

CHEMICAL TRIGGERS IN BREEDING CYCLES

Murray S. Blum

Department of Entomology, University of Georgia, Athens, Georgia 30602 USA

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Summary

The very widespread distribution of compounds that function as agents of intraspecific communication between the sexes emphasizes the great importance that these sex attractants can possess both as reproductive stimuli and species-isolating agents. The sex pheromones of both invertebrates and vertebrates are usually secreted as blends of natural products, the individual compounds possessing varying pheromonal activities. These chemical releasers of sexual behavior have been detected frequently as female-derived natural products but males in a variety of classes have been demonstrated to produce these pheromones, and in some cases attracted males secrete sex pheromones as well.

Sex pheromones have been adapted to function as mating stimulants by a great variety of aquatic plants and animals. Communication in aquatic media is often predicated on the secretion of pheromones that are quite volatile and readily diffusible, as are the cases for the sexual attractants of some brown algae and polychaete worms. A variety of copepod species possess sex attractants which may be derived from either females or males. Females of some copepod species promote male encounters by hopping and setting up hydrodynamical signals.

Blends of insect pheromones, particularly those of species of moths, beetles, and true bugs, have been studied in considerable detail, and it has been established that structural eclecticism of their sex pheromones is pronounced, especially in the case of the beetles. Maximum pheromonal activity is correlated with a variety of factors including ratios of

compounds, the concentrations of major pheromones, enantiomeric purity, and recognition of correct geometric isomers.

A wide variety of amphibians and reptiles appear to utilize sex pheromones and it is probable that more is known about the role of sexual attractants in the red-sided garter snake than that of any other species of vertebrate. Chemical releasers of sexual behavior have been extensively analyzed in rodents and a boar-produced steroid has been marketed for promoting artificial insemination in sows. The search for human-produced sexual excitants, with great commercial applications, continues unabated with periodic reports in the media that human sweat has yielded its great sexual secrets which can be made available to anyone who is willing to part with 50 quid. Fortunately, this recurrent hyperbole has not been identified with the availability of a commercial product with established pheromonal attributes.

1. Introduction

The evolution of mating systems predicated on the utilization of chemical releasers of sexual behavior undoubtedly reflected the fact that olfaction constituted the major sensory process available for signaling. Sexual attraction based on acoustical or optical stimuli is not widespread in the animal kingdom, whereas a host of disparate species secrete sex pheromones of great specificity that can rapidly attract large numbers of individuals of the opposite sex. Even over considerable distances, pheromonal attractants can be functional at very low light intensities (i.e., night), only requiring that the receiver individual be downwind from the emitter. In the case of some European silkmoths, males, whose plumose antennae have a large surface area that is ideally suited for trapping pheromonal molecules; have been reported to be attracted to females at distances exceeding 2 km? The underdeveloped female antennae are obviously poorly adapted as pheromone traps. Certainly the vulnerability of the sexes to avian predators is reduced if mating is a nocturnal phenomenon.

Plant and animal aquatic species have adapted a large variety of natural products to function as sex pheromones. Among marine plants, species of brown algae have been demonstrated to biosynthesize a diversity of compounds that subservise the function of gametic attractants. In a sense, these algal species have partitioned the environment by utilizing very idiosyncratic sex pheromones that are highly species-specific and in some cases capable of interfering with the pheromonal communication of other species. Similarly, sex pheromone utilization by a potpourri of marine animals including rotifers, nematodes, mollusks, annelids, and crustaceans documents the widespread evolution of sexual attractants in animals found in the aquatic environment.

Among the fungi, yeasts and mycelial fungi produce a diversity of mating pheromones that induce morphological changes in the receiver individuals. However, these fungi are particularly distinctive in producing sex pheromones that require the metabolic input of two strains of the same species. In essence, the synthesis of the final sex pheromone reflects the alternate production by the two strains of pheromonal intermediates, until the final precursor is converted to the physiologically active end product.

Chemical releasers of sexual behavior in arthropod species in the classes Crustacea,

Arachnida, and Insecta have been characterized in a large number of species. Insects have proven to be a particularly rich source of sex pheromones, especially species of true bugs, moths, beetles, and ants. Often mating is virtually an en masse phenomenon which contributes to a concentrated reproductive output provided that the males do not habituate to the pheromonal signal. The male silkworm, *Bombyx mori*, may be a typical lepidopteran by rapidly degrading the pheromone on its antennae immediately after electrophysiological stimulation. Males of ants, wasps, and bees form dense aggregations, pheromonally mediated, which act as mating sites for attracted females.

Vertebrates appear to be no less dependent on sex pheromones than invertebrate species. Lampreys, boney fish, amphibians, reptiles, and a variety of mammals are reported to promote mating by the utilization of sex pheromones. In a rare case of the commercial utilization of a vertebrate sexual stimulant, a synthetic compound, identical to a boar excitant, is presented to a sow, in estrous, in order to induce a copulatory position that is suitable for artificial insemination. This compound, which is ordinarily present in a secretion on the muzzle of the male, is introduced as an aerosol that is identified as "Boar Mate."

While sex pheromones have been characterized in rodents and even elephants, the search for chemical releasers of sexual behavior in humans has not been particularly rewarding. Obviously, the isolation and identification of sex pheromones from humans (female or male) would be of considerable commercial interest, but repeated efforts to achieve this objective do not appear to have been successful. Collections of dermal exudates have yielded products that have been ultimately marketed (and very costly at that) with claims that one's sex life will improve considerably if this product is applied to one's body. At this juncture the only unambiguously identified sexual pheromonal system that has been recognized in humans is a female-produced secretion that synchronizes the menstrual cycles of women living together in small groups. This phenomenon was previously known as the "French boarding house syndrome", after it was observed that the menstrual cycles of young women living together in Parisian rooming houses became synchronized after they moved from rural France.

On the other hand, a human "pheromone" is available for women, although the product is completely artificial. A perfume, "Pheromone", that is the mainstay of a company, can be easily obtained, at a price. Until someone establishes that human beings produce sexually stimulating volatiles (releaser pheromones that produce a rapid response), it appears that the artificially produced product may constitute the only "Pheromone" that is available.

2. Sex Pheromones as Reproductive Stimuli

Many animals constitute pheromone factories that synthesize a variety of these compounds in glands whose contents may be stored in glandular reservoirs distributed throughout the body. Because of their critical role in reproduction, optimization of sex pheromone perception has probably been emphasized in both plants and animals. The foundation for this pheromonal analysis reflects the isolation and identification, more than 40 years ago, of bombykol, a fatty acid derivative that is the sex pheromone of the silkworm. Today we know a great deal about chemical communications in moths and

other animals, especially in regard to chemical structures, biological activities, biosyntheses, and activities of related compounds. On the other hand, our understanding of how the information in volatile molecules can be transduced into an electrical signal by a nerve cell is not extensive. Nevertheless, the bombykol paradigm provides considerable insight into a variety of factors that have contributed to sex pheromones being so eminently adaptive in promoting mating.

Bombykol, a 16 carbon alcohol with two sites of unsaturation, possesses a highly distinctive structure which should contribute considerably to the specificity of the signal. Electrophysiological recordings from male *B. mori* antennae indicate single-molecule sensitivity for the sex pheromone. In terms of chemical communication, this is equivalent to the theoretical detection limit. In addition, in order for the male to follow turbulent wind-borne pheromone trails, he must exhibit a fast response time, and values of 0.5 seconds have been measured. Obviously, molecular mechanisms identified with antennal receptor proteins, binding proteins, and degrading enzymes must exhibit rapid responses in order to optimally support this chemical sensor. A rapid degradation of bombykol would avoid nonadaptive prolongation of the signal molecules. Investigations of the fate of bombykol on the male antennae support this molecular scenario.

The plumose antennae of male silkworms are covered with sensilla, the so called olfactory 'hairs.' Chemical signals are detected by the male with an abundance of olfactory sensilla, numbering 15,000-20,000 sensilla. Significantly, half of these olfactory sensilla are specialized for the detection of bombykol. Since the male does not feed, olfactory specialization is clearly dedicated to processing information related to the sex pheromone.

In terms of particulars, the male silkworm and bombykol provide a useful olfactory duet for examining the adaptive utilization of a sex pheromone. The sex pheromone is of great structural distinctiveness, resulting in a molecule that can provide considerable species specificity to the receiver (male *B. mori*). Detection on the part of the male reflects a degree of hypersensitivity to the sex pheromone that is identified with single molecule sensitivity. Thus, the silkworm male has been able to adapt its pheromonal response to function at the theoretical detection limit of chemical communication. Accompanying this great olfactory sensitivity is a very rapid response to wind-borne pheromone trails as a device for optimizing the mating potential. And certainly the great sensitivity of the male to its sex pheromone must be greatly enhanced by the presence of thousands of specialist chemoreceptors rendering the antennae bombykol traps.

3. Glandular Origins of Sex Pheromones

Although the anatomical origins of sexual attractants and excitants are very eclectic, it is clear that the glandular producers of these compounds are highly adaptive in terms of releasing their products so as to optimize their reproductive potential. Anatomical specializations notwithstanding, these chemical releasers of sexual behavior must be delivered to intraspecific targets at concentrations that are highly stimulatory.

Fertile female gametes of a variety of species of marine brown algae utilize sex pheromones to attract conspecific males which first release spermatozoa and then are subsequently attracted to the "calling" females. The spermatozoal release is exceptional because it represents one of the fastest signal response actions identified in the plant kingdom.

Among animals, sex pheromones are synthesized both in glands that appear to have arisen *de novo* for the biogenesis of these compounds and in tissues that are considered to be dedicated to other metabolic functions. In the rotifer *Brachionus plicatilis*, a mate-recognition pheromone is concentrated in the corona or foot. Volatile sex pheromones have been identified in the coelomic fluid of several species of polychaete worms in the genera *Arenicola*, *Platynereis*, and *Nereis*. In *A. marina* male spawning water elicited pumping behavior in females, ensuring transport of spermatozoa into the female's tube. On the other hand, the pheromone-fortified coelomic fluid of males of *Platynereis dumerilii* initiates egg release in swarming females.

In insects the biosynthesis of chemical releasers of sexual behavior occurs in a variety of tissues, particularly in the head and abdomen. Females of diverse species produce sex pheromones in glands located near the tip of the abdomen, externalizing these pheromone factories at the appropriate mating time. This activity is described as "calling" behavior, in reference to the female's apparent receptivity as she broadcasts her sex pheromone. This behavior, which is particularly characteristic of moths in a large number of genera, has also been detected in many species of bees, ants, beetles, and termites. Virgin queens of some ponerine and myrmicine ant species are distinctive in signaling with sex pheromones produced in the poison gland of the sting. On the other hand, the occurrence of a diversity of other sex pheromone glands is characterized by great anatomical variation, often as male-derived structures.

In the Hymenoptera, male carpenter ants (*Camponotus* spp.) produce sex pheromones in mandibular glands that both stimulate female flight and function as sexual attractants. Bumblebee queens have also adapted these glands as the source of a pheromone that releases copulatory behavior in males. Queen honey bees (*Apis mellifera*), often at altitudes of at least 100 meters, attract drone bees with a powerful sex pheromone produced in the mandibular glands. By contrast, males of many species of true bugs (Heteroptera) often synthesize their sex pheromones in hypertrophied metathoracic or dorsal abdominal glands. Males of many species of moths (Tortricidae), when close to the "calling" female, secrete glandular constituents which can function as sexual stimulants. The pyralid wax moth, *Galleria melonella*, emits a female attractant from costal wing glands. Thoracic sex attractants are also liberated by female grasshoppers (*Romalea* and *Taeniopoda* species) from glands present in the metathoracic spiracles. Males of some species of hepialid moths are particularly distinctive in emitting female attractants from tibial scent brushes located on the hind legs that have lost their normal functions. By contrast, dipterous (e.g., flies) sex pheromones are often identified with long-chain cuticular hydrocarbons that stimulate males to land in the vicinity of the female.

Vertebrates also secrete sex pheromones from glands distributed throughout the body, the locations of which appear to be sometimes correlated with the mating behaviors of

the pheromone producers. Male sea lampreys (*Petromyzon marinus*) discharge sex pheromones as urinary products that elicit a strong response in spawning-run females. Sexually ripe male sticklebacks (*Hypsoblennius* spp.) also secrete sex pheromones in the presence of receptive females but in this case the chemical releasers of sexual behavior are present in the seminal ejaculate. On the other hand, female goldfish secrete steroidal sex hormones of presumed ovarian origin.

In the last decade the presence of sexual excitants in a variety of terrestrial vertebrates has been confirmed. A pheromone has been isolated from the submandibular (mental) gland of the male terrestrial salamander, *Plethodon jordani*, and it has been demonstrated that application of the pheromone to the female greatly increases her receptivity. On the other hand, males of the newt *Cynops pyrrhogaster* produce a sex pheromone in the cloacal gland. Recently, parotid and rostral glands of males of the tree frog *Litoria splendida* have been identified as the source of an aquatic sex pheromone. The glands, situated in the front and rear of the head, appear to produce a species-specific secretion that is highly attractive to the female.

It is probable that the most thoroughly analyzed sex pheromone system among vertebrates is that of the garter snake *Thamnophis sirtalis parietalis*. Pheromonal skin lipids produced by the females are detected by the males with their tongues and the large surface area of the female's skin generally attracts enough males to form a dense mating ball.

Mammalian sex pheromones have been difficult to characterize possibly because the behavioral repertoires of mammals are not easily standardized. However, several significant sex pheromonal systems have been detected in a variety of mammals. For example, the vaginal discharge of the female hamster clearly possesses copulation-inducing activity for the male and must be regarded as a true sex pheromone. A commercially available sex pheromone for sows, inducing a copulatory response, is based on compounds transferred from the muzzle of the boar. This commercialization of a proven mammalian sexual stimulant is exceptional and reflects both the identification of the boar pheromones and the availability of a rapid-response bioassay for the sow.

A sex pheromone has been identified as a product of the female Asian elephant, *Elephas maximus*. This compound, which is discharged as a urinary constituent, elicits several mating-associated behaviors in male elephants. Males exhibit flehmen responses to the discharge of urine, tasting and smelling the discharging urine. Flehmen responses can occur in other mammals (e.g., bovines) and subsequent olfactory responses to pheromones may reflect the utilization of the vomeronasal organ (VNO), an olfactory system independent of the classical system for odor detection. There is no strong evidence for human beings processing odorants with their VNO.

4. Sex Pheromones as Eclectic Natural Products

The evolution of sex pheromones by multifarious plants and animals is consistent with the great structural diversity that characterizes these compounds which are often idiosyncratic natural products. Although it is beyond the scope of this review to

present an inclusive summary of the chemistry of these pheromonal products, it seems appropriate to identify, whenever possible, the particularly distinctive sex pheromones produced by the organisms that are treated. Whenever possible, the adaptive significance of these chemical releasers of sexual behavior will be emphasized.

Species of brown algae in the advanced orders Laminariales, Desmarestiales, and Sporochnales synthesize cyclic hydrocarbons that function as novel marine sex pheromones. 6-Substituted cyclohepta-1,4-dienes (e.g., ectocarpene) are generated from vinylalkenylcyclopropane (pre-ectocarpene), which in some algal species functions as a powerful male attractant.

The biosynthesis of fungal pheromones is identified with several novel developments. For example, all characterized saccharomycetous pheromones are small linear peptides containing 9 and 15 amino acids. Significantly, the pheromones of heterobasidiomycetous yeasts are lipopeptides with a carboxy-terminal S-farnesylated cysteine residue that is often additionally carboxy-methylated. This suggests that this type of hydrophobic modification is advantageous in signal transmission between yeast cells. The increase in hydrophobicity resulting from the introduction of a farnesyl residue constitutes a novel biosynthetic development in yeasts.

Investigations on the marine sand-dwelling protozoan ciliate *Euplodes raikovi* demonstrate that mating type-specific pheromones secreted into the environment, regulate conjugation in this protozoan. The mating pheromone, euplomone r-1, is a diffusible polypeptide with a molecular weight of about 12,000.

A large glycoprotein, probably functioning as a contact sex pheromone, has been identified in the rotifer, *Brachionus plicatilis* (Rotifera). This is the first pheromone characterized from a zooplankter, and it is distinguished by the presence of oligosaccharides containing N-acetylglucosamine and mannose and fucose residues.

Varieties of chemical releasers of sexual behavior have been identified as products of nereidid polychaetes (Annelida). Marine polychaetes in several genera secrete pheromones in the coelomic fluid which include different isomers of 5-methyl-3-heptanone, as well as 3,5-octadien-2-one, uric acid, and glutathione derivatives. In the case of the two ketones, the sexes of *Platynereis dumerilii* each produce a different enantiomer (optical form) of 5-methyl-3-heptanone, which should considerably increase the specificity of the signal for the males and females.

The major research thrust on the chemistry of sexual pheromones has been undertaken with insect species since about 1960. At this juncture the structures of the sexual releasers of a multitude of moths (Lepidoptera), beetles (Coleoptera), ants, bees, and wasps (Hymenoptera), cockroaches (Orthoptera), and flies (Diptera) have been determined. Although these compounds are usually present as mixtures, maximum pheromonal activity is generally associated with a few specific structures. An examination of the structures of these highly active insect sex pheromones can provide important insights into the biosynthetic versatility of these abundant arthropods.

For nearly 25 years adults of female moths constituted the major experimental animals

for investigating sex pheromone structure, biosynthesis, and field activities. For the most part, the active compounds have proven to be unsaturated and polyunsaturated fatty acid derivatives. Geometrical isomers of alkenyl acetates are commonly produced, and these key sex pheromones are often accompanied by unsaturated alcohols and saturated acetates. The pheromonal blend of *Archips argyrospilus*, consisting of (*Z*)-11-tetradecenyl acetate, (*E*)-11-tetradecenyl acetate, (*Z*)-9-tetradecenyl acetate, and dodecyl acetate, is characteristic of the classes of compounds produced by female moths. In some cases polyunsaturated aldehydic sex pheromones are secreted by females, and these compounds are probably highly specific male attractants. Females of the salt marsh caterpillar, *Estigmene acraea*, utilize diunsaturated((*Z,Z*)-9,12-octadecadienal), triunsaturated (*Z,Z,Z*)-9,12,15-octadecatrienal), and related compounds, as nocturnal attractants for aggregated males.

Structural diversity characterizes the sexual attractants secreted by females and males in a variety of families. Queens of the honey bee, *Apis mellifera*, attract drone bees with a very distinctive sex pheromone, (*E*)-9-oxo-2-decenoic acid. Aromatic sex pheromones such as methyl anthranilate, methyl 6-methylsalicylate, and mellein are utilized as female stimulants by male carpenter ants (*Camponotus* species). In contrast, sex pheromonal specificity is achieved by utilizing distinctive optical isomers. Females of sawfly species in the genus *Neodiprion* attract males with the acetate ester of 3,7-dimethylpentadecan-2-ol, a compound with three potential centers of optical activity. Some species are attracted to the (*S,S,S*) isomer of this rather long-chain acetate.

Well-developed exocrine glands are associated with the synthesis of characteristic sex pheromones by males of many species of true bugs (Heteroptera). *Podisus maculiventris*, the spined soldier bug, releases a pheromonal blend dominated by (*E*)-2-hexenal and (+)-*R*-terpineol which, in combination, serve as a potent sex pheromone. However, in some species of true bugs the chemistry of the sex pheromone is correlated with the presence of geographic strains. Comparison of Japanese and North American strains of the southern green stink bug, *Nezara viridula*, demonstrated a major chemical difference in their sex pheromones. The Japanese strain produces a pheromonal blend containing nearly equal amounts of *trans*(*Z*)-bisabolene epoxide and *cis*(*Z*)-bisabolene epoxide whereas the North American strains synthesize pheromones in which *cis*(*Z*)-bisabolene epoxide greatly predominates. In contrast, qualitative variation distinguishes the sex pheromone of species in the genus *Euschistus*. The sexual attractant of male *E. obscurus* is dominated by methyl (2*E*,4*Z*)-dodecadienoate along with methyl 2,6,10-trimethyltridecanoate. On the other hand, the major volatile secreted by *E. heros* is 2,6,10-trimethyltridecanoate.

In the Orthoptera, the chemistry of the sex pheromones of cockroaches has received considerable attention. Females of *Periplaneta americana*, the American cockroach, emit their sex pheromone from the body surface. The pheromone, (1*Z*,5*E*)-1,10(14)-diepoxy-4(15),5-germacradien-9-one, is a powerful sexual stimulant for males. The sexual stimulant from the German cockroach, *Blattella germanica*, is 3*S*,11*S*-dimethyl-2-nonacosanone, a long-chain ketone with two optically active centers.

Diversity is a hallmark of coleopterous sex pheromones. The number of beetle species

is fulsome, and it will not prove surprising if structural multifariousness of these chemical releasers of sexual activity accompanies this explosion of beetle species. For example, females in the dermestid genus *Trogoderma* release sex pheromones containing (*E*) or (*Z*) 14-methyl-8-hexadecenal whereas a simple aromatic compound, phenol, is utilized by the grass grub beetle, *Costelytra zealandica* (Scarabaeidae).

Another scarab, the Japanese beetle, *Popillia japonica*, produces a sexual attractant, (*R,Z*)-5-(-)-(1-decenyloxy)cyclopentan-2-one, which requires enantiomeric purity in order to exhibit maximum activity. By contrast, females of the scarabs *Anomala rufocuprea* and *Blitopertha orientalis* produce methyl 5-(*Z*)-tetradecenoate and a mixture of (*Z*)- and (*E*)-tetradec-7-en-2-one, respectively, none of which are optically active. Scarab sex pheromone diversity is further emphasized in the case of the large black chafer *Holotrichia parallela*, which utilizes a simple amino acid derivative, L-isoleucine methyl ester, as a very active attractant for males. The identification of (*R*)-linalool as a key component of this pheromone system further emphasizes the structural eclecticism that characterizes beetle sex pheromones.

In the last decade considerable progress has been made on studies on the chemistry of vertebrate sex pheromones. The urine of male sea lampreys, *Petromyzon marinus* (Agnatha), contains steroids that elicit a response in female lampreys. Similarly, in boney fish steroidal hormones function as sex hormones in male goldfish and salmon.

Amphibian sex pheromones have been recently isolated and identified in salamanders and a frog. A proteinaceous pheromone, termed plethodontid receptivity factor, has been isolated from the submandibular gland of the male terrestrial salamander, *Plethodon jordani*. This protein, which increases female receptivity, is the second sex pheromone identified in salamanders, the first being sodefrin, a decapeptide produced by males of an aquatic-breeding species, *Cynops pyrrhogaster*. A larger peptide, splendipherin, has been identified from the parotoid and rostral glands of the male tree frog, *Litoria splendida*. This compound contains L-amino acids as confirmed by the synthesis of L-splendipherin which possessed the same pheromonal activity as the natural product. Females of the red-sided garter snake, *Thamnophis sirtalis parietalis*, produce a contact sex pheromone, which is in admixture with a proteinaceous secretion. The sex pheromone is a mixture of C₂₉-C₃₇ saturated and unsaturated methyl ketones which are of such low volatility that perception by the male requires extended contact chemoreception.

Sex pheromones have been identified in a variety of mammalian species. In common with male boney fish, steroids have been identified in boars and demonstrated to possess sexual releaser activity for sows. Synthetic pheromones, marketed under the name "Boar Mate," have been utilized for the artificial insemination of sows. In contrast, females of the Asian elephant, *Elephas maximus*, release an aliphatic sex pheromone in their urine that can be readily detected by males. The pheromone has been identified as (*Z*)-7-dodecen-1-yl acetate.

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products as reproductive enhancers].

Biographical Sketch

Murray S. Blum received his B.S., M.S., and Ph.D. in entomology at the University of Illinois minoring in chemistry, biochemistry, and biophysics. He taught and undertook research at Louisiana State University and the University of Georgia, retiring as an Emeritus Research Professor. His initial research was in toxicology following which he undertook studies in chemical ecology, specializing in the chemistry of social insect pheromones and defensive compounds (allomones). Ultimately his investigations encompassed a wide variety of arthropods, particularly species of ants and bees which served as models for studying the chemical basis of insect sociality.

In addition, these social insects constituted ideal candidates for investigating the chemistry and mode of action of poison gland products (venoms) of a wide variety of ants, bees, and wasps. He also studied the novel toxic proteins produced by mites that were structurally characterized and demonstrated to belong to a new class of toxins. Analytical, biochemical, and behavioral studies of a variety of arthropods were used to examine their chemical defenses.

He has undertaken field research in North America, South America, Europe, Asia, Australia, and Africa. He has taught ecology courses in Costa Rica and presented lecture programs at the University of Bourgogne and the University of Natal. He is a fellow of the American Association for the Advancement of Science and was appointed Research Professor at the University of Georgia. He was appointed a Senior Postdoctoral Fellow of the U.S. National Science Foundation at the University of Bristol and a Fulbright Fellow at the University of Paris (VI).

Dr. Blum has published more than 300 papers, reviews, and chapters in a variety of publications. He has edited books on sexual selection in insects (with his wife N.A. Blum), insect physiology, and the chemistry and functions of alkaloids. He authored a book on the chemical ecology of arthropod allomones that dealt with the chemistry, functions, mode of action, and biosynthesis of these eclectic natural products.