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REPRODUCTIVE ISOLATION IN CLEARWING MOTHS (LEPIDOPTERA: SESIIDAE): A TROPICAL–TEMPERATE COMPARISON¹

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Abstract. To elucidate the factors promoting reproductive isolation in a diverse tropical community of clearwing moths (Lepidoptera: Sesiidae), I compared the results of pheromone trapping studies conducted in Panama with previously published studies involving Wisconsin Sesiidae. Pair-forming behavior in sesiids is facilitated by female-emitted sex pheromones which serve as long-range attractants for conspecific males. Pheromones of the various species appear to be closely related in terms of chemical structure. Prior work in Wisconsin demonstrated that species maintain reproductive isolation through specificity in sex pheromone chemistry and differences in seasonal or daily pattern of sexual activity. In both Wisconsin and Panama, data were obtained by trapping male sesiids with synthetic pheromone baits.

An objective comparison of reproductive isolation in the two regions is accomplished through an application of metrics (breadth, overlap) developed originally to measure niche segregation. The atmospheric channel along which sex communication occurs is considered as an entity, and the chemical and temporal axes along which the communication channels of species may differ are viewed as dimensions. Interspecific differences in channels along a dimension constitute a reproductive isolating mechanism. The calculations of channel breadths and overlaps along these dimensions permit a quantitative comparison of isolating mechanisms. Theory predicts that in species-rich communities either breadths are narrower, overlaps greater, or channel availability (space) is more extensive along one or more dimensions.

Species richness of sesiids was significantly greater in Panama on both a regional and a local basis. Seasonal breadths of sesiids were greater in Panama than in Wisconsin. However, when seasonal breadths were standardized to account for the extended favorable season in Panama, values in both regions were equivalent. Chemical breadths of species that apparently utilized mixtures of different compounds as sex pheromones (binary species) were comparable in Panama and Wisconsin, as were overlaps along the seasonal and chemical dimensions. However, a higher proportion of the Panamanian fauna were binary isomer species, and Panamanian sesiids appeared to utilize a greater diversity of compound mixtures as pheromones. This indication that greater channel space distinguishes two communities differing in species richness agrees with several recent findings, regarding niche segregation, in other taxa.

Key words: channel breadth; channel overlap; channel space; coexistence; communication channel; niche breadth; niche overlap; pheromone; reproductive isolation; Sesiidae; species richness; tropical–temperate comparison.

INTRODUCTION

The species richnesses of most taxa are higher in the tropics than in temperate regions (Fischer 1960), although exceptions do exist (Patrick 1966, Janzen 1981). Because of this increased diversity, factors related to the coexistence of species (mechanisms of resource partitioning, niche segregation, sexual isolation, etc.) in tropical communities are expected to differ from factors found in temperate areas. One aspect of coexistence is the maintenance of reproductive isolation through various “isolating mechanisms” (Mayr 1942). Species coexisting in a community must be segregated by prefertilization mechanisms if individuals

are to avoid loss of time, energy, and gametes in mate seeking. The present study investigates the expectation that patterns of reproductive isolation differ between tropical and temperate communities; in particular, I compare the nature of isolating mechanisms among clearwing moths (Lepidoptera: Sesiidae) in Panama with that found among Wisconsin species.

Most studies of species coexistence have investigated the resource partitioning (niche segregation) of food or shelter by species forming a guild (Schoener 1974). Several workers, however, have regarded other commodities (e.g., escape space [Ricklefs and O'Rourke 1975], pollinators [Parrish and Bazzaz 1975, Stiles 1975]) as potential subjects of resource partitioning. While the direct application of resource partitioning to reproductive isolation is debatable, Greenfield and Karandinos (1979a) quantitatively considered the atmospheric channel used for sexual communica-

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tion as an entity needed for reproductive isolation. Consequently, quantitative indices such as niche breadth and overlap, developed initially to analyze resource partitioning, may be borrowed to measure sexual communication channels. In the present study, I compare, by computing breadths and overlaps of species' communication channels, how members of a tropical and a temperate community of moths avoid interspecific interference during pair formation. Thus, I attempt to understand how moths in species-rich tropical communities are able to cope with the greater number of closely related species from which they must maintain reproductive isolation.

Using the now classical niche hypervolume model of Hutchinson (1957), Mac Arthur (1972:216) illustrated how coexistence in species-rich communities can be hypothetically accounted for by one or more of the following factors: (1) narrower niche breadths of the various species, (2) higher niche overlaps, (3) greater spectrum of resources (available niche space) along a dimension, (4) increased dimensionality enhancing available niche space. Later, Pianka (1974:234) added the possibility of greater exploitation of available niche space, but distinguishing this from factors 3 and 4 above could be difficult. Ricklefs and O'Rourke (1975) and Ricklefs (1979:754) report several recent empirical studies that suggest that greater available niche space is responsible for coexistence in the tropics. In this study, I adapt the above factors to a comparison of atmospheric communication channels of clearwing moths in Panama and Wisconsin.

Sexual communication and reproductive isolation in Sesiidae

As in most moths, the initial stage of pair-formation in sesiids is accomplished via female-emitted pheromones (Duckworth and Eichlin 1974, Greenfield 1981). Recently, the sex pheromones of two sesiids were isolated, identified, and synthesized. These compounds were discovered to be the (Z,Z) and (E,Z) isomers of 3,13-octadecadien-1-ol acetate (ODDA) (Tumlinson et al. 1974). Field and laboratory studies of sesiids in North America, Europe, and Japan indicate that many species use these compounds, or related ones (isomers of 3,13-octadecadien-1-ol [ODDOH]), singularly or in various mixtures, as sex pheromones (Yaginuma et al. 1976, Duckworth and Eichlin 1978a, Underhill et al. 1978, Voerman et al. 1978). In Wisconsin, 21 of the 29 sesiid species present were captured in traps baited with these compounds (Greenfield and Karandinos 1979a). Observations of males exhibiting copulatory behavior near these baits (Greenfield and Karandinos 1979a) and the tendency for taxonomically related species to utilize chemically similar sex pheromones (Tamaki 1977) strengthen the hypothesis that the ODDA and ODDOH isomers are the natural sex pheromones of these species.

Insect species in which pair-formation is mediated

by structurally related pheromones can achieve "long-range" premating reproductive isolation in a variety of manners. In a chemical fashion, species can differ according to the geometric isomers comprising their sex pheromones (Roelofs and Comeau 1969). Among Lepidoptera, the sex pheromones of many species include several components and species distinction can be acquired through the isomeric blend comprising the multicomponent pheromone (Roelofs and Comeau 1971) and/or by the specific ratio of those components forming the pheromonal bouquet (Minks et al. 1973). Species can also differ temporally, restricting sexual activity to different times of the day (Brown 1972), season (Purrington and Nielsen 1977, Greenfield and Karandinos 1979b), or year (for periodical, biennial species). Finally, species can maintain a segregation of reproductive activities by confining these activities to distinct habitats. Chemical, seasonal, and diel factors have been found, singularly and in various combinations, to maintain premating reproductive isolation among clearwing moths in Wisconsin.

To compare various aspects of reproductive isolation between two communities, an objective method of assessing the degree of isolation must be employed. I accomplish this by considering the various attributes of the atmospheric communication channel in which species can differ as dimensions. These chemical, temporal, and spatial dimensions are indicated above. Interspecific differences in the atmospheric channel along a dimension are then a reproductive isolating mechanism. The "diversity" of a species' channel along each dimension constitutes its "channel breadth" along that dimension, and the amount of sharing, of the atmospheric channel, between species is their "channel overlap." These metrics can be used to quantify the degree of reproductive isolation (= the complement of channel overlap along a given dimension) among the various species.

Reproductive isolation in tropical communities

The relevance of Mac Arthur's (1972) four coexistence factors to reproductive isolation in species-rich communities can be visualized hypothetically as follows. The first factor, narrower channel breadth, may be manifested in several ways. Each species may be sexually active during a very limited portion of the day or season. Along the chemical dimension, if a group of species are all utilizing a particular multicomponent pheromone (e.g., combination [=blend] of isomers), each species may emit and respond to only a narrow range of isomeric ratios of that blend's components.

Species in a tropical community may exhibit higher mean levels of overlap of their long-range communication channels. In Wisconsin, sesiid species were found to maintain reproductive isolation through long-range mechanisms that operate during the initial stage of the pair-forming sequence (Greenfield and Karandinos 1979a). However, species in a tropical commu-

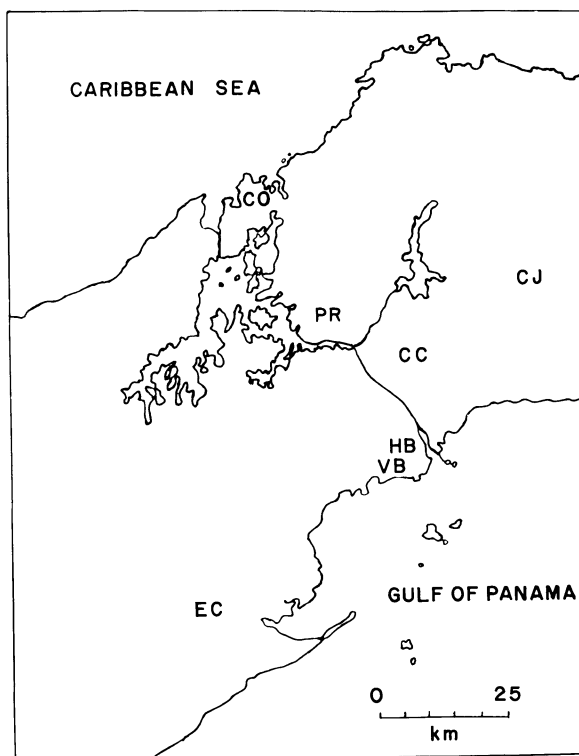


FIG. 1. Study sites used in Panama during 1978–1979.

nity may tend to rely more on close-range isolating mechanisms involved in courtship. Thus, tropical species would still maintain premating reproductive isolation, yet the isolation would not be manifested until individuals enter a close-range "courtship arena." The specific behavioral (courtship) factors referred to above may also exist among the Wisconsin species, but reproductive isolation would not strongly depend on them because of the extensive segregation of communication channels along chemical, seasonal, and diel dimensions. An implication of the above possibility for reproductive isolation is that tropical organisms might suffer a greater loss of time and energy in mate seeking.

Available communication channel "space" may be enlarged in a tropical community in several ways. "Space" may be more extensive along a single dimension; e.g., longer duration of favorable temperature conditions in the tropics extends the seasonal dimension. On the other hand, greater space may result from the presence of additional dimensions. The increased structural complexity of tropical forests, compared with temperate forests, may allow species to stratify vertically the microhabitats in which sexual activity occurs, thereby introducing a second spatial dimension along which species' communication channels may differ. Such stratification is documented for the activity of many butterflies of neotropical forests

(Papageorgis 1975). Tropical species could also more frequently utilize complex pheromonal mixtures containing several components, a factor contributing to increased chemical dimensionality. In the present study I explore these possible mechanisms by which Panamanian sesiids may maintain reproductive isolation.

STUDY SITES

The temperate zone sites used in this comparative study are 31 localities in southern Wisconsin. Precise locations and vegetation at these sites are provided elsewhere (Greenfield 1978, Greenfield and Karandinos 1979a), and the abbreviations used to identify Wisconsin sites later in this paper correspond with the coding used in these two references. These sites had been selected to include all major plant communities found within a broad geographic region. Thus, an attempt was made to survey all resident sesiid species. The survey was conducted between 1975 and 1977 but was most intensive during 1977.

During 1978 and 1979 sesiid moths were surveyed at seven sites in central Panama (Fig. 1, Table 1). The sites were chosen to encompass a transisthmian precipitation gradient (sites CO, PR, CC, HB, VB) within lowland tropical moist and dry forests (Holdridge System) and two premontane locations (sites EC, CJ), ≈ 800 m elevation, mutually isolated by the lowlands along the Panama Canal. These seven locations included most major natural habitats existing in central Panama.

MATERIALS AND METHODS

Both the temperate and tropical phases of this comparative study were trapping surveys in which male sesiids were captured in sticky traps baited with synthetic sex attractants (isomers of 3,13-ODDA and 3,13-ODDOH). At each site an array of traps, each trap baited with a different isomer or isomeric combination, was employed. A critical assumption regarding this trapping is that a bait eliciting maximal attraction of males of a species corresponds closely with the natural sex pheromone of that species. However, several difficulties arise from this assumption. The synthetic baits used may lack certain components of the actual pheromone, and the compounds may also be emitted at release rates different from those of the female. Cardé et al. (1977) and Roelofs (1978) have addressed these problems, indicating how their occurrence can affect captures of male moths in pheromone traps. Another shortcoming of the trapping approach toward understanding pheromonal communication concerns the possibility of the individual compounds of a multicomponent pheromone mediating different behaviors in the pair-forming sequence (Baker and Cardé 1979). The presence or absence of compounds eliciting "short-range behaviors" may affect trapping efficacy, yet such compounds should not be included in an analysis purporting to examine long-range communication.

TABLE 1. Trapping sites used in Panama during 1978 and 1979 with climatological data from nearby meteorological stations.

Site	Location	Elevation (m)	Mean annual temp. (°C)	Total annual precipitation (cm)	Months between which 90% of precipitation occurs
VB	8°53'N, 79°36'W	10	27.5*	173.5*, 184.8†	May–December*, April–November†
HB	8°54'N, 79°35'W	20	27.5*	173.5*, 184.8†	May–December*, April–November†
CC	9°03'N, 79°35'W	100	25.7‡	240.7‡	April–November‡
PR	9°07'N, 79°43'W	60	§	211.1	April–November
CO	9°20'N, 79°52'W	30	27.1¶	258.8¶	April–November¶
EC	8°41'N, 79°56'W	800	21.9#	271.0#	April–November#
CJ	9°10'N, 79°25'W	720	22.5**	457.2**	May–December**

* United States Air Force, Howard Air Force Base Station, 32-yr average (1941–1972).

† United States Air Force, Howard Air Force Base Station, 1978–1979.

‡ Tropic Test Center, Chiva Chiva Antenna Site, 1978–1979.

§ Data not available.

|| Panama Canal Company, Gamboa Station, 1978–1979.

¶ Panama Canal Company, Gatun Station, 1978–1979.

Institute de Recursos Hidraulicos y Electrificación (IRHE), Campana Capira Station, 11-yr average (1948–1958).

** IRHE, Cerro Azul Station, 1978–1979.

Trapping also provided data on temporal (seasonal periodicity) aspects of sexual activity in each species abundantly captured. Details concerning the design of traps, their deployment in the field, and preparation of synthetic sex attractant baits are published elsewhere (Greenfield and Karandinos 1979a).

Several aspects of the phase of the study conducted in Panama differ from the previously published Wisconsin survey and need to be described here. At each of the seven sites located in Panama, a spectrum of 22 traps baited with attractive compounds was used (Table 2). This array included the four compounds (E,Z-3,13-ODDA [EZAC]; Z,Z-3,13-ODDA [ZZAC]; E,Z-3,13-ODDOH [EZOH]; Z,Z-3,13-ODDOH [ZZOH]) previously found attractive in Wisconsin and other nearctic localities. Each site also included two additional traps baited with 200 µg E,E- and Z,E-3,13-ODDA, isomers previously found inactive in Wisconsin. (They were not attractive to any sesiids, and they did not synergize nor inhibit the attractiveness of E,Z- or Z,Z-3,13-ODDA to any species. Synergism and inhibition are defined here by a significant increase and decrease, respectively, in trap catch.) Inclusion of these traps in Panama served to corroborate the inactivity of the compounds. The four attractive compounds were each used singly and in their six possible binary combinations. For each of these six combinations, three ratios (9:1, 5:5, 1:9) were prepared. The above arrangement of traps was designed to encompass the basic combinations of active isomers as simply as possible. Arrays of traps used during 1977 at Wisconsin sites included different sets of baits. At "group I sites" in Wisconsin the array consisted of EZAC and ZZAC singly and in 10 different ratios of the blend of these two isomers (Greenfield and Karandinos 1979a). "Group II sites" in Wisconsin had an array including EZAC, ZZAC, EEAC, and ZEAC, singly and in various combinations, and the array at "group III sites"

was similar to that used in Panama, but the 9:1 and 1:9 ratios of the six binary combinations of EZAC, ZZAC, EZOH, and ZZOH were omitted (Greenfield 1978, Greenfield and Karandinos 1979a). "Control traps," baited with dispensers containing only hexane (the solvent used for preparing the attractant solutions) were employed at all sites in Panama and Wisconsin to confirm that sesiids were not attracted to the traps in the absence of any baits.

Traps were maintained at the seven sites in Panama from ≈25 September 1978 to 25 September 1979. Fresh baits were replaced in the traps every 3 mo to provide a uniform emission of attractant during the study period. (Gas chromatographic analysis had revealed that the various compounds were emitted from the dispensers used at relatively constant rates for 120 d [Greenfield and Karandinos 1979a].) Approximately once each week all traps at every site were examined. During these checks the sticky inserts (8 × 17 cm pieces of stiff paper coated on one side with an adhesive) situated in the bottom of the traps were returned to the laboratory in specially constructed grooved carrying cases and were replaced with fresh inserts. Since attracted moths were ensnared on these inserts, this procedure allowed all captured sesiid specimens to be saved for future identification and maintained the adhesiveness of the inserts (trap effectiveness) at a relatively constant level. In Panama these inserts received an additional treatment of white enamel paint prior to application of the adhesive. This treatment, unnecessary in Wisconsin, increased the water resistance of the inserts, prolonging their stickiness in the humid climate.

Information on the diel periodicity and habitat specificity of Wisconsin sesiids had been obtained earlier (Greenfield and Karandinos 1979a). However, no data were collected in Panama on daily activity patterns, and the seven sites used were insufficient to assess

TABLE 2. Quantities of isomers of 3,13-ODDA and 3,13-ODDOH (synthetic sex attractants for Sesiidae) used as baits in each of the 22 traps placed at Panamanian sites (1978–1979), with numbers of males (pooled from all sites) of the various sesiid species abundantly captured (pooled $n \geq 5$) at each trap. Trapline position is the randomized placement of the trap (used at all sites) in relation to the end of the trapline. Traps baited with EE-, ZE-3,13-ODDA, and control dispensers never caught sesiids and are not included in the table below.

Trapline position	3,13-ODDA isomer (μg)		3,13-ODDOH isomer (μg)		Species*					
	EZ	ZZ	EZ	ZZ	CC6	HB4	HB20	CC18	CJ7	PR7
7	200	36	22
18	200	22	21
10	200	200	9
4	22	200	56
13	200	...	22	20
9	200	...	200	2
6	22	...	200	...	63	...	2
16	200	22	1
8	200	200
21	22	200
12	...	200	6
5	...	200	22
14	...	200	200
20	...	22	200	39
15	...	200	...	22	...	24
19	...	200	...	200	...	1
11	...	22	...	200
22	200	3
3	200	22	1
17	200	200
1	22	200
2	200

* Coded species designations are used because formal species names have not yet been assigned.

adequately the habitat specificity of Panamanian species. Consequently, the tropical–temperate comparison will be restricted to the chemical and seasonal dimensions.

Species designation

The proper determination of species, important in any ecological study, is critical in an investigation of reproductive isolation. Unlike the Nearctic sesiid fauna, for which several monographs and taxonomic keys have been published, no current systematic treatment of Sesiidae exists for central Panama or any other neotropical region (Duckworth and Eichlin 1978*b*). Therefore, “species” in the Panamanian phase of this comparative study were coded and assigned to the established genera to which they belonged. The assignment of individual specimens to these various species was based on morphological characteristics (scaling, genitalia) known to be taxonomically pertinent in Sesiidae (these designations of species were verified by T. D. Eichlin [*personal communication*]). Possible occurrence of cryptic species presents a disadvantage to this reliance on morphological criteria, but at this time the use of any behavioral or ecological characters toward species determination could generate tautology. Quantitative measurements of behavioral and ecological characters (compounds eliciting sexual attraction, seasonality) will later be used to calculate channel metrics, thereby necessitating the use

of other characters in species designation. Fortunately, previously discovered cryptic species among Nearctic Sesiidae have been separable on a morphological basis (Duckworth and Eichlin 1977, Greenfield and Karandinos 1979*b*, Purrington and Nielsen 1979). In addition, none of the morphologically defined species in this study exhibited disjoint behavioral or ecological characters suggestive of unrecognized cryptic species within the erected taxa.

Channel metrics.

“Channel breadth” of a species along the seasonal dimension, “seasonal breadth,” was computed as the seasonal standard deviation (SSD), a parameter found by Wolda (1979) to reflect most accurately the phenology of a species sampled in low numbers. For both Wisconsin and Panamanian data, the year was divided into 24 ≈15-d periods. Individuals were assigned to these phenological periods based on the dates between which they were trapped, and the SSD was:

$$SSD_j = \left| \sum_{i=1}^s (x_{ij}i^2) - \left(\sum_{i=1}^s x_{ij}i \right)^2 / \sum_{i=1}^s x_{ij} \right| / \left(\sum_{i=1}^s x_{ij} - 1 \right),$$

where x_{ij} is the number of individuals of species j trapped during phenological period i , and s is the total number of phenological periods (24). For all species,

TABLE 2. Continued.

Species*										
EC18	CC19	HB18	CC4	EC4	CC12	EC15	CJ10	CC15	CO19	CC1
...	3
12	...	13	1
1	1	...	3
...	13	10
...
...
...
...
...	1
...	8
...	5
...	3
...
...	2	8	...	6	5	...
...	29	9	...
...
...
...
...	14
...	1

separate SSDs were computed for each site at which five (an arbitrary minimum) or more individuals were collected. Pooling the data could bias a species' seasonal distribution toward higher values because of the likelihood of minor between-site variation in seasonality. However, separating data obtained at different sites created very low sample sizes for several species. Despite the potential inaccuracies that might result from using small samples, I considered that a tropical-temperate comparison based on many species (albeit some with little data) would be more robust than a comparison of only a few species captured very abundantly. This judgment was also used in establishing the arbitrary minimum at five individuals. In addition to SSD, the seasonal maximum (SM), defined as the ratio of the maximal number of individuals captured during any 15-d period to the mean value per period (Wolda 1980), was calculated to provide a measure of the sharpness of the seasonal peak.

Because the portion of the year during which adult sesiids were active was far greater in Panama than Wisconsin, the SSD and SM values from Panama were then standardized. This was accomplished by dividing that portion of the year during which insect activity (trap captures of any sesiid species) occurred into the same number of phenological periods (6) at every site. Thus, periods for Panamanian sites were ≈ 61 d in length, while for Wisconsin they remained ≈ 15 d. Individuals trapped in Panama were reassigned to these adjusted periods, and the standardized SSDs and SMS

were determined. Comparison of standardized values from Wisconsin and Panama allowed examination of the effects of season length (duration of favorable climatic conditions) on coexistence.

"Chemical breadth" was computed only for those species captured in numbers ≥ 5 and appearing to utilize a binary mixture of isomers as a sex pheromone, "binary species." This included 4 species in Wisconsin utilizing various ratios of the EZAC:ZZAC blend (the only blend of the six used at group III sites in Wisconsin found attractive to more than one species) and 13 species in Panama utilizing the EZAC:ZZAC, EZAC:EZO, EZAC:ZZO, ZZAC:EZO, ZZAC:ZZO, and EZO:ZZO blends. The various ratios of these blends that were tested were considered as distinct categories. Chemical breadth of species j is calculated (Levins 1968) as:

$$B_{cj} = 1/\sum_{i=1}^s p_{ij}^2,$$

where p_{ij} is the proportion of males of species j found in category i (captured in trap i), and s is the number of categories (12 in Group I sites in Wisconsin [data from Group I sites will be used in the Panama-Wisconsin comparison] along the EZAC:ZZAC gradient and 5 [10:0, 9:1, 5:5, 1:9, 0:10] along each of the six gradients tested in Panama). These B_{cj} values were scaled by the method of Colwell and Futuyma (1971) (in this procedure each species was considered equally abundant) to correct for the difference in ecological

TABLE 3. Species richness of sesiids trapped with 3,13-ODDA and/or 3,13-ODDOH isomers at Panamanian and Wisconsin sites.

Panama		Wisconsin*	
Site	Number of species trapped	Site	Number of species trapped
VB	4	P	9
HB	8	W	12
CC	17	AV	12
PR	10		
CO	20		
CJ	11		
EC	20		

* The three Wisconsin sites listed were those that had been surveyed with an array of traps during 1977 comparable to the array of 22 traps (Table 2) used at each site in Panama during 1978–1979. Data obtained from Greenfield and Karandinos (1979a).

range (number of categories) between the chemical gradient in Panama and that in Wisconsin (Colwell and Futuyma 1971:573). Unlike the treatment of seasonal breadth, data used to determine B_{cj} were pooled from all sites at which species j was trapped. Although this pooling of data could prevent detection of channel shifts along the chemical dimension between sites, it is necessary to reduce potential bias introduced by “position effects” (anomalous results at a site resulting from the unequal placement of traps, favoring some traps over others, in relation to the spatial distribution and movement of the moths).

“Seasonal overlap” between species j and k at a given site is computed as:

$$O_{sjk} = d_{jk}/SSD_{jk},$$

where d_{jk} equals the temporal difference (measured in phenological periods) between the mean trapping dates of species j and k (mean trapping date of species j =

$$\sum_{i=1}^s x_{ij}i / \sum_{i=1}^s x_{ij}), \text{ and}$$

$$SSD_{jk} = [(SSD_j^2 + SSD_k^2)/2]^{1/2}$$

(Southwood 1979:444). This index (O_{sjk}) is a measurement of separation of species and decreases as overlap increases. “Chemical overlap” between species j and k is calculated as:

$$O_{cjk} = \sum_{i=1}^s \min(p_{ij}, p_{ik})$$

(Schoener 1968), scaled by the method of Colwell and Futuyma (1971). For Wisconsin data, O_{cjk} values were determined for all possible pairs of species along the EZAC:ZZAC gradient, including the “single-isomer species” appearing to utilize solely E,Z- or Z,Z-3,13-ODDA as a sex pheromone. Chemical overlap values among Panamanian species were computed similarly except that six different gradients were examined. Overlap values were only calculated for species cap-

tured in samples of five or greater at each site (O_{sjk}) or at all sites combined (O_{cjk}).

RESULTS AND DISCUSSION

Species richness

Forty-seven species of sesiids in the “ODDA-ODDOH group” were captured in Panama, as opposed to 21 species in Wisconsin. The more-intensive sampling in Wisconsin (more sites and 3 yr of trapping) substantiates the higher species richness in Panama. This tropical–temperate difference is also found when the numbers of species at individual sites (α diversity) are compared (Table 3: sites CC, CO, and EC in Panama), dismissing the possibility that high species turnover rates (β diversity) between sites in Panama fully account for the high overall richness found there (γ diversity). The three Wisconsin sites listed in Table 3 were ones (group III sites) that had been surveyed with an array of traps comparable to the array of 22 used at each site in Panama.

Phenology and seasonal breadth

The seasonal distributions of abundantly captured ($n \geq 5$) sesiid species at three sites in Panama are illustrated in Fig. 2. In general, Panamanian species were active between December and June, months coinciding with the annual dry season and the beginning of the wet season (Table 1). Previously, Wolda (1980) reported that Homoptera light-trapped in Panama were abundant throughout the rainy season, whereas Buskirk and Buskirk (1976) noted a peak in general arthropod abundance, indicated by sweep sampling and malaise trapping, during the late dry season and early rainy season in Costa Rica.

Contrary to initial expectations regarding coexistence, SSDs of Panamanian sesiids were significantly greater than those of Wisconsin species (Table 4). This comparison includes data from the two Panamanian sites at which the greatest numbers of sesiids (both species and individuals) were collected and the eight group I sites in Wisconsin. The precision of this comparison is enhanced by the absence of distinctly multimodal distributions of seasonal activity among sesiid species (SSD will not accurately reflect the seasonal breadth of a species exhibiting a multimodal seasonal distribution). Additional support for the validity of this comparison was derived by recomputing seasonal breadth as:

$$1/\sum_{i=1}^s r_{ij}^2,$$

where r_{ij} is the proportion of males of species j captured during phenological period i . This is the same index that was used to calculate chemical breadth. Comparing seasonal breadths of sesiids computed in this manner, values of species trapped at Panamanian sites were still found to be significantly greater ($P < .05$; Mann-Whitney U tests, one-tailed) than those of

Wisconsin species. Seasonal maxima (SMS) were significantly lower in Panama (Table 4), indicating that sharp seasonal peaks did not exist. These findings, which agree with those of Wolda (1980) for various Homoptera, will be reanalyzed in the seasonal diversity section.

Chemical breadth

Chemical breadth (B_{ci}) of Panamanian sesiids was also not significantly narrower than that of Wisconsin species (Table 5). Only binary species (species exhibiting maximal attraction to a blend of two isomers) were examined in this comparison because such species exhibit varying ranges of response to a gradient of ratios of an isomeric blend (Greenfield and Karandinos 1979a). Single-isomer sesiid species (species exhibiting maximal attraction to one isomer), however, are not suitable for comparative purposes. They are generally inhibited from responding to their sex pheromone (attractant) by the addition of small percentages of other isomers (Greenfield and Karandinos 1979a), and therefore possess uniformly narrow chemical breadths along a gradient of isomeric ratios. Inclusion of single-isomer species could affect the comparison by reflecting the prevalence of such species in a given community (a parameter interesting in its own right that will be treated in the Chemical diversity section) rather than the chemical breadths of those species that typically exhibit varying ranges of response.

Complications existed in analyzing chemical breadth for several species (HB4, HB20, CCI) from Panama that were attracted to baits along more than one blend gradient. Fig. 3 illustrates a typical example in which various ratios of three different blends (EZAC:EZOH, ZZAC:EZOH, EZOH:ZZOH) attracted males of species HB20. In this case, 1:9 is the optimal ratio for attraction along the ZZAC:EZOH gradient, but minor attraction to ratios of the EZAC:EZOH and EZOH:ZZOH blends must be accounted for. This is done by recognizing that the absolute quantities of EZOH in the 1:9 and 5:5 ratios of EZAC:EZOH and in the 9:1 and 5:5 ratios of EZOH:ZZOH are all equivalent to the quantity of EZOH in the bait containing only this isomer (Table 2). Noting this and the fact that responses to 1:9 and 5:5 ratios of EZAC:EZOH and to 9:1 and 5:5 ratios of EZOH:ZZOH do not differ significantly from response to pure EZOH ($P \geq .05$; Friedman two-way ANOVA), it can then be assumed that EZAC and ZZOH exert a "neutral effect" (neither synergism nor inhibition) on response of species HB20 males to EZOH. Trap catches for EZOH, EZAC:EZOH (1:9), EZAC:EZOH (5:5), EZOH:ZZOH (9:1), and EZOH:ZZOH (5:5) are then pooled, the pooled sum is divided by 5 (the number of equivalently baited traps), and the quotient (1.6) is taken as the response value to pure EZOH along the ZZAC:EZOH gradient. Without such a correction factor, we would mistakenly conclude that moths were responding to

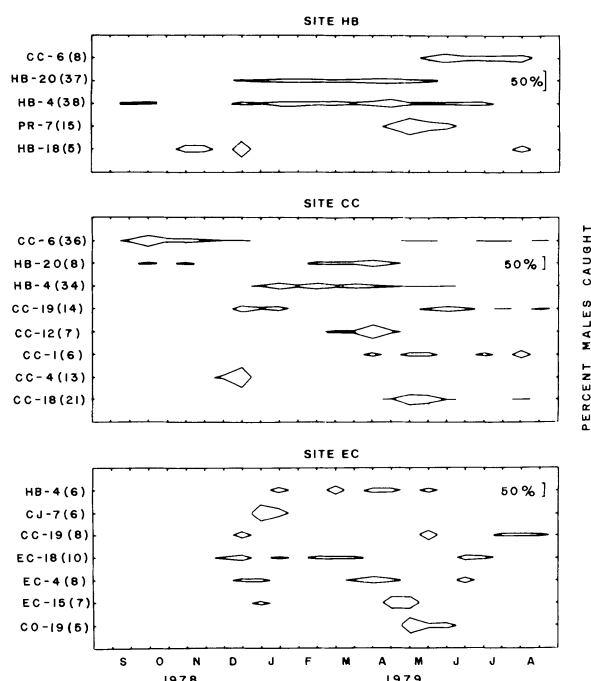


FIG. 2. Seasonality of sexual activity, as indicated by captures in pheromone-baited traps, of sesiid species abundantly caught ($n \geq 5$ at a given site) at three sites (sites at which the greatest number of sesiid individuals were collected) in Panama, 1978-1979. Coded species designations given along the Y-axis are used because formal species names have not yet been assigned. Parenthetical values are sample sizes. Values shown are the percentages of males caught during each 15-d time interval (phenological state i) given along the X-axis.

EZAC or to ZZOH, when in fact these isomers attracted moths only because they were associated with EZOH (the primary attractant). Chemical breadth is computed using the corrected value, and the species' response is considered to lie entirely along the ZZAC:EZOH gradient. The other species (HB4, CCI) are treated in an analogous fashion. This methodology is also used in determining chemical overlaps.

Overlap: seasonal and chemical

Values of O_{sjk} are not significantly lower in Panamanian sites than in Wisconsin locations (Table 6). This equivalence still holds ($P \geq .05$; Mann-Whitney U tests, one-tailed) when seasonal overlap is recomputed as:

$$\sum_{i=1}^8 \min(r_{ij}, r_{ik}),$$

the same index that was used to calculate chemical overlap. In addition, when O_{sjk} values between species j and its nearest neighbor (species k for which O_{sjk} is minimal) are examined, values are not significantly lower in Panama than in Wisconsin (Table 6). Values of O_{cjk} (and the corresponding nearest neighbor values) are likewise not significantly higher in Panama

TABLE 4. Seasonal standard deviations (SSDs) and seasonal maxima (SMS) of total captures per week, for abundantly ($n \geq 5$ at a given site) captured sesiids at various Panamanian and Wisconsin sites. The two Panamanian sites for which data are shown are those at which the greatest numbers of sesiids (both species and individuals) were collected and the Wisconsin locations comprised all eight Group I sites. Parenthetic values are corrected for differences in season length between sites. SSDs at Panamanian sites are significantly greater than at Wisconsin sites ($P < .05$; Mann-Whitney U tests, one tailed), but corrected SSDs do not differ significantly ($P > .05$; Mann-Whitney U tests, two tailed). SMS at Panamanian sites are significantly lower than at Wisconsin sites ($P < .05$), but corrected SMS do not significantly differ ($P > .05$). See text for details.

Panama sites (1978–1979)								
Species code*	CC				EC			
	SSD	SM	(SSD)	(SM)	SSD	SM	(SSD)	(SM)
CC6	2.98	12.67	(0.70)	4.17)				
HB4	2.54	5.65	(0.89)	3.53)	2.79	8.00	(0.75)	3.00)
HB20	4.90	6.00	(1.16)	3.75)				
CC18	1.38	11.43	(0.32)	5.43)				
CJ7					0.52	16.00	(0.52)	4.00)
EC18					5.36	4.80	(1.69)	1.80)
CC19	5.91	5.14	(1.49)	2.57)	5.38	9.00	(2.07)	2.25)
CC4	0.38	20.30	(0.00)	6.00)				
EC4					4.41	6.00	(1.55)	2.25)
CC12	0.95	13.71	(0.00)	6.00)				
EC15					2.88	12.29	(1.13)	5.14)
CO19					0.89	14.4	(0.45)	4.80)
CC1	3.33	8.00	(0.82)	3.00)				
Wisconsin† sites (1977)								
Species	TH		LR		BL		BZ	
	SSD	SM	SSD	SM	SSD	SM	SSD	SM
<i>Carmenta bassiformis</i>	0.89 (0.89)	9.39 (2.35)	0.82 (0.82)	12.52 (3.13)			0.72 (0.72)	10.67 (2.67)
<i>Paranthrene pellucida</i>	0.47 (0.47)	18.86 (4.72)			0.73 (0.73)	14.19 (3.55)	(0.62 (0.62)	14.40 (3.60)
<i>P. simulans</i>	0.16 (0.16)	23.34 (5.84)	0.24 (0.24)	22.56 (5.64)	0.10 (0.10)	23.75 (5.94)	0.00 (0.00)	24.00 (6.00)
<i>Podosesia syringae</i>	0.33 (0.33)	21.14 (5.29)	0.51 (0.51)	19.38 (4.85)	0.41 (0.41)	20.00 (5.00)	0.58 (0.58)	19.50 (4.88)
<i>Synanthedon decipiens</i>					0.57 (0.57)	16.80 (4.20)		
<i>S. exitiosa</i>					0.97 (0.97)	12.00 (3.00)	0.49 (0.49)	17.14 (4.29)
<i>S. pictipes</i>	2.08 (2.08)	14.00 (3.50)	0.73 (0.73)	13.33 (3.33)	2.02 (2.02)	16.80 (4.20)	1.22 (1.22)	9.60 (2.40)
<i>S. scitula</i>	0.58 (0.58)	14.40 (3.60)	0.66 (0.66)	18.86 (4.72)	0.66 (0.66)	15.88 (3.97)	0.72 (0.72)	13.71 (3.43)
	AR		KZ		M		MN	
	SSD	SM	SSD	SM	SSD	SM	SSD	SM
<i>Carmenta bassiformis</i>	0.68 (0.68)	12.00 (3.00)			0.88 (0.88)	9.60 (2.40)	0.67 (0.67)	11.43 (2.86)
<i>Paranthrene pellucida</i>			0.56 (0.56)	14.46 (3.62)			0.63 (0.63)	14.38 (3.60)
<i>P. simulans</i>	0.86 (0.86)	22.28 (5.57)	0.11 (0.11)	23.69 (5.92)	0.08 (0.08)	23.86 (5.97)	0.05 (0.05)	23.95 (5.99)
<i>Podosesia syringae</i>	0.40 (0.40)	21.33 (5.33)	0.55 (0.55)	14.40 (3.60)	0.17 (0.17)	23.29 (5.82)	0.18 (0.18)	23.25 (5.81)
<i>Synanthedon decipiens</i>			0.28 (0.28)	22.00 (5.50)			0.52 (0.52)	15.00 (3.75)
<i>S. exitiosa</i>			0.55 (0.55)	14.40 (3.60)			0.83 (0.83)	13.71 (3.43)
<i>S. pictipes</i>			1.03 (1.03)	14.77 (3.69)			1.06 (1.06)	13.09 (3.27)
<i>S. scitula</i>	0.47 (0.47)	18.86 (4.72)	0.69 (0.69)	13.60 (3.40)			0.83 (0.83)	12.48 (3.12)

* See Table 2.
† Data obtained from Greenfield (1978).

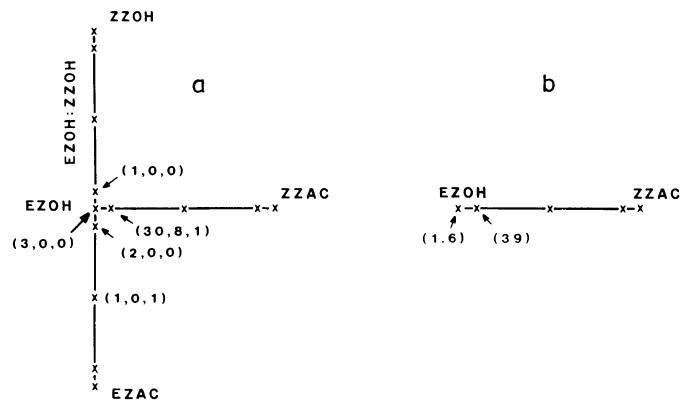


FIG. 3 (a) Attraction of males of species HB20 to 3,13-ODDA (EZAC and ZZAC isomers) and 3,13-ODDOH (EZOH and ZZOH isomers) baits in Panama. Parenthetic values are the numbers of males captured with the given bait (x) at sites HB, CC, and CO, respectively. (b) Corrected values for attraction of species HB20. Parenthetic values indicate the expected range of response of males along the ZZAC:EZOH gradient. See text for details.

than in Wisconsin (Table 7). It appears that tropical coexistence in the present case is not achieved through adaptation to higher levels of overlap. A caveat regarding this interpretation must be indicated, however. Sample sizes of many sesiid species in Panama were very small (30 of 47 were below the minimal criterion of $n = 5$), and the omission of such species from analysis could bias mean overlaps among the Panamanian fauna toward lower values.

Seasonal diversity

Despite a marked increase in species richness and numbers of individuals during the dry and early wet seasons, sesiids could be collected in Panama throughout the year (Fig. 2). This presents the possibility that coexistence results from greater channel space (diversity) along the seasonal dimension: ssds in Panama

may be greater than those in Wisconsin, but due to the extended favorable season more species could be "packed" along this axis. To assess this potentiality, standardized ssds and SMS of the Panamanian and Wisconsin faunas were compared (Table 4). No significant interregional differences were detected. Evidently, the seasonal distributions of Panamanian sesiids are no different, relative to the entire "season," than those of Wisconsin species. In other words, the increased length of season in the tropics does not appear to enhance the opportunities for coexistence regarding reproductive isolation.

Chemical diversity

The significant conditions affecting coexistence in the tropical community surveyed involve channel space (diversity) along the chemical dimension(s), or chem-

TABLE 5. Chemical breadth (B_{cj}) of abundantly captured ($n \geq 5$) sesiid species which responded maximally to an isomeric blend (binary species). Values for Panamanian species are not significantly lower than for Wisconsin species ($P > .05$; Mann-Whitney U test, one tailed). See text for details.

Panama			Wisconsin†		
Species*	Isomeric blend to which species responded	B_{cj}	Species	Isomeric blend to which species responded	B_{cj}
CC6	EZAC : EZOH	.18	<i>P. pellucida</i>	EZAC : ZZAC	.28
HB4	EZAC : ZZAC	.44	<i>S. decipiens</i>	EZAC : ZZAC	.35
HB20	ZZAC : EZOH	.33	<i>S. exitiosa</i>	EZAC : ZZAC	.18
CC18	EZAC : ZZAC	.32	<i>S. viburni</i>	EZAC : ZZAC	.06
EC18	EZAC : ZZAC	.37			
CC19	ZZAC : ZZOH	.32			
HB18	EZAC : ZZAC	.32			
CC4	EZAC : ZZAC	.29			
EC4	EZAC : ZZAC	.29			
EC15	ZZAC : ZZOH	.28			
CO19	ZZAC : ZZOH	.57			
CC1	EZOH : ZZOH	.33			
CC15	ZZAC : ZZOH	.28			

* See Table 2.
† Data obtained from Greenfield and Karandinos (1979a).

TABLE 6. Seasonal overlap (O_{sjk}) between abundantly ($n \geq 5$ at a given site) captured sesiids at selected Panamanian and Wisconsin sites. The two Panamanian sites for which data are shown are those at which the greatest numbers of sesiids (both species and individuals) were collected. The Wisconsin site (AV), a Group III site, used for comparison below had been surveyed with an array of traps comparable to that used at the two Panamanian sites. NN = seasonal overlap between species j and its nearest neighbor (species k for which O_{sjk} is minimal). O_{sjk} and NN values at Panamanian sites are not significantly lower than values at the Wisconsin site ($P > .05$; Mann-Whitney U tests, one tailed). See text for details.

Panama species*								
Site CC	HB20	HB4	CC19	CC12	CC1	CC4	CC18	NN
CC6	2.38	3.05	2.66	6.12	5.72	2.08	7.40	2.08
HB20		0.15	0.61	0.91	2.07	1.52	2.06	0.15
HB4			0.54	0.94	2.24	2.24	2.38	0.15
CC19				0.07	1.05	1.96	0.86	0.07
CC12					2.29	∞	4.42	0.07
CC1						5.74	0.53	0.53
CC4							13.26	1.52
CC18								0.53
Site EC	CJ7	CC19	EC18	EC4	EC15	CO19		NN
HB4	2.85	0.53	0.28	0.03	0.42	1.67		0.03
CJ7		1.77	1.18	1.56	2.55	5.90		1.18
CC19			0.64	0.48	0.26	0.13		0.13
EC18				0.20	0.54	1.13		0.20
EC4					0.32	0.94		0.03
EC15						0.73		0.26
CO19								0.13
Wisconsin species†								
Site AV	<i>P. simulans</i>	<i>P. tabaniformis</i>	<i>A. fraxini</i>	<i>P. syringae</i>	<i>C. bassiformis</i>	<i>S. acerni</i>	<i>S. pictipes</i>	NN
<i>Paranthrene dollii</i>	1.01	0.39	1.97	0.93	2.04	0.54	0.01	0.01
<i>P. simulans</i>		1.17	5.61	0.33	5.85	0.72	0.80	0.33
<i>P. tabaniformis</i>			3.57	0.98	3.70	0.26	0.32	0.26
<i>Albuna fraxini</i>				5.28	0.01	3.64	1.67	0.01
<i>Podosesia syringae</i>					5.50	0.57	0.74	0.33
<i>Carmentia bassiformis</i>						3.77	1.72	0.01
<i>Synanthedon acerni</i>							0.45	0.26
<i>S. pictipes</i>								0.01

* See Table 2.
† Data obtained from Greenfield (1978).

ical dimensionality. Six of 15 (40%) Wisconsin sesiids ($n \geq 5$) are binary species, whereas 13 of 17 (76%) Panamanian species ($n \geq 5$) are binary. If all species in both regions are included in the comparison, 7 of 21 Wisconsin species are binary (Greenfield 1978) as opposed to 42 of 47 Panamanian species (M. D. Greenfield, *personal observation*). In both cases, a significantly higher proportion of species in Panama are binary ($P < .05$; Fisher's exact test, one-tailed).

A more meaningful difference in chemical dimensionality is evident if the distributions of species along the six gradients of ratios of isomeric blends are examined (Fig. 4). In Wisconsin, species appear to "occupy" (exhibit maximal response to) 8 of the 12 chemical categories tested. Panamanian species ($n \geq 3$), however, occupy 12 of the 22 categories tested, and if all species are included, 20 categories are occupied. To compare Wisconsin and Panamanian sesiids, I computed the probability of 4 (or more) categories remaining unoccupied when 21 species are randomly assigned to 12 categories (Wisconsin) and the probability

of 2 (or more) categories remaining unoccupied when 47 species are randomly assigned to 22 categories (Panama). For Wisconsin, P (four empty categories) = .05 and P (four or more empty categories) = .06, whereas for Panama, P (two empty categories) = .08 and P (two or more empty categories) = .82. (Note also that P [two or fewer empty categories] = .26.) These probabilities were calculated as:

$$P(m \text{ empty categories})$$
$$= \binom{n}{m} \sum_{v=0}^{n-m} (-1)^v \binom{n-m}{v} \left(1 - \frac{m+v}{n}\right)^r,$$

and $P(m \text{ or more empty categories})$
$$= \binom{n}{m} \sum_{v=0}^{n-m} (-1)^v \binom{n-m}{v} \left(1 - \frac{m+v}{n}\right)^r \left(\frac{m}{m+v}\right),$$

where n = number of categories, and r = number of species (Feller 1970:60, 102). The values given above reveal that the situation in Wisconsin (P [four or more empty categories]) is unlikely to have arisen by chance

TABLE 7. Chemical overlap (O_{cjk}) between abundantly ($n \geq 5$) captured sesiids in Panama and Wisconsin. The two blends for which O_{cjk} is computed among Panamanian species were those attractive to five or more species. O_{cjk} values are confined to species pairs using the same blend gradient. NN = Chemical overlap between species j and its nearest neighbor (species k for which O_{cjk} is maximal). For comparative purposes, O_{cjk} values are only considered when both species j and k occur at a given site. Thus, O_{cjk} values from 4, 18, and 13 species pairs at Panamanian sites HB, CC, and EC, respectively, are compared with values from 36 species pairs at Wisconsin site MN. O_{cjk} and NN values at Panamanian sites are not significantly higher than values from Wisconsin ($P > .05$; Mann-Whitney U tests, one tailed). See text for details.

EZAC : ZZAC blend	Panama species*									NN†
	CC18	CJ7	PR7	EC18	HB18	CC4	EC4	CC12	CJ10	
abc HB4	0.0	0.0	0.0	.01	0.0	.66	.66	.33	.01	.66
b CC18		0.0	0.0	.78	.79	0.0	0.0	0.0	.11	.79
c CJ7			.77	0.0	0.0	0.0	0.0	0.0	.48	.48
a PR7				0.0	0.0	0.0	0.0	0.0	.48	0.0
bc EC18					.78	0.0	0.0	.01	.13	.78
ab HB18						0.0	0.0	0.0	.11	.79
b CC4							.76	0.0	0.0	.66
c EC4								0.0	0.0	.66
b CC12									.06	.33
c CJ10										.48
ZZAC : ZZOH blend	CC12	EC15	CC15	CO19						NN†
abc CC19	0.0	.04	.04	.82						.82
ab CC12		0.0	0.0	0.0						0.0
c EC15			.70	.04						.04
b CC15				.25						.04
c CO19										.82
Wisconsin species‡										
EZAC : ZZAC blend	<i>P. pel- lucida</i>	<i>P. syringae</i>	<i>C. bassi- formis</i>	<i>S. decipiens</i>	<i>S. exitiosa</i>	<i>S. pictipes</i>	<i>S. scitula</i>	<i>S. viburni</i>	<i>NN</i>	
<i>Paranthrene simulans</i>	.07	.34	.32	.04	.49	.01	.32	.01	.49	
<i>P. pellucida</i>		.03	.01	.52	.01	.06	.01	.19	.52	
<i>Podosesia syringae</i>			.55	.02	.16	0.0	.55	0.0	.55	
<i>Carmenta bassiformis</i>				.01	.15	0.0	.55	0.0	.55	
<i>Synanthedon decipiens</i>					.01	.01	.01	.37	.52	
<i>S. exitiosa</i>						0.0	.15	0.0	.49	
<i>S. pictipes</i>							0.0	.01	.06	
<i>S. scitula</i>								0.0	.55	
<i>S. viburni</i>									.37	

* See Table 2. *a* = Found at site HB; *b* = found at site CC; *c* = found at site EC.
† Species j and k for which NN is computed must coexist at one or more sites.
‡ Data obtained from Greenfield and Karandinos (1979a). All nine species coexist at site MN.

and that the distribution of species' channels among chemical categories probably differs between the two regions. A source of potential bias in this comparison is that some species may actually utilize blends of three or more isomers as pheromones, some of which might additionally be compounds not tested, yet will respond to the blends presented in the study. However, this possibility is unlikely to distort the basic difference reported above: a "trinary species" should be more likely to respond to a bait containing two of three, rather than one of three, of its pheromone's components (Carde et al. 1977). Consequently, I reach the tentative conclusion that reproductive isolation among Panamanian sesiids is primarily acquired through greater available channel space. Considered from another viewpoint, Pianka's (1974) "greater exploitation of available space" may represent a more accurate interpretation. Assuming that the isomer(s) attracting male sesiids correspond with the sex pheromones of conspecific females, there are no a priori reasons for believing that the various isomeric blends existing only among Panamanian species could not have evolved in the Wisconsin fauna. This lack of evolution of a diversity of blends (the presence of unoccupied chemical categories) by Wisconsin sesiids may be due to the smaller number of species.

Although preliminary, this comparative study supports Ricklefs' (1979) contention that available (niche) space is greater in tropical (diverse) communities. Several explanations for this finding in the present study can be proposed. To understand the absence of decreased seasonal breadths in communities with increased species richness and potentially greater interspecific interference, it should be realized that phenology may be influenced primarily by climate and host plant conditions; i.e., the adults of Panamanian

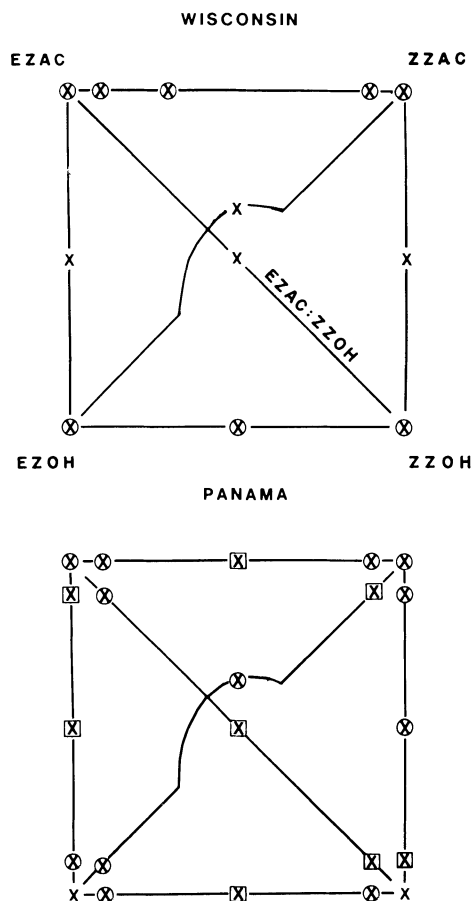


FIG. 4. Chemical diversity of sex pheromones of sesiids in Panama and Wisconsin. X's correspond with the baits tested. Circles indicate that one or more sesiid species ($n \geq 3$) are maximally attracted to the given bait (assumed utilizing it as a sex pheromone). Squares indicate that one or more sesiid species ($n < 3$) are maximally attracted to the given bait (assumed utilizing it as a sex pheromone).

sesiids may emerge and mate provided that temperature is favorable and host plant conditions suitable for oviposition exist, regardless of the presence of other sesiid species. The similarity of chemical breadths in both regions may reflect the range of response, exhibited by a male sesiid, to ratios of an isomeric blend that is most conducive to efficient mate seeking. However, the diversity of chemicals (blends and ratios thereof) that apparently serve as sex pheromones of Panamanian sesiids could indicate a different type of lability along the chemical dimension, over evolutionary time, of the communication channel. While chemical breadth may be fixed by behavioral factors as noted above, the actual chemical(s) (category) utilized for sexual communication may often shift. This lability may manifest itself in the evolution of novel pheromonal blends and ratios in a diversifying community,

a point first alluded to by Roelofs and Cardé (1974), rather than an increasing specificity in response (narrower chemical breadth, the finer subdivision of previously utilized blends). Consequently, chemical overlap values are not higher in the more diverse community, despite the approximate equivalence of chemical breadths in both regions. As such, future research on this topic may reveal the relationship(s) between phylogeny and pheromonal chemistry in the Lepidoptera, a question that has been asked (Roelofs and Comeau 1969, Tamaki 1977, 1979), but which remains unexplored.

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