Available online at www.sciencedirect.com
SCIENCE DIRECT®
Journal of Theoretical Biology 235 (2005) 199–206
Journal of Theoretical Biology
www.elsevier.com/locate/yjtbi

Chemical constraints on the evolution of olfactory communication channels of moths

John A. Byers*

Western Cotton Research Laboratory, USDA-ARS, 4135 East Broadway Road, Phoenix, AZ 85040-8830, USA

Received 14 September 2004; received in revised form 10 December 2004; accepted 5 January 2005
Available online 17 February 2005
Communicated by James Cushing

Abstract

It is estimated there are over 100,000 moth species (Lepidoptera) that produce sex pheromones comprising communication channels used in specific-mate-recognition systems (SMRS) involved in pre-zygotic mating isolation and speciation. About 1572 moth species have been found to use 377 pheromone components, the majority being alcohols, aldehydes or acetate esters of olefinic chains of 10–22 carbons. Since there are limited numbers of possible unsaturated (double bonded) *E*- and *Z*-configured isomers of these chains, there may be constraints on incipient species evolving new pheromone components, especially if they are utilized by existing species. Here I develop algorithms that count and name all possible structures of chains with or without a functional group. The results show that for acetate esters there are only seven or nine monounsaturated isomers of six or seven carbon chains, respectively, suggesting use of these compounds could limit the number of communication channels available for radiation of new species (no moths use these short chains). For commonly used 14-carbon chains with an acetate ester functional group, and 1–3 unsaturations, there are 1039 isomers. A total of 2,096,883 isomers were counted from all multiply unsaturated 10–22-carbon chain acetate esters. The number of possible signals quickly extends into millions when considering pheromone blends of 2–4 components used by most species. There should be little chemical constraint on evolution of new communication channels based on compounds of 10 or more carbons, even for closely related species (e.g. ermine moths, *Yponomeuta*).

Keywords: Lepidoptera; Pheromone components; Speciation; Geometric isomers; Programming geometric sums

1. Introduction

Pheromone communication in moths (Lepidoptera) is an integral part of the specific-mate-recognition systems (SMRS) of all species investigated (Marin, 1994; Linn and Roelofs, 1995; Eldredge and Spencer, 1995; White et al., 1995; Zhu et al., 1997; Etges and Ahrens, 2001). The SMRS concept of Paterson (1978, 1985) proposes that speciation is not a gradual process of natural selection but rather a punctuated equilibrium, where selection occurs primarily during the relatively quick transitions to new species as the SMRS is altered during adaptation to a new habitat. The SMRS is a coadapted complex of traits that are under stabilizing selection to ensure syngamy within a population of organisms occupying a preferred habitat. Variation in the elements of the mate recognition system such as pheromone amounts produced by female moths is intraspecific and relatively minor, and this variation in the signal is generally not perceived or acted upon by responding males (Linn and Roelofs, 1995; White et al., 1995).

Over 100,000 moth species are estimated worldwide (Holloway et al., 1987). Male moths orient tens of meters upwind to females releasing pheromone components that comprise a unique communication channel for each species (Baker, 1989; Sasaerila et al., 2000). However, many species use compounds in common, e.g. the Pherolist Internet site (Arn et al., 1992; Arn, 2001) reports about 377 components from 1572 moth species

*Tel.: +1 602 437 0121x231; fax: +1 602 437 1274.
E-mail address: jbyers@wcrl.ars.usda.gov.

0022-5193/$ - see front matter © 2005 Elsevier Ltd. All rights reserved.
doi:10.1016/j.jtbi.2005.01.003

(Byers, 2002, unpublished). The majority of these components are structurally related, being unsaturated olefinic chains from 10 to 22 carbons with an end functional group (either alcohol, aldehyde or acetate ester). The positions of unsaturated, carbon–carbon double bonds can be in either the *E*- (*trans*-) or *Z*- (*cis*-) configuration except at the end opposite the functional group (Fig. 1). Usually there are one, two, and sometimes three unsaturations in the components of moths investigated to date (Byers, 2002, unpublished).

If the number of possible different isomers of chain lengths up to 22 carbons is relatively small, then this may have implications on evolution of communication channels and speciation given that there are hundreds to thousands of species in a region that may compete for the limited set of components. A species might have been hindered in the evolution of a communication channel because sympatric species already used some or all of the relatively few possible geometric configurations of these molecules. For example mutant females releasing a new pheromone blend of components might attract primarily males of a dominant species using the same blend that would interfere with mating or spawn poorly adapted offspring (McMillan et al., 1997; Lynch and Force, 2000; Jiggins et al., 2001). This might then constrain speciation such that the number of species would in some way be limited by the number of possible components theoretically available.

The present study develops methods for determining the number of possible olefinic (aliphatic) molecules that are available for use as pheromone components given certain chemical assumptions about chain length, unsaturation, and end functional groups. In addition, combinatorial mathematics can provide limits on the number of sex pheromones comprised of blends of two, three, or four components that are possible to evolve given certain chemical and biological assumptions (Byers, 2002, unpublished). Another objective was to explore the cases where there could be constraints on the evolution of moth pheromone components (e.g. in the moth genus *Yponomeuta*) that would restrict species to existing communication channels.

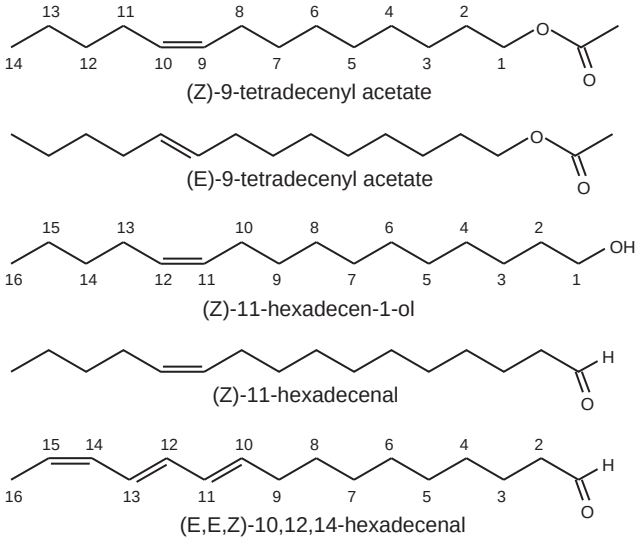

Fig. 1. Examples of moth pheromone components: (*Z*)-9-tetradecenyl acetate (acetate ester, most common component used by 199 species), (*E*)-9-tetradecenyl acetate (component of 17 species), (*Z*)-11-hexadecen-1-ol (most common alcohol, used by 50 species), (*Z*)-11-hexadecenal (most common aldehyde, used by 119 species), and (*E,E,Z*)-10,12,14-hexadecatrienal (used by tobacco hornworm, *Manduca sexta*) (Arn et al., 1992; Arn, 2001; Byers, unpublished).

2. Methods

2.1. Characteristics of moth pheromone components

The known moth pheromone components from species in 49 families (Pherolist) comprised of olefinic chains with an end functional group have certain structural characteristics in common. For example two unsaturated (double) bonds are always separated by at least one single bond in the carbon chain (Fig. 1). Also, position one, next to the end functional group, is never unsaturated in aldehydes, alcohols, and acetate esters due to a maximum of four carbon bonds, keto-enol tautomerism, and dipole moments, respectively (Morrison and Boyd, 1973; Byers, 2002). All possible geometric isomers of olefinic acetate esters, alcohols, or aldehydes (or any functional group at carbon 1) can be represented as a simplified chemical name as well as counted by computer iteration (BASIC code available from author). However, for each unsaturation a nested loop is required which means that additional loops are required for each additional unsaturation.

2.2. Enumeration of moth pheromone analogs and blends

A more efficient algorithm was found for purposes of counting isomers of 9–22 carbon chains that requires only one program loop, but a summation variable was required for each additional unsaturation above one (Fig. 2). This method was generalized to allow counting of isomers of molecules with from 1 to 100 unsaturations, a far larger range than that encompassing natural pheromone components of moths. The smallest chain that can accommodate the number of desired unsaturations is found and then the algorithm calculates the number of isomers for this and the next 19 larger chain lengths with the specified number of unsaturations.

It is more difficult to count all isomers of olefinic chains without a functional group since unsaturations could be counted from either end, but the lowest combination of numbers has priority according to accepted chemical nomenclature. For example (*Z*,*Z*)-8,10-dodecadiene should not be counted as a possible

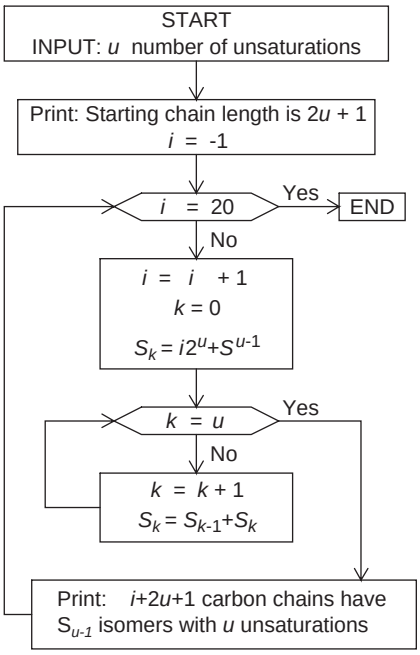

Fig. 2. Flow diagram of method to calculate number of unsaturated isomers of olefinic chains with end functional group (e.g. acetate ester, alcohol, aldehyde).

isomer but rather be counted as (*Z*,*Z*)-2,4-dodecadiene (these compounds are identical and the first name is not correct). Although all isomers are created as above, only the lowest sum of unsaturation positions when counting from either end is used (program code available from author).

Once an estimate of the numbers of possible components available to moth species is made, the number of blends of components can be calculated from the formula for combinations. The equation for combinations of n things taken r at a time (e.g. $n = 100$, $r = 3$) is given by

$$C_r^n = \frac{n!}{r!(n-r)!} = \frac{100 \cdot 99 \cdot 98}{3 \cdot 2 \cdot 1} = 161,700. \quad (1)$$

To avoid calculating factorials of large n, it is convenient to reduce the common factor, $(n-r)!$, as indicated in the second part of Eq. (1).

3. Results

3.1. Numbers of moth pheromone analogs with functional groups

A BASIC program names the positions and configurations (E/Z) of all geometric isomers of various olefinic chain lengths from 5 to 22 carbons and a specified number of unsaturations (isolated or conjugated) that have a functional group (e.g. acetate ester, alcohol, aldehyde) on carbon number one. The *trans*-, *cis*- configurations are represented here as small e, z letters to more easily discriminate them visually from position numbers. An X represents a double bond that cannot isomerize (a delta bond) since it is between the last two carbons opposite the functional group (the end carbon has two hydrogens). For example output from the program with appropriate numbers of FOR:NEXT loops, shows that 9-carbon length acetate esters can have the following isomers:

13 monounsaturated isomers:

2e, 2z, 3e, 3z, 4e, 4z, 5e, 5z, 6e, 6z, 7e, 7z, 8X

50 diunsaturated isomers:

2e4e, 2e4z, 2z4e, 2z4z, 2e5e, 2e5z, 2z5e, 2z5z, 2e6e, 2e6z, 2z6e, 2z6z, 2e7e, 2e7z, 2z7e, 2z7z, 2e8X, 2z8X, 3e5e, 3e5z, 3z5e, 3z5z, 3e6e, 3e6z, 3z6e, 3z6z, 3e7e, 3e7z, 3z7e, 3z7z, 3e8X, 3z8X, 4e6e, 4e6z, 4z6e, 4z6z, 4e7e, 4e7z, 4z7e, 4z7z, 4e8X, 4z8X, 5e7e, 5e7z, 5z7e, 5z7z, 5e8X, 5z8X, 6e8X, 6z8X

56 triunsaturated isomers:

2e4e6e, 2e4e6z, 2e4z6e, 2e4z6z, 2z4e6e, 2z4e6z, 2z4z6e, 2z4z6z, 2e4e7e, 2e4e7z, 2e4z7e, 2e4z7z, 2z4e7e, 2z4e7z, 2z4z7e, 2z4z7z, 2e4e8X, 2e4z8X, 2z4e8X, 2z4z8X, 2e5e7e, 2e5e7z, 2e5z7e, 2e5z7z, 2z5e7e, 2z5e7z, 2z5z7e, 2z5z7z, 2e5e8X, 2e5z8X, 2z5e8X, 2z5z8X, 2e6e8X, 2e6z8X, 2z6e8X, 2z6z8X, 3e5e7e, 3e5e7z, 3e5z7e, 3e5z7z, 3z5e7e, 3z5e7z, 3z5z7e, 3z5z7z, 3e5e8X, 3e5z8X, 3z5e8X, 3z5z8X, 3e6e8X, 3e6z8X, 3z6e8X, 3z6z8X, 4e6e8X, 4e6z8X, 4z6e8X, 4z6z8X

8 isomers with four unsaturations:

2e4e6e8X, 2e4e6z8X, 2e4z6e8X, 2e4z6z8X, 2z4e6e8X, 2z4e6z8X, 2z4z6e8X, 2z4z6z8X while five conjugated unsaturations will not fit in a 9-carbon acetate ester.

There are 2,096,883 different geometrical isomers of olefinic acetate esters of chain lengths 10–22 (Table 1). Equal numbers can be added for the aldehydes and for the alcohols. The number of geometrical isomers at each particular chain length is a complex geometrical progression produced from a series of summations:

$$G_{2u+1+n} = \sum_{Z_1=0}^{n} \sum_{Z_2=0}^{Z_1} \cdots \sum_{Z_{u-1}=0}^{Z_{u-2}} Z_{u-1} \cdot 2^u + 2^{u-1}, \quad (2)$$

where u is the number of unsaturations, the number of Σ is equal to $u-1$, and n is the number of increments in the chain length beginning with a length of $2u+1$. However, implementation of the formula is more efficiently done as shown in Fig. 2. There is a dramatic increase in the number of possible isomers of 14-carbon acetate esters available for use as pheromone components as the number of unsaturations is increased from 1 to 3 (23, 200, and 816 isomers, respectively; Table 1, Fig. 3). A computer analysis of the Pherolist literature database (Byers, unpublished) showed that the number of different attractive components discovered in moths with 1 and 2 unsaturations are higher for chain lengths

Table 1
Number of different possible geometric isomers of unsaturated olefinic chains from 5 to 22 carbons with a functional group at carbon position one

Length	Number of unsaturations									
	1	2	3	4	5	6	7	8	9	10
5	5	2								
6	7	8								
7	9	18	4							
8	11	32	20							
9	13	50	56	8						
10	15	72	120	48						
11	17	98	220	160	16					
12	19	128	364	400	112					
13	21	162	560	840	432	32				
14	23	200	816	1568	1232	256				
15	25	242	1140	2688	2912	1120	64			
16	27	288	1540	4320	6048	3584	576			
17	29	338	2024	6600	11424	9408	2816	128		
18	31	392	2600	9680	20064	21504	9984	1280		
19	33	450	3276	13728	33264	44352	28800	6912	256	
20	35	512	4060	18928	52624	84480	71808	26880	2816	
21	37	578	4960	25480	80080	151008	160512	84480	16640	512
22	39	648	5984	33600	117936	256256	329472	228096	70400	6144
Total[a]	396	4218	27744	118048	326144	572000	604032	347776	90112	6656

[a]Grand total = 2,097,126.

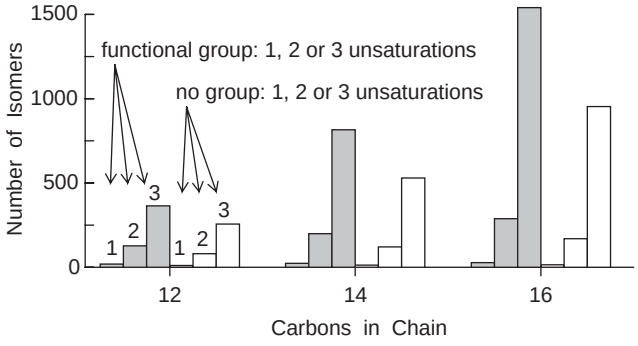

Fig. 3. Number of possible geometric isomers of unsaturated olefinic chains of 12, 14 or 16 carbons with a functional group (e.g. aldehyde, alcohol, or acetate ester) or without a group (hydrocarbons).

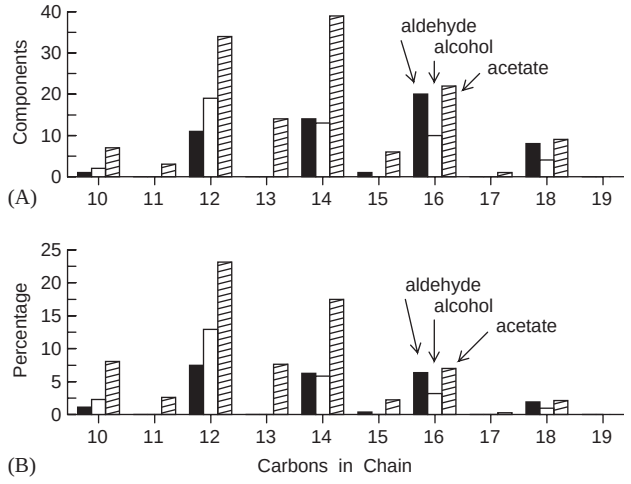

Fig. 4. (A) Number of moth pheromone components with aldehyde, alcohol, and acetate ester groups with chain lengths of 10–20 carbons. (B) Percentage of moth pheromone components with aldehyde, alcohol, and acetate ester groups of all possible isomers of one or two unsaturations in chain lengths of 10–20 carbons (Byers, unpublished).

with even numbers from 10 to 18 carbons, with peaks for aldehydes, alcohols, and acetate esters at 16, 12, and 14 carbon chain lengths, respectively (Fig. 4A). The percentages of these discovered moth components with 1 and 2 unsaturations of the possible isomers (Table 1) follow a similar pattern. However, the percentages of the possible isomers used by moths of all three functional group types peak at 12 carbon chain lengths (Fig. 4B).

3.2. Numbers of hydrocarbon moth pheromone analogs

In Table 2, all possible isomers of straight chain hydrocarbons from 10 to 22 carbons with no functional groups are presented yielding a total of 1,641,292. These, in addition to the isomers with aldehyde, alcohol, and acetate ester functional groups counted above gives a total of 7.9 million prospective components available to moths. Although the less common olefinic epoxide pheromones of moths (Millar, 2000) are not considered in the examples here, they have even more possible isomers than hydrocarbons since any unsaturation position can have the one epoxide in the

Table 2
Number of different possible geometric isomers of unsaturated olefinic chains from 5 to 22 carbons without a functional group

Length	Number of unsaturations										
	1	2	3	4	5	6	7	8	9	10	11
5	3	3									
6	5	9	2								
7	5	15	6								
8	7	25	24	4							
9	7	35	44	16							
10	9	49	98	64	8						
11	9	63	146	160	32						
12	11	81	256	348	160	16					
13	11	99	344	664	416	80					
14	13	121	530	1160	1136	400	32				
15	13	143	670	1888	2240	1280	160				
16	15	169	952	2924	4688	3536	960	64			
17	15	195	1156	4328	7872	8272	3200	384			
18	17	225	1554	6192	14120	17536	10400	2304	128		
19	17	255	1834	8600	21472	34032	25152	9088	768		
20	19	289	2368	11652	34816	61952	61344	29696	5376	256	
21	19	323	2736	15448	49504	106608	122496	82624	21760	1792	
22	21	361	3426	20112	74752	175552	251328	204224	82048	12544	512
Total[a]	216	2460	16146	73560	211216	409264	475072	328384	110080	14592	512

[a]Grand total = 1,641,502.

cis-configuration with two chiral forms, (*R*, *S*) and (*S*, *R*). For example a modified algorithm showed there to be 509 isomers of a 19-carbon chain with one unsaturation and one epoxide as compared to 255 isomers of diunsaturated hydrocarbons of 19 carbons.

A more conservative and probably more appropriate estimate of the number of isomers available for moths would be to limit the unsaturations from 1 to 3 since these are most commonly found in moth species. Also, only chains of 10–22 carbons are commonly used. For example about 57.5%, 18.2%, and 0.3% of the moth species use acetate ester components with 1, 2, or 3 unsaturations, respectively (Pherolist: Arn et al., 1992; Arn, 2001; Byers, unpublished). Among the alkene hydrocarbons, 0.06%, 0.7%, and 3.5% of the species use components with 1, 2, or 3 unsaturations, respectively. Thus, from Tables 1 and 2, there are 32,123 mono- to triunsaturated alkenyl acetate esters and 18,632 similarly unsaturated alkene hydrocarbons with chains of 10–22 carbons. The total for aldehydes, acetate esters, alcohols, and without a group is then 115,001 potential components of 10–22 carbons.

Since most moths use 2–4 components (Byers, 2002, unpublished), the number of possible different blends is calculated by Eq. (1). Thus, the number of blends for two, three, and four components are then calculated at an astounding 6.6 billion, 253 trillion, and 7.3E+18, respectively. Much larger numbers can be obtained using higher numbers of unsaturations, but these have not been discovered in nature (except in two cases as discussed subsequently).

4. Discussion

Constraints on evolution of pheromone communication systems can involve pheromone biosynthesis, sensory physiology, chemical volatility/stability, and inter-specific competition for limited numbers of chemical isomers. Considering that several million possible chemical isomers of unsaturated carbon chains could be used, relatively few are reported as sex pheromone components of moth species (Fig. 4B). Most components are carbon chains of 12, 14, or 16 length that are used by 49%, 63%, and 31% of species with identified attractant pheromones, respectively (Pherolist). Of these, only a few species are known to use carbon chains larger than 18, suggesting larger chains have comparatively too little volatility to be sufficiently released for male detection. Of those moth species that use aldehydes (19% of species), alcohols (20%), or acetate esters (71%) as functional groups, there are about 69%, 24%, and 1% that use components with 1, 2, or 3 unsaturations, respectively (Pherolist; Byers, unpublished). Only one species uses 4 unsaturations in a 22-carbon chain with a functional group (Leonhardt et al., 1991) even though up to 10 unsaturations are possible in this chain.

Probably the most obvious hypothesis to account for the relatively few unsaturations in moth components is that some fatty acid precursors (oleic, linoleic, and linolenic acids) have 1, 2 or 3 unsaturations, respectively. However, moths in general have the ability to unsaturate practically any position in the molecule by

using one or more Δdesaturases (5, 9, 10, 11, 12, and 14) and chain-shortening enzymes (Bjostad et al., 1981; Roelofs and Wolf, 1988; Foster and Roelofs, 1988, 1996; Zhao et al., 1990; Jurenka, 1997; Tillman et al., 1999). A few moths have even made 4 unsaturations in either 19-carbon hydrocarbon chains or 22-carbon chains of butyrate ester (Wong et al., 1984; Leonhardt et al., 1991). There probably is no fitness benefit in making a pheromone component more complex (more unsaturations or groups) once a unique species-specific structure has evolved. From a chemical perspective, relatively more unsaturation complexity in a molecule would make it less stable due to more points that can be chemically altered by hydrogenation, epoxidation, or geometric isomerization (Morrison and Boyd, 1973). Natural selection would not favor the evolution of a less stable pheromone component that would otherwise require production of much larger quantities to be effective. If there are constraints on the evolution of biosynthetic enzymes, there could also be limits on the antennal receptors to discriminate between higher numbers of unsaturated bonds (and constraints on the evolution of more complexity).

Early in evolution of a species, it can be supposed that only one pheromone component was utilized first and that later a second would be added to form a blend. The second component might be necessary to differentiate the species for mating isolation from other species (immigrant species or sibling species) using the first component. The limited numbers of monounsaturated isomers (Tables 1 and 2) probably required moths to evolve multiple component pheromones during speciation to avoid fitness costs of miss-communication. The Pherolist reports that 55% of moth species have two or more components, while some of the single component species may use blends that have not yet been elucidated (Byers, 2002, unpublished). If a moth species could select any isomer of the 14-carbon aldehydes with 1–3 unsaturations (1039 isomers available, Table 1), then there are 539,241 possible 2-component blends or 519 times more than the number of single compounds (Eq. (1)).

This indicates that moths when restricted to subsets of the known pheromone analogs would have practically no constraints on evolution of new pheromones due to lack of unique isomers to comprise blends. On the other hand, no moths are known to use components with chains of 5 or 6 carbons (Pherolist) possibly because there are only 7 and 15 isomers possible for acetate esters or other functional group (Table 1). These may not provide enough communication channels to readily allow radiation of species, especially when in competition with other species using larger chains that could more readily find new channels. A few species in the Eriocraniidae and Nepticulidae use pheromone components with chains of only 7 or 9 carbons, while species of Psychidae use 8 carbons (Pherolist). In these cases, there may also be constraints on evolution of pheromones since there are fewer isomers of various functional groups possible (Tables 1 and 2). A competing theory is that the relatively few communication channels for chains of 5 or 6 carbons means that proportionately few moth species would use the isomers given equal chances. For example 5–6 carbon chains have only 3% of the monounsaturated isomers of all chains up to 22 carbons, so about 3% of moths (i.e. 47 of 1572 species reported) might be expected to use the shorter chains, but so far no species have been found (Pherolist; Byers, unpublished). These estimates based on the Pherolist will need to be updated in future, probably with the newly created Pherobase covering moth and insect pheromones (www.pherobase.com).

In order for a moth to evolve the use of another analog as a component (Tables 1 and 2), at least one and probably several mutations coding for the biosynthetic enzymes would be necessary. However, it is more likely that a new mutant species arises from one mutation rather than from several occurring simultaneously. Thus, we may consider a more limited number of potential isomers for a particular group. For example many species of ermine moths, *Yponomeuta* (Yponomeutidae), use monounsaturated 14- and 16-carbon acetate esters and alcohols (Löfstedt et al., 1986, 1990; Pherolist). From Table 1, there are 23 different 14-carbon chains of each functional group and 27 of each group for 16-carbon chains or a total of 100 different possible components, assuming conservatively that only single unsaturations are easily biosynthesized. The majority of moths studied (55% or 870 species, Pherolist) have two or more synergistic components (many of the 702 species with one reported component probably have at least two). Blend combinations of 2, 3, and 4 components could be selected from among the theoretically 100 to choose from. Thus, from formula (1), if the pheromone is comprised of two, three, or four components, there are 4950, 161,700 and 3,921,225 possible blends, respectively. It seems that using 2 or 3 component blends allows enough possibilities that a random selection of an isomer by a mutation would most likely not be the same as any existing component blends in use by sympatric species (blends of the 100 possible compounds). Mutations that allowed use of other chain lengths or functional groups would drastically increase the possibilities. However, if a mutant species of *Yponomeuta* could only select a new blend using compounds already produced by females of the genus, then of the 18 compounds identified (Pherolist) there are 153, 816 and 3060 possible blends using 2, 3, or 4- components per blend. In this case, there may be some limited constraints on the evolution of new pheromone blends in this genus (8 sympatric species in The Netherlands), at least when using only two

components. This could also provide selection pressure for the evolution of closely related species using opposite ratios of *E*:*Z* isomers (e.g. 98:2 and 2:98; Linn and Roelofs, 1995) that perhaps doubles the number of possible 2-component blends.

Insects use auditory, visual, and olfactory senses to find mates and suitable reproductive habitats and food. Sound can be varied in frequency and pulse duration to give in theory many possible signals (Gogala, 1985; Kalmring, 1985). Emitted or reflected light is usually of constant frequency (of many possible) or pattern (butterfly wings), but can be varied in pulse duration (flapping of wings or light pulses of lightning beetles, Lampyridae) to yield many possible signals (Forrest and Eubanks, 1995; Cronin et al., 2000). Moths, and other insects, have used combinations of chemicals to produce many possible signals. Although sound and light can be pulsed, the signals are emitted constantly over several minutes to hours as are releases of sex and aggregation pheromones (Baker, 1989; Byers, 1989). The complexity of these signals is undoubtedly limited by the aptitude of the insect brain as compared to brains of higher animals such as birds and humans (Marler, 1970), where language as a signal is virtually unlimited.

The moth system of chemical communication is digital in nature, comprised of discrete binary states of *E* or *Z* unsaturations at various integer positions and chain lengths with a few possible functional groups. Finally, the signal "bandwidth" is greatly expanded by chemical combinations resulting in a multitude of unique communication channels or "frequencies".

Acknowledgements

My appreciation for evolution of moth pheromones grew out of stimulating discussions with colleagues at Lund University, especially Christer Löfstedt.

References

Arn, H., 2001. The Pherolist. Internet address: http://www-pherolist.-slu.se/index.html.

Arn, H., Toth, M., Priesner, E., 1992. List of Sex Pheromones of Lepidoptera and Related Attractants. International Organization for Biological Control.

Baker, T.C., 1989. Sex pheromone communication in the Lepidoptera: New research progress. Experientia 45, 248–262.

Bjostad, L.B., Wolf, W.A., Roelofs, W.L., 1981. Total lipid analysis of the sex pheromone gland of the redbanded leafroller moth, *Argyrotaenia velutinana*, with reference to pheromone biosynthesis. Insect Biochem. 11, 73–79.

Byers, J.A., 1989. Chemical ecology of bark beetles. Experientia 45, 271–283.

Byers, J.A., 2002. Internet programs for drawing moth pheromone analogs and searching literature database. J. Chem. Ecol. 28, 787–797.

Cronin, T.W., Järvilehto, M., Weckström, M., Lall, A.B., 2000. Tuning of photoreceptor spectral sensitivity in fireflies (Coleoptera: Lampyridae). J. Comp. Physiol. A. 186, 1–12.

Eldredge, N.D.M., Spencer, H.G., 1995. Species, selection, and Paterson's concept of the specific-mate recognition system. In: Lambert, D.M., Spencer, H.G. (Eds.), Speciation and the Recognition Concept: Theory and Application. Johns Hopkins University Press, Baltimore, MD, USA, pp. 464–477.

Etges, W.J., Ahrens, M.A., 2001. Premating isolation is determined by larval-rearing substrates in cactophilic *Drosophila mojavensis*. V. Deep geographic variation in epicuticular hydrocarbons among isolated populations. Am. Nat. 158, 585–598.

Forrest, T.G., Eubanks, M.D., 1995. Variation in the flash pattern of the firefly, *Photuris versicolor quadrifulgens* (Coleoptera: Lampyridae). J. Insect Behav. 8, 33–45.

Foster, S.P., Roelofs, W.L., 1988. Sex pheromone biosynthesis in the leafroller moth *Planotortrix excessana* by Δdesaturation. Arch. Insect Biochem. Physiol. 8, 1–9.

Foster, S.P., Roelofs, W.L., 1996. Sex pheromone biosynthesis in the Tortricid moth, *Ctenopseustis herana* (Felder and Rogenhofer). Arch. Insect Biochem. Physiol. 32, 135–147.

Gogala, M., 1985. Vibrational communication in insects (biophysical and behavioural aspects). In: Kalmring, K., Elsner, N.E. (Eds.), Acoustic and Vibrational Communication in Insects. Verlag Paul Parey, Berlin, Germany, pp. 117–126.

Holloway, J.D., Bradley, J.D., Carter, D.J., 1987. Lepidoptera. In: Betts, D.J. (Ed.), CIE Guides to Insects of Importance to Man. CAB International Institute of Entomology. British Museum of Natural History, Oxford, UK, pp. 3–22.

Jiggins, C.D., Nalsbit, R.E., Coe, R.L., Mallet, J., 2001. Reproductive isolation caused colour pattern mimicry. Nature (London) 411, 302–305.

Jurenka, R.A., 1997. Biosynthetic pathway for producing the sex pheromone component (*Z,E*)-9,12-tetradecadienyl acetate in moths involves a Δ12 desaturase. Cell. Mol. Life Sci. 53, 501–505.

Kalmring, K., 1985. Vibrational communication in insects (reception and integration of vibratory information). In: Kalmring, K., Elsner, N.E. (Eds.), Acoustic and Vibrational Communication in Insects. Verlag Paul Parey, Berlin, Germany, pp. 127–134.

Leonhardt, B.A., Mastro, V.C., Schwarz, M., Tang, J.D., Charlton, R.E., Pellegrini-Toole, A., Warthen Jr., J.D., Schwalbe, C.P., Cardé, R.T., 1991. Identification of sex pheromone of browntail moth *Euproctis chrysorrhoea* L. (Lepidoptera: Lymantriidae). J. Chem. Ecol. 17, 897–910.

Linn Jr., C.E., Roelofs, W.L., 1995. Pheromone communication in moths and its role in the speciation process. In: Lambert, D.M., Spencer, H.G. (Eds.), Speciation and the Recognition Concept: Theory and Application. Johns Hopkins University Press, Baltimore, MD, USA, pp. 263–300.

Löfstedt, C., Herrebout, W.M., Du, J.W., 1986. Evolution of the ermine moth pheromone tetradecyl acetate. Nature (London) 323, 621–623.

Löfstedt, C., Hansson, B.S., Dukerman, H.J., Herrebout, W.M., 1990. Behavioural and electrophysiological activity of unsaturated analogues of the pheromone tetradecyl acetate in the small ermine moth *Yponomeuta rorellus*. Physiol. Entomol. 15, 47–54.

Lynch, M., Force, A.G., 2000. The origin of interspecific genomic incompatibility via gene duplication. Am. Nat. 156, 590–605.

Marin, I., 1994. Sexual isolation in Drosophila. II. Intraspecific variation in mate recognition systems. J. Evol. Biol. 7, 303–314.

Marler, P., 1970. Birdsong and speech development: could there be parallels? Am. Sci. 58, 669–673.

McMillan, W.O., Jiggins, C.D., Mallet, J., 1997. What initiates speciation in passion-vine butterflies? Proc. Natl Acad. Sci. USA 94, 8628–8633.

Millar, J.G., 2000. Polyene hydrocarbons and epoxides: a second major class of lepidopteran sex attractant pheromones. Annu. Rev. Entomol. 45, 575–604.

Morrison, R.T., Boyd, R.N., 1973. Organic Chemistry. Allyn and Bacon, Inc., Boston, Massachusetts, USA.

Paterson, H.E.H., 1978. More evidence against speciation by reinforcement. S. Afr. J. Sci. 74, 369–371.

Paterson, H.E.H., 1985.The recognition concept of species. In: Vrba, E.S. (Ed.), Species and Speciation, pp. 21–29. Transvaal Museum Monograph No. 4. Transvaal Museum, Pretoria, South Africa.

Roelofs, W.L., Wolf, W.A., 1988. Pheromone biosynthesis in Lepidoptera. J. Chem. Ecol. 14, 2019–2031.

Sasaerila, Y., Gries, G., Gries, R., Boo, T.C., 2000. Specificity of communication channels in four limacodid moths: *Darna bradleyi*, *Darna trima*, *Setothosea asigna*, and *Setora nitens* (Lepidoptera: Limacodidae).

Tillman, J.A., Seybold, S.J., Jurenka, R.A., Blomquist, G.J., 1999. Insect pheromones—an overview of biosynthesis and endocrine regulation. Insect Biochem. Mol. Biol. 29, 481–514.

White, C.S., Lambert, D.M., Foster, S.P.D.M., Spencer, H.G., 1995. Chemical signals and the recognition concept. In: Lambert, D.M., Spencer, H.G. (Eds.), Speciation and the Recognition Concept: Theory and Application. Johns Hopkins Univ. Press, Baltimore, MD, USA, pp. 301–326.

Wong, J.W., Palaniswamy, P., Underhill, E.W., Steck, W.F., Chisholm, M.D., 1984. Novel sex pheromone components from the fall cankerworm moth, *Alsophila pometaria*. J. Chem. Ecol. 10, 463–473.

Zhao, C.-H., Löfstedt, C., Wang, X., 1990. Sex pheromone biosynthesis in the Asian corn borer *Ostrinia furnacalis* (II): Biosynthesis of (*E*)- and (*Z*)-12-tetradecenyl acetate involves Δdesaturation. Arch. Insect Biochem. Physiol. 15, 57–65.

Zhu, J., Chastain, B.B., Spohn, B.G., Haynes, K.F., 1997. Assortative mating in two pheromone strains of the cabbage looper moth, *Trichoplusia ni*. J. Insect Behav. 10, 805–817.