Ecological Entomology (1986) **11**, 411–423

Vertical community structure and resource utilization in neotropical forest cockroaches

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ABSTRACT. 1. Patterns of vertical habitat use of ten species of cockroaches are examined. Three assemblages of cockroaches are recognized on the basis of morphology, foraging behaviour, foraging heights, and overlaps and breadths of vertical distributions.

2. Three apterous and brachypterous species occur near the ground and comprise one assemblage. They feed mainly on material in the leaf-litter.

3. Species that perch higher either migrate into the leaf-litter on a diel basis and feed on both leaf-litter and epiphyllic materials, or some are strictly arboreal and forage on algae, liverworts, lichens, spores, pollen and trichomes on the surfaces of leaves.

4. Trophic and behavioural correlations with perch height are described and the functions of perching are examined.

5. We conclude that studies of interactions among species are confounded by our lack of understanding of stage- and sex-specific interactions of coexisting species. A simplistic 'species' approach to such interactions is inadequate because it does not recognize intraspecific variation.

Key words. Cockroaches, perching, vertical distribution, competition, guild, assemblage, community.

Introduction

Closely related sympatric species differ in use of resources. Numerous studies report on vertical zonation of animals resulting from environmental factors and/or biological interactions such as competition, predation and mate-finding. Birds (review: Cody, 1974) and lizards (reviews: Schoener, 1974; Pianka, 1973) have been studied extensively, and perch partitioning has been interpreted as an evolutionary consequence of competition. Conversely, the vertical distribution of insects has received little attention.

Cockroaches are rarely used as models in ecological research. Although some information is available on distributions, foraging and movement, and sexual recruitment in the ubiquitous domestic species, there is a dearth of information about the more than 4000 species which live in forests, deserts, grasslands, caves, nests of various animals, and other predominantly tropical habitats (review: Schal *et al.*, 1984). Most

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information on tropical cockroaches is based primarily on collection records and observations of day-time resting sites.

Hawke & Farley (1973) and Edney *et al.* (1974) investigated seasonal and diel variations in vertical (depth) distribution of the cockroach *Arenivaga* sp. (Polyphagidae) in desert sand dunes. Gautier (1974) found differences in perching heights among life-stages of *Blaberus atropos* and *Blaberus colosseus* (Blaberidae) in caves in Trinidad, and Gautier (1980) and Deleporte (1976) noted sexual differences in the cavernicoulous species *Gyna maculipennis* (Blaberidae) and *Periplaneta americana* (Blattidae), respectively. Dreisig (1971) showed that adults of the temperate species *Ectobius* (Blattellidae), when active, migrate upward in the vegetation. He suggested that differential activity and distribution patterns in adults and nymphs may result from physiological differences. Based on differences in perch heights in cockroaches in northeastern Kansas, Gorton (1980) suggested that 'intersexual, interspecific, and probably inter-lifestage competition' were responsible for structuring the community. Schal (1982) reported that cockroaches in the understorey of a tropical forest stratify inter- and intra-specifically.

The aim of the present study was to describe the vertical structure of the cockroach community in the lowest 2 m of a Costa Rican forest, to examine temporal, spatial and trophic similarities and differences among several species, and to document ontogenetic shifts in habitats of cockroaches.

Materials and Methods

The study was conducted during March to July 1979, February to May 1980 and March to June 1981 at Finca la Selva, an Organization for Tropical Studies field station in the Caribbean lowlands of Costa Rica at a latitude of 10°28'N. Holdridge *et al.* (1971) describe the field site in great detail with reference to its history, abiotic factors, vegetational composition and soil types. We utilized two study plots in a 25–30-year-old abandoned plantation. A mark–recapture study to examine individual variations in perch height was conducted in a 400 m^2 plot. A 100 m^2 area with a different vegetation profile was used to examine the effect of perch availability on abundance and vertical distributions of cockroaches.

In nightly sessions of a 5-month capture–mark–recapture programme, adults of ten species were collected by hand, the site of capture was marked, and we recorded: (1) the species identification, (2) sex, (3) perch height, (4) time, and (5) behavioural notes. Marking was done in the laboratory without anaesthesia. The pronotum was scraped with an insect pin and a drop of Eastman 910 adhesive, a dot of coloured Testor's enamel paint and a second coating of glue were placed successively at predesignated positions on the pronotum, which, along with a colour code, corresponded to a number. The insects were returned to their sites of capture on the same night. In subsequent nights sighting of marked individuals was recorded; marked cockroaches were not captured. Traps baited with banana and beer were deployed at ground level (pitfall), 0.5 m, 3 m and 10 m above the ground as an independent assessment of the vertical distribution of cockroaches.

Temporal and relative abundance calculations were made on the basis of a 'conspicuousness' record. The number of individuals of each category (species, sex, age-class) seen was divided by the cumulative time spent searching (observation time) to calculate 'relative activity' values for hourly or 2 h time intervals.

Niche breadth and overlap are measures of ecological specialization and the degree to which sympatric organisms share resources. Here, resources are perches along the vertical niche axis and hourly intervals during the night. As a measure of vertical overlap of perches, O, we used Schoener's (1968) index of ecological similarity,

$$O=1-(1/2)\sum_{i=1}^{n} p_{ij}-p_{ik}$$

where p_{ij} and p_{ik} are the proportions of individuals of species j and species k which are associated with resource interval i.

Breadth, B, along the vertical axis was calculated as

$$B=1\Big/\sum_{i=1}^{n} p_i^2,$$

and as

$$B=\exp\,(-p_i \log p_i).$$

Because a high positive correlation was calculated between these two niche breadth measures

($r=0.995$, $P<0.0001$), only the former was used in correlation analyses.

To determine the relative availability of perches at both plots we chose randomly two 20×20 cm squares within every square metre of both plots and recorded the presence or absence of leaves within 5 cm of a 3 m tall graduated stick positioned in their centres. The vertical distributions of perches for the large and small plots were the averages of 800 and 200 individual 3 m vertical profiles, respectively.

Diel locomotory activity patterns were investigated outdoor in a screened insectary. We divided all the surfaces of 30×15×15 cm cages into squares 7.5×7.5 cm. The frequency at which five individuals crossed these lines was a relative measure of activity (see Block & Bell, 1974). These data were recorded for 3 min at either 0.5 h or 1 h intervals during continuous 24 h periods.

To determine whether vision was involved in selection of perch height, the eyes of thirty field-collected *Epilampra involucris* males were painted with India ink; these and unaltered control males were caged in an outdoor insectary. In experimental series, equal numbers of blinded and control males were allowed to walk out of glass vials onto leaves at 25 cm and at 100 cm above the ground. We recorded the time spent on the leaf before locomotion ensued. Preliminary observations indicated that whereas early in the night (about 19.00 hours) perching individuals were restless and tended to move about, by about 22.00 hours they were more apt to remain on the perch for longer periods of time. Therefore, we started the experiments at 22.00 hours.

Results

General activity patterns

Notes about the biology and habits of the species discussed here are presented in the Appendix. Adults of all species except *I.impar*, *I.* n.sp. 'G', and *C.imitans* rest in the leaf-litter during the day. At dusk (18.00 hours) males and females climb or fly onto understorey foliage. Before sunrise (*c.* 05.00 hours) they move downward to the leaf-litter. The height to which they move and the temporal patterns of these behaviours vary both inter- and intra-specifically. Adults and nymphs of *Imblattella* and *Cariblatta* spend the day in folded dead leaves and other above-ground refugia.

On leaves, cockroaches feed on epiphylls, bird droppings, or fallen materials which are trapped as 'aerial litter'. They commonly perch at the edge of leaves. Females of several species were seen in 'calling' postures, evidently emitting pheromones to which males are attracted (Schal, 1982; Schal & Bell, 1985). Flight

TABLE 1. Comparison of trap catches at four heights.

Species		Height			
		Ground	0.5 m	3 m	10 m
Epilampra involucris	Males	15	3	0	0
	Females	21	0	0	0
Nesomylacris sp.	Males	22	9	0	0
	Females	25	2	0	0
Hyporhicnoda reflexa	Males	9	1	0	0
	Females	12	0	0	0
Xestoblatta hamata	Males	1	11	1	0
	Females	8	6	0	0
Epilampra rothi	Males	12	27	6	1
	Females	5	1	1	0
	Nymphs	106	13	0	0
Xestoblatta cantralli	Males	12	22	8	0
	Females	7	25	1	0
Plectopterine species	Males	3	3	3	1
	Females	4	2	3	0
	Nymphs	3	5	11	2

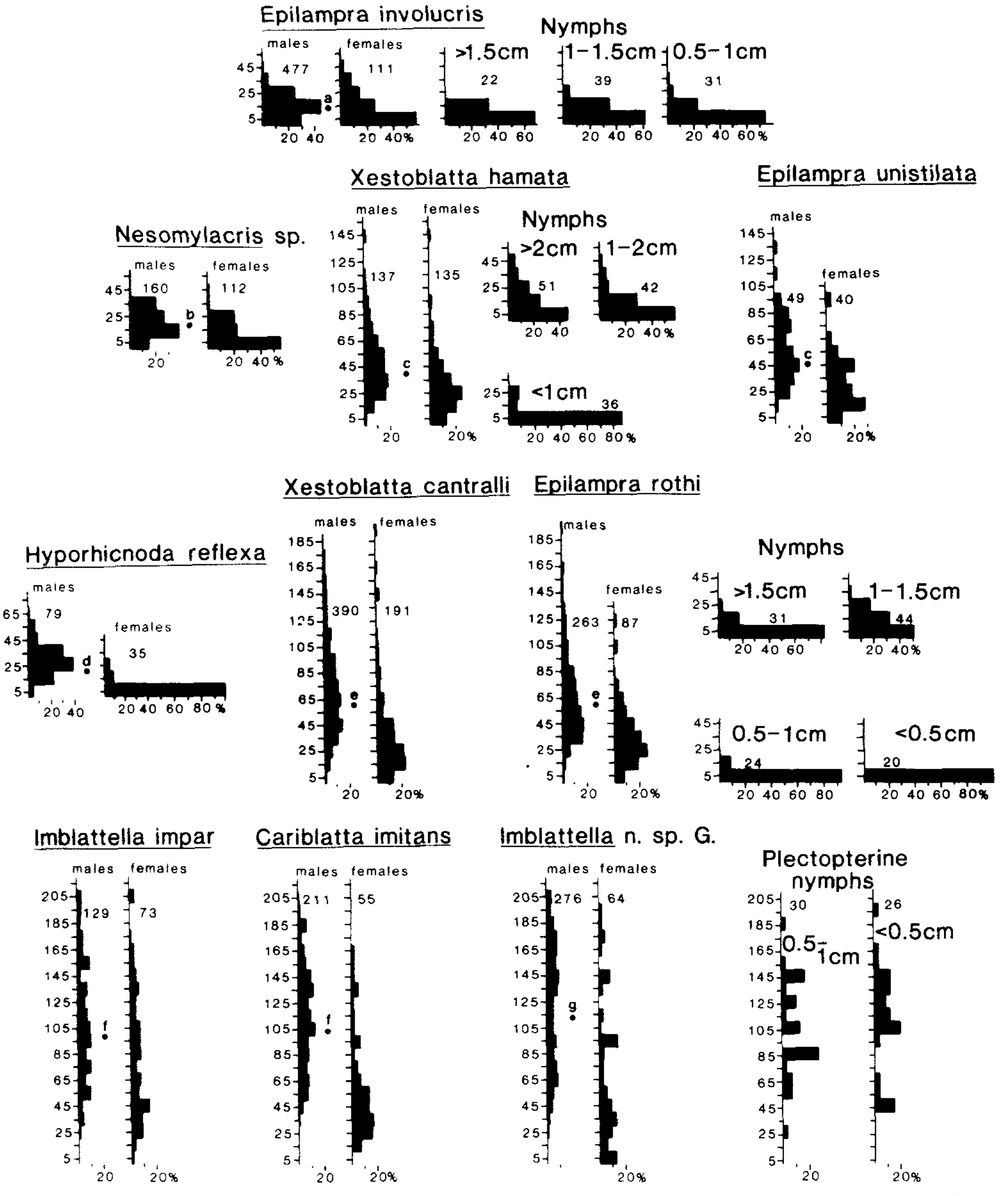

FIG. 1. Vertical distributions of species, sexes and life-stages of cockroaches. The ordinate is perch height in cm. Abscissa is percentage of all cockroaches found at each height interval. The points between males and females for each species are the mean perch height for that species. Statistically different ($P<0.05$, Student–Newman–Keuls test) distributions are labelled with different letters (above species mean). *Imblattella* and *Cariblatta* nymphs are grouped together (plectopterines) because we could not identify them to species.

between perches is common in all winged species.

Perch heights of species

Most individuals of all species were trapped either at ground level or at 0.5 m above the ground (Table 1). The number of adults captured in the 3 m and 10 m traps was only 8.5% of the total adult catch. Because sampling commenced at 21.00 hours when cockroaches were active above ground, we propose that the lower 2 m of the vegetation represents the true range of these species.

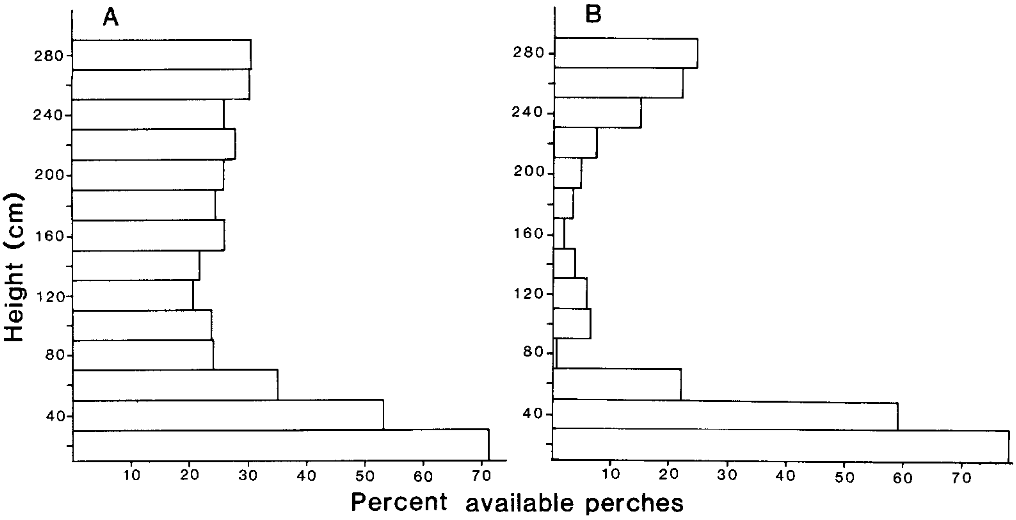

FIG. 2. Vegetation profiles of two study sites. (A) is a typical forest site; (B) is a plot dominated by *Selaginella*.

The distributions of adults of most species are significantly different from each other ($P<0.05$, Student–Newman–Keuls test) (Fig. 1). Overlaps in vertical distributions between pairs of species are negatively correlated with differences between their mean perching heights ($r=0.600$, $P=0.033$). To reflect the probability of co-occurrence of species in a given height interval, the proportion of individuals at each height was corrected on the assumption that perch use is related to the availability of leaves, and that individuals sample randomly from the available

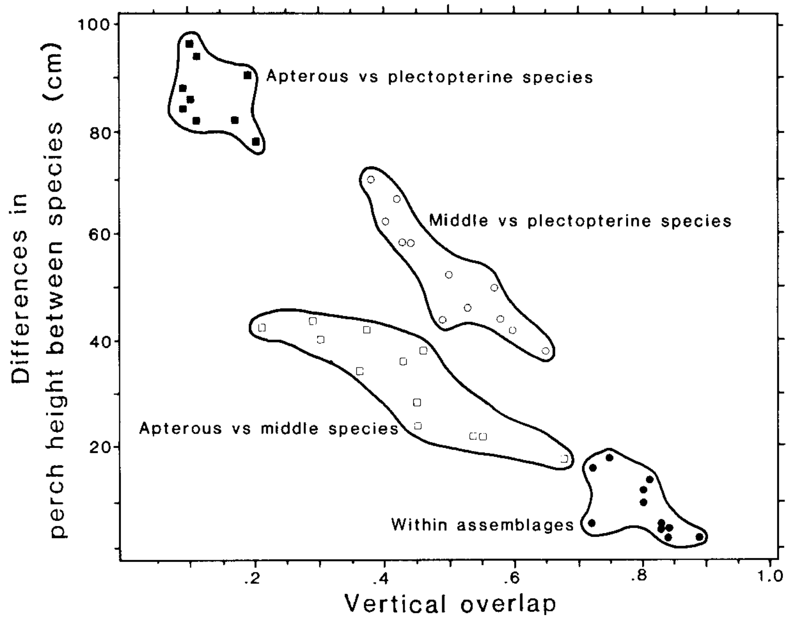

FIG. 3. Relationship between differences in species mean height and vertical overlap. Middle species are *X.hamata*, *X.cantralli*, *E.unistilata* and *E.rothi*. 'Within assemblages' are comparisons of species within each assemblage (e.g. *E.unistilata* versus *Nesomylacris*, *E.rothi* versus *E.unistilata*).

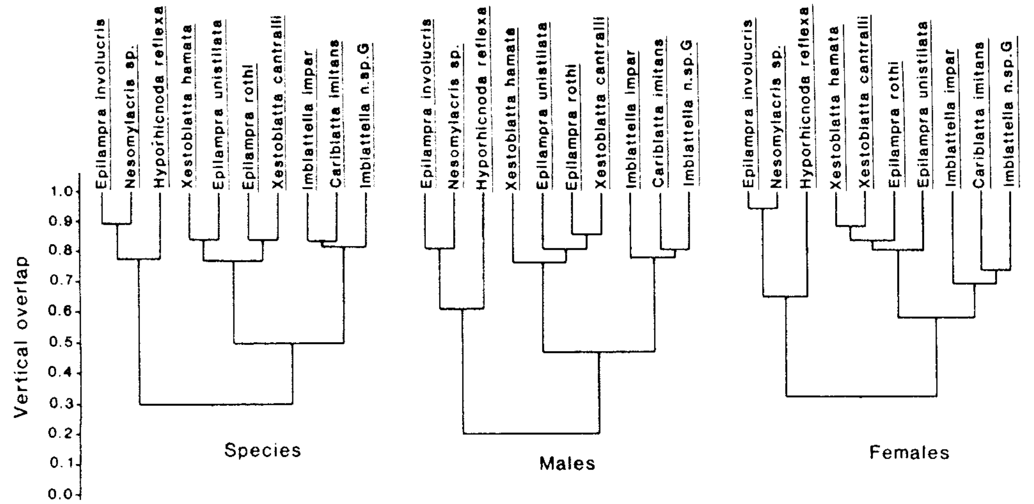

FIG. 4. Dendrogram of ecological similarity of species and consexuals, based on overlaps in vertical distributions. Overlaps within clusters were averaged in the amalgamation procedure.

perches. Because vegetation was most dense close to the ground (Fig. 2), overlaps between low perchers (*E.involucris, Nesomylacris, H.reflexa*) and high perchers (*Imblattella* and *Cariblatta*) were most significantly affected by these correction factors. However, the correlation between vertical overlaps and the corrected vertical overlap measures is 0.985 ($P \leqslant 0.001$, Pearson correlation).

Three assemblages of cockroaches separate along vertical perches (Fig. 3). Adults of *E.involucris* and *Nesomylacris* and *H.reflexa*

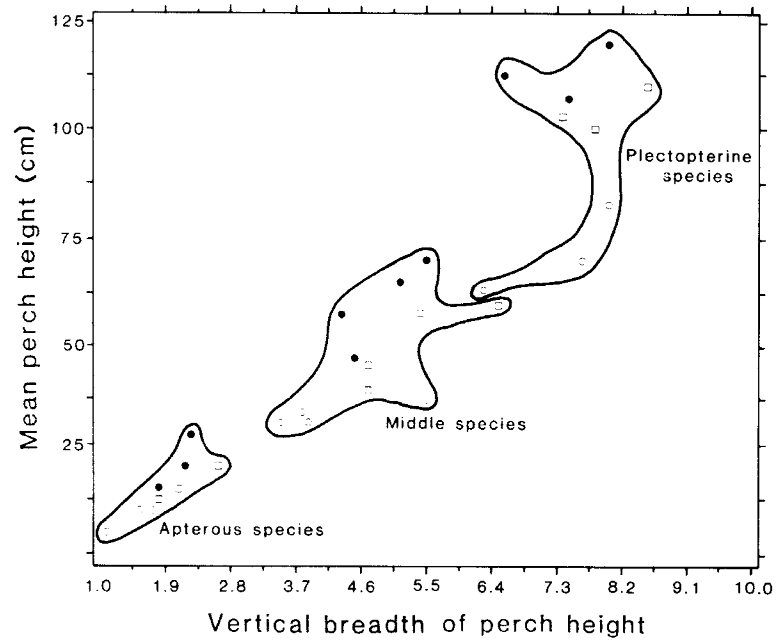

FIG. 5. Relation between mean perch height and vertical breadth of perch height for species (□) and sexes (○, female; •, male). Assemblages are best separated when males in one group are compared to males in the other groups, females are compared with females, and species are compared with species. Boundaries for groups were drawn to delimit the three assemblages; no statistical procedure was used to do so.

females are brachypterous and perch close to the ground. *X.hamata, E.unistilata, E.rothi* and *X.cantralli* comprise an intermediate group; all four species are good fliers and spend the day in the leaf-litter. Approximately 20 cm separate means of *X.hamata* and *H.reflexa* (Fig. 1). The mean perches of plectopterine species (*I.impar, C.imitans* and *I.*n.sp. 'G'; see Appendix) are separated by 40 cm from that of *X.cantralli.*

Vertical overlap values were arranged into symmetrical community matrices using cluster analysis; these are summarized as dendrograms of vertical range similarity. The same three clusters of species separate on the basis of overlaps of perch heights (Fig. 4). Moreover, similar arrangements result when consexuals are clustered.

The three assemblages are distinguishable also on the basis of breadth of vertical distributions (Fig. 5). Apterous and brachypterous species occupy a narrow vertical region close to the ground, while the plectopterine species perch higher and have greater vertical breadths; the others are intermediate between these two groups. Vertical breadths of perches correlate directly with mean perch heights (r=0.968, P=0.001) (Fig. 5). As vertical breadth increases, vertical overlap with the nearest neighbour decreases (r=0.630, P=0.025). Thus, high perchers overlap less with their neighbours than do low perching species with their neighbours.

Intraspecific vertical distributions

Although the vertical ranges of conspecific females and males overlap considerably, their distributions differ significantly (P<0.05, Student–Newman–Keuls test) (Fig. 1) with males always perching higher than females. Trapping results (Table 1) indicate increasingly male biased sex ratios with increasing height, corroborating the 'male above' pattern.

The differences in perch heights between conspecific females and males increase with height above the ground (r=0.852, P=0.0009; Fig. 6). As for species, the vertical breadths of males and females relate to their respective mean perching heights (Fig. 6). Thus, low perching males and females overlap more with their nearest consexual neighbours than with conspecifics of the opposite sex.

Perch heights of immatures were examined in detail in four species; the pattern is similar in the others (Fig. 1). In all species except *Imblattella* and *Cariblatta*, early instars are found in the leaf-litter where parturition occurs or oothecae are

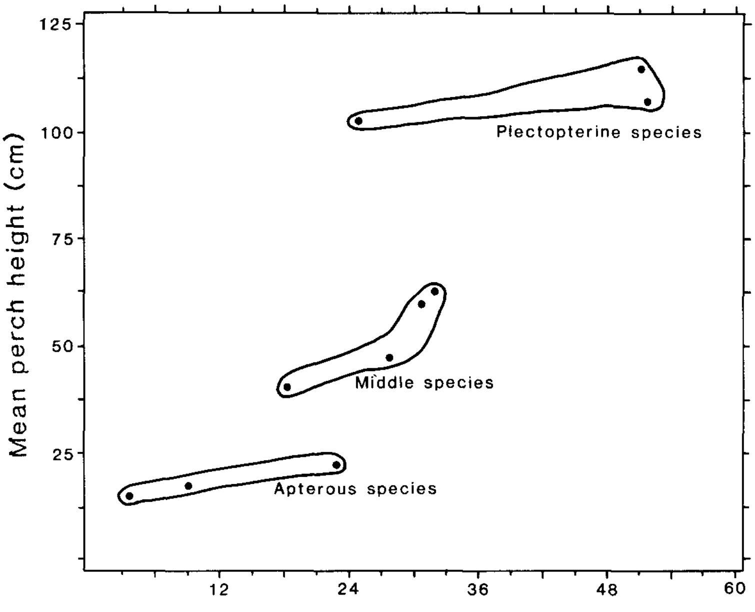

FIG. 6. Relation between mean perch height and the difference in mean heights of conspecific males and females. As perch height increases, separations of conspecific males and females increase.

deposited; older nymphs perch higher in the foliage. Perch heights of the largest nymphs (mostly females) are closest to perches of adult females (Fig. 1). Nymphs of *Imblattella* and *Cariblatta* could not be separated to species; all instars overlap in ranges with each other as well as with the adults.

Diel activity

H. reflexa males initiate perching within minutes after sunset (18.00 hours), and they remain above ground for only 3–4 h (Fig. 7). Because locomotory activity in the laboratory did not correspond to this perching pattern (Fig.

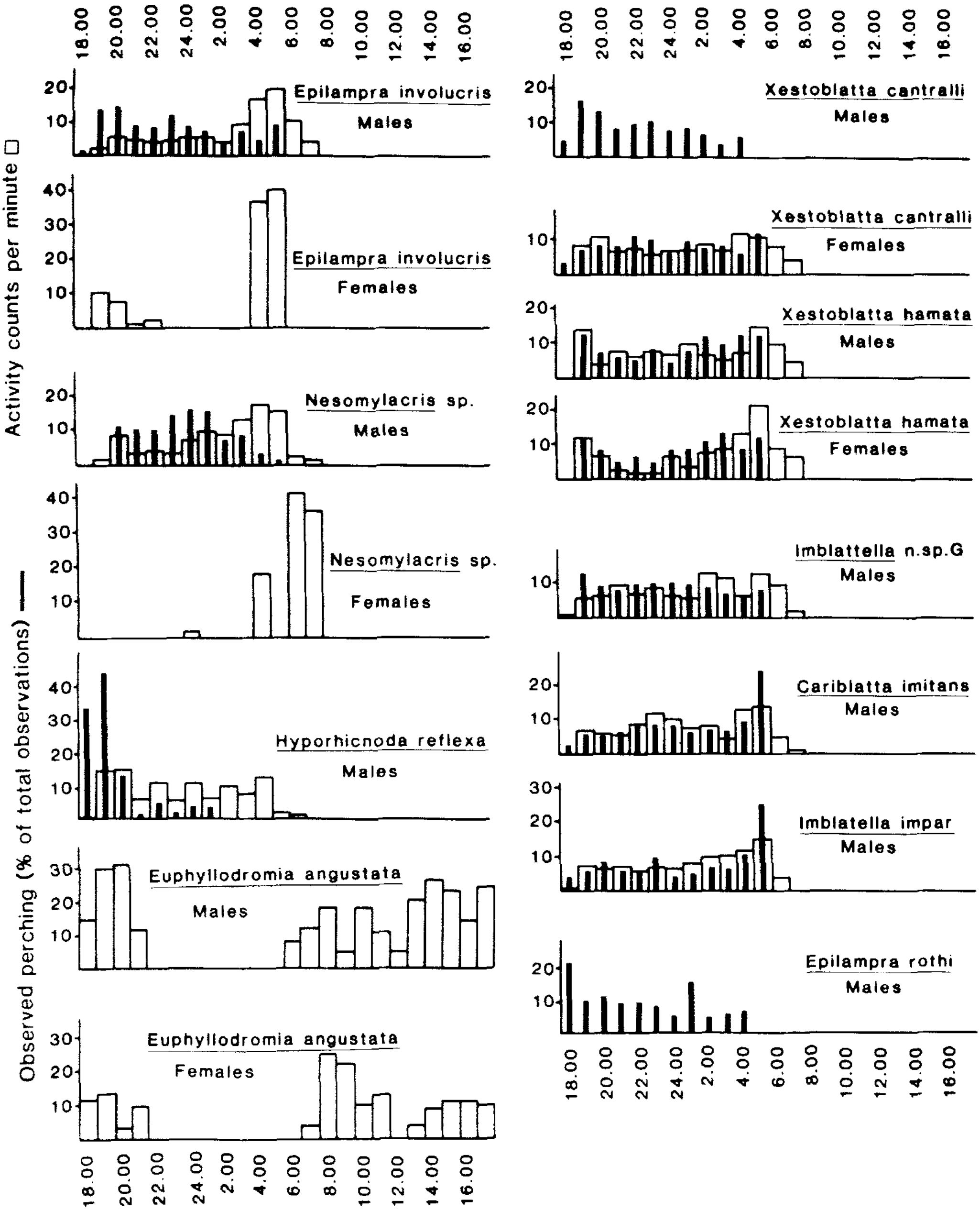

FIG. 7. Activity of cockroaches in the field (a measure of conspicuousness; solid bars), and locomotory activity in an outdoor insectary (open bars).

TABLE 2. Percentage abundance of cockroaches in two plots of different vegetation profiles.

Species	Forest plot	*Selaginella* plot
E.involucris	19.1	41.3
Nesomylacris	8.8	18.3
H.reflexa	3.7	13.7
X.hamata	8.8	4.0
X.cantralli	18.9	5.4
E.unistilata	2.9	0.9
E.rothi	11.4	7.6
I.impar	6.6	2.1
*I.*n.sp. 'G'	11.1	3.0
C.imitans	8.6	3.7

7), and males were trapped in leaf-litter pitfall traps throughout the night (unpublished), they probably remain active in the leaf-litter.

For most species, laboratory and field data are in general agreement (Fig. 7). However, the laboratory measures accentuate the 'on–off' nature of locomotory activity. Some species (e.g. *E.involucris* and *X.hamata*) have bimodal activity patterns with the 'on' peak probably corresponding to the locomotion which initiates perching, and the 'off' peak corresponding to the return back to the leaf-litter.

With few exceptions, temporal overlap among species is large. For males of nine species for which sufficient activity data are available, a positive correlation exists between overlap of perch heights and overlap of temporal activity with the nearest neighbours (r=0.857, P=0.007).

Habitat complexity and height preferences

To determine whether perching heights are related to the availability of perches, we examined perching patterns in an adjacent area wherein *Selaginella* sp. (Selaginellaceae) was most dominant in the understorey. Between 40 cm and 250 cm perches were less available than in the larger plot (Fig. 2). Both *Xestoblatta* species, *E.unistilata, E.rothi, Imblatella* and *Cariblatta* were significantly under-represented in the *Selaginella* plot. The abundance and perch heights of *E.involucris, Nesmylacris* and *H.reflexa* did not differ in the two plots (Table 2).

Individual variations and height selection

Species variations in perch heights were mainly due to large variations in nightly perch choice within rather than between individuals (*E.involucris*: F=1.157, P=0.389; *E.rothi*: F=1.546, P=0.194; *X.cantralli*: F=1.801, P=0.244).

Normal and blinded *E.involucris* males moved down from 100 cm high perches more frequently than males placed at 25 cm (Table 3). We interpret these results to indicate that males at 100 cm employ non-visual cues in orientating to more preferred lower perches.

Discussion

This study was designed to describe perching patterns of a cockroach community within 2 m of the ground. Significant differences in perch heights among species, sexes and age classes suggest that perching above ground may have several functions in the life-history of cockroaches.

Predator avoidance

Cockroaches may enhance their chances for survival by moving out of the leaf-litter, where ground dwelling predators (spiders, ants, frogs)

TABLE 3. Time that experimental *Epilampra involucris* males remained on a leaf after release.*

Experimental condition	Height (cm)	N	Mean±SEM (min)	Significance† (P<0.05)
Normal	25	15	26.7±4.13	a
Blinded	25	15	23.7±3.67	a
Normal	100	15	8.7±1.24	b
Blinded	100	15	7.7±0.96	b

*Recorded at 5 min intervals.

†Conditions labelled with the same letter are not significantly different from each other (ANOVA; SNK, P>0.05).

are more active at night, and onto foliage. However, many spiders in the Ctenidae, Lycosidae and Pisauridae perch on leaves, and detect prey mainly through low frequency vibrations emanating from the prey (Barth & Seyforth, 1979). It appears that cockroaches perching at the edges of leaves may detect such signals from the approaching spider; slight vibration of the substratum elicits running rapidly under the leaf (*Imblatella* and *Cariblatta*), flight to a new perch (*Xestoblatta, Epilampra rothi*), jumping into the leaf-litter (*E.involucris, Nesomylacris*) or 'playing dead' (*H.reflexa*).

Hard, non-resonating surfaces such as tree-trunks and the ground are inferior for this type of predator detection system. Indeed, it appears (unpublished) that the type of perch utilized may be related to the size of the cockroach and its escape behaviour. Large species (*Megaloblatta blaberoides, Nyctibora noctivaga* (Blattellidae) and *Blaberus colosseus* (Blaberidae)), which are rare, perch mainly on tree-trunks. When disturbed, they retreat several centimetres into crevices or crouch down on the substrate, hiding the antennae under the pronotum; they rarely fly.

Gradwohl & Greenberg (1982) demonstrated heavy predation by a diurnal antwren on cockroaches in arboreal leaf-litter in Panama. Most species of cockroaches are well camouflaged in leaf-litter but relatively conspicuous in daylight on green leaves. Thus, the early morning migration to ground and foliage hiding places may be in response to predation by visual predators (lizards, birds) and parasitoids (flies, wasps) above ground. This pattern of vertical migration is similar to that suggested for zooplankton, which evade visual predators by spending the day in deeper, darker waters (Hutchinson, 1967). Conversely, adults and nymphs of *E.angustata* perch on exposed surfaces during the day and hide in and under leaves at night. The black, orange and white coloration of *Euphyllodromia* adults, resembling wasps, and black and white disruptive bands of nymphs may play a role in this reversal.

Microhabitat preferences

Studies of temperature tolerance (e.g. Appel *et al.*, 1983) and temperature and humidity preferences reveal that although cockroaches may tolerate broad environmental ranges, they select narrow microhabitats in choice situations. Since temperature, humidity and wind in tropical forests vary with both height and time of day (Richards, 1952; Schal, 1982), choice of perches may reflect microhabitat selection based on physiological preferences and constraints. These are likely to be size-related in poikilotherms, thus resulting in age (size) related shifts in perch heights in species with incomplete metamorphosis. The translocation experiments, showing that blinded *E.involucris* males select low perches (Table 3), lend credence to the suggestion that cockroaches may follow environmental gradients to orientate to preferred heights. Thus, when perches are not available at preferred heights (Fig. 2), species which are normally found at these heights are under-represented; shifts in perching heights do not occur (Table 2).

Young (1984) suggested that perching may be a form of behavioural thermoregulation in neotropical dung beetles, based on observations of perching only at mid-morning and in sun patches, dark coloration, a decrease in temperature in the rainy season, and general daily activity patterns. Interestingly, *H.reflexa* shows similar activity patterns, but at night rather than in mid-day (Fig. 7), suggesting that much more intensive physiological data are needed before assigning a behavioural thermoregularity function to perching.

Localization of food and feeding

The heights at which cockroaches perch correlate well with their respective diets. *E.involucris* females perch close to the ground; they feed mainly on detritus in the leaf-litter and have more elaborate, sclerotized proventriculi (unpublished). On the basis of stomach contents, *E.involucris* males, which perch at heights up to 50 cm (Fig. 1), also eat epiphyllic algae, bryophytes, lichens, pollen, spores, and other organic matter such as fruits, and flakes of shed bark trapped on the surfaces of leaves. *Imblattella* and *Cariblatta* feed almost exclusively on leaf trichomes, blue-green algae, liverworts, and spores which they obtain from grazing surfaces of leaves; they have relatively small and unspecialized proventriculi (unpublished). *Xestoblatta* and higher perching *Epilampra* feed on epiphylls, fermenting fruits, and bird droppings (Schal & Bell, 1982), trapped on understorey leaves and on the ground. Epiphylls are most common within 1–2 m of the ground and their species composition changes markedly with height within this zone (B. Bentley, pers. comm.).

Localization of mates

Females of some species emit pheromones while perching (Schal & Bell, 1985). Slow winds (Schal, 1982) and dense understorey vegetation may retard horizontal pheromone dispersion (see Aylor *et al.*, 1976). Therefore, perching above the ground may facilitate mate-recruitment. Convection originating on leaf surfaces (Gates & Benedict, 1963) and unstable temperature conditions may explain the 'male-above' perching pattern observed for all species. Thus, initial divergence in perch height of the sexes may be driven by sexual selection pressures rather than by differential niche use. The problem of mate-finding resulting from habitat differentiation of the sexes is less severe in mobile animals than in plant communities (see Meagher, 1980), thus permitting greater ecological divergence.

The largest nymphs of Epilampra and *Xestoblatta* perch lower than intermediate sized nymphs (Figs. 1 and 4) because almost all are females, and adult females perch lower than adult males. Thus, sexual shifts in habitat use modulate gradual ontogenetic shifts.

Morphology and perching

Flightless cockroaches perch close to the ground, and among flying species, smaller species occur higher in the foliage. This pattern is corroborated by fogging of trees with pyrethrum in the same Costa Rican forest, which indicates that few flightless species spend the day in the canopy, and that small plectopterines are more diverse and abundant than other cockroach subfamilies (Fisk, 1983).

We found no apparent differences in perching between the families Blattellidae and Blaberidae. However, by incorporating other habitats (unpublished observations), it is evident that members of the Blatellidae are found mainly in forest and woodland habitats, whereas blaberid cockroaches are more common in 'patchy' microhabitats such as caves, hollow trees, rotting logs, bird nests, and in underground cavities. With the exception of *Epilampra*, which represents a phylogenetic intermediate between the Blattellidae and the Blaberidae (Roth, 1970; Fisk & Schal, 1981), few blaberids occur in the forest above 1 m. Indeed, Fisk (1983) found eight blattellids and only one blaberid species in the canopy of the same forest, and only seven blaberid species compared to about forty blattellid species when data from Panamanian and Costa Rican trees are combined. Most likely, the prevalence of blaberids in 'closed' habitats (caves, hollow trees, under bark) and near the ground is related to their ovoviviparous reproduction and nutritional requirements.

Niche breadth and overlap

Breadth and overlap in perching heights may indicate the degree of potential interaction among species. However, the use of these measures as indices of competition (e.g. Gorton, 1980) may be misleading because the relationships between them are not known (Abrams, 1980), and unrelated species may share common non-limiting resources, and hence overlap extensively. We observed few agonistic contests for perches under natural conditions, and perches seem to be abundant at all heights and during all seasons.

This study shows that the cockroach community is structured on several levels. With respect to sex, the vertical distributions of species represent the combined vertical ranges of males and females which indeed differ significantly from each other. Low overlaps between females and males more likely reflect differing roles in sexual recruitment (Schal, 1982) than intersexual competition. With respect to age, conspecific adults and juveniles perch at different heights. The interaction of age with sex is documented by the progressively higher perches of older nymphs, and differences in perch heights between late instar males and females (Fig. 1). Thus, this cockroach community emphasizes a critical question of community ecology, namely, how do the various life-stages and sexes interact with those occupying similar niches, and not how species interact with sympatric species. We conclude that an understanding of the habitat of different classes of individuals within a population is essential for discussions of community structure. Guild classification based on overlap measures, therefore may serve an important function in presenting a visual representation of the cockroach community, which facilitates nearest neighbour comparisons and comparison with other communities.

Acknowledgments

We thank G. Otis for introducing C.S. to Costa Rica, and the Organization for Tropical Studies for providing logistic support at La Selva field station. Gunter Seelinger assisted with monitoring activity in the laboratory and was an inspiration in the field. We thank M. Grayum for identifying plants in the study plots, R. Holt for a critical discussion of niche metrics, and K. Armitage, R. Jander, C. Michener, O. Taylor and H. Wolda for reviewing earlier drafts of the manuscript. P. Estes assisted with statistical-computer analysis, and F. Fisk identified voucher specimens. Supported in part by NSF grants BNS 80-06284 and BNS 77-24898 to W.J.B. and DEB 80-07556 to W.J.B. and C.S., a Sigma Xi Grant-in-Aid of Research to C.S., and State funds from the New Jersey Agricultural Experiment Station.

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Accepted 24 March 1986

Appendix

The species involved in the study were:

Epilampra involucris Fisk & Schal (Blaberidae) is very common in mature and successional forests. Both sexes are brachypterous. Females are larger than males.

Epilampra rothi Fisk & Schal (Blaberidae) is not a common species; females are rarely seen. More common at fallen ripe fruits.

Hyporhicnoda reflexa Saussure & Zehtner (Blaberidae) males are winged; females are apterous. Both sexes and nymphs exhibit tonic immobility when disturbed (Schal, unpublished).

Nesomylacris sp. near *asteria* (Blattellidae) is very similar in morphology to *E.involucris* (both sexes are brachypterous) but significantly smaller. Behaviourally and in egg case morphology it is more similar to *Xestoblatta cantralli.* A common leaf-litter species.

Xestoblatta hamata Giglio-Tos (Blattellidae), although not very common in the 'open' forest, is conspicuous at specific feeding sites. Both sexes are winged and superficially resemble the American cockroach (*Periplaneta americana*).

Xestoblatta cantralli Fisk & Gurney (Blattellidae) is very common. Both sexes are winged but are smaller than *X.hamata.*

Imblattella impar Hebard, *Cariblatta imitans* Hebard, and *Imblattella* new species 'G' (Fisk, 1971) (Blattellidae). All three species are similar morphologically and behaviourally and are found in the same habitats. Other members of these genera occur at La Selva but are not common. All adults are winged and are similar in size to the German cockroach (*Blattella germanica*). Both genera are in the subfamily Plectopterinae.