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ALTITUDINAL PATTERNS IN SPECIES RICHNESS OF NEOTROPICAL TREEHOPPERS (HOMOPTERA: MEMBRACIDAE): THE ROLE OF ANTS

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Abstract.—Treehoppers are sap-feeding insects that vary widely in degrees of both sociality and ant mutualism. Based on these life histories, treehoppers may be classified as (1) species that are ant mutualists and that aggregate as individuals, (2) species exhibiting parental care that are not ant mutualists, and (3) solitary species that rarely interact with ant mutualists. We predicted the availability of ants should influence the distribution of treehopper species that depend upon ants for protection. Because ant abundance has been shown to decline with increasing altitude in tropical regions, we examined the elevational distribution of treehopper species in Colombia that are obligate ant mutualists and those treehopper species that are not. The proportion of treehopper species that are dependent upon ants for defense declined with increasing altitude. Those species having parental care, that do not rely on ants for defense, were more common at higher elevations. Solitary treehoppers, species that only occasionally interact with ants, did not show a changing relationship with altitude. Thus, mutualistic ants are not only important in the evolution of treehopper life histories but also appear to be important in determining the geographic distribution of treehoppers.

Key Words: membracids, mutualism, altitude, Colombia

Sociality in treehoppers (Homoptera: Membracidae) ranges from solitary species to those with highly developed parental care. Additionally, many species rely on ant mutualists for protection from natural enemies (Wood 1984). In return, treehoppers provide ants with a source of carbohydrates, free amino acids and amides, and water in the form of honeydew (Way 1963). Thus, treehopper sociality and ant mutualism may allow alternative defenses against predators (Wood 1982b). For example, aggregations of nymphs and young adults of many species are tended by ants (Wood 1984). In some of these species, parent females also guard eggs and early instars, but their survival is still dependent on the defense provided by ants (Wood 1977, Bristow 1983, Olmstead 1984). The size of treehopper aggregations and the volume of honeydew produced are important factors contributing to the constancy of ant attendance (McEvoy 1979, Fritz 1982, Wood 1982a, Cushman and Whitham 1989).

Other treehopper species also aggregate, but do not interact with ant mutualists. In these presocial species (species with parental care) parent females actively guard eggs and nymphs protecting them from predators (Hinton 1976, 1977, Wood 1976, 1982b, Eberhard 1986). The benefit of aggregation in these species is the effective guarding of offspring by parent females rather than the attraction of ants (Wood 1976).

Alternatively, some treehopper species are solitary throughout their life cycle, are rare, and may incur lower levels of predation simply by virtue of their crypsis. Because a relatively small volume of honeydew is produced by solitary treehoppers, ant-treehopper mutualisms are relatively uncommon in these species (Wood 1984).

Based on their level of sociality and interactions with ant mutualists, treehoppers may be classified as (1) species that are ant mutualists and that form aggregations as individuals, (2) species with parental care that are not ant mutualists, or (3) solitary species that rarely interact with ant mutualists.

In the tropics, ant mutualisms decline with increasing altitude in myrmecophilous animals (Wood 1984) and plants (Bentley 1977a, b, Koptur 1985). This pattern reflects the decline in ant abundance along an increasing elevational gradient (Janzen 1973, Janzen et al. 1976, Bentley 1977a). The cool air temperatures and high soil moisture of tropical montane regions preclude ants from exploiting these habitats (Bentley 1977a). Koptur (1985) and Bentley (1977b) have shown that nectary plants in areas of low ant activity have alternative defenses against herbivores. Thus, the plasticity of the defensive repertoire of these plants (*Inga* and *Bixa*) permits them to grow in areas where ant activity is low. In contrast, the defensive mechanisms of treehoppers are not labile within species. Consequently, treehopper species that rely solely upon ants for defense are relatively undefended in the absence of ants. Furthermore, the increased conspicuousness of individuals in aggregations formed by ant-dependent species elevates their risk of predation compared to species that do not rely upon ants. Non-attended species reduce their risk of predation in other ways. Specifically, aggregations formed by presocial species are protected by parent females while solitary species are cryptic.

Given the effects of altitude on ant abundance and the importance of ants to some treehopper species, we predicted a decline with increasing altitude in the number of tropical treehopper species that depend upon ants for protection. We also predicted that species not dependent on ants for defense should be more common at higher altitudes in the tropics where ants are rare. We used treehoppers to test our predictions because they have a wide geographic distribution and they exhibit diverse life history types (Wood 1982b, 1984). We chose to restrict our study to the treehoppers of Colombia because it has an altitudinal range of 5000 m and membracid taxonomists have made extensive collections there.

METHODS

We obtained locality and altitude records for all treehopper species from the literature (Richter 1940, 1941a, b, 1942a, b, c, 1943, 1945, 1955, Strümpel 1972, 1973, Strümpel and Strümpel 1975, 1978) and used gazetteers and relief maps to determine the altitude of those localities for which authors did not provide this information. We divided the altitudinal gradient into 13 classes of 250 m increments, from sea level to 3000 m and above. We found no records of treehoppers collected above 4200 m in Colombia.

One problem inherent in analyzing collection data from published works is the accuracy of locality records. For example, workers may designate the nearest large city as the collection site rather than a more accurate locality. Because we used published data, such errors may exist in our data set.

We followed Metcalf and Wade (1965) for species synonymies and Deitz (1975, 1983, 1985) for classification at the subfamily and tribal levels. We assumed an equal error rate in species identification across taxa relative to life history type. We used Wood's (1976, 1977, 1984) studies of membracids as well as those by Eberhard (1986), Ekkens (1972), Fritz (1982), Haviland (1925), and Hinton (1976, 1977) to determine sociality and ant mutualism for 330 (86%) of the 384 treehopper species recorded from Colombia.

Table 1. The number of treehopper species within each 250 m altitudinal class are given for Colombian treehoppers exhibiting one of three life history types. The number of species for which life history types was not available or could not be inferred is also given (see text for explanation of life history types).

Altitude Range (in Meters)	Midpoint	No. of Ant Dependent Species	No. of Presocial Species (No Ant Mutualism)	No. of Solitary Species	No. of Species with Unknown Life History Types	Total
0–249	125	40	1	21	2	64
250–499	375	61	2	40	3	106
500–749	625	72	1	35	7	115
750–999	875	51	2	25	6	84
1000–1249	1125	32	3	14	6	55
1250–1499	1375	32	6	11	5	54
1500–1749	1625	5	7	8	4	24
1750–1999	1875	17	11	8	7	43
2000–2249	2125	10	3	8	1	22
2250–2499	2375	0	3	4	1	8
2500–2749	2625	3	7	4	9	23
2750–2999	2875	8	22	14	18	62
3000+	3125	1	3	7	4	15
Total Number of Species		156	45	129	54	384

When sociality or ant mutualism information was not available for a particular species, we designated the life history type on the basis of congeners for which these data were available. In the Membracidae, life history patterns are often invariable within tribes, and with few exceptions, are consistent at the generic level (Wood, personal observation). We categorized each species as one of three types (1) species that aggregate as individuals and that are ant mutualists, (2) presocial species that are not ant mutualists, and (3) solitary species. Appendix A is a list of the treehopper genera and includes data on level of sociality and the presence of ant mutualism.

To control for unequal sampling effort throughout Colombia, we evaluated species richness as the proportion of species with a particular life history type relative to all species with known life history types that occur at that elevational class. For example, in our data set 21 solitary species occurred between sea-level and 250 m. Because 62 treehopper species occur in Colombia between 0 and 250 m, solitary species represent 33.87% of the treehopper species in this elevational class. We assumed that although some zones may be less well sampled than others, the proportions of species approximate the relative richness of species with different life history types. Proportional values were arcsine transformed prior to analysis.

We employed polynomial regression models (SAS Institute 1986) to describe the relationship between altitude and the proportion of treehopper species of each life history type. These models are appropriate because there was no reason to assume the relationship between species richness and altitude was linear. This approach also made it possible to describe the form of the relationship. We used sequential (Type I) sums of squares to determine the order of the polynomial regression that was appropriate (Freund et al. 1986). Initially, we used fourth degree polynomials and retained terms significant at $P < .05$ in the models. We examined the Studentized residuals to determine if our data met the assumptions of the models.

Results and Discussion

We were able to assign life history classification to 330 species of treehoppers in our data set. Of these species, 156 (47.27%) were dependent upon ant mutualists, 45 (13.64%) were presocial species that do not interact with ants, and 129 (39.09%) were solitary. The species richness of treehoppers with each of these three life history types across the altitudinal gradient is given in Table 1.

In Colombia, the proportion of treehopper species that depend upon ants for protection declines with increasing altitude (Figure 1a). A linear model best described the relationship ($y = 61.99 - 0.014x^1$, $R^2 = .62$, $P < .01$). Because ants are less common at higher elevations (Janzen 1973, Janzen et al. 1976, Bentley 1977a, b, Koptur 1985), treehoppers in these zones may be at a higher risk of predation than those occurring at lower elevations where ants are more abundant. Thus, our data supported our hypothesis that the altitudinal distribution of treehoppers that depend upon ants for protection reflects the availability of ant mutualists.

We found a significant positive relationship between altitude and the proportion of presocial treehopper species that are not ant mutualists. A linear model best described the relationship (Fig. 1b; $y = 2.71 + 0.135x^1$, $R^2 = .77$, $P < .01$). Because protection of offspring is provided by parent females rather than by ant mutualists, these species are less likely to be restricted to areas where ants are abundant. For this reason, species with parental care are overrepresented at higher elevations where ants, and consequently ant-dependent treehoppers, are rare.

Because ant-treehopper mutualisms are not common but do occur in solitary treehoppers (Wood 1984), these species should not be restricted to areas in which ant mutualists are common. Our data supported this hypothesis since the proportion of solitary species is nearly equal over the elevational gradient (Fig. 1c) and the proportion of solitary treehopper species was not statistically related to elevation in any of the models tested. Solitary species represent on average 36.77 ± 7.23% (arcsine transformed mean ±1 SD) of the membracid species at any elevation.

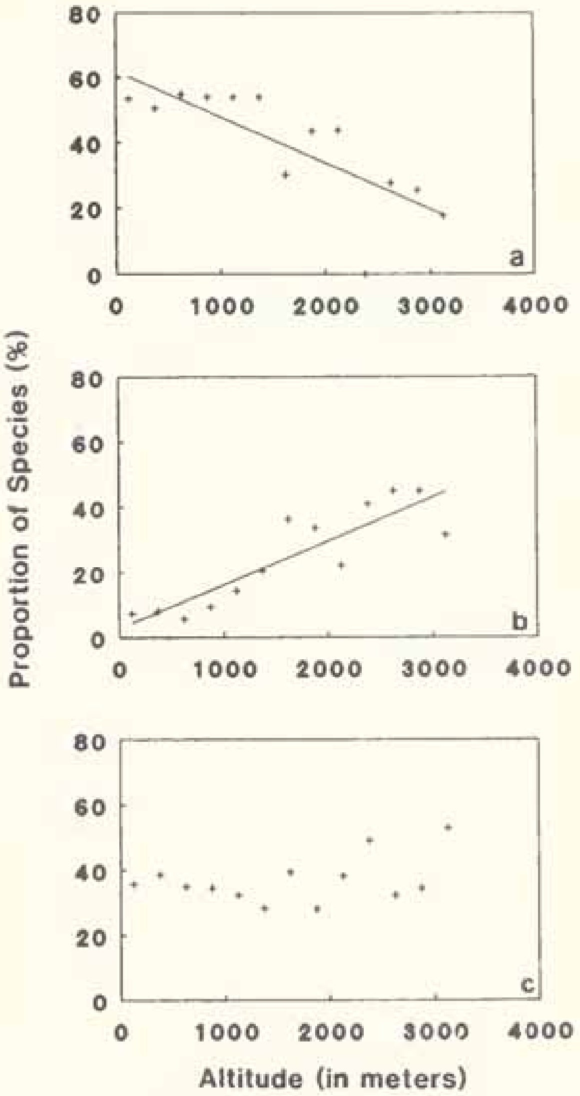

Fig. 1. The relationship between altitude and the proportion of Colombian treehopper species of three life history types: 1a) aggregating ant-dependent species, 1b) presocial species that do not interact with ants, and 1c) solitary species. Proportional values were arcsine transformed. Solid lines represent significant regressions (see text for regression equations and explanation of life history type).

We have focused here upon the relationships between ants, altitude, and treehopper life histories. Admittedly, ant mutualism is not the only selective factor varying across the environmental gradient. Differential plant productivity, seasonality, and a number of other factors may also affect the elevational distribution of phytophagous insects (Begon et al. 1986, Descimon 1986). We assume, however, that the differing selective pressures resulting from the clinal variation in these factors are evenly imposed on species with all three life history types. It appears that the decline with increasing altitude in the relative richness of treehopper species that depend upon ants for protection is due in large part to the corresponding decline in the abundance of mutualistic ants.

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Appendix A. A list of the treehopper genera reported in Colombia including the number of species, life history type, ant mutualism, and references. Life histories were categorized as one of three types: aggregative/ant-dependent, presocial, or solitary.

Genus	No. of Species	Life History Type (Reference)*	Ant Mutualism (Reference)*
Subfamily Centrotinae			
Tribe Abelini			
Ischnocentrus	3	Aggregative (8)	Yes (8)
Subfamily Membracinae			
Tribe Aconophorini			
Aconophora	14	Presocial (3, 5, 8)	Yes (8)
Guayaquila	1	Presocial (8)	No (8)
Tribe Hoplophorionini			
Potnia	2	Presocial (8)	No (8)
Ochropepla	2	Presocial (8)	No (8)
Hoplophorion	10	Presocial (8)	No (8)
Alchisme	12	Presocial (8)	No (8)
Umbonia	4	Presocial (1, 5, 6, 8)	No (8)
Tribe Membracini			
Bolbonota	7	Aggregative (1, 8)	Yes (8)
Tritropidia	5	Aggregative (3)	Yes (9)
Erechtia	5	Presocial (8)	Yes (8)
Tylopelta	3	Aggregative (8)	Yes (8)
Leioscyta	14	Aggregative (8)	Yes (8)
Campylenchia	2	Aggregative (8)	Yes (8)
Enchophyllum	6	Aggregative (8)	Yes (8)
Enchenopa	8	Aggregative (8)	Yes (8)
Membracis	28	Aggregative (5, 8)	Yes (8)
Tribe Hypsoprorini			
Notocera	11	Aggregative (8)	Unknown
Philya	4	Solitary (8)	No (8)
Hypsoprora	8	Unknown	Unknown
Sphongophorus	15	Solitary (8)	Unknown
Subfamily Darninae			
Darnoides	4	Unknown	Unknown
Hypheodana	1	Unknown	Unknown
Tribe Cymbomorphini			
Cymbomorpha	1	Solitary (8)	No (8)
Tribe Darnini			
Darnis	3	Solitary (8)	No (8)
Hebetica	2	Unknown	Unknown
Stictopelta	2	Solitary (8)	No (8)
Alcmeone	1	Solitary (8)	No (8)
Tribe Hyphinoini			
Bubalopa	2	Unknown	Unknown
Hyphinoe	2	Solitary (5, 8)	No (8)
Tomogonia	2	Unknown	Unknown
Tribe Hemikypthini			
Proterpia	1	Unknown	Unknown
Atypa	1	Solitary (8)	No (8)
Subfamily Smiliinae			
Tribe Acutalini			
Acutalis	4	Solitary (8)	No (8)

Appendix A. Continued.

Genus	No. of Species	Life History Type (Reference)*	Ant Mutualism (Reference)*
Euritea	2	Unknown	Unknown
Thrasymedes	4	Solitary (8)	No (8)
Tribe Micrutalini			
Micrutalis	9	Solitary (8)	Yes (8)
Tribe Ceresini			
Antonae	4	Unknown	Unknown
Centrogonia	4	Solitary (9)	Unknown
Penichrophorus	11	Solitary (9)	Unknown
Ilithucia	2	Unknown	Unknown
Melusinella	1	Unknown	Unknown
Ceresa	9	Solitary (9)	No (9)
Stictolobus	2	Solitary (9)	No (9)
Vestistilus	2	Solitary (8)	No (8)
Cyphonia	8	Solitary (8)	No (8)
Poppea	3	Aggregative (8)	Yes (8)
Tribe Amastrini			
Vanduzea	2	Aggregative (8)	Yes (2, 8)
Harmonides	3	Aggregative (8)	Yes (8)
Tynelia	2	Aggregative (3)	Unknown
Lallemandia	1	Unknown	Unknown
Amastris	7	Solitary (8)	Yes (1, 8)
Tribe Smiliini			
Telamona	1	Solitary (9)	Unknown
Antianthe	3	Presocial (5, 8)	Yes (8)
Tribe Tragopini			
Horiola	2	Presocial (3, 8)	Yes (8)
Tragopa	23	Solitary (8)	Yes (8)
Stilbophora	2	Aggregative (9)	Unknown
Chelyoidea	1	Aggregative (9)	Unknown
Tropidolomia	2	Aggregative (9)	Yes (9)
Tribe Polyglyptini			
Eucatoriana	1	Unknown	Unknown
Heranice	7	Unknown	Unknown
Adippe	2	Presocial (8)	Yes (8)
Dioclophara	2	Unknown	Unknown
Ennya	10	Presocial (8)	No (8)
Hille	4	Presocial (3)	Unknown
Polyglyptodes	2	Presocial (8)	No (8)
Maturnaria	6	Unknown	Unknown
Metheisa	1	Presocial (8)	Yes (8)
Polyrhyssa	1	Unknown	Unknown
Entylia	1	Presocial (5, 7, 8)	Yes (7, 8)
Polyglypta	2	Presocial (1a, 5, 8)	No (8)
Aphetea	3	Presocial (3, 8)	Yes (1, 8)
Phormophora	1	Unknown	Unknown
Subfamily Stegaspidinae			
Tribe Stegaspidini			
Bocydium	5	Solitary (8)	No (8)
Stylocentrus	1	Solitary (8)	No (8)
Oeda	2	Solitary (8)	No (8)
Lycoderes	8	Solitary (8)	No (8)

Appendix A. Continued.

Genus	No. of Species	Life History Type (Reference)*	Ant Mutualism (Reference)*
Stegaspis	5	Aggregative (9)	Unknown
Euwalkeria	1	Unknown	Unknown
Subfamily Heteronotinae			
Tribe Heteronotini			
Nassunia	2	Aggregative (8)	Yes (8)
Anchistrotus	2	Aggregative (9)	Unknown
Heteronotus	3	Aggregative (1)	Yes (1, 8)
Smiliorachis	1	Unknown	Unknown
Rhexia	11	Aggregative (9)	Yes
Total Number of Genera = 84		Total Number of Species = 384	

* 1a) Eberhard 1986, 1) Ekkens 1972, 2) Fritz 1982, 3) Haviland 1925, 4) Hinton 1976, 5) Hinton 1977, 6) Wood 1975, 7) Wood 1977, 8) Wood 1984, 9) Wood, personal observation.