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THE INSECT FAUNA OF MISTLETOE (*PHORADENDRON TOMENTOSUM*, LORANTHACEAE) IN SOUTHERN TEXAS

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ABSTRACT.—The insect fauna of American mistletoe (*Phoradendron tomentosum* Engelmann) growing on mesquite (*Prosopis glandulosa* Torrey) in southern Texas is described. (*P. tomentosum* supports at least twelve species of host-restricted insect herbivores, including four or five lepidopterans, two weevils, one coreid bug and four homopterans. Several generalist herbivores are found regularly, and ant tending of homopterans is common. The two most destructive herbivores are *Cyathissa* (*Emarginea*) *percara* Morrison (Lepidoptera: Noctuidae) and *Atlides halesus* Cramer (Lepidoptera: Lycaenidae). Both feed on leaves and younger stems. The stem feeding bug, *Leptoglossus brevirostris* Barber (Hemiptera: Coreidae) tends to be found on the same plants as *C. percara*, and the stem feeding weevil, *Smiracraulax tuberculatus* Pierce (Coleoptera: Curculionidae) tends to occur with *A. halesus*. Most of the host restricted herbivores reach peak abundance in late spring.

Some biologists (e.g., Lawton & Strong, 1981) have argued that insect herbivores are rarely resource limited and that competition plays at most a minor role in structuring insect herbivore communities. Data on phytoplagous insect communities are often limited to listing the pests of a particular plant species, and "island biogeographic" models developed by Strong (1979) and others have proven effective in explaining some of the trends obtained from these data. Species listing permits evaluation of "taxonomic resource partitioning", or radiation of related insect species onto different host species; however Gilbert and Singer (1975) suggested that insects can partition parts of the same plant species, habitat, phenology, adult resources or predators. In order to understand the dynamics of an association, information is needed on phenologies, parts of the host plant utilized, responses to host density, mutualists, predators, parasitoids, and the impact of herbivores on their food supply. *Phoradendron tomentosum* Engelmann is the only loranthaceous plant in most parts of Texas. It supports a fauna of mainly host-restricted insect herbivores, making it a good subject for studying non-taxonomic resource partitioning. This article provides a detailed description of the insect fauna of *P. tomentosum* at one site in southern Texas.

P. tomentosum is a hemiparasite on a variety of mainly deciduous trees, including elm (*Ulmus*), hackberry (*Celtis*), *Acacia*, mesquite (*Prosopis*) and occasionally oaks (*Quercus*). It is usually dioecious, though plants with both male and female inflorescences are encountered. Leaves and stems are photosynthetic. Stem diameters of 40-50 mm. are common. Fruit mature during the winter, and are fed on by several species of birds, that act as seed dispersers. Deer, as well as insects, are known to feed on *P. tomentosum*.

STUDY AREA.—The Chaparral Wildlife Management Area (CWMA) near Artesia Wells, Texas was used as a study area. The CWMA is about 60 miles north of the Mexican border at Laredo,

and 10 miles west of U. S. Inter-Regional Highway #35, in Dimmit and LaSalle counties. It is owned and operated by the Texas Parks & Wildlife Department and comprises some 15,000 acres of former ranchland. Vegetation is desert grassland dominated by mesquite (*Prosopis glandulosa* Torrey) on sandy soils and *Acacia* spp. on shallower, more calcareous soil. Other common species include desert hackberry (*Celtis pallida* Torrey), prickly pear (*Opuntia lindheimeri* Engelm.), *Colubrina texensis* Gray and *Diospyros texana* Scheele. Elm and hackberry are common along creekbeds. *P. glandulosa* is the only major host of *P. tomentosum*, with a few individuals found on *Acacia farnesiana*. Whittaker, Gilbert & Connell (1979) give more information on the vegetation and history of the area.

Since 1900, several windmills have been at the CWMA. Most are surrounded by fencing, and brush inside the fence is cleared periodically. Water is pumped into a tank near the windmill. Mesquite trees near water tanks which survive the repeated clearing live longer and reach basal diameters of up to 50 cm. Most of the *P. tomentosum* is found on the large trees near the tanks. Under undisturbed conditions, *Prosopis* is usually found in dense clumps of several species, and rarely attains basal diameters of more than 20 cm.

METHODS.—375 *P. tomentosum* plants were marked in 1980 at four of the windmill sites. There were originally 75 plants at one site (Guajalote East) and 100 at each of the others. A host tree would be chosen, and "all" accessible *P. tomentosum* were marked. Both large and small host trees were used, until the number of marked mistletoe was 100. Marking was done with wire or a small nail driven into the host branch. A few more *P. tomentosum* were added in early 1981 to replace ones that had died. I recorded location (relative to the nearest tank), basal diameter and number of live mistletoe present (in 1980) for each host tree. I recorded host branch diameter, height and vertical and horizontal angle of the host branch for each marked plant. This allowed relocation of marked plants. Basal diameter of the host proved to be correlated with density of infestation (number of mistletoe) and negatively correlated with distance from the tank: in other words, large mesquite trees with many mistletoe growing on them were found close to the tanks. (Whittaker, 1982).

Marked mistletoe were assigned a number and censused once a month for insects between 13 March 1981 and 10 October 1981. Limited observations indicated that there were few insects present in other months. Whenever an insect was observed on a marked plant, I recorded the plant number, the species of the insect, the stage of development (egg, larval instar, pupa, adult), the location on the plant (leaf, stem or inflorescence) and the size class of the leaf or stem. Leaves and stems were divided into four size categories, with type 1 the largest. Size categories for stems were: type 1, greater than 10 mm. diameter; type 2, 5-10 mm. diameter; type 3, 2.5-5.0 mm.; type 4, less than 2.5 mm. For leaves, the size categories were: type 1, surface area (estimated) greater than 500 $mm.^2$; type 2, 300-500 $mm.^2$; type 3, 100-300 $mm.^2$; type 4, less than 100 $mm.^2$. For sedentary herbivores, these observations are believed to accurately reflect feeding preferences. Emphasis in data collecting was on common herbivores: rare species and transients were sometimes omitted. Collections were made of all species which were encountered more than once. Lepidopteran larvae were taken back to the lab for rearing of adults or parasitoids. Presence of ants on the plant and behavioral observations such as predation were recorded. Voucher specimens were left with the Will C. Hogg Collection at the University of Texas, Austin.

RESULTS.—At least twelve species of insect herbivores depend exclusively on *Phoradondron tomentosum* for larval food (Table 1). *Tacoma feriella, Carmenta phoradendri* and *Atlides halesus* are all *Phoradendron* specialists (Tim Friedlander, pers. comm.; Howe, 1975). Members of the genus *Smiracraulax* are also restricted to *Phoradendron* (Horace Burke, pers. comm.). *Leptoglossus brevirostris* is restricted to *P. tomemtosum*, but other *Leptoglossus* species use hosts in other plant families. Host plants of *Cyathissa percara* were previously unknown. *Cyathissa percara* and *A. halesus* caterpillars would not feed on any other species which I offered them, including *Prosopis*. Weevils of the genus *Myrmex* use a variety of hosts in other geographic areas, but I found them only on *P. tomentosum*.

TABLE 1.—*Insect species encountered on* Phoradendron

Specialist Herbivores	Order:Family	Abundance, Phenology	Parts of Plant
Atlides halesus Cramer	Lepidoptera: Lycaenidae	Common, especially in spring to early summer	Leaves, non-woody stems
Cyathissa percara Morrison	Lepidoptera: Noctuidae	Extremely common, outbreaks in April, September-October	Leaves, non-woody stems, inflorescences
Tacoma feriella Hurst	Lepidoptera: Pyralidae	Scarce, summer to fall	Leaves, stems
undetermined	Lepidoptera: Geometridae	Uncommon, may feed on other plant species	mainly leaves
Carmenta phoradendri Engelhardt	Lepidoptera: Sesiidae	Scarce	woody stems
Smiracraulax tuberculatus Pierce	Coleoptera: Curculionidae	Common, especially in spring to early summer	Non-woody stems, adults rasp young leaves
Myrmex sp. (prob. *estriatus* Csy.)	Coleoptera: Curculionidae	Fairly common in April, may use other hosts	Larvae bore stems
Leptoglossus brevirostris Barber	Hemiptera: Coreidae	Very common, first instar larvae mostly emerge in April	stems, leaves
undetermined	Homoptera: Aphididae	Common, especially in spring	leaves, non-woody stems
undetermined	Homoptera: Coccidae	Very common, spring to summer	Leaves, stems
undetermined	Homoptera: Pseudococcidae	Common, especially in summer	Leaves, stems, haustoria
undetermined	Homoptera: Diaspididae	Scarce	Leaves, stems

The homopterans showed no affinity for other host plants in limited rearing experiments.

Cyathissa percara was the most destructive insect herbivore. Caterpillars fed on leaves and non-woody stems. Large outbreaks in April were observed in 1980 and 1981, with smaller outbreaks in the fall. Many plants were defoliated by *C. percara*, with only woody (greater than 4 mm. diameter) stems left standing. Defoliated plants sometimes regenerated new growth and sometime died.

Leptoglossus brevirostris is a common coreid bug which causes little apparent damage to the host plant. Eggs were laid along stems in rows of about 20 and usually hatched in April. *Leptoglassus brevirostris* fed extensively on stems as well as leaves, and they were often found feeding on plants that were recently defoliated by *Cyathissa percara*. Adults are good flyers, but seem to be fairly sedentary, as they were usually found on plants that had larvae on them earlier in the year.

Atlides halesus, the Great Purple Hairstreak, is the largest lycaenid butterfly in most of the United States (Howe, 1975). Larvae are highly cryptic on *Phoradendron tomentosum*, and have a feeding preference similar to *Cyathissa percara*. Host defoliation by *A. halesus* larvae was observed occasionally. Caterpillars were common from April to early June,

TABLE 2.—*Insect species encountered on* Phoradendron

Specialist Herbivores	Order:Family	Abundance, other food plants
Ophryastes decipiens LeConte	Coleoptera: Curculionidae	Fairly common, probably on *Prosopis*, larvae are root feeders
Aphrastus unicolor Leconte & Horne	Coleoptera: Curculionidae	Common on *P. tomentosum* in 1980 but not 1981; *Verbesina*, other plants
Amphicerus cornutus	Coleoptera: Bostrichidae	Common, bores dry stems of *Phoradendron*, *Prosopis*, possibly other species
Brochymena sp. (prob. *quadri-pustulata* Fabr., *arborae* Say	Hemiptera: Pentatomidae	Very common, feeds mainly on *Prosopis*
Vanduzea laeta Goding	Homoptera: Membracidae	Very common, also on *Prosopis, Colubrina Humboldtiana, Verbesina,* others
Metcalfa pruinosa Say	Homoptera: Flatidae	Common, also on *Prosopis*, other species
Texananus sp. (prob. *excultus* Uhler)	Homoptera: Cicadellidae	Fairly common, may be host-restricted
Pseudostermyle strigata Scudder	Orthoptera: Phasmidae	Scarce, also on *Prosopis*, other species
Paraidemona mimica Scudder	Orthoptera: Acrididae	Fairly common
Aidemona azteca Scudder	Orthoptera: Acrididae	Uncommon, feeds on many other plant species

and adults were sometimes found flying in midwinter. Ovipositing adults may place as many as 20 eggs at different points on the same plant.

Smiracraulax tuberculatus is a small (2 mm.), black anthonomine weevil. Larvae bore into non-woody stems (Burke and Hafernik, 1971) and adults rasp young leaves. It is common, especially in late spring. *Myrmex* sp. has a similar life history (I found dormant adults inside of *Phoradendron tomentosum* stems) but is larger and less common.

The pyralid moth *Tacoma feriella* feeds on both leaves and stems, sometimes girdling larger, woody stems that are left behind by *Cyathissa percara*. The sesiid moth *Carmenta phoradendri* bores older, woody stems, and pupal cases are sometimes found protruding.

Four species of host-restricted homopterans occur on *P. tomentosum*. The aphids and coccids were mainly on leaves and younger stems, while the diaspidids were on older, woody stems but restricted to a few plants. The pseudococcids were found at the bases of stems and inside of bored out stems, as well as on leaves. The four species were tended by a variety of ants. Heavy homopteran infestations cause leaves to wrinkle and lose turgor.

Common generalist herbivores are listed in Table 2. *Vanduzea laeta* was common on *Phoradendron tomentosum* as well as several other plants. It is a medium sized (5 mm.), green or brown membracid tree hopper, tended by most of the same ants that tend the aphids and scale insects. A thousand or more individuals were found on a few plants. *Metcalfa pruinosa*, a large, white solitary homopteran and *Paraidemona mimica*, a wingless acridid grasshopper, use *P. tomentosum* for food. *Amphicerus cornutus* was found

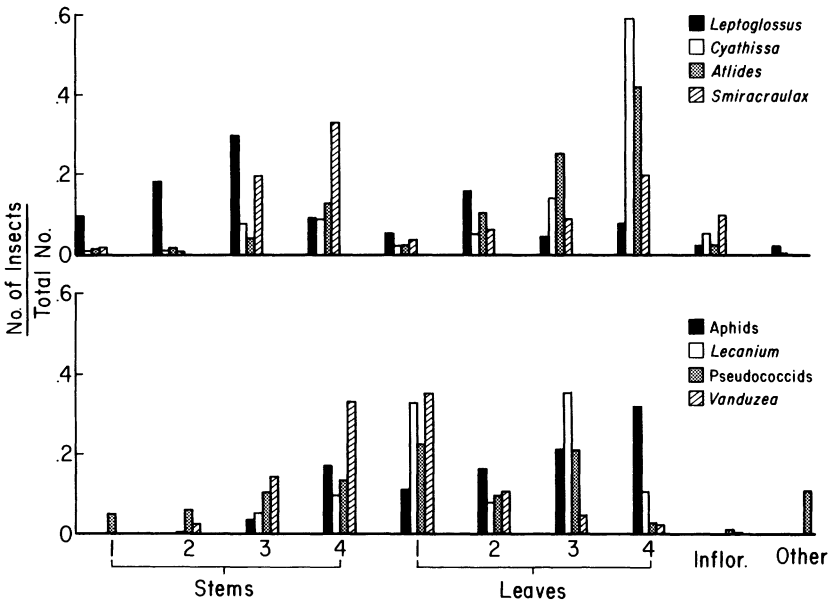

FIG. 1.—Feeding preferences of eight major *Phorandendron* herbivores.

in dead, drying tissue. Associations of some of the insects (*Ophryastes, Brochymena*) with *P. tomentosum* may be coincidental. *Largus cinctus*, an omnivorous largid bug, often oviposits on *P. tomentosum*, and early instars apparently use it for food.

Densities of most of the major herbivores peaked in April, apparently timing their reproduction to the spring growth of the host plant and not partitioning the resource phenologically. Predators, parasites, hot weather, depleted food, and accumulation of secondary chemicals in the mistletoe all offer explanations for the summer decline in herbivore populations. Eighty-two of the 375 plants (22%) marked in 1980 were dead a year later, with herbivore defoliation a contributing factor.

Figure 1 shows the proportion of total observations on different size classes of leaves, stems and inflorescences, for eight herbivore species. *Atilides halesus* and *Cyathissa percara* prefer young leaves, while *Leptoglossus brevirostris* and *Smiracraulax tuberculatus* depend more on stems. The type 3 and 4 stems used by *S. tuberculatus* were readily eaten by *A. halesus* larvae. The homopterans all have slightly different preferences. Figure 2 shows the relative positions of major herbivores on *Phoradendron tomentosum*.

Figure 3 shows the relative numbers of *Leptoglossus, Cyathissa, Atlides* and *Smiracraulax* on *Phoradendron tomentosum* growing on host trees of different diameters. Expected values are based on a uniform distribution for each species, or the same number of insects per mistletoe regardless of host (*Prosopis*) diameter. *Atilides halesus* and *Smiracraulax tuberculatus* were more common on small *Prosopis*, while *Leptoglossus brevirostris* and

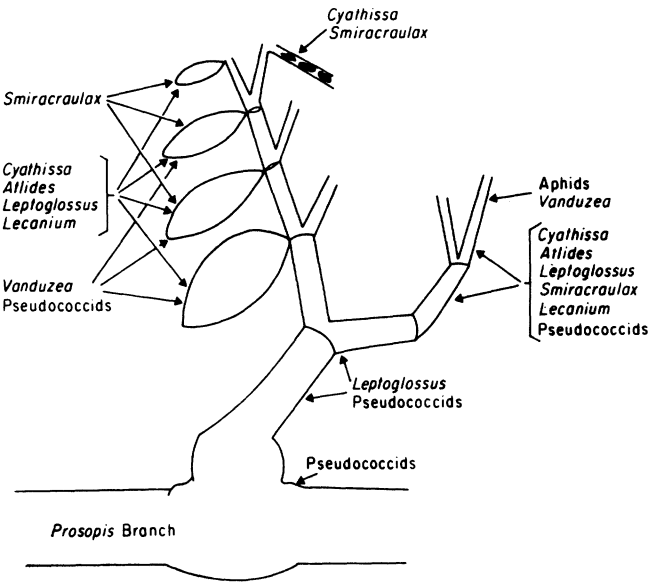

FIG. 2.—Schematic diagram of feeding preferences.

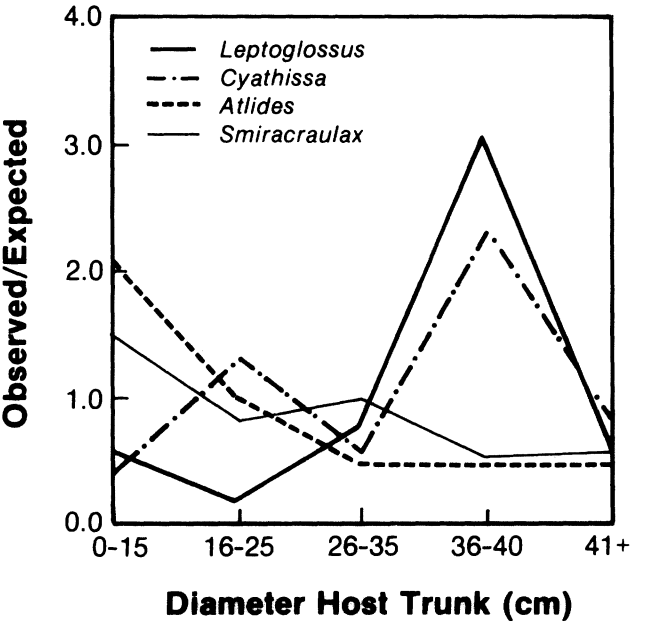

FIG. 3.—Relative abundance of *Cyathissa, Leptoglossus, Atlides*, and *Smiracraulax* in relation to mesquite trunk diameter.

Cyathissa percara were more common on large *Prosopis*. Insect abundance show similar patterns when plotted against density of mistletoe infestation and distance from the tank, with *L. brevirostris* and *C. percara* being more

common on densely infested *Prosopis* trees and close to the tanks. Size of individual mistletoe plants was negatively correlated with *Prosopis* diameter, and *A. halesus* and *S. tuberculatus* showed less preference for large mistletoe plants than did *L. brevirostris* or *C. percara*. *Leptoglossus brevirostris* and *C. percara* tended to be found on the same individual more often then expected, as did *A. halesus* and *S. tuberculatus* (Whittaker, 1982, Appendix 7). Homopterans were usually found in dense populations on a few individual host plants. More detailed data and discussion of insect distributions are presented elsewhere (Whittaker, 1982).

Table 3 lists other species which were encountered frequently on *Phoradendron tomentosum*, including predators, parasitoids and mutualists of major herbivores. *Cyathissa percara* was preyed on by hemipterans including *Largus cinctus* and the pentatomid *Podisus acutissimus*, and parasitized by *Casinaria limenitides* (Hymenoptera: Ichneumonidae). Caterpillars were attacked by ants, such as *Crematogaster laeviuscula*, that tend the homopterans. *Atilides halesus* is attacked by an unidentified hymenopteran egg parasite, by a braconid wasp (*Apanteles* sp.) that emerges from third or fourth instar larvae, and by the large chalcidoid *Metadontia amoena*, that emerges from pupae. Malicky (1970) stated that lycaenid larvae are protected by their thick integuements from ant and hemipteran attacks, and this appears to be true for *A. halesus*, since no interactions with ants or predators were observed. *Crematogaster* ants were observed attacking the coccinellid beetle *Olla v-nigrum*, that feeds on aphids. *Crematogaster* ants are beneficial to *Phoradendron tomentosum* because they attack *Cyathissa percara* larvae, but detrimental because they increase homopteran densities and use stems for nesting. Figures 4 and 5 show ecological interactions between different members of the *P. tomentosum* insect community.

Discussion.—*Phoradendron tomentosum* carries a heavy load of insect herbivores and is frequently subject to defoliation. Food appears to be one of several important limiting factors for the herbivore populations. *Cyathissa percara* larvae in particular often deplete their food source and are found wandering around the bark of the host tree. The association of leaf feeding *Cyathissa percara* with stem feeding *Leptoglossus brevirostris* and of leaf feeding *Atilides halesus* with stem feeding *Smiracrulax tuberculatus* offers some support for the importance of competition in determining community structure. Food resources of all the host restricted herbivores, however, depend on continued reproduction of *P. tomentosum*. MacArthur and Levins' (1964) widely cited argument that the number of consumers should not exceed the number of functionally independent resources is not supported by my results. Given the destructive capacity of the major herbivore species (*A. halesus* and *C. percara*), partitioning of the mistletoe biomass is not an adequate explanation for the coexistence of the other host-restricted insects. *Atilides halesus* and *C. percara* have different secondary consumers and ecological antagonists, and I suggest that the presence of independent limiting factors at higher trophic levels reduces the need for dietary character displacement. Dense populations of *P. tomento-*

TABLE 3.—*Insect species encountered on* Phoradendron

Other Species	Order:Family	Food	Uses of *Phoradendron*
Olla v-nigrum Muls.	Coleoptera: Coccinellidae	Aphids, other small homopterans	
Chrysopis sp.	Neuroptera: Chrysopidae	Aphids, other small homopterans	
Largus cinctus Herrich-Schaeffer	Hemiptera: Largidae	*Cyathissa, Prosopis* pods, other plants and insects	oviposition, possibly food
Podisus acutissimus Stal	Hemiptera: Pentatomidae	*Cyathissa, other insects*	
Phytocoris breviusculus Reuter	Hemiptera: Miridae	*Small insects*	common on *P. tomentosum*
Oecanthus niveus	Orthoptera: Gryllidae	*Aphids, other small homopterans*	
Rehnia spinosa	Orthoptera: Tettigonidae	*Insects*	
Cycloptilum squamosum Scudder	Orthoptera: Gryllidae	*unknown*	
Trypoxolon punctivertex Richards	Hymenoptera: Sphecidae	*small spiders*	pupation, possibly nesting
Apanteles sp.	Hymenoptera: Braconidae	*Atlides, Tacoma* (parasitoid)	
Metadontia amoena Say	Hymenoptera: Chalcididae	*Atlides*, other lepidopteran larvae (parasitoid)	
Casinaria limenitides Howard	Hymenoptera: Ichneumonidae	*Cyathissa* (parasitoid)	
Crematogaster sp.	Hymenoptera: Formicidae	nectar	tends homopterans, nesting
Pseudomyrmex pallida	Hymenoptera: Formicidae	nectar	
Pseudomyrmex sp. (prob. *mexicanus* Roger)	Hymenoptera: Formicidae	nectar	
Neoponera villosa Fabr.	Hymenoptera: Formicidae	nectar	
Monomorium minimum Buckley	Hymenoptera: Formicidae	nectar	Tends homopterans
Forelius foetida Buckley	Hymenoptera: Formicidae	nectar	Tends homopterans
Conomyrma insana Buckley	Hymenoptera: Formicidae	nectar	Tends homopterans
Pheidole sp.	Hymenoptera: Formicidae	nectar	Tends homopterans
Camponotus sp.	Hymenoptera: Formicidae	nectar	Tends homopterans

sum on older trees seem to favor the more sedentary herbivores (*C. percara, L. brevirostris,* aphids and scale insects). *Atilides halesus* is a much better flyer than *C. percara* and may use its flying ability to seek out relatively

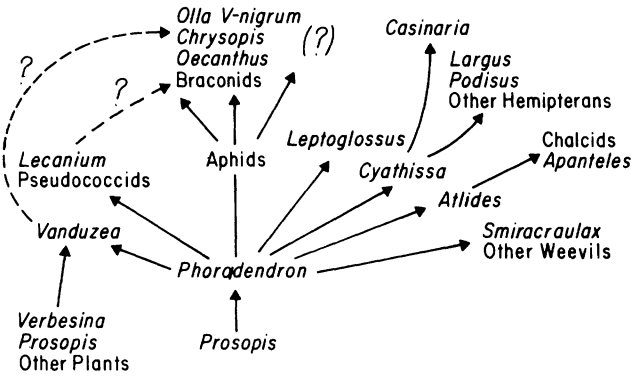

FIG. 4.—Food web showing interactions of herbivores and secondary consumers.

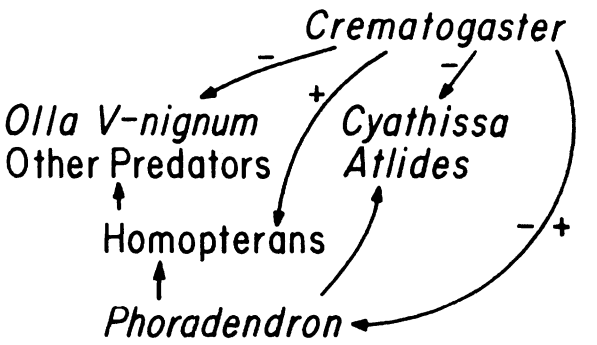

FIG. 5.—Flow diagram to illustrate the role of ants.

isolated plants, before *C. percara* eggs have had time to accumulate. The homopterans apparently escape intensive competition with *C. percara* by reproducing rapidly on a few individual hosts, and through the protection of ant mutualists. Future studies should seek understanding of natural systems in their full complexity, instead of trying to support or rebut competition as a general theory of community structure.

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LITERATURE CITED

ARNOLD, L. A. AND D. L. DRAWE. 1979. Seasonal food habits of deer in South Texas Plains. Jour. Range Manage. 32:175-178.

BURKE, H. R. AND J. E. HAFERNIK. 1971. Biology and taxonomy of the genus *Smiracraulax* Pierce. Southwest. Nat. 15:309-317.

GILBERT, L. E. AND M. C. SINGER. 1975. Butterfly ecology. Ann. Rev. Ecol. and Syst. 6:365-397.

HOWE, W. H. 1975. The butterflies of North America. Doubleday, New York, 633 pp.

LAWTON, J. H. AND D. R. STRONG. Community patterns and competition in folivorous insects. Amer. Nat. 118:317-338.

MACARTHUR, R. H. AND R. LEVINS. 1964. Competition, habitat selection and character displacement in a patchy environment. Proc. Nat. Acad. Sci. 51:1207-1210.

MALICKY, H. 1970. New aspects on the association between lycaenid larvae and ants. Jour. Lepid. Soc. 24:190-202.

STRONG, D. R. 1979. Biogeographical dynamics of insect-host plant communities. Am. Rev. Entomol. 24:89-119.

WHITTAKER, P. L. 1982. Community ecology of *Phoradendron tomentosum* in southern Texas. Ph.D. dissertation, Univ. of Texas, Austin, 122 pp.

———. Multiple coexistence of insect hebivores on herbivores on mistletoe (*Phoradendron tomentosum*). In press, Proc. Tamaulipan Biotic Province Symp., Texas Parks and Wildlife Dept., Austin.

WHITTAKER, R. H., L. E. GILBERT AND J. H. CONNELL. 1979. Analysis of two-phase pattern in a mesquite grassland, Texas. Jour. Ecol. 67:935-952.

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