

Male Pheromones in Moths

Reproductive Isolation, Sexy Sons, and Good Genes

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Introduction

The amount of information published on the pheromones of moths is voluminous, and the great majority of it focuses on the female attractants of pest insects because of their economic importance (Cardé and Minks 1997; Blomquist and Vogt 2003; Cardé and Millar 2004; El-Sayed 2011; Ando 2012). From the perspectives of an animal behaviorist and an evolutionary biologist, however, male pheromones are of equal if not greater interest. Male courtship pheromones and the structures and behaviors associated with their release are the grist of sexual selection. This chapter is devoted to male moth pheromones, their biology, chemistry, and evolution. It will begin with a discussion of the genetic architecture of sex determination in Lepidoptera and how it predisposes males to extravagance. We will describe the benefits accrued by females who exercise mate choice based on male courtship pheromones, and we will emphasize empirical tests of the models for sexual

selection through mate choice using the case study of *Utetheisa ornatrix* (Erebidae). We will also describe the diversity of male pheromone releasing structures, the propensity for diet dependence in male pheromones, and the unusual behaviors and physiology associated with pheromone precursor collection. Our primary objective is to demonstrate that male pheromones are worth studying and their stories are some of the most interesting in chemical ecology. Previous reviews of male courtship pheromones in moths include those of Birch (1970a, 1970b, 1972, 1974), Weatherston and Percy (1977), Haynes and Birch (1985), Tamaki (1985), Birch and Hefetz (1987), Baker (1989), Birch et al. (1990), and Krasnoff (1997).

Genetic Architecture in Lepidoptera

Lepidopterans and birds share a “reversed” genetic architecture that determines sex. In both birds and Lepidoptera, and

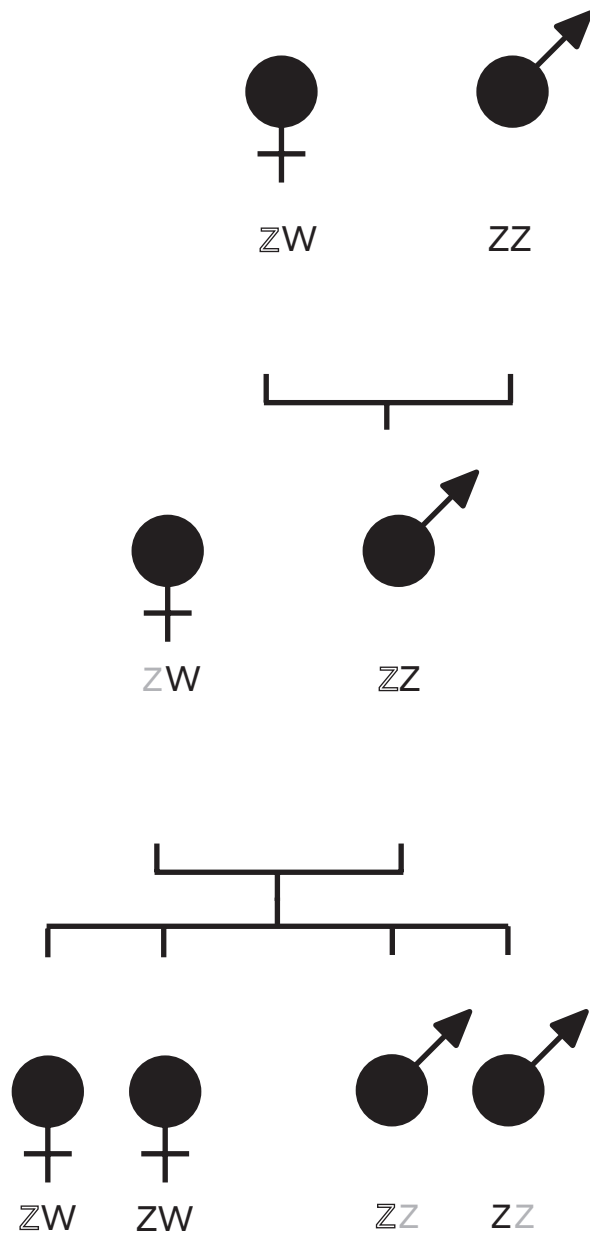


FIGURE 12.1 Inheritance of a Z-linked mating preference. The white Z represents the sex chromosome bearing the preference gene(s), shown here to be introduced into the lineage by the paternal grandmother. The gray Z is that possessed by the mother but not transmitted to daughters. Therefore, granddaughters can only acquire Z-linked gene(s) by way of their father (after Iyengar et al. 2002 and reprinted with permission from *Nature*).

unlike humans, the female is the heterogametic sex. The implications of this are profound and may have preadapted males to evolve exaggerated traits in these prominent taxa (Reeve and Pfennig 2003; Iyengar and Reeve 2010). Female moths are ZW and males are ZZ (figure 12.1). The protected invasion theory of Reeve and Shellman-Reeve (1997) predicts that female mating preference alleles should be inherited from their fathers and will be transmitted to all of a female's sons that have the father's attractive trait (Iyengar et al. 2002). Such alleles will be less vulnerable to chance loss when rare and more likely to fuel the evolution of exaggerated male

traits through sexual selection. The protected invasion theory also predicts that the female preference alleles will be correlated with the preferred male trait alleles, a prerequisite for both Fisherian and good genes models of sexual selection (see below). Experimental evidence for the paternal inheritance of a female moth's mating preference and a correlation of female mating preference and male target traits have been found in the mating system of *Utetheisa ornatrix* (see case study).

Mate Choice

Given the diversity of scents and disseminating structures in male moths (see figure 12.2 and Table 12.1), there can be little doubt that male courtship pheromones have arisen through sexual selection (Birch et al. 1990). The roles played by males and females in moth courtship are consistent with those predicted by disparities in parental investment between the two sexes (Trivers 1972; Thornhill 1979; Cardé and Baker 1984). In keeping with their large contribution to offspring in the form of nutrient-rich eggs, females play a less costly role in the communication system (Hammerstein and Parker 1987). Females generally remain stationary and emit vanishingly small amounts of pheromones that draw males upwind to them. Females are said to be the limiting, choosy sex because of the time and energy necessary to produce and replenish eggs (Trivers 1972; Andersson 1994) and they maximize their fitness through the choice of high-quality mates. Because of their smaller per capita contribution to offspring and ability to replenish sperm quickly, males, the non-limiting sex, bear the cost of searching for and competing for females. Male courtship pheromones with their associated elaborate disseminating structures frequently mediate female mate choice (Baker and Cardé 1979; Greenfield 2002) and males maximize their fitness through multiple matings. Phelan (1992) nicely summarized and extended the logic behind the disparate roles of the sexes in moth chemical communication in his asymmetric tracking hypothesis.

Beyond these general patterns the critical questions are those concerned with the specific benefits of female mate choice. In this sense studies of moth courtship and the role of male pheromones have mirrored the trends of the sexual selection literature over the last three decades (Bradbury and Andersson 1987).

Species or Mate Recognition

One of the key ideas of modern biology is the concept of reproductive isolation. It is the foundation of the biological species concept and fundamental to the process by which species form and are maintained (Coyne and Orr 2004). It has been suggested that one important function of male scent disseminating structures in moths and the pheromones that they release is that they promote species recognition, maintain reproductive isolation, and prevent hybridization and the loss of fitness associated with it. Evidence for these functions for male pheromones, however, is scant (Birch et al. 1990). An exception is an insightful meta-analysis by Phelan and Baker (1987) in which they measured whether the presence of scent disseminating structures in members of five families of moths (Phycitinae of North America and Europe, Yponomeutidae of Japan, Tortricidae and Noctuidae of Great

Britain, and Ethmiidae from the western United States) was correlated with sharing the same host plant. They reasoned that if two species shared a host plant they would be more likely to make mating mistakes increasing the relative strength of selection for species recognition. They found a significant correlation between sharing a host plant and the presence of male scent disseminating structures across these groups and concluded that male pheromones promote reproductive isolation. Further, they suggest that the mechanism for the evolution of reproductive isolation was runaway sexual selection, a mechanism consistent with the pattern of male pheromones arising repeatedly and independently across taxa. Although correctly criticized for analyzing species as independent units and for not analyzing independent evolutionary events phylogenetically (Krasnoff 1997; Greenfield 2002), the study stands alone as the most comprehensive cross-taxa test of the species-recognition hypothesis in moths. Additional meta-analyses with proper controls are needed (Krasnoff 1997). For a model phylogenetically controlled study of the evolution of male moth pheromones see Wagner and Rosovsky (1991) who studied the evolution of male scent disseminating structures in the Hepialidae, a primitive family of Lepidoptera.

Additional evidence for a species-recognition function has been gathered by focusing on small clades of insects like *Ephestia elutella*, *Cadra figulilella*, and related phycitinae Pyralidae (Phelan and Baker 1990a, 1990b, and references therein) which have complex courtship sequences, the choreography of which involve the delivery of male pheromones. Similarly the multicomponent pheromone blend of *Grapholita molesta* and a complex courtship ritual point to a species-recognition function (Baker and Cardé 1979; Baker et al. 1981). The role of male courtship pheromones in reproductive isolation in members of the genus *Heliiothis* (Noctuidae) has received renewed interest (Hillier and Vickers 2004, 2011; Hillier et al. 2007) and the recent studies of Lassance and Löfstedt (2009) suggest a similar function for the hairpencil pheromones of *Ostrinia* species (Crambidae) (for additional examples see Table 12.1).

Yet in some moth groups like the Arctiinae of the Erebiidae (formerly the Arctiidae) there is a profound lack of species specificity in male courtship pheromones. This is true despite efforts to identify minor pheromone components (Schulz 2009) and pheromone components, when they do exist, can vary with diet (Krasnoff and Roelofs 1989). This is difficult to reconcile with a species-recognition function and requires a different focus, that of mate assessment.

Mate Assessment

Biologists have also looked at mating systems from the perspective mate assessment, usually exercised through female preferences for male traits (Andersson 1994; Johansson and Jones 2007). Traditionally the benefits of mate assessment have been divided into discrete categories: direct phenotypic or material benefits and indirect genetic benefits including good genes and sexy sons (Fisherian runaway sexual selection). It is important to note that these are not mutually exclusive and indeed may coexist in the same population. We briefly summarize the evidence for mate assessment based on male courtship pheromones in moths and benefits that females may accrue through mate choice.

Benefits of Mate Assessment

Direct (Phenotypic) Benefits

In some species, females have a propensity to choose mates based on tangible resources provided to the female during courtship. Direct (phenotypic) or material benefits are the result of nongenetic quantities that have a positive impact on the survivorship and offspring production of the female such as enhanced paternal care (Davies 1992), the transmission of antipredator defensive chemicals (González et al. 1999), and the acquisition of nutrient-rich nuptial gifts (Thornhill and Alcock 1983; Gwynne 1984).

In Lepidoptera, sperm, nutrients, and defensive chemicals are transferred from the male to the female in the form of a spermatophore during prolonged copulation (Thornhill and Alcock 1983; Dussourd et al. 1988, LaMunyon and Eisner 1994; Vahed 1998). The nongametic constituents have been referred to as nuptial gifts (Thornhill and Alcock 1983) and they can represent a significant fraction of a male's body mass (LaMunyon and Eisner 1994). Much of the information on direct phenotypic benefits comes from tiger moths (Erebidae, Arctiinae) and/or the convergent evolutionary system in the Ithomiine and Danaine butterflies (not covered here; for an excellent review see Boppré 1990). The spermatophores of some arctiines contain nutrients plus pyrrolizidine alkaloids—PAs (Dussourd et al. 1988), defensive chemicals sequestered during larval life (Hartmann 2009) and/or collected from plant sources in adulthood—pharmacophagy (Conner and Jordan 2009). Male pheromones in this group are dihydropyrrolizines derived from the necine base of the PAs with the main pheromonal components being danaidal, hydroxydanaidal, and rarely danaidone (Schulz 2009). The PA-derived pheromones have the potential to act as indicators of male quality in the form of alkaloid load, potential to transfer alkaloids to the female, and additional correlated phenotypic characters.

In the eretid *Cosmosoma myrodora* (figure 12.2) the nuptial gift is bestowed in spectacular fashion (Conner et al. 2000). The male possesses a ventral abdominal pouch filled with deciduous flocculent scales laden with the pyrrolizidine alkaloids intermedine and lycopsamine obtained through adult pharmacophagy. During courtship the male showers the female with up to four doses of flocculent. The alkaloidal cloak bestowed by the male at least temporarily protects the female from predation (as evidenced by the experiments showing that *Nephila clavipes*, the golden orb-weaving spider, cut females cloaked in flocculent scales from their webs). Males also transfer additional alkaloids to the female in a more traditional spermatophore. Males that do not utilize the flocculent in courtship are discriminated against by virgin females.

In erebids the pyrrolizidine alkaloids transferred during courtship are quickly transferred to the eggs (Dussourd et al. 1988). In species like *Cosmosoma* this is particularly critical, because the female does not normally forage for alkaloids on her own. As predicted by the parental investment theory described above, it is the male that takes on the costly task of collecting alkaloids and females “forage” only by mating with alkaloid-laden males. The critical question in species with nuptial gifts is whether direct material benefits are the prime benefits for females or whether indirect genetic benefits are more important.

TABLE 12.1
Moth species with known male courtship pheromones (restricted to those with chemical characterization and measured female response)

Taxon	Behavioral role ^a	Disseminating structure	Chemical components	Female response	Male sound production	References
Tortricidae						
<i>Grapholita molesta</i>	RI MA SS	Abdominal hair pencils	Methyl 2-epijasmonate trans-ethyl cinnamate	Short range attraction of female		Baker and Cardé (1979) Baker et al. (1981) Nishida et al. (1982) Löfstedt et al. (1989, 1990)
Pyralidae						
Pyraloidea						
<i>Corcyra cephalonica</i>	RI	Wing glands	(E,E)-farnesal (Z,E)-farnesal	Short range attraction of female	+	Spangler (1987) ^s Zagatti et al. (1987)
<i>Eldana saccharina</i>	RI MA	Wing gland Abdominal hair pencils	(E)-3,7dimethyl-6-octen-4olide (many additional components) Vanillin 4-hydroxybenzaldehyde (many additional components)	Short range attraction of female Female acceptance	+	Kunesch et al. (1981) Bennett et al. (1991) ^s Burger et al. (1993) Zagatti (1981) Zagatti et al. (1981)
<i>Ephesia elutella</i>	RI MA	Costal fold wing gland	(E)-phytol γ -decalactone γ -undecalactone	Ventral flexion of abdomen	+	Krasnoff and Vick (1984) Phelan et al. (1986) Trematerra and Pavan (1994) ^s
<i>Galleria mellonella</i>	RI	Wing glands	<i>n</i> -undecanal <i>n</i> -nonal	Attracts female (minor components including aldehydes, alcohols, and ketones)	+	Roller et al. (1968) Spangler (1986) ^s Lebedeva et al. (2002)
<i>Achroia grisella</i>	SS	Wing glands	<i>n</i> -undecanal <i>n</i> -11-octadecenal	Excites female	+	Dahm et al. (1971, but see Greenfield and Coffelt 1983) Spangler (1984) ^s Collins et al. (1999) ^s Jang and Greenfield (1996) ^s Jia and Greenfield (1997) ^s Jang et al. (1997) ^s Jang and Greenfield (2000) ^s

Crambidae						
<i>Ostrinia nubilalis</i>	RI MA	Abdominal and genital hair pencils	Hexadecanyl acetate (Z)-9 hexadecenyl acetate (Z)-11 hexadecenyl acetate (Z)-14 hexadecenyl acetate	Female acceptance behavior	Lassance and Löfsted (2009) Nakano et al. (2008)*; sound in <i>O. furnacalis</i>	
Noctuoidea						
Erebidae						
Arctiinae						
Arctiini						
<i>Cretonotus gangis</i>	MA	Abdominal coremata	R-(-)-hydroxydanaidal	Lek formation	Schneider et al. (1982) Bell and Meinwald (1986) Wunderer et al. (1986)	
<i>Cretonotus transiens</i>	MA	Abdominal coremata	R-(-)-hydroxydanaidal	Lek formation	Schneider et al. (1982) Bell et al. (1984) Bell and Meinwald (1986) Wink et al. (1988) Egelhaaf et al. (1990) Wink and Schneider (1990) von Nickisch-Roseneck and Wink (1994) Wunderer et al. (1986)	
<i>Estigmene acrea</i>	MA	Abdominal coremata	Hydroxydanaidal	Lek formation	Willis and Birch (1982) Krasnoff and Roelofs (1989) Davenport and Conner (2003) Jordan et al. (2005, 2007) Jordan and Conner (2007)	
<i>Phragmatobia fuliginosa</i> (L.)	lost	Abdominal coremata	Danaidal Hydroxydanaidal	Tymbalar sound	Krasnoff et al. (1987) Krasnoff and Roelofs (1989, 1990) von Nickisch-Roseneck and Wink (1993)	
<i>Pyrrharctia isabella</i> (JE Smith)	lost	Abdominal coremata	Hydroxydanaidal	Tymbalar sounds	Krasnoff et al. (1987) Krasnoff and Yager (1988) Krasnoff and Roelofs (1989, 1990)	
<i>Callimorphini</i> (s.l.)						
<i>Euplagia quadripunctataria</i>	MA	Abdominal coremata	Hydroxydanaidal Danaidal Ethyl esters	EAG response	Schneider et al. (1998)	

(continued)

TABLE 12.1 (continued)

Taxon	Behavioral role ^a	Disseminating structure	Chemical components	Female response	Male sound production	References
<i>Haploa clymene</i>	MA	Abdominal coremata	Hydroxydanaidal	Female acceptance		Davidson et al. (1997)
<i>Pareuchaetes pseudoinsulata</i> (Rego Barros)	MA	Abdominal	Hydroxydanaidal	EAG response		Schneider et al. (1992)
<i>Utetheisa ornatrix</i>	MA	Genitalic coremata	R(-)-hydroxydanaidal	Female acceptance	-	Conner et al. (1981)
	MB					Dussourd et al. (1988)
	GG					Dussourd et al. (1991)
	SS					Lamunyon and Eisner (1993)
	SSP					Lamunyon and Eisner (1994)
						Iyengar and Eisner (1999a)
						Iyengar and Eisner (1999b)
						Iyengar et al. (2001)
						Iyengar et al. (2002)
						Bezerides et al. (2005)
						Iyengar and Reeve (2010)
Noctuidae						
<i>Conogethes punctiferalis</i>	RI	Abdominal hair pencils	Tiglic acid	Female acceptance		Takayoshi and Hiroshi (1999)
	MA					
<i>Heliothis virescens</i>	RI	Abdominal hair pencils	Tetradecanoic acid	Abdominal extension in female; inhibition of upwind flight by male		Teal and Tumlinson (1989)
	MA		Hexadecanoic acid			Teal et al. (1989)
			Hexadecanyl acetate			Hillier and Vickers (2004)
			Octadecanol			Hillier and Vickers (2011)
			Octadecanoic acid			Hillier et al. (2007)
			Octadecanyl acetate			
<i>Helicoverpa armigera</i>	RI	Abdominal hair pencils	(Z)-11-hexadecen-1-ol	Inhibition of male response to female		Huang et al. (1996)
<i>Mamestra brassica</i>	RI	Abdominal scent brushes	2-phenyl ethanol	Female acceptance		Jacquin et al. (1991)
	MA		2-methyl butanoic acid			
			benzaldehyde			
			2-methyl propanoic acid			
			Benzyl alcohol			
			Phenol			

<i>Phlogophora meticulosa</i>	RI MA	Abdominal scent brushes	6-methyl-5-heptene-2-one 6-methyl-5-heptene-2-ol 2-methyl butyric acid	Female acceptance	Aplin and Birch (1970) Birch (1970a)
<i>Plodia interpunctella</i>	RI	Wing gland	Palmitic acid Oleic acid Linoleic acid Ethyl esters	Female exposes abdominal tip between wings	Grant (1974) Phelan (1992) Tramaterra and Pavan (1994) ^s
<i>Pseudaletia unipunctata</i>	RI MA	Abdominal scent brushes	Benzyl alcohol Benzaldehyde Acetic acid	Female acceptance	Fitzpatrick and McNeil (1988)
<i>Trichoplusia ni</i>	RI MA	Genitalic hair pencils	(S)-(+)-linalool p-cresol m-cresol	Long range attraction of female	Landolt and Heath (1989) Landolt and Heath (1990) Heath et al. (1992) Landolt et al. (1994) Landolt (1995)

a. RI = reproductive isolation; MA = mate assessment; MB = material benefit; GG = good genes; SS = sexy sons; SSP = sexy sperm.

s. Sound production reference.

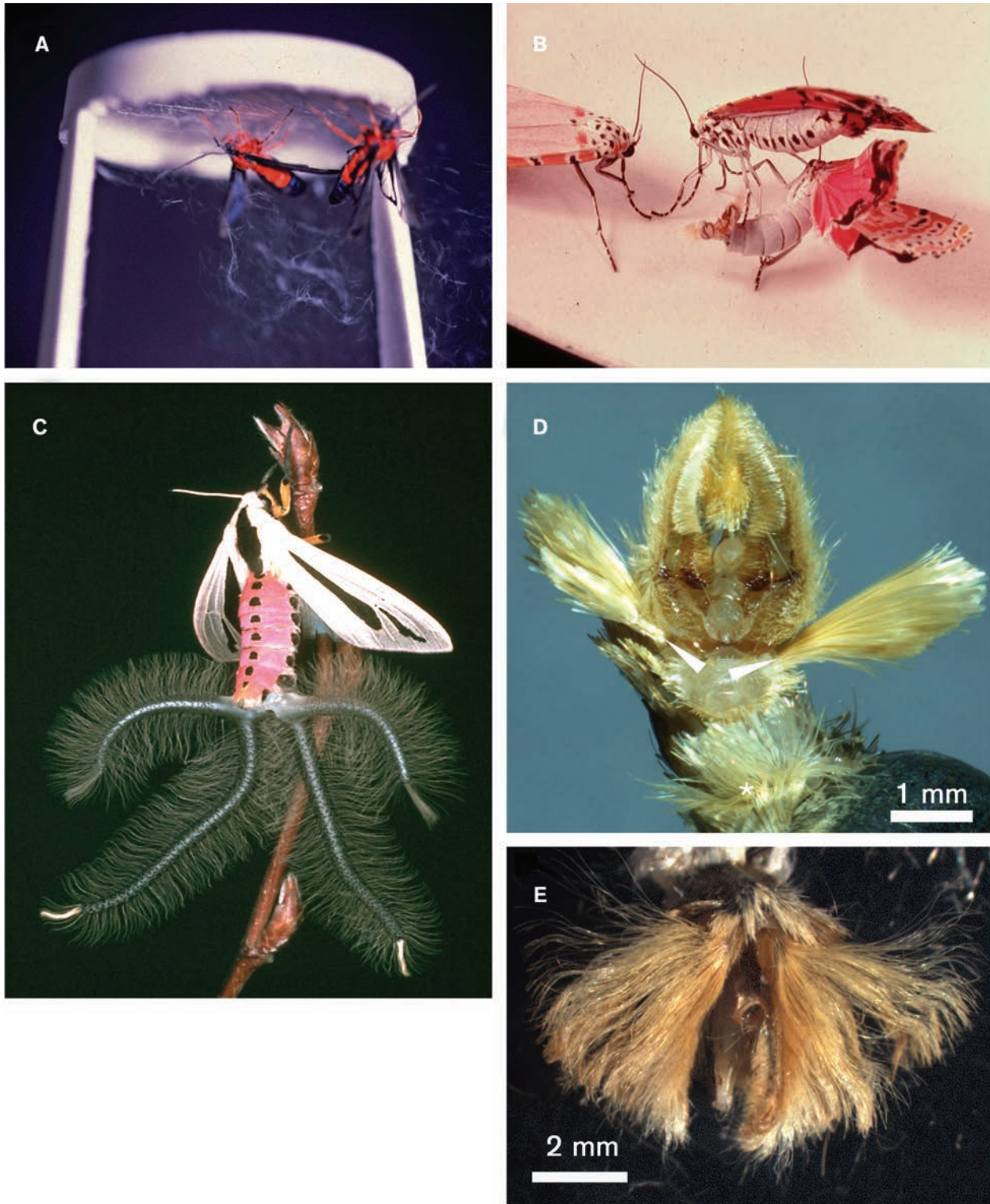


FIGURE 12.2 (A) Courtship of *Cosmosoma myrodora* (Erebidae). Explosive release of flocculent by the male (right) festooning the female (left) with pyrrolizidine alkaloid-laden scales. (B) Courtship of *Utetheisa oratrix* (Erebidae). Male (bottom) flexing abdomen and airing genitalic coremata near the antennae of the female (top). (C) Male *Creatonotus transiens* (Erebidae) with abdominal coremata fully inflated (courtesy of Michael Boppré). (D) Abdominal hairpencils of *Ostrinia nubilalis* (Crambidae) (photo provided by Christer Löfsted and reprinted with permission of *BMC Biology*). (E) Abdominal scent brushes of *Heliopsis virescens* (Noctuidae) (photo provided by Kirk Hillier and reprinted with permission of *Chemical Senses*).

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Indirect Genetic Benefits

Indirect (genetic) benefits are those that are experienced in the next generation in the form of increased offspring survivorship (“good genes”) and mating success of sons (“sexy sons”) (Andersson 1994). There are numerous models (verbal, mathematical, and genetic) that explain the evolution of mate assessment (Bradbury and Andersson 1987), but here we emphasize empirical methods for testing the predictions of the models.

GOOD GENES

To demonstrate a good gene’s benefit, four criteria must be met: (1) males in a given population must vary genetically with respect to their survivorship; (2) male behavior and ornamentation (scent disseminating structures, courtship pheromones, and display behaviors for the purposes of this chapter) should provide accurate information on the survival value of their possessors; (3) females must base their choice of mates on male behavior and ornamentation; and (4) offspring should benefit from their mother’s choice by increased survival (Heisler et al. 1987). In only one moth species have these criteria been met. In the rattlebox moth, *Utetheisa ornatrix*, the quantity of male courtship pheromone hydroxydanaidal is correlated with male body size and is heritable. Females that choose males with greater quantities of hydroxydanaidal benefit through increased fecundity (Iyengar and Eisner 1999b) and their offspring have an enhanced ability to compete for PA-rich food sources (Kelly et al. 2012).

A subcategory of the good genes argument is the healthy mate hypothesis (Hamilton and Zuk 1982). This idea suggests that females may choose males with strong resistance to diseases and parasites and that courtship cues will sometimes be honest indicators of good health. This idea has never been vetted in the male courtship pheromone arena. Given the recent finding that generalist tiger moth caterpillars preferentially feed on PA-containing host plants when infested with parasitoids (Bernays and Singer 2005; Singer et al. 2009), this hypothesis should be investigated. In this context the benefit of choosing a male with the genetic competence to find and utilize PAs could be the reduced incidence of disease/parasitism in progeny.

SEXY SONS

The idea that the only benefit to a choosy female might be that her male offspring will be chosen in the next generation (Lande 1981) dominated the literature on sexual selection for several decades (Andersson 1994). It is an idea that finds its roots in Darwin’s (1871) *The Descent of Man and Selection in Relation to Sex* and was formalized first by Fisher (1930) when he realized that female preference for male traits could theoretically give rise to an evolutionary positive feedback loop. The result would be the exaggeration of male sexually selected traits in a runaway process that continues until the traits become sufficiently deleterious to survival that natural selection brings the process to a halt. Theoretical models are numerous and demonstrate that runaway sexual selection can occur (O’Donald 1967, 1980; Lande 1981; Kirkpatrick 1982), but the underlying assumptions of the models are numerous and critical to outcomes (Andersson 1987). The

diversity of male courtship pheromones and the behaviors associated with their release are consistent with Fisherian runaway sexual selection (Baker and Cardé 1979; Baker 1989; Birch et al. 1990). Empirical tests of the Fisherian process are, however, rare, as four criteria must be met. The first is that the signals, courtship pheromones, should arise frequently and randomly across taxa. As a result of their multiple independent origins, courtship pheromones should thus vary in their chemistry and in their mode of release. Studies should have adequate phylogenetic controls as emphasized by Krasnoff (1997). The second requirement is that the male trait be shown to be heritable or correlated with a heritable trait (Iyengar and Eisner 1991a). The third requirement is that the female preference be shown to be heritable (Iyengar et al. 2002). And last it must be shown that the female preference and the male trait are genetically linked (Iyengar et al. 2002). This linkage completes the positive feedback loop that results in runaway sexual selection. This sets the bar for support of Fisherian runaway sexual selection very high.

SEXY SPERM

As described above it has been argued that females will always be the choosy sex and maximize their fitness through the quality of their choices and not their quantity (Williams 1966; Trivers 1972; Parker 1979). Many recent studies have challenged these assumptions and have found that females may be more promiscuous than was predicted (Birkhead and Møller 1998; Arnqvist and Nilsson 2000). Multiple mating could benefit females in many contexts. They could provide the female with serial nuptial gifts and be an unusual form of nutrient and chemical defense “foraging.” They could increase the odds of finding a mate of superior genetic quality and they could increase female fecundity (LaMunyon 1997). Keller and Reeve (1995) hypothesized that female promiscuity and male sperm competitiveness could coevolve in a runaway sexual selection process that would ultimately promote sperm competition within the body of the female. This has been dubbed the “sexy sperm” hypothesis. Iyengar and Reeve (2010) have gathered evidence in support of this hypothesis by showing that female promiscuity genes in *Utetheisa ornatrix*, which mates up to 22 times, are Z-linked, a pattern consistent with the sexy sperm hypothesis (see case study on *U. ornatrix*).

It is not possible for all of the potential benefits of mate assessment to be measured in all species; however, they should be addressed for a number of “model” species. Only then will we begin to fully understand the intricacies of moth courtship and the mechanisms that underlie their evolution.

Scent Structures in Male Lepidoptera

The scent disseminating structures of male Lepidoptera are impressive in several respects. They are exceedingly common across taxa, and their varied location, shape, and chemistry suggest repeated evolutionary origins. This pattern is consistent with the genetic bias toward elaboration that stems from the genetic architecture of Lepidoptera described above and can be construed as circumstantial evidence for runaway sexual selection. Depending on their morphology, the disseminating structures are referred to as androconial scales, scent brushes, scent fans, hairpencils, and coremata (Birch et al.

1990). They are also frequently large relative to body size and reminiscent of the feathered displays of male birds (Andersson 1994). The most notable examples are the magnificent abdominal coremata of *Cretonotos* species (figure 12.2). The diversity of male scent disseminating structures is highest in the Gelechiidae, Tortricidae, Pyralidae, Notodontidae, Erebidae, and Noctuidae (Brown et al. 2011).

The newest addition to the list of potential scent disseminating structures involved in courtship are the deciduous flocculent scales associated with pouches located on the venter of the second and third segments of the abdomen (Weller et al. 2000). Although originally described in the context of defense (Blest 1964), deciduous scales that pack these pockets are shed in clouds in the vicinity of the female during courtship as described for *Cosmosoma* above (figure 12.2). They are found in Euechromina arctiines (Erebidae) and have evolved multiple times as evidenced by their association with different segments and fine structure (Weller et al. 2000). Thus far they are restricted to clades associated with PA-containing plants, again strengthening the relationship between defensive chemicals and sex in the Erebidae (Conner and Jordan 2009).

Scent dissemination is usually linked to behaviors associated with normal sexual excitement in males such as wing fanning for wing glands, genital extrusion for scent brushes and coremata associated with male genitalia, and copulatory flexion of the abdomen for the coremata on the intersegmental membranes of the abdomen (figure 12.2). The latter mechanisms take advantage of biomechanical changes during the flexion of the abdomen of the male during copulatory attempts. Abdominal flexion associated with copulatory attempts pressurizes the air-filled tracheal system and hemolymph spaces within the insect. The intersegmental membranes respond to the increased pressure and bulge outward. Pressurization is likely the first evolutionary step in scent dissemination in these species. Elaboration of the intersegmental and genital membranes into coremata and related structures follows. Baker and Cardé (1979) referred to the courtship behavior of *Grapholita molesta* as ritualized copulation referring to the link between copulatory attempts, the scent dissemination mechanism, and sexual selection.

The scent disseminating structures themselves appear to be optimized for the release of small volatile molecules at high flux rates. They are composed of highly modified scales with large surface areas and associated secretory cells (Birch 1970a, 1970b). They are deployed rapidly in time frames frequently measured in milliseconds. Our understanding of the evolution of male courtship pheromone disseminating structures is hampered by a dearth of genetic and developmental studies. The so-called evo-devo studies have illuminated the origins of insect epidermal outgrowths such as sexually selected beetle horns (Moczek et al. 2007). Such studies frequently discover fundamental bauplan genes that can be redeployed to produce new structures and functions. For moth coremata, particularly because they are sexually dimorphic and can be diet dependent, these are tractable questions that would clarify how scent structures arise and diversify. Also as pointed out by Krasnoff (1997), Krasnoff and Roelofs (1990), and Phelan (1992), further gaps in our understanding of the evolution of male courtship pheromones are the result of a lack of comparative phylogenetic studies (but see Phelan and Baker 1990a; Weller et al. 1999). This is being rectified but at a frustratingly slow rate for behaviorists.

Courtship Characteristics

The courtship of moths varies in complexity from the unadorned and simple to the more complicated choreographic exchange of both female and male signals. The primitive condition is exemplified by a female releasing her sex attractant blend (Löfstedt and Kozlov 1997; Greenfield 2002). The male flies upwind and mates with the female without foreplay. We have attempted to arrange the following vignettes in three sections: female responses to male pheromones, male responses to male pheromones, and lekking. The first two sections are generally arranged in order of increasing complexity.

Female Responses to Male Pheromones

INCREASED FEMALE ACCEPTANCE

Removal of scent disseminating structures in male moths frequently diminishes their probability of mating (Birch, 1970a, 1974; Clearwater 1972; Grant 1974, 1976; Hendrikse 1986; Phelan and Baker 1986; Fitzpatrick and McNeil 1988; Cibrian-Tovar and Mitchell 1991; Royer and McNeil 1992; Kimura and Honda 1999). In some cases the proximate cause is not immediately obvious. This prompted the labeling of the male courtship pheromones “aphrodisiac” pheromones—pheromones that increase the likelihood of copulation (Birch 1974).

FEMALE QUIESCENCE

In some cases the only observable behavior is a decrease in the probability of female taking flight or in other ways moving away from the male (Conner 1981; Hillier and Vickers 2004).

SPECIFIC ACCEPTANCE BEHAVIORS

Fine-grained behavioral analysis, often through video recording, has allowed the description of discrete acceptance behaviors. In *Heliothis virescens* abdominal extension, which may be associated with increased female pheromone release, is elicited by natural hairpencil eversion, hairpencil extracts, and blends of synthetic chemicals combined in the proportions of the natural courtship pheromones (Hillier and Vickers 2004). Female acceptance behavior sometimes includes curling of the abdomen toward the substrate, a behavior that has been interpreted as scent marking (Teal et al. 1981; Thibout et al. 1994; Hillier and Vickers 2004). In phycitinae pyralid species female acceptance behavior often involves curling the abdomen upwards between the wings, an adjustment that is necessary for coupling in these species (Krasnoff and Vick 1984; Phelan and Baker 1990a, 1990b; and references therein). Abdominal curling can also be directed toward the male, bringing the genitalia of the female into apposition with the male genitalia and thereby facilitating copulation. An alternative method for exposing the genitalia is to raise the wings allowing a male to approach from the side (Conner 1981; Krasnoff and Roelofs 1990).

FEMALE MOVES AWAY

When exposed to extracts of male courtship pheromones of heterospecific males (*Helicoverpa zea* or *Heliothis subflexa*),

H. virescens females move away suggesting a role of male courtship pheromones in reproductive isolation (Hillier and Vickers 2004).

FEMALE ATTRACTED (SHORT RANGE)

In *Grapholita molesta* males wing fan and extrude their abdominal hairpencils in a pulsatile fashion in the vicinity (<2 cm) of a calling female. Females orient to the wing-generated air currents and move toward the male (Baker and Cardé 1979). Through orientation toward the male, females express a clear “preference” for males with courtship pheromones. Males of the lesser wax moth, *Achroia grisella*, attract females from close range with a combination of courtship pheromones and ultrasound (Dahm et al. 1971; but see Greenfield 2002). In *Galleria mellonella* wing-gland pheromones also attract females from close range (Röller et al. 1968; Leyrer and Monroe 1973; Finn and Payne 1977).

FEMALE ATTRACTED (LONG RANGE)

In *Trichoplusia ni* exposure of genitalic hairpencils attracts females from long (distances greater than those typically associated with moth courtship, i.e., greater than 25 cm) range (Landolt and Heath 1990). Combinations of male pheromones with plant odors or female sex attractants are synergistic in triggering female attraction (Landolt et al. 1994). Female attraction has also been described for *Heliothis virescens* (Heath et al. 1992).

FEMALE DECREASES CALLING

Male hairpencil odors have been reported to trigger a decrease in female calling in tobacco budworm moths, *Heliothis virescens*, and cotton bollworm moths, *Helicoverpa zea* (Hendricks and Shaver 1975; Huang et al. 1996). It is possible that males have exploited a mechanism for the control of female pheromone release that allows them to decrease their competitive interactions with other males. Such a mechanism would operate just prior to copulation, an event that will also decrease female pheromone release.

FEMALE SOUND PRODUCTION

Females of *Phragmatobia fuliginosa* and *Pyrharctia isabella* (Erebidae) produce tymbalar clicks in response to the eversion of the coremata of males and their dihydropyrrrolizine pheromone hydroxydanaidal (Krasnoff and Yager 1988). This behavior can be used as a remarkably sensitive bioassay for hydroxydanaidal. While intriguing, Krasnoff and Roelofs (1989) were unable to demonstrate a function for either eversion of the coremata or the “pheromone” hydroxydanaidal and tentatively suggested that the acoustic response is a vestige of a no longer functional communication system (Krasnoff and Roelofs 1990). Perhaps there is an errepid species for which the pheromone/acoustic exchange remains salient. Cryptic (at least to us) ultrasonic signals are being found to play important roles in the courtship in many moth species previously thought to be silent (Nakano et al. 2008).

Male Responses to Male Pheromones

ATTRACTION OF CONSPECIFIC MALES

Male *Grapholita molesta* are attracted to the hairpencil secretions of conspecifics (Baker 1983). This attraction appears to represent an alternative mating strategy in which males may “sneak” matings in the presence of conspecifics. A similar phenomenon was demonstrated for the male courtship pheromone of *Anticarsia gemmatalis* (Heath et al. 1988), suggesting that exploitation of conspecific male courtship signals by male moths foraging for mates may be common (Birch et al. 1990).

REPULSION OF CONSPECIFIC MALE

The inhibition of upwind orientation of male moths by conspecific male courtship pheromone (Hirai et al. 1978; Huang et al. 1996; LeComte et al. 1998; Hillier and Vickers 2004) is a controversial putative male response to courtship pheromone. While early studies (Hirai et al. 1978) were criticized for technical flaws (Fitzpatrick and McNeil 1988), group selection arguments for why a male would break off an approach, and for the necessity to use excessive amounts of the pheromone to show an effect (Phelan 1992), more recent studies (Huang et al. 1996; Hillier and Vickers 2004) support early reports. A male that detects male courtship pheromone components in the pheromone plume of a conspecific female may conserve energy and search time by breaking off an approach to an already taken female (Greenfield 2002; but see Baker and Cardé 1979). It is also possible that a male may gain a competitive advantage by inserting a “false pheromone component” into the pheromone plume of a conspecific female (Hillier et al. 2007). Downwind males would interpret the pheromone blend as one of a heterospecific female and break off pursuit toward what appears to be an inappropriate target. Also see Davie et al. (2010) for additional competitive interactions among males.

Lekking (Sex Role Reversal)

There are now several examples of sex role reversal in moths (i.e., males attract females from long distance) (Willis and Birch 1982; Wunderer et al. 1986; Wagner and Rosovsky 1991). Parental investment theory predicts that sex role reversal should occur when the male becomes the limiting sex (Phelan 1992, 1997). The way in which this could happen is most clear in the errepid *Cretonotos gangis* with its enormous, four-branched, inflatable coremata deployed for a few hours each night in “lek-like” behavior (Schneider et al. 1982; Wunderer et al. 1986). Their coremata scents attract additional males to the lek and also females. After use the coremata are deflated and fold neatly (without the aid of retractor muscles) into the abdomen leaving no trace of their existence. Bifid versions of the coremata can be seen in the common salt marsh moth *Estigmene acrea* where they play a similar behavioral role (Willis and Birch 1982; Jordan et al. 2005). In *C. gangis*, *C. transiens*, and *E. acrea* male pheromone precursors are potent morphogens—specific chemicals that stimulate growth and development. Males deprived of pheromone precursors (PAs) in their larval food do not produce male pheromone and do not produce fully formed coremata for their release (Boppré and Schneider

1985; Schmitz et al. 1989; Jordan et al. 2005, 2007; Jordan and Conner 2007). This prevents the energy wasting process of construction of a large scent disseminating structure with no signal to convey.

In both *C. gangis* and *E. acraea*, the primitive condition of the mating system is still evident. The females of both species release pheromone and attract males late in the evening. The derived strategy, lekking, occurs earlier in the evening when the males inflate their coremata. One possible explanation is that the males' contribution to the female—a nuptial gift in the form of spermatophore—has become large relative to the contribution of the female to her offspring. At this tipping point a sex role reversal would take place and females would be attracted to males (Gwynne 1984). It is also possible that *Cretonotos* and *Estigmene* are practicing alternative mating strategies depending on larval access to PAs (Jordan and Conner 2007). Males that find PA-containing plants as caterpillars and have an ample supply of PAs develop robust coremata (see morphogenetic effect above), join aggregations, and display. Mating with such males would be highly advantageous to females, especially those that did not find PAs as caterpillars. Males without PAs could revert to the normal mating system in which they detect the female sex attractant and fly upwind. The occurrence of lekking would thus depend on the local availability of PAs in the habitat. From the female's perspective alternative mating strategies are also available. If she is PA-deprived because of an inferior larval diet she can attend the lek to obtain PAs from males. Alternatively, if she acquired sufficient PAs during larval feeding she can avoid the costs of searching for a lek by remaining stationary and attracting males. Additional examples of sex role reversal, such as the pheromonal/acoustic leks of the lesser wax moth (Greenfield and Coffelt 1983), are resource related (Emlen and Oring 1977; Phelan 1992).

Source of Male Pheromones

Past reviews have drawn attention to the fact that many male moth pheromones are minimally altered host plant volatiles (figure 12.3). These include floral and fruit odors and pyrrolizidine alkaloid derivatives. The most likely reason is that males have exploited existing chemoreceptors that were present in females for locating their host plants (Baker 1989; Phelan 1992). Preexisting receptors remove one step in the evolutionary pathway to a courtship pheromone and all that remains is changing (sometimes minimally) the behavioral response to the pheromone.

More recent studies indicate that there are some notable exceptions to the plant-derived pheromone trend (Heath et al. 1988; Hillier and Vickers 2004; Lassance and Löfstedt 2009). In these cases the male courtship pheromones are long-chained hydrocarbons with various degrees of unsaturation and/or functional groups and they are chemically related to female pheromone components. They are processed with receptors (Baker et al. 2004) and neural centers (olfactory lobe glomeruli) analogous to those used by males to receive and recognize female sex attractants (Hillier et al. 2006, 2007). Indeed, the production of the male pheromone components is regulated by neuropeptides that they share with females (Bober and Rafaeli 2010). Again this may be an illustration of the expedient use of preexisting features. In this case the evolution of the male signal may be facilitated by preexisting biochemical pathways and the female response by preexisting

chemoreceptors in the female (e.g., Lim and Greenfield 2006, 2008; Lim et al. 2007).

It seems clear the sources of male courtship pheromones are more diverse than originally thought (Birch 1970a, 1970b; Birch et al. 1990) and reflect the different selective advantages of their use. Given that the number of species investigated remains less than 0.01% of species with male scent disseminating structures, it seems likely that additional classes of male pheromones will be discovered in the future.

Quest for Pheromone Precursors

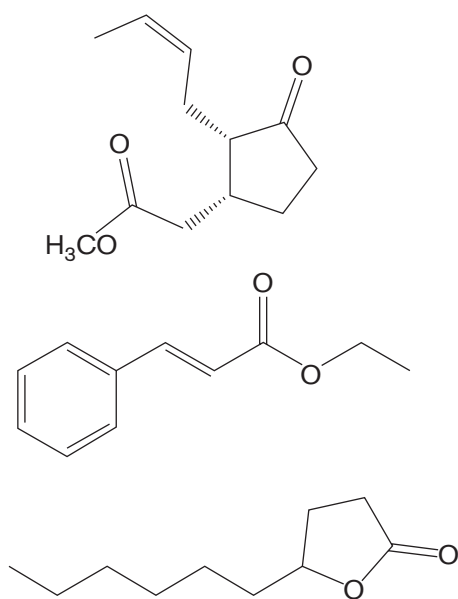
The diet dependence of some male pheromones is no better illustrated than by the extraordinary behavior termed pharmacophagy. As redefined by Boppré (1984) pharmacophagous (literally “drug eating”) insects seek out non-host plant species and collect specific chemicals for sexual or defensive (non-nutritional) purposes. Our knowledge of this behavior can be traced to the early collectors of Lepidoptera in central and South America, including William Beebe in Trinidad (Beebe 1955; Beebe and Kenedy 1957). They found that the dead shoots of *Heliotropium indicum* attracted swarms of erebids by night and ithomiine and danaine butterflies by day. Researchers later found that virtually any plant with high concentrations of pyrrolizine alkaloids served as excellent bait (Pliske 1975; Goss 1979; Boppré 1986; DeVries and Stiles 1990; Häuser and Boppré 1997; Brehm et al. 2007; Conner and Jordan 2009). The visitors are most often (but not always) male-biased, in keeping with parental investment theory. Upon arrival at the bait they unfurl their proboscis regurgitate on the surface of the plant and imbibe an extract of surface alkaloids. These serve as chemical defenses, male courtship pheromones, or their precursors (Krasnoff and Dussourd 1989; Conner et al. 2000; figure 12.4). The tip of the proboscis of pharmacophagous moths possesses clusters of sensilla stylconica that appear to be gustatory chemoreceptors for PAs and their derivatives (Zaspel et al. 2013; figure 12.4D) similar to those found on the maxillary palps of pharmacophagous larvae (Bernays and Singer 2005).

The attraction of male moths to rotting fruit, mud puddles, feces, blood, and tears provides opportunities to collect exogenous chemicals that may be incorporated into courtship and all merit further study (Baker et al. 1989; Smedley and Eisner 1995; Zaspel et al. 2011). It is notable that plants containing cardenolides, a major class of defensive chemicals found in some Erebididae, are not known to be attractive to males of these groups (Baker 1989; Birch et al. 1990). Why plants containing PAs attract erebids and plants containing cardenolides do not remains a mystery.

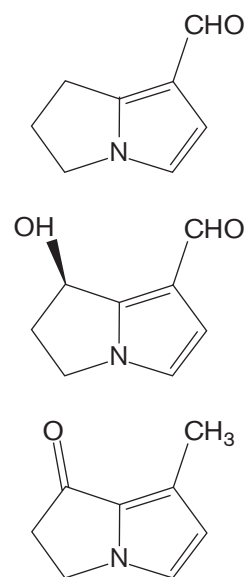
Role of Sound in Courtship

Although this review has focused exclusively on the chemical modality, it is becoming increasingly apparent that moth courtship involves multimodal cues. Many of the species that use male courtship pheromones combine them with acoustic and usually ultrasonic signals (Nakano et al. 2008; Table 12.1). The acoustic signals can potentially play roles in both reproductive isolation and mate choice. Their frequent use in courtship is likely a result of exploitation of preexisting structures that evolved for bat detection (Conner 1999). The use of multimodal courtship signals raises the bar for studying moth

Herbal and Floral Scents



PA Derivatives



Long Chained Hydrocarbons

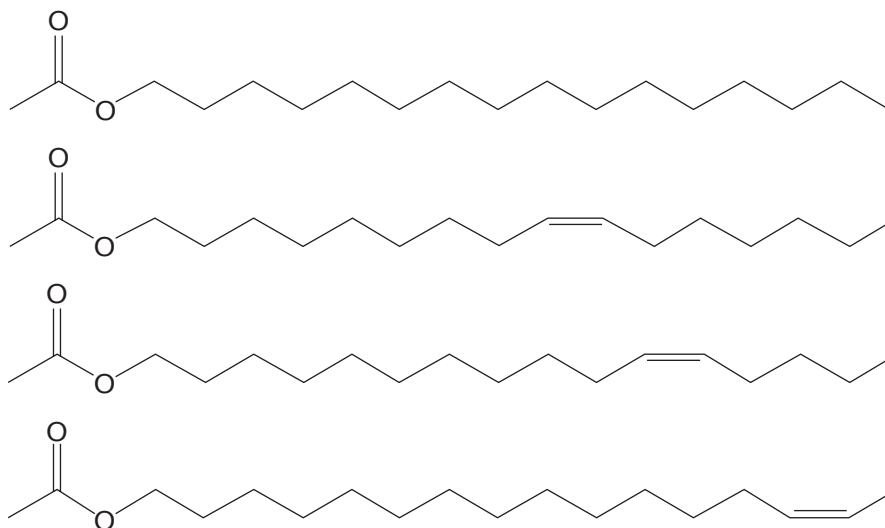


FIGURE 12.3 Examples of male courtship pheromones. Herbal and floral scents: (1) methyl 2-epijasmionate; (2) ethyl *trans*-cinnamate; (3) γ -decalactone. PA derivatives: (4) danaidal; (5) *R*-hydroxydanaidal; (6) danaidone. Long-chained hydrocarbons: (7) hexadecanyl acetate; (8) (Z)-9 hexadecenyl acetate; (9) (Z)-11 hexadecenyl acetate; (10) (Z)-14 hexadecenyl acetate.

courtship. Researchers will need to use sophisticated technologies in both the fields of chemical ecology and bioacoustics. Experimental protocols will need to incorporate controls for both sound and chemistry and early studies will need to be reexamined in light of the possibility of redundant chemical and acoustic signals.

Future Directions

Detailed studies of male courtship pheromones have been largely restricted to the Erebiidae and select noctuids and pyral-

ids. Understudied groups include the Gelechiidae, Tortricidae, and the Notodontidae, all of which have a high diversity of androconial scales. The latter groups deserve special attention.

With the advent of new technologies it is becoming clear that moths are combining chemical and acoustic modalities in their courtship repertoires. Acoustic signals provide another opportunity to study the evolutionary forces influencing moth courtship. Evolutionary studies that map both chemical and acoustic cues on phylogenies will be particularly instructive.

Studies of the evolution and development of male courtship pheromone disseminating structures are needed. They

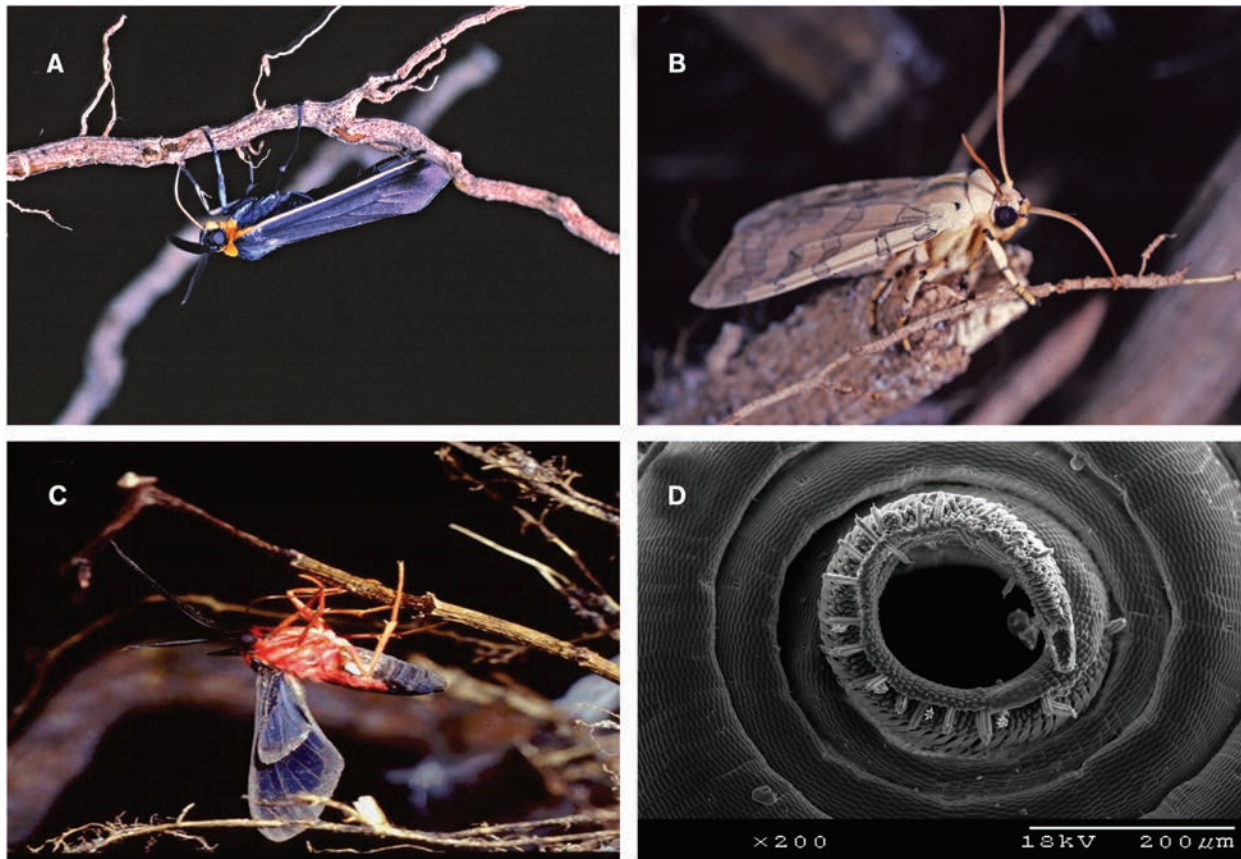


FIGURE 12.4 Pharmacophagy in Erebidae.

A Male *Cisseps fulvicollis* imbibing pyrrolizidine alkaloids from the roots of *Eupatorium capillifolium*.

B Adult *Halysidota tessellaris* collecting alkaloids.

C Male *Cosmosoma myrodora* visiting roots.

D Scanning electron micrograph of presumed alkaloid receptors on the tip of the proboscis of a male *Cosmosoma auge* (photograph provided by Jennifer Zaspel).

SOURCE: Photos A through C reprinted with permission of Cambridge University Press.

will provide clues about how scent structure arise and diversify and would also ultimately explain how specific dietary requirements can control scent structure development. In addition understanding the neural processing of male courtship pheromones would help clarify the early steps in the evolution of male courtship pheromones.

Before conclusions can be made about the selective pressures that gave rise to male courtship pheromones, the assumptions and predictions of the various models of sexual selection must be tested empirically in a variety of species. It is likely that there will be no single answer, because females and males have a number of options for increasing their fitness through mate choice and in some cases they may be using them all. Detailed genetic analyses, physiological studies, quantitative measurements of behavior, and, especially, phylogenetic treatments will play important roles in our understanding of what must be considered one of the pinnacles of chemical communication.

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References Cited

- Andersson, M. B. 1987. Genetic models of sexual selection: some aims, assumptions, and tests. Pp. 41–53. In J. W. Bradbury and M. B. Andersson, eds. *Sexual Selection: Testing the Alternatives*. Chichester: John Wiley and Sons.
- Andersson, M. B. 1994. *Sexual Selection*. Princeton, NJ: Princeton University Press.
- Ando, T. 2012. Sex pheromones of moths. Available online at: <http://www.tuat.ac.jp/~antetsu/LepiPheroList.htm>.
- Aplin, R. T., and M. C. Birch. 1970. Identification of odorous compounds from male Lepidoptera. *Experientia* 26:1193–1194.
- Arnqvist, G., and T. Nilsson. 2000. The evolution of polyandry: multiple mating and female fitness in insects. *Animal Behaviour* 60:145–164.
- Baker, T. C. 1983. Variations in male oriental fruit moth courtship patterns due to male competition. *Experientia* 39:112–114.
- Baker, T. C. 1989. Origin of courtship and sex pheromones of the oriental fruit moth and a discussion of the role of phytochemicals in the evolution of lepidopteran male scents. Pp. 401–418. In C. H. Chou and G. R. Waller, eds. *Phytochemical Ecology: Allelochemicals*,

- Mycotoxins and Insect Pheromones and Allomones*. Institute of Botany Sinica Monograph Series, No. 9. Taipei, China.
- Baker, T. C., and R. T. Cardé. 1979. Courtship behavior of the oriental fruit moth (*Grapholitha molesta*): experimental analysis and consideration of the role of sexual selection in the evolution of courtship pheromones in the Lepidoptera. *Annals of the Entomological Society of America* 72:173–188.
- Baker, T. C., R. Nishida, and W. L. Roelofs. 1981. Close-range attraction of female oriental fruit moths to herbal scent of male hairpencils. *Science* 214:1359–1361.
- Baker, T. C., S. A. Ochieng, A. A. Cossé, S. G. Lee, J. L. Todd, C. Quero, and N. J. Vickers. 2004. A comparison of responses from olfactory receptor neurons of *Heliothis subflexa* and *Heliothis virescens* to components of their sex pheromone. *Journal of Comparative Physiology A* 190:155–165.
- Beebe, W. 1955. Two little-known selective insect attractants. *Zoologica: Scientific Contributions of the New York Zoological Society* 40:27–36.
- Beebe, W., and R. Kenedy. 1957. Habits, palatability, and mimicry in thirteen ctenuchid moth species from Trinidad, B.W.I. *Zoologica: Scientific Contributions of the New York Zoological Society* 42:147–158.
- Bell, T. W., and J. Meinwald. 1986. Pheromones of two arctiid moths (*Cretonotus transiens* and *C. gangis*): chiral components from both sexes and achiral female components. *Journal of Chemical Ecology* 12:385–409.
- Bell, T. W., M. Boppré, D. Schneider, and J. Meinwald. 1984. Stereochemical course of pheromone biosynthesis in the arctiid moth, *Cretonotus transiens*. *Experientia* 40:713–714.
- Bennett, A. L., P. R. Atkinson, and N. J. S. La Croix. 1991. On communication in the African sugarcane borer, *Eldana saccharina* Walker (Lepidoptera: Pyralidae). *Journal of the Entomological Society of South Africa* 54:243–259.
- Bernays, E. A., and M. S. Singer. 2005. Taste alteration and endoparasites. *Nature* 436:476.
- Bezzerides, A., V. K. Iyengar, and T. Eisner. 2005. Corematernal function in *Utetheisa ornatrix*: interpretation in light of data from field-collected males. *Chemoecology* 15:187–192.
- Birch, M. C. 1970a. Structure and function of the pheromone-producing brush organs in males of *Phlogophora meticulosa* (L.) (Lepidoptera: Noctuidae). *Transactions of the Royal Entomological Society of London* 122:277–292.
- Birch, M. C. 1970b. Pre-courtship use of abdominal brushes by the nocturnal moth *Phlogophora meticulosa* (L.) (Lepidoptera: Noctuidae). *Animal Behaviour* 18:310–316.
- Birch, M. C. 1972. Male abdominal brush-organs in British noctuid moths and their value as a taxonomic character. *The Entomologist* 105:185–205; 233–244.
- Birch, M. C. 1974. Aphrodisiac pheromones in insects. Pp. 115–134. In M. C. Birch, ed. *Pheromones*. Amsterdam: North-Holland Publishing.
- Birch, M. C., and A. Hefetz. 1987. Extrusible organs in male moths and their role in courtship behavior. *Bulletin of the Entomological Society of America* 33: 222–229.
- Birch, M. C., G. M. Poppy, and T. C. Baker. 1990. Scents and eversible scent structures in male moths. *Annual Review of Entomology* 35:25–58.
- Birkhead, T. R., and A. P. Møller. 1998. *Sperm Competition and Sexual Selection*. San Diego, CA: Academic Press.
- Blest, A. D. 1964. Protective display and sound production in some New World arctiid and ctenuchid moths. *Zoologica: Scientific Contributions of the New York Zoological Society* 49:161–181.
- Blomquist, G. J., and R. G. Vogt. 2003. *Insect Pheromone Biochemistry and Molecular Biology: The Biosynthesis and Detection of Pheromones and Plant Volatiles*. London: Elsevier Press.
- Bober, R., and A. Rafraeli. 2010. Gene-silencing reveals the functional significance of pheromone biosynthesis activating neuropeptide receptor (PBAN-R) in a male moth. *Proceedings of the National Academy of Sciences of the United States of America* 107:16858–16862.
- Boppré, M. 1984. Redefining “pharmacophagy”. *Journal of Chemical Ecology* 10:1151–1154.
- Boppré, M. 1986. Insects pharmacophagously utilizing defensive plant chemicals (pyrrolizidine alkaloids). *Naturwissenschaften* 73:17–26.
- Boppré, M. 1990. Lepidoptera and pyrrolizidine alkaloids: exemplification of complexity in chemical ecology. *Journal of Chemical Ecology* 16:165–185.
- Boppré, M., and D. Schneider. 1985. Pyrrolizidine alkaloids quantitatively regulate both the scent organ morphogenesis and pheromone biosynthesis in male *Cretonotus* moths (Lepidoptera: Arctiidae). *Journal of Comparative Physiology A* 157:569–577.
- Bradbury, J. W., and M. B. Andersson. 1987. *Sexual Selection: Testing the Alternatives*. Chichester: John Wiley and Sons.
- Brehm, G., T. Hartmann, and K. Willmott. 2007. Pyrrolizidine alkaloids and pharmacophagous Lepidoptera visitors of *Prestonia amabilis* (Apocynaceae) in a montane forest in Ecuador. *Annals of the Missouri Botanical Garden* 94:463–473.
- Brown, R. L., J. Baixeras, and S. Lee. 2011. Male sex scales of moths. Available online at: <http://lepcourse.wikispaces.com/file/view/sex+scales.AZ.+aug.12.pdf>.
- Burger, B. V., A. E. Nell, D. Smit, H. S. C. Spies, W. M. Mackenroth, D. Groche, and P. R. Atkinson. 1993. Constituents of wing gland and abdominal hair pencil secretions of male African sugarcane borer, *Eldana saccharina* Walker (Lepidoptera: Pyralidae). *Journal of Chemical Ecology* 19:2255–2277.
- Cardé, R. T., and T. C. Baker. 1984. Sexual communication with pheromones. Pp. 355–383. In W. J. Bell and R. T. Cardé, eds. *Chemical Ecology of Insects*. London: Chapman & Hall Press.
- Cardé, R. T., and J. G. Millar. 2004. *Advances in Insect Chemical Ecology*. Cambridge: Cambridge University Press.
- Cardé, R. T., and A. K. Minks. 1997. *Insect Pheromone Research: New Directions*. New York: Chapman & Hall.
- Cibrian-Tovar, J., and E. R. Mitchell. 1991. Courtship behavior of *Heliothis subflexa* Gn. Lepidoptera, Noctuidae and associated backcross insects obtained from hybridization with *Heliothis virescens* F. *Environmental Entomology* 20:419–426.
- Clearwater, J. R. 1972. Chemistry and function of a pheromone produced by male of the southern armyworm *Pseudaletia separata*. *Journal of Insect Physiology* 18:781–789.
- Collins, R. D., Y. Jang, K. Rheinhold, and M. D. Greenfield. 1999. Quantitative genetics of ultrasonic advertisement signaling in the lesser waxmoth *Achroia grisella* (Lepidoptera: Pyralidae). *Heredity* 83:644–651.
- Conner, W. E. 1999. “Un chant d’appel amoureux”: acoustic communication in moths. *Journal of Experimental Biology* 202:1711–1723.
- Conner, W. E., and A. T. Jordan. 2009. From armaments to ornaments: the relationship between chemical defense and sex in tiger moths. Pp. 155–172. In W. E. Conner, ed. *Tiger Moths and Woolly Bears: Behavior, Ecology, and Evolution of the Arctiidae*. Oxford: Oxford University Press.
- Conner, W. E., T. Eisner, R. K. VanderMeer, A. Guerrero, and J. Meinwald. 1981. Precopulatory sexual interactions in an arctiid moth (*Utetheisa ornatrix*): role of pheromone derived from alkaloids. *Behavioral Ecology and Sociobiology* 9:227–235.
- Conner, W. E., R. Boada, F. Schroeder, and T. Eisner. 2000. Chemical defense: bestowal of a nuptial alkaloidal garment by a male moth on its mate. *Proceedings of the National Academy of Sciences of the United States of America* 97:14406–14411.
- Coyne, J. A., and H. A. Orr. 2004. *Speciation*. Sunderland, MA: Sinauer.
- Dahm, K. H., D. Meyer, W. E. Finn, V. Reinhold, and H. Röller. 1971. The olfactory and auditory mediated sex attraction in *Achroia grisella* (Fabr.). *Naturwissenschaften* 5:265–266.
- Darwin, C. 1871. *The Descent of Man, and Selection in Relation to Sex*. London: John Murray.
- Davenport, J. W., and W. E. Conner. 2003. Dietary alkaloids and the development of androconial organs in *Estigmene acrea*. *Journal of Insect Science* 3:3. PMID: PMC524643.
- Davidson, R. B., C. Baker, M. McElveen, and W. E. Conner. 1997. Hydroxydanaidal and the courtship of *Haploa* (Arctiidae). *Journal of the Lepidopterists’ Society* 51:288–294.
- Davie, L. C., T. M. Jones, and M. A. Elgar. 2010. The role of chemical communication in sexual selection: hair pencil displays in the diamondback moth, *Plutella xylostella*. *Animal Behaviour* 79:391–399.
- Davies, N. B. 1992. *Dunnock Behaviour and Social Evolution*. Oxford: Oxford University Press.
- DeVries, P. J., and F. G. Stiles. 1990. Attraction of pyrrolizidine alkaloid-seeking Lepidoptera to *Epidendrum paniculatum* orchids. *Biotropica* 22:290–297.
- Dussourd, D. E., K. Ubik, C. Harvis, J. Resch, J. Meinwald, and Eisner, T. 1988. Biparental defensive endowment of eggs with acquired

- plant alkaloid in the moth *Utetheisa ornatrix*. *Proceedings of the National Academy of Sciences of the United States of America* 85:5992–5996.
- Dussourd, D. E., C. A. Harvis, J. Meinwald, and T. Eisner. 1991. Pheromonal advertisement of a nuptial gift by a male moth (*Utetheisa ornatrix*). *Proceedings of the National Academy of Sciences of the United States of America* 88:9224–9227.
- Egelhaaf, A., C. Coelln, B. Schmitz, M. Buck, M. Wink, and D. Schneider. 1990. Organ specific storage of dietary pyrrolizidine alkaloids in the arctiid moth *Cretonotos transiens*. *Zeitschrift für Naturforschung C* 45:115–120.
- El-Sayed, A. M. 2011. The pherobase: database of pheromones and semiochemicals. Available online at: <http://www.pherobase.com>.
- Emlen, S. T., and L. W. Oring. 1977. Ecology, sexual selection, and the evolution of mating systems. *Science* 197:215–223.
- Finn, W. E., and T. L. Payne. 1977. Attraction of greater wax moths females to male-produced pheromones. *Southwestern Entomologist* 2:62–64.
- Fisher, R. A. 1930. *The Genetical Theory of Natural Selection*. Oxford: Clarendon Press.
- Fitzpatrick, S. M., and J. N. McNeil. 1988. Male scent in lepidopteran communication: the role of male pheromone in mating behaviour of *Pseudaletia unipunctata* (Haw.) (Lepidoptera: Noctuidae). *Memoirs of the Entomological Society of Canada* 146:131–151.
- González, A., C. Rossini, M. Eisner, and T. Eisner. 1999. Sexually transmitted chemical defense in a moth (*Utetheisa ornatrix*). *Proceedings of the National Academy of Sciences of the United States of America* 96:5570–5574.
- Goss, G. J. 1979. The interaction between moths and plants containing pyrrolizidine alkaloids. *Environmental Entomology* 8:487–493.
- Grant, G. G. 1974. Male sex pheromone from the wing glands of the Indian meal moth, *Plodia interpunctella* (Hbn.) (Lepidoptera: Phycitidae). *Experientia* 30:917–918.
- Grant, G. G. 1976. Courtship behavior of a phycitid, *Vitula edmandsae*. *Annals of the Entomological Society of America* 69:445–449.
- Greenfield, M. D. 2002. *Signalers and Receivers: Mechanisms and Evolution of Arthropod Communication*. Oxford: Oxford University Press.
- Greenfield, M. D., and J. A. Coffelt. 1983. Reproductive behavior of the lesser waxmoth, *Achroia grisella* (Pyralidae: Galleriinae): signaling, pair formation, male interactions, and mate guarding. *Behaviour* 84:287–315.
- Gwynne, D. T. 1984. Courtship feeding increases female reproductive success in bushcrickets. *Nature* 307:361–363.
- Hamilton, W. D., and M. Zuk. 1982. Heritable true fitness and bright birds: a role for parasites? *Science* 218:384–387.
- Hammerstein, P., and G. A. Parker. 1987. Sexual selection: games between the sexes. Pp. 119–142. In J. W. Bradbury and M. Andersson, eds. *Sexual Selection: Testing the Alternatives*. New York: John Wiley Press.
- Hartmann, T. 2009. Pyrrolizidine alkaloids: the successful adoption of a plant chemical defense. Pp. 55–81. In W. E. Conner, ed. *Tiger Moths and Woolly Bears: Behavior, Ecology, and Evolution of the Arctiidae*. Oxford: Oxford University Press.
- Häuser, C. L., and M. Boppré. 1997. A revision of the Afrotropical taxa of the genus *Amerila* Walker (Lepidoptera: Arctiidae). *Systematic Entomology* 22:1–44.
- Haynes, K. F., and M. C. Birch. 1985. The role of other pheromones, allomones, and kairomones in the behavioral responses of insects. Pp. 225–255. In G. A. Kerkut and L. I. Gilbert, eds. *Comprehensive Insect Physiology, Biochemistry, and Pharmacology*, Vol. 9. London: Pergamon Press.
- Heath R. R., P. J. Landolt, N. C. Leppla, and B. D. Dueben. 1988. Identification of a male-produced pheromone of *Anticarsia gemmatalis* (Hübner) (Lepidoptera: Noctuidae) attractive to conspecific males. *Journal of Chemical Ecology* 14:1121–1130.
- Heath, R. R., P. J. Landolt, B. D. Dueben, R. E. Murphy, and R. E. Schneider. 1992. Identification of male cabbage looper pheromone attractive to females. *Journal of Chemical Ecology* 18:441–453.
- Heisler, L., M. Andersson, S. J. Arnold, C. R. Boake, G. Borgia, G. Hausfater, M. Kirkpatrick et al. 1987. Evolution of mating preferences and sexually selected traits. Pp. 97–118. In J. W. Bradbury and M. Andersson, eds. *Sexual Selection: Testing the Alternatives*. New York: John Wiley and Sons.
- Hendricks, D. E., and T. N. Shaver. 1975. Tobacco budworm: male pheromone suppressed emission of sex pheromone by the female. *Environmental Entomology* 3:555–558.
- Hendrikse, A. 1986. The courtship behavior of *Yponomeuta padellus*. *Entomologia Experimentalis et Applicata* 42:45–55.
- Hillier, N. K., and N. J. Vickers. 2004. The role of heliothine hairpencil compounds in female *Heliothis virescens* (Lepidoptera: Noctuidae) behavior and mate acceptance. *Chemical Senses* 29:499–511.
- Hillier, N. K., and N. J. Vickers. 2011. Hairpencil volatiles influence interspecific courtship and mating between two related moth species. *Journal of Chemical Ecology* 37:1127–1136.
- Hillier, N. K., C. K. Kleinedam, and N. J. Vickers. 2006. Physiology and glomerular projections of olfactory receptor neurons on the antenna of female *Heliothis virescens* (Lepidoptera: Noctuidae) responsive to behaviorally relevant odors. *Journal of Comparative Physiology A* 192:199–219.
- Hillier, N. K., D. Kelly, and N. J. Vickers. 2007. A specific male olfactory sensillum detects behaviorally antagonistic hairpencil odorants. *Journal of Insect Science* 7:1–12.
- Hirai, K., H. H. Shorey, and L. K. Gaston. 1978. Competition among courting male moths: male-to-male inhibitory pheromone. *Science* 202:644–645.
- Huang, Y., S. Xu, X. Tang, Z. Zhao, and J. Du. 1996. Male orientation inhibitor of cotton bollworm: identification of compounds produced by male hairpencil glands. *Insect Science* 4:173–181.
- Iyengar, V. K., and T. Eisner. 1999a. Heritability of body mass, a sexually selected trait, in an arctiid moth (*Utetheisa ornatrix*). *Proceedings of the National Academy of Sciences of the United States of America* 96:9169–9171.
- Iyengar, V. K., and T. Eisner. 1999b. Female choice increases offspring fitness in an arctiid moth (*Utetheisa ornatrix*). *Proceedings of the National Academy of Sciences of the United States of America* 96:15013–15016.
- Iyengar, V. K., and H. K. Reeve. 2010. Z linkage of the female promiscuity genes in the moth *Utetheisa ornatrix*: support for the sexy-sperm hypothesis? *Evolution* 64:1267–1272.
- Iyengar, V. K., C. Rossiniand, and T. Eisner. 2001. Precopulatory assessment of male quality in an arctiid moth (*Utetheisa ornatrix*): hydroxydanaidal is the only criterion of choice. *Behavioral Ecology and Sociobiology* 49:283–288.
- Iyengar, V. K., H. K. Reeve, and T. Eisner. 2002. Paternal inheritance of a female moth's mating preference. *Nature* 419:830–832.
- Jacquin, E., P. Nagnan, and B. Frerot. 1991. Identification of hairpencil secretion from male *Mamestra brassicae* (L.) (Lepidoptera: Noctuidae) and electroantennogram studies. *Journal of Chemical Ecology* 17:239–247.
- Jang, Y., and M. D. Greenfield. 1996. Ultrasonic communication and sexual selection in wax moths: female choice based on energy and asynchrony of male signals. *Animal Behavior* 51:1095–1106.
- Jang, Y., and M. D. Greenfield. 2000. Quantitative genetics of female choice in an ultrasonic pyralid moth, *Achroia grisella*: variation and evolvability of preference along multiple dimensions of the male advertisement signal. *Heredity* 84:73–80.
- Jang, Y., R. D. Collins, and M. D. Greenfield. 1997. Variation and repeatability of ultrasonic sexual advertisement signals in *Achroia grisella* (Lepidoptera: Pyralidae). *Journal of Insect Behavior* 10:87–98.
- Jia, F.-Y., and M. D. Greenfield. 1997. When are good genes good? Variable outcomes of female choice in wax moths. *Proceedings of the Royal Society of London B* 264:1057–1063.
- Johansson, B. G., and T. M. Jones. 2007. The role of chemical communication in mate choice. *Biological Reviews* 82:265–289.
- Jordan, A. T., and W. E. Conner. 2007. Dietary basis for developmental plasticity of an androconial structure in the salt marsh moth *Estigmene acrea* (Drury). *Journal of the Lepidopterists' Society* 61:32–37.
- Jordan, A. T., T. H. Jones, and W. E. Conner. 2005. If you've got, flaunt it: ingested alkaloids affect corematal display behavior in the salt marsh moth, *Estigmene acrea*. *Journal of Insect Science* 5:1. PMID: PMC1283882.
- Jordan, A. T., T. H. Jones, and W. E. Conner. 2007. Morphogenetic effects of alkaloidal metabolites on the development of the coremata in the salt marsh moth, *Estigmene acrea* (Drury) (Lepidoptera: Arctiidae). *Archives of Insect Biochemistry and Physiology* 66:183–189.
- Keller, L., and H. K. Reeve. 1995. Why do females mate with multiple males? The sexually-selected sperm hypothesis. *Advances in the Study of Behavior* 24:291–315.
- Kelly, C. A., A. J. Norbutus, A. F. Lagalante, and V. K. Iyengar. 2012. Male courtship pheromones as indicators of genetic quality in an arctiid moth (*Utetheisa ornatrix*). *Behavioral Ecology* 23:1009–1014.

- Kimura, T., and H. Honda. 1999. Identification and possible functions of the hairpencil scent of the yellow peach moth, *Conogethes punctiferalis* (Guenée) (Lepidoptera: Pyralidae). *Applied Entomology and Zoology* 34:147–153.
- Kirkpatrick, M. 1982. Sexual selection and the evolution of female choice. *Evolution* 36:1–12.
- Krasnoff, S. B. 1997. Evolution of male lepidopteran pheromones: a phylogenetic perspective. Pp. 490–504. In R. T. Cardé and A. K. Minks, eds. *Insect Pheromone Research: New Directions*. New York: Chapman & Hall.
- Krasnoff, S. B., and D. D. Dussourd. 1989. Dihydropyrrrolizidine attractants for arctiid moths that visit plants containing pyrrolizidine alkaloids. *Journal of Chemical Ecology* 15:47–60.
- Krasnoff, S. B., and W. L. Roelofs. 1989. Quantitative and qualitative effects of larval diet on male scent secretions of *Estigmene acrea*, *Phragmatobia fuliginosa* and *Pyrrharctia isabella* (Lepidoptera: Arctiidae). *Journal of Chemical Ecology* 15:1077–1093.
- Krasnoff, S. B., and W. L. Roelofs. 1990. Evolutionary trends in the male pheromone systems of arctiid moths: evidence from studies of courtship in *Phragmatobia fuliginosa* and *Pyrrharctia isabella* (Lepidoptera: Arctiidae). *Zoological Journal of the Linnean Society* 99:319–338.
- Krasnoff, S. B., and K. W. Vick. 1984. Male wing gland pheromone of *Ephestia elutella*. *Journal of Chemical Ecology* 10:667–679.
- Krasnoff, S. B., and D. D. Yager. 1988. Acoustic response to a pheromonal cue in the arctiid moth *Pyrrharctia isabella*. *Physiological Entomology* 13:433–440.
- Krasnoff, S. B., L. B. Bjostad, and W. L. Roelofs. 1987. Quantitative and qualitative variation in male pheromones of *Phragmatobia fuliginosa* and *Pyrrharctia isabella* (Lepidoptera: Arctiidae). *Journal of Chemical Ecology* 13:807–822.
- Kunesch, G., P. Zagatti, J. Y. Lallemand, A. Debal, and J. P. Vigneron. 1981. Structure and synthesis of the wing gland pheromone of the male African sugar-cane borer: *Eldana saccharina* (Wlk.) (Lepidoptera: Pyralidae). *Tetrahedron Letters* 22:5271–5274.
- LaMunyon, C. W. 1997. Increased fecundity, as a function of multiple mating, in an arctiid moth, *Utetheisa ornatrix*. *Ecological Entomology* 22:69–73.
- LaMunyon, C. W., and T. Eisner. 1993. Postcopulatory sexual selection in an arctiid moth (*Utetheisa ornatrix*). *Proceedings of the National Academy of Sciences of the United States of America* 90:4689–4692.
- LaMunyon, C. W., and T. Eisner. 1994. Spermatophore size as determinant of paternity in an arctiid moth (*Utetheisa ornatrix*). *Proceedings of the National Academy of Sciences of the United States of America* 91:7081–7084.
- Lande, R. 1981. Models of speciation by sexual selection on polygenic traits. *Proceedings of the National Academy of Sciences of the United States of America* 78:3721–3725.
- Landolt, P. J. 1995. Attraction of female cabbage looper moths (Lepidoptera: Noctuidae) to males in the field. *Florida Entomologist* 78:96–100.
- Landolt, P. J., and R. R. Heath. 1989. Attraction of female cabbage looper moth (Lepidoptera: Noctuidae) to male-produced sex pheromone. *Annals of the Entomological Society of America* 82:520–525.
- Landolt, P. J., and R. R. Heath. 1990. Sex role reversal in mate-finding strategies of the cabbage looper moth. *Science* 249:1026–1028.
- Landolt, P. J., R. R. Heath, J. G. Millar, K. M. Davis-Hernandez, B. D. Dueben, and K. E. Ward. 1994. Effects of host plant, *Gossypium hirsutum* L., on sexual attraction of cabbage looper moths, *Trichoplusia ni* (Hübner) (Lepidoptera: Noctuidae). *Journal of Chemical Ecology* 20:2959–2974.
- Lassance, J.-M., and C. Löfstedt. 2009. Concerted evolution of male and female display traits in the European corn borer *Ostrinia nubilalis*. *BMC Biology* 7:10.
- Lebedeva, K. V., N. V. Vendilo, V. L. Ponomarev, V. A. Pletnev, and D. B. Mitroshin. 2002. Identification of pheromone of the greater wax moth *Galleria mellonella* from the different region of Russia. *International Organization of Biological and Integrated Control of Noxious Animals and Plants: West Palaearctic Regional Section Bulletin* 25:1–5.
- LeComte, C., E. Thibout, D. Pierre, and J. Auger. 1998. Transfer, perception, and activity of male pheromone of *Acrolepiopsis assectella* with special reference to conspecific male sexual inhibition. *Journal of Chemical Ecology* 24:655–671.
- Leyrer, R. L., and R. E. Monroe. 1973. Isolation and identification of the scent of the moth *Galleria mellonella* and a reevaluation of its sex pheromone. *Journal of Insect Physiology* 19:2267–2271.
- Lim, H., and M. D. Greenfield. 2006. Female pheromonal chorusing in an arctiid moth, *Utetheisa ornatrix*. *Behavioral Ecology* 18:165–173.
- Lim, H., and M. D. Greenfield. 2008. Female arctiid moths, *Utetheisa ornatrix*, orient towards and join pheromonal choruses. *Animal Behaviour* 75:673–680.
- Lim, H., K. C. Park, T. C. Baker, and M. D. Greenfield. 2007. Perception of conspecific female pheromone stimulates female calling in an arctiid moth, *Utetheisa ornatrix*. *Journal of Chemical Ecology* 33:1257–1271.
- Löfstedt, C., and M. Kozlov. 1997. A phylogenetic analysis of pheromone communication in primitive moths. Pp. 473–489. In R. T. Cardé and A. K. Minks, eds. *Insect Pheromone Research: New Directions*. New York: Chapman & Hall.
- Löfstedt, C., N. J. Vickers, W. L. Roelofs, and T. C. Baker. 1989. Diet related courtship success in the oriental fruit moth, *Grapholitha molesta* (Tortricidae). *Oikos* 55:402–408.
- Löfstedt, C., N. J. Vickers, and T. C. Baker. 1990. Courtship, pheromone titre and determination of male mating success in the oriental fruit moth *Grapholitha molesta* (Lepidoptera: Tortricidae). *Entomologia Generalis* 15:121–125.
- Moczek, A. P., J. Andrews, T. Kijimoto, Y. Yerushalmi, and D. J. Rose. 2007. Emerging model systems in evo-devo: horned beetles and the origins of diversity. *Evolution and Development* 9:323–328.
- Nakano, R., N. Skals, T. Takanashi, A. Surlykke, T. Koike, K. Yoshida, H. Maruyama, S. Tatsuki, and I. Ishikawa. 2008. Moths produce extremely quiet ultrasonic courtship songs by rubbing specialized scales. *Proceedings of the National Academy of Sciences of the United States of America* 105:11812–11817.
- Nishida, R., T. C. Baker, and W. L. Roelofs. 1982. Hairpencil pheromone components of male oriental fruit moths *Grapholitha molesta*. *Journal of Chemical Ecology* 8:947–959.
- O'Donald, P. 1967. A general model of sexual and natural selection. *Heredity* 22:499–518.
- O'Donald, P. 1980. *Genetic Models of Sexual Selection*. Cambridge: Cambridge University Press.
- Parker, G. A. 1979. Sexual selection and sexual conflict. Pp. 123–166. In M. S. Blum and N. A. Blum, eds. *Sexual Selection and Reproductive Competition in Insects*. New York: Academic Press.
- Phelan, P. L. 1992. Evolution of sex pheromones and the role of asymmetric tracking. Pp. 265–314. In B. D. Roitberg and M. B. Isman, eds. *Insect Chemical Ecology: An Evolutionary Approach*. New York: Chapman & Hall.
- Phelan, P. L. 1997. Evolution of mate-signaling in moths: phylogenetic considerations and predictions from the asymmetric tracking hypothesis. Pp. 240–256. In J. C. Choe and B. J. Crespi, eds. *Mating Systems in Insects and Arachnids*. Cambridge: Cambridge University Press.
- Phelan, P. L., and T. C. Baker. 1986. Male-size-related courtship success and intersexual selection in the tobacco moth, *Ephestia elutella*. *Experientia* 42:1291–1293.
- Phelan, P. L., and T. C. Baker. 1987. Evolution of male pheromones in moths: reproductive isolation through sexual selection. *Science* 235:205–207.
- Phelan, P. L., and T. C. Baker. 1990a. Comparative study of courtship in twelve phyticine moths (Lepidoptera: Pyralidae). *Journal of Insect Behavior* 3:303–326.
- Phelan, P. L., and T. C. Baker. 1990b. Information transmission during intra- and interspecific courtship in *Ephestia elutella* and *Cadra figulilella*. *Journal of Insect Behavior* 3:589–602.
- Phelan, P. L., P. J. Silk, C. J. Northcott, S. H. Tan, and T. C. Baker. 1986. Chemical identification and behavioral characterization of male wing pheromone *Ephestia elutella* (Pyralidae). *Journal of Chemical Ecology* 12:135–146.
- Pliske, T. E. 1975. Attraction of Lepidoptera to plants containing pyrrolizidine alkaloids. *Environmental Entomology* 4:455–473.
- Reeve, H. K., and D. W. Pfennig. 2003. Genetic biases for showy males: are some genetic systems especially conducive to sexual selection? *Proceedings of the National Academy of Sciences of the United States of America* 100:1089–1094.
- Reeve, H. K., and J. S. Shellman-Reeve. 1997. The general protected invasion theory: sex biases in parental and alloparental care. *Evolutionary Ecology* 11:357–370.
- Röller, H., K. Biermann, J. S. Bjerke, D. W. Norgard, and W. H. McShan. 1968. Sex pheromones of pyralid moths. I. Isolation and

- identification of sex attractant of *Galleria mellonella* L. (greater waxmoth). *Acta Entomologica Bohemoslovaca* 65:208–211.
- Royer, L., and J. N. McNeil. 1992. Evidence of a male pheromone in the European corn borer, *Ostrinia nubilalis* (Hübner) (Lepidoptera: Pyralidae). *The Canadian Entomologist* 124:113–116.
- Schmitz, B., M. Buck, A. Egelhaaf, and D. Schneider. 1989. Ecdysone and a dietary alkaloid interact in the development of the pheromone gland of a male moth (*Cretonotos*, Lepidoptera: Arctiidae). *Developmental Biology* 198:1–7.
- Schneider, D., M. Boppré, J. Zweig, S. B. Horsely, T. W. Bell, J. Meinwald, K. Hansen, and E. W. Diehl. 1982. Scent organ development in *Cretonotos* moths: regulation by pyrrolizidine alkaloids. *Science* 215:1264–1265.
- Schneider, D., S. Shulz, R. Kittmann, and P. Kanagaratnam. 1992. Pheromones and glandular structures of both sexes of the weed defoliator moth, *Pareuchaetes pseudoinsulata* Rego Barros (Lep., Arctiidae). *Journal of Applied Entomology* 113:280–294.
- Schneider, D., S. Schulz, E. Priesner, J. Ziesmann, and W. Franke. 1998. Autodetection and chemistry of female and male pheromone in both sexes of the tiger moth, *Panaxia quadripunctaria*. *Journal of Comparative Physiology A* 182:153–161.
- Schulz, S. 2009. Alkaloid-derived male courtship pheromones. Pp. 145–153. In W. E. Conner, ed. *Tiger Moths and Woolly Bears: Behavior, Ecology, and Evolution of the Arctiidae*. Oxford: Oxford University Press.
- Singer, M. S., K. C. Mace, and E. A. Bernays. 2009. Self-medication as adaptive plasticity: increased ingestion of plant toxins by parasitized caterpillars. *Public Library of Science ONE* 4: e4796.
- Smedley, S., and T. Eisner. 1995. Sodium uptake by puddling in a moth. *Science* 270:1816–1818.
- Spangler, H. G. 1986. Functional and temporal analysis of sound production in *Galleria mellonella* L. (Lepidoptera: Pyralidae). *Journal of Comparative Physiology A* 159:751–756.
- Spangler, H. G. 1987. Ultrasonic communication in *Coccyra cephalonica* (Stainton) (Lepidoptera: Pyralidae). *Journal of Stored Product Research* 23:203–211.
- Takayoshi, K., and H. Hiroshi. 1999. Identification and possible functions of the hairpencil scent of the yellow peach moth, *Conogethes punctiferalis* Guenée (Lepidoptera: Pyralidae). *Applied Entomology and Zoology* 34:147–153.
- Tamaki, Y. 1985. Sex pheromones. Pp. 145–191. In G. A. Kerkut and L. I. Gilbert, eds. *Comprehensive Insect Physiology, Biochemistry, and Pharmacology*, Vol. 9. London: Pergamon Press.
- Teal, P. E. A., and J. H. Tumlinson. 1989. Isolation, identification and biosynthesis of compounds produced by male hairpencil glands for *Heliothis virescens* (F.) (Lepidoptera: Noctuidae). *Journal of Chemical Ecology* 15:413–427.
- Teal, P. E. A., J. R. McLaughlin, and J. H. Tumlinson. 1981. Analysis of the reproductive behavior of *Heliothis virescens* (F.) (Lepidoptera: Noctuidae) under laboratory conditions. *Annals of the Entomological Society of America* 74:324–330.
- Teal, P. E. A., J. R. McLaughlin, and J. H. Tumlinson. 1989. Analysis of the reproductive behavior of *Heliothis virescens*. *Annals of the Entomological Society of America* 74:324–330.
- Thibout, E., S. Ferary, and J. Auger. 1994. Nature and role of the sexual pheromones emitted by males of *Acrolepiopsis assectella*. *Journal of Chemical Ecology* 20:1571–1581.
- Thornhill, R. 1979. Male and female sexual selection and the evolution of mating strategies in insects. Pp. 81–121. In M. M. Blum and N. A. Blum, eds. *Sexual Selection and Reproductive Competition in Insects*. New York: Academic Press.
- Thornhill, R., and J. Alcock. 1983. *The Evolution of Insect Mating Systems*. Cambridge: Harvard University Press.
- Trematerra, P., and G. Pavan. 1994. Role of ultrasound production and chemical signals in the courtship behavior of *Ephestia cautella* (Walker), *Ephestia kuehniella* Zeller and *Plodia interpunctella* (Hubner) (Lepidoptera: Pyralidae). *Proceeding of the 6th International Working Conference on Stored-Product Protection* 1:591–594.
- Trivers, R. L. 1972. Parental investment and sexual selection. Pp. 136–179. In B. Campbell, ed. *Sexual Selection and the Descent of Man*. London: Aldine Publishing Company.
- Vahed, K. 1998. The function of nuptial feeding in insects: a review of empirical studies. *Biological Reviews of the Cambridge Philosophical Society* 73:43–78.
- von Nickisch-Roseneck, E., and M. Wink. 1993. Sequestration of pyrrolizidine alkaloids in several arctiid moths (Lepidoptera: Arctiidae). *Journal of Chemical Ecology* 19:1889–1903.
- von Nickisch-Roseneck, E., and M. Wink. 1994. Influence of previous feeding regimes and ambient temperatures on degradation and storage of pyrrolizidine alkaloids in the moth species *Cretonotos transiens* (Lepidoptera: Arctiidae). *Entomologia Generalis* 19:159–170.
- Wagner, D. L., and J. Rosovsky. 1991. Mating systems in primitive Lepidoptera, with emphasis on the reproductive behavior of *Korscheltellus gracilis* (Hepialidae). *Zoological Journal of the Linnean Society* 102:277–303.
- Weatherston, J., and J. E. Percy. 1977. Pheromones of male Lepidoptera. Pp. 295–307. In K. G. Adiyodi and R. G. Adiyodi, eds. *Advances in Invertebrate Reproduction, Vol. 1*. Kerala: Peralam-Kenoth.
- Weller, S., J., N. L. Jacoben, and W. E. Conner. 1999. The evolution of chemical defenses and mating systems in tiger moths (Lepidoptera: Arctiidae). *Biological Journal of the Linnean Society* 68:557–578.
- Weller, S. J., R. B. Simmons, R. Boada, and W. E. Conner. 2000. Abdominal modifications occurring in wasp mimics of the ctenuchine-euchromiine clade (Lepidoptera: Arctiidae). *Annals of the Entomological Society of America* 93:920–928.
- Williams, G. C. 1966. *Adaptation and Natural Selection*. Princeton, NJ: Princeton University Press.
- Willis, M. A., and M. C. Birch. 1982. Male lek formation and female calling in a population of the arctiid moth, *Estigmene acrea*. *Science* 218:168–170.
- Wink, M., and D. Schneider. 1990. Fate of plant-derived secondary metabolites in 3 moth species (*Syntomis mogadorensis*, *Syntomeida epilais*, and *Cretonotos transiens*). *Journal of Comparative Physiology B* 160:389–400.
- Wink, M., D. Schneider, and L. Witte. 1988. Biosynthesis of pyrrolizidine alkaloid-derived pheromones in the arctiid moth, *Cretonotos transiens*: stereochemical conversion of heliotrine. *Zeitschrift für Naturforschung* 43c:737–741.
- Wunderer, H., K. Hansen, T. W. Bell, D. Schneider, and J. Meinwald. 1986. Sex pheromones of two Asian moths (*Cretonotos transiens*, *C. gangis*; Lepidoptera—Arctiidae): behavior, morphology, chemistry, and electrophysiology. *Experimental Biology* 46:11–27.
- Zagatti, P. 1981. Comportement sexuel de la pyrale de la canne à sucre *Eldana saccharina* (Wlk.) lie a deux phéromones émises par le mâle. *Behaviour* 78:81–89. [In French]
- Zagatti, P., G. Kunesch, and N. Morin. 1981. La vanilline, constituant majoritaire de la sécrétion aphrodisiaque émise par les androconies du mâle de la Pyrale de la Canne à sucre: *Eldana saccharina* (Wlk.) (Lépidoptères, Pyralidae, Gallerinae). *Comptes Rendus de l'Académie des Sciences, Série III* 292:633–635. [In French]
- Zagatti, P., G. Kunesch, F. Ramiandrasoa, C. Malosse, D. R. Hall, R. Lester, and B. F. Nesbit. 1987. Sex pheromones of rice moth, *Coccyra cephalonica* Stainton. I. Identification of male pheromones. *Journal of Chemical Ecology* 13:1561–1573.
- Zaspel, J. M., S. J. Weller, and M. A. Branham. 2011. A comparative survey of proboscis morphology and associated structures is fruit-piercing, tear-feeding, and blood-feeding moths in the subfamily Calpinae. *Zoomorphology* 130:203–225.
- Zaspel, J. M., S. Coy, K. Habanek, and S. J. Weller. 2013. Presence and distribution of sensory structures on the mouthparts of self-medicating moths. *Zoologischer Anzeiger* 253:6–10.