BIOLOGY OF THE SCOLYTIDAE AND PLATYPODIDAE (COLEOPTERA) IN A TROPICAL DECIDUOUS FOREST AT CHAMELA, JALISCO, MEXICO

THOMAS H. ATKINSON
Instituto de Biologia
Universidad Nacional Autónoma de México
Apdo. 21 San Patricio 48980,
Jalisco, Mexico
and
ARMANDO EQUIHUA
Centro de Entomología y Acarología
Colegio de Postgraduados
56230 Chapingo, Mexico, Mexico

ABSTRACT

The feeding habits, degree of host specificity, and mating systems were examined for 96 species of Scolytidae and Platypodidae in a tropical deciduous forest at Chamela, Mexico. The dominant feeding habit was phloeophagy (59.4%), followed by xylomycetophagy (13.5%), myelophagy (13.5%), and xylophagy (12.5%). Most phloeophagous species were monophagous (limited to one plant genus); the other three groups were largely polyphagous. The mating systems found in order of importance were monogyny (40%), harem (heterosanguineous) polygyny (20.2%), inbred (consanguineous) polygyny (19.1%), and bigyny (18.1%). Monogynous species were mostly phloeophagous, to a lesser extent xylomycetophagous. Phloeophagy and xylophagy were equally represented among bigynous species. Harem polygynous species were almost exclusively phloeophagous while inbred polygynous species were mostly myelophagous or xylomycetophagous. All inbred polygynous species were polyphagous. The overall biological patterns of these beetles differed from those reported for Scolytidae and Platypodidae of temperate or tropical regions.

RESUMEN

Los hábitos alimenticios, grado de especificidad respeto al hospedero y sistemas de apareamiento se examinaron en 96 especies de Scolytidae y Platypodidae en un bosque tropical caducifolia en Chamela, México. El hábito alimenticio dominante era fleofagía (59.4%) seguido por xilomicetofagía (13.5%), mielofagía (13.5%) y xilofagía (12.5%). La mayoría de las especies fleófagas eran monófagas (limitadas a un género de plantas); los otros 3 grupos eran polífagos. Los sistemas de apareamiento encontrados en orden de importancia eran monoginia (40%), poliginia de harém (heterosanguinea) (20.2%), poliginia endógama (consanguinea) (19.1%), y biginia (18.1%). Especies monoginas eran principalmente fleófagas, o xilomicetófagas en menor grado. Floeofagia y xilofagia estaban igualmente representadas entre especies biginas. Especies poliginas de harém eran casi exclusivamente fleófagas; especies poliginas endógamas eran principalmente mielófagas o xilomicetófagas. Todas las especies poliginas endógamas eran polífagas. Los patrones globales de la biología de estos coleópteros diferieron de los reportados para Scolytidae y Platypodidae de otras regiones templadas o tropicales.

The Scolytidae and Platypodidae form a compact group, both taxonomically and ecologically. Most are borers of the woody tissues of shrubs, vines, and trees. The common names "bark beetles" and "ambrosia beetles" refer to the most common feeding habits found in the group; i.e. consuming phloem (inner bark) (phloeophagy) and ectosymbiotic fungi that grow in their galleries (xylomycetophagy), respectively. Other habits include the consumption of wood (xylophagy), pith in twigs and branches (myelophagy), herbaceous plants (herbiphagy) and fruits or seeds (spermatophagy) (Wood, 1982). Generally, feeding habit is characteristic of a given species although there is some overlap of feeding guilds.

Reproductive biology in the Scolytidae and Platypodidae has recently been reviewed by Kirkendall (1983). Mating systems of outbreeding species are monogyny or harem polygyny (heterosanguineous polygamy of Wood (1982)). Depending on the species either males or females initiate gallery construction in monogynous species, while males initiate attack in polygynous species. Bigyny is a special case of polygyny, in which a male initiates attacks and is associated with only two females. Another important mating system is inbred polygyny (spanandry of Beaver (1977, 1979); consanguineous polygamy of Wood (1982)) in which females mate with their siblings prior to emergence and then construct new galleries alone. In this last case, males are few in number, reduced in size and are flightless.

In a comparison of 2 tropical and 2 temperate areas Beaver (1979) reported that the ambrosial habit was more common in the humid tropics and that the overall degree of host specificity was lower (*i.e.*, more polyphagous) there. However, 3 of the 4 areas compared were large and ecologically heterogeneous (France, California, West Malaysia). The practice of inbred polygyny is more prevalent in tropical areas and is related to low host specificity (Browne 1961, Beaver 1977, Wood 1982).

We present here an analysis of the host tissues consumed, degree of host specificity, and mating systems for the Scolytidae and Platypodidae in tropical deciduous forest on the Pacific Coast of Mexico. Preliminary results were presented by Equihua et al. (1984). Our current analysis is based on our recent, more complete annotated checklist of the 96 species of Scolytidae and Platypodidae in the region (Equihua and Atkinson, in press).

Methods

The Estación de Biología Chamela is a biological reserve and field station of the National University of Mexico on the coast of Jalisco, Mexico (19°30′ N, 105°03′ W). The station covers 1600 ha, mostly below 150 m above sea level and is 2 km from the coast at its closest point. The mean annual temperature is 24.9°C and the 10 year average rainfall is 748 mm, most of which (80%) falls within the 4-month period from July through October (S. H. Bullock, Estación de Biología Chamela, personal communication). The vegetation of the station is mostly tropical deciduous forest with some tropical subdeciduous forest along the courses of the larger drainages (forest types from Rzedowski, 1978). Estuarine and riparian communities are found nearby. Despite the low rainfall and its strong seasonality a diverse flora occurs in this forest type, both in terms of numbers of species and variety of different life forms (Rzedowski 1978, Lott 1985). More than 750 species of vascular plants are known from the station (Lott 1985), of which approximately 60% are woody (Lott, personal communication).

We observed feeding habits (type of tissue consumed), mating systems, and degree of host specificity for most of the Scolytidae and Platypodidae at the station and nearby areas (within 5 km) from early 1982 until mid 1985. Feeding habits were inferred from observations on the location of adult and larval galleries. Degree of host specificity was

assigned based on our observations in the area, subjective judgment, and a critical review of the literature; doubtful cases were not included. We consider species that utilize host plants of the same genus as monophagous; those which utilize hosts within the same family or occasionally from related families as oligophagous; those that utilize several to many unrelated hosts are classified as polyphagous. Mating systems were inferred from the number and sex of adults constructing galleries and gallery architecture.

Results and Discussion

Feeding Habits

Phloeophagy is the dominant feeding habit; xylomycetophagy, xylophagy, and myelophagy are of approximately equal importance (Table 1). Only one spermatophagous species and no herbiphagous species were found. In the 2 temperate areas compared by Beaver (1979) phloeophagy was the dominant habit (more than 80%), followed by xylomycetophagy; in his two humid tropical areas xylomycetophagy predominated (57% in Fiji, 76% in West Malaysia) while phloeophagy was a distant second (30.3% and 11.6%, respectively). In the same study none of the other four feeding guilds included more than 10% of the total species in any locality. The relatively high importance of xylophagy (12.5%) and myelophagy (13.5%) in the Chamela fauna is unprecedented. The dominance of phloeophagy at Chamela is more similar to the pattern characteristic of temperate areas than to that of humid tropical ones. The relatively low importance of xylomycetophagous species at Chamela (13.5%) compared with that in humid tropical areas (Beaver 1979) may be related to the long (8 months) dry season, during which moisture may limit growth of ambrosial fungi in wood. In the Chamela area, ambrosia beetles were primarily limited to the shadier, more humid watercourses, particularly during the dry season, lending credence to the above hypothesis. In addition the relatively large number of xylophagous species, mostly Micracini, may partly exclude ambrosia beetles by competition for wood. Fungi are apparently present in the wood surrounding gallery systems of most (all?) xylophagous Scolytidae and Platypodidae and stain and/or alter the texture of the wood (Wood 1982, Atkinson, personal observations). Since xylophagous Scolytidae and Platypodidae directly consume xylem along with any included fungal hyphae they may be less limited by low atmospheric moisture than xylomycetophagous species that require an abundant growth of ambrosial fungi on their gallery walls.

Host Specificity

Monophagous species (50%) were slightly more numerous than polyphagous species (41%) in the Chamela fauna (Table 1). Eighteen species were excluded from the analysis because their degree of host specificity was not known; most belonged to the genera *Pseudothysanoes*, *Araptus*, and *Pityophthorus*. Based on our experience with other species of these genera, most are expected to be monophagous. Oligophagy is by far the least common of the 3 host-specificity categories, suggesting that it is the least successful adaptive strategy in tropical deciduous forest. The relative importance of the different host specificity categories at Chamela more nearly resembles temperate (57% in France, 70% in California restricted to single genus or species of host) than humid tropical (14% in Fiji, 4% in Malaysia) patterns (Beaver 1977, 1979).

Apparently the type and condition of host tissue consumed influences the degree of host specificity (Table 1). Although 15 combinations were possible (3 degrees of host specificity × 5 feeding habits), only 3 were well represented: phloeophagous

TABLE 1. CROSS-TABULATION OF FEEDING HABITS AND DEGREE OF HOST SPECIFICITY FOR 94 SPECIES OF SCOLYTIDAE AND PLATYPODIDAE IN A TROPICAL DECIDUOUS FOREST AT CHAMELA, MEXICO.

Feeding Habit	Degree of Host Specificity[a] (No. of spp.)				Total spp.	
	Monophagy	Oligophagy	Polyphagy	Unknown	No.	%
Phloeophagy	34	5	4	14	57	59.4
Xylomycetophagy	—	1	12	—	13	13.5
Myelophagy	2	—	11	—	13	13.5
Xylophagy	3	—	5	4	12	12.5
Spermatophagy	—	1	—	—	1	1.0
Total spp. No.	39	7	32	18	96	
% [b]	50.0	9.0	41.0	—[c]		

[a]Monophagy = restriction to one plant genus; Oligophagy = restriction to one plant family; Polyphagy = use of hosts from 2 or more unrelated plant families.
[b]Values based on the 78 species with known host specificity.
[c]18.8% of all 96 species.

monophages, xylomycetophagous polyphages, and myelophagous polyphages (35.4%, 12.5%, and 11.5% of all 96 species, respectively). Beaver (1977, 1979) reported that ambrosia beetles are basically polyphagous in both temperate and humid tropical areas, a conclusion supported here. He attributed decreased host specificity in xylomycetophagous species to several factors, of which the most important was that these feed on fungi rather than directly on host tissues. Perhaps more important is the association between utilization of dead tissues and polyphagy. Most ambrosia beetles breed in heartwood which consists of dead cells. A relatively high percentage of the myelophages (*Hypothenemus, Cryptocarenus*) and xylophages (*Hylocurus, Thysanoes*) at Chamela are also polyphagous. The species of these genera at Chamela breed in obviously dead hosts. Three of the 4 polyphagous phloeophages (*Hypothenemus*) are also found in dead, dry material.

The high degree of host specificity among the phloeophages probably reflects the fact that they usually breed in living or recently killed hosts which produce resin or latex (Table 2). The strong association of host-specific phloeophages with this type of defense system suggests that latex/resin defenses are effective against generalist phloeophages and have been a selective factor leading to host specialization (see Cates and Alexander 1982). The relative scarcity of host-specific Scolytidae in plants which do not produce latex or resin may indicate that they are at a competitive disadvantage with respect to generalist species or to other organisms (Cerambycidae, Buprestidae, Bostrichidae) in those hosts.

Although relatively few plants at Chamela are associated with host-specific Scolytidae and Platypodidae, all woody plants which we observed were subject to attack by one or more polyphagous species belonging to different feeding guilds. Apparently the presence or absence of a given species or guild is determined mostly by physical characteristics of the host plant and microhabitat.

MATING SYSTEMS

Monogyny is the most prevalent mating system in the Chamela fauna; bigyny, harem polygyny, and inbred polygyny are of similar rank (Table 3). The 2 species with unknown

TABLE 2. HOST PLANTS OF THE MONOPHAGOUS AND OLIGOPHAGOUS SCOLYTIDAE AND PLATYPODIDAE AT CHAMELA, MEXICO. (R = RESIN PRESENT, L = LATEX PRESENT, NC = NO CONGENERIC PLANTS IN CHAMELA AREA[a], PH = PHLOEOPHAGOUS, XM = XYLOMYECETOPHAGOUS, X = XYLOPHAGOUS, M = MYELOPHAGOUS, S = SPERMATOPHAGOUS).

Plant Family	Plant Species	Insect Species
Anacardiaceae	*Astronium graveolens* (R,NC)	*Pityophthorus indefessus* (ph)
	Mangifera indica (R,NC)[b]	*Hypocryphalus mangiferae* (ph)
	Spondias purpurea (R,NC)	*Pityophthorus nanus* (ph)
		Dendroterus luteolus (ph)
Apocynaceae	*Plumeria rubra* (L,NC)	*Scolytodes plumeriacolens* (ph)
		Scolytodes plumeriae (ph)
	Thevetia ovata (L,NC)	*Pityophthorus costabilis* (ph)
		Pityophthorus costatulus (ph)
Asclepiadaceae	*Sarcostemma clausum* (L,NC)	*Araptus delicatus* (m)
	several genera, fruits (l)	*Araptus fossifrons* (s)
Burseraceae	*Bursera arborea* (R)	*Dendroterus sallaei* (ph)
	Bursera instabilis (R)	*Phloeoterus burserae* (ph)
		Dendoterus luteolus (ph)
Cactaceae	*Stenocereus chrysocarpus* (R)	*Cactopinus atkinsoni* (ph)
	Stenocereus standleyi (R)	*Cactopinus setosus* (ph)
	Acanthocereus occidentalis (R,NC)	*Cactopinus setosus* (ph)
Combretaceae	*Conocarpus erecta* (NC)	*Scolytopsis puncticollis* (ph)
	Laguncularia racemosa (NC)	*Scolytopsis puncticollis* (ph)
Convolvulaceae	*Ipomoea wolcottiana* (L)	*Scolytogenes rusticus* (ph)
Euphorbiaceae	*Celaenodendron mexicanum* (L,NC)	*Pseudothysanoes thomasi* (ph)
	Croton spp. (L)	*Chramesus exul* (ph)
	Euphorbia colletioides (L)	*Araptus* sp.4 (m)
	Hippomane mancinella (L,NC)	*Cnemonyx splendens* (ph)
	Hura polyandra (L,NC)	*Cnemonyx equihuai* (ph)
Julianaceae	*Amphipterygium adstringens* (R,NC)	*Pityophthorus ingens* (ph)
Leguminosae	*Acacia* spp. (R)	*Hylocurus scitulus* (x)
	Cynometra oaxacana (NC)	*Pseudochramesus* sp. (ph)
	Lonchocarpus spp. (R)	*Chramesus vitiosus* (ph)
	several genera[c]	*Araptus* sp.1 (ph)
		Pseudothysanoes squameus (ph)
		Chaetophioeus minimum (ph)
		Chramesus securus (x)
		Platypus excisus (sm)
		Scolytus propinquus (ph)
Malpighiaceae	*Heteropterys laurifolia*	*Scolytus cristatus* (ph)
Moraceae	*Brosimum alicastrum* (L,NC)	*Phloeotribus setulosus* (ph)
		Pycnarthrum amersum (ph)
	Chlorophora tinctoria (L,NC)	*Pseudothysanoes spinatus*
	Ficus spp. (L)	*Araptus consobrinus* (ph)
		Gymnochilus reitteri (ph)
		Pycnarthrum furnerium (ph)
		P. hispidum (ph)
		P. reticulatum (ph)
		Scolytodes amoenus (ph)
		S. tenuis (ph)

(Cont. next page)

TABLE 2. HOST PLANTS OF THE MONOPHAGOUS AND OLIGOPHAGOUS SCOLYTIDAE AND PLATYPODIDAE AT CHAMELA, MEXICO. (R = RESIN PRESENT, L = LATEX PRESENT, NC = NO CONGENERIC PLANTS IN CHAMELA AREA[a], PH = PHLOEOPHAGOUS, XM = XYLOMYECETOPHAGOUS, X = XYLOPHAGOUS, M = MYELOPHAGOUS, S = SPERMATOPHAGOUS).

Plant Family	Plant Species	Insect Species
Nyctaginaceae	*Guapira* sp. (NC)	*Dendrosinus mexicanus* (x)
Ulmaceae	*Celtis iguaneus*	*Chramesus subopacus* (ph)
		Phloeotribus opimus (ph)
	Phyllostylon brasilense (NC)	*Phloeotribus* (sp. (ph)

[a]Based on Lott (1985, personal communication).
[b]Plant and host-specific insect introduced.
[c]Genera not the same for different beetles.

mating habits are species of *Pseudothysanoes*. All species of this genus with known mating habits are bigynous (Wood 1982, Atkinson and Equihua 1985a,b, Equihua and Atkinson, in press). Little comparative information is available on the relative importance of the various mating systems in different parts of the world except that inbred polygyny is the dominant habit in the humid tropics. (Browne 1961, Beaver 1977, 1979, Wood 1982). In this context, the relatively low ranking of inbred polygyny in the Chamela fauna is noteworthy. The high incidence of bigyny (18.1%) is unusual. If bigyny were considered a special case of harem polygyny then combining these 2 categories would make harem polygyny about equal in rank to monogyny in the Chamela fauna.

Mating systems were related to feeding habits and degree of host specificity. Monogyny was the most frequent mating system exhibited by phloeophagous insects, followed by harem polygyny and bigyny (Table 3). This mating system was also important among the xylomycetophagous species. Inbred polygyny was most common among the myelophages and xylomycetophages. Most xylophages were bigynous. All species exhibiting inbred polygyny were also polyphagous while species with harem polygyny were monophagous (8 spp.) or oligophagous (1 sp.) (Table 4). The largest group of bigynous species of known specificity were polyphagous. Monogynous species were mostly monophagous although an appreciable number were polyphagous.

Harem polygynous species at Chamela were basically phloeophagous and monophagous. This is consistent with the hypothesis of Kirkendall (1983) regarding the origin of this mating system, which has evolved at least 7 times independently in the Scolytidae. Kirkendall (1983) proposed that harem polygyny arose from monogyny in situations in which resource quality varied widely. This made it "profitable" for males to find and defend patches of high quality tissue and attract females instead of searching for females directly. Of all the tissues consumed by Scolytidae in living woody plants, phloeom (including the cambium), is initially the highest in nutrient value, and would change most in quality after the death of the plant.

Bigynous species were either phloeophagous or xylophagous (Table 3). The former were mostly monophagous while the latter were mostly polyphagous. In all but one case (*Scolytus propinguus*), these insects belong to the tribe Micracini. Most Micracini with known mating habits are bigynous except *Micracisella* spp. which are monogynous (Wood 1982, Kirkendall 1983, Atkinson and Equihua 1985a, b).

Species exhibiting inbred polygyny were associated with several feeding habits (Table 3) but all were polyphagous (Table 4). The Chamela species belong to two unre-

TABLE 3. CROSS-TABULATION OF FEEDING HABITS AND MATING SYSTEMS FOR 64 SPECIES OF SCOLYTIDAE AND PLATYPODIDAE IN A TROPICAL DECIDUOUS FOREST AT CHAMELA, MEXICO.

Feeding Habit	Mating System (No. of spp.)					Total spp.	
	Monogyny	Bygyny	Polygyny	Inbred Polygyny	Unknown	No.	%
Phloeophagy	27	9	18	3	—	57	59.4
Xylomycetophagy	8	—	—	5	—	13	13.5
Myelophagy	3	—	—	10	—	13	13.5
Xylophagy	2	8	—	—	2	12	12.5
Spermatophagy	—	—	1	—	—	1	1.0
Total spp. No.	40	17	19	18	2	96	
%[a]	42.6	18.1	20.2	19.1	—[b]		

[a]Values based on the 94 species with known mating systems.
[b]2.2% of all 96 species.

TABLE 4. CROSS-TABULATION OF DEGREE OF HOST SPECIFICITY AND MATING SYSTEMS FOR 96 SPECIES OF SCOLYTIDAE AND PLATYPODIDAE IN A TROPICAL DECIDUOUS FOREST AT CHAMELA, JALISCO.

Degree Specificity	Mating System					Total spp.	
	Monogyny	Bygyny	Polygyny	Inbred Polygyny	Unknown	No.	%[a]
Monophagy	28	2	9	—	—	39	50.0
Oligophagy	3	2	2	—	—	7	9.0
Polyphagy	8	6	—	18	—	32	41.0
Unknown	1	7	8	—	2	18	
Total spp. No.	40	17	19	18	2	96	
%[a]	42.5	18.1	20.2	19.1			

[a]Values based on the 78 (host specificity) or 94 (mating systems) species for which information is available.

lated tribes, the Cryphalini (*Hypothenemus*, *Cryptocarenus*) and the Xyleborini (all species). This strong correlation of inbred polygyny and polyphagy agrees strongly with the results of Beaver (1977) although the species he examined were mostly xylomycetophagous (Xyleborini) while most at Chamela were myelophagous (Cryphalini). No completely satisfactory explanation has been advanced for the origin of inbred polygyny, although it has evolved at least 5 times in the Scolytidae. Comparative studies of biology of species with comparable feeding habits but different mating systems would allow a better understanding of the relationship between resources and reproductive biology of the Scolytidae and Platypodidae.

ACKNOWLEDGMENT

Field work for this study was supported in part by the Centro de Entomología y Acarología, Colegio de Postgraduados, Chapingo, Mexico. Emily Lott and Stephen Bullock critically reviewed the manuscript. Special thanks are due R. A. Haack for his editorial comments.

References Cited

ATKINSON, T. H., AND A. EQUIHUA M. 1985a. Listado comentado de los Scolytidae y Platypodidae (Coleoptera) del Valle de México. Folia Ent. Mex. 65: 63-108.

———, AND ———. 1985b. Notes on Biology and Distribution of Mexican and Central American Scolytidae. I. Hylesininae, Scolytinae except Cryphalini and Corthylini. Coleopterists Bull. 39: 227-238.

BEAVER, R. A. 1977. Bark and ambrosia beetles in tropical forests. Pages 133-147 *in* Proc. Symp. on Forest Pests & Diseases in Southeast Asia, Bogor, Indonesia, April, 1976. BIOTROP. Spec. Publ. 2.

———. 1979. Host specificity of temperate and tropical animals. Nature 281: 139-141.

BROWNE, F. G. 1961. The biology of Malayan Scolytidae and Platypodidae. Malayan For. Rec. 22: 1-225.

CATES, R. G., AND H. ALEXANDER. 1982. Host resistance and susceptibility. Pages 212-263 *in* J. B. Mitton & K. Sturgeon, eds., Bark Beetles of North American Conifers. Univ. Texas Press, Austin, Texas.

EQUIHUA, M. A., T. H. ATKINSON, AND E. J. LOTT. 1984. Scolytidae y Platypodidae (Coleoptera) de la Estación de Biología Chamela, Jalisco. Agrociéncia 57: 179-193.

———, AND ———. 1986. Annotated checklist of the bark and ambrosia beetles (Coleoptera: Scolytidae and Platypodidae) associated with tropical deciduous forest in Chamela, Jalisco, Mexico. Florida Ent. (in press).

KIRKENDALL, L. R. 1983. The evolution of mating systems in bark and ambrosia beetles (Coleoptera: Scolytidae and Platypodidae). Zool. J. Linnean Soc. 77: 293-352.

LOTT, E. J. 1985. Listado florístico de la Estación de Biología Chamela. Instituto de Biología, Univ. Nacional Autónoma de México, Mexico City. (in press).

RZEDOWSKI, J. 1978. Vegetación de México. Editorial Limusa, Mexico City. 432 pp.

WOOD, S. L. 1982. The bark and ambrosia beetles (Coleoptera: Scolytidae) of North and Central America, a taxonomic monograph. Great Basin Natur. Mem. 6, 1359 pp.