J. Insect Physiol. Vol. 31, No. 8, pp. 611–617, 1985
Printed in Great Britain.

0022-1910/85 $3.00 + 0.00

PHYSIOLOGICAL REGULATION OF LONG-TERM OVIPOSITION IN THE HOUSE CRICKET, *ACHETA DOMESTICUS*

MICHAEL P. MURTAUGH* and DAVID L. DENLINGER
Department of Entomology, The Ohio State University, 1735 Neil Avenue, Columbus, OH 43210, U.S.A.

(*Received* 15 *October* 1984; *revised* 2 *January* 1985)

Abstract—In house crickets [*Acheta domesticus* (L.)] a single mating early in adult life sufficed to induce egg laying for the duration of the life of a female. Female house crickets mated readily shortly after adult emergence but oviposition did not commence until about 12–14 days after emergence, even though females matured eggs by 7 days. The egg-laying factor associated with mating remained active during prolonged periods of substrate deprivation during which the female did not oviposit. If the spermatophore was removed prematurely shortly after a mating, the long-term, egg-laying response was truncated and was correlated with a dramatic decline in the fertility of eggs which were oviposited. The egg-laying stimulus appeared to act in the spermatheca, apparently through neural means, since denervation of the spermatheca abolished mating-induced oviposition. These results indicate that the oviposition factor found in the testes is able to act for long periods of time and has to be present continually in order to be effective. Furthermore, the long-term oviposition stimulus in the house cricket may be different from prostaglandin E2 which induces a prompt ovipositional response.

Key Word Index: *Acheta*, cricket, oviposition, spermatheca

INTRODUCTION

Reproductive success in insects requires that oviposition be regulated to assure fertilization and a favourable environment for egg development. Thus in a large number of insects, oviposition is stimulated by male-derived factors transferred with sperm at the time of mating. Oviposition stimuli range from the physical mating act itself to chemical activators secreted by male accessory glands and testes and sperm (see Engelmann, 1970 for review). In addition, reproductive success is maximized by stimuli which promote oviposition throughout the reproductive life of the female.

For these reasons we were interested in factors regulating oviposition in the house cricket, *Acheta domesticus*. Adults of this species survive for 60 days or more and are reproductively active continuously. To have adaptive value, therefore, factors that regulate oviposition in the house cricket must stimulate the laying of fertilized eggs for an extended period of time. Attention was also focused on house crickets because (1) the male accessory reproductive gland contains extremely high levels of cyclic GMP and it is transferred to the female during mating (Fallon and Wyatt, 1975a,b; Murtaugh *et al.*, 1985) and (2) males synthesize E and F prostaglandins in the testes and deliver prostaglandin synthetase to the female during mating (Destephano *et al.*, 1974; Destephano and Brady, 1977; Murtaugh and Denlinger, 1982). Prostaglandins are potent regulatory molecules in vertebrate reproduction (Karim, 1975) and prostaglandin E2 stimulates a burst of ovipositional activity in *Acheta domesticus* (Destephano *et al.*, 1982) and in *Teleogryllus commodus* (Loher, 1979; Loher *et al.*, 1981) when injected into unmated females.

The long-term regulation of oviposition in *Acheta domesticus* was not addressed in the studies described above. Because we were interested in the possibility that male-derived prostaglandins play a role in long-term control of egg laying, we needed detailed baseline data describing the ovipositional activity of female house crickets throughout their adult life and its regulation by the male. The findings presented here demonstrate that long periods of ovipositional activity extending more than 50 days are stimulated by a single mating, even though mating can precede the onset of egg laying by almost 2 weeks. The ovipositional signal appears to be received in the spermatheca since it must have intact neural connections in order for oviposition to ensue.

MATERIALS AND METHODS

Insect rearing

Acheta domesticus (L.) adults and mid- to late-instar nymphs were maintained in continuous culture at 25 ± 1°C with 12 h light and 12 h dark. Free-standing water and a finely ground diet consisting of 95% rodent lab chow (Ralston Purina, St Louis, MO) and 5% liver powder (U.S. Biochemicals, Cleveland, OH) were available *ad libitum* to all developmental stages. The diet was optimized for growth and reproduction (Clifford *et al.*, 1977; Tennis *et al.*, 1977, 1979). Shelter was provided by egg cartons and corrugated cardboard. Newly emerged nymphs were

*Address correspondence to: Dr Michael Murtaugh, Department of Pharmacology, University of Texas Medical School at Houston, P.O. Box 20708, Houston, TX 77225, U.S.A.

maintained at 30–32°C in sealed containers to increase humidity and accelerate the growth rate. Other conditions were the same as for adults. Under these rearing conditions nymphal development lasted 40–50 days.

Males and females of known age and mating history were obtained by culling a colony of developing nymphs daily. The sexes were then reared apart individually or in age-matched groups as needed.

Egg collection

In order to recover eggs quantitatively and reproducibly, females were kept in pint containers with screen bottoms resting on petri dishes filled with moist perlite (Terra-lite, W. R. Grace, Cambridge, MA). Females readily deposited eggs which were collected by filtration through aluminum window screen (which retained the perlite) into tap water. To hatch the eggs or determine fertility, eggs were placed on moist filter paper in a petri dish at 30–32°C. Humidity was maintained at 75% with saturated potassium chloride (Winston and Bates, 1960). Fertility was determined by the appearance of eyespots about 10 days after egg deposition and was used to confirm the successful transfer of sperm during mating. Hatching occurred within 13–14 days.

Surgical procedures

Removal, implantation and manipulation of the spermatheca was done through a ventral incision in the seventh sternite just anterior to the bursa copulatrix. In denervated-spermatheca experiments, the spermatheca was drawn out, attached nerves were severed, and the spermatheca was reinserted without damaging or cutting the spermathecal duct. Control animals received the same incision, the spermatheca was touched, and a piece of fat body was removed. For implantation studies, spermathecae were dissected from surface sterilized, mated females in sterile cricket saline (Fallon and Wyatt, 1975b) and placed in Grace's insect tissue culture medium (Grand Island Biological, Grand Island, NY) for not more than 2 h prior to implantation. Spermathecae were inserted through incisions in the seventh sternite. Control animals were given spermathecae taken from virgin animals.

RESULTS

Effect of mating on oviposition

Under the rearing conditions employed in these studies, vitellogenin uptake into eggs was detected 4 days after eclosion and at 7 days the ovaries were filled with mature, chorionated eggs. Since these animals were presumed to be competent to respond to an oviposition stimulus, 7-day old females were mated individually with males for 24 h then isolated in containers on moist perlite to monitor long-term oviposition. After mating, no eggs were laid for 5 days (Fig. 1). Beginning on day 14, though, eggs were deposited by all of the females at a rate averaging 25–30 eggs per day until the females were 60-days old. Egg production then declined but persisted beyond 70 days. In comparison, unmated females laid almost no eggs. If moist perlite was not available as an oviposition substrate, eggs were not laid by mated or unmated females (data not shown).

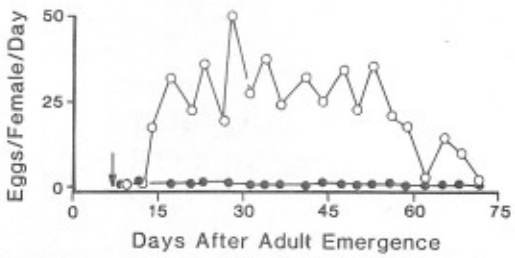

Fig. 1. Effect of mating on long-term oviposition in house crickets. Newly emerged adult females were provided with moist perlite for oviposition and maintained without mating (closed circles, $n = 8$) or were mated (arrow) on day 7 (open circles, $n = 8$). Data represent the mean number of eggs laid per female per day and were obtained by counting eggs collected at 2–3-day intervals.

Figure 1 also illustrates the temporal variability in ovipositional activity. The data presented are means derived from eggs laid by eight females and collected at 2–3 day intervals. Nevertheless, the graph still fluctuates markedly. It also indicated that egg-laying data needs to be collected from large numbers of individuals over long periods in order to yield reliable estimates of long-term ovipositional behaviour.

Since the delay between mating and oviposition observed in Fig. 1 was not expected we examined the relationship between female receptivity to mating and the onset of egg laying. One-day old females did not mate, but females only 2-days old were already receptive to males and about 50% accepted spermatophores (Fig. 2A). After 5 days of adulthood,

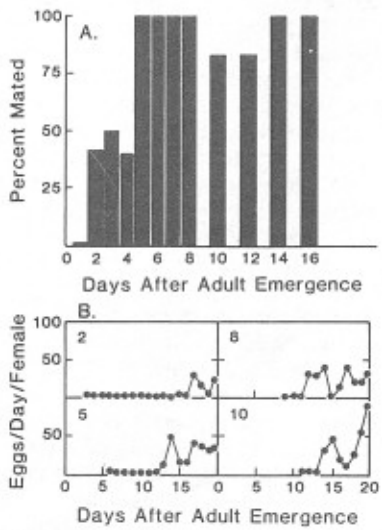

Fig. 2. Effect of age on mating receptively and the onset of oviposition in young female house crickets. Females were collected and isolated individually within 24 h of adulthood. A. Females from 1–16 days old were given mature males for 1 day then maintained in isolation on moist perlite until 20 days of age. Mating success was determined by the presence or absence of sperm in the spermatheca. Five to seven females were used for each determination. B. Females which mated successfully at the age of 2 days, 5 days, 8 days or 10 days, as indicated in each quadrant, were maintained on moist perlite. Eggs were collected daily until the age of 20 days. Data represent the mean number of eggs laid per female per day by 3 (2 days), 6 (5 and 8 days), or 5 (10 days) mated females.

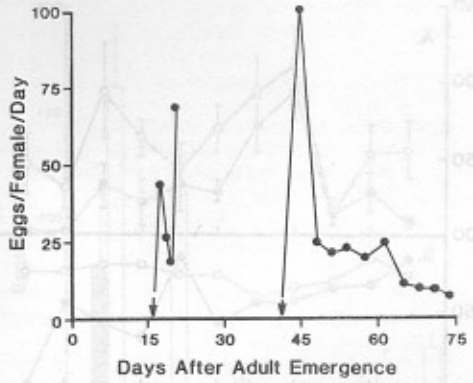

Fig. 3. Effect of age on the onset and duration of oviposition in mature females. Sixteen-day old or 42-day old females were mated with mature males (arrows) and provided with moist perlite. Eggs were collected as shown (closed circles). Data are means obtained from 16 (mated at 16 days) and 8 (mated at 42 days) females.

females mated within 24 h in nearly all cases (Fig. 2A). The egg-laying patterns of mated females depicted in Fig. 2A were followed to 20 days of age. Four groups are presented in Fig. 2B. In all age groups oviposition was delayed until the animals were about 13–14 days old. Females mated on day 2 did not lay eggs until day 17, an interval of 15 days between receptivity to mating and onset of oviposition. Mating on day 10 still failed to promote egg laying for 4 days, until day 14. The delay between mating receptivity and the onset of egg laying was apparent only in young females. Older animals responded differently after mating, showing no lag as they commenced oviposition within 24 h. As shown in Fig. 3, females mated at 16 or 42 days (Fig. 3, arrows) laid eggs within 24 h and continued to oviposit for several weeks.

The number of times a female mated was not determined in the preceding experiments. It was possible that the intensity of the oviposition stimulus was proportional to the number of matings (Sakaluk and Cade, 1982) and that unequal numbers of matings contributed to the observed fluctuations in egg production. Therefore we determined the effect of a second mating on oviposition. Mating was documented by observing the transfer and attachment of a spermatophore to the bursa copulatrix. All the matings were successful, based on subsequent oviposition of fertile eggs. For the second mating, females were given a different male and spermatophore attachment was again verified. Females were isolated individually and oviposition was monitored for 20 days. No difference in the number of eggs laid was observed between females mated once or twice. The egg-laying patterns of the two groups, representing 33 individuals, are virtually identical (Fig. 4). The data for females mated twice were offset slightly to see the standard error bars better. The results indicated that a single mating is sufficient to fully stimulate long-term oviposition. A stimulatory effect of a second mating was only observed in very old females in whom egg production had declined to only 1–5 eggs per day. Figure 5 shows that a second mating temporarily reversed the gradual decline in

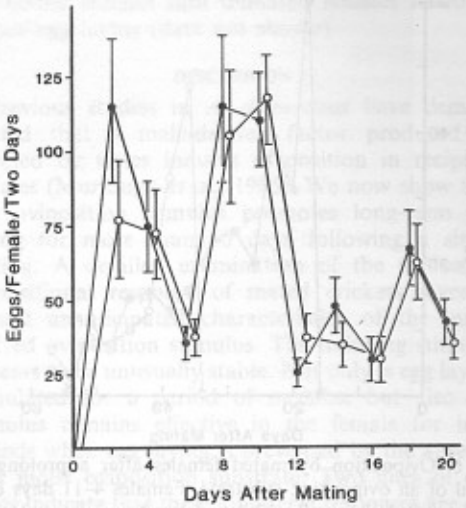

Fig. 4. Lack of effect of a second mating on long-term oviposition by female house crickets. Females 10–13 days old were mated once or twice with mature males. Matings were confirmed by noting the transfer and attachment of a spermatophore to the bursa copulatrix. After mating females were maintained individually on moist perlite and eggs were collected at 2-day intervals. Data represent the mean ± SE of females mated once (closed circles, $n = 16$) or twice (open circles, $n = 17$). The open circles are offset slightly to the right to simplify the presentation of the data.

egg production in these females and induced an immediate large burst of egg laying (61.4 ± 24.1 eggs/female/day, $\bar{X} \pm SE$) in 60-day old animals. Thus aged animals were still responsive to an oviposition stimulus. It was not clear whether this was a temporary or long-term effect.

Retention of the oviposition stimulus in the absence of an egg-laying substrate

Since in nature an oviposition substrate is not always available at the time of mating, we allowed young females to mate and then investigated the effect of a protracted deprivation of an oviposition

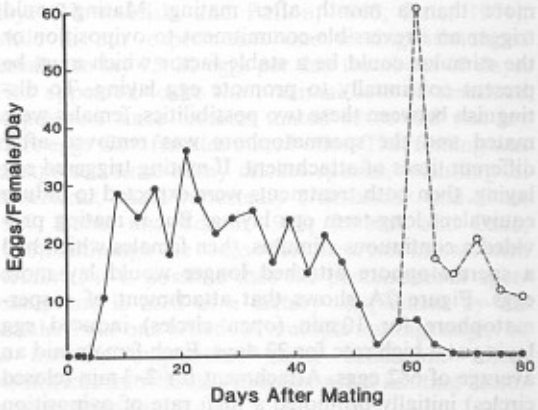

Fig. 5. Stimulatory effect of a second mating on oviposition in aged females. Twenty-five females age 4–11 days were mated to mature males and transferred in groups of 1–3 to moist perlite. Egg production was monitored as indicated (closed circles). Fifty-eight days after mating, 8 females were mated again. Oviposition by this group is shown by the open circles.

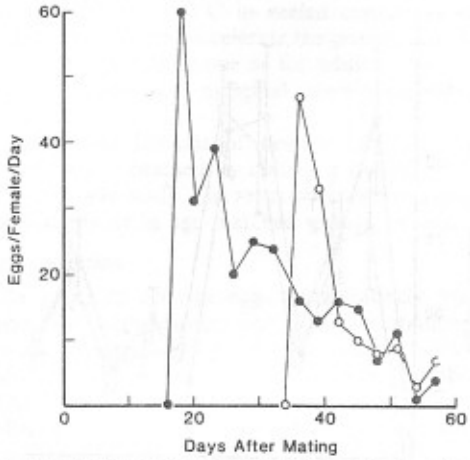

Fig. 6. Oviposition by mated females after a prolonged denial of an ovipositior substrate. Females 4–11 days old were mated then kept for 17 days (closed circles, $n = 16$) or 34 days (open circles, $n = 14$) before being placed on moist perlite. Eggs were collected at 2–3-day intervals.

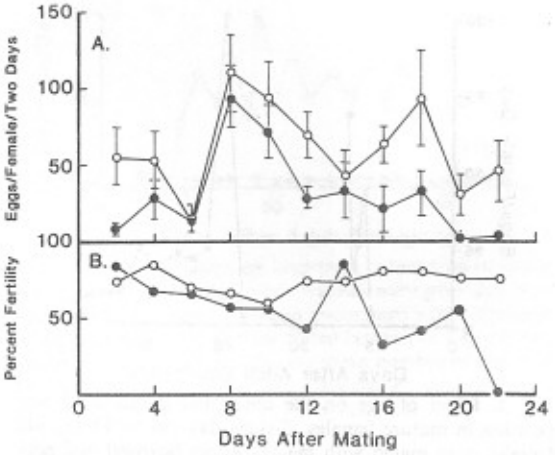

Fig. 7. Effect of time of spermatophore attachment on long-term oviposition and egg fertility. Females 13–14 days old were mated to mature males. Spermatophores were removed after 2–3 min (closed circles, $n = 8$ females) or after 10 min (open circles, $n = 10$ females). Females were maintained individually on moist perlite and eggs were collected at 2-day intevals. A. Mean $\pm$ SE of the number of eggs laid per female per 2 days. B. All of the eggs laid (by the crickets shown in panel A) were collected and incubated to determine fertility. Data shown are means at each time point. The standard errors of the means averaged 11% for the open circles and 12% for the closed circles.

substrate on egg laying behaviour. As shown in Fig. 6, 30 females 4–11 days old were allowed to mate then were deprived of moist perlite for 16 (closed circles) or 34 (open circles) days after mating. Immediately upon being placed on a moist substrate both groups initiated a burst of ovipositional activity, laying up to 60 eggs/female/day, and continued to oviposit until the experiment was terminated 57 days after mating. We do not believe that the intial burst of ovipositional activity nor the prolonged egg laying response resulted simply from a moist substrate stimulus. Unmated females of this species did not lay eggs at a significant rate at any time in their lives, even when maintained continuously on a moist oviposition substrate (Fig. 1).

Does mating trigger a response in females or provide a continuous stimulus?

The preceding experiment raised two interesting possibilities for how oviposition could be stimulated more than a month after mating. Mating could trigger an irreversible commitment to oviposition or the stimulus could be a stable factor which must be present continually to promote egg laying. To distinguish between these two possibilities, females were mated and the spermatophore was removed after different times of attachment. If mating triggered egg laying, then both treatments were expected to induce equivalent long-term egg laying. But if mating provided a continuous stimulus, then females which had a spermatophore attached longer would lay more eggs. Figure 7A shows that attachment of a spermatophore for 10 min (open circles) induced egg laying at a high rate for 22 days. Each female laid an average of 682 eggs. Attachment for 2–3 min (closed circles) initially promoted a high rate of oviposition which declined steadily after 8 days to near 0. In this group females laid only 339 eggs each.

When the fertility of the eggs in Fig. 7A was determined it was observed that egg fertility remained constant in the 10-min group at about 75% until the experiment was terminated (Fig. 7B, open circles). By contrast, in the 2–3 min spermatophore attachment group, fertility was at or near 75% for about 14 days but then decreased dramatically. Thus, a brief period of spermatophore attachment was associated with lack of long-term fertility as well as decreased egg laying potential. These observations suggested that the inability to fertilize eggs, perhaps due to a lack of sperm, was correlated with a marked reduction in ovipositional activity.

Role of the spermatheca in the stimulation of oviposition

After the spermatophore is attached to the female during mating, it is evacuated. The insemination mixture passes through the bursa copulatrix and the spermathecal duct to the spermatheca, where it is stored. The oviposition stimulus is known to be in the insemination mixture since castrated males cannot induce oviposition even though they transfer spermatophores (Murtaugh *et al.*, 1985). Therefore the spermatheca was the most likely tissue to receive the oviposition stimulus. To test this possibility the spermatheca was removed surgically before mating. Figure 8 shows that females which were sham-operated 15 days before mating displayed a prompt and sustained ovipositional response. Ablation of the spermatheca, however, blocked long-term egg laying. Only a brief egg-laying burst was observed in the first 24 h. Afterwards, the number of eggs deposited was identical to sham-operated, unmated females (Fig. 8). The surgery did not interfere with the primary ovipositional mechanism or its regulation since some eggs were laid.

To determine if the oviposition stimulus in the spermatheca acted neurally or hormonally to induce egg laying, females were surgically altered to make an

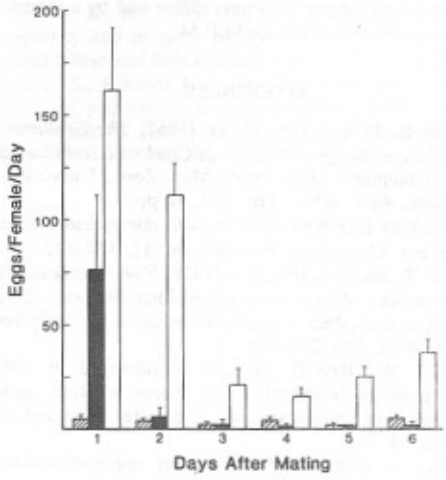

Fig. 8. Effect of removal of the spermatheca on egg deposition by female house crickets. Spermathecae were extirpated from 12–13-day old females and the females were mated 15 days later. After mating females were isolated on moist perlite and eggs were collected daily for 6 days. Data represent the mean ± SE of the number of eggs laid per female per day from sham-operated, unmated females (cross-hatched bars, $n = 11$), mated females lacking spermathecae (black bars, $n = 12$) and sham-operated, mated females (open bars, $n = 12$).

intact spermatheca which filled with sperm on mating but from which the nerves had been detached. The data shown in Fig. 9 clearly demonstrate that simple denervation of the spermatheca completely inhibited oviposition even though visual inspection at the end of the experiment showed that the spermathecae were filled with sperm. Further evidence that the signal was transmitted neurally rather than hormonally in the female was that implantation of spermathecae from

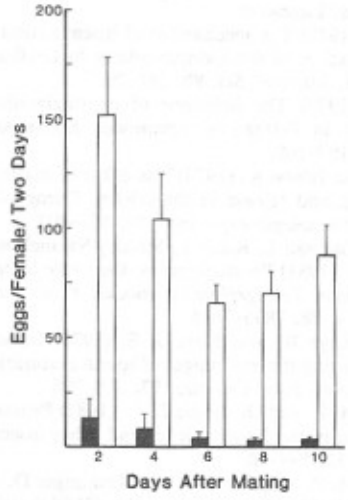

Fig. 9. Denervation of the spermatheca blocks oviposition in female house crickets. Spermathecae from 2–5-day old females were denervated. Twelve days later, females were mated and eggs were collected at 2-day intervals. Data shown are the mean ± SE from females with denervated spermathecae (black bars, $n = 9$) and sham-operated females (open bars, $n = 14$).

just-mated females into unmated females failed to induce egg laying (data not shown).

DISCUSSION

Previous studies in *A. domesticus* have demonstrated that a male-derived factor produced or secreted by testes induces oviposition in recipient females (Murtaugh *et al.*, 1985). We now show that this oviposition stimulus promotes long-term egg laying for more than 60 days following a single mating. A detailed examination of the prolonged ovipositional response of mated crickets revealed several unanticipated characteristics of the male-derived oviposition stimulus. The inducing stimulus appears to be unusually stable. Not only is egg laying stimulated for a period of months, but also the stimulus remains effective in the female for long periods when egg laying is prevented by the absence of a moist oviposition substrate. Two lines of evidence indicate that these long-term responses are due to the persistence of a stable factor from the male (or induced quantitatively in the female), and not to an irreversible switching on of a female ovipositional programme. Since a second mating stimulates another burst of egg-laying activity in aged females, the decline in fecundity is probably due to the degradation or depletion of the oviposition stimulus. In addition, in young females the number of eggs laid is correlated with time of spermatophore attachment. A spermatophore normally remains attached to the female for about 30 min (Sakaluk and Cade, 1980) which is sufficient to allow for complete evacuation of the insemination mixture (Khalifa, 1949). Removal of the spermatophore shortly after attachment, within 2–3 min, did not prevent the initial induction of oviposition, but resulted in a lower oviposition rate after approx. 8 days. The decline in egg laying from 8–20 days after mating was also associated with decreased fertility, presumably due to a lack of sperm.

The results also indicate that the insemination contents from a single spermatophore are sufficient to stimulate female oviposition in natural populations maximally. Adult crickets usually survive less than 40 days (Nowosielski and Patton, 1965; Bate, 1971), while in our experiments one mating stimulated females to lay 25–30 eggs per day for about 40 days. This appeared to be the maximal rate of sustained oviposition since females mated twice did not lay more eggs than females mated once. This finding was unexpected since many cricket species, including *A. domesticus*, mate repeatedly (Alexander and Otte, 1967; Loher and Edson, 1973; Sakaluk and Cade, 1980). Although the reason for this is not known with certainty, it is possible that the proteinaceous spermatophore is used as a dietary supplement by the female. Thus one benefit of multiple matings might be to increase oviposition under conditions where insufficient nutritional resources are a limiting factor in reproduction.

Recently emerged females become receptive to and mate with males long before they initiate egg laying. Females accept spermatophores 2 days after becoming adults (Fig. 2), and they contain mature, fully chorionated eggs after 6 days (Bradley and Edwards, 1978 and unpublished observations). Even

though they are mated and have received the oviposition stimulus, oviposition does not commerce until approx. day 14. These observations indicate that the oviposition stimulus enters the female in a latent form and must be activated by the female. Activation could be achieved by biochemical modification or through developmental maturation. The final stages of sperm maturation in *A. domesticus*, for example, occur in the spermatheca (McMaster-Kaye and Kaye, 1976). The ability of females to activate the oviposition stimulus appears to be age-dependent. Females that are older than 15 days initiate ovipositional activity within 24 h of mating, whereas younger females do not oviposit.

Reception and processing of the oviposition stimulus takes place in the spermatheca. Removal of the spermatheca blocks long-term oviposition but does not prevent an immediate, short-term egg laying response. Denervation studies further suggest that the oviposition signal that is transmitted from the spermatheca is neural, not hormonal. Neural regulation of oviposition emanating from the spermatheca is also found in *Cimex* (Davis, 1965), while in *Rhodnius* hormonal regulation of oviposition from the spermatheca has been inferred (Davey, 1965).

The nature of the oviposition stimulus was not determined in the present studies. However, pharmacological and biochemical studies show that prostaglandins induce a short-term ovipositional episode in *A. domesticus* and *T. commodus* (Loher, 1979; Loher *et al.*, 1981; Destephano *et al.*, 1982). Prostaglandins of the E and F series and their key biosynthetic enzymes have been identified in testes, in spermatophores and in the spermathecae of mated females (Destephano *et al.*, 1974; Destephano and Brady, 1977; Loher *et al.*, 1981; Murtaugh and Denlinger, 1982). Although the role of prostaglandin E2 in short-term oviposition in crickets is well described, the effects of prostaglandins on long-term oviposition are less dramatic. The only evidence so far showed that the egg laying activity of unmated *T. commodus* females between 3 and 13 days after injection with prostaglandin E2 was the same as uninjected controls (Loher, 1979).

Alternatively, the long-term egg laying stimulus might be a factor associated with sperm. Sperm are maintained in a viable state for long periods in the spermatheca in the presence or absence of ovipositional activity. Using egg fertility as an index of sperm availability, the depletion of sperm from the spermatheca is correlated with a decline in egg laying activity. In addition the age-related delay in the onset of oviposition may be related to a requirement for the final stages of sperm maturation, which occur in the spermatheca (McMaster-Kaye and Kaye, 1976). In any event, the persistence and stability of the egg laying response induced in mated females by the contents of a single spermatophore indicate that the stimulating factor exerts a powerful and prolonged influence on female reproductive behaviour.

Acknowledgements—We thank Ms Mary Lou Cervenak for technical assistance. This research was supported in part by the Science and Education Administration of the U.S. Department of Agriculture under grant No. 8300051 from the Competitive Research Grants Office and by a Sigma Xi Grant-in-Aid of Research to M.P.M.

REFERENCES

Alexander R. D. and Otte D. D. (1967) *The Evolution of Genitalia and Mating Behavior in Crickets (Gryllidae) and other Orthoptera*. Misc. Publ., Mus. Zool., University of Michigan, Ann Arbor. No. 133, 62 pp.

Bate J. (1971) Life history of *Acheta domesticus* (Insecta; Othoptera, Gryllidae). *Pedobiologia*. **11,** 159–172.

Bradley J. T. and Edwards J. S. (1978) Yolk proteins in the house cricket, *Acheta domesticus*: identification, characterization, and effect of ovariectomy upon their synthesis. *J. exp. Zool.* **204,** 239–248.

Clifford C. W., Roe R. M. and Woodring J. P. (1977) Rearing methods for obtaining house crickets, *Acheta domesticus*, of known age, sex, and instar. *Ann. ent. Soc. Am.* **70,** 69–74.

Davey K. G. (1965) Copulation and egg production in *Rhodnius prolixus*: the role of the spermathecae. *J. exp. Biol.* **42,** 373–378.

Davis N. T. (1965) Studies of the reproductive physiology of Cimicidae (Hemiptera). III. The seminal stimulus. *J. Insect Physiol.* **11,** 1199–1211.

Destephano D. B. and Brady U. E. (1977) Prostaglandin and prostaglandin synthetase in the cricket, *Acheta domesticus*. *J. Insect Physiol.* **23,** 905–911.

Destephano D. B., Brady U. E. and Farr C. A. (1982) Factors influencing oviposition behavior in the cricket, *Acheta domesticus*. *Ann. ent. Soc. Am.* **75,** 111–114.

Destephano D. B., Brady U. E. and Lovins R. E. (1974) Synthesis of prostaglandin by reproductive tissue of the male house cricket, *Acheta domesticus*. *Prostaglandins.* **6,** 71–79.

Engelmann F. (1970) *The Physiology of Insect Reproduction*. Pergamon Press, Oxford.

Fallon A. M. and Wyatt G. R. (1975a) An improved assay for cyclic GMP using an insect binding protein. *Analyt. Biochem.* **63,** 614–619.

Fallon A. M. and Wyatt G. R. (1975b) Cyclic guanosine 3′,5′-monophosphate. High levels in the male accessory gland of *Acheta domesticus* and related crickets. *Biochim. biophys. Acta.* **411,** 173–185.

Karim S. M. M. ed. (1975) *Prostaglandins and Reproduction*. MTP Press, Lancaster.

Khalifa A. (1949) The mechanism of insemination and the mode of action of the spermatophore in *Gryllus domesticus*. *Q. J. Microsc. Sci.* **90,** 281–292.

Loher W. (1979) The influence of prostaglandin E2 on oviposition in *Teleogryllus commodus*. *Entomologia exp. Appl.* **25,** 107–109.

Loher W. and Edson K. (1973) The effect of mating on egg production and release in the cricket *Teleogryllus commodus*. *Entomologia exp. Appl.* **16,** 483–490.

Loher W., Ganjian I., Kubo I., Stanley-Samuelson D. and Tobe S. S. (1981) Prostaglandins: their role in egg-laying of the cricket *Teleogryllus commodus*. *Proc. natn. Acad. Sci., U.S.A.* **78,** 7835–7838.

McMaster-Kaye R. and Kaye J. S. (1976) Basic protein changes during the final stages of sperm maturation in the house cricket. *Expl Cell Res.* **97,** 378–386.

Murtaugh M. P. and Denlinger D. L. (1982) Prostaglandins E and F2α in the house cricket and other insects. *Insect Biochem.* **12,** 599–603.

Murtaugh M. P., Kapoor C. L. and Denlinger D. L. (1985) Extracellular localization of cyclic GMP in the house cricket male accessory reproductive gland and its fate in mating. *J. exp. Zool.* **233,** 413–423.

Nowosielski J. W. and Patton R. L. (1965) Life-tables for the house cricket, *Acheta domesticus* L., and the effect of intra-specific factors on longevity. *J. Insect Physiol.* **11,** 201–209.

Sakaluk S. K. and Cade W. M. (1980) Female mating frequency and progeny production in singly and doubly mated house and field crickets. *Can. J. Zool.* **58,** 404–411.

Tennis P. S., Koonce J. F. and Teraguchi M. (1977) The effects of population density and food surface area on body weight of *Acheta domesticus* (L.) (Orthoptera: Gryllidae). *Can. J. Zool.* **55,** 2004–2010.

Tennis P. S., Koonce J. F. and Teraguchi M. (1979) Studies on food size as a selection pressure on body size. I. Effects of food size on fitness of two size strains of *Acheta domesticus* L. *Evolution.* **33,** 95–103.

Winston P. W. and Bates D. H. (1960) Saturated solutions for the control of humidity in biological research. *Ecology* **41,** 232–237.