rate with their nonphysogastric queens (group 2). After five more weeks, the queens in the two groups were weighed, killed by freezing, and tested for the inhibitory pheromone (*11*).

The mean weight of the queens of group 1 was 20.1 mg (S.D., 1.17) and of group 2, 10.7 mg (S.D., 1.52). The mean times taken by virgin queens to dealate were controls, 1.2 days ($N = 9$); group 1 queens, 8.6 days; and group 2 queens, 1.6 days. The difference between the queens of groups 1 and 2 was significant [$P < .001$, $t(26) = 5.3$], but group 2 queens were not significantly different from the controls. This result showed that queens produce different amounts of inhibitory pheromone and that the amount is positively correlated with fecundity. However, we do not yet know whether this pheromone is causally involved in the selection of queens for execution by workers. There is a distinct possibility that it is, but we believe that fire ant queens (and the queens of other social insects) produce a number of pheromones (*12*) that interact with each other and that the first step in understanding their effects should be to define their integrated functions and develop bioassays for these.

Although we developed our quantitative pheromonal hypothesis to explain the role of workers in maintaining monogyny in colonies of social insects, it may also explain the occasional occurrence of polygyny in essentially monogynous species. A lower fecundity of queens in polygynous colonies is evidently a general feature in the social insects (*13*) and is indicative of a lower pheromone production. More queens may therefore be present in a colony before the tolerance threshold of the workers is exceeded. Our experimental results suggest that this threshold is, in any case, higher among the workers of polygynous colonies.

The hypothesis also suggests explanations for other well-known social phenomena. For example, it seems probable that the behavioral dominance hierarchies formed in colonies of primitively eusocial Hymenoptera, such as paper wasps, *Polistes* spp., reflect quantitative pheromonal hierarchies, since position in the dominance order is positively correlated with the degree of ovarian development, with the queen occupying the alpha position (*14*). Further, temporary social parasitism occurs in a variety of ant genera, for example, *Formica* and *Lasius* (*1*), and acceptance of the parasitic queen by the workers of the host colony may well depend on her being pheromonally superior to the host queen. Since host and parasite are closely related taxonomically, their pheromones are probably very similar or even identical, and quantitative superiority would be a relatively minor evolutionary adaptation.

Our hypothesis may well have implications for the management of both beneficial and harmful species of social insects.

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3. The assumption of Wilson that workers recognize queens by their odor is reasonable, although workers may have to touch a queen in order to receive the complete pheromonal signal, as is evidently the case in the honey bee [J. Simpson, *J. Apic. Res.* **18**, 233 (1979)]. The probability that audio, visual, or other signals are involved in recognition seems negligible. Evidence for the existence of genetically controlled "odor" differences between individuals has been obtained for both honey bee queens [M. D. Breed, *Proc. Natl. Acad. Sci. U.S.A.* **78**, 2635 (1981)] and workers (M. D. Breed, *Anim. Behav.*, in press) and also for primitively social bees of the species *Lasioglossum zephyrum* [L. Greenberg, *Science* **206**, 1095 (1979)].
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9. Each half-colony consisted of an estimated 15,000 to 20,000 workers and abundant worker brood, but no adult or immature sexuals.
10. The fecundity of a queen may be conveniently measured by weighing her, since physogastry of mated queens in established colonies is caused almost exclusively by the greatly enlarged ovaries.
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An Unusual Lepidopteran Sex Pheromone System in the Bagworm Moth

Abstract. *The female sex pheromone of the bagworm moth is* (R)*-1-methylbutyl decanoate. The antipode is biologically inactive and it neither enhances nor detracts from the potency of the* R *enantiomer. Unlike other moths for which female pheromones have been identified, the female secretes the pheromone from glands on her thorax and it is disseminated from hair that is shed from her body.*

We report a novel sexual communication system in the bagworm moth, *Thyridopteryx ephemeraeformis* (Haworth). Unlike other moths that secrete sex pheromones (*1*) from glandular tissue on the tips of their abdomens (*2*), the wingless adult female bagworm produces pheromone from glands situated on its thorax. The cryptic female dispenses the chemical from morphologically specialized, deciduous hairs that are cast from her body. We have identified the pheromone as (*R*)-1-methylbutyl decanoate; the males are ostensibly anosmatic to the antipode. The pheromone is among the first long-chain fatty acid esters to be identified as a sex pheromone in the Lepidoptera (*3*), and it is one of the rare chiral pheromones discovered in the order.

The herbivorous bagworm is a biological curiosity and a serious defoliator of

Table 1. Male bagworm responses to the enantiomers and racemate of 1-methylbutyl decanoate on cotton rolls or to a virgin female placed in Pherocon 1C (Zoecon) insect traps positioned 20 m apart, 1.5 m from the ground, and baited daily. The test was replicated five times on each of 5 days in mid-September 1981, near Beltsville, Maryland; a randomized complete-block design was used. Means followed by the same letter are not significantly different from each other according to Duncan's New Multiple Range Test. Male responses to *S* enantiomer treatments was due to 2 percent *R* in the *S* enantiomer (*9*).

Treatment	Capture (males per trap per day)
R (0.5 mg)	27.3 a
Racemate (1.0 mg)	24.6 a
Racemate (0.1 mg)	7.3 b
R (0.05 mg)	4.1 b
Virgin female (one)	3.0 c
S (0.5 mg)	2.1 cd
S (0.05 mg)	0.2 e

ornamental shrubs and trees throughout the Southeast and lower Midwest. Like most members of its family (Psychidae), it spends the greater part of its life confined to a fusiform bag, which is open at both ends and which the larva constructs from silk and bits of host plants. The larva carries the bag about and enlarges it as it grows; only its head and thoracic legs protude from the top opening (Fig. 1A). Before pupation, the larva seals the top of its bag with silk and spins a cocoon within the hanging bag, positioning itself with its head pointed down. After pupation, the winged diurnal flying male emerges from his bag to search for a mate; the adult female, an amorphous creature without functional appendages, remains in her bag with merely her head and thorax protruding from a fracture in the pupal shell. Pheromone-laden hairs dislodged from a female's thorax (*4*) are expelled through the anterior aperture in the pupal shell (Fig. 1B) toward the bottom opening of the bag. The male perceives the pheromone, flies to the bag, and inseminates the female by a rather extraordinary process: he hangs upside down on the bag containing the inverted female, thrusts his abdomen into the bottom of the bag, and extends it (Fig. 1C) pneumatically about 4 cm into the female's pupal shell, past the length of her body, to contact her caudal genitalia. We have shown that this copulatory behavior is mediated by the pheromone, (*R*)-1-methylbutyl decanoate. Visual cues (such as those that might be associated with the female bag) are apparently not required to elicit such behavior. In a field experiment, males alighted on a white cylindrical roll of cotton containing 50 μg of the compound and telescoped their abdomens specifically into the treated end (Fig. 1D). Inspection of the probed cotton revealed that the males had not transferred sperm to the cotton. Therefore, sperm delivery undoubtedly requires additional stimuli that may be provided by the female. These observations, however, make it clear that (*R*)-1-methylbutyl decanoate plays an essential role in the insect's reproductive behavior.

For identification, the thoracic hair from approximately 200 females was washed with hexane and the concentrated solution was fractionated by preparative gas chromatography, yielding a single compound (~ 75 μg) that was attractive to males in the field (*5*). This substance was identified by gas chromatography, high- and low-resolution mass spectrometry, infrared and nuclear magnetic resonance spectroscopy, and microchemical reactions (*6*). It was found to be a C_5 ester of decanoic acid. Synthesis of all possible C_5 esters showed that the pheromone was identical to 1-methylbutyl decanoate. The alcohol portion of the structure contained an asymmetric center; therefore both antipodes were synthesized (*7*) from commercially available (*S*)- and (*R*)-2-pentanol, and field tests showed that only the *R* enantiomer was biologically active. The alcohol from the natural ester was derivatized and shown to have only the *R* configuration (*8*).

Males responded with equal intensity to the *R* enantiomer or to a quantity of racemate that contained the same amount of the *R* enantiomer; they showed no response to the antipode (Table 1) (*9*). Ten times more males were attracted into traps by 500 μg of synthetic pheromone than by the virgin female (*10*). The optical isomer differentiation exhibited by the males is not surprising, inasmuch as the involvement of chirality in pheromone perception is well known in other orders of insects (*11*). The bagworm pheromone perception system, however, differs from the only other species of moth in which pheromone chirality is documented, the gypsy moth [*Lymantria dispar* (L.)]. Although the male gypsy moth is attracted to only one enantiomer, the antipode has a definite biological effect (*12, 13*). In the case of the bagworm, the antipode in the racemic mixture acts only as a diluent. It may well be that while the gypsy moth possesses sensory chemoreceptors to ac-

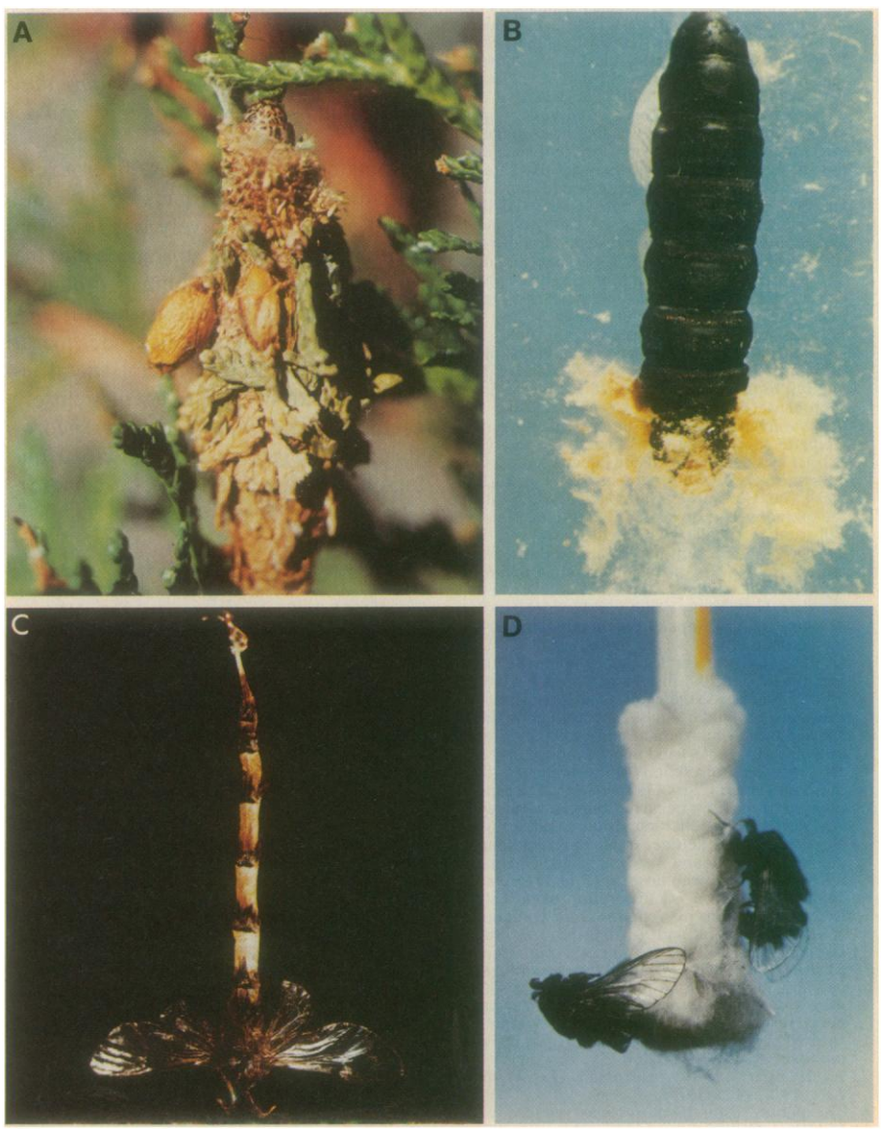

Fig. 1. (A) Bagworm larva feeds on arborvitae with only its head protruding from the top of the bag. (B) Adult female bagworm sequestered in her pupal shell expels golden pheromone-laden hair to attract a mate. (C) The winged male bagworm pneumatically extends its abdomen to inseminate the female. Each chitinous abdominal segment is connected by translucent intersegmental membrane. (D) Male bagworms respond sexually to a cotton roll treated with synthetic female sex pheromone.

commodate both optical isomers, the bagworm has one type of receptor that is tuned to receive the *R* enantiomer exclusively.

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4. The entire body of the adult female is hirsute but only morphologically distinct hair from membranous lateral and ventral surfaces of the thorax is dispensed from the pupal shell. Scanning electron microscopy and histological study showed that these deciduous hairs occur in association with large nucleated subcuticular cells that are characteristically secretory. Analyses by gas chromatography (GC) of heptane rinses made of the female's abdomen, ovipositor, and head and thorax showed that all but the head and thorax rinses were devoid of pheromone. Replicated analyses of 15 individual females showed that pheromone could be extracted from the head and thorax ($\bar{X}$ = 0.24 μg per female) and from the expelled hair ($\bar{X}$ = 0.53 μg per female). These results indicated the thoracic site of pheromone production and the function of the deciduous hair as a pheromone dispenser.
5. Female pupae were collected in the field, removed from their bags, placed in individual petri dishes, and incubated: 80 percent relative humidity, 16-hour photophase (26°C), and 8-hour scotophase (16°C). Hairs expelled by the females were aspirated onto a plug of glass wool in a pipette and washed with 50 ml of hexane. The extract was concentrated and injected onto a GC column packed with 4 percent SE-30 on 80/100 mesh Gas Chrom Q. The major constituent in the extract was trapped and found to be biologically active. Capillary GC analysis showed that it was > 99 percent pure, and its retention indices [E. Kovats, in *Advances in Chromatography*, J. C. Giddings and R. A. Keller, Eds. (Dekker, New York, 1966), vol. 1] of 1660 (polar column) and 1592 (apolar column) indicated that the compound was weakly polar.
6. Capillary GC was carried out by polar (SP1000) and apolar (SP2100) fused silica columns (60 m by 0.25 mm inside diameter) (J & W Scientific). Low resolution GC–mass spectrometry (MS) showed a molecular ion at mass to charge ratio (*m/e*) 242 ($C_{15}H_{30}O_2$) and intense ions at *m/e* 173 and 155; high-resolution MS established that these ions were $C_{10}H_{21}O_2$ and $C_{10}H_{19}O$, respectively. No reaction occurred on treatment with O_3, $NaBH_4$, or acetic anhydride–pyridine; thus olefin, aldehyde, ketone, or alcohol functionalities for the compound were excluded. The infrared spectrum showed absorption at 1745 cm^{-1}, compatible with C=O absorption of an ester. Reduction of a few micrograms of the compound at 250°C with Pt and $LiAlH_4$ [B. A. Bierl-Leonhardt and E. D. DeVilbiss, *Anal. Chem.* **53**, 936 (1981)] yielded *n*-pentane, according to GC-MS. Without Pt, a similar reduction at 300°C gave *n*-decane and *n*-pentane. The nuclear magnetic resonance spectrum of the compound showed a triplet at 2.3 ppm ($C\underline{H}_2C=O$) and multiplet at 4.9 ppm ($C\underline{H}O$).
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9. The GC analysis of the diastereomers of the optically active alcohols used in synthesis of the enantiomers of the pheromone showed that each optical isomer of the alcohol contained 2 percent opposite enantiomer. In a field test similar to but separate from the test described in Table 1, traps baited with 500 μg of *S* enantiomer captured males at about the same rate as traps baited with 10 μg of *R* enantiomer. Thus, the small number of males attracted to the *S* enantiomer were most likely responding to the trace of *R* in the *S* isomer.
10. The 1-methylbutyl decanoate in a crude extract of the females' pheromone-laden hairs was assayed by GC and field-tested against the same amount (5.5 μg per trap) of synthetic pheromone. The number of males captured in traps baited with this extract was not different from those baited with the synthetic pheromone. Thus, the superiority of the synthetic pheromone over females in causing male capture (Table 1) is attributed to the comparatively small quantity of pheromone produced by the female.
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Quinolinic Acid: An Endogenous Metabolite That Produces Axon-Sparing Lesions in Rat Brain

Abstract. *A current hypothesis links the neuroexcitatory properties of certain acidic amino acids to their ability to cause selective neuronal lesions. Intracerebral injection of the neuroexcitatory tryptophan metabolite, quinolinic acid, has behavioral, neurochemical, and neuropathological consequences reminiscent of those of exogenous excitotoxins, such as kainic and ibotenic acids. Its qualities as a neurotoxic agent suggest that quinolinic acid should be considered as a possible pathogenic factor in neurodegenerative disorders.*

Kainate and ibotenate are neuroexcitatory and toxic amino acids of plant and fungal origin, respectively (*1*). Injection of either of these two substances into the brains of experimental animals produces effects that have been construed to provide models of human neurodegenerative disorders. In particular, striatal lesions caused by these agents closely resemble the neuropathologic and neurochemical changes characteristic of Huntington's disease (*2*). Intraventricular (*3*), intrahippocampal (*4*), or systemic (*5*) administration of kainate results in seizures and concomitant nerve cell changes similar to those observed in temporal lobe epilepsy in the human. The structural resemblance of exogenous amino acids, such as kainic and ibotenic acids, to endogenous excitatory amino acids, such as glutamic and aspartic acids, has led to the hypothesis that hyperfunction of the body's own "excitotoxins" may be related to neuronal damage in certain

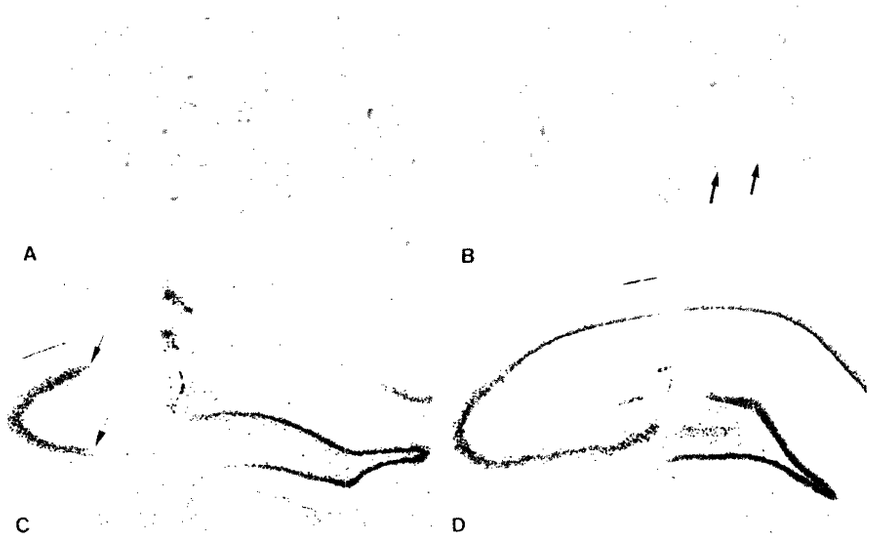

Fig. 1. Light microscopic analysis of 30-μm thionin-stained cryostat sections. (A and B) Micrographs of rat striatum 4 days after intrastriatal infusion of 60 nmole quinolinic (A) or 800 nmole nicotinic (B) acid. Arrows in (B) delineate the track of the injection needle (×50). (C and D) Effects of intrahippocampal administration of 30 nmole of quinolinic acid (C) or 800 nmole of nicotinic acid (D). Rats were killed 4 days after operation. Tracks of the injection needles are clearly identifiable in both micrographs. Arrows in (C) indicate the sharp border between degenerated and intact pyramidal cells (×10).