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Sexual Communication with Pheromones

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13.1 INTRODUCTION

A critical event in sexual reproduction is location or recruitment of a mate. In a number of insect groups, the necessary movements in time and space are often mediated by pheromones. One sex may recruit the other, or both sexes may be attracted to the chemical emitters. Aggregation may be viewed as the end result of movement reactions that reduce the distance between individuals in their environment. Such clustering may be brought about by a combination of attraction and arrestment, which are themselves not orientation mechanisms but rather end results, i.e., displacements, caused by movement reactions (Kennedy, 1978). For sex- and aggregation-pheromone communication, we define attraction as the net displacement of one individual toward the chemical source. Conversely, arrestment is the lack of net displacement toward or away from the chemical source. Both displacement phenomena may be viewed as part of a continuum caused by pheromone mediation of quite disparate movement reactions, such as orthokinesis, klinotaxis and anemotaxis (see Bell, Chapter 4 and Cardé, Chapter 5). That attraction and arrestment are only outcomes, not mechanisms, does not diminish the heuristic value of these terms; they are a capsule summary of the change in spacing between an individual and the chemical source. To an organism responding to sex pheromone, proximate cues and orientation mechanisms notwithstanding, such outcomes are the result of evolutionary selection.

13.2 DIVERSITY OF COMMUNICATION SYSTEMS

Among the insect groups in which chemical attraction is a major means of

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sexual recruitment are the moths (Lepidoptera), many Coleoptera, Hymenoptera, Orthoptera, Diptera and Homoptera. In these groups, females are predominantly the emitters and males the receivers. Hence, the reduction in spacing is due primarily to chemically mediated movements of males. Where attraction of females by males does occur, interesting ecological and evolutionary situations are being discovered that involve sexual selection and parental investment in gametes and offspring. The following examples of chemical communication in a number of insect groups illustrates the variety of these chemical communication systems.

Within the Lepidoptera, only in a few cases discovered so far do male-emitted chemicals attract females. The vast majority of aggregation is initiated by females who release volatiles from a gland typically located at the end of their abdomen. In some species, a sort of dual system is used, in which both female and male-emitted chemicals cause aggregation. As discussed in more detail later in this chapter, male oriental fruit moths, *Grapholitha molesta*, chemically attract females from a few centimeters away after they have been attracted from long distances by the females' pheromone (Baker and Cardé, 1979b). In the salt marsh caterpillar, *Estigmene acraea*, males hang from plants just after sunset and inflate huge coremata at the end of their abdomens (Willis and Birch, 1982). A yet-to-be-identified pheromone released from these organs apparently attracts other males which land and evert their coremata, resulting in the formation of an aggregation of sexually displaying males, or lek. Females are attracted to a male or males in this group, one of which then mates with her. Later in the night, females attract males with a blend of (*Z*,*Z*)-9,12-octadecadienal,(*Z*,*Z*,*Z*)-9,12,15-octadecatrienal, and (*Z*,*Z*)-3,6-*cis*-9,10-epoxyheneicosadiene (Hill and Roelofs, 1981). In the pyralid wax moths, *Galleria melonella* and *Achroia grisella*, males emit pheromone from costal wing glands to lure flying females, although in the latter species the chemicals, *n*-undecanal and (*Z*)-11-octadecenal, apparently only 'prime' females to respond to auditory cues generated by males' vibrating wings (Dahm *et al.*, 1971). In *G. melonella* it is not clear whether the chemicals, *n*-nonanal and *n*-undecanal (Roller *et al.*, 1968; Leyrer and Monroe 1973), attract females from a distance or merely cause arrestment of randomly flying individuals (Finn and Payne, 1977). However, in another pyralid species, *Eldana saccharina*, the African sugarcane borer, an unidentified pheromone emitted from male wing glands causes females to walk rapidly and search the grassy vegetation until they locate the male and touch his abdominal hairpencils (Zagatti *et al.*, 1981). Vanillin and *p*-hydroxybenzaldehyde have been identified from these hairpencils, which function during courtship to aid in females' acceptance of males during copulatory attempts (Zagatti, 1981).

In the Coleoptera, most knowledge of sexual communication pertains to bark beetles, family Scolytidae (discussed in detail by Birch, Chapter 12), where one of the sexes, depending on the species, initiates aggregation by boring into host trees. The blend of pheromone plus host-tree volatiles attracts predominantly members of the opposite sex. In the curculionid species *Anthonomus grandis*, the boll weevil, a male-emitted blend of two terpene alcohols plus two terpene aldehydes (Tumlinson *et al.*, 1969) results primarily in the attraction of females, although a close-range, female-emitted pheromone plus cotton plant volatiles attracts principally males (Hedin *et al.*, 1979). Much work has also been done in the dermestid genus *Trogoderma*, in which solitary females release either (*E*) or (*Z*), 14-methyl, 8-hexadecenal or a blend of both from an intersegmental abdominal gland (Cross *et al.*, 1976). Males are not only attracted preferentially to a precise geometrical isomeric blend, but also respond specifically to the correct optical enantiomers (Silverstein *et al.*, 1980). In the Scarabaeidae, female Japanese beetles, *Popilla japonica* release the sex pheromone (*Z*)-5-(1-decenyl)dihydro-2(3H)-furanone, attracting males from many tens of meters away (Tumlinson *et al.*, 1977). A small amount of the (*S*) form added to the pure (*R*) form of this compound reduces the attraction of males, and therefore optical configuration also plays a role in pheromone channel partitioning in this family.

For hymenopterans, much is known about chemically mediated aggregation in the sawflies, subfamily Symphyta. Female-emitted pheromone attracts males from some distance. In the species *Neodiprion lecontei*, *N. sertifer* and *N. pinetum*, females emit, and males respond most strongly to, the acetate ester of 3,7-dimethyl pentadecan-2-ol (Jewett *et al.*, 1976), whereas in *Diprion similis* the propionate ester is used. Communication channel segregation is thus achieved between the latter species and the others by functional moiety; however, *N. lecontei* and *N. pinetum* males both preferentially respond to the same (*S,S,S*) optical isomer of the acetate compound (Kraemer *et al.*, 1979, 1981). It is unclear how partitioning is accomplished, except that there are some host-tree preference differences between these species. Presumably, optical differences in pheromone structure could play a role in isolating some of the other members of this genus that apparently use this acetate in sexual communication. In the subfamily Apocrita, a variety of sexual communication systems is employed. Queens of some primitive ant species in the subfamilies Myrmicinae, Myrmeciinae, and Ponerinae (such as *Rhytidoponera metallica*) raise their abdomens in a typical calling posture and release an unidentified sex pheromone from a tergal gland to attract males (Hölldobler and Haskins, 1977). More advanced species such as the socially parasitic *Harpagoxenus sublaevis*, *Doronomyrmex pacis* and *Leptothorax kutteri* also employ female-emitted pheromone for sexual communication (Buschinger and Alloway, 1979). Queen honey bees emit sex pheromone from their mandibular glands, which initiates mate-finding by drones (males), evokes upwind flight and heightens visual orientation to the female flying several meters above the ground. A mandibular gland chemical, (*E*)-9-oxo-2-decenoic acid has been implicated as a sex pheromone component (Boch *et al.*, 1975). Bumblebee queens also produce from their mandibular glands a sex pheromone that evokes copulatory attempts from males (Van Honk *et al.*, 1978). Females are arrested on vegetation at the sites of mandibular gland deposits made by males (Svensson and Bergstrom, 1979), who patrol particular routes along their chemically marked territory.

Most work on sexual communication in the Orthoptera has centered on the cockroaches, including many elegant studies on orientation covered in Chapter 4 by Bell. Female American cockroaches, *Periplaneta americana* emit sex pheromone, (1*Z*,5*E*)-1,10(14)-diepoxy-4(15),5-germacradien-9-one from their body surfaces (Persoons *et al.*, 1979; Adams *et al.*, 1979); this chemical elicits increased rates of locomotion, upwind movement, and wing-raising by males (Tobin *et al.*, 1981). Wing-raising attracts females from a few centimeters away, and in the German cockroach, *Blattella germanica* is elicited by the female's cuticular constituent 3*S*,11*S*-dimethyl-2-nonacosanone (Nishida *et al.*, 1979). In both species, the male accomplishes copulation while the female is arrested and feeding on the male's dorsal abdominal cuticule. Hence, a 'dual' system of sexual aggregation is found also in the order Orthoptera. Both males and females take part in a chemical dialog that reduces spacing and results in mating.

In the Diptera, a wide variety of sexual aggregating systems is known. A female sciarid, *Bradysia impatiens*, attracts males from at least 1 m downwind using a pheromone evidently released from the thorax and legs (Alberts *et al.*, 1981). Cuticular hydrocarbons such as the blend of (*Z*)-9-tricosene and branched alkanes of 28–30 carbons from female houseflies (*Musca domestica*) cause males to fly and to land on fly-like models (Uebel *et al.*, 1976). Such cuticular pheromones are also known in the stable fly (*Stomoxys calcitrans*) (Sonnet *et al.*, 1979) and face fly (*Musca autumnalis*) (Uebel *et al.*, 1975). Among tephritid fruit flies, a variety of systems is used, some in which females attract males with pheromone, and others involving males attracting females, either by isolated or group emission (leks), depending on the species (Prokopy, 1980). Lekking males are also found in some tropical *Drosophila* species, in which pheromone apparently attracts females into the group whereupon one male may mate with her (Spieth, 1968).

Investigations of homopteran sexual communciation have focused on the economically important scale insects and mealybugs. Female diaspidid scales are sedentary and release blends of terpenoid-type compounds such as (3*S*,6*R*)-3-methyl-6-isopropenyl-9-decen-1-yl acetate plus (3*S*,6*R*)-3-methyl-6-isopropenyl-3,9-decadien-1-yl acetate by the California red scale, *Aonidiella aurantii* (Roelofs *et al.*, 1978; Gieselmann *et al.*, 1980). Such blends attract the vagile, flying males from several meters away. Mealybug females of the family Coccidae also produce terpenoid compounds that attract males, such as 2,6-dimethyl-1,5-heptadien-3-ol acetate by the Comstock mealybug, *Pseudococcus comstocki* (Bierl-Loenhardt *et al.*, 1980). The preferential attraction of male scale insects and mealybugs to only the 'correct' geometrical and optical isomers (Gieselmann *et al.*, 1979; Bierl-Leonhardt *et al.*, 1981) indicates myriad possibilities for maintaining separate communication channels by sympatric species in this group.

These have been brief descriptions of sexual communication in a variety of groups. In the remainder of our contribution we will define the major selective forces that shape chemical sexual communication systems: environmental conditions, competition for an exclusive communication channel (a function of the signal-to-noise ratio), reproductive isolation, stabilizing selection, and sexual selection. These factors could be explored with any of the aforementioned insect groups, but we will use moth species as examples because of the comparative wealth in our current understanding of their chemical communication systems. A related discussion for the bark beetles is found in Chapter 12.

13.3 SELECTIVE FORCES

13.3.1 Competition and reproductive isolation

A major ecological paradigm contends that interspecific competition plays a major role in the structuring of communities; this belief has been applied to the analyses of the partitioning of pheromone communication channels in moths (e.g., Comeau, 1971; Roelofs and Cardé, 1974; Cardé *et al.*, 1977; Greenfield and Karandinos, 1980). If the competing species are closely related, distinct pheromone communication channels also provide premating isolation mechanisms that prevent hybridization (Roelofs and Cardé, 1974; Cardé *et al.*, 1977). Although these two, related selective agents provide ample hypotheses to explain distinct communication channels, a rigorous demonstration of the importance of either competition or reproductive isolation in the initial evolution and continued maintenance of these distinct channels is not so readily forthcoming. Autecological constraints can be expected to influence these communication systems, particularly in their daily temporal patterning. The avoidance of avian and chiropteran predation, flight energetics in various air temperatures and insolations and dispersal of pheromone in different wind fields (see Elkinton and Cardé, Chapter 3) can all be expected to offer substantial effects.

In the following examples, description of the communication channels and their degree of overlap between sibling and congeneric species, as well as species in different families, will be straightforward, although the elucidation of these phenomena is by no means complete even in these cases. The selective forces apparently shaping these patterns will be presented as hypotheses. There may be several plausible explanations for differences among the communication channels of the species, and it may be difficult to test experimentally any hypothesis. It could be argued that we rarely observe direct competition between species for a communication channel in nature because the selective effects of competition are so powerful. Character displacement, in the form of a narrower partitioning of the pheromone communication channel where competing species overlap, would provide direct support of the competition paradigm. Insight into the importance of these factors can be gained by experimental manipulation of the natural blend of synthetic pheromone components or by emitting the pheromone at uncharacteristic times or emission rates and documenting the effects upon behavioral response. Similarly, observing the effects of natural fluctuations in environmental conditions upon the animal's communication success may reveal the influence of autecological factors in shaping the communciation channel.

The preponderance of attractant pheromones identified to date for various moth species are even-numbered 10–18 carbon-chain acetates, alcohols and aldehydes, typically with one or two double bonds along the chain. Of course, some moth families employ quite different pheromones, as in the long-chain epoxides and ketones in the Lymantriidae. Yet other major families (e.g., Sphingidae and Geometridae) currently remain with few identified attractants; these groups probably possess unique structures.

Now although some species evidently use only a single chemical for attraction, most species use a blend of two to four related chemicals to create a distinct communication channel. Moths in phylogenetically distant groups may 'share' the same attractant components. (*Z*)-11- and (*E*)-11-tetradecenyl acetates, for example, are used by two co-existing moths in North America, the tortricid, *Argyrotaenia velutinana* and the pyralid, *Ostrinia nubilalis* (Klun *et al.*, 1973; Kochansky *et al.*, 1975). These species nonetheless maintain non-overlapping chemical channels by employing slightly different ratios of these chemicals (93:7 and 97:3, respectively) and through the use of an additional component, dodecyl acetate, emitted by *A. velutinana* (Roelofs *et al.*, 1975).

One of the most thoroughly investigated attractant pheromone systems in any group of moths are the attractants in the Tortricidae. The Tortricidae is generally divided into two subfamilies, the Oleuthreutineae, which are characterized by somewhat food plant-specialized, internally feeding larvae and the Torticineae, which are primarily folivorous. In species occurring worldwide (especially North America, Europe and Japan), much is known of the chemical structures of their pheromones. But our knowledge of the tortricids of northeastern North America is particularly detailed, principally due to the efforts of Wendell Roelofs and his colleagues. A typical attractant pheromone in the Tortricidae is comprised of one to four compounds of either 12 or 14 carbon-chain length and possesses either an acetate, alcohol or aldehyde moiety. The compounds eliciting upwind flight typically contain one or two double bonds between the C_7 to the terminal position. A major difference among species in the two subfamilies is the nearly exclusive use of 12-carbon-chain attractants by oleuthreutines and 14-carbon-chain attractants by tortricines (Roelofs and Comeau, 1971; see the discussion by Roelofs and Brown, 1982).

Within the tortricines of northeastern North America many species overlap broadly in their spatial and temporal distributions, and thus we may surmise that the chemical communication channel is partitioned in some fashion. Indeed cross-communication, in which a female lures a non-conspecific mate, appears negligible (Comeau, 1971), despite the relatively few structures employed by the species examined to date.

The partitioning of the chemical channel in tortricines feeding on apple (*Malus*) in this region is especially instructive because in a given locality most of the species emerge some three to five weeks after the late spring optimal feeding period for the larvae. Because of the initial larval dispersal from the egg mass and the solitary leaf-rolling habits of the larvae, adults of many species emerge over the entire tree at the same time (Chapman and Lienk, 1971). One might expect that differing daily times of sexual recruitment would offer an effective partitioning mechanism.

The importance of mating periodicity in creation of an exclusive communication channel between some moth species has long been recognized (Rau and Rau, 1929; see discussion in Roelofs and Cardé, 1974). For example, discrete, non-overlapping daily mating rhythms appear to be primary barriers to cross-attraction in three saturniid moths in South Carolina. *Callosamia promethea* is active from about 10.00 to 15.00–16.00 h; *C. securifera* from the latter time until dusk and *C. angulifera* from dusk to about midnight (Collins and Weast, 1961; Ferguson, 1971–2). Among the *Hemileuca* species of the California Sierra Nevada mountains, specificity also seems to be based in part upon different diel rhythms of attraction (Collins and Tuskas, 1979). But among the apple-feeding tortricines in eastern North America exclusive rhythms of mating appear relatively unimportant. First, if the average times of attraction of males to synthetic pheromone (and where data are available to females) are calculated for a typical June evening (Table 13.1), then it is apparent that the daily rhythms of attraction in these species are so broadly overlapping as to be ineffective partitioning mechanisms. Second, the rhythms shift according to the daily temperature conditions: female calling and male response are altered by the current temperature conditions. This plasticity evidently allows optimization of flight times so that for these tortricines mating occurs late at night when temperatures are warm and early in the evening (or even before dusk) when temperatures are cool (Comeau, 1971; Cardé *et al.*, 1975a; Comeau *et al.*, 1976). An example of such daily alterations in time of attraction for *Archips argyrospilus* in New York is given in Fig. 13.1.

The effect of energetics upon the rhythms of sexual activity would be expected to be most pronounced in small moths, i.e., those possessing a high surface area to volume ratio (Comeau, 1971, Cardé *et al.*, 1975a). Among the nocturnal species, we might expect (at least in temperate regions) that large species would fly later in the night than small ones, as seems to be the case in central New York (Comeau, 1971).

Among moths a large proportion of the day-flying species are either mimics (e.g., male *C. promethea* mimics the butterfly *Battus phelinor*, and sesiids are wasp mimics), or distasteful and aposomatically colored as in many arctiids. Thus, daytime flight among temperate and tropical moths is not typical, unless the species is comparatively well protected against predation.

Table 13.1 Attractant blend ratio and inhibitors*

Species	Z11–14:Ac	E11–14:Ac	Z9–14:Ac	12:Ac	Z11–14:OH	E11–14:OH	Adult seasonal distribution†	Regression for attraction in June–July‡	Typical activity time in June–July§	Structure references¶
Archips argyrospilus	60* ~	40* ~	4* ~	200*	—	—	June to early July	$10.46 + 0.63T_{2050}$	22.5	Cardé *et al.*, 1977
Archips mortuanus	90 ~	10 ~	1 ~	200			June to early July	$14.98 + 0.43T_{2220}$	22.3	Cardé *et al.*, 1977
Archips cervasivoranus	20* ~	80* ~		—			July	$20.00 + 0.27T_{2415}$	24.5	Roelofs *et al.*, 1980
Archips semiferanus	30* ~	70* ~					June to early July	$18.18 + 0.25T_{12215}$	22.4	Miller *et al.*, 1976
Argyrotaenia velutinana	90* ~	10* ~	—	150*	—		April; late June to mid July; August to early September	$17.45 + 0.22T_{2300}$	21.1	Roelofs *et al.*, 1975
Christoneura rosaceana	95* ~	5* ~	—	—	5*		June to early July; August	$16.74 + 0.40T_{2300}$	23.4	Hill and Roelofs, 1979
Christoneura fractivittana	—				100		June	$17.65 + 0.25T_{2200}$	21.9	Roelofs and Comeau, 1970
Pandemis limitata	90* ~	—	10* ~	—			June			Roelofs *et al.*, 1976
Platynota ideausalis	—	50*			—	50*	June; August			Hill *et al.*, 1974
Platynota flavedana	—				15* ~	85* ~	June; August			Hill *et al.*, 1977

* Compounds asterisked have been identified as present in either the female's abdominal tip or her effluvium. The remaining compounds have been determined as attractants or antagonists of attraction (−) by empirical screening in the field

† Flight periods for the lower Hudson Valley of New York according to Chapman and Lienk (1971)

‡ Regression equations for the hour of attraction as modified by the temperature at the mean time of attraction for this species. See Comeau (1971) and Comeau *et al.* (1976). All times are Eastern Daylight Time

§ Peak time of attraction for a typical June evening where the temperature is 23°C at 1800, 19°C at 2000, 17°C at 2200, 16.5°C at 2400, and 15.5°C at 0200

¶ Additional references to compound identifications and biological activities are given in these references

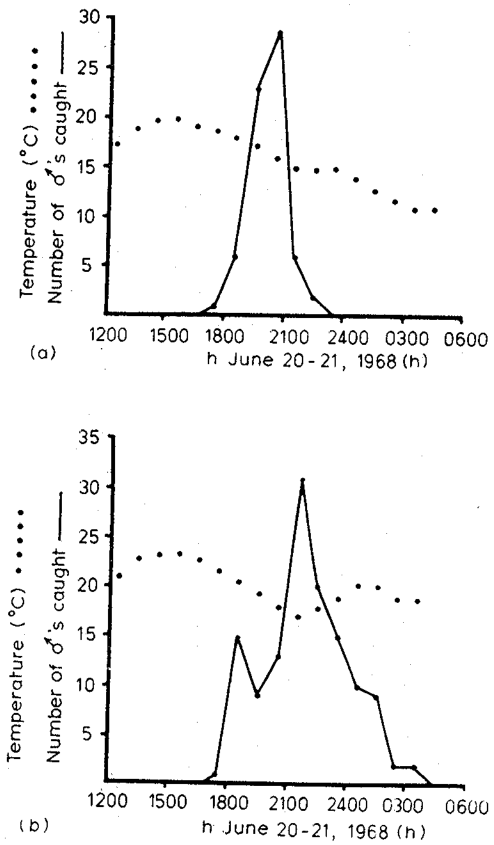

Fig. 13.1 Diel rhythms of male *Archips argyrospilus* attraction to female pheromone extract on (a) a typical June night and on (b) an unusually warm evening (after Comeau, 1971).

The sibling *Archips* species *argyrospilus* and *mortuanus* exhibit nearly identical times of attraction to caged virgin females (Fig. 13.2); specificity in attraction is mediated largely by the ratio of the (*Z*) and (*E*) isomers of 11-tetradecenyl acetate. The same pattern of chemical blend specificity holds for the other species (Table 13.1) and evidently it is enhanced by the antagonistic effects upon attraction by the pheromone components emitted by the *other* species. For example, *Pandemis limitata* utilizes the same proportion of (*Z*)-11- and (*Z*)-9-tetradecenyl acetates as *A. mortuanus*, but males of *P. limitata* are not lured to this blend when the two additional blend components for *A. mortuanus*, (*E*)-11-tetradecenyl and dodecyl acetates, are added.

Apart from energetic and predation considerations, the pattern of the

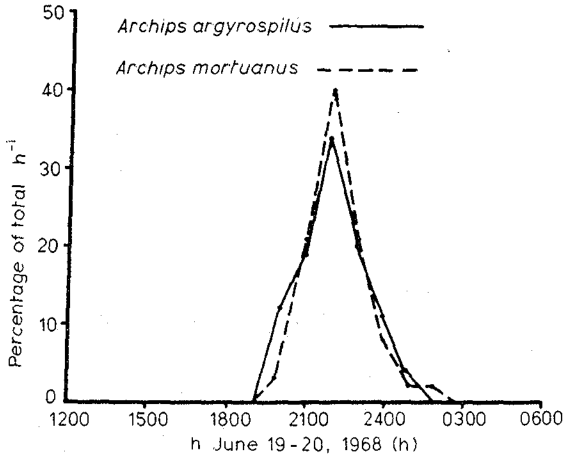

Fig. 13.2 Periodicities of attraction of the sibling species male *Archips argyrospilus* and *A. mortuanus* to female pheromone extracts of these species (after Comeau, 1971). Specificity in attraction is achieved mainly by differences in the ratio of (*Z*) to (*E*) isomers of 11-tetradecenyl acetate (Table 13.1).

pheromone dispersal can be modified greatly by atmospheric conditions. First, wind speed and dispersion coefficients, for example, on average vary with time of day (Fig. 13.3; see Chapter 3) and such daily patterns modify the dimensions of the active space. Second, sending and receiving individuals may alter their patterns of emission and response in accord with the current conditions. *Trichoplusia ni* females call in bouts the duration of which are adjusted from about 20 min at wind velocities of <0.1 m sc^{-1} to 5 min at velocities of 3 m sc^{-1} (Kaae and Shorey, 1972). But the overall daily timing of sexual activity undoubtedly is influenced by daily cycles of fluctuation in atmospheric conditions and their modification of the patterns of pheromone dispersion.

A quite different partitioning of the sex communication channel evidently occurs in the day-active Sesiidae (Greenfield and Karandinos, 1979). Most of their data on attraction specificity is based on male attraction to synthetic lures; for, in nearly all of the species studied, the identities of the natural pheromone system remains unknown. Presumably, however, they are identical or very similar to the empirically determined attractants. Greenfield and Karandinos found that year of emergence (some sesiids have a 2-year life cycle) or habitat preference are not involved in isolation; instead the species are partitioned by a combination of diel and seasonal differences and the ratio of the (*Z*,*Z*) and (*E*,*Z*)-3,13-octadecadienyl acetate attractants. In 93% of the species pairs examined, a communicational channel (niche) overlap of less than 5% was achieved by partitioning along a *single* channel dimension (chemical, seasonal or diel), with the remaining 7% of species pairs being isolated by a combination of factors (Greenfield and Karandinos, 1979).

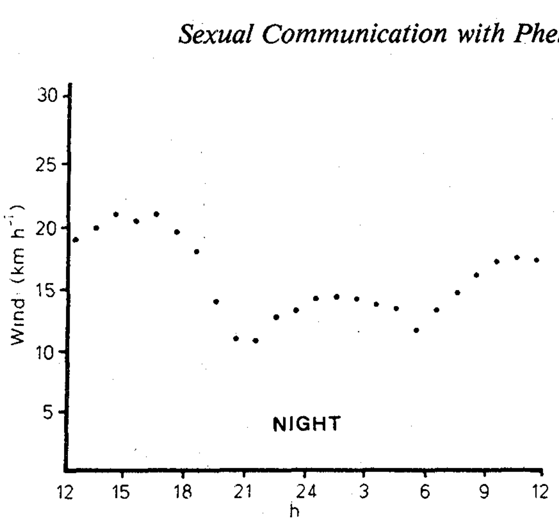

Fig. 13.3 Mean hourly wind speeds recorded in Geneva, New York during the last half of July, 1968 (after Comeau, 1971).

13.3.2 Variation in communication systems

As suggested earlier, the view that either reproductive isolation or interspecific competition dictate the variance of the communication channel may be illuminated by examining the variance of features of the channel in localities where the number of competitive species (and hence the intensity of competition) differ. Where there are few species we might expect the channel to be comparatively broad; conversely, in places where there were many species potentially employing overlapping channels, we might expect relatively narrow tuning. For example, *A. argyrospilus* in New York seems to be more acutely tuned to the proportion of the Z9-14:Ac, in its blend than populations in British Columbia (Cardé *et al.*, 1977). Although the number of tortricines on apple is similar in the two localities (Chapman and Lienk, 1971; Mayer and Beirne, 1974a, b), in New York a sibling species, *A. mortuanus*, competes for the same channel (Table 13.1). Most of the specificity of attraction comes from using different proportions of the 11-14:Ac's. In British Columbia, male *A. argyrospilus* were attracted to mixtures lower in E11-14:Ac or 12:Ac or higher in Z9-14:Ac than in New York (Roelofs *et al.*, 1974; Cardé *et al.*, 1977), suggesting character displacement (a narrowing of the communication channel) in the New York population due to competition with *A. mortuanus*.

Geographical variation in male response also appears to be documented in the noctuid *Agrotis segetum*. The attractant components Z5-10:Ac, Z7-12:Ac and Z9-14:Ac and their blends that evoke male catch appear to differ in Denmark, Switzerland, France and Hungary (Arn *et al.*, 1982). Geographical differences in pheromone production and response occur in *Ostrinia nubilalis*, the European corn borer, and will be considered in Section 13.3.6.

Interpretation of the published attraction spectra of different populations of a given species is obscured by several factors. First, most traps employed in these studies ensnare responding animals on a sticky surface; as a trap's capacity is approached, it retains proportionally fewer responders than traps baited with less active treatments (see Cardé, 1979). Second, trap (treatment) interaction is dependent upon the intertrap distance and the position of treatments (Wall and Perry, 1978). The same experimental design (such as a Latin Square with a constant intertrap distance) should be employed in comparative field trials. Third, general population activity levels seem to influence the apparent variance of response spectra (e.g., Baker and Cardé, 1979a), possibly by altering the number of trap visitations per animal. These factors mean that variances of response spectra among different populations, particularly when test conditions vary and non-saturating traps are employed, must be compared cautiously.

We know even less about the ratio of *emitted* pheromone components. The variance in ratio of the Z11 and E11-14:Ac components extracted from the pheromone gland has been determined for *A. velutinana* (Miller and Roelofs, 1980), and for various strains of *O. nubilalis* (see Section 13.3.6), but as yet we do not know if these ratios remain constant over time in individuals or if the ratios in the pheromone gland match the ratios actually released.

13.3.3 Physiochemical constraints upon blends

One interesting feature of the multichemical attractant systems is the dissimilarity among species in the effect of modifications of the optimal blend ratio. Relatively subtle alterations of the optimal blend for some species greatly decreases the field trap catches. For example, a 5% alteration in the optimum ratio of Z11-14:Ac to E11-14:Ac drastically lowers the male catch in *A. velutinana* (Klun *et al.*, 1973; Roelofs *et al.*, 1975). However, the addition of 12:Ac in widely varying proportions (1:5 to 2:1) to the 9:1 Z11-14:Ac, E11-14:Ac attractant combination increases the trap catch ten-fold over the attractant alone (Roelofs *et al.*, 1975). Similar cases of noncritical ratios are given in Table 13.1.

The *raison d'être* of these divergent blends may be explained by the relative volatility of the components. Those compounds differing in the position or geometrical configuration of the double bond but which have identical carbon-chain lengths and functionalities possess essentially identical vapor pressures at different environmental temperatures. Such components would emanate from a pheromone gland and diffuse within the active space at nearly the same rates. (Most models of pheromone dispersion in wind do not consider molecular diffusion as a major factor in dispersion (see Elkinton and Cardé, Chapter 3); but in still air, over relatively short distances differences in molecular diffusivity may be important (see Bradshaw and Howse, Chapter 15)). Ratios would remain constant throughout the active space, provided that the components are transported at equal rates to the surface of the pheromone gland.

Blend components with either different functional moieties or chain lengths would evaporate at slightly different rates at typical environmental temperatures (e.g., 16–30°C). Hence, the ratio of components emitted from the gland would vary with temperature and thus preclude the use of such compounds in very precise ratios.

13.3.4 Parental investment and stabilizing selection

Features of the chemical communication system are also likely to be molded by the probabilities of mate finding under different population densities. In the absence of any other pressures, stabilizing selection (selection for the population norm) should prevail, favoring (in species with a multichemical pheromone) those males most sensitive to the blend emitted by the majority of females, and those females emitting the blend to which males are most sensitive. Individuals varying from the norm should have a reduced probability of finding a mate, especially at moderate to low population densities, even in the absence of competition with other species. At high densities, however, discrimination by females for 'better' males may also mold the system.

It is possible that lepidopterous sex pheromone systems, in which, as a rule, females are the emitters, arose originally due to the disparity in parental investment between the two sexes (Trivers, 1972; Thornhill, 1979). Female moths produce fewer gametes than males, but furnish each egg with a large supply of nutrients, representing a larger 'investment' in each potential offspring than males give each sperm cell. Females' production of offspring is limited by the number of eggs they can produce, whereas male offspring production depends upon how many matings males can procure. Females therefore become a limiting resource competed for among males. Males able to detect and locate females more rapidly and from greater distances than other males would be at a reproductive advantage, and volatile chemicals emanating from the females' body surfaces might be likely cues originally utilized for detection by males. Thornhill (1979) has proposed just such a scenario for the origin of sex pheromones in *Bittacus* and *Panorpa* scorpionflies (Mecoptera). In these groups, however, males are a limiting resource for reproductive success since they provide nutrients needed for females' egg production, in the form of proteinaceous saliva balls or prey items. Accordingly, these mecopteran males' chemical emanations are detected from a distance by females who fly upwind and locate males and their gifts.

In the Lepidoptera where females are limiting, why, among all the potential volatiles arising from females' bodies would such a narrow range of chemicals be selected to enable early detection by males of each species? Stabilizing selection must be part of the explanation, as males that can detect what the majority of females are producing should be able to locate more females and presumably gain more matings than other males, assuming, of course, an equal probability of courtship success among those males locating females. In addition, it would seem that males should be under pressure to produce not only more receptors and a decoding mechanism tuned to the norm of female emissions, but also to detecting the emissions of 'abnormal' females on the extremes of the distribution. One of the costs of such broad tuning would be an increase in chemical background noise from the environment, thus effectively reducing detection sensitivity through a decrease in the signal : noise ratio. Time and energy lost to responding to airborne volatiles from non-conspecifics could be another cost of the broader tuning, bringing about a decline in male reproductive success.

Once males began tuning their receptors to emissions common to most conspecific females, presumably selection should have favored those females producing greater quantities of these volatiles, as such females would be most likely to attract males and succeed in mating, especially at low population densities. However, the amounts of lepidopterous sex pheromone emitted by females, usually of the order of 1–100 billionths of a gram per hour, are miniscule compared to emissions of courtship compounds by males (Birch, 1974) or of defensive compounds by insects of both sexes.

For a given species there is a characteristic rate of pheromone release as well as a range (minimum to maximum) of pheromone concentrations that elicit normal behavioral responses. Indisputably, of course, there will be variation in the Q (emission rate) and K (threshold of response) features of individuals, although at present we have only fragmentary information on how much variation exists or its genetic basis. Leaving aside the important question of biosynthetic capability, it can be suggested that an increase in Q (and therefore the generated active space) would seem to confer an advantage to an emitter in locating a mate. In sparse populations, particularly, a female emitting a higher than average rate of pheromone should have an increased probability of luring a mate over typical females. Why, then, does there appear to be such a range of release rates among the various moth species and why are many of these rates so low? The difference between *G. molesta* which releases at about 2 ng h^{-1} (Baker *et al.*, 1980) and *T. ni* which emits at up to 1 $\mu g\ h^{-1}$ (Bjostad *et al.*, 1980) cannot be attributed to the differences in gland surface area alone.

Part of this disparity could relate to the *demographics* of calling females and responsive males. In populations in which males are sparse, selection should favor high Q values. However, females releasing pheromone with a higher than average Q may lure mates possessing on average an above-normal K. These responders could enter the active space relatively close to the female and assuming that the higher K is heritable, her sons could be less sensitive to pheromone. Also, responders possessing a normal K might respond to pheromone from such high Q females at optimal concentrations occurring far from the source and then exhibit less than optimal performance of orientation and mating behaviors in the abnormally high concentration of pheromone near the female. This would be most likely in species possessing an upper threshold limit such as *G. molesta* (Baker and Roelofs, 1981).

A corollary to the hypothesis that the limiting sex is competed for by the non-limiting sex is that the limiting sex can afford to be 'choosy' or discriminating (Trivers, 1972; Thornhill, 1979). Possibly, one of the reasons for the small quantities of pheromone emitted by female moths of some species is that under average-to-high population densities the parsimonious emission of pheromone by (discriminating) females selects for males having lowest K's and most acute mate-finding abilities (Greenfield, 1981). At the same time this would put further pressure on the males' sensory systems to optimize their tuning by narrowing the bandwidth (variance in the receptor's response spectrum) and amplifying the signal (number of receptors), thereby improving the signal : noise ratio. Hence, the narrow range of pheromone blend ratios and low emission rates often utilized by Lepidoptera could be the result of selective pressures relating to reproductive (communication) success and parental investment, and not reproductive isolation *per se*, resource partitioning of the communication channel, or other pressures such as avoidance of detection by predators, as in some beetles (see Birch, Chapter 12).

These examples show that, in addition to the posited interspecific effects of competition for an exclusive communication channel, other factors including energetics, predation, pheromone dispersion, physiochemical constraints, and stabilizing selection, may dictate the design of these signals. We will now consider in detail the sexual communication system of the oriental fruit moth, *G. molesta*, as an example of the interplay of the chemical and non-chemical signals in sexual communication and the potential role of sexual selection.

13.3.5 Integration of chemical and other cues in the sexual behavior of the oriental fruit moth

Sexual communication in the oriental fruit moth is initiated by the female, who, a few hours before dusk, raises her wings and abdomen and releases four compounds from a gland near her extended ovipositor. Three of these compounds elicit behavioral changes in males: (*Z*)-8-dodecenyl acetate (Z8-12:Ac) (Roelofs *et al.*, 1969), (*E*)-8-dodecenyl actate (E8-12:Ac), and (*Z*)-8-dodecenyl alcohol (Z8-12:OH) (Cardé *et al.*, 1979) (Fig. 13.4). The fourth compound,

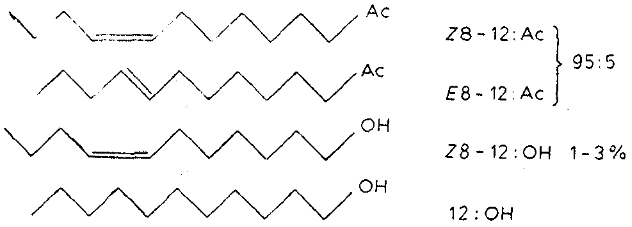

Fig. 13.4 Pheromone components emitted by female *Grapholitha molesta*, the Oriental fruit moth.

dodecyl alcohol (12:OH) seems to increase males' reactions only if Z8-12-OH is at or lower than normal levels. The first three compounds appear to act in concert to elicit movement reactions resulting in attraction to the female (Baker and Cardé, 1979b). It is clear that the ratio of these components is crucial to optimal attraction, as demonstrated in field experiments with synthetic sources. When more or less than 6% E8-12:Ac relative to Z8-12:Ac is present, the number of approaches of males toward the source diminishes significantly (Baker and Cardé, 1979b), as reflected in reduced trap captures of males to these off-ratios (Baker *et al.*, 1981a) (Fig. 13.5). Wind tunnel observations support the field results, and indicate that reduced upwind flights to the source in response to too little E8-12:Ac is due to the tendency of males to lose contact with the plume during erratic, rapid velocity flights. The reduction in source location by males flying upwind to an excess of E8-12:Ac is characterized by arrestment within the plume at some distance downwind of the source, followed by upward flight out of the plume. Too little or too much Z8-12:OH added to the optimal Z8:12:Ac mixture also reduces attraction of males, the optimal percentage being ca. 3% relative to Z8-12:Ac. Not surprisingly, those ratios that elicit optimal attraction of males to synthetic sources are nearly identical to those emitted by females. Interestingly, Z8-12:OH appears important for the reproductive isolation of the oriental fruit moth from a congener, *G. prunivora,* the lesser appleworm. This component reduces captures of *G. prunivora* males when added to the two acetates while it simultaneously increases attraction of *G. molesta.*

Female *G. molesta* release this blend of components at a rate of ca. 2 ng h^{-1} (Baker *et al.*, 1980). Trapping experiments indicate that rubber septum dispensers releasing the synthetic blend at between 1 and 12 ng h^{-1} capture the maximum number of males, demonstrating that emission rates close to the females' are optimal. Emission rates higher or lower than these reduced captures (Fig. 13.5), but for different reasons. The lower concentrations are not sufficient to elicit upwind flight from males more than a few meters on average from the source. Conversely, super-normal rates evoke upwind flight from more than 80 m away but result in within-plume arrestment more than a meter away from the source (Baker and Roelofs, 1981). More detailed observations in a wind tunnel confirmed that only an intermediate range of dosages and (*E*)-(*Z*) ratios resulted in attraction to the source without prematurely causing arrestment.

Once the male has landed near a female, these same pheromone components elicit close approach to the female by walking while wing-fanning. Of all the incomplete combinations of components, only the two acetates are sufficient to evoke some close approaches, but inclusion of Z8-12:OH in the blend increases close approaches and courtship behaviors dramatically.

The most striking behavior seen when the complete blend is present is the hairpencil display of courtship. The natural blend of chemicals alone, however, is not all that is needed before males will display at a female. The visual cues

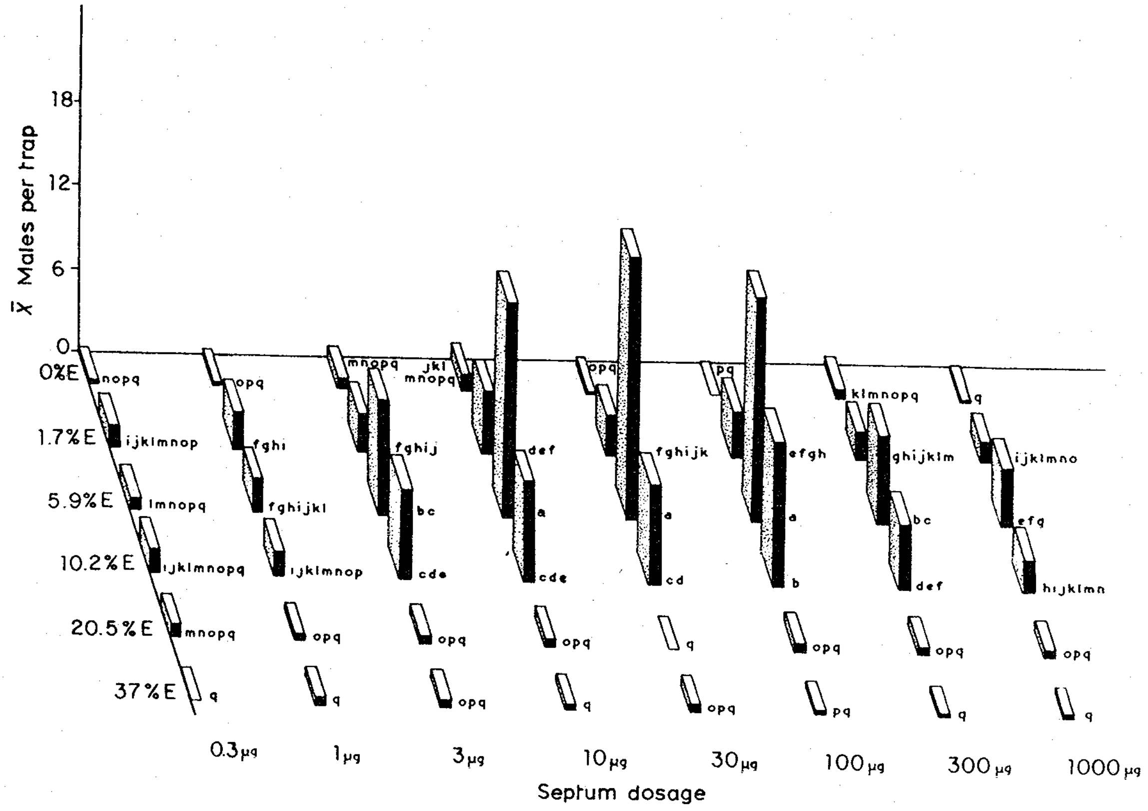

Fig. 13.5 Captures of male *Grapholitha modesta* in traps baited with different combinations of (*Z*)-8-dodecenyl and (*E*)-8-dodecenyl acetates in different dosages (Baker *et al.*, 1981a).
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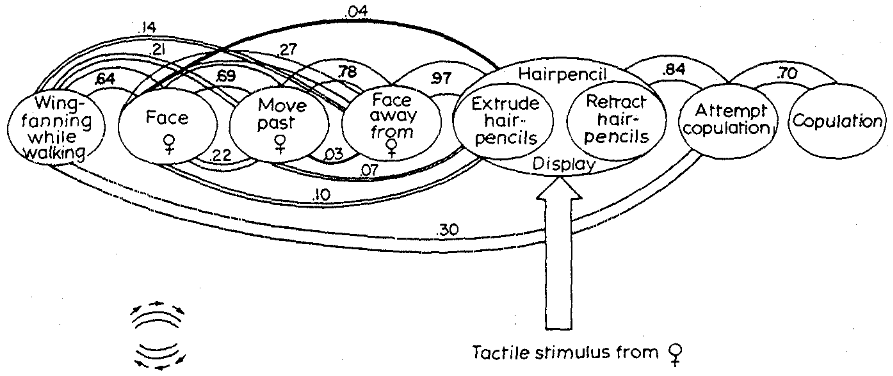

Fig. 13.6 The conditional probabilities of male and female *Grapholitha molesta* courtship behaviors occurring in cases where the female delivers a tactile stimulus to the male by hitting her head into his abdominal tip (Baker and Cardé, 1979a).

from a sitting female (or artificial model) need to be coupled with the presence of pheromone (Baker and Cardé, 1979a). However, apparently males are not able to discriminate between potential mates on the basis of visual cues alone, for a large red rubber septum is very effective at evoking hairpencil displays. If the model is not within, or at the source of, the pheromone plume, displays will not be evoked as frequently.

When the visual and chemical stimuli are correct, a fairly rigidly 'fixed action pattern' of male behaviors is evoked, one of which is the hairpencil display (Fig. 13.6) (Baker and Cardé, 1979a). Chemical, anemotactic (wind), and possibly visual cues from the hairpencil display now elicit movement by the female, over a few cm to the male's abdominal tip. The predominant cues effecting female attraction are chemicals released by the rhythmically extruded and retracted hairpencils that give them a pleasant herb-like odor to the human nose. Four hairpencil compounds (Fig. 13.7) have been identified: ethyl-*trans*-cinnamate (I), (−)-mellein (II), methyl-jasmonate (III), and methyl 2-epijasmonate (IV). The combination of I and IV is behaviorally active in attracting females, unlike many other combinations of the four compounds (Baker *et al.*, 1981b). Wind of ca. 90 cm sc^{-1} generated by the male's vibrating wings propels these compounds to the female, possibly imparting directionality to the signal. Although typically the male walks upwind of the female before displaying, he can display from any position because his wind-producing ability would confer independence from the ambient wind. His wind also might allow the female to use anemotaxis to orient more accurately to him. Visual cues from the male's body, including the rhythmic extension of the light-colored hairpencils, do not seem to affect the accuracy of the female's orientation, although the contribution of the hairpencils' visual cues to attraction cannot yet be dismissed entirely.

The final stimulus in the aggregation process, as one might expect, is tactile; the attracted female touches the tip of the male's abdomen, and experimental

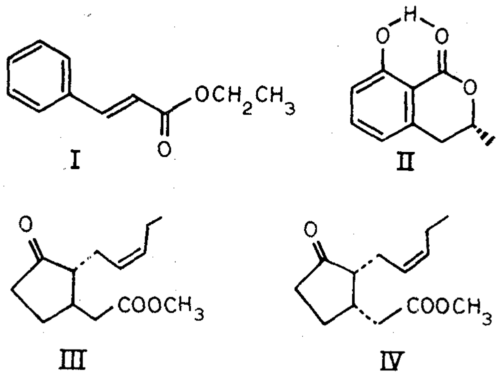

Fig. 13.7 Compounds present in male *Grapholitha molesta* hairpencils: ethyl-*trans*-cinnamate (I), (−)-mellein (II), methyl-jasmonate (III), and methyl 2-epijasmonate (IV) (Baker *et al.*, 1981b).

manipulations confirm that it is this touch that evokes the male's copulatory attempt (Baker and Cardé, 1979a). Only those males that display and induce females to touch their abdomens copulate. However, the situation is quite different if two or more males arrive near a female at about the same time (Baker, 1983). If a male is displaying when a second male approaches, the latter male may attempt to copulate (often successfully) with the female without first displaying. Such late-arriving males appear to 'sneak' in for a copulatory attempt under the cover of the first male's chemical barrage. Other alterations in the normal male courtship sequence also occur, including late-arriving males being attracted to first-arrivals' displays, and the touches they deliver causing misdirected copulatory attempts by displaying males and reduced mating success. Two may display simultaneously toward one female, whereupon she will 'choose' one male over the other by touching his hairpencils. Simultaneous displaying occurs infrequently, but even for sequentially arriving males, females sometimes choose late arrivals after not responding to earlier males' displays. Females fail to respond to males that are prevented experimentally from everting their hairpencils, even though the rest of their courtship sequence is otherwise unaltered.

Because females control whether copulation will occur, it is possible that female-choice sexual selection could have been responsible for the evolution of the hairpencil organs, the courtship pheromone blend, and the rigidly fixed sequence of movements that comprise the display (Baker and Cardé, 1979a). As discussed above, as the limiting sex, females can exercise discrimination in selecting mates, considering their larger parental investment in potential offspring. However, here the benefit received by females choosing males with 'better' displays would be the mating advantage conferred upon their sons in the presence of discriminating females in the next generation. Protandry (early seasonal emergence of male adults), or a skewed sex ratio with a predominance of males, are two conditions that could result in a proportion of the male population being excluded from mating, but in the oriental fruit moth a third situation effectively creates a shortage of females during the mating period. Most females mate only once whereas males can mate an average of more than once per evening (Dustan, 1964).

Thus, some males could acquire a disproportionate share of matings at the expense of other males. For the highly rapid, directional selection (selection for an extreme) of male courtship traits to proceed, first a small percentage of discriminating females and males with an appropriate trait must be present in the population. Initially, such characters may confer an advantage in *reproductive* rather than courtship success (Thornhill, 1979). After that, sexual selection could proceed on its own to produce more extreme male scent dissemination structures and increasingly selective females.

13.3.6 Speciation

The most commonly accepted view of speciation in sexually reproducing animals assumes that the diverging populations are geographically isolated from one another for many generations, during which time differing selective pressures acting upon the two populations cause them to acquire substantial genetic differences. If they have not thus acquired effective premating reproductive isolating mechanisms and hybrids are less fit, then it is posited that barriers to hybridization could develop during periods of secondary contact between the populations when traits, such as differences in the sex pheromone communication channel, would be accentuated. Such an allopatric model is most compatible with multicomponent pheromone communication systems (cf. Shorey, 1970) that have the ready possibility of modification of the communication system. This traditional allopatric view of speciation is currently being challenged in two ways. First, many suggest that speciation may occur in 'quantum' or rapid steps. Rapid speciation is viewed as most likely to occur in isolated or peripheral segments of a species' distribution. A second model holds that new species can arise, presumably also quite rapidly, within the general distribution of the species. The latter process is termed sympatric speciation and has been most cogently advocated by Bush (1975).

As with the previous discussions of the selective forces that mold the communication channel, it is difficult to arrive at either definitive proofs or absolute refutations of these models. Notwithstanding such difficulties, several cases provide illuminating evidence of the potential contribution of sex pheromones to the speciation process. In many of the bark beetles it is known that the aggregation pheromone is biosynthesized from precursors obtained by the feeding adult beetles from the phloem of the host trees. In *Ips paraconfusus* the pheromone component *cis*-verbenol is biosynthesized from the host terpene (−)-pinene. Ingestion of the opposite isomer produces the opposite optical form of the pheromone (Renwick *et al.*, 1976). Clearly this suggests that beetles colonizing a tree species that contains a 'wrong' precursor either alone or in combination with the correct precursor would possess a new communication system. If this occurred in individual animals colonizing inappropriate hosts, however, we cannot readily assume that this process will lead to a rapid evolution of a new pheromone, because there would have to be numerous males and females *responsive* to this new communication system if the colonizing beetles are to attack a tree successfully (see Chapter 12). Thus, the rapid alteration of pheromone communication channel of bark beetles through colonization of new hosts containing novel precursor materials may be limited.

Ips pini from eastern and western North America produce and respond preferentially to pheromone produced by their own aggregating populations (Lanier *et al.*, 1980; see Section 11.3). These differences presumably arose in isolation, character displacement, or possibly clinal divergence.

Roelofs and Comeau (1969) hypothesized that rapid evolution of new pheromone communication channels could occur within relatively few generations. The rare female homozygous (recessive trait) for a novel pheromone component or blend would lure the rare male homozygous (recessive trait) for the ability to perceive the same pheromone. The resulting progeny, of course, would have a normal phenotype. If, however, some of these siblings mated, as might be feasible in very small populations, then recombination of traits in males responsive to the novel system and females releasing it could carry this new communication system to fixation within a relatively few generations. If either the production or response traits were not completely recessive, or if the traits were carried on the X-chromosome, then the model would be more appealing.

The occurrence of an insect's pheromone trait on the X-chromosome (in the Lepidoptera the female is the heterogametic sex) has been demonstrated for the major 'species-recognition' pheromone in *Colias eurytheme*, sulfer butterfly, by Grula and Taylor (1979). Another signal used by males in courtship is the ultraviolet reflection pattern of the wing, which is also transmitted on the X-chromosome. In contrast to the evidently close linkage of courtship signals in *C. eurytheme*, it was found that genes controlling a multicomponent courtship pheromone system in *Drosophila melanogaster* were dispersed throughout the genome. Such an independent assortment of loci would enhance the diversity of genotypes and promote the outbreeding found with the negative assortative mating system of this species (Averhoff and Richardson, 1976). That genes controlling a species-specific communication system should be inherited as a co-adapted complex in *C. eurytheme* (Grula and Taylor, 1979) substantiates the theoretical analyses of Alexander (1962) and O'Donald (1962). The documented systems in *C. eurytheme* and *D. melanogaster* raise 'the interesting possibility that insect communication systems have both variable and invariable components and that different sets of genes with different modes of inheritance give rise to this dichotomy' (Grula and Taylor, 1979).

Populations of *O. nubilalis* in North America (which were introduced from unknown European localities several times in the early 1900s) vary in their production and response to the ratio of the two pheromone components, Z11- and E11-14:Ac. Populations from Iowa and New York, for example, produce and are most attracted to 97:3 and 4:96 ratios, respectively, of the two acetates (Klun *et al.*, 1973; Kochansky *et al.*, 1976). Isozyme studies of males attracted to these two blends in central Pennsylvania suggest that these strains are not panmictic (Cardé *et al.*, 1975b, 1978; Harrison and Vawter, 1977). In some areas such as Maryland and North Carolina captures of males in traps occur across the spectrum of attractant blends from the predominantly (*Z*) to (*E*) isomer mixes (Klun, 1975; Kennedy and Anderson, 1980). The so-called Z and E strains both occur in Europe, but evidently not in the same localities, so that an allopatric origin of these strains is the most plausible explanation. The Klun and Maini (1979) study of the genetics of pheromone production and laboratory response in hybrid crosses of these strains indicates that the major features of these traits are controlled by simple Mendelian inheritance. As White (1978 p. 332–3) notes,

> 'An important unresolved question in speciation theory is whether the primary role in initiating speciation is usually a premating isolating mechanism, such as a pheromonal or bio-acoustic difference between the two diverging populations, or a postmating one, whether due to chromosomal rearrangements or gene mutation. Only a series of investigations on suitable cases in various stages of speciation, in which both the ethological and the cytogenetic factors are intensively studied, will resolve this basic question. The answer will not necessarily be the same for all cases or for all groups of organisms. In all but a minute number of instances closely related species differ in karyotype. But, at the same time, the great majority of closely related animal species differ in courtship behavior. Thus, most studies of sibling species are likely to be uninformative on this point, since both kinds of differences will exist. The cases that may help to resolve this problem will be those few instances of semispecies or sibling species that differ in a single respect only.'

13.4 CONCLUSION

During the past 20 years the burgeoning study of pheromone communication has resulted in the characterization of the chemistry and behavioral responses in numerous insect species. Despite the rapid accumulation of identified pheromones and a description of the behaviors elicited, for a large number of the pheromone systems, we do not as yet know all of the chemical components involved, nor do we have a thorough understanding of the orientation mechanisms that are involved in many pheromone responses. The selective forces that shape these communication systems largely remain uncharted.

The rhythms of daily communication cycles and the proximate environmental cues regulating their expression have been described for a large number of temperate insects, and these general patterns can be expected to be similar for other insect species. But how the timing of these events relates to ultimate selection factors, such as flight energetics of the responder, predation, optimal conditions for atmospheric transmission of the pheromone message, light and wind conditions favorable for successful orientation, and numerous other factors, has scarcely been documented. The paradigm of interspecific partitioning of the communication channel appears to be a likely explanation for differences among closely allied species in chemical blends, the daily timing of reproductive activity, and other differences in the communication channel. However, rigorous proof of the importance of these selective forces in the creation and maintenance of such partitioning is lacking. Future studies, if they are to resolve these questions, will need to separate the effect of environmental factors that favor particular daily patterns of communication from divergences resulting from interspecific competition for discrete communication channels. In part, distinctions between the effects of environmental and species partitioning forces may become evident by careful description and comparison of the communication channels of given species in different localities where the number of species sharing pheromone components varies and therefore the degree of competition differs.

Stabilizing or normalizing selection would act to keep characteristics of the communication channel at some intermediate level, as in the ratio of two pheromone components. Unfortunately, we have little information on individual variation in production of and response to ratios of components. Sexual selection and choice of a partner by the non-resource limited sex may be powerful agents, promoting new and elaborate courtship behaviors and pheromones. The seemingly advantageous strategy of increasing the rate of pheromone emission in the calling sex, thereby increasing the active space and the opportunity for luring a mate, may have disadvantageous consequences. This practice may tend to result in females attracting males that have a higher threshold of response and thus their male offspring would be less successful in mate location. To test these hypotheses it will be necessary to have descriptions of natural variation in the communication channel and to determine its genetic basis.

The degree to which pheromones are involved in speciation will probably remain speculative, inasmuch as allopatric speciation generally is not amenable to experimentation. It is clear that a bark beetle could alter its aggregation pheromone simply by selecting a host tree species that provides a precursor for a novel pheromone. If speciation occurs primarily in an allopatric mode, then changes in the pheromone communication channel that effect reproductive isolation may come about or at least be reinforced after initial changes in the communication system that occurred in isolation.

The present attempt to summarize the selective forces molding the pheromone systems in insects has emphasized moth examples. This restriction has limited our exploration of phenomena such as aggregation, lekking, male-produced attractants, and the effects of plant hosts upon sexual behavior, all of which appear to occur infrequently in this group. McNeil and Turgeon (1982) have suggested that both temperature and larval food source modify the rapidity of the onset of sexual behavior (including pheromone emission) in the cutworm moth *Pseudaletia unipuncta*. This in turn determines the reproductive success of the fall generation and the likelihood of wide-scale epidemics occurring in the ensuing year. Except for this example (and of course the phenomenon of mass host attack in bark beetles), interactions between population dynamics and pheromone-mediated sexual behavior have been little explored in the non-social insects.

Much remains to be unravelled if we are to understand how environmental factors, the community, and intraspecific mating success shapes the pheromone communication channel. The exciting prospect of defining and testing these hypotheses is one of the future challenges in elucidating the chemical ecology of insects.

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