spatial cues, such as colors, sounds, and shapes, stay learning should be more rapid than shift learning. This difference may be due to the nature of position as a cue, for each position in space is unique.

Differences between and within species in the ease of shift and stay learning may depend on the influence of the spatial and temporal scale of resource depletion after feeding. Shift learning should occur whenever the positions are divided so finely that visits always produce depletion; stay learning should occur whenever visits do not result in appreciable resource depletion. In hummingbirds, for example, stay learning may occur more easily at patches of inflorescences. Temporal scales may also be important for resources that are renewed, since the rate of renewal should determine the value of a site for future visits.

An ecological approach to learning, based on an analysis of the problems animals face in their natural environments, can generate useful predictions about differences in learning between and within species. This is in contrast to the recent approach called biological "constraints" on learning (*11*), which requires the analysis of apparent anomalies in arbitrary learning situations. Our results suggest that the ecology of food resource distribution in space and time generates important evolutionary influences on learning.

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5. The Department of Interior Fish and Wildlife Service, the Arizona Department of Fish and Game, and the New York State Department of Conservation provided the necessary permits.
6. Nutritional components were provided by K.-L. Schuchmann [see K.-L Schuchmann, *Kolibris: Haltung, und Pflege* (Biotropic Verlag, Frankfurt, 1979)].
7. The *Archilochus* obtained 30 μl per rewarded flower while the *Lampornis* and *Eugenes* obtained 20 μl per flower. These amounts are much less than the average meal size for these birds so several trials could be conducted in a short time.
8. The rate of improvement in shift learning was much greater when the shift learning followed stay learning than when the shift learning came first. This may represent a ceiling effect, since those birds who learned to shift first and showed lower rates of improvement began training at relatively high levels of shift behavior. Alternatively, this difference could represent some more basic difference in the learning process.
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12. Supported by grants from the National Science Foundation and the Syracuse University Undergraduate Honors Program. We also acknowledge the Department of the Interior Fish and Wildlife Service and the Arizona Department of Fish and Game for permits. We thank C. L. Gass, T. Goldsmith, B. Heinrich, J. Krebs, S. E. G. Lea, W. Roberts, and S. Shettleworth for their comments on an earlier version of this report.

12 May 1982

Sex Pheromone of the Winter Moth, a Geometrid with Unusually Low Temperature Precopulatory Responses

Abstract. *The sex pheromone for the winter moth,* Operophtera brumata *(L.), has been identified as the novel compound* (Z,Z,Z)-*1,3,6,9-nonadecatetraene. The male moths respond to the pheromone at low temperatures (4° to 15°C) and exhibit an upper response limit that coincides with the lower response limit for other reported moth sex pheromone systems. The pheromone attracted two other geometrid species,* O. bruceata *(Bruce spanworm) and* O. occidentalis.

The winter moth *Operophtera brumata* (L.) is a common forest pest in Europe and was accidently introduced into Canada in the early 1930's. It has become a serious defoliator of oak, elm, flowering plum, apple, and filbert in expanding areas of eastern and western Canada and in the northwestern United States. A trap including synthetic sex pheromone of this species would have immediate utility in monitoring the spread of this pest, and an analysis of this moth's sex pheromone system would be important for other reasons as well. Although sex pheromones have been reported for species in most other lepidopteran families, there has been a conspicuous absence of characterized pheromones for any species in the Geometridae. Since pupal diapause of the winter moth is broken only in late fall when temperatures drop to about 7°C (*1*), the wingless female moths are dependent on a mating communication system that must function at temperatures well below the lowest temperature (around 16°C) at which males of most other species respond to their pheromones (*2*).

A previous study showed that a sex pheromone system was utilized by the winter moth (*3*). Using behavioral assays and electroantennagraphy (EAG) on abdominal tip extracts from female winter moths, we have now identified a novel sex pheromone, (*Z,Z,Z*)-1,3,6,9-nonadecatetraene **1**. This compound elicits the full range of precopulatory behavioral responses in flight tunnel bioassays and, in Nova Scotia, was as active as live females in attracting males to traps. The males responded to pheromone in the flight tunnel at temperatures as low as 4°C, but were unresponsive at temperatures above 15°C.

A sample of crude extract from the abdominal tips of 10,000 female winter moths (*4*) was subjected to chromatography on Florisil (~ 48 g) and eluted with 0, 1, 5, and 10 percent diethyl ether in Skelly B. EAG analysis (*5*) with male moths showed large antennal responses only to the fraction eluted with 1 percent diethyl ether in Skelly B. A portion of the active fraction was injected onto a gas-liquid chromatography (GLC) column (OV-101, 180°C) (*6*), and the effluent was collected at 2-minute intervals in glass capillary tubes. EAG analysis showed activity (5 mV) only in the 8- to 10-minute fraction (retention time of nonadecane was 9.15 minutes). The material obtained at 8 to 10 minutes was injected onto a polar XF-1150 column (160°C) (*6*), and the effluent was collected in 1-minute fractions. High EAG activity (8 mV) was elicited only with the 4- to 5-minute fraction (nonadecane, 2.9 minutes; heneicosane, 5.6 minutes). The active material collected from both GLC columns was used for the subsequent analyses.

Injection of the collected active material produced a peak corresponding to a

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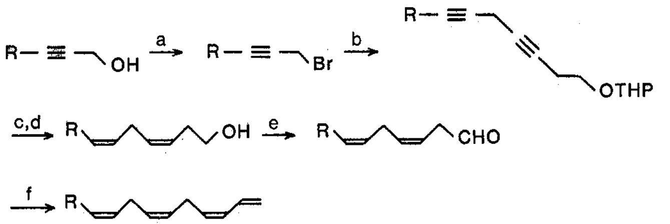

1

R, n-C_9H_{19}
a, PBr_3
b, ≡—OTHP (OTHP, tetrahydropyran) and ethyl magnesium bromide
c, p-toluenesulfonic acid
d, P-2 nickel
e, CrO_3 and pyridine
f, 2-propenyltriphenylphosphonium bromide and n-butyllithium

Scheme 1. Synthesis of *O. brumata* pheromone.

carbon number of 18.95 on the nonpolar OV-101 column and a carbon number of 20.9 on the polar CHDMS column (*6*). Microhydrogenation of the active material (with Pd and $CaCO_3$ in ethanol) produced a product that had GLC retention times identical to those of nonadecane on OV-101, CHDMS, and XF-1150 columns, and gave an electron-impact mass spectrum identical to that of nonadecane. An electron-impact mass spectrum of the active material exhibited a molecular ion at a mass-to-charge ratio (*m*/*e*) of 260 and other major ions at 147, 133, 119, 106, 105, 91, 80, 79, and 67. A chemical ionization mass spectrum (isobutane) gave an intense MH^+ ion at *m*/*e* 261. These data are consistent with expectations for a 19-carbon straight-chain tetraene.

Microozonolysis of the active material yielded a product with a retention time identical to that of *n*-decanal on OV-101. There were no peaks at the retention times of any other 3- to 12-carbon aldehydes. This showed that all unsaturation is found before carbon-10 in the chain. (*Z*,*Z*,*Z*)-1,3,6,9-Heneicosatetraene **2** already had been identified as a possible pheromone component of some populations of the arctiid moth *Utetheisa ornatrix* (*7*), and the (*Z*,*Z*,*Z*)-3,6,9 system was found in 20- and 21-carbon-chain compounds as a pheromone component in a number of species in the Arctiidae, Lymantriidae, and Noctuidae (*8*). The electron-impact mass spectrum of compound **2** was similar to that of the bioactive winter moth component, and the chemical ionization spectra were similar except that the 21-carbon tetraene had a larger MH^+ ion (at 289) than the MH^+ ion (at 261) of the winter moth component. Data collected thus far supported structure **1** as the active component in the sex pheromone of the winter moth.

The proposed compound was synthesized as outlined in scheme 1, and the product was compared with the natural material (*9*). Standard EAG analyses (10 μg per cartridge) showed that synthetic compound **1** produced, by far, the greatest male antennal response (10 mV) of all di- and tri-unsaturated 18- to 21-carbon-chain standards tested. Synthetic **1** had retention times identical to the natural compound on two capillary columns (Carbowax 20 M, 18.47 minutes; OV-101, 20.47 minutes). Analyses of single female tips by capillary GLC on both columns showed that each female stored less than 1 ng of **1**.

The responses of male *O. brumata* to synthetic **1** were tested in field trials and in a sustained-flight tunnel. In the flight tunnel, males exhibited high levels of response when tested at 12°C during the scotophase period (*10*). Male response was found to be optimal between 7° and 15°C (Fig. 1), with significant loss of activity below 4°C and above 17°C (*11*). Field trapping studies (*12*) in Nova Scotia also demonstrated high attraction of male *O. brumata* to the synthetic material. Traps containing 30, 100, or 1000 μg of **1** on a rubber septum captured 311, 438, and 675 males, respectively; these results were significantly better than those obtained with unbaited traps (total of two males) at the 5 percent level by analysis of variance and Duncan's multiple range test. Male flight activity occurred predominantly during the scotophase, within a temperature range of 5° to 12°C. The characteristic 1,3,6,9-tetraene mass spectral pattern, the capillary GLC retention times, and the high biological activity all indicate that **1** is the main pheromone component of the winter moth.

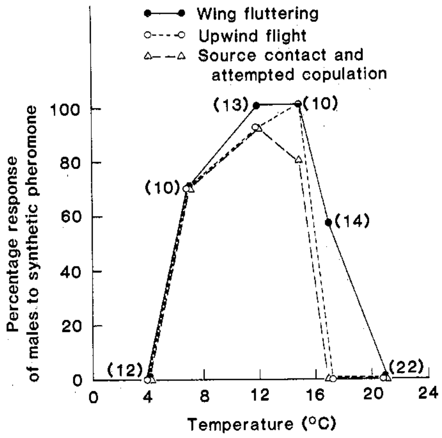

Fig. 1. Responses of *O. brumata* to (*Z*,*Z*,*Z*)-1,3,6,9-nonadecatetraene in a sustained-flight tunnel. Number of males tested at each temperature is given in parentheses.

Trap tests conducted in upstate New York in November 1981 showed that synthetic **1** was very attractive to the native species, *O. bruceata* (Bruce spanworm), and trap tests conducted late in the flight period (16 to 20 December) in Oregon resulted in captures of over 100 males of *O. brumata* and over 200 males of the native species *O. occidentalis* (*13*).

The observations that male *O. brumata* respond optimally to their sex pheromone at temperatures between 7° and 15°C is unique among reported pheromone studies. While numerous Lepidoptera are able to maintain high body temperatures and exhibit flight activity at lower temperatures (*14*), lower temperature thresholds for pheromone response are typically between 15° and 17°C (*2*). Males of *O. brumata* apparently have adapted their mating chemical communication system and their physiological requirements for extended flight activity to function in an otherwise unfavorable seasonal period.

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10. Flight tunnel as in J. R. Miller and W. L. Roelofs, *J. Chem. Ecol.* **4**, 187 (1978). Males were tested with 30 μg of synthetic **1** on a rubber septum (A. H. Thomas Co.) at ~ 1 lux, 3 hours into the scotophase of a photoperiod of 14 hours of light and 10 hours of darkness. Males were acclimated to tunnel condition for 2 hours before they were tested. Initially, 33 males were tested, with 33, 29, and 27 males exhibiting wing fluttering, upwind flight 150 cm to the source, and source contact with attempted copulation, respectively.
11. At temperatures above and below the optimal range, males were typically inactive, often lying on their sides and exhibiting very little movement, even when touched. Within the optimal range, nonpheromone-stimulated basal activity was significantly increased, with males exhibiting upright posture and frequent periods of walking and wing fluttering.
12. Field trapping was conducted (6 November to 21 December 1981) in an orchard containing Cortland, McIntosh, and Red Delicious apples. Zoecon 1CP traps with synthetic lures were hung in trees in a Latin square design of three replicates with traps randomized each of 19 count days (Monday, Wednesday, and Friday at 1000 EST). A virgin female approximately 72 hours old was used in each replicate on 16 November, but only one male was captured compared to 141 males captured on that night in the traps baited with **1**. On two occasions, lure traps were checked hourly from dawn to dusk to determine flight occurrence. No males were taken during the daylight hours.
13. J. C. Miller, D. Kimberling, G. E. Daterman, unpublished results.
14. Individuals of the genus *Ennominae* (Geometridae), similar in external morphology and size to *O. brumata*, exhibited flight activity at 7°C and had a mean thoracic temperature of 17°C [G. A. Bartholomew and B. Heinrich, *J. Exp. Biol.* **58**, 123 (1973); B. Heinrich, *Insect Thermoregulation* (Wiley-Interscience, New York, 1981)].
15. Supported by NSF grant PCM 78–13241 and by PHS grant AI-12020. We thank J. Franclemont for identification of the Bruce spanworm specimens caught in New York.

22 February 1982; revised 12 May 1982

Sex and Handedness Differences in Cerebral Blood Flow During Rest and Cognitive Activity

Abstract. *Cognitive activity resulted in increased flow of blood to the cerebral hemispheres. The increase was greater to the left hemisphere for a verbal task and greater to the right hemisphere for a spatial task. The direction and degree of hemispheric flow asymmetry were influenced by sex and handedness, females having a higher rate of blood flow per unit weight of brain, and females and left-handers having a greater percentage of fast-clearing tissue, presumably gray matter.*

Sex differences in cognitive functioning have been extensively documented (*1*). A consistent finding is that males perform better than females in spatial tasks, whereas females have greater verbal fluency (*2*). These findings have been linked to research on sex differences in hemispheric specialization of function (*3, 4*). Evidence on the effects of brain lesions shows that for most right-handers the left and right hemispheres are specialized for verbal and spatial functioning, respectively (*5, 6*). However, females are less likely than males to suffer speech impairment after left hemispheric damage (*4, 6*) or to have deficits in spatial function after right hemispheric damage (*6*). Furthermore, when verbal and spatial tasks are presented for initial processing by the right or the left hemisphere in visual, auditory, or tactile stimulation modalities, females tend to show less lateralization (*7, 8*).

Handedness also seems to have an effect on cognitive functioning and this effect in left-handed subjects has been attributed to a lesser degree of hemispheric specialization. Left-handed patients recover faster than right-handed patients from speech disorders resulting from cortical lesions (*9*), and a significant proportion of left-handed patients have verbal deficits after injuries to the right hemisphere (*6*). Likewise, studies of lateralization of function in normal subjects indicate that left-handers show smaller and sometimes reversed effects in comparison with right-handers (*7, 10*).

The neurophysiological basis of these sex and handedness differences is unknown. We present data of isotope clearance in humans showing sex and handedness differences in regional cerebral blood flow (rCBF) and in the amount and distribution of fast-perfusing tissue, presumably gray matter.

Using the ^{133}Xe inhalation technique (*11*), we measured rCBF in 62 normal healthy volunteers aged 18 to 26. The sample included 15 right-handed males, 15 right-handed females, 15 left-handed males, and 17 left-handed females (*12*). Measurements were taken from each subject during periods of resting, solving verbal analogies, and solving a spatial line orientation task (*13*). The order of tasks was counterbalanced across subjects (*14*). For each measurement, the subject inhaled trace amounts of ^{133}Xe mixed with air, and the clearance of xenon from the brain was measured by 16 sodium iodide crystal detectors, with collimators 19 mm in diameter and 21 mm in length, placed anteriorly to posteriorly over eight homologous regions (*15*) of each hemisphere. Each detector measures flow in a cylinder of tissue that includes primarily cortex and underlying white matter, and to a diminished extent deeper structures.

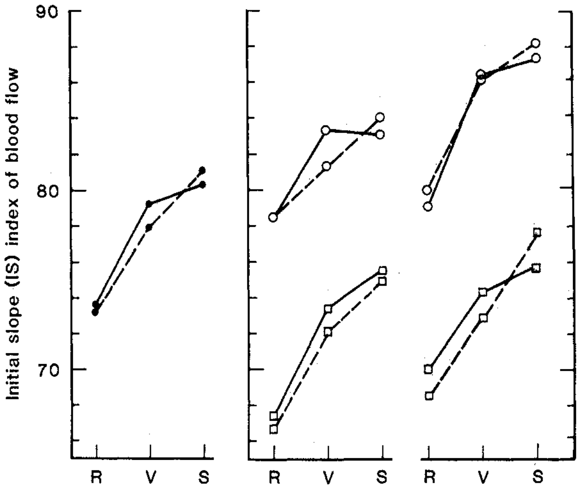

Fig. 1. Initial slope (*IS*) index of blood flow to the left (——) and right (- - - -) hemispheres for the total sample and for right- and left-handed females (○) and right- and left-handed males (□) during performance of resting (*R*), verbal (*V*), and spatial tasks (*S*).