All observations to date are consistent with the view that the ureilite diamonds were formed by shock during the breakup of the meteorite parent body (*10*). A detailed discussion of this point will be given elsewhere (*8*).

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10. I thank the Materials Research and Development Section, Spacecraft Systems Branch, NASA, for lending equipment for this investigation. I am on active duty with the U.S. Army at NASA.

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Hypersexual Activity Induced in Females of the Cockroach Nauphoeta cinerea

Abstract. Corpora allata control mating in females principally by inducing feeding on the tergum of a displaying male. Mating induces an inhibitory nervous mechanism, the seat of which is posterior to the last abdominal ganglion, causing an immediate loss of receptivity by suppressing feeding behavior. After parturition, females may again be receptive. Transection of the nerve cord before or just after mating causes excessive sexual behavior.

The basic features of precopulatory behavior of *Nauphoeta cinerea* (Olivier) are raising of the wings by the male and feeding by the female on the exposed tergites of the male (*1, 2*). Females less than 3 days old do not mate, although they are courted by males. Eight percent ($N = 50$) will mate on the third day, 46 percent ($N = 50$) on the fourth, 66 percent ($N = 50$) on the fifth, and 96 percent ($N = 50$) on the sixth. More than 95 percent ($N = 600$) of virgin females older than 6 days remain receptive until they oviposit (24 to 35 days or more) (*3*). After females mate they become unreceptive during preoviposition and pregnancy periods. After parturition about 70 percent ($N = 106$) mate again (*4*).

Engelmann suggested that the corpus allatum hormone conditions females of *Leucophaea maderae* (Fabricius) to respond to the male (*5*) but he did not observe the behavior of males toward allatectomized females (in *6*). Barth (*6*) stated that the corpora allata regulate mating behavior of *Byrsotria fumigata* (Guérin) by controlling female sex pheromone production. Male display by *Nauphoeta* is evoked readily, even by females that are unreceptive. The sex pheromone, if it exists, appears to be a nonvolatile substance on the surface of the female and the male apparently recognizes her by contact chemoreception (*2*), a mechanism similar to that in *Blattella germanica* (Linnaeus) (*7*).

Receptivity of females of *Nauphoeta* can be correlated with activity of the corpora allata. In females less than one day after emergence, the oöcytes are 0.86 ± 0.03 mm long ($N = 5$) and do not contain yolk. Oöcytes of females that mated when they were 3, 4, and 5 days old were 1.02 ± 0.04 mm ($N = 4$), 1.03 ± 0.01 mm ($N = 23$), and 1.16 ± 0.02 mm ($N = 15$) long, respectively. Oöcytes 1 mm long usually contain yolk. Although yolk in the oöcytes may not be apparent in some of the youngest females that mate, the occurrence of colleterial gland secretion indicates activity of the corpora allata; this secretion is a more sensitive indicator of the presence of corpus allatum hormone than is yolk in the oöcytes (*8*). Females become receptive when there is a very low concentration of hormone and remain receptive, unless mated, until the oöcytes mature and are oviposited (*9*).

After a female oviposits, the basal oöcytes are about 0.51 mm long. These increase in length until parturition, when they are usually from 0.75 to 0.92 mm long. The corpora allata become inactive at oviposition and usually remain inhibited during pregnancy (*10*) probably because of a nervous stimulus resulting from the stretched uterus. Removal of the oötheca from the uterus results in premature resumption of activity of the corpora allata. The time required to reactivate the corpora allata varies with the age of the oötheca at the time it is removed. The younger the oötheca, the longer it takes for the corpora allata to become active again (*11, 12*). If the receptivity of the female is controlled by the corpora allata, then females in different stages of pregnancy whose oöthecae have been removed should subsequently become receptive at different times, depending upon when their corpora allata are reactivated.

Table 1. Multiple matings resulting from nerve cord transection in 15 females of *Nauphoeta*. The ten controls were with males for 88 hours.

Spermatophores recovered		No. and site of insertion of spermatophores		
Total	Per ♀	Bursa and vestibule	Body cavity	Uterus
		Nerve cord cut (15 ♀)		
93	3 to 11	38*	45	10
		Unoperated controls (10 ♀)		
10	1	10†	0	0

* Only one large spermatophore can normally be inserted in the bursa at one time. However, sometimes two may be forced into the bursa; others may be stuck to the spermatophore that was inserted first or they may be deposited in the vestibule. One spermatophore in the bursa of each female represents the first normal mating prior to nerve cord transection. † In bursa only.

To test this hypothesis pregnant females were taken from cultures and their oöthecae were removed. The females were divided into two groups on the basis of the size of their eggs (*13*). Those females whose eggs in the oötheca were 4.5 to 5.3 mm long were considered to be in "late" stages of gestation and females whose eggs were 3.5 to 4.0 mm long were considered to be in "early" stages of gestation. A third group of females with intact oöthecae were used for controls. All females were exposed to an equal number of males for 1 hour daily for 23 days. Females that mated were removed and their oöcytes were measured, or the colleterial glands examined for secretion.

The results are shown in Fig. 1. Females that were in late pregnancy when their oöthecae were removed began to mate earlier than females that

Table 2. Effect of nerve cord transection at two places, on receptivity of females of *Nauphoeta*; the ratio of female to male was 3:1, the time allowed was 20 to 22 hours.

Treatment	Ratio of No. mating more than once to No. used	No. of spermatophores recovered per ♀ (Mean ± S.E.)*
Anterior to last abdominal ganglion		
Virgins	13/19 (68%)	3.5 ± 0.5
Mated	16/20 (80%)	4.5 ± 0.4†
All nerves arising from last abdominal ganglio		
Virgins	9/11 (82%)	4.8 ± 0.5
Mated	20/28 (71%)	4.1 ± 0.4†
Controls (mated)		
Unoperated	0/10	
Sham operated‡	0/10	

* Based only on females that mated more than once. † One of the spermatophores in each of these females represents the first mating before nerve cord transection. ‡ Incisions made between third and fourth sternites and some fat or tracheal tissue removed.

were in the earlier stages of pregnancy. All oöcytes were about the same length when the females mated. They averaged 0.96 ± 0.04 mm for the early pregnancy group and 1.03 ± 0.05 for the late pregnancy group. The females mated again when their oöcytes had resumed growth and contained yolk, or if no yolk was noticeable when secretion was present in the colleterial glands. The oöcytes of 56 females that mated within a few hours to 5 days after parturition averaged 1.07 ± 0.02 mm long.

Since copulation is principally initiated by the feeding of females on tergites of displaying males, it is apparent that a very low titer of corpus allatum hormone controls mating by inducing this receptive feeding behavior.

The following experiments were done to determine the time of suppression of female receptivity. Mating of 40 females was manually interrupted by pulling pairs apart after 5 to 14 minutes of copulation, but prior to transfer of spermatophore. In subsequent mating trials, 35 females mated during the first trial, and three others during a second trial (*14*). Mating of 18 females was interrupted after the spermatophore was transferred but before the female was released by the male. The spermatophore was then easily removed because it was not cemented in the bursa. Fourteen females mated in four trials. Thirty-three females were allowed to complete copulation and their spermatophores were removed within 1 to 2 minutes after the pairs had separated but before any sperm had entered the spermathecae. Only two females mated in seven trials. When mating was completed, the spermatophore was cemented tightly in the bursa. Loss of receptivity occurred just before the male released the female, when the spermatophore was firmly inserted or cemented into the bursa. Females that were separated prior to this time remained receptive. Some females in copula fed on the tergites of other males that courted them. Unlike *Drosophila* (*15*), the receptivity of *Nauphoeta* females apparently is uninfluenced by sperm in the spermathecae.

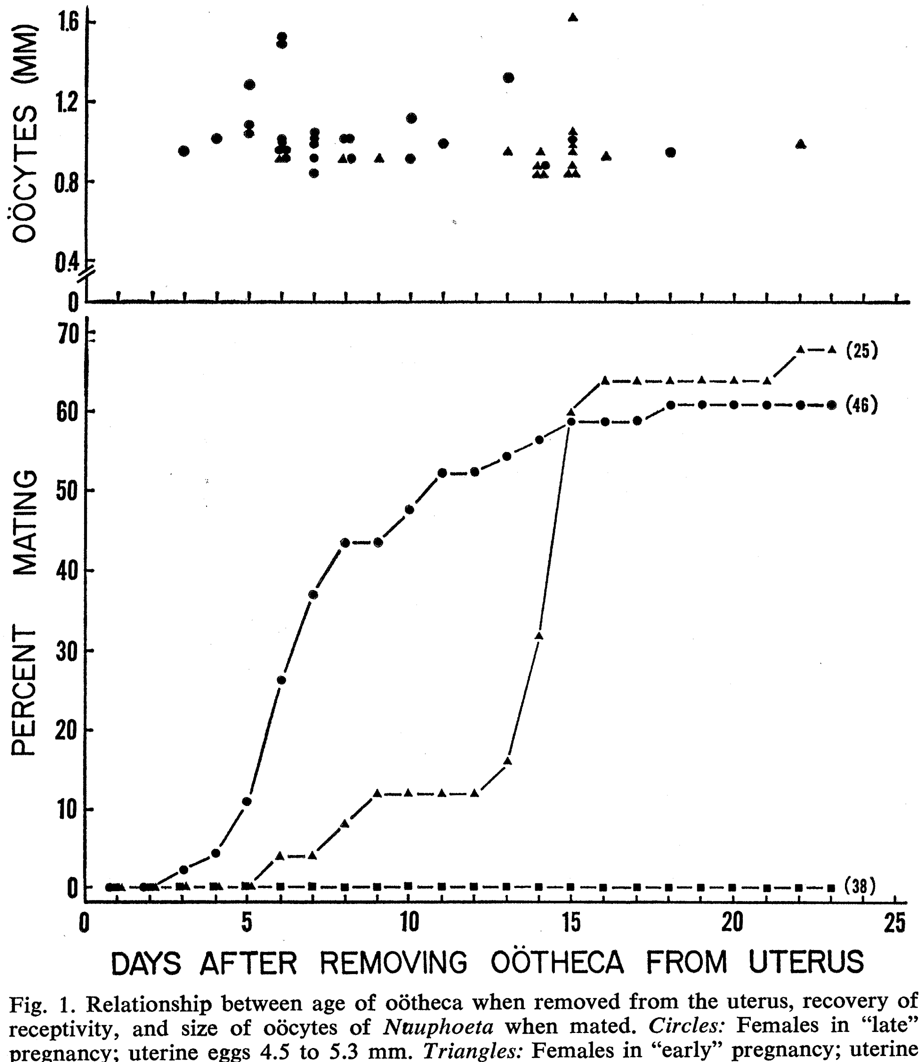

Fig. 1. Relationship between age of oötheca when removed from the uterus, recovery of receptivity, and size of oöcytes of *Nauphoeta* when mated. *Circles:* Females in "late" pregnancy; uterine eggs 4.5 to 5.3 mm. *Triangles:* Females in "early" pregnancy; uterine eggs 3.5 to 4.0 mm. *Squares:* Females with oötheca left in uterus. The percentage mating is expressed as accumulative data. Numbers in parentheses represent the number of insects used.

The rapid loss of receptiveness after mating suggested that a nervous mechanism was involved. The nerve cords of 35 females were transected less than 4 hours after mating and they were tested for 2-hour periods on 3 days following the operations; pairs that mated were removed from the container. Five females did not mate again, 15 mated twice, 6 mated three times, and 9 mated four times (*16*). Females with transected nerve cords had difficulty in mating and copulation was often unsuccessful. A female would feed on the tergites of the male but the male could not grasp her properly and they would stay joined for only a few seconds. Nineteen unoperated mated females did not mate again.

The nerve cords of 15 mated females were transected within one hour after mating. These females were exposed, together with ten mated controls, to 50 males. Groups of five operated females were sacrificed and examined for spermatophores after being with males for 42, 65, and 88 hours, respectively; some of the males were replaced during the experiment. The results are shown in Table 1. All of the operated females mated more than once ($\bar{x}$ = 6.2 ± 0.6 matings). Most supernumerary spermatophores were inserted in the body cavity among the oöcytes of the right ovary (*17*). Transection of the nerve cord in receptive virgins also resulted in excessive copulations (Table 2).

Insertion of the spermatophore into the bursa during mating prior to the release of the female, resulted in an inhibitory input in the female which suppressed sexual receptivity by inhibiting female feeding behavior on the tergites of the courting male. This inhibitory effect originates in an area posterior to the last abdominal ganglion, because transecting the cord above this ganglion, or cutting all nerves arising from the ganglion induces excessive sexual behavior (Table 2) (*18*).

Note added in proof. Transecting the nerve cords of females of *Leucophaea maderae* before and just after mating also results in multiple matings.

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3. These females, when tested for receptivity, were exposed to males in metal containers, 12 by 18 by 7 inches, that were covered to exclude most of the light. Males 10 or more days old, at which time they usually show courting behavior, were used (2♂ : 1♀). Although receptive females usually mate within a few minutes under these conditions, each test period lasted 1 hour.
4. A female mated when 6 days old would not mate again for about 60 days (approximately 10 days to oviposition following copulation plus about 50 days of gestation; these periods vary with temperature).
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7. L. M. Roth and E. R. Willis, *Am. Midland Naturalist* **47**, 66 (1952).
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9. Engelmann stated that females of *Leucophaea* mate only if the titer of corpus allatum hormone is low and once the hormone concentration increases the females do not mate (*5*). We have found, to the contrary, that virgin *Leucophaea* will mate after their oöcytes have grown markedly in size, which may be indicative of a high concentration of hormone (*11*).
10. The oöcytes of most *Nauphoeta* females do not contain yolk when parturition occurs, but in some individuals inhibition of the corpora allata apparently ceases prior to parturition and yolk is present in the oöcytes when the female gives birth (*11*).
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14. One trial consisted of exposing females to males (2:1) for 1 hour once a day.
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16. During one of the trials ten females that had mated were again exposed to males immediately and nine of them mated again.
17. The abnormal insertion of the spermatophore into females with transected nerve cords has been reported for *Leucophaea* (*11*).
18. This study was made while I was a postdoctoral fellow at Harvard University.

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Aversive Training: Long-Term Effects

Abstract. Three years ago a tone ending in unavoidable electric shock was periodically presented to pigeons while they pecked a key for food. When pecking was disrupted by tone, shock was disconnected and the training tone and tones of different frequencies were presented. At first all tones caused a reduction in the rate of pecking, but as testing proceeded the gradient narrowed. In our study, testing was resumed after a 2½-year interruption. Despite the interruption the tones still suppress behavior.

The study reported here was concerned with the retention of a conditioned emotional response. Such a response results from a training history in which a neutral stimulus has typically preceded an unavoidable noxious event. It can be detected by determining whether subsequent presentations of the stimulus cause a reduction in the rate of ongoing hunger-motivated responses (*1*).

In earlier work (*2*) we investigated the degree to which this reduction (conditioned suppression) was mediated by stimuli which were like, but not identical to, the stimulus that was used in the original training. This phenomenon, the stimulus generalization of conditioned suppression, commanded special attention because it represents one of the mechanisms by which aversive training can affect large segments of an organism's behavior (*3*). In order to examine it, a 48-second tone accompanied for the last 8 seconds by unavoidable electric shock was periodically presented to pigeons (maintained at 80 percent of their normal body weight) while they pecked a key for food. When pecking was completely disrupted by the 40 seconds of preshock tone, the use of shock was discontinued and tests for stimulus generalization were begun. In these test sessions, the tone used in training (1000 cy/sec) and tones of different frequencies (300, 450, 670, 1500, 2250, and 3400 cy/sec) were presented sequentially and in random order, without shock, at intervals of approximately 10 minutes. Each tone lasted 40 seconds, and all tones were equated for intensity (80 db sound pressure level relative to 2×10^{-4} dyne/cm^2). The entire series of seven tones was presented once per session, and sessions occurred every day.

Initially, the gradient of generalization was broad: all tones caused some degree of conditioned suppression. As testing proceeded, however, the gradient systematically narrowed until only the tone used in training produced substantial reductions in the rate of pecking. These results were of particular interest for a least two reasons. (i) They appeared to reflect the development of a discrimination without either previous or concurrent differential reinforcement. (ii) The extinction of conditioned suppression appeared to proceed at a very slow pace (*3*). In our study we sought to examine these effects further. In particular, we wished to determine how the gradient changes with the passage of time.

We used two of the surviving birds (Nos. 21 and 9) from the earlier experiments. In that work testing had been discontinued when the birds exhibited a fairly strong tendency to suppress pecking in response to the tone that had previously been paired with shock and a reduced tendency to suppress pecking in response to the other test tones. At the termination of the tests the birds were returned to their home loft, where they were kept for approximately 2½ years. Then, with no further aversive training, testing was continued—that is, the seven tones were presented sequentially and in random order (without shock) while the birds pecked a key for food. The experimental situation in these tests was identical with that in the previous work with these birds.

Figure 1 shows the results of these recent tests (solid lines) as well as the results of the tests that had been conducted more than 2 years earlier (dashed lines). Each gradient represents data averaged across four successive sessions. The top gradient for bird No. 9 represents the first block of sessions for that bird. The top gradient for bird No. 21 represents the second block of sessions for that bird (*4*). The remaining gradients, for both birds, represent successive blocks of sessions, in descend-

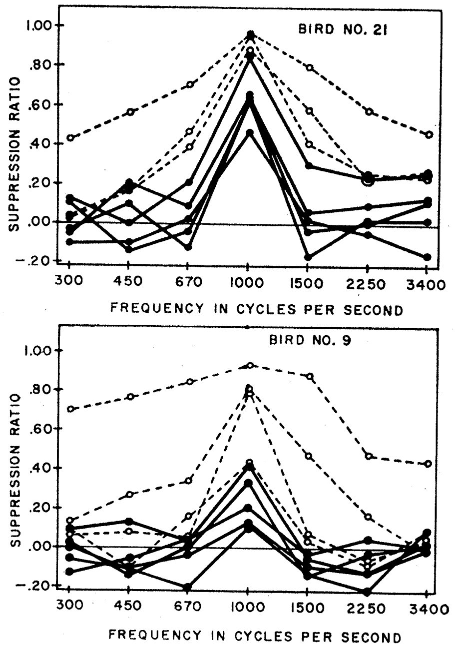

Fig. 1. Generalization gradients for birds Nos. 21 and 9. The suppression ratio equals (pre-tone R's − tone R's) / (pre-tone R's). The solid lines show the results of the sequence of tests reported here, whereas the dashed lines show results obtained more than 2 years previously. Each gradient represents data averaged across four successive sessions. The top gradient for bird No. 9 represents the first block of sessions for that bird. The top gradient for bird No. 21 represents the second block of sessions for that bird. The remaining gradients, for both birds, represent successive blocks of session, in descending order.