SEASONAL AND SIZE PATTERNS, TROPHIC STRUCTURE, AND RICHNESS OF COLEOPTERA IN THE TROPICAL ARBOREAL ECOSYSTEM: THE FAUNA OF THE TREE *LUEHEA SEEMANNII* TRIANA AND PLANCH IN THE CANAL ZONE OF PANAMA

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ABSTRACT

Samples of Coleoptera were obtained by fogging trees (*Luehea seemannii* Triana and Planch) in a moist seasonal forest in the Canal Zone of Panama. More than 945 species, 56 families, were represented in the 7712 specimens obtained. Species richness and abundance were highest in the minor rainy season (July) samples, less so in major rainy season samples (October) and much less so in dry season samples (March-April). Trophic groups respond differently to seasonal change: herbivores and fungivores have peak abundance in the minor rainy season and steady decline until end of the dry season; predators and scavangers also have a peak in the minor rainy season, decline to the end of the rainy season and level off through the dry season. Herbivores constitute the major component of the samples, followed by predators, scavengers, and fungivores. Taxon distribution throughout the 19 sampled trees was low; a herbivor species was found on average in only 2.36 trees, a predator species in only 1.76 trees. Size distribution data showed that dry season species tend to be smaller than wet season ones and it is suggested that water loss, not heat buildup, is an important factor governing tropical arthropod size.

The tropical arboreal ecosystem is the last frontier in regard to general knowledge of Coleoptera. Past collecting and sampling of arboreal beetles has been fortuitous; collectors normally search the ground and scan under canopy vegatation using standard techniques; ecologists use standard trapping or sampling techniques and mostly do not look at the beetle species *per se*. The few truly arboreal specimens available for study are those collected at malaise or light traps, thus the animals' microhabitats and habits are unknown; hard data are altogether lacking even though Beebe (1917) pointed out years ago, "Yet another continent of life remains to be discovered, not upon earth, but one to two hundred feet above it . . . At present we know almost nothing of it. Up to now gravitation and tree-trunk swarming with terrible ants have kept us at bay, and of the tree-top life we have obtained only unconnected facts and specimens."

Although techniques used for this study (see Methods) were not precise, nor did they lend themselves to accumulation of microhabitat data, they did sample a portion of the anthropod fauna of a tropical canopy section. These samples underwent great attrition due to storage and sorting limitations, but on the whole Coleoptera were little affected and survived intact. Thus, these beetle samples could be counted, weighed and measured,

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trophic levels could be ascertained, and certain faunal descriptors could become known. With this in mind, we examined all specimens of all the families of Coleoptera, except weevils (Curculionidae), in the samples, sorted the species represented, measured their total lengths, widths, and depths, and computed total volume and biomass[1], and determined their feeding types. Correlations of these data with tree size, season, and species richness led us to a faunal description of the Coleoptera (excluding weevils) of the lowland tropical tree *Luehea seemannii* (Tiliaceae) in the Canal Zone of the Republic of Panama.

Our data (Figure 6) indicate that species richness and biomass are highest during early rainy season flush (Figure 7). Faunal attrition occurs through late rainy season decreasing to slightly over half its earlier strength. Dry season initiates nearly complete faunal turnover and the dry season fauna is depauperate with very low biomass. We also note that the various trophic groups respond differently to seasonal change. Herbivores and fungivores have a three-phase population cycle; predators and scavengers have a two-phase cycle.

Herbivores are dominant in the fauna followed by predators, scavengers, and finally fungivores. Distribution of taxa among the *Luehea* "habitat" is low, that is a herbivorous species on average was found in only 2.36 of the trees sampled, a predator species is on 1.76 of the trees. Species of the dry season fauna were somewhat smaller than wet season ones.

Materials and Methods

Sampling methods were described elsewhere (Montgomery *et al.* MS). The beetles were extracted by hand from the total samples by Montgomery, Lubin, the senior author (in part), and others at the Smithsonian Tropical Research Institute; the weevils were sorted and taken by H. P. Stockwell. The remaining Coleoptera were packaged dry and sent to Washington where the junior author pinned and labelled them. Sorting the material to species was done by the junior author and T. Gruenwald; final checking was done by the senior author and all problems were taken to U.S.D.A. Coleopterists residing in NMNH. Upon completion of the final sorting, L. E. Schimmel and G. N. House measured specimens with an electronic measuring device (Erwin 1978). Determination of trophic groups was made by the junior author mostly through recourse to literature, and partly by the senior author through discussion with colleagues at NMNH. A. F. Newton and M. K. Thayer (Museum of Comparative Zoology, Harvard) also helped in this endeavor. Measurements and counts were facilitated and accomplished by use of a Hewlett-Packard 97 desk calculator; the senior author and L. E. Schimmel performed the data input. Final analysis and text were the responsibility of the senior author. G. L. Venable and A. L. Halpern provided tables and graphic illustrations and the latter typed the draft manuscript.

[1]Biomass was computed as a function of volume. Representative families were selected to cover the range of varibility in beetle body structure-loosely built (Cantharidae) to compactly built (Buprestidae). Thirty specimens of selected species of ten families were dried and weighed to determine the average weight/volume of the beetle samples. This figure (K) of 1.473×10^{-4}gm/mm^2 was then used to compute a "standard" biomass figure for the rest of the families. See text for further details.

Measurements. – As insect-oriented ecologists become more and more aware of the need to look at their data in terms of individual species rather than mixed size classes and trophic groups, they also become aware of the difficulty in dealing with the myriad of life forms we call Arthropoda. For this study we wanted to deal with species and that meant preparing the material for sorting (hence pinning/pointing and labelling). Once the material is pinned and sorted regular biomass determination (dry weight method) techniques at the species level are not feasible, therefore we decided to determine "standard volume" (total length × widest elytral width × depth at hind coxal level). Once a mean standard volume was made for each species and a mean grams/mm^3 was determined for a cross sample of various Coleoptera, "standardized biomass" (mean grams per species) could be computed. The mean grams/mm^3 was designated "K" and in Table III total volume was converted to standardized biomass. Since standardized biomass only approximates real biomass, figures given in this paper cannot be compared directly with other biomass figures. However, relative *proportions* of the fauna should be comparable.

Measurements of total length, total width, and total depth were made on two specimens of each species series, the largest and smallest selected by eye. A mean was then calculated. This method is commonly used in taxonomic revisions and faunal works where "approximate species size" is conveyed to the reader for field recognition purposes. We tested the merits of the method by independently measuring several total series (n= 30+ in each series), calculated means, and compared them with the means determined by the method described above. The highest mean length error of one species was 0.25mm, but mean width error of the same species was 0.05mm and mean depth error only 0.01mm; thus mean volume error was 1.79mm^3. The lowest errors were 0.02mm mean length and 0.005mm^3 mean volume. We thus felt confident to use the eye selection method to facilitate measurement of the 945+ species. Regardless of which method we choose, the presence of numerous species represented by only one specimen would tend to make our biomass averages somewhat imprecise. However, we assume here that all taxa are varying in similar fashion and that things tend to even out. We also report our findings with full recognition of their imprecise nature and hope only to show relative trends as an aid to direction of future research.

The Fauna

Herbivores. – Nineteen families of herbivorous beetles are represented in the samples, 12 of these by more than 10 species. Five families are represented by only one species, four of these by a single specimen. These four, Byturidae, Limnichidae, Rhipiphoridae, and Throscidae are considered accidental. Monommidae (one species, 17 specimens) is regarded as a resident.

Anobiids, Buprestids, Cerambycids, Elaterids, Languriids, Mordellids, and Scolytids are wood boring in the larval stage and feed on inner parts of their host plants. As adults they may feed on pollen, scavenge, or not feed at all. The presence of their species in the sample indicates a possible host-link with *Luehea seemannii*, but does not prove it; some or all the individuals may be simply resting in the foliage or on bark.

Bruchiids are seed eaters in the larval stage, but none present in the samples are known to feed on *Luehea*. The sampled bruchiids were probably accidental visitors, or associated with lianas growing on the sampled trees. Chrysomelids and the sampled Scarabaeids are leaf eaters. Many of the former are undoubtedly tied to *Luehea* as their host plant.

Cantharids and Phalacriids are pollen feeders as adults. Helodids and Ptilodactylids are semiaquatic as larvae and the adults are known to rest on near-water vegetation. Whether they feed on the vegetation upon which they rest is unknown. The complete absence of the family Ptilodactylidae in the dry season is of particular interest in that 35 species are involved.

Fungivores.—Eleven families of fungivorous beetles are represented, only two of them with more than 10 species. There are also two families with one species, one specimen (Biphyllidae, Heteroceridae) and must be regarded as accidental.

Anthribids, Melandryids, and Platypodids are wood boring as larvae, the latter maintaining its own fungus gardens in its borrows. Ciids are fungus borers as both larvae and adults. Endomychids, Erotylids, lathridiids, Pselaphids and Scaphidiids are grazers.

Scavengers.—Seven families of scavengers are represented in the samples, four of them by more than 10 species. No families appear to be accidental. The Hydrophilids are apparently behaving like the other aquatic forms mentioned above.

Predators.—Seventeen families of predators are represented in the samples, 10 of them by more than 10 species. Dytiscidae and Rhizophagidae are represented by one species, one specimen, and are therefore considered accidential. Colydiids, Cucujids, Histerids, and Trogositids have species which are under bark predators; the remaining families usually are surface predators feeding on arthropods, arthropod eggs, or other small invertebrates. The Carabid species are the top predators in regard to size; the genus *Agra* has species members in the samples of over 20.0mm in length.

SEASONAL DISTRIBUTION OF THE FAUNA

The Coleoptera (exclusive of weevils) obtained from the Arthropod samples from 19 *Luehea seemannii* trees represent 56 families plus two species presently unassignable to families (Table I). These "58" family-group taxa[2] contained representatives of 945+[3] species. There were 7712 specimens collected and processed. Representatives of the dominant family, Chrysomelidae or leaf beetles, were so numerous and diverse we treat them here after in part as subfamilies, 11 in number. The minor rainy season (July samples) was the most diverse with 59 family-group taxa represented, followed by the dry season (March-April samples) with 51, and late rainy season (October samples) with 50. In terms of species, richness is somewhat more dramatic; early rainy-609, late rainy-385, dry-232 (Summary, Figure 1). Figure 1 also shows richness of specimens and species of beetles, and number of lianas/trees arranged by trees sampled. There appears to be no correlation with numbers of lianas unless season is also taken into account, however documentation of lianas was incomplete. Rearrange-

[2]Families, leaf-beetle subfamilies, unidentified families.

[3]The rove beetle family Staphylinidae, subfamily Aleocarinae, is impossible to determine to species at the present time. Our estimate of 50 additional aleocarines is reasonable but these were not included in the 945 total species nor in the figure given below for predators, 296.

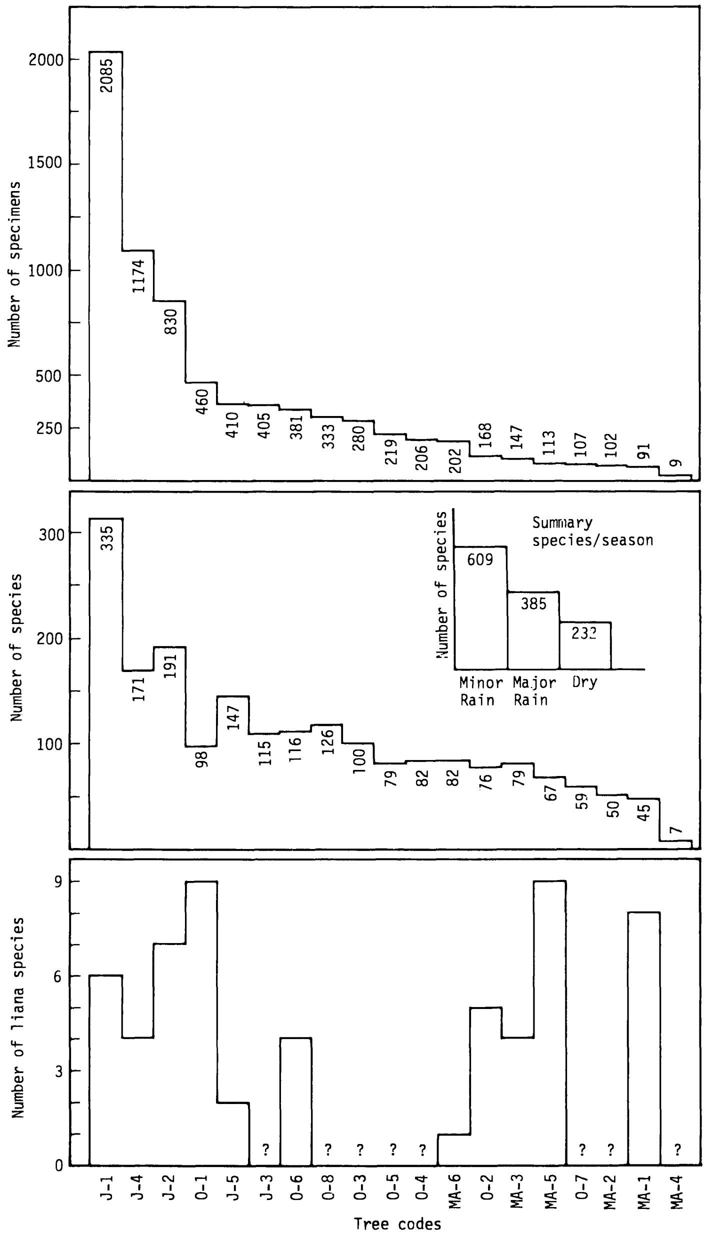

Figure 1. Richness in trees sampled; trees coded July (J), October (O), March-April (M-A) listed in order of highest number of total specimens to the left. Top – Number of specimens per tree; Middle – Number of species per tree and seasonal summary of total species; Bottom – Number of liana species per tree.

TABLE I. List of families, numbers of species and specimens, total volume (standardized), mean total length of species with standard error and coefficient of variation.

Family	Number of Species	Number of Specimens	Total Volume mm^3	Mean Total Length mm	s.	c.v.
Anobiidae	14	50	61.42	1.57	0.27	0.17
Anthicidae	15	250	175.12	2.74	0.87	0.32
Anthribidae	11	15	78.16	2.96	1.28	0.43
Biphyllidae	1	1	2.67	3.16	0	0
Bruchidae	6	6	92.33	3.82	1.14	0.30
Buprestidae	14	21	90.44	3.44	1.28	0.37
Byturidae	1	1	12.61	5.10	0	0
Cantharidae	19	67	1,258.03	6.80	2.93	0.43
Carabidae	41	134	3,872.45	7.25	4.54	0.63
Cerambycidae	62	170	2,910.85	5.83	2.43	0.42
Chrysomelidae						
a. Alticinae	66	1,068	8,370.44	3.25	1.52	0.47
b. Chalamisinae	2	4	44.70	2.98	0.66	0.22
c. Cassidinae	11	44	2,772.30	6.11	1.57	0.26
d. Chrysomelinae	2	2	532.85	9.36	0.47	0.05
e. Clytrinae	2	13	135.00	4.24	2.11	0.50
f. Cryptocephalinae	30	201	4,265.45	3.61	1.47	0.41
g. Eumolpinae	36	708	10,896.76	3.72	1.02	0.28
h. Galerucinae	41	752	5,865.97	4.78	1.40	0.29
i. Hispinae	9	14	158.89	5.68	1.42	0.25
j. Lamprosomatinae	1	12	43.80	2.18	0	0
k. Zeugophorinae	5	55	464.84	4.34	0.71	0.16
Ciidae	8	11	9.49	2.00	0.43	0.22
Cleridae	12	55	226.13	4.46	0.86	0.19
Coccinellidae	36	99	77.605	2.30	0.87	0.38
Colydiidae	5	11	26.73	3.53	0.95	0.27
Cryptophgidae	9	44	82.91	2.21	0.67	0.30
Cucujidae	18	45	32.54	2.53	0.92	0.36
Curculionidae						
Dermestidae	6	6	23.30	2.40	0.82	0.34
Dytiscidae	1	1	10.11	4.74	0	0
Elateridae	12	80	446.62	4.32	1.53	0.35
Endomychidae	5	54	4,611.11	4.57	1.86	0.41
Erotylidae	9	80	2,266.73	4.41	1.01	0.23
Euchnemidae	11	16	104.94	4.73	1.43	0.30
Euglenidae	11	37	20.34	1.81	0.33	0.18
Helodidae	12	17	80.76	2.55	0.71	0.28
Heteroceridae	1	1	1.46	2.74	0	0
Histeridae	3	6	14.12	2.49	0.25	0.10
Hydrophilidae	2	19	28.70	1.70	0.04	0.02
Lampyridae	12	23	442.02	6.53	2.61	0.41
Languriidae	14	46	206.70	3.53	2.77	0.78
Lathridiiae	3	21	6.33	1.26	0.19	0.15
Limnichidae	1	1	3.12	2.56	0	0
Lycidae	9	16	117.78	6.09	1.87	0.31
Melandryidae	14	60	997.22	4.88	2.81	0.58
Melyridae	2	5	36.81	2.80	1.94	0.69
Monommidae	1	17	102.26	3.03	0	0
Mordellidae	43	187	431.09	2.72	0.70	0.26
Mycteridae	11	21	25.46	2.84	1.08	0.38
Nitidulidae	22	178	447.97	2.72	1.01	0.37
Orthoperidae	10	23	13.98	1.25	0.30	0.24
Phalacridae	28	164	348.00	1.98	0.52	0.26
Platypodidae	2	2	5.86	3.69	0.47	0.13
Pselaphidae	7	13	5.18	1.64	0.15	0.09
Ptilodactylidae	35	736	3,388.40	3.99	1.31	0.33
Rhipiphoridae	1	1	14.62	5.65	0	0
Rhizophagidae	1	1	0.31	1.81	0	0
Scarabaeidae	3	4	383.30	6.33	4.52	0.71
Scaphidiidae	8	22	129.50	2.20	1.04	0.47
Scolytidae	10	11	8.96	1.98	0.49	0.25
Scydmaenidae	3	6	9.03	2.26	0.45	0.20
Staphylinidae	114	1,876	2,140.56	2.85	1.94	0.68
Tenebrionidae	31	109	1,753.83	5.18	2.57	0.50
Throscidae	1	1	0.92	2.19	0	0
Trogositidae	7	16	243.64	4.63	3.58	0.77
Family ?#1	1	3	12.46	3.60	0	0
Family ?#2	1	3	3.54	2.45	0	0
TOTAL	946	7,735	59,370.67			

ment of histograms in Figure 1 to correspond to tree age (judged by trunk diameter) or size of crown indicate no apparent correlation of these factors to numbers of species or specimens. Season, particularly as reflected in numbers of species and specimens, is responsible for richness—the dry season being particularly depauperate. There is almost a complete faunal shift between seasons although late rainy season is partially the tail end of early rainy season richness. Table II shows species per family per season, that is seasonal preference. Of particular note is the fact that 40% of the annual fauna is found only in early rainy season; only 1% shares late rainy and dry season; there is only 5% similarity between early rainy and dry seasons; only 18% of the species last throughout the entire rainy season; and only 4.7% can be found all year.

The four major trophic groups respond differently to seasonal change (Figure 2). All groups, as could be predicted from field observations, are at maximal richness in the early rainy season. Herbivores steadily decrease in species from early rainy to late rainy (324 to 217) and the dry season has only 93 species. Fungivores probably are responding to drought (lack of food source) with 48 early rainy species, 35 late rainy, and a mere 12 dry season species. The predators constitute 167 species in early rainy season dropping to slightly less than 2/3 that in late rainy season (100) and holding at 99 in the dry season. The predator pattern is also seen in the scavenger group (70 to 33, and 28 for the dry season). Thus species dependent upon plant food (herbivores and fungivores) have 3-phase annual populations with density and richness fluctuations which correspond to the three seasons. Species which depend on animal food (alive or dead) have 2-phase annual populations which peak in the early rainy season and level off during the rest of the year.

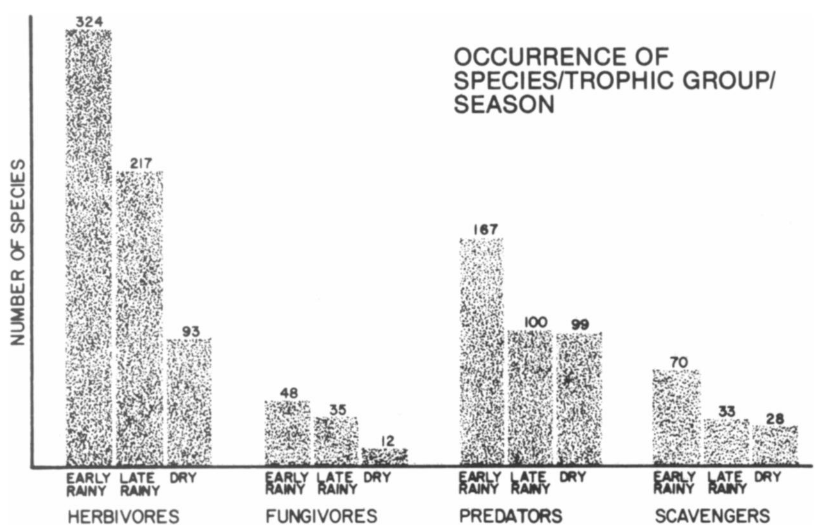

Figure 2. Seasonal distribution of species per trophic group.

TABLE II. Number of species/family/season with total sample summary.

NUMBER OF SPECIES

Trophic type Family	October	March/April	July	October + March/April	October + July	March/April + July	October + March/April + July	Total Species
Herbivores								
Anobiidae	3	3	2	0	2	4	0	14
Bruchidae	0	1	5	0	0	0	0	6
Buprestidae	0	0	13	0	1	0	0	14
Byturidae	1	0	0	0	0	0	0	1
Cantharidae	1	2	13	0	2	1	0	19
Cerambycidae	10	9	34	0	5	4	0	62
Chrysomelidae	54	9	67	1	46	11	17	205
Elateridae	2	3	3	0	4	0	0	12
Helodidae	3	2	6	0	0	1	0	12
Languriidae	0	1	7	0	3	2	1	14
Limnichidae	0	0	1	0	0	0	0	1
Monommidae	0	0	0	0	0	1	0	1
Mordellidae	16	4	14	0	5	1	3	43
Phalacridae	6	6	11	0	3	1	1	28
Ptilodactylidae	16	0	9	0	10	0	0	35
Rhipiphoridae	0	1	0	0	0	0	0	1
Scarabaeidae	0	0	3	0	0	0	0	3
Scolytidae	1	2	7	0	0	0	0	10
Throsidae	0	1	0	0	0	0	0	1
Subtotal (no. species)	113	44	195	1	81	26	22	482
%total Herbs.	23.44	9.13	40.46	0.21	16.80	5.39	4.56	
Fungivores								
Anthribidae	1	2	7	0	1	0	0	11
Biphyllidae	0	0	1	0	0	0	0	1
Ciidae	3	1	3	0	1	0	0	8
Endomychidae	1	0	2	0	1	0	1	5
Erotylidae	3	0	1	1	3	0	1	9
Heteroceridae	1	0	0	0	0	0	0	1
Lathrididae	1	0	0	0	1	1	0	3
Melandryidae	2	0	5	1	4	0	2	14
Platypodidae	0	0	2	0	0	0	0	2
Pselaphidae	2	1	2	0	2	0	0	7
Scaphidiidae	1	0	5	0	2	0	0	8
Subtotal	14	5	28	2	15	1	4	69
%total Fungi.	20.29	7.25	40.58	2.90	21.74	1.45	5.80	

Scavengers								
Anthicidae	0	2	4	1	2	4	2	15
Crytophagidae	2	1	4	0	1	0	1	9
Dermestidae	1	0	5	0	0	0	0	6
Euglenidae	4	1	3	0	1	0	2	11
Hydrophilidae	0	0	1	0	0	1	0	2
Nitidulidae	3	2	15	0	2	0	0	22
Tenebrionidae	4	5	13	0	3	2	4	31
Subtotal	14	11	45	1	9	7	9	96
%total Scav.	14.58	11.46	46.88	1.04	9.38	7.29	9.38	
Predators								
Carabidae	10	4	18	0	6	2	1	41
Cleridae	2	0	6	1	2	0	1	12
Coccinellidae	3	5	17	0	3	6	2	36
Colydiidae	0	0	4	0	0	0	1	5
Cucujidae	1	9	5	5	1	0	1	18
Dytiscidae	0	0	1	0	0	0	0	1
Eucnemidae	2	3	4	1	0	1	0	11
Histeridae	0	2	1	0	0	0	0	3
Lampyridae	5	0	6	1	0	0	0	12
Lycidae	3	1	2	1	1	1	0	9
Melyridae	0	1	0	0	1	0	0	2
Mycteridae	5	4	0	2	0	0	0	11
Orthoperidae	0	3	3	0	1	2	1	10
Rhizophigidae	0	0	1	0	0	0	0	1
Scydmaenidae	0	0	2	0	0	1	0	3
Slaphylinidae	26	30	41	0	12	4	2	110
Trogositidae	0	4	3	0	0	0	0	7
Subtotal	57	66	114	7	27	17	9	297
%total Pred.	19.19	22.22	38.38	2.36	9.09	5.72	3.03	
Total no. species	198	126	382	11	132	51	44	944
%total Fauna.	20.97	13.35	40.47	1.17	13.98	5.40	4.66	
Unknowns								
Family ?#1	0	0	1	0	0	0	0	1
Family ?#2	0	0	1	0	0	0	0	1

SUMMARY

Trophic Types							
Herbivores	113(23.44)	44 (9.13)	195(40.46)	1(0.21)	81(16.80)	26(5.39)	22(4.56)
Fungivores	14(20.29)	5 (7.25)	28(40.58)	2(2.90)	15(21.74)	1(1.45)	4(5.80)
Scavengers	14(14.58)	11(11.46)	45(46.88)	1(1.04)	9 (9.38)	7(7.29)	9(9.38)
Predators	57(19.19)	66(22.22)	114(38.38)	7(2.36)	27 (9.09)	17(5.72)	9(3.03)
Total	198	126	382	11	132	51	44
%	20.97	13.35	40.47	1.17	13.98	5.40	4.66

TABLE III. Taxa arranged by trophic groups per season with mean volume ($\bar{x}$V), standard error (s.), coefficient of variation (c.v.), total volume (TV), and standardized biomass (gm/family x 10^{-3}). K - .0001473 (see text).

	July					October		
Trophic Group / Family / Subfamily	$\bar{x}$V/sp. mm^3	s.	c.v.	TV/family mm^3	gm/family $X10^{-3}$	$\bar{x}$V/sp. mm^3	s.	c.v.
Herbivores								
Anobiidae	1.22	.77	.63	23.15	3.410	1.27	.61	.48
Bruchidae	17.82	10.25	.58	89.10	13.124	-	-	-
Buprestidae	4.36	3.56	.82	87.22	12.848	3.22	-	-
Byturidae	-	-	-	-	-	12.61	-	-
Cantharidae	18.67	14.09	.75	1,026.64	151.224	21.72	30.59	1.41
Cerambycidae	21.09	30.66	1.45	2,445.98	360.293	16.16	12.94	.80
Chrysomelidae								
Alticinae	10.44	10.38	.99	4,676.79	688.891	6.22	6.75	1.08
Chlamisinae	12.51	-	-	12.51	1.843	-	-	-
Cassidinae	43.03	12.06	.28	1,075.00	158.348	102.86	81.65	.79
Chrysomelinae	-	-	-	-	-	312.80	-	-
Clytrinae	3.97	-	-	27.76	4.089	3.97	-	-
Cryptocephalinae	25.94	24.77	.96	4,046.16	595.999	4.39	3.69	.84
Enmolpinae	15.75	10.11	.64	7,481.70	1,102.054	14.96	10.89	.73
Galerucinae	6.81	7.52	1.11	4,329.17	637.687	13.31	12.87	.96
Hispinae	6.91	2.46	.36	27.64	4.071	18.86	16.14	.86
Lamprosomatinae	3.65	-	-	10.95	1.613	3.65	-	-
Zeugophorinae	8.25	1.98	.24	396.14	58.351	9.85	1.63	.17
Elateridae	6.71	2.77	.41	335.58	49.431	3.35	2.84	.85
Helodidae	5.88	4.89	.83	52.93	7.797	1.38	1.02	.74
Languriidae	7.47	7.83	1.05	186.86	27.524	.36	.66	1.84
Limnichidae	3.12	-	-	3.12	.460	-	-	-
Monommidae	6.02	-	-	90.25	13.294	-	-	-
Mordellidae	2.80	3.35	1.20	302.05	44.492	1.92	1.43	.74
Phalacridae	1.94	1.24	.64	131.95	19.436	2.28	1.30	.57
Ptilodactylidae	3.97	3.76	.95	2,202.74	324.464	6.05	10.34	1.71
Rhipiphoridae	-	-	-	-	-	-	-	-
Scarabaeidae	15.33	6.77	.44	46.00	6.776	337.30	-	-
Scolytidae	1.02	.38	.37	8.13	1.198	.26	-	-
Throsidae	-	-	-	-	-	-	-	-
Total					4,288.716			
Scavengers								
Anthicidae	.74	.26	.35	71.74	10.567	1.33	.60	.45
Cryptophagidae	2.16	.78	.36	54.07	7.965	1.70	.53	.31
Dermestidae	4.36	4.73	1.08	21.82	3.214	1.40	-	-
Euglenidae	.56	.16	.28	8.43	1.242	.53	.15	.28
Hydrophilidae	1.53	.08	.05	27.55	4.058	-	-	-
Nitidulidae	2.47	4.29	1.74	407.30	59.995	2.67	4.21	1.58
Tenebrionidae	13.82	25.50	1.84	953.80	140.495	24.29	36.63	1.51
Total					227.536			
Fungivores								
Anthribidae	6.97	8.52	1.22	69.72	10.270	2.20	1.42	.65
Biphyllidae	2.67	-	-	2.67	.393	-	-	-
Ciidae	1.30	.94	.72	5.21	.767	.65	.35	.54
Endomycidae	93.09	44.36	.48	4,468.49	658.209	21.71	11.80	.54
Heteroceridae	-	-	-	-	-	1.46	-	-
Lathrididae	.28	.06	.20	.85	.144	.23	.05	.19
Melandryidae	23.94	27.73	1.16	694.13	102.245	12.82	20.63	1.61
Platypodidae	2.93	.97	.33	5.86	.863	-	-	-
Pselaphidae	.43	.12	.27	2.59	.382	.37	.12	.33
Scaphidiidae	6.99	8.60	1.23	125.76	18.524	.94	.10	.11
Total					791.798			
Predatores								
Carabidae	34.53	60.26	1.75	2,658.79	391.640	32.00	26.02	.81
Cleridae	4.77	2.30	.48	162.11	23.879	3.00	1.86	.62
Coccinellidae	10.52	43.30	4.11	547.29	80.616	1.41	1.72	1.22
Colydiidae	2.73	1.84	.68	21.81	3.213	1.64	-	-
Cucujidae	1.09	.76	.70	14.15	2.084	.70	.42	.59
Dytiscidae	10.11	-	-	10.11	1.489	-	-	-
Eucnemidae	8.11	3.89	.48	40.54	5.971	4.19	6.39	1.53
Histeridae	1.87	-	-	1.87	.275	-	-	-
Lampyridae	39.42	65.55	1.66	275.93	40.644	11.48	10.75	.94
Lycidae	5.77	5.19	.90	23.08	3.400	11.37	12.51	1.10
Melyridae	9.08	-	-	18.16	2.675	9.08	-	-
Mycteridae	-	-	-	-	-	1.45	1.41	.97
Orthoperidae	.70	.58	.84	6.95	1.024	.62	.10	.16
Rhizophagidae	.31	-	-	.31	.046	-	-	-
Scydmaenidae	1.51	.64	.44	7.54	1.111	-	-	-
Staphylinidae	.92	3.07	3.34	1,055.51	155.477	1.23	.99	.81
Trogositidae	72.82	53.95	.74	218.47	32.181	-	-	-
Total					745.724			
				July total	6,053.774			

		March/April					
TV/family mm^3	gm/family X10^{-3}	$\bar{X}$V/sp. mm^3	s.	c.v.	TV/family mm^3	gm/family X10^{-3}	3 Seasons Total gm X10^{-3}
20.34	2.996	1.20	.67	.56	17.93	2.641	9.047
-	-	3.23	-	-	3.23	.476	13.620
3.22	.474	-	-	-	-	-	13.321
12.61	1.857	-	-	-	-	-	1.857
173.73	25.590	14.42	14.19	.98	57.66	8.493	185.308
201.09	29.621	10.99	26.85	2.44	263.78	38.855	428.768
3,631.68	534.947	1.72	2.50	1.45	61.97	9.128	1,232.966
-	-	10.73	-	-	32.19	4.742	6.584
1,440.04	212.118	51.45	17.96	.35	257.26	37.894	408.360
312.80	46.075	220.04	-	-	220.04	32.412	78.487
15.86	2.336	45.69	-	-	91.37	13.459	19.884
171.31	25.234	8.00	9.70	1.21	48.01	7.072	628.305
3,291.36	484.817	9.52	14.36	1.51	123.70	18.221	1,605.093
1,424.22	209.788	12.51	18.52	1.48	112.58	16.583	864.057
113.10	16.660	4.54	.58	.13	18.15	2.673	23.404
21.90	3.226	3.65	-	-	10.95	1.613	6.452
68.92	10.152	-	-	-	-	-	68.503
90.33	13.306	6.90	7.68	1.11	20.71	3.051	65.787
6.88	1.013	6.98	2.00	.29	20.95	3.086	11.896
5.76	.848	2.82	4.54	1.61	14.08	2.074	30.447
-	-	-	-	-	-	-	.460
-	-	6.02	-	-	12.03	1.772	15.060
111.46	16.418	.84	.61	.73	17.58	2.590	63.500
168.35	24.798	2.17	.97	.45	47.70	7.026	51.260
991.88	146.104	-	-	-	-	-	470.568
-	-	14.62	-	-	14.62	2.154	2.154
337.30	49.684	-	-	-	-	-	56.460
.26	.038	.29	.04	.12	.57	.084	1.320
-	-	.92	-	-	.92	.136	.136
	1,858.101					216.233	6,363.051
15.91	2.344	.62	.42	.68	87.47	12.884	25.795
23.80	3.506	1.01	.33	.33	5.04	.742	12.213
1.48	.218	-	-	-	-	-	3.432
9.45	1.392	.62	.44	.72	2.46	.362	2.996
-	-	1.20	-	-	1.20	.177	4.235
29.38	4.328	5.65	3.75	.67	11.29	1.663	65.986
631.58	93.032	12.03	21.47	1.78	168.45	24.813	258.339
	104.819					40.642	37.996
6.60	.972	.92	.16	.17	1.84	.271	11.151
-	-	-	-	-	-	-	.393
3.92	.577	.36	-	-	.36	.053	1.398
108.55	15.989	34.07	-	-	34.07	5.019	679.216
1.46	.215	-	-	-	-	-	.215
1.63	.240	.35	-	-	3.85	.567	.929
269.13	39.643	3.40	.34	.10	33.96	5.002	146.891
-	-	-	-	-	-	-	.863
1.46	.215	.38	-	-	1.13	.166	.763
1.88	.277	.93	-	-	1.86	.274	19.075
	58.129					11.352	861.279
832.04	122.560	12.31	11.97	.97	381.58	56.207	570.406
57.08	8.407	3.47	2.11	.61	6.94	1.022	33.309
30.92	4.555	6.83	6.16	.90	170.84	25.165	110.335
3.28	.483	1.64	-	-	1.64	.242	3.937
9.86	1.452	.47	.47	.99	8.53	1.256	4.793
-	-	-	-	-	-	-	1.489
20.94	3.084	6.21	4.74	.76	43.46	6.402	15.458
-	-	2.45	.72	.29	12.25	1.804	2.080
160.73	23.675	2.68	-	-	5.36	7.895	65.110
56.87	8.377	5.40	.95	.18	37.83	5.572	17.349
18.16	2.675	.49	-	-	.49	.072	5.422
17.43	2.567	.89	.77	.87	8.03	1.183	3.750
3.09	.455	.49	.57	1.16	3.94	.580	2.059
-	-	-	-	-	-	-	.046
-	-	1.49	-	-	1.49	.219	1.330
751.79	110.739	.45	.42	.95	61.05	8.993	275.208
-	-	1.94	1.25	.64	25.17	3.708	35.888
	289.031					113.215	1,147.969
October total	2,310.060				March/April total	381.442	8,745.300

Trophic Groups

For purposes of analysis the 58 family-group taxa samples were divided into four trophic groups. Although assignment to trophic groups was done in somewhat of a simplistic manner, the resultant groups conveniently allowed faunal description and did show some differences. The difficulties in assigning Coleoptera to trophic groups are, 1) insufficient published data on beetle feeding habits and, 2) often striking differences of feeding types within a single family thus precluding generalizations. However, some generalizations are made here with full realization that the analyses are based on only approximations and the conclusions tentative.

We assigned taxa to one of four trophic groups: herbivores, scavengers, fungivores, or predators, based on literature, our own field experience, or discussions with beetle experts. Table III depicts the trophic nature of the beetle fauna of *Luehea seemannii.* As expected, herbivores constitute the bulk of the fauna both in number of specimens (4421) and standard biomass (6.363 gm) and represent the greatest species richness (482). These are followed by predators (2342 specimens; 1.147 gm; 296+ species)[4], scavengers (643 specimens; 0.372 gm; 96 species), and finally fungivores (200 specimens; 0.861 gm; 60 species)[5]. Figure 3 shows distribution of trophic groups per trees sampled (trees arranged in descending order by total number of all specimens per tree); note significant lack of correlation in trees J-4, J-5, MA-3, O-7. Since it is doubtful that predator beetles feed exclusively on herbivorous beetles there should be no positive correlation in ratios of these trophic groups to each other, but there does seem to be a trend in this direction generally, perhaps reflecting the overall nature of the arthropod fauna.

The number of species (Table II) found to carry over from one season to the next is highest among the fungivores (31.89%), followed by scavengers (27.09%), herbivores (26.96%), and finally by predators (20.20%). The highest carry-over rates are found between the early and late rainy seasons as could be expected; the lowest rates are between the late rainy season and dry season where only 55 (5.83%) species make the transition and 44 of these are species which are present in the fauna all year. Seasonal endemicity is highest for all trophic groups in the early rainy season (Table II) with about 40% of each confined to the single season. Notable is the high number (66) of predator species restricted to the dry season. Notable too is that only 23 herbivore species (4.77%) carry over from late rainy season into the dry season. Of particular interest is the distribution of species (per trophic group) in the trees sampled. Each herbivorous species was found on an average in every 2.36 trees; each scavenger species was found in every 2.15 trees; fungivore in every 2.09 trees; and predator in every 1.76 trees. From these data we might conclude that herbivorous species are likely to be encountered nearly twice as often in the tropical lowland forests than predator species, the others somewhere in between.

The question thus arises, why are not the herbivores common to all the *Luehea* trees if they are eating it? Why are these herbivorous species distributed in only 12% of the available habitat? As pointed out recently by Edmunds and Alstad (1978) certain trees or parts of trees may have

[4]Undetermined Staphylindae would add at least 50 to the number of species.
[5]Note that funigivores are fewer in number but larger in size than scavengers.

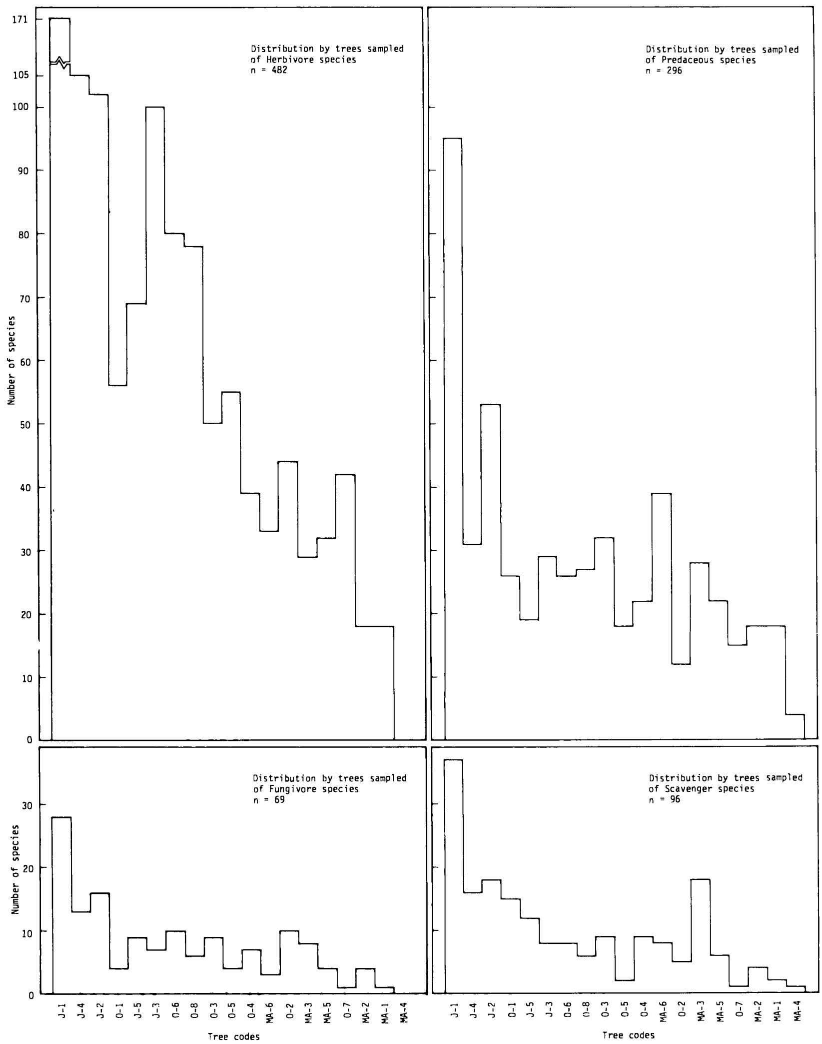

Figure 3. Distribution by trees sampled of trophic groups; trees listed in order of highest number of total specimens to the left (see Figure 1).

chemically defensive aspects determined by variation in the tree species gene pool. Their work was with northern pines, but this may be worth study for tropical trees.

SIZE

From Table III it can be seen that mean total length of beetle families in the samples range from 1.25 mm (Orthoperidae) to 7.25 mm (Carabidae), with the overall average between 3.0 and 4.0 mm (Figure 5). As can be seen

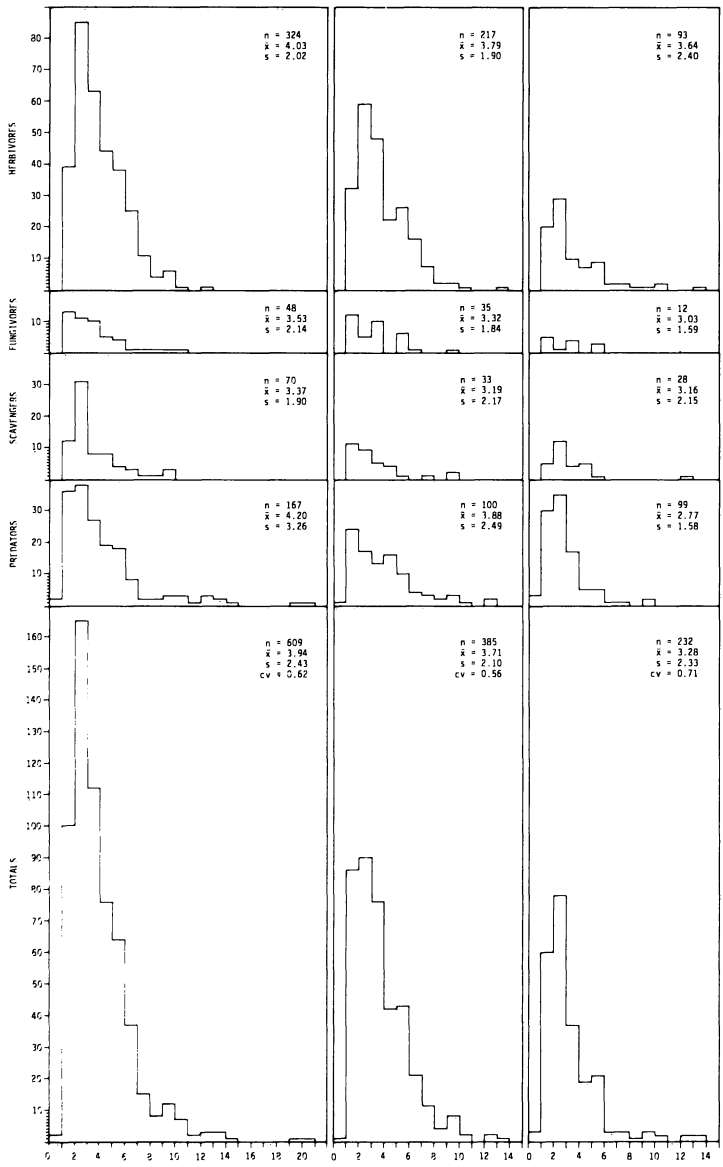

Figure 4. Number of species by total lengths; size classes (mm) per trophic groups and seasons with mean lengths ($\bar{x}$) and standard error (s); coefficient of variation (c.v.) given for season's totals.

in Figure 4, species of the dry season are somewhat smaller than those of the wet seasons. This is opposite to the findings of Janzen and Schoener (1968) for a dry season transect from moist bottomlands (wet equivalent) to dry hillside (dry equivalent) where the numbers of small insects (1 to 3 mm) decrease toward the hilltop. However, since their samples are differentiated by four habitats within a single season and ours are one habitat within "three" seasons there may be no grounds for comparison. However, our size data show that for beetles of the moist tropical forest canopy smallness is selected for in that habitat. The larger wet season species are replaced (94%) by smaller dry season species. Why? What factors would influence a faunal shift of this scale? Janzen and Schoener (1968) suggest that larger species are more successful at their hilltop site because they loose heat better due to a higher surface to volume ratio. Our size data apparently conflict with this idea. First it must be noted that the heat loss hypothesis was generated from the study of warm-blooded animals which must lose heat or store it depending on seasonal needs. We suggest that for insects water loss during the dry season is as critical, if not more so, as heat loss. Water loss must not exceed the threshold of the species in question; heat gain may be secondary, or not critical, because the insect can take cover easily, and even in hot climates small cool refugia exist for small animals. It is likely the answer to the question involves water loss, heat gain, as well as other complexities of nature, for example, size bimodality of carabid beetle faunas. Elsewhere (Erwin 1979) it was noted that carabid beetles of the forest floor community have a bimodal size distribution, and it was suggested that ants of a certain size eliminate the emigration or evolution of Carabids of the

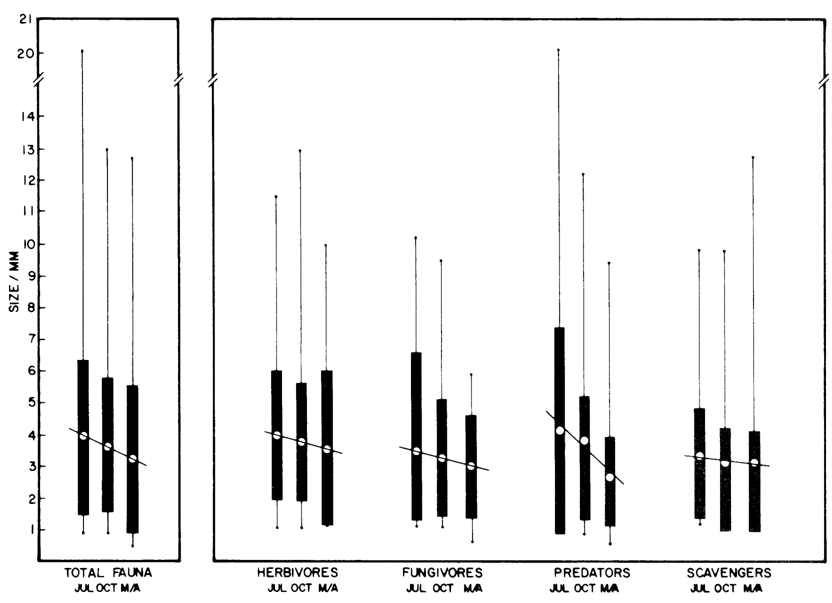

Figure 5. Size ranges with mean lengths, standard error, and coefficient of variation of taxa by Trophic class and season.

same size into the forest floor habitat. The Carabids of the canopy samples are not bimodal in size and it must be assumed that selective pressures of the canopy may be different from those of the forest floor in regard to size.

SUMMARY

In summary, the tropical arboreal ecosystem as represented by *Luehea seemannii* crowns is much richer in beetle species than we expected. Peak richness and abundance are present in the early rainy season as expected; the dry season is relatively depauperate. There is hardly any carry-over of species between rainy and dry seasons, and each season, including both parts of the rainy season has a high degree of uniqueness. Mean size of beetles in the dry season is significantly smaller than that of rainy season beetles. Plant eating beetles (herbivores and fungivores) have 3-phase annual populations, that is a peak in early rainy season, drop in numbers in late rainy season and a further decrease in the dry season. Predators and scavengers, on the other hand, peak in early rainy season, drop in number later in the rainy season, and maintain this level through the dry season. There appears to be no correlation between tree size or age and density of beetles, nor is there a correlation between number of lianas and beetle density or abundance.

ACKNOWLEDGMENTS

We greatly appreciate the help given by those people cited under "Methods". In addition, we heartily thank Vera Krischik and Robert Denno for criticizing a preliminary draft thus adding substantially to the final product. As usual however, we take full credit for any blunders that remain.

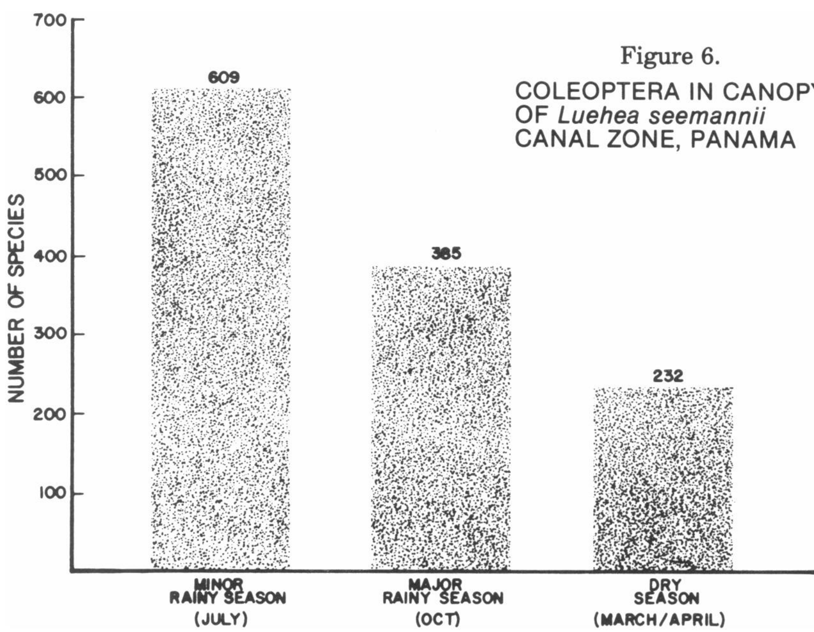

Figure 6.
COLEOPTERA IN CANOPY OF *Luehea seemannii* CANAL ZONE, PANAMA

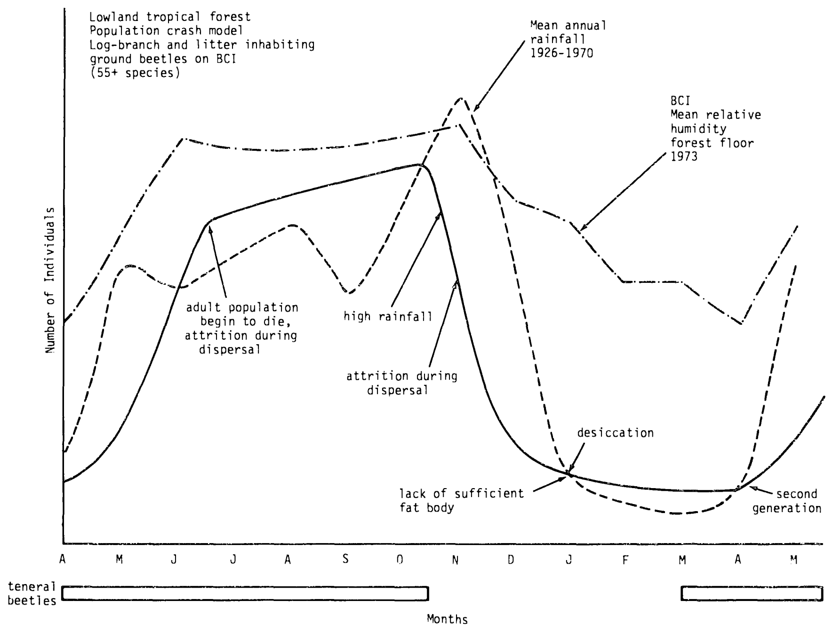

Figure 7. Summary of annual carabid faunal cycles and sequence of seasonal events at Barro Colorado Island, Panama.

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Addendum

Unfortunately, two small families of beetles were overlooked during

processing, thus figures in the Tables and text are incomplete. Since the families are small no signigicant adjustments were necessary however, and the data are presented here.

Lagriidae–7 species, 29 specimens; October–2 spp., 9 specimens, TV = 237.75, $\bar{x}$ = 26.42, s = 40.78, c.v. = 1.54; March-April–1 sp., 2 specimens, TV = 25.64, $\bar{x}$ = 12.82, s and c.v. = 0.0; July–6 spp., 18 specimens, TV = 637.27, $\bar{x}$ = 35.40, s = 17.06, c.v. = 0.48. Trees–0-3, 1 sp., 4 specimens; 0-5 and 0-6, 1 sp., 1 specimen each; 0-7, 2 spp., 2 specimens; 0-8, 1 sp., 1 specimen; M-A-2, 1 sp., 2 specimens; J-1, 4 spp., 13 specimens; J-2, 1 sp., 1 specimen; J-3, 1 sp., 1 specimen; J-4, 3 spp., 3 specimens.

Nilionidae–2 species, 8 specimens; October–1 sp., 3 specimens, TV = 3.60, $\bar{x}$ = 1.20, s and c.v. = 0.0; March-April–none; July–2 spp., 5 specimens, TV = 5.49, $\bar{x}$ = 1.10, s = 0.23, c.v. = 0.21. Trees–0-2, 1 sp., 1 specimen; 0-3, 1 sp., 2 specimens; J-1, 2 spp., 2 specimens; J-2, 1 sp., 3 specimens.