductive diapause in *Lygus hesperus* Knight. *J. Econ. Ent.*, **59**: 1280–1281.

LEWIS, T., AND L. R. TAYLOR, 1965. Diurnal periodicity of flight by insects. *Trans. Roy. Ent. Soc. London*, **116**: 393–469.

LONG, D. B., 1958. Observations on oviposition in the wheat bulb fly, *Leptohylemyia coarctata* (Fall.). *Bull. Ent. Res.*, **49**: 355–366.

OUYE, M. T., R. S. GARCIA, H. M. GRAHAM AND D. F. MARTIN, 1965. Mating studies on the Pink Bollworm, *Pectinophora gossypiella* (Lepidoptera: Gelechiidae) based on presence of spermatophores. *Ann. Ent. Soc. Amer.*, **58**: 880–882.

PARKER, A. H., 1962. Studies on the diurnal rhythms of the housefly, *Musca domestica* L., in a dry tropical environment. *Acta Trop.*, **19**: 97–119.

PITTENDRIGH, C. S., 1960. Circadian rhythms and the circadian organization of living systems. *Cold Spring Harb. Symp. Quant. Biol.*, **25**: 289–308.

PITTENDRIGH, C. S., AND D. H. MINIS, 1964. The entrainment of circadian oscillations by light and their role as photoperiodic clocks. *Amer. Natur.*, **98**: 261–294.

SHOREY, H. H., 1964. Sex pheromones of noctuid moths. II. Mating behavior of *Trichoplusia ni* (Lepidoptera: Noctuidae) with special reference to the role of the sex pheromone. *Ann. Ent. Soc. Amer.*, **57**: 371–377.

SHOREY, H. H., AND L. K. GASTON, 1965. Sex pheromones of noctuid moths. V. Circadian rhythms of pheromone-responsiveness in males of *Autographa californica, Heliothis virescens, Spocloptera exiqua,* and *Trichoplusia ni* (Lepidoptera: Noctuidae). *Ann. Ent. Soc. Amer.*, **58**: 597–600.

WILLIAMS, C. B., 1935. The times of activity of certain nocturnal insects, chiefly Lepidoptera, as indicated by a light trap. *Trans. Roy. Ent. Soc.*, **85**: 523–555.

WILLIAMS, C. B., 1936. The influence of moonlight on the activity of certain nocturnal insects, particularly of the family Noctuidae, as indicated by a light trap. *Phil. Trans. Roy. Soc., B,* **226**: 357–389.