ceptor blocking agent naloxone hydrochloride. The disruption of the onset and quality of maternal responsiveness in the morphine-treated animals appeared to be somewhat specific, since activity in the open field test was enhanced rather than depressed in these animals. Taken together, these findings indicate that morphine affects maternal behavior by way of an opiate receptor mechanism, and lend support to the hypothesis that the normal expression of pup-oriented behaviors is opiate mediated.

That the intensity of behavioral responsiveness rather than the absolute incidence of the responses to pups was affected by morphine indicates that the action of the opiate system on maternal behavior is modulatory. One neural site of morphine's disruptive action on maternal behavior appears to be the medial preoptic area (*11*). Direct application of morphine to the medial preoptic area, an area involved in the estrogen-stimulated onset (*12*) and the nonhormonally regulated maintenance (*13*) of maternal behavior in the rat, disrupts pup-oriented responses in previously maternal rats. The site of morphine's action appears to occur with some degree of neural specificity, since application of morphine to the ventromedial nucleus of the hypothalamus fails to disrupt ongoing maternal behavior (*11*). It is not known whether morphine disrupts hormonal events responsible for the onset of maternal behavior or whether it has an independent nonhormonal mode of action.

The effect of morphine on maternal behavior does not appear to be simply a performance effect, since maternal behavior appeared in the morphine-treated rats after about 5 days of exposure to pups, at about the same time that morphine treatment affected open-field activity. Furthermore, the appearance of the behavior at this time does not appear to result from habituation or tolerance to morphine, since retrieval of young from the arms of the T-maze was relatively absent in the morphine-treated females that showed full home cage maternal responsiveness. Given these disruptive effects of morphine on maternal behavior in rats, the possible effects of opiate administration and opiate addiction on maternal responsiveness in other animals, including humans, warrant examination.

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Male Lek Formation and Female Calling in a Population of the Arctiid Moth *Estigmene acrea*

Abstract. *Abdominal coremata in male* Estigmene acrea *(Lepidoptera: Arctiidae) are inflated and displayed in aggregations to which females and males are attracted and where mating occurs (leks). Female* E. acrea *also release a sex pheromone which attracts males. These two mating behaviors occur in the same populations at different peak times on the same nights. Thus male lek formation and female calling occur in the same species, and the male coremata, or related structures, appear to be integrally associated with lek behavior.*

Males of the North American salt marsh moth, *Estigmene acrea* (Drury), aggregate and inflate paired abdominal coremata (air-filled tubes covered with hairs) (Fig. 1). Male brushes, hair-pencils, and analogous organs are found throughout the Lepidoptera, in both butterflies and moths, where precopulatory eversion by males is associated with the release of scent (pheromone) (*1*). Large coremata are inflated by males of the Asian arctiid moths, *Creatonotos gangis* and *C. transiens* (*2*), but their biological role has not yet been determined. Only in one species of arctiid moth, *Utetheisa ornatrix*, has the biological function of the coremata been defined (*3*) and, in this species, males that inflate the coremata and release pheromone just before making genital contact are more likely to succeed in mating. Males of many other arctiid moths also have a variety of morphologically different coremata and hair-bearing structures whose behavioral roles are not known (*4*). The few reports of live male *E. acrea* with inflated coremata are of isolated males and not in the context of natural behavior (*5*).

As is typical of moths, female *E. acrea* release a sex attractant pheromone (*6*) which stimulates upwind flight and orientation to the female by males. In this case, copulation occurs without any display of the coremata. In addition, however, male *E. acrea* form aggregations in which they adopt a specific display posture with their coremata fully extended and inflated (Fig. 1). We observed aggregations on alfalfa plants or other low vegetation, and some males would display extended coremata while on fence posts or barbed wire adjacent to plants. Males adopted a display posture from almost ground level up to about 1 m above ground and did so on the tips of vegetation (Fig. 1) or other structures where they were clearly visible and accessible. Females and males oriented upwind to these male aggregations; males would join the aggregations, and females would fly directly to them and mate with males in them. Females were

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only observed to mate with males that were in full display posture. Once in this posture, males were not observed to move nor were any male-male behavioral interactions observed, which might have indicated that males competed for optimal sites in an aggregation.

To investigate this behavior further, we recorded the number of males displaying inflated coremata, the number mating, and the number that were neither mating nor displaying in natural aggregations in an alfalfa field in Davis, California. The responses of males and females to mating stations that contained either five male or five virgin female *E. acrea* were measured (*7*), and the composition and changes within male aggregations were followed throughout the natural period of nocturnal activity (2000 to 0130 hours).

Aggregations contained an average of 9.2 males [maximum 22, minimum 3 (by definition): $N = 55$]. Just over half of the males in natural aggregations mated during the course of observation (mean, 56 percent). For all aggregations there was an initial peak in the proportion of males in display posture, and this occurred just after dark (that is, between 2000 and 2030 hours, with sunset at 2000 hours) (Fig. 2A). The number of displaying males then decreased as males mated with females that were attracted to the aggregations, retracted their coremata, and remained quiescent or left the aggregations. A second, smaller peak of male display activity consistently occurred about 2 hours after the first, but little mating occurred during it.

Male response to virgin females was monitored by means of pheromone traps (*7*), each containing two virgin females. Males were not caught in these traps until an hour after the initial peak in the proportion of males displaying and mating in aggregations. Also, maximum male response to females (between 2230 and 2330 hours) occurred about 2 to 3 hours after maximum female response to male aggregations (Fig. 2B). Observed natural matings of calling females in the field coincided with the time of male attraction to the pheromone traps. The mean time of onset of matings resulting from female response to males (in natural aggregations and at mating stations) between 2100 to 2130 hours (peak 2030 to 2100 hours) was significantly different ($P < .05$) from the mean time of matings resulting from male response to females (in traps and at mating stations) which occurred between 2230 and 2300 hours (peak 2300 to 2330 hours).

These mating behaviors have apparently not been described from the Lepidoptera. In the vast majority of species females attract males, either with pheromones (moths) or by visual cues (butterflies) (*8*). In a few species of moths, males attract females (though from what distance is not clear) (*9*). In the tortricid moth, *Grapholitha molesta*, the eversion of brushes and release of pheromones by the male during courtship stimulate the female to orient toward him over a short distance (a few centimeters) just before copulation (*10*). But long-range orientation behaviors to both male and female have not been reported from other species (*11*), nor have coremata been shown to produce pheromones stimulating long-range attraction.

The male aggregations, and behavior of females toward them, fit the classical concept of lek behavior (*12*), in which the males aggregate at sites which are not associated with any resource (*13*). Females respond and select males from within the aggregations. Where leks occur in other species they are, as in this species, a rare alternative to other mating strategies more typical of species in the taxon. However, an alternative female-based mating strategy available in the same population has apparently not been reported. We have no information about the relative success of mating by either strategy (*14*), but the proportion of males mating in larger aggregations was not significantly different from that in the smaller ones.

The role of the coremata in aggregations, though as yet undetermined, may be visual, complementing the brilliant white and yellow appearance of the males (*15*), or olfactory. No chemical secretion has been identified from the coremata, but their structure and mechanism of inflation appear to be similar to those in *Utetheisa*, from which hydroxydanaidal, a pyrrolizine, has been isolated as the principal pheromone in facilitating female acceptance (*3*). In *Creatonotos*, where the behavioral function of the coremata is not known, hydroxydanaidal

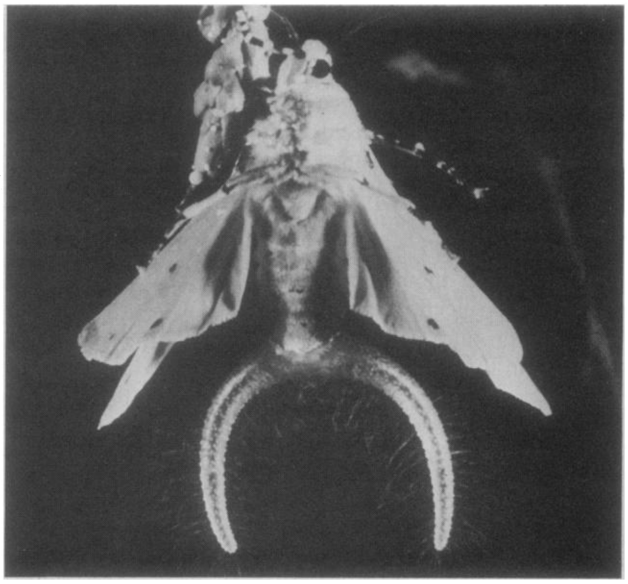

Fig. 1. Male *Estigmene acrea* in the typical display posture with coremata fully extended in the field.

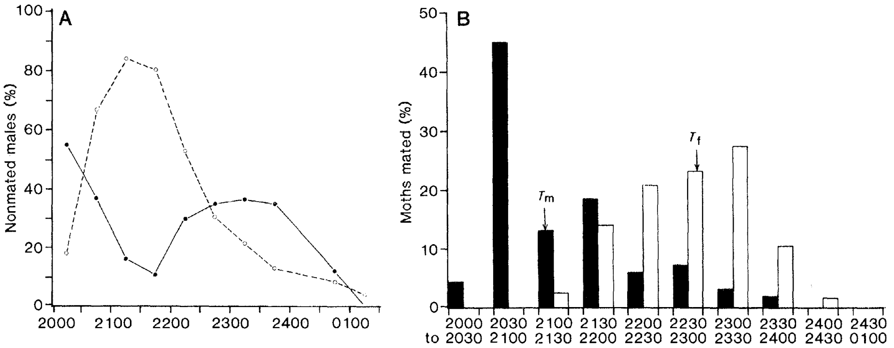

Fig. 2. (A) Structure of natural aggregations of *E. acrea*, Davis, California, 1979–1981. Each point represents the mean proportion of displaying (●) or nondisplaying (○) males for each time period for 55 aggregations. (B) Time of onset of mating in natural male aggregations (solid bars) and on mating stations baited with virgin females (open bars); T_m and T_f indicate the mean time of mating in male aggregations ($N = 245$) and on mating stations ($N = 45$), respectively.

on the coremata is derived (as in *Utetheisa*) from defensive pyrrolizidine alkaloids sequestered in the larval food plants (*2*). The morphogenesis and pheromone content of the coremata are influenced by the dietary alkaloid so that females might be able to directly assess the alkaloid content—that is, the degree of chemical protectiveness—of the males by the size of their coremata, the pheromone content, or both. However, neither *Creatonotos* nor *Utetheisa* are known to form leks.

If a similar situation occurs in *E. acrea*, females visiting leks may be able to assess the fitness of assembled males, although we never observed females to move from one male to another: they flew straight in and mated with the first displaying male contacted. Unlike *Creatonotos*, however, *E. acrea* shows no readily discernible natural variation in the size of male coremata with diet, and the larvae feed on a wide range of garden and crop plants without any apparent deleterious dietary effects (*16*).

Male leks have not been well substantiated in the Lepidoptera, especially moths, nor has the use of male brushes or coremata in long-range attraction. Furthermore, the occurrence of a dual system of mating, one based on female attraction and the other on male attraction, in the same species (and population) has apparently not been reported. What sort of stimuli are provided by the coremata and by the lek as a whole, and what sort of selection pressures led to the evolution and maintenance of both strategies in this species is not known.

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Ecological Correlates of Paternal Investment of Urates in a Tropical Cockroach

Abstract. *Females of the tropical cockroach* Xestoblatta hamata *feed on urates offered by the male after copulation. Females on nitrogen-deficient diets ingest and transfer to their maturing oocytes more male-derived uric acid than do females on high-protein diets. In isolated females, the greatest uptake of uric acid by the ovaries occurs during the mating stage in the reproductive cycle. Uric acid from males contributes significantly to the female's nitrogen pool and may help shorten the time between mating and oviposition. In both field and laboratory experiments males choose high-protein foods and dietary uric acid.*

Cockroaches, unlike many terrestrial insects, void little uric acid (*1*). Instead, they store urates in specialized cells of the fat body or secrete them into accessory glands in males of some species. In three subfamilies of cockroaches the male coats his sperm package with uric acid after inserting it into the female (*2*). Roth (*3*) suggested that uric acid might protect the spermatophore from being prematurely consumed by the female or by other insects, and Cornwell (*4*) that it might act like a plug to prevent females from mating repeatedly. Mullins and Keil (*5*) reported, however, that the spermatophore-urate complex may disappear shortly after mating and that male uric acid could be recovered from mated *Blattella germanica* females and their oothecae. They found that the transfer of the urates was related to the nutritional state of the female: those on a low-protein diet transferred more to oothecae than did those on a high-protein diet. Mullins and Keil (*5*) suggested that the transfer of urates might represent "paternal investment of a nitrogen resource from which the female and her progeny might benefit."

We report a postcopulatory behavior in the tropical rain-forest cockroach *Xestoblatta hamata* that supports the paternal investment proposal (*6*). After copulation the male raises his wings, tele-

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