

Sweep samples of tropical deciduous forest foliage-inhabiting insects: seasonal changes and inter-field differences in adult bugs and beetles

by

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Abstract: Sweep samples in four different pasture sites and adjacent deciduous forest understory in Guanacaste Province, Costa Rica produced some tentative conclusions about the structure of the "community" of adult beetles and bugs: a) during the dry season, the different areas in the deciduous forest understory are of widely different value to beetles and bugs; b) the density and species-richness of beetles and bugs is severely reduced by the dry season in all sites except the portions of the forest understory beneath occasional evergreen trees; c) among the four pasture sites in the rainy season, there is nearly as wide a range of numbers of species and individuals as had been found in all the different secondary vegetation sites sampled previously in Costa Rica; d) during the dry season, there appears to be a higher per cent of the beetle species in common between forest understory and pasture sites than in the rainy season; and e) in one of the richest sites swept previously, 312 species of beetles were taken with 800 sweeps, while in the present study, 16,000 sweeps in five habitats and two seasons were required to accumulate 320 beetle species—the figures for adult bugs are generally the reverse, emphasizing that two major orders may display quite different patterns of community structure.

To the degree that it can be determined from standardized sweep samples, a rough image of the dynamics of tropical foliage-inhabiting insects in response to environmental change is emerging (Janzen and Schoener, 1968; Schoener and Janzen, 1968; Janzen 1973a, 1973b; Allan *et al.*, 1973; Janzen *et al.*, 1975; Janzen and Pond, 1975). Here, I report the results of a sweep sample comparison of the adult bugs (Hemiptera) and beetles (Homoptera) to be found in four old fields (pastures) and in an adjacent deciduous forest understory in the Pacific coast lowlands of Costa Rica. Comparable samples were taken in the wet season and following dry season.

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METHODS

The methods were the same as those described in the above mentioned papers. In brief, 800 sweeps were taken in 100-sweep subsamples while moving at a rapid walk through a patch of vegetation regarded as one "habitat". A given patch of vegetation was contacted only once during a particular sample. However, when a site was re-swept the following season, every effort was made to follow the same path. All diurnal sweeps were taken on clear mornings between 8:30 and 10:00 AM (after nearly all dew was gone from the foliage); the night sweeps were taken in black dark (8:00 to 9:30 PM) under starlit skies without the use of flash-lights. During the rainy season sweeps (1971), the air temperature was 28 to 29C in the open pasture and 27 to 28C in the forest understory. In the dry season (1972), the analogous temperatures were about 30 and 29C though it seemed hotter in the forest owing to a lack of breeze.

The insects in the subsamples were placed in plastic bags, killed with ethyl acetate, and removed immediately from the vegetation. As this study was conducted in part during courses taught by the Organization for Tropical Studies, thereby limiting time available for sorting, only adult beetles (Coleoptera) and bugs (Hemiptera-Heteroptera) were retained (see Janzen, 1973a, 1973b for a similar situation). These were sorted immediately to morphospecies and enumerated with respect to the 100-sweep subsample in which they were found. A reference collection was made at the time, and these specimens were later tentatively identified and checked for synonymy by Dr. D. Whitehead (using the collections of the U. S. National Museum). As an indication of the accuracy of the morphospecies identifications, 7% of the 320 beetle morphospecies in the reference collections were found to be synonyms; the comparable figure for the 95 bug species was 1%. With more attention to avoiding the more obvious of the duplications in putting together the beetle reference collection, the figure of 7% could have been reduced to about 3%, with sexual dimorphism being responsible for most of this error.

SWEEP AREAS

The habitats are all within a few kilometers of Hacienda Palo Verde, which lies about 24 km southwest of the main entrance to the COMELCO Ranch north of Bagaces, Guanacaste Province, Costa Rica. The sweep sites are all slightly hilly and near the bases of the 50 to 150 m tall limestone hills and ridges that lie along the east and north sides of the many square km of swamp at the west end of COMELCO and in the floodplain to the Rio Tempisque.

The Palo Verde Forest site (see below for detailed descriptions) was chosen as exemplary of mixed deciduous forest that could be contrasted with nearby pastures with quite different vegetation. During the rainy season, the Baltimora Pasture represented a site with few species of plants where the pollen and nectar of the dominant plant (*Baltimora scolospermum*) was an abundant food source for generalist insects; the Aeschynomene Pasture also had a dense and nearly monospecific stand of herbaceous plants but the numerous flowers were only rarely visited by insects. The Cow Pasture represented an ungrazed (in the rainy season) mixture of grasses and dicots, no one dicot exceeded 10% of the total cover. The Horse Pasture was the same, but was under heavy grazing during the rainy season. During the dry season, the Aeschynomene Pasture became the most barren of all the sites and the continuously grazed Horse Pasture ran a close second. During the

dry season, the Baltimore Pasture lost most of its rainy season dominant plants, but retained a considerable amount of vegetation in the form of sucker shoots of trees and shrubs. The Cow Pasture had by far the largest amount of vegetation at any site swept during the dry season, primarily because the species in it were allowed to grow to a large size before cattle were turned loose in it (late rainy season) and the plants were mostly perennials or annuals with long-lived foliage (grasses, *Croton*).

Palo Verde Forest: The area swept was in the understory of 10 to 25 m tall deciduous forest lying to the west and north of the road from Hacienda Palo Verde to Hacienda Colmenar, beginning at the point where the road leaves the last old pasture (Baltimore Pasture, see below) behind and penetrates the forest. This site is about 7 km north of Hacienda Palo Verde by road.

The portion of the forest that was swept contained scattered evergreen trees (*Brosimum costaricanum*, *Ficus*, *Licania arborea*, *Sloanea terniflora*, *Ardisia revoluta*) but no riparian evergreen vegetation; some of the common deciduous species of trees are *Bursera simaruba*, *Guazuma ulmifolia*, *Enterolobium cyclocarpum*, *Spondias mombin*, *Rehdera trinervis*, *Luehea seemannii*, *Calycophyllum candidissimum*, *Pithecellobium saman*, *Bombacopsis quinata*, *Lysiloma seemannii*, *Stemmadenia donell-smithii*, *Tabebuia neochrysantha*, *T. rosea*, *Lonchocarpus costaricensis*, *Guettarda deamii*, *Chlorophora tinctoria*, *Sapindus saponaria*, *Cochlospermum vitifolium*, *Swietenia humilis*, and *Simarouba glauca*.

This forest is essentially unbroken by major clearing for at least 4 km to the west and north of the sweep site, though there are occasional patches burnt out by accidental fires, and selective logging had taken place in the distant past. During the dry season, cattle have access to this forest, but their damage is not conspicuous. Peccaries, deer, agoutis, pacas, coatis, capuchin and howler monkeys are occasionally encountered, but are probably not as common as they would be were they not occasionally hunted.

The forest is generally leafless from about January to the end of April. There are no weather records for the site but weather stations at nearby Cañas and Liberia receive about 1900 and 1700 mm of rain annually (Costa Rica. Servicio Meteorológico Nacional, 1965).

The dry season sweeps were taken during the middle of the dry season; the rainy season samples were taken during its driest part (commonly called the "veranillo"), when it rained only about once every three days.

The site is roughly analogous to the Taboga Primary Hillside site described by Janzen (1973a), except that the latter site is within a few hundred meters of evergreen riparian vegetation (and the Río Higerón) and is in a much smaller piece of forest that has been severely hunted and highgraded for timber in recent years.

Baltimore Pasture: This is a long strip (30 x 500 m) of an old pasture cut into the Palo Verde Forest site from its southeast edge. It is bordered on three sides by relatively intact forest and its southeast end is contiguous with hundreds of hectares of pasture. Sweeps were taken in two parallel lines of 400 sweeps each down the length of the pasture, about 10 m apart and 10 m from the forest edge.

During the rainy season, most of the vegetation swept was 0.8 to 1.2 m tall *Baltimora scolospermum* (compositae). This herbaceous annual bears large numbers of pollen- and nectar-rich yellow flowers, which attract a large number of flying insects. Scattered through the *Baltimora* were seedling and saplings of forest trees,

shrubs of *Acacia collinsii*, *Mimosa invisa* (in flower), *Pseudocalymma alliateum*, *Sida*, *Stachytarpheta*, and *Bauhinia unguolata*, and a scattered understory of the grass *Brachiaria fasciculata* (SW) S. T. Blake. During the 1972 dry season, the *Baltimora* was reduced to a few straggly stems and this lowered the amount of vegetation contacted by the net at least ten-fold. This site was a nearly pure stand of *B. fasciculata* during the 1972 rainy season, with no trace of *Baltimora*. Cattle wandered through it during the 1972 dry season, but it was only very lightly grazed compared to the other pasture sites.

Cow Pasture: The area swept was about 200 m by 500 m in the northeast edge of a 50 ha pasture lying between forest on limestone ridges, the swamp (to the west) and the airstrip and Organization for Tropical Studies field station (to the north). The rainy season vegetation swept was a dense 0.5 to 0.7 m tall stand of *B. fasciculata* and other pasture grasses, heavily mixed with scattered sucker shoots of *Bauhinia pauletia*, *Bignonia*, *Pseudocalymma alliateum*, *Acacia collinsii*, *Rauwolfia vomitoria*, *Casearia*, *Randia subcordata*, *Luehea seemanni*, *Pithecellobium dulce*, *Acacia farnesiana*, and dense patches of *Croton*. The portion of the pasture swept has scattered tall trees (*Enterolobium cyclocarpum*, *Bombacopsis quinata*, *Albizzia caribaea*, *Pithecellobium saman*, *Sideroxylon tempisque*, *Gliricida sepium*).

During the dry season, the grass was trampled and grazed down to 0.1 to 0.3 m tall tufts but most of the other plants were evergreen and unchanged (almost all were species not eaten by cattle). During the 1971 rainy season, cattle had not been pastured at the site prior to the sweeps, and the *Croton* flowers were a prominent source of nectar for insects; several species of common *Apion* weevils bred in the abundant seeds. At the time of the dry season sweeps, the *Croton* flowers were still moderately abundant and the seeds were still producing *Apion* weevils.

Bounded on one side by forest and the other by a swamp (with permanent but greatly fluctuating water levels), the insects at this site are only a few hundred meters from refuges from the extremes found in the open pasture in the dry season.

Horse Pasture: This site is the pasture to the west of the road between Hacienda Palo Verde and Hacienda Colmenar, after the third gate, going north from Hacienda Palo Verde. This sweep area is contiguous with at least 10 ha of similar pasture and the closest forest is 200 m to the east. The swamp is about 500 m to the southwest. During both seasons, the vegetation swept was heavily grazed (primarily by horses) and consisted of grass clumps with scattered tufts of sucker shoots from one-half as many species of broad-leaved plants as described above for the Cow Pasture. The grasses and other plants were 0.1 to 0.6 m tall in both seasons. The site had an occasional tall tree left from earlier forest and scattered clumps of 2-3 m tall regeneration (*Acacia collinsii*, *Muntingia calabura*, *Luehea seemanii*, etc.) but these were avoided when sweeping.

Aeschynomene Pasture: This site is about 6 ha of flat pasture cut out of the forest 1 km north of Hacienda Colmenar (where the Hacienda Palo Verde-Hacienda Colmenar road ends). The site is bounded on the southeast by a forested limestone ridge and on the other three sides by the forested (but disturbed by old selective logging) floodplain of the Rio Tempisque (about 400 m west). This river occasionally floods as far as the sweep site itself.

During the rainy season sweeps, the site was a nearly pure ungrazed stand of the annual fabaceous legume *Aeschynomene americana* L. in full flower. The plants

ranged from 1 to 2 m tall and the vegetation was almost impenetrably dense. Below the *Aeschynomene* were scattered grasses, sedges and Marantaceae, but these were rarely contacted with the sweep net. The widely scattered patches of *Mimosa pigra*, 2-4 m in diameter, were avoided in both the wet and dry season sweeps. No livestock had been in the site during that portion of the rainy season prior to the sweeps. In strong contrast with *Baltimora* flowers, *Aeschynomene* flowers were not heavily visited by insects.

During the dry season, *Aeschynomene* disappeared *totally*, through trampling, grazing and biotic litter decomposition, leaving no tall vegetation to be swept. Thus, these sweeps differ from the others reported in the present study and elsewhere in that the net was held so that it brushed along the surface of the ground, with the lower rim cutting through 2 to 15 cm tall grass, herbaceous weeds and litter. Horse dung was occasionally captured by the sweep net.

RESULTS

The results are given in Table 1 and Figures 1 and 2.

DISCUSSION

Intrahabitat variation

Within one season: Two of the series of 800-sweep samples are long enough within a habitat to permit some conclusions about both the technique and microecological variation in beetle and bug community parameters.

In the *Baltimora* Pasture during the rainy season, the numbers of species of adult beetles (86 to 110) and adult bugs (24 to 36) are quite similar on the four sample dates (Table 1). The 5 July low is correlated with the fact that the *Baltimora* was just coming into flower; at the times of the following three samples, *Baltimora* was producing maximum amounts of nectar and pollen. It is noteworthy that the 15 July night and day samples are almost identical in species-richness and numbers of individuals; they had 76% of their beetle species in common and 83% of their adult bug species in common. Unfortunately, after counting in the field, part of the data for the 15 July night sample and the 26 July sample were lost so that a species-sweep curve cannot be plotted for all 3,200 sweeps. However, if this is begun with the 5 July and 15 July samples (Fig. 1), it is clear that it would have leveled off by the time it reached its total of 151 species taken in 3,200 sweeps, since 92% of the beetle species in the 26 July sample had been taken in one of the three previous samples. Based on the same kind of calculation (96% of the adult bugs in the 26 July sample had been collected in one of the three previous samples), the species sweep curve of the adult bugs in 3,200 sweeps in Figure 2 was well leveled off by the time it reached the total of 64 species that were actually caught.

The story is quite different for the four samples taken during the dry season in the Palo Verde Forest. This forest appears superficially to be one habitat but it is obviously not. At the one extreme, 800 sweeps yielded 73 species of adult beetles and 10 of adult bugs and at the other extreme, 800 sweeps yielded 21 and 6, respectively (Table 1). When the smoothest species-sweep curve is plotted for this data by cumulating from the most species-rich to the most species-poor sample (Figs. 1, 2), the beetles level off at about 110 species (but still climbing slowly). However, these four forest samples may be combined in other ways to give a less

smooth approach to the asymptote, as can be seen from the four individual curves plotted in the inserts in both figures. The separate curves show that while the adult bug samples are all beginning to level off by the 800th sweep, all four of the beetle samples were still adding more species at this point. Within the Palo Verde Forest site, the progression from high to low species-richness in the samples is correlated with an obvious ecological gradient. The higher the proportion of the sweeps that were taken through the shady sites below occasional evergreen trees (*Brosimum*, *Ardisia*, *Ficus*, etc.), the larger were the numbers of species and individuals in the samples. In the most species-rich sample, at least half of the sweeps were taken under such trees; the air literally buzzed with insects flying off the foliage as the net passed through such a microhabitat. The most species-poor sample was taken along the sides of a slight ridge with none of these evergreen trees growing on it; the vegetation contacted with the net was almost totally leafless. While these four forest samples were taken by four different people, after having watched them sampling, I am convinced that the intrahabitat differences are not due to differences in sweeping technique.

Between seasons: The differences among the Palo Verde Forest samples in the wet and the dry seasons depend on which dry season forest sample is used for comparison. The dry season sample taken in the most shady part of the forest has the same species-richness and twice as many individuals as each of the wet season forest samples (Table 1). On the other hand, the more leafless portions of the forest have much reduced species-richnesses and numbers of individuals when compared to the wet season forest samples. In short, part of the forest understory serves as a dry season refuge, while the other parts fluctuate seasonally between being very low productivity sites and desert.

In all four of the secondary vegetation sites, the dry season reduces the adult beetle and bug species-richness to about one-fourth that in the wet season samples and the number of individuals is reduced to about 0.1 to 0.05 of that in the wet season (Table 1).

Over all sites, there is surprisingly little overlap in the species composition of the adult beetles and bugs between the wet and dry seasons. Out of the 135 species of beetles taken with 8,800 sweeps during the dry season, only 22 per cent were also taken in the rainy season sweeps. Of the 214 species of beetles taken with 7,200 sweeps in the rainy season, only 14 per cent were also taken in the dry season sweeps (320 total beetle species). The analogous figures for the bugs are 48 species taken with 8,800 sweeps and 15 per cent overlap with the wet season sweeps, and 57 species taken with 7,200 sweeps and 12 per cent overlap with the dry season sweeps (95 total bug species). In retrospect, this low seasonal overlap is probably mostly due to at least half of the insect species taken in the rainy season being associated with an abundant nectar-pollen-seed host (*Baltimora*) which is totally absent in the dry season. The other main contributor to the low overlap is the fact that the shady forest sites, which were major contributors to dry season species-richness (Sample A, 7 March, Table 1), are refuges for insects from all vegetational levels in the forest and not just the level of the sweeps.

Interhabitat variation

Within one season: Perhaps the most dramatic contrast is that between the four secondary vegetation sites during the rainy season. In these four sites, all carved out

TABLE 1

Numbers of species (bold face) and individuals of adult beetles (Coleoptera) and adult bugs (Hemiptera) taken in 800-sweep samples in forest understory and four nearby secondary vegetation habitats

Forest	5 July		15 July		7 March									
Beetles	60	276	80	262										
Bugs	7	12	8	11	73	A	503	41	B	137	C	28	73	D
					10		30	6		13		3	7	21
														6
														11
Baltimore Pasture	5 July		15 July		15 July (night)		26 July		29 February					
Beetles	86	948	99	2769	110	2514	98	1824				22	72	
Bugs	26	205	35	414	36	400	24	262				6	9	
Cow Pasture					21 July				29 February					
Beetles					97	1926			A			B	227	
Bugs					34	315			23	86			41	92
									18	78			25	
Horse Pasture					18 July				29 February					
Beetles					48	124			A			B	11	
Bugs					17	70			9	13			8	16
									9	32			9	
Aeschynomone Pasture					21 July				29 February					
Beetles					20	623							9	
Bugs					8	40			6	30			4	1
									2	6			1	

are adjacent to and 400 m from, the Palo Verde Forest site, respectively. Of the Cow Pasture and Aeschynomene Pasture, 33 and 38 per cent of the beetle species were the same as those in the forest. For the bugs, the comparable figures are 33 and 10 per cent. These two sites are about 4 and 5 km in opposite directions from the Palo Verde Forest site. It appears that local distance effects are operating.

The degree to which the dry season influences the various secondary sites as compared among themselves and with the Palo Verde Forest is evident by inspection of Table 1. The Horse Pasture is most severely reduced of all, probably reflecting the lowered numbers of transients being generated by the small dry season populations. The forest can be viewed as the least or the second-most greatly reduced, depending on which of the four samples is contrasted with the rainy season samples. For beetles, the Baltimora Pasture and Cow Pasture sites have quite similar reductions, but the Baltimora Pasture bugs were depressed much more by the dry season than were those of the Cow Pasture. It may be pertinent that the Baltimora Pasture bugs had a somewhat shady forest very nearby to retreat to, but the forest available to the Cow Pasture bugs is totally deciduous. The Aeschynomene Pasture is far less damaged by the dry season than expected when one remembers that it changed from a lush and nearly impenetrable stand of vegetation during the rainy season to a site with little more vegetation than a cattle feed lot during the dry season.

It was stressed earlier that even within the rainy season the interhabitat variation in beetle and bug species-richness and numbers approaches that found at a wide variety of sites in Costa Rica. If we include the seasonal variation as well, the differences between the richest sample (110 species of beetles for 2,514 individuals, 36 species of bugs for 400 individuals) and the poorest sample (4 species of beetles with 9 individuals, 1 species of bug with 1 individual), the range is about equal to that found at all Costa Rican sites with the exception of the highest rainfall sites at intermediate to low elevations (compare with Table 1 of **Janzen**, 1973b). However, if we select these other Costa Rican samples for comparisons, these ranges are not so impressive. For example, in the San Vito primary sample there were 312 species of beetles in 800 sweeps (Table 1, **Janzen**, 1973b). The present study required 16,000 sweeps in five habitats and two seasons to accumulate 320 total beetle species. By way of contrast, the same San Vito sample had only 21 bug species, a number surpassed in 6 of the present 800-sweep samples.

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Fig. 1. Species-sweep curves for adult beetles. Solid lines are dry season sweeps (February) and dotted are rainy season sweeps (July). The inset shows the four forest samples as separate species-sweep curves, with the letters corresponding to those in Table 1. If all thirty-two 100-sweep subsamples of the Baltimora Pasture site in the rainy season could have been plotted, the species-sweep curve would have approached an asymptote before the total of 151 species at the end of 3,200 sweeps.

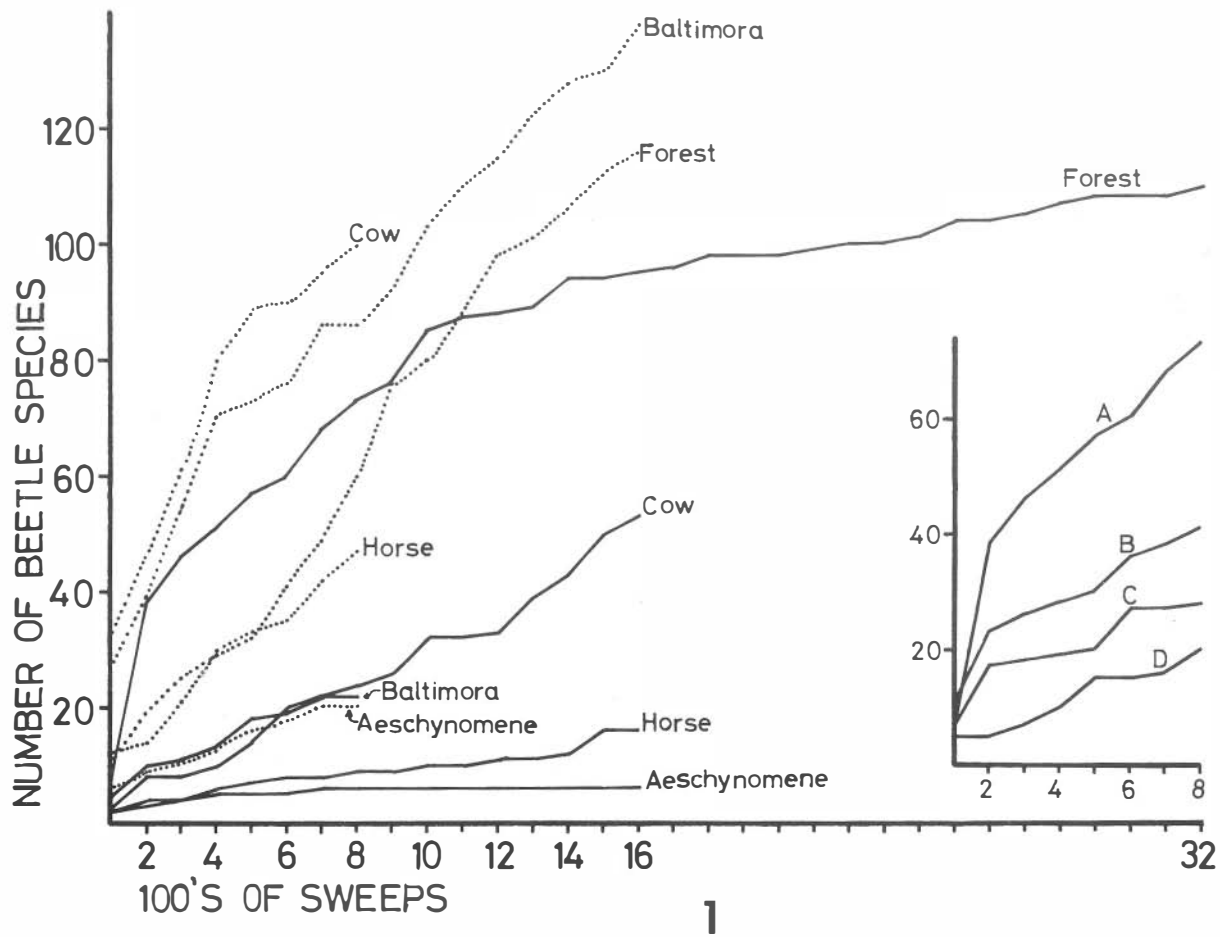
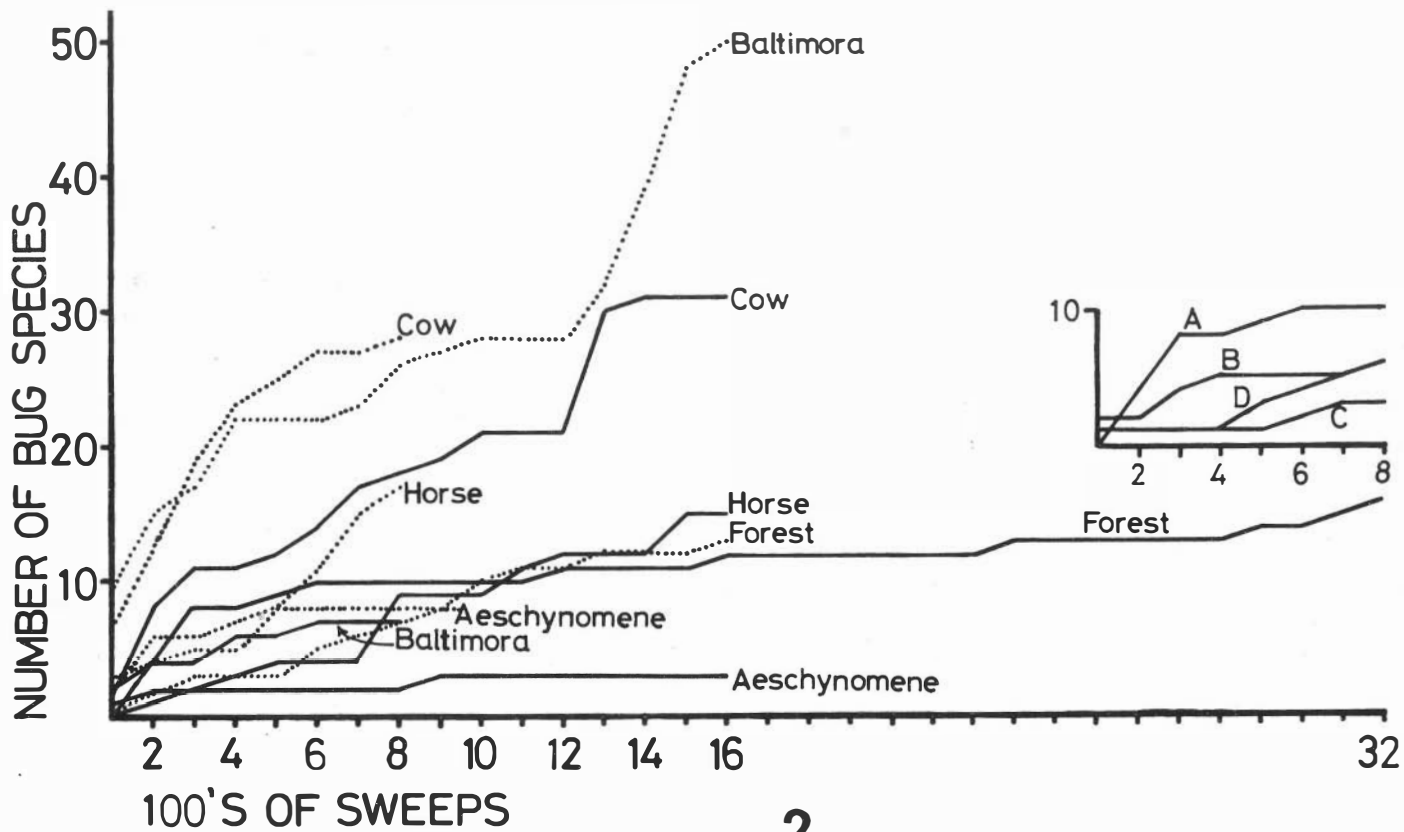


Fig. 2. Species-sweep curves for adult bugs. Analogous to Fig. 1. If all thirty-two 100-sweep subsamples of the Baltimora Pasture site in the rainy season could have been plotted, the species-sweep curve would have approached an asymptote before the total of 64 species at the end of 3,200 sweeps.



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