parent that the species of North American birds are well known, but that much work is still necessary in regard to subspecies. The congruence of curve with dots here is very good. It should be noted that with such a beloved group, we started in 1758 with a fair amount of knowledge. Even in the lower primates [Fig. 1*b* (*8*)], we note that a few species must still be unknown. The tree-frogs, or Hylidae [Fig. 1c (*9*)], yield a curve with surprising congruence of line and dots and one that indicates a large number of unknown species. The discovery of the importance of the Culicidae, or mosquitoes (Fig. 1*g*), as carriers of disease at the end of the last century together with the use of genitalia in identifying them brought a sharp rise in the number of species. Probably only the curves in Fig. 1*a* (species), 1*b*, and 1*d* really indicate that completion is near. It should also be noted that there is little correlation between the economic importance of a group and the smoothness of its curve; the curve for tree-frogs (Fig. 1*c*), which are of practically no economic importance, is much smoother than those for butterflies (Fig. 1*d*) and Vespid wasps (Fig. 1*f*), many of which are of economic importance.

The last chart (Fig. 1*h*) is a composite of all the preceding groups plus several not figured, representing a combined total of 8045 species. This is but a small sample of the Animalia, possibly only about 0.4 percent, but it should provide us with an indication of the long road still ahead.

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Insect Mating Behavior: Endocrine Control of a Chemical Communication System

Abstract. *Experiments on several species of moths and cockroaches indicate that the production of sex pheromone (a male attractant) in virgin females is under endocrine control in some species but not in others. The presence or absence of endocrine control over pheromone production may be correlated with the type of life cycle exhibited.*

Virgin females of many species of insect produce sex pheromones which attract males and initiate male precopulatory behavior (*1*). A relatively simple chemical communication system of this type underlies the mating behavior of the cockroach, *Byrsotria fumigata* (Guérin) (*2*). The mating behavior of this cockroach is under the control of the endocrine system—specifically, the production of the female sex pheromone is under the control of the corpora allata (*3*, *4*). Results previously reported may be summarized as follows: (i) adult females ordinarily fail to produce sex pheromone if their corpora allata have been removed shortly after the imaginal molt; (ii) there is a high correlation between the production of sex pheromone and successful mating (that is, insemination); and (iii) the implantation of corpora allata into previously allatectomized females can induce pheromone production. Subsequently, mating tests in which allatectomized females (artificially coated with sex pheromone to enhance their attractiveness) were exposed to males have shown that pheromone production is the only aspect of the female's sexual behavior affected by the removal of these endocrine organs (*5*).

These data suggest that mating behavior may be similarly regulated in other insects. In the light of this possibility, the results of allatectomy will be examined in three other insect species; one cockroach, *Pycnoscelus surinamensis* (L.), and two moths; a saturniid, *Antheraea pernyi* Guérin, and a pyralid, *Galleria mellonella* (L.).

There are two different strains of the cockroach *P. surinamensis*; one strain is bisexual and the other parthenogenetic (*6*). Roth (*7*) discovered that females of the parthenogenetic strain (as well as those of the bisexual strain) produce a sex pheromone which stimulates the courtship behavior of males of the bisexual strain, when assayed by the filter-paper technique (*3*). In the present study, the effect of allatectomy on the production of pheromone by virgin females differed in the two strains (Table 1). In the bisexual strain, removal of the corpora allata less than 24 hours after the imaginal molt resulted in a failure of sex pheromone production in most experimental animals. Thus, the corpora allata appear to control the production of sex pheromone in animals of the bisexual strain as they do in *B. fumigata*. By contrast, removal of the corpora allata just after the imaginal molt had no effect on pheromone production in parthenogenetic females. Pheromone production occurred normally in the adult even in females allatectomized during the last nymphal instar. Thus, in the parthenogenetic strain the corpora allata seem to have lost their ability to control pheromone production. Further evidence for this conclusion may be derived from observations on females carrying egg cases. The corpora allata control oocyte maturation in females of both strains and the activity of these glands is inhibited while an egg case is being carried (*8*). Females of the bisexual strain do not produce pheromone while carrying egg cases, which is as would be expected from the known inhibition of the corpora allata at this time. By contrast, in most parthenogenetic females tested while carrying egg cases, pheromone production persisted, thus indicating its independence from control by the corpora allata. Hence, in this case in which there can no longer be any selective advantage in being able to signal to the male the female's ability to mate, the endocrine control over the necessary communication system appears to have been lost (*9*).

These results lead to the hypothesis that the regulation of mating behavior by means of endocrine control of sex pheromone production may not be a widespread phenomenon in insects. Rather, it may be expected to occur only in those instances in which selection pressures favor the evolution of such a mechanism. This would be the case in insects such as cockroaches which are long-lived in the adult stage and which have repeated reproductive cycles in which there are periods during which successful mating is not possible. In insects which are short-lived as adults, which lay eggs and die within a few days, the female must attract a male within a very

Table 1. Sex pheromone production in *Pycnoscelus surinamensis* virgin females. The numbers producing or not producing the pheromone are shown.

Group	No. tested	Sex pheromone	
		Produced	Not produced
Bisexual strain			
Control	12	12	0
Allatectomized*	33	6†	27‡
Parthenogenetic strain			
Control	10	10	0
Allatectomized*	16	16‡	0

* Allatectomized within 24 hours after the imaginal molt. † Showed oocyte maturation and accessory gland secretion. ‡ Showed neither oocyte maturation nor accessory gland secretion.

brief time span. Here it would seem advantageous to have a simpler arrangement in which the communication system for mating is genetically built in as a part of the adult developmental process so that it appears automatically as soon as the adult stage is reached. Thus, in moths such as the oak silkworm, *Antheraea pernyi*, and the wax moth, *Galleria mellonella*, which have short-lived nonfeeding adult stages, one would not expect the endocrine system to have any influence on the production of sex pheromone once the adult stage is reached. It is known that egg maturation itself is a part of the adult developmental process in these moths and that, in contrast to other insects which have been studied, egg maturation proceeds normally in the absence of corpora allata, even if the latter are removed prior to the initiation of adult development (*10, 11*).

According to my findings, the corpora allata appear to be unnecessary for sex pheromone production in *Antheraea pernyi*. Röller, Piepho, and Holz (*11*) have reported similar results for *Galleria mellonella*. In the experiments with *Antheraea*, the corpora allata were removed from female pupae chilled for long periods. These pupae were then placed at 25°C and allowed to develop into adults. The production of pheromone was assayed by testing the ability of these adult females to attract males in nature from distances of at least 25 or 30 yards. Allatectomized females were tied to wooden and wire frames and placed out of doors at dusk. Males (in a ratio of four males to one female) were released 25 to 30 yards downwind from the females. The frames were then checked early in the morning for the presence of copulating pairs. Similar experiments were performed at another location 8 km away, unoperated and sham-operated control females being used. Observations at night indicated that the allatectomized females "called" (*12*) normally and that mating occurs between 4 and 6 a.m. in this species. Preliminary results indicate that allatectomized females are able to attract males successfully (five of eight allatectomized females mated successfully as compared with seven of eight control females). These results agree with those obtained by Röller, Piepho, and Holz from a much larger number of individuals of the wax moth, *Galleria mellonella*. The results of these two sets of experiments indicate that the corpora allata do not control sex pheromone production in these moths; the results thus conform with the hypothesis stated previously.

It should be pointed out that the insects I have discussed so far, represent the two extremes in terms of reproductive cycles in insects. It would be of interest to study this phenomenon in an insect with an intermediate type of reproductive cycle, such as occurs in the cockroach, *Periplaneta americana* (L.). This cockroach is long-lived as an adult, but lacks the long gestation periods (during which mating is not feasible) which characterize the other cockroaches discussed in this report. Females produce egg cases which are oviposited externally at 7- to 14-day intervals, the shorter period referring to mated females, the longer one to virgin females (*13*). Within each interovipositional period there are several days while the egg case is being formed and extruded during which mating is not possible. My evidence that pheromone production in virgin females ceases during this period and commences again after the egg case is laid (*14*) suggests that an endocrine mechanism is involved. Recently, Yamamoto (*15*) found that the corpora allata do, in fact, control the production of sex pheromone in this species, and thus it conforms with the hypothesis proposed here. Another intermediate type of life cycle occurs in certain Lepidoptera, which, though short-lived in the adult stage, do actually feed as adults. Pheromone production may not begin in such species until several days after the adult molt. Here, endocrine or neuroendocrine control over the communication system for mating might occur independent of the endocrine events occurring during adult development; this possibility should be investigated.

This hypothesis concerning the presence or absence of endocrine control over the chemical communication system governing mating behavior, depending upon the type of life cycle of the insect in question, seems to fit the data now available. Furthermore, it suggests the possibility of discriminating, on the basis of the life cycle, those insects in which endocrine control over mating behavior might be expected to occur (*16*).

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9. Virgin females of some species of ovoviviparous cockroaches have normal cycles of oothecal production in the absence of mating, and may carry oothecae composed of infertile eggs for a considerable time before they are aborted (*8*). Successful mating is mechanically impossible for a female carrying an egg case. Herein lies the evolutionary significance of the alternating cycles of pheromone production and inhibition which are correlated with cycles of oothecal production in these virgin females. For if a male were to court a female carrying an egg case, he would be "wasting his courting energies" and in addition might well be exposing both to the danger of predation.
   The act of mating itself further complicates the endocrine control system. Pheromone production in many species ceases as a result of mating, but may be initiated again after parturition. Females of ovoviviparous species frequently mate again at this time (*5*).
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12. The behavior known as "calling" entails, in this species, the protrusion of the abdominal tip (which is normally somewhat telescoped) to expose the openings of the pheromone producing glands.
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16. In connection with this hypothesis, it is interesting that in females of the acridid, *Gromphocerus rufus*, endocrine control (via the corpora allata) is exercised over a different type of signaling system, namely, stridulation, which the female employs to communicate her sexual receptivity to males [W. Loher, *Naturwissenschaften* **49**, 406 (1962); W. Loher and F. J. Huber, *J. Insect Physiol.* **10**, 13 (1964)]. In theory, the hypothesis should apply not only to chemical communication, but to all communication concerned with female receptivity in whatever sensory modality.
17. These experiments were undertaken at the Biological Laboratories, Harvard University, with the assistance of Prof. Carroll M. Williams, Dr. Terrell H. Hamilton, Peter Bunyard, and Mrs. Baltasar Cruz. Financial support from NSF grant G-19962 is gratefully acknowledged.
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