

Behavioral and Physiological
Ecology and Community
Structure of Tropical Cockroaches
(Dictyoptera: Blattaria)

by Coby Schal

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CHAPTER 1

Introduction

In the introduction to their treatise on the biotic associations of cockroaches, citing some 1700 references, Roth and Willis (1960) concluded that, "our detailed knowledge of cockroaches is based on studies of few domiciliary pests that man attempts to eradicate. Comparable studies of the bionomics of the less well known species should add much valuable information to our knowledge of this ancient group." In the years since the treatise, and to a large extent because of Roth's continued research, the cockroach has become a "white rat" of invertebrate biological research. Yet, the gloomy picture presented above has changed little. Of the 109 studies listed in the 1980 Biological Abstracts under the heading "cockroach", 55% deal with physiological aspects and/or control of Periplaneta americana or Blattella germanica. The other 49 reports examine one or several species maintained in laboratory cultures. Of these, 65% address developmental, genetic, cellular, or molecular questions. Methodological, psychological, and papers dealing primarily with other animal groups comprise the bulk of the remaining 17 papers. With few exceptions, the behavioral and ecological studies are conceived and implemented in the laboratory. These statistics are representative of other recent years as well. Our total ecological information on several species which are well studied in laboratories is provided by the labels accompanying museum specimens. For instance, both Gromphadorhina portentosa and

Nauphoeta cinerea have been studied extensively with regard to their social behavior, neurophysiology, and endocrinology (see Bell and Adiyodi, 1981). Yet, our understanding of their natural habitats and ecological associations is limited to vague geographic distribution data.

A. Classification of Blattaria

Cockroaches are placed in five families comprising two major phyletic lineages separated on the basis of reproductive strategies and morphology (McKittrick, 1964).

Members of the primitive Cryptocercidae are oviparous and they are physiologically and ecologically similar to termites. The Blattidae are also oviparous, producing egg cases frequently; embryogenesis proceeds in the discarded ootheca. Blattellidae is the largest family with members ranging from the blattid reproductive mode to a strategy conferring greater protection on the developing embryos; the female may rotate and then carry an ootheca externally (attached at the genital pouch) until the young hatch. Females in the family Polyphagidae also carry the ootheca externally after rotating it in a manner similar to some of the blattellids. The most advanced forms occur in the largely tropical Blaberidae. In all of the Blaberidae the egg case is rotated and retracted internally into the uterus where embryogenesis occurs. Pseudo-viviparous Diploptera punctata represents the most highly evolved strategy within the Blaberidae. The implications of these reproductive strategies will be discussed in relation to spatial distributions, communication and social behavior of cockroaches.

B. Habitat preferences and microhabitat selection

Few studies deal with cockroach habitat preferences under natural conditions, although laboratory investigations document preferences for temperature (Gunn, 1934, 1935; Gunn and Cosway, 1938; Edney et al., 1978; Appel, 1982), humidity (Gunn, 1935; Gunn and Cosway, 1938; Edney et al., 1978; Appel, 1982), light conditions (Goustand, 1958; Crawford and Cloudsley-Thompson, 1971), types of shelters (Berthold and Wilson, 1967; Mizuno and Tsuji, 1974), and substrate (Takagi, 1979; Crawford and Cloudsley-Thompson, 1971).

Gautier (1974a,b) studied the spatial distribution of burrowing blaberid nymphs in caves. The number of nymphs found in each 50 cm square sample correlated positively with both the depth and quantity of organic matter in the substrates tested. Nymphs concentrate in zones in the substratum where bat guano, fruit, and twigs dropped by bats accumulated. Nymphs are absent from zones of dry soil, stones, or pebbles. Therefore the positions of bats in the cave, which determine the placement of guano, are related to the horizontal distribution of nymphs.

Cockroaches employ behavioral strategies to cope with adverse desert climates. Arenivaga and Polyphaga (Polyphagidae) avoid the heat and low humidity of the desert by associations with burrowing turtles and rodents during the day (Roth and Willis, 1960). The relative humidity inside kangaroo rat burrows, for example, is several fold higher than that recorded on the desert surface (Schmidt-Neilsen, 1949, in Roth and Willis, 1960). Desiccated A. investigata can absorb water vapor from

the surrounding air at relative humidities of 82% or above (Edney, 1966). Relative humidities of 82% and above are available only 45 cm below the sand surface (Edney et al., 1974). Hence these microhabitats may provide cockroaches with a predictable source of water.

The patchy diurnal distribution of cockroaches near desert plants also can be explained by water relations (Hawke and Farley, 1973; Edney et al., 1974). Micorrhizae that coat adventitious roots of desert shrubs (Harley, 1959) and contain 35-38% moisture are found in gut smears of Arenivaga sp. These fungi are probably utilized as sources of water as well as nutrients. Arenivaga sp. is never seen on branches or leaves of plants above the desert floor, and surface activity ceases if the temperature reaches 40^o C (Hawke and Farley, 1973). By contrast, adult males of A. investigata emerge above the surface, perch on bushes, and fly to lights (Edney et al., 1974).

Studies that delineate microhabitat preferences in forest communities are limited to species descriptions with qualitative information on distribution, life histories, and general habitats (e.g., Blatchley, 1920), and classification of habitats based on soil types, drainage, slope, and floral compositions (e.g., Cantrall, 1943; Friauf, 1953). Lawson's (1967) work is a summary of trapping data, but no information is provided on the methods employed, types of traps used, or the schedule of trapping. Gorton's (1980) study of six wood cockroaches (Blattellidae) in Kansas examined vertical and horizontal distributions, relative abundance, and seasonal variations in grassland and forest habitats.

The need for intensive work on temperate cockroaches is best

illustrated by the contrasting results of these and other papers. For instance, Lawson stated, on the basis of a few captures, that "Parcoblatta bolliana was strictly a grassland cockroach species in Kansas, and P. lata was frequently in open woodlands." Gorton, on the basis of two "nonforest" and 12 "forest" sightings considers, the former a forest species; on the basis of 110 captures he found P. lata most commonly in prairie and disturbed grasslands. Both studies agree that P. uhleriana and P. virginica are forest species, but Friauf (1953) found the latter only in scrub habitats. Unfortunately, differences between the field sites and methods preclude a direct comparison of these studies.

Four species of Ectobius (Blattellidae) were observed by Morvan (1972) in Brittany in the following biotopes: E. lapponicus on mesophilous heathlands under pine trees, E. lividus along borders between forest and mesophilous heathlands, dry heathlands, and edges of peat bogs, E. panzeri on meso- and xerophilous heathlands and E. sylvestris on mesophilous heathlands, peat bogs, and forest borders. Other data from Europe indicate localizations of E. lapponicus and E. panzeri in deciduous forest. Strict relationships between a given habitat and any one of these species are not evident.

Other reports of microhabitat selection include investigations of specialized niches. Roth and Willis (1960) reviewed associations of cockroaches with termites, ants, bees, wasps, and birds. Although no studies attempt to delineate preferences of commensal cockroaches, much information is available about the biotic and physical characteristics of these microhabitats. Many cockroach commensals are restricted to

their myrmecophilous or termicophilous habitats, although other occasional or accidental associations were reported (Roth and Willis, 1960). Commensal associations are no doubt the result of ecological convergence of unrelated species on similar microhabitats (Chopard, 1924).

Rotting logs and loose boards offer a microhabitat for many tropical and temperate species. Best studied is Cryptocercus punctulatus (Cryptocercidae) in the Appalachian mountains and in Oregon and northern California in the U.S. (Cleveland et al., 1934; Seelinger and Seelinger, unpublished). Family groups of a male, female, and nymphs excavate in fallen rotting logs which are used as food. Other congenerees occur in similar habitats in the Far East (Bobyleva, 1975). Extensive work of Cleveland et al. (1934) on this cockroach and its symbiotic protozoans examines, among other topics, the geographical and microhabitat distribution of C. punctulatus. Forested localities with dense leaf-litter provide a suitable cool environment for C. punctulatus, but "the main factor (controlling the distribution of this insect) is probably the effect of temperature on its cellulose-digesting protozoa without which it cannot exist" (Cleveland et al., 1934).

Many species have been collected under loose bark of live or fallen logs, including North American species of Parcoblatta (see Roth and Willis, 1960). Schal and Seelinger (unpublished) noted that Capucina patula juveniles in Costa Rica were restricted to these habitats, whereas adults were occasionally seen on nearby foliage. Being cryptically colored and dorso-ventrally depressed, C. patula is well adapted for burrowing in crevices.

C. Objectives of present research

My overall goal was to gain insight into the distributional ecology of some tropical cockroaches and to relate ecological patterns to interspecific, intraspecific, and trophic relations among cockroaches. Most cockroaches are tropical. Studies of temperate species concern ecologically marginal (usually domiciliary) species. Therefore, this study of some tropical species is a start for investigations of cockroaches in the habitats where they are most abundant and diverse.

Chapter 2 is a taxonomic treatment of three of the common species at the La Selva field site, and a related species from San Vito, Costa Rica. It was essential that these species be named and their phylogenetic relationships understood in order to record and understand the biological information concerning them.

Chapter 3 reports the framework of the research. In it I describe the cockroach community and present data relating to perch height and various niche metrics. Differences in resource utilization between the major phyletic lines are discussed.

In Chapter 4 I address the problem of differential habitat utilization by the sexes and examine its role in mate-finding.

Chapter 5 is a study of sexual selection in one species. It relates male contribution of urates to females to nitrogen deficient environment. This study was part of a larger effort to relate sexually divergent habitats to trophic differences between males and females.

CHAPTER 2

New Species of Epilamprine Cockroaches from Costa Rica and Panama
(Blattaria: Blaberidae)

Four new species of Epilampra are described, E. involucris and E. belli from Costa Rica, and E. unistilata and E. rothi from Costa Rica and Panama. The first three, along with E. carinulata (Saussure), are designated as the Carinulata Group of Epilampra.

INTRODUCTION

Several undescribed species of cockroaches were encountered in Costa Rica and Panama in recent years. In this chapter four new species are described, and some biological notes given in order to facilitate future studies. I follow Roth's (1969, 1970a,b, 1973) methods of dissection and preparation of the genitalia and his system (as derived from McKittrick, 1964) for naming the parts. Roth (1970b) in his study of the genus Epilampra Burmeister, 1838, discussed the close affinities of Audreia Shelford, 1910, to Epilampra and the ambiguities encountered by other specialists (Hebard, 1920; Rehn and Hebard, 1927) resulting from Shelford's characterization of Audreia. Consequently, Roth transferred all the Audreia species which he examined, except the type-species, A. carinulata (Saussure), 1895, into either Subgroup A of his Burmeisteri Group or his monotypic Heusseriana Group of Epilampra or to the genus Poeciloderrhis Stal, 1874. Roth based his conclusions chiefly on the morphology of the male genitalia, noting that the primary character used by Shelford, the reduced subquadrate tegmina in both sexes, is not shared by all Audreia. For example, A. exploratrix Gurney has lateral lobate tegmina, while A. bromeliadarum Caudell and A. cicatricosa (Rehn) are apterous. Three of the species described here share characters of the male genitalia and lack of a left style with A. carinulata, yet the nymphal color patterns, where known, are typical of Epilampra. I consider these four species to comprise a new species group within the genus Epilampra.

The holotypes and allotypes of all four species described here are

deposited in the Ohio State University Entomology Museum. Paratypes are divided about equally between the Snow Entomological Museum, University of Kansas, and the F.W. Fisk collection.

Carinulata Group

Adults usually shining reddish brown; tegmina usually short, subquadrate in both sexes (but may be full length); sub-genital plate of male asymmetric, single right style; hooked phallomere, R2, stout, without subapical incision, sheath proximal to base of R2 without row of slender setae noted for most Epilampra; sclerotization of left phallomere, L2d, diagnostic for the group and species within it; nymph tan or gray, numerous dark punctations as typical for Epilampra. Appearance of R2 in this group very similar to R2 in Poeciloderrhis (as defined by Roth, 1970a), but no Carinulata Group species shows abdominal tergal glands as noted for male Poeciloderrhis.

KEY TO SPECIES OF THE CARINULATA GROUP

1. Adult fully winged in both sexes ----- unistilata, new species
 Adult with tiny wing rudiments and short subquadrate tegmina in both sexes ----- 2
2. Smaller, length of male under 14 mm, of female under 18 mm
 ----- carinulata (Saussure)
 Larger, length of male 16-23 mm, of female 22-28 mm ----- 3
3. Male with flattened sclerotization of left phallomere, L2d, L-shaped and blunt-tipped (Fig. 2-1A); female with latero-posterior angles of abdominal tergum 7 acute; supra-anal plate with very shallow (0.15 mm deep) median notch ----- involucris, new species

Male with flattened sclerotization of left phallomere, L2d, hammer-head-shaped (Fig. 2-1D); female with latero-posterior angles of abdominal terga 3-7 acute, spinelike; supra-anal plate without median notch ----- belli, new species

Epilamra involucris Fisk and Schal, NEW SPECIES

Figs. 2-1A, 2-1B, 2-1C

Male holotype. Measurements in Table 2-1. Head broad and flat, interocular distance nearly half width of head, distance between white ocellar spots one third width of head; maxillary palpus pale, distal (fifth) segment covered with gray microtrichiae giving it a velvety appearance; segment 5 longer than 4, slightly shorter than 3; mouthparts lighter colored than reddish brown of head and body; antennae brown, shorter than body. Pronotum convex, semicircular in outline, latero-posterior angles rounded, right and left posterior margins straight, meeting at obtuse angle (160 degrees); pronotum covering most of head; tegmina truncated, one and a third times as long as pronotum, their latero-posterior angles broadly rounded, posterior margins nearly straight, exposing 7 abdominal terga but covering tiny wing rudiments; tegmina smooth, venation feebly indicated by lines of shallow punctations between scarcely elevated veins.

Abdominal terga, except tergum 7, bear acute spines at latero-posterior angles, smooth except for up to 18 low longitudinal ridges (cicatrices) on distal quarter of each tergum; tergal glands or specializations not evident; supra-anal plate extends beyond sub-genital

plate, broadly rounded posteriorly with shallow (0.2 mm deep) median notch; plate reddish brown proximally, distal half nearly transparent with scattered small raised black spots, each surrounded by a setal socket; cercus light brown, flattened, stout, apparently 10-segmented; terminal segment finger-shaped, black-tipped. Genitalia (Figs. 2-1A,B,C) similar to those of carinulata (Roth, 1970b, Figs. 347-352); hooked right phallomere (R2) small, stout, blunt-tipped except for minute distal spine; subapical incision lacking. R2 of holotype has apparent split on outer circumference of hook, but split lacking in dissected paratypes. Flat sclerotization of left phallomere (L2d) blunt-tipped and L-shaped as in carinulata, but membranous prepuce readily visible due to thick covering of microtrichiae; phallomere L1 with deep, well defined cleft, setal brush lacking.

Abdominal sterna smooth, transverse except posterior margin of sternum 7 with sharp lateral emarginations at base of each cercus, the remainder broadly concave; sub-genital plate with anterior margin broadly convex, posterior margin convex laterally, broadly emarginate centrally with simple (0.5 mm) right style, left style absent. Legs and ventral body surface brown, less reddish than dorsal surface; ventro-anterior margin of front femur with 4 large spines separated by row of minute setae from 2 apical spines; ventro-anterior margins of mid- and hind femora with 4 spines plus apical spine, of hind-femur with 4 spines only; mid- and hind femora with dorso-apical (genicular) spine. Tibiae fully spined; tarsi with obvious pulvilli on 4 proximal tarsomeres, large arolium and simple symmetrical claws on fifth tarsomere.

Female allotype. External form and color similar to those of male except as follows: Tegmina with posterior margins broadly rounded, merging imperceptibly with latero-posterior angles; tergum 7 with latero-posterior angles acute; supra-anal plate uniform reddish brown, lacking color pattern noted for type, plate more transverse, not extending beyond sub-genital plate; median notch shallow (0.15 mm deep). Sub-genital plate fused with sternum 7 (as in all female blaberid cockroaches), its anterior margin slightly convex, posterior margin semicircular with sinuate outline. Genitalia not studied.

Male nymph (subimago). Head broad, distance nearly half head width, interocellar distance 0.35X head width; front of head brown with scattered dark punctations, mouthparts lighter colored, maxillary palpus as in adult. Antenna brown; pronotum convex, semicircular in outline, posterior margin transverse, latero-posterior angles broadly rounded and extending posteriorly; meso- and metanota exposed; transverse wing pads seen as broadly rounded latero-posterior angles; color of entire notum light gray, heavily marked with black punctations and dark brown spots, spots concentrated centrally along posterior margins of terga. Abdominal terga bear acute spines at latero-posterior angles and raised cicatrices as described for adult; each cicatrix marked by dark brown spot; other spots on terga apparently formed by clusters of scattered dark punctations. Overall coloration shows "salt and pepper" effect characteristic of Epilampra. Supra-anal plate semicircular with broadly rounded latero-posterior margins reflexed and median notch at posterior end; coloration gray with numerous punctations; tan, black-tipped cerci

stout, weakly segmented. Abdominal sterna light brown with dark punctations; sub-genital plate with right style present, left absent (earlier instars have symmetrical paired styles).

Types. Holotype male, allotype female, 6 male and 3 female paratypes and 2 nymphs all from Costa Rica, Heredia Province, Finca La Selva near Puerto Viejo, collected by me during 1979 and 1980; other male and female paratypes from same locality collected by F.W. Fisk in March 1974.

Remarks. Epilampra involucris may be separated from other species in the Carinulata Group by means of the key. Based on external morphology alone it is difficult to separate from E. belli, but the male genitalia are distinct. Also, based on present knowledge, the species are allopatric; involucris is found in the Caribbean lowlands of north-central Costa Rica while belli occurs in the Pacific highlands in southern Costa Rica near the Panama border. Epilampra involucris is commonly found in both primary and secondary (older than 20 years) forests. The males rest in leaf-litter by day but climb onto vegetation at dusk, rarely climbing higher than 50 cm above the ground (see Chapter 3). Females and nymphs occur in the leaf-litter though occasionally late instar nymphs and females climb as well. The courtship sequence is somewhat similar to that of Gromphadorhina portentosa (Schaum) (Barth, 1968). Following contact with a female the male arches his abdomen down and then up in a sweeping motion until he contacts the female's genitalia. The more common sequence noted in Blattaria, namely, mounting of the male by the female, does not occur in this

species. Copulation takes place in the usual opposed position and lasts 20 to 30 minutes. As in other blaberid cockroaches, the oothecae are not deposited externally but are held in the genital pouch until the young are hatched. Dissection of six oothecae disclosed 50 ± 2.53 (mean \pm standard deviation) developing embryos in each.

The name involucris refers to the flightless condition which this species shares with most members of the Carinulata Group.

Epilampra belli Fisk and Schal, NEW SPECIES

Figs. 2-1D, 2-1E, 2-1F

Male holotype. Measurements in Table 2-2. Head broad and flat; interocular distance just over half head width, interocellar distance one third head width; dark reddish brown color of body and head extends to clypeus; clypeus and mouthparts buff; expanded distal segment of clypeus velvety gray; antenna brown. Pronotum and tegmina as in involucris; both species show suffused sprinkling of darker spots around margins of pronotum and tegmina comparable to black punctations of other Epilampra. Latero-posterior angles of abdominal terga 2-4 about 90 degrees, of terga 5 and 6 acute, spinelike, of tergum 7 rounded. Terga smooth except for cicatrices along distal margins; tergal specializations absent. Supra-anal plate extends beyond sub-genital plate, broadly rounded posteriorly with very shallow notch; exposed portion of plate mostly transparent with scattered setae; cercus light brown, apical segment slender, black-tipped. Abdominal sterna and sub-genital plate as in involucris (right style present, left absent).

Genitalia (Figs. 2-1D,E,F) similar to those of involucris except as follows: R2 lacks any split on its outer circumference, L1 more sclerotized, L2d with free sclerotized portion shaped like hammerhead, proximal extension truncate, apical extension blunt-tipped; additionally, a sclerotized portion extends into membranous prepuce; prepuce nearly transparent, lacking microtrichiae. Legs differ from those of involucris only in 3 (rather than 4) large spines on ventro-posterior margin of hind-femur and smaller tarsal arolia.

Female allotype. External features similar to holotype except as noted: Posterior margins of tegmina broadly rounded, merging with latero-posterior angles; abdominal terga 3-7 with latero-posterior angles acute, spinelike; supra-anal plate uniform dark reddish brown, posterior margin without median notch; sub-genital plate with anterior margin slightly convex, posterior margin semicircular.

Types. Holotype male and allotype female from Costa Rica, Puntarenas Province, Finca Las Cruces near San Vito, collected by W.J. Bell January 27, 1980; one male paratype collected by M. Kosztarab February 12, 1970 at same locality; one male, 3 female paratypes collected by F.W. Fisk February 4-6, 1974 from same locality.

Remarks. Epilampra belli is closest to E. involucris but can be separated from it as noted in the key and remarks under involucris. Very little is known of its biology except that it favors very moist habitats. The species is named after Dr. William J. Bell who collected the type specimens.

Epilampra unistilata Fisk and Schal, NEW SPECIES

Figs. 2-1G, 2-1H, 2-1I, 2-2B

Male holotype. Measurements in Table 2-3. Head flat; interocular and interocellar distances nearly equal, about a quarter head width; vertex tan; nearly black interocellar band present; face and mouthparts mostly buff; maxillary palpus with fifth (distal) segment covered with gray microtrichiae, segments 3 and 4 subequal in length, shorter than 5; antenna brown; pronotum exposing vertex of head and dorsal areas of compound eyes; pronotum vaulted, anterior and lateral margins forming a semicircle; latero-posterior angles broadly rounded, right and left posterior margins straight, meeting at 120 degrees angle; base color mottled red brown, interrupted by poorly defined pale median line. Tegmina fully developed, extending beyond tips of cerci; discoidal sectors (M + Cu veins) oblique; wings and tegmina transparent, tinted with reddish brown, but tegmina also with darker brown mottling. Light brown abdominal terga have latero-posterior angles broadly rounded, cicatrices barely visible, tergal specializations lacking; supra-anal plate semicircular, rounded posterior margin with oblique median emargination; cercus slender, nearly 7X longer than wide.

Genitalia (Figs. 2-1G,H,I) characteristic for Group; R2 small and stout with blunt tip, no subapical incision or slender setae on sheath; L1 with a deep open cleft; L2d with flattened sclerotized portion ovate distally, proximal portion (adjacent to L2vm) with deep U-shaped emargination. Sub-genital plate (Fig. 2-2B) convex anteriorly and posteriorly, posterior margin with ample median emargination, single

style arising from right edge of emargination. Abdominal sterna light reddish brown with scattered darker tiny spots, no spots on legs and ventral thorax; ventro-anterior margin of front femur with 3 large spines separated by row of widely spaced minute setae from 2 apical spines; ventro-anterior margins of mid- and hind-femora also ventro-posterior margins of front and mid-femora all with 3 large spines plus apical spine, ventro-posterior margin of hind-femora as above but lacks apical spine; in addition, mid- and hind-femora bear genicular spine. Tibiae fully spined; tarsi with obvious pulvilli on 4 proximal tarsomeres; arolium present; claws simple, symmetrical.

Female allotype. Similar to male in external form and color except as follows: Interocellar band not so dark; supra-anal plate with large posterior median emargination; cerci less slender, about 4X longer than wide; sub-genital plate with posterior semicircular margin entire; ventro-anterior margin of front femur with 4 large spines (rather than 3); ventro-posterior margin of hind femur with 4 spines plus genicular spine.

Types. I collected the holotype and allotype in copulo May 4, 1979 in Costa Rica, Heredia Province, Finca La Selva near Puerto Viejo; 5 male and 3 female paratypes collected by me in 1979, same locality; 3 male paratypes collected in light traps by H. Wolda July 10 and October 13, 1977 in Panama, Chiriqui Province, Fortuna; 5 male paratypes collected in light traps by H. Wolda February 17 and May 10, 1980 in Panama, Bocas del Toro Province, Corriente Grande, on Rio Changuinola.

Remarks. Epilampra unistilata is the only member of the Carinulata Group to have fully developed, functional wings and tegmina. It is placed in the group because of the single right style (from which the name is derived; Latin Stilus) and the morphology of the male genitalia which are most similar to those of carinulata.

Variations among the paratypes are noted in the intensity of coloration and the spination of the legs, that is, the ventro-anterior margin of the front femur has 4 (sometimes 3) spines separated by a row of fine setae from the 2 (sometime 1) apical spines; the ventro-posterior margin of the mid-femur usually has 4 plus a distal spine; and the hind-femur usually has 4 large spines but no distal spine.

Epilampra unistilata occurs in the lower understory of lowland rain-forests (see Chapter 3). Males are active starting around sunset. They usually climb to 0.5 to 1.5 m above the ground. As noted above, they have been taken in light traps. Females are rarely seen and usually occur lower in the vegetation. Courtship was not observed, but copulation is in the typical opposed position. The ootheca of one female contained 36 developing embryos.

Epilampra rothi Fisk and Schal, NEW SPECIES

Figs. 2-1J, 2-1K, 2-1L, 2-2A, 2-2C

Male holotype (light form). Measurements in Table 2-4. Head flat, with interocular and interocellar distances equal, one fourth as wide as head; vertex pale cinnamon, interocular space suffused with dark brown,

darkest adjacent to inner margins of eyes and ocellar spots; central brown mark just below ocelli and separated from interocular band by pale tan area, the mark connected dorso-laterally with pair of commalike spots, their "heads" directly beneath but not touching ocelli; pair of median brown spots on clypeus below central mark; remainder of head pale except gray-brown segments 4 and 5 of maxillary palpus; antenna brown. Vaulted pronotum covering most of head; ground color of pronotum and tegmina cinnamon, disc with diffuse pattern of darker areas; wide borders of pronotum and costal margins of tegmina pale with scattered darker spots; tegmina and wings translucent. Abdominal terga tan, latero-posterior angles rounded, no cicatrices or tergal specializations; supra-anal plate semicircular with median emargination not evident in holotype (but present in some paratypes); cercus slender, about 5X longer than wide; genitalia as in Figs. 2-1J,K,L; R2 with obvious subapical incision and row of slender spines proximal to base; L1 with short open cleft, setal brush lacking but a few widely scattered microtrichiae at that site; L2d shaped like mitten with thumb extended at near right angle; prepuce clearly defined by its scalelike covering. Legs and ventral surfaces of thorax and abdomen tan with a few darker spots, abdominal sterna increasingly darker towards posterior; reddish brown sub-genital plate (Fig. 2-2C) convex anteriorly, trigonal posteriorly with nearly straight latero-posterior margins meeting at midline as a blunted right angle, simple style located at center of each latero-posterior margin; right style somewhat larger. Ventro-anterior margin of front femur with 5 large spines separated by row of close-set, short setae from 2 apical spines; ventro-anterior margins of mid- and

hind femora with 3 large spines plus apical spine, of mid femur with 4 spines plus apical spine, of hind femur with 4 spines only; tibiae fully spined; tarsi with pulvilli on 4 proximal tarsomeres and arolium on fifth tarsomere between simple, symmetrical claws.

Male paratype (dark form). Differs from holotype in color as follows (Fig. 2-2A): Ground color of whole body buff, contrasting with numerous dark brown markings; vertex of head pale with dark stripes just dorsal and ventral to it, the 2 ventral stripes filling most of the interocular plus interocellar space (stripes fused on the midline in some paratypes); below stripes, but separate, is central dark mark with its dorso-lateral commalike extensions; this mark fused with clypeal spots noted in holotype, resulting in very dark central mark with well defined margins which, along with small lateral spots and black mandibles, comprises characteristic facial pattern; maxillary palpus with light and dark bands on all segments. Dark disc of pronotum contrasts sharply with pale but spotted borders; very dark marks irregular (but consistent) in shape; obvious central pale area within disc enclosing 2 pairs of small black dots; tegmina with numerous dark brown spots, some fused into mottled dark areas especially along radial vein; venter of thorax and abdomen plus legs marked with numerous nearly black spots; some larger marks on coxae and femora and dark bands on tibiae and tarsi; sub-genital plate and 2 adjacent sterna reddish brown except for narrow pale latero-posterior borders.

Female allotype (light form). Similar to male holotype except as follows: General coloration more intense, dark markings on face as in

dark form except the 2 clypeal spots not fused with central face mark; disc of pronotum and most of tegmina pale with numerous dark spots; abdominal terga shading to dark reddish brown towards supra-anal plate; plate dark with narrow pale borders and short median stripe extending anteriorly from posterior margin about a quarter length of plate; posterior margin with oblique median emargination; legs and venter of thorax and abdomen colored as in dark form males; sub-genital plate semicircular in outline.

Female paratypes. Other Costa Rican females less intensively colored than allotype, correspond more to cinnamon colored light-form males, while Panamanian females correspond to dark form males; that is, they have 2 clypeal spots fused with central facial mark, dark pronotal disc with central pale area and no cinnamon color on dorsum.

Types. Holotype and allotype taken in copulo by me February 23, 1980, Costa Rica, Heredia Province, Finca La Selva near Puerto Viejo; 6 male and 3 female paratypes also collected by me in 1979 and 1980, same location; 2 female paratypes collected by M. Kosztarab and A. Young in light trap, January 10, 1970, same location; 2 female and 2 male paratypes taken by H. Wolda in light traps, May 1978, May and June 1979, Panama, Chiriqui Province, Fortuna; 24 male and female paratypes taken by H. Wolda in light trap between January 13 and May 10, 1980, Panama, Bocas del Toro Province, Corriente Grande on Rio Changuinola.

Remarks. Epilampra rothi appears to represent the "n. sp. D" of Dr. Louis M. Roth (1970b) for whom I have named the species. As

pointed out by Roth it is closest to but distinct from Epilampra azteca Saussure and falls in Group C of the Burmeisteri Group of Epilampra. It exhibits considerable range in coloration. The dark form (from Panama) with striking dark markings against a pale background (Fig. 2-2A) most closely resembles azteca and has been mistakenly identified as azteca in the past (Roth, 1970b), while the light form (from Costa Rica and the adjacent Chiriqui Province of Panama) with suffused chestnut brown markings on a cinnamon brown background appears quite different. Both populations agree in external morphology and male genitalia, and I am treating them as one species. As noted in the descriptions some individuals show color patterns between the dark and light extremes.

Epilampra rothi is probably the most common species of its size in the lower understory of the Costa Rican lowland rain-forest, but it is apparently more restricted in its Panamanian distribution. Males are common on leaves starting about sunset usually 0.5 to 1.5 m above ground (see Chapter 3). Females are relatively scarce and occur lower in the vegetation, while nymphs are common in the leaf-litter. Copulation is in the opposed position. Courtship was not observed. I collected 3 males of this species in north central Nicaragua along the Rio Bocay.

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Table 2-1. Measurements of adult Epilampra involucris in mm.

	Holotype	6 Paratype	Allotype	3 Paratype
	male	males	female	females
		(Range)		(Range)
Total length	19.0	16.6-22.6	25.6	25.4-28.2
Pronotum, length	5.3	5.0-5.5	7.0	5.5-6.9
Pronotum, width	7.5	7.7-8.5	10.2	9.1-10.2
Tegmen, length	6.3	5.9-6.9	7.9	5.9-9.0
Tegmina, width	9.0	8.7-10.2	12.2	10.9-12.4
Abdomen, length	11.9	11.8-14.0	14.5	12.4-14.6
Hind-tibia, length	7.2	6.6-8.5	9.2	8.3-9.8

Table 2-2. Measurements of Epilampra belli in mm.

	Holotype	2 Paratype	Allotype	3 Paratype
	male	males	female	females
		(Range)		(Range)
Total length	*	18.6-19.0	22.2	22.4-26.5
Pronotum, length	5.2	5.1-5.8	6.0	6.3-8.0
Pronotum, width	7.2	7.1-7.3	8.4	9.1-10.0
Tegmen, length	6.3	5.9-6.1	7.7	7.9-9.8
Tegmina, width	8.8	8.9-9.1	10.9	10.9-12.4
Abdomen, length	*	9.5-10.1	15.8	14.5-17.1
Hind-tibia, length	6.5	6.6-6.8	8.2	7.5-9.5

* Tip of abdomen removed for dissection of genitalia.

Table 2-3. Measurements of Epilampra unistilata in mm.

	Holotype	8 Paratype	Allotype	3 Paratype
	male	males	female	females
		(Range)		(Range)
Total length	20.2	20.8-22.4	23.0	24.4-24.8
Pronotum, length	4.0	4.0-4.3	4.4	4.8-5.0
Pronotum, width	4.9	5.1-5.6	6.6	6.7-7.2
Tegmen, length	16.7	17.7-19.7	19.4	20.0-20.8
Tegmina, width	9.1	9.1-10.5	10.5	9.3-10.3
Abdomen, length	9.3	9.1-10.4	10.7	--
Hind-tibia, length	6.7	6.5-6.8	7.3	7.4-7.7

Table 2-4. Measurements of Epilampra rothi in mm.

Light Form (Costa Rica)	Holotype male	8 Paratype males (Range)	Allotype female	5 Paratype females (Range)
Total length	20.0	19.4-20.2	20.8	19.4-22.3
Pronotum, length	4.2	3.7-4.1	4.3	4.1-4.7
Pronotum, width	5.1	4.7-5.7	5.7	5.4-6.6
Tegmen, length	16.8	16.6-17.3	17.0	16.0-19.4
Tegmina, width	8.2	7.5-9.4	9.0	8.4-9.9
Abdomen, length	10.8	10.4-11.0	11.1	11.5-13.8
Hind-tibia, length	6.3	5.4-6.5	6.0	6.0-6.6
Dark Form (Panama)		24 Paratype males (Range)		3 Paratype females (Range)
Total length		18.2-20.6		20.7-21.3
Pronotum, length		3.9-4.4		3.7-4.7
Pronotum, width		4.7-5.0		5.0-5.9
Tegmen, length		16.0-18.3		16.1-17.9
Tegmina, width		7.7-9.3		9.1-10.0
Abdomen, length		10.3-11.1		9.9-12.4
Hind-tibia, length		5.1-6.4		5.2-6.6

Figure 2-1. Male genitalia of Epilampra species. A,B,C, E. involucris. D,E,F, E. belli. G,H,I, E. unistilata. J,K,L, E. rothi. A,D,G,J, Ventro-medial sclerite of left phallomere (L2vm), dorsal sclerite of L2 (L2d), prepuce (P). B,E,H,K, Hooked sclerite of right phallomere (R2), subapical incision (SI). C,F,I,L, First sclerite of left phallomere (L1), cleft (C). Scale bars = 0.5 mm. Fig. J from Roth (1970b, fig. 281).

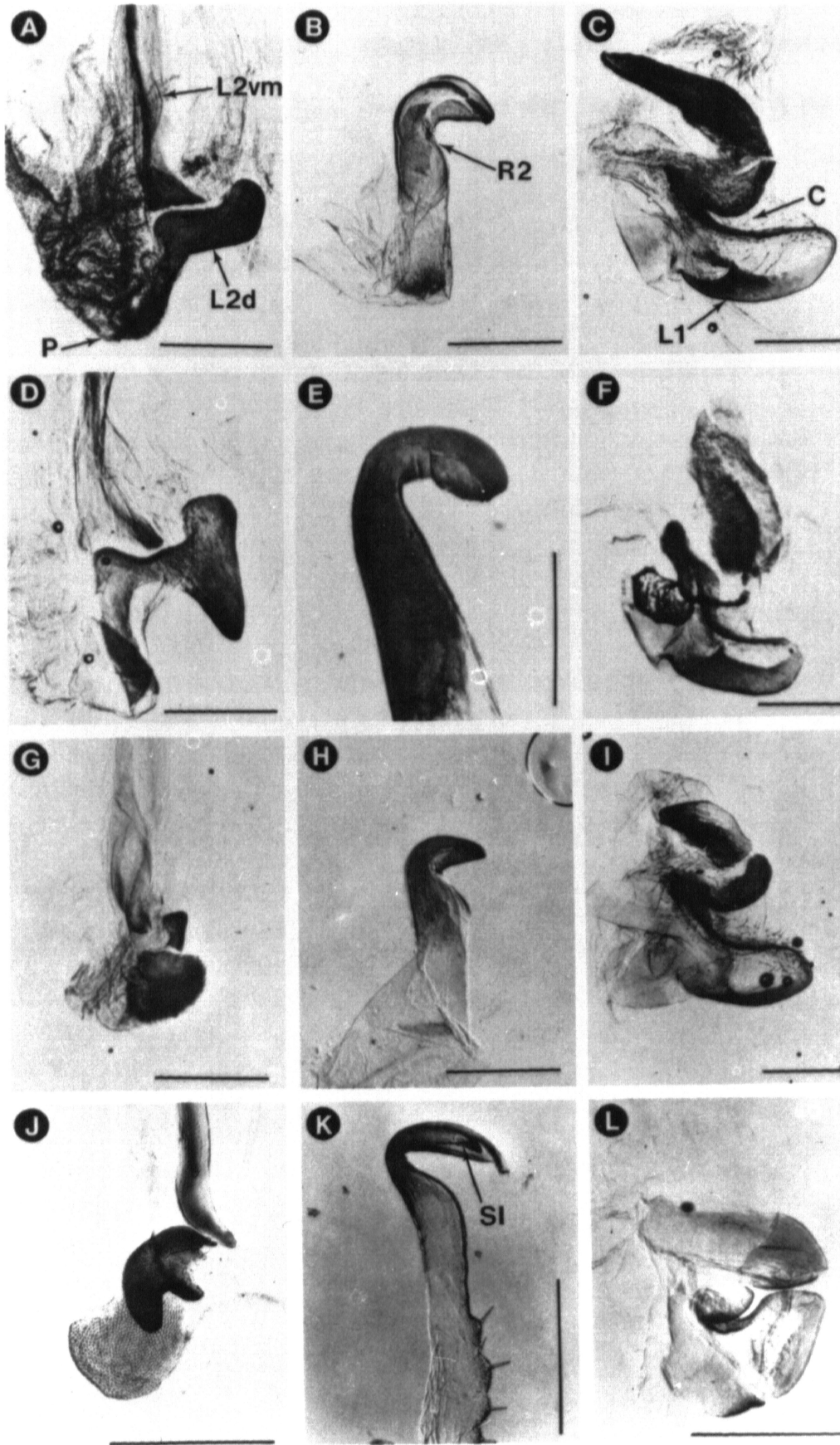
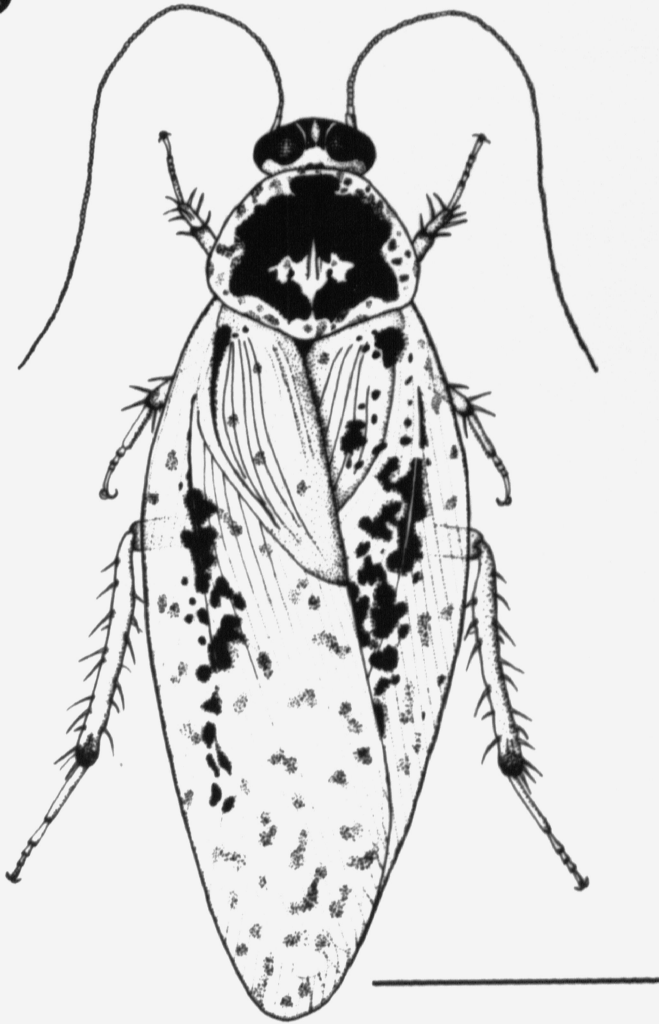
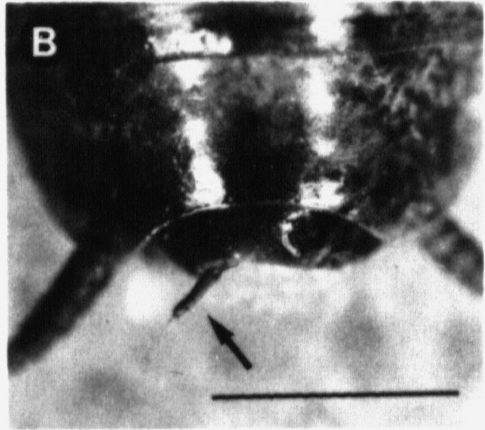


Figure 2-2. A. Male Epilampra rothi, habitus of dark form; scale bar = 6.2 mm. B,C, Ventral aspect of distal part of abdomen. B, E. unistilata. C, E. rothi. Scale bars for B and C = 2.0 mm.

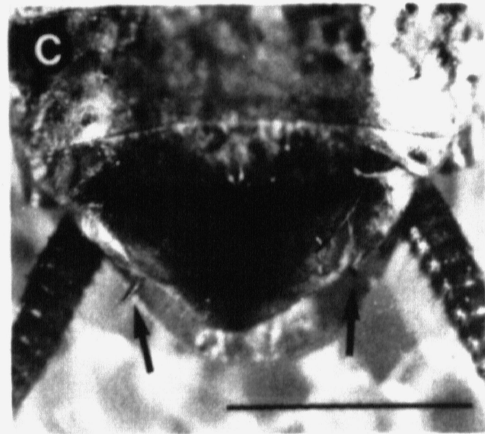
A



B



C



CHAPTER 3

Vertical Community Structure and Resource Utilization of Some
Costa Rican Rain-Forest Cockroaches

The patterns of vertical habitat use among ten species of cockroaches are examined. Three assemblages of cockroaches are separated on the basis of overlaps and breadths of vertical distributions. Three apterous or brachypterous species occur near the ground and comprise one assemblage. Higher perchers separate into those which migrate into the leaf-litter on a diel basis, and those which hide in above-ground refugia during the day. Trophic and behavioral correlations with perch height are described.

INTRODUCTION

Closely related sympatric species differ in their utilization of environmental resources. Numerous studies report direct or indirect evidence of vertical stratification of animals. The following is merely a sampling from the vast natural history literature. Adams (1941) noted that "some animals are commonly found on the ground, others on the herbs and still other species at different levels in the shrubs and trees." Zooplankton migrate upward at sunset to feed on phytoplankton, and down at sunrise, probably to avoid visual predators in the epilimnion (Zaret and Suffern, 1976). Narver (1970) and Eggers (1978) showed that some filter-feeding fish follow vertically migrating zooplankton in a diel pattern. Beginning with the work of Dunlavy (1935) and Colquhoun and Morley (1943), birds formed a model for the study of vertical niche separation (see MacArthur, 1965; Cody, 1974; Lack, 1971). Schoener (1974) and Pianka (1973) reviewed the pertinent literature in the study of lizard community structure. The increased interest in stratification of forests into vertical layers stimulated the studies of Napier (1966) and Charles-Dominique (1977) on primate distributions. Enders (1974) found that two closely related spider species coexisted as adults because of high mortality among the vertically stratified immatures. Differences in the vertical distributions of life stages and seasonal variations have been documented in soil mites by using core samples (e.g., Mitchell, 1978), and in spiders (Barth and Seyfarth, 1979).

The vertical distribution of insects has received little attention. Howden and Nealis (1978) reported on vertical separation of seven

species of beetles; they suggested that different sized beetles perch at different heights because they forage on different sized food. Hadow (1966), Corbet (1961) and others, looked at biting activity of mosquitoes as a function of vertical distribution, among other factors. Trapping pest species in forests and agricultural crops indicate that they occur in specific regions along the vertical profile. For example, male gypsy moths tend to fly near the ground at low population densities (Richerson et al., 1976). Late instar larvae and adult gypsy moths have diel patterns of vertical movement in temperate woodlands (Leonard, 1970).

Hawke and Farley (1973) and Edney et al. (1974) investigated intraspecific niche separation of the cockroach Arenivaga (Polyphagidae) in desert sand dunes. Gautier (1974a) found ontogenetic and sexual differences in the vertical distribution of Blaberus atropos and B. colosseus (Blaberidae) in caves in Trinidad. Gautier (1980) and Deleporte (1976) noted similar patterns for the cavernicolous species Gyna maculipennis (Blaberidae) and Periplaneta americana (Blattidae), respectively. For temperate species, Dreisig (1971) showed that Ectobius (Blattellidae) adults migrate upward in the vegetation during the active phase of the circadian cycle. He proposed that physiological limitations result in differential activity and distribution patterns in adults and nymphs. Gorton (1980) investigated inter and intraspecific vertical segregation of cockroaches in northeastern Kansas. He attributed this to "intersexual, interspecific, and probably inter-lifestage competition," but the evidence which he reported to support this thesis was rather meager.

Schal (1982 [Chapter 4]) reported that cockroaches in the understory of a tropical forest stratify inter and intraspecifically. The aim of the present study was to attempt to explain coexistence of several syntopic species. Utilizing behavioral observations, stomach analyses, micro-environmental measurements, distributional data, and temporal activity patterns, the overall objective was to document the vertical structure of the cockroach community in the lowest 2 m of a Costa Rican forest and to examine temporal, spatial, and trophic differences among several species.

The following specific questions are considered: 1) How are species and classes of individuals within species distributed vertically? 2) What factors contribute to variations in vertical distributions? 3) Are there morphological or trophic correlates with the vertical ranges of species? 4) How important is time in separating syntopic species? 5) What relationships can be calculated between the average height of a species and its vertical range?

MATERIALS AND METHODS

This study was conducted during three periods (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 $10^{\circ}28'N$. Holdridge et al. (1971) describe the field site in great detail with reference to its history, abiotic factors, vegetational composition, and soil types.

I utilized two study plots in a successional abandoned plantation.

A large plot (400 m²) was used in a mark-recapture study to examine individual variations in perch height. A smaller (100 m²) area was used to examine the effect of different vertical vegetation profiles on abundance and vertical distributions of cockroaches.

In nightly sessions of a five month capture-mark-recapture program in 1979 adults of ten species were collected by hand and the site of capture was marked. I recorded on magnetic tape which was later transcribed (1) the species identification, (2) sex, (3) height above the ground, (4) time of capture, and (5) behavioral notes. Nightly weather patterns were also recorded.

Marking was done in the laboratory without anesthesia. The pronotum was scraped with an insect pin and a drop of Eastman 910 adhesive, a dot of colored Testor's enamel paint and a second coating of glue were placed successively at predesignated positions on the pronotum, which along with a color code corresponded to a number. The insects were returned to their capture sites on the same night. In subsequent nights sighting of marked individuals was recorded; marked cockroaches were not captured.

The analysis of vertical distributions and temporal activity patterns included data collected in the large plot and in adjacent regions of similar vertical structure. Thus, unmarked cockroaches seen outside of the mark-recapture program and not captured were included. Temporal and relative abundance calculations were made on the basis of this "conspicuousness" record. Dreisig (1971), Gorton (1980), and others used this procedure in their studies. The number of individuals of a given category (species, sex, age-class) which were seen was

divided by the cumulative time spent searching (observation time) to calculate "relative activity" values. I divided the nocturnal activity period of cockroaches into hourly intervals for most common species; a two hour activity index was computed for the less abundant species.

Niche breadth and overlap are measures of ecological specialization and the degree to which sympatric organisms share resource intervals. Here, resource intervals are defined as regions along the vertical niche axis and as hourly intervals during the night. As a measure of vertical overlap, I utilized Schoener's (1968) index of ecological similarity,

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

where p_{ij} and p_{ik} are the proportions of individuals of species j and species k which are associated with resource interval i (see Abrams, 1980; Linton et al., 1981, for critical discussions of niche overlap measures).

Niche breadth along the vertical axis was calculated as

$$B = 1 / \sum_{i=1}^n p_i^2 \quad (2)$$

and as

$$B = \exp(-\sum p_i \log p_i) \quad (3)$$

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.

Diel locomotory activity patterns were investigated outdoor in a screened insectary. I divided all the surfaces of 30 x 15 x 15 cm cages into 7.5 x 7.5 cm squares. The frequency at which 5 individuals crossed

these lines was a relative measure of activity (see Block and Bell, 1974). These data were recorded for 3 min at either 0.5 hr or 1 hr intervals during continuous 24 hr periods.

To determine whether vision was involved in perch height selection the eyes of 30 field collected E. involucris males were painted with India ink and they were caged in an outdoor insectary. Unaltered males were maintained under similar conditions. 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. I recorded the time spent on the leaf before locomotion ensued. Preliminary observations indicated that whereas early in the night (ca 19.00 hr) perching individuals were restless and tended to move about, by ca 22.00 hr they were more apt to remain on the perch for longer periods of time. Therefore, I started the experiments at 22.00 hr.

The species involved in the study are as follows:

Epilampra involucris Fisk and Schal- Blaberidae. This species is very common in all the forest types which I examined. Both sexes are brachypterous. Females are larger than males.

Epilampra rothi Fisk and Schal- Blaberidae. Males of this species are probably the most conspicuous insect on understory foliage at night. Females are common only at feeding sites. Both sexes are winged.

E. unistilata Fisk and Schal- Blaberidae. Not a common species. Females are rarely seen.

Hyporhienoda reflexa Saussure and Zehntner- Blaberidae. Males are winged; females are apterous. Both sexes and nymphs exhibit tonic immobility when disturbed (Schal, in preparation).

Nesomylacris sp. near asteria - Blattellidae. Very similar in morphology to E. involucris (both sexes are brachypterous) but significantly smaller. Behaviorally 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, it is conspicuous at specific feeding sites. Both sexes are winged and superficially resemble the American cockroach (Periplaneta americana).

X. cantralli Fisk and Gurney- Blattellidae. Very common. Both sexes are winged but are smaller than X. hamata.

Imblattella impar Hebard, Cariblatta imitans Hebard, and I. new species "G" (Fisk, 1971)- Blattellidae. All three species are similar morphologically and behaviorally 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.

RESULTS

(1) Activity Patterns and Perch Types

Adults of all species except I. impar, I. new sp. "G", and C. imitans rest in the leaf-litter during the day. At dusk (ca. 18.00 hr) males and females climb or fly onto understory foliage. Before sunrise (ca. 05.00 hr) they move downward to the leaf litter. The height to which they move and the temporal patterns of these behaviors 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; flight between leaves is common in some species. Females of several species were seen in "calling" postures, evidently emitting volatile sex pheromones to which males are attracted (Schal, 1982 [Chapter 4]; Schal et al., in preparation).

The type of perch utilized seemed to be a function of the size of the cockroach and its particular escape behavior. Large species (Megaloblatta blaberoides, Nyctibora noctivaga (Blattellidae), and Blaberus colosseus (Blaberidae) were found mostly on trunks of trees at various heights. When disturbed, they usually retreated several cm into crevices or crouched down on the substrate; they rarely took flight. Other species tended to perch on foliage and commonly flew away or jumped off the leaf into the leaf-litter when disturbed.

(2) Interspecific Vertical Stratification and Niche Metrics

The distributions of adults of all species (with the exception of X. hamata vs. E. unistilata, X. cantralli vs. E. rothi, and I. impar vs. C. imitans) are significantly different from each other ($P < 0.05$, Student's t-Test of log transformed data and Wilcoxon Rank Sum Test) (Fig. 3-1). These distributions represent the total number of observations regardless of the time of night or the climatic conditions.

To justify the use of means as evidence for vertical habitat partitioning, the true ranges of species must not extend far above the 2.2 m upper limit of sampling. Food baited traps at ground level, 0.5 m, 3 m, and 10 m above the ground were deployed to independently assess the vertical distribution of cockroaches. Most individuals of all species were trapped either at ground level or at 50 cm above the ground (Table 3-1). The adult catch in the 3 m and 10 m traps was only 8.5% of the total adult catch. Because sampling commenced at 21.00 hr when cockroaches were active above ground, it was safe to conclude that the lower 2 m of the vegetation did indeed represent the true range of these species.

The vertical distribution results (Fig. 3-1) indicate that the variance in the vertical range is related to the mean perching height. To reflect the probability of co-occurrence of species in a given resource interval, I applied a weighting factor to each one based on the vegetation profile (Fig. 3-2). That is, the proportion of individuals utilizing each resource interval was corrected on the assumption that resource utilization is related to the availability of

leaves (or with indirect vegetation affects on temperature, humidity, radiation, etc.), and that individuals of a species sample randomly from the available resources. Such weighting of niche measures accounted for the relative abundance or availability of resources (perches) (see Schoener, 1974; Hanski, 1978; Hurlbert, 1978). Since in the present study the vegetation was most dense close to the ground, overlap indices between low perchers (E. involucris, Nesomylacris, H. reflexa) and high perchers (Imblattella and Cariblatta) were most affected by these correction factors. For interspecific overlap measures the correlation between niche overlap and the corrected overlap measures (Fig. 3-3) is 0.985 ($P < 0.001$, Pearson Correlation). As intuitively expected, species overlaps are negatively correlated with differences between mean species heights ($r = -0.910$, $P < 0.001$; Fig. 3-4). A negative correlation also exists between height and the largest overlap of each species with its nearest neighbor ($r = -0.600$, $P = 0.033$).

Three morphologically different assemblages of cockroaches separate along the height dimension (Figs. 3-4, 3-5). Adults of E. involucris and Nesomylacris, and H. reflexa females are brachypterous and perch close to the ground; on average, less than 5 cm separate means of adjacent species. Approximately 20 cm separate means of X. hamata and H. reflexa. X. hamata, E. unistilata, E. rothi, and X. cantralli comprise an intermediate guild; all four species are good fliers and spend the day in the leaf-litter. The mean perch heights of I. impar, C. imitans, and I. n. sp. "G" are within a 12 cm range separated by 40 cm from that of X. cantralli. These three species are smaller than the other species and spend the day in above-ground refugia.

Vertical overlap values were arranged into symmetrical community matrices which are summarized as dendrograms of vertical range similarity (see Cody, 1974 for discussion). As expected, three clusters of species separate on the basis of vertical overlap (Fig.3-6). Similar arrangements result when consexuals are clustered.

The three assemblages are also distinguishable on the basis of vertical breadth. Apterous species occupy a narrow vertical region close to the ground, the plectopterine species perch higher and exhibit greater vertical breadths; the others are intermediate between these two groups. The widths (breadths) of species' vertical ranges correlate directly with the species mean perch heights ($r=0.968$, $P=0.001$) (Fig. 3-7).

Because both vertical overlap and breadth are correlated with perch height (negatively and positively, respectively), I examined the relationship between breadth and overlap. As vertical breadth increases, vertical overlap with the closest neighbor decreases ($r=-0.630$, $P=0.025$). That is, plectopterine species (high vertical breadths) exhibit less overlap with their neighbors than do brachypterous species (low vertical breadths) with their neighbors.

Low perching males or females (with small vertical breadths) have ranges that overlap more with their closest consexual neighbors than do high perchers (with greater breadths). This relationship is statistically significant for both the male and female populations, but not for each of the three consexual assemblages.

(3) Intraspecific Vertical Stratification

Intraspecific vertical separation is as statistically significant as interspecific stratification, and in several closely related species (e.g., Imblattella and Cariblatta), differences in sexual separation are more significant than species differences (Fig. 3-1). Although their vertical ranges overlap considerably, the distributions of conspecific females and males are significantly different for all species ($P < 0.05$, Student's t-Test of log transformed data and Wilcoxon Rank Sum Test).

The direction of sexual differences in distributions are consistent for all species; males always perch higher than females. Trapping results (Table 3-1) indicate increasingly male biased sex ratios with increasing height, suggesting that the "male above" pattern may hold for the entire vertical community profile.

The differences in perch heights between females and conspecific males increase with height above the ground ($r = 0.852$, $P = 0.0009$; Fig. 3-8). Here, as in the interspecific patterns, the same three assemblages of cockroaches are recognized. The sexes of apterous species which are close to the ground are separated by small distances; in the plectopterine species greater distances separate the males from the females.

Similarly, the three groups are recognized in the analysis of vertical breadths. As for species metrics, the vertical breadths of males and females relate to their respective mean perching heights (Fig. 3-7). For the two lower assemblages males have broader vertical ranges than conspecific females; in the higher perching plectopterine species,

females and males have similar ranges (Fig. 3-7). In the analysis of sexual and species vertical breadths, females tend to bridge the gap between the assemblages.

For the whole community, no significant relationship exists between vertical overlaps and the distances between the sexes ($r=-0.387$, $P=0.135$). However, for each assemblage, the two measures are significantly negatively correlated, as in overlap between species.

Separation of age classes was examined in detail in four species; the pattern is similar in the others (Fig. 3-1). Except for the plectopterine species (Imblattella and Cariblatta), early instars are found exclusively in the leaf-litter where parturition occurs or oothecae are deposited. Older nymphs perch at higher levels in the vegetation. The distributions of last instar nymphs are closest to those of adults of the same sex. For example, most large nymphs of E. rothi are females; instead of ranging higher than smaller nymphs they perch closer to the ground, as do adult females.

All instars of Imblattella and Cariblatta overlap in ranges with each other as well as with the adults. It is not known whether sexual separation of the nymphs occurs in these species.

(4) Diel Activity

H. reflexa males exhibited a unique activity pattern (Fig. 3-9). They were found on foliage within minutes after sunset (ca. 18.00 hr) and were very common until ca. 20.00-21.00 hr, at which time their above-ground activity dropped abruptly and remained low for the rest of the night. Laboratory data (Fig. 3-9) suggest that activity on foliage

may be followed by other kinds^{of} activity. After the males moved into the leaf-litter at ca. 21.00 hr they probably remained active (possibly for the rest of the night) as indicated by the locomotory measure in the laboratory. This suggestion was also corroborated by the trapping results; males were trapped in the leaf-litter late in the night.

E. involucris males moved upward onto foliage early but remained active all night. Nesomylacris sp. adults occurred in the <40 cm zone with E. involucris and H. reflexa, but they initiated activity later at night and were less active after 01.00 hr.

Higher up, X. cantralli followed a pattern similar to E. involucris. The activity of X. hamata adults was bimodally distributed; both males and females were conspicuous between 19.00 and 20.00 hrs and between 01.00 and 04.00 hrs.

For most species, laboratory and field data are in general agreement (Fig. 3-9). However, the laboratory measures accentuate the "on-off" nature of locomotory activity. Most species have bimodal activity patterns with the "on" peak probably corresponding to the locomotion which initiate perching, and the "off" peak corresponding to the return back to resting sites.

Species with high spatial overlaps may reduce competition between them by overlapping little in time. Temporal shifts in activity are most obvious in the diurnally active Euphyllodromia angustata. I did not detail the vertical habitat use in this species, but both laboratory and field data indicate that E. angustata adults roost on the underside of leaves at night and are active during the day-light hours (Fig. 3-9). Behaviorally, they are similar to the plectopterine species.

With few exceptions, temporal overlap among species was large. For males of nine species for which sufficient activity data were available, a positive correlation existed between spatial and temporal overlap with the nearest neighbors ($r=0.857$, $P=0.007$). A positive relationship between these measures persisted when all vertical and temporal overlaps among all males in the community were analyzed ($r=0.169$, $P=0.009$).

(5) Habitat Complexity and Height Preference

The average preference of individuals for specific resources is reflected in their relative distribution among resource intervals when all resources are equally abundant. The analyses of perch distributions of species and sexes were conducted in a forest with a vertical profile as in Figure 3-2. To determine whether the distributions of low perching species are modulated by competition with high perchers, I examined species diversity and perching patterns in an adjacent study plot. This area was dominated by Selaginella sp. (Selaginellaceae), a short fern ally. Between 40 cm and 250 cm the density of leaves was much lower than in the larger study plot. Above 2.5 m leaf density increased in both areas.

Xestoblatta, E. unistilata, E. rothi, Imblatella, and Cariblatta were significantly underrepresented in the Selaginella plot. The abundance of E. involucris, Nesomylacris, and H. reflexa did not differ in the two plots.

(6) Individual Variations in Perch Height

Since marked cockroaches were recaptured repeatedly at different heights, I tested whether the variations in the within species distributions (Fig. 3-1) might be attributed to differences in height preferences between or within individuals on different nights. Data on perch heights between 20.00 and 21.00 hrs for males of three species were analyzed. This time period encompassed the greatest numbers of recaptures for which such data were available. The variations in height distributions were mainly due to large variations within individuals (Table 3-2). At 20.00 hr a marked X. cantralli may perch at 20 cm on one night and at 150 cm at the same time on another night. I have no evidence to suggest that individual height preferences contribute to variation in the species height distribution.

(7) Vision and Height Selection

Of the two variables (vision, height) examined in four conditions, changes in height affected the duration of perching most significantly (Table 3-3). Normal and blinded males moved down from high perches more frequently than males placed at 25 cm. I interpret these results to indicate that males at 100 cm employ non-visual sensory cues in orienting to more preferred lower perches.

DISCUSSION

(1) Why Perch ?

Amongst the more likely functions of perching in cockroaches are a) predator avoidance, b) selection of preferred structural (physical) microhabitats, c) feeding, and d) orientation to mates.

a. Predator Avoidance

That perching on foliage may be a predator avoidance strategy is suggested by the high activity of ground dwelling (spiders, ants, frogs) and flying (bats) predators at night. Blattellid cockroaches comprise 23% and 92% of the respective diets of Australian Dinopis and Menneus net casting spiders (Dinopidae) (Austin and Blest, 1979). Cockroaches thus may enhance their chances for survival by moving out of the leaf-litter and onto foliage at night.

Spiders in the Ctenidae, Lycosidae, and Pisauridae perch on leaves in banana and coffee plantations (Barth and Seyfarth, 1979) and in the La Selva forest (pers. obs.). Prey localization in these spiders is transduced mainly through low frequency vibrations emanating from the prey and transmitted at least 25 cm. across a leaf (Barth and Seyforth, 1979). Presumably, the prey may detect such signals from the approaching spider. Cockroaches typically perch at the edges of leaves, and as a spider approaches, the cockroach assumes an alert stilt posture. Slight vibration of the substratum elicits evasive responses, such as running rapidly under the leaf (as in Imblatella and Cariblatta), abandoning the perch either by flying or gliding to a new

perch (e.g., Xestoblatta, Epilampra rothi), jumping directly into the leaf-litter (e.g., E. involucris), or "playing dead" (e.g., H. reflexa). Hard, non-resonating surfaces as tree-trunks and the ground are inferior for this type of predator detection system.

The early morning migration to ground and foliage hiding places is probably in response to predation by visual predators (lizards, birds) above ground. Most species of cockroaches are well camouflaged in leaf-litter but relatively conspicuous on green leaves. This pattern of vertical migration is similar to that of zooplankton which evade visual predators by spending the day in deeper, darker waters (Hutchinson, 1967). Large, conspicuous late instar gypsy moth larvae (Lymantria dispar) exhibit a diel migration to the bases of host trees, possibly to avoid diurnal bird predation in the canopy (Leonard, 1970).

b. Microhabitat Preferences

Perching at specific heights may be a form of microhabitat selection related to physiological constraints. The cockroach Arenivaga sp. (Polyphagidae) exhibits circadian and seasonal vertical movements through the sand in the Colorado desert in California (Hawke and Farley, 1973; Edney et al., 1974). The activity patterns of females and immatures correlate with temperature and humidity. Similarly, in Ectobius (Blattellidae), a temperate forest and grassland cockroach, when low temperatures prevail during the preceding night, males shift their above-ground activity to late afternoon (Dreisig, 1971). In both species, meteorological factors seem to determine the time and place where activity occurs.

Temperature, humidity, and wind measurements in the tropical rain-forest covary with both height and time of day (Richards, 1952; Schal, 1982 [Chapter 4]). Physiological studies of temperature tolerance (Appel, 1982) and behavioral studies of temperature and humidity preferences of several cockroach species (see Cornwell, 1968) reveal that many species select narrow environmental ranges, though they may tolerate significantly greater ranges. Hence, differences in perch heights of species, sexes, and life-stages may reflect microhabitat selection based on physiological tolerance. The problem of mate-finding resulting from habitat differentiation (especially in perch height) of the sexes is less severe in mobile animals than in plant communities (see Meagher, 1980), thus permitting greater ecological divergence.

I did not determine whether individuals select specific heights above the ground or abiotic factors which covary with height (as temperature, humidity, refugia, and food).

c. Localization of Food and Feeding

While on foliage, cockroaches feed on epiphylllic algae, bryophytes, lichens, pollen, spores, and other organic matter trapped on the surfaces of leaves. Schal and Bell (1982a; [Chapter 5]) reported that Xestoblatta hamata and other species (unpublished) feed on bird droppings, fruits, and flakes of shed bark, which are intercepted on the surfaces of leaves. These studies (and related work with scarabs - Howden and Nealis, 1978) indicate that perching on leaves enhances food finding, food localization and feeding in several species of cockroaches.

The heights at which cockroaches perch correlate well with their respective diets. E. involucris adults perch close to the ground and feed mainly on detritus in the leaf-litter. Interestingly, males which perch at heights up to 50 cm (Fig. 3-1) supplement their diets with epiphyllic material, whereas females which are more common in the leaf-litter rarely graze on surfaces of leaves. Imblattella and Cariblatta feed almost exclusively on leaf trichomes, blue green algae, liverworts, and spores which they obtain from leaves while perching. Xestoblatta and Epilampra, except E. involucris, feed on fermenting fruits trapped on understory leaves and on the ground. Possibly, a finely resolved separation of cockroaches may operate above ground based on the distribution of epiphylls. 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.).

Ontogenetic differences in heights also correlate with trophic differences within species. Whereas adults are thought to be nitrogen limited as evidenced by the high rate of oocyte resorption and the mobilization of stored uric acid in natural populations (Schal and Bell, 1982a), nymphs of Xestoblatta, Nyctibora, Megaloblatta, and probably many other species (see Roth and Alsop, 1978) secrete proteinaceous defensive materials (Schal et al., 1982), suggesting that nitrogen is not as limited for ground-dwelling nymphs.

d. Localization of Mates

In Chapter 4 (Schal, 1982) I propose a convective pheromone plume model to account for differential vertical, sexual stratification in

cockroaches. Females emit volatile sex pheromones which mix vertically in convective and turbulent eddies and reach conspecific males which are on the average higher than the females. Since convection plumes originate on leaf surfaces (Gates and Benedict, 1963), and dense vegetation retards pheromone flow (see Aylor et al., 1976), perching on leaves may enhance the mate-finding process (Schal, 1982).

My results (Fig. 3-2) and other studies of vertical vegetation profiles (leaf area measurements) of dense tropical forests suggest that a "chemical communication channel" may exist up to 2 m. above the ground. Within this corridor the vegetation is more sparse, close to leaf-litter shelters, and rich in epiphylls and fermenting fruits on which cockroaches feed. Unfortunately, because nothing is known of the chemical nature of sex pheromones of forest cockroaches, I do not know if vertical stratification partitions this stratum among species with similar pheromones. In X. hamata and X. cantralli, differences in the temporal and spatial patterning of diurnal cycles of perching, calling, and mating may be adequate to isolate the two species even if they utilize similar or identical sex attractants (see below; also, Roelofs and Carde, 1971, for a similar situation in Lepidoptera).

(2) Morphology and Perching

In the "open" tropical wet forest, the nightly height distributions of the ten cockroach species seem to correlate primarily with modes of locomotion and with body size. However, the close correlation between height and body size may be a consequence of the relation between body

size and escape behavior, maneuverability, and other behaviors which are differentially selected for at different heights. Moreover, I do not know whether all wingless species occur close to the ground, but perching higher may be inefficient if volatile pheromones are utilized as described above.

Nyctibora noctivaga (Blattellidae) and Blaberus colosseus (giganteus) (Blaberidae), two large, winged species, occur on tree trunks above the present sampling range. However, the apparent relation between size and perch height is not without exceptions. X. hamata individuals perch lower than the smaller X. cantralli. E. azteca, of similar size to E. rothi, seems to range up to the forest canopy.

In communities which are structured on the basis of body size, the latter correlates well with food size (e.g., Hespenheide, 1973). In the present study all species seem to forage on similar sized food, but its location may vary from the ground up to the canopy. In this respect, the studied cockroach community resembles other grazing, plant, and filter-feeding communities.

Ecologically, cockroaches do not separate along higher taxonomic lines in this study. There are no apparent consistent differences in habitat utilization between the blattellidae and the Blaberidae (both are most abundantly represented). By incorporating other habitats (unpublished observations), a clearer phylogenetic pattern emerges. Members of the Blattellidae are found mainly in "open" forest habitats, whereas blaberid cockroaches are more common in "closed" microhabitats such as caves, hollow trees, rotting logs, bird nests, and in underground cavities. With the exception of Epilampra, few blaberids

occur in the forest above ~1 m. Epilampra represents a phylogenetic intermediate between the Blattellidae and the Blaberidae (Roth, 1970b; Fisk and Schal, 1981 [Chapter 2]).

It remains to be determined whether the prevalence of blaberid cockroaches in "closed" habitats is related to their ovoviviparous reproductive mode (blattellids are oviparous) and consequently to long periods of internal incubation of embryos by the female. Caves offer a nutritionally more stable habitat than "open" tropical forests. Accumulated bat guano represents an abundant source of amino nitrogen which is limiting in the forest. Hence, availability of usable nitrogen may have selected for the divergence of blaberids and blattellids in modes of communication, social organization, and parental strategies. In the Blattellidae, uric acid contributed by males to females is transferred into the eggs and is used as a source of nitrogen (Schal and Bell, 1982a [Chapter 5]).

(3) Temporal Partitioning

It is sometimes easier to document differences in spatial habitat use than differences in temporal activity patterns. Two species which overlap spatially and temporally may in fact at the same time segregate on a finer behavioral level. For instance, when species A feeds, species B calls; when A calls, B mates, etc. Such temporal differences in activity seem to occur in the two closely related Xestoblatta species. X. hamata mates for 248 ± 18.5 min (N=9) and pairs do not couple until ca. 23.00 hr (Schal and Bell, 1982a). On the other hand,

X. cantralli matings usually begin earlier (ca. 21.00 hr) and last ca. 3 hours. The two species have similar feeding patterns and requirements (Schal and Bell, in manuscript), and females of both species engage in "calling" or pheromonal attraction of males (Schal et al., in preparation). The timing of matings and perching activity in Xestoblatta seem to represent a case of "nonsynchronous spatial overlap" (Schoener, 1970) by two species.

Temporally staggered habitat utilization by related species may sometimes be related to noncircadian factors. For instance, rainfall may elevate or depress the level of activity or abundance (conspicuousness) of some species and not others. Similarly, seasonal changes in activity may result from differences in moisture, temperature, availability of food, shelter, etc. Wolda and Fisk (1981) documented changes in the abundance of cockroaches in sites with a pronounced dry season and in relatively aseasonal sites in Panama. Unfortunately, the use of light traps precluded examination of many understory species which are not attracted to lights.

Imblattella and Cariblatta are good candidates for elucidating seasonal effects because the three species overlap considerably in their diel activity patterns (Fig. 3-9) and spatial habitat (Fig. 3-1), and are similar in morphology and behavior. Correlations of rainfall and species abundance between March and July 1979 indicate that I. impar and C. imitans respond to proximate changes in rainfall (unpublished). The abundance of I. n. sp. "G" declined during this period irrespective of rainfall, suggesting a more general seasonal response. Similar patterns seem to exist between E. rothi and E. unistilata but

much more intensive investigations are necessary to elucidate these relationships.

(4) Niche Metrics and Competition

The use of niche overlap and breadth measures as indices of competition (e.g., Gorton, 1980) may be misleading because the relationships between them are not known (see Abrams, 1980). Lawlor (1980), Abrams (1980), Schoener (1974), and others argue that use of overlap measures as substitutes for competition coefficients may overestimate competition. Unrelated species may share common non-limiting resources and hence overlap extensively. The relative rates of resource renewal determine the importance of the resource in competition (Lawlor, 1980).

Mechanisms for interference competition in cockroaches involve agonistic interactions (e.g., Schal and Bell, 1982b), yet I observed few such contests for perches. Interspecific and intrasexual encounters on foliage most commonly resulted in avoidance behavior, except when naturally or experimentally baited with food. Moreover, the relatively low abundance of some species in the Sellaginella community did not result in expansion of perch height distributions of other species.

In the present paper the presence or intensity of competition for perches is unknown. Rain-forest perches seem to be abundant at all heights and during all seasons, but I do not know what constitutes a suitable perch and whether perches at different heights have different fitness values for cockroaches. It is premature to draw inferences

about interspecific competition from the present data. It is also important to recognize that I measured only two major niche axes: perching height and perching time. No doubt other dimensions separate seemingly overlapping species and reduction to vertical and temporal overlap measures may ignore additive and multiplicative interactions among resource axes (May, 1975). For example, I do not know whether seasonal shifts in habitat use (other than changes in species abundance) occur in any of these species, how the availability of food (i.e., fruiting phenology of plants) modulates overlap indices, or on a finer level, what I define as the vertical distribution of females of species A may in fact comprise several physiologically distinct subsamples. A case in point is the observation that females remain in the leaf-litter or close to the ground when ready to oviposit.

Field observations indicate that sexual partitioning among conspecifics is related to enhanced probabilities of finding mates (Schal, 1982 [Chapter 4]). Hence, low overlap measures between females and males more likely reflect sexual selection and differing roles in mate acquisition than reduced intersexual competition. This study indicates that these populations of cockroaches are structured on several levels. With respect to sex, the vertical distributions of species represent the combined vertical ranges of males and females which in fact statistically differ from one another. With respect to age, adults and juveniles occupy different vertical and in some cases also horizontal ranges. The interaction of age with sex is documented by the progressively higher mean perch height of nymphs with increasing age, and the differences between late instar males and females. I

conclude that an understanding of the habitat of different classes of individuals within a population is essential for discussions of community structure.

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Table 3-1. Comparison of trap catch at four heights.

Species		Height			
		Ground	0.5 m	3 m	10 m
<u>Epilampra involucris</u>	males	15	3	0	0
	females	21	0	0	0
<u>Nesomylacris</u> sp.	males	22	9	0	0
	females	25	2	0	0
<u>Hyporhionoda reflexa</u>	males	9	1	0	0
	females	12	0	0	0
<u>Xestoblatta hamata</u>	males	1	11	1	0
	females	8	6	0	0
<u>Epilampra rothi</u>	males	12	27	6	1
	females	5	1	1	0
	nymphs	106	13	0	0
<u>Xestoblatta cantralli</u>	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

Table 3-2. Comparison of individual and species variations in height preferences.

Epilampra involucris males

Source	d.f.	S.S.	Mean Squares	F Ratio	P
Between individuals	5	250	50	1.157	0.389
Within individuals	11	476	43		

Epilampra rothi males

Source	d.f.	S.S.	Mean Squares	F Ratio	P
Between individuals	9	17352	1928	1.546	0.194
Within individuals	22	27443	1247		

Xestoblatta cantralli males

Source	d.f.	S.S.	Mean Squares	F Ratio	P
Between individuals	2	1451	726	1.801	0.244
Within individuals	6	2417	403		

Table 3-3. Time that experimental Epilampra involucris males remained on a leaf after release.¹

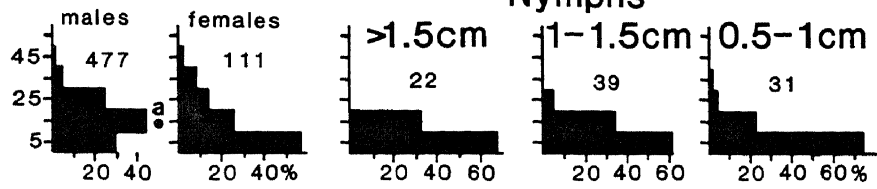
Experimental Height Condition (cm)	N	mean \pm SEM (minutes)	Significance ² (P<0.05)
Normal 25	15	26.7 \pm 4.13	a
Blinded 25	15	23.7 \pm 3.67	a
Normal 100	15	8.7 \pm 1.24	b
Blinded 100	15	7.7 \pm 0.96	b

¹ Recorded at 5 minute intervals.

² Conditions labeled with different letters are different.

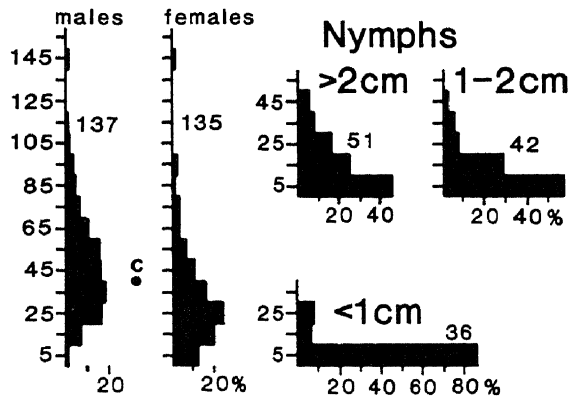
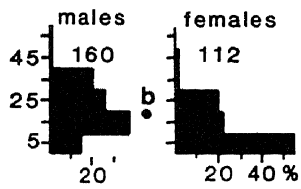
Figure 3-1. Vertical distributions of species, sexes, and life-stages of cockroaches. The ordinate is perch height in cm. The sample size for each group is next to the respective histogram. The mean species perch heights are graphed between the distributions of the males and females. Statistically different ($P < 0.05$, Student's t-Test of log transformed data and Wilcoxon Rank Sum Test) species distributions are labeled with different letters (above species mean). Imblattella and Cariblatta nymphs are grouped together (plectopterines) because I could not identify the species.

Epilampra involucris

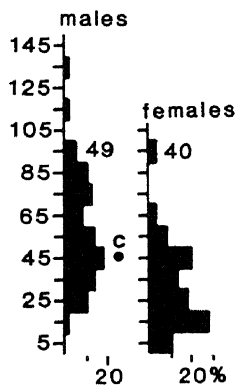


Xestoblatta hamata

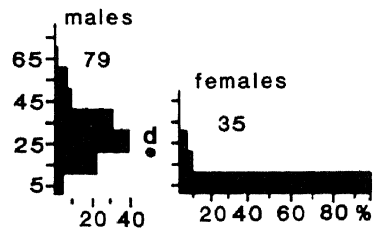
Nesomylacris sp.



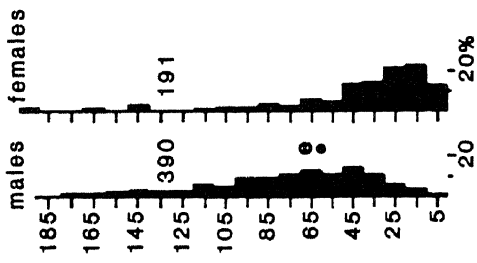
Epilampra unistilata



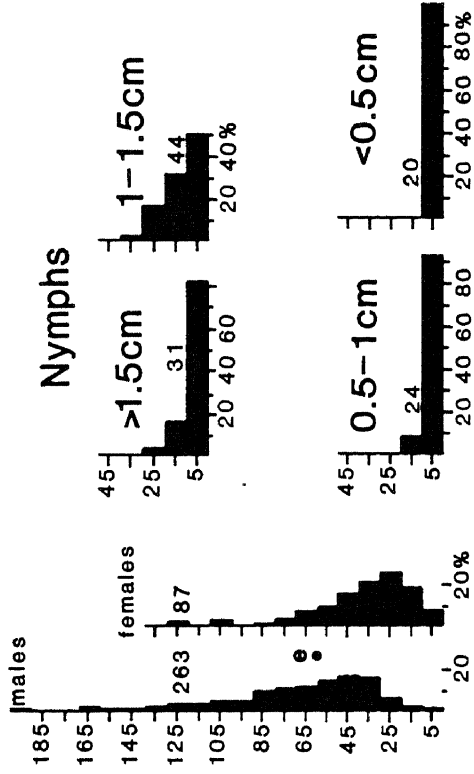
Hyporhichnoda reflexa



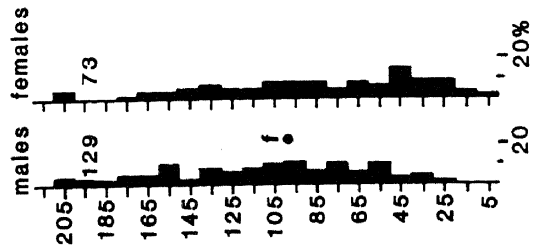
Xestoblatta cantralli



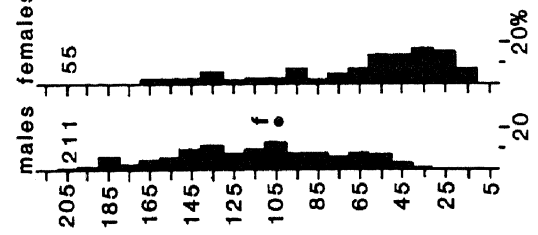
Epilampra rothi



Imblattella impar



Cariblatta imitans



Imblattella n. sp. G.

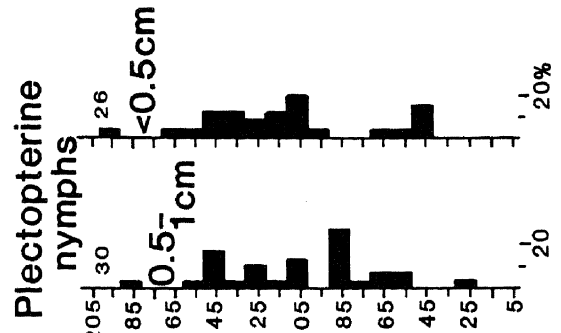
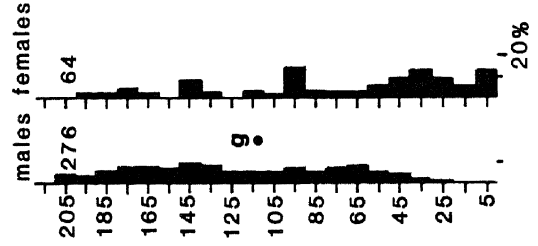


Figure 3-2. Vertical vegetation profile of the study area. A 400 m² plot was divided into 1 x 1 m squares which in turn were subdivided into 25 areas each. Two 20 x 20 cm squares were selected randomly within each 1 m² and I recorded the presence or absence of leaves within 5 cm of a 3 m vertical stick positioned in their centers. This profile is the average of 800 individual 3 m vertical profiles.

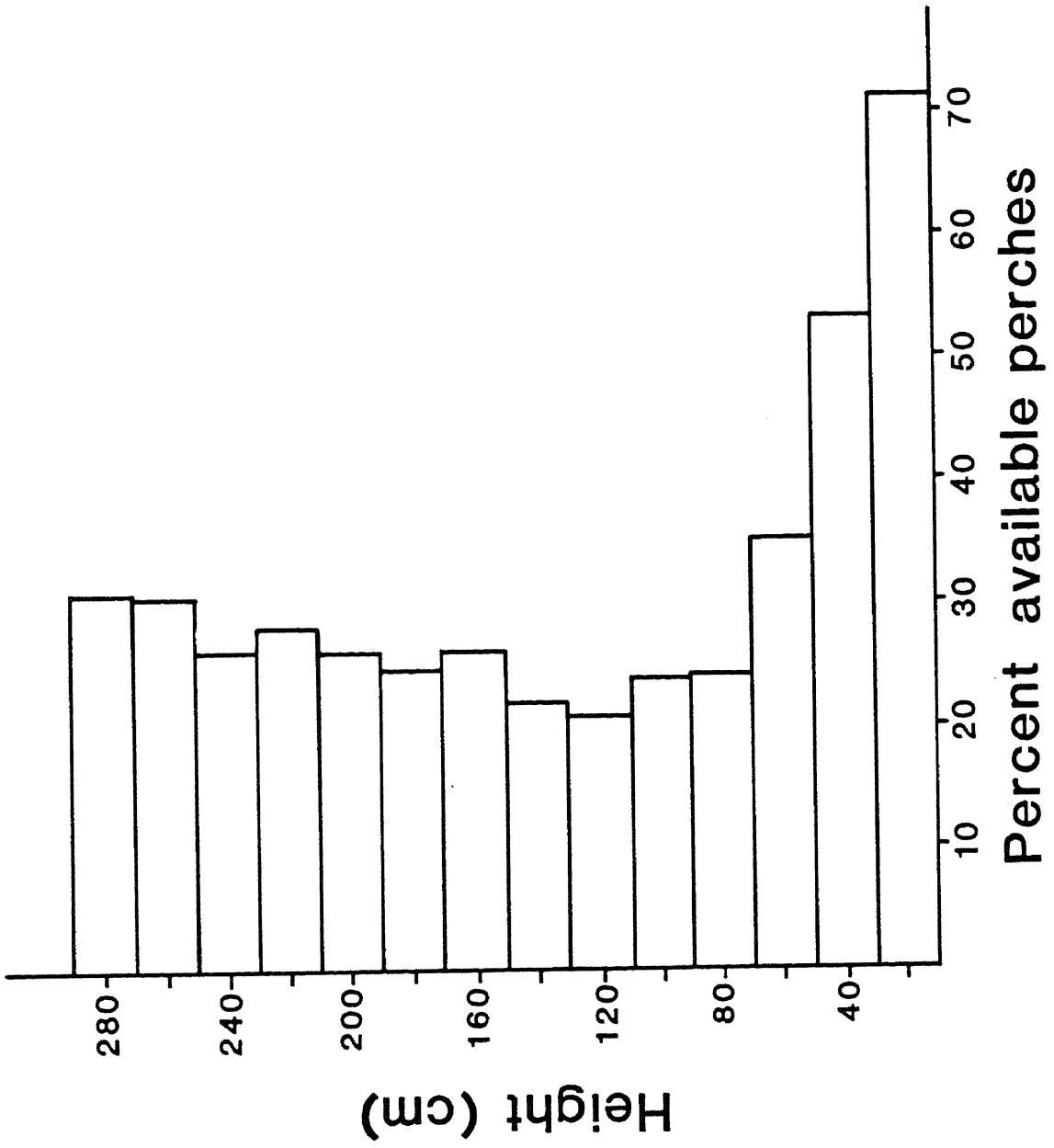


Figure 3-3. Relation between vertical overlap (equation 1) and overlap corrected for the availability of perches (see text).
each ○ represents 2 correlations,
each ⊙ represents 4 correlations,
each ● represents 6 correlations.
A total of 90 correlations are presented, 9 for each of the 10 species.

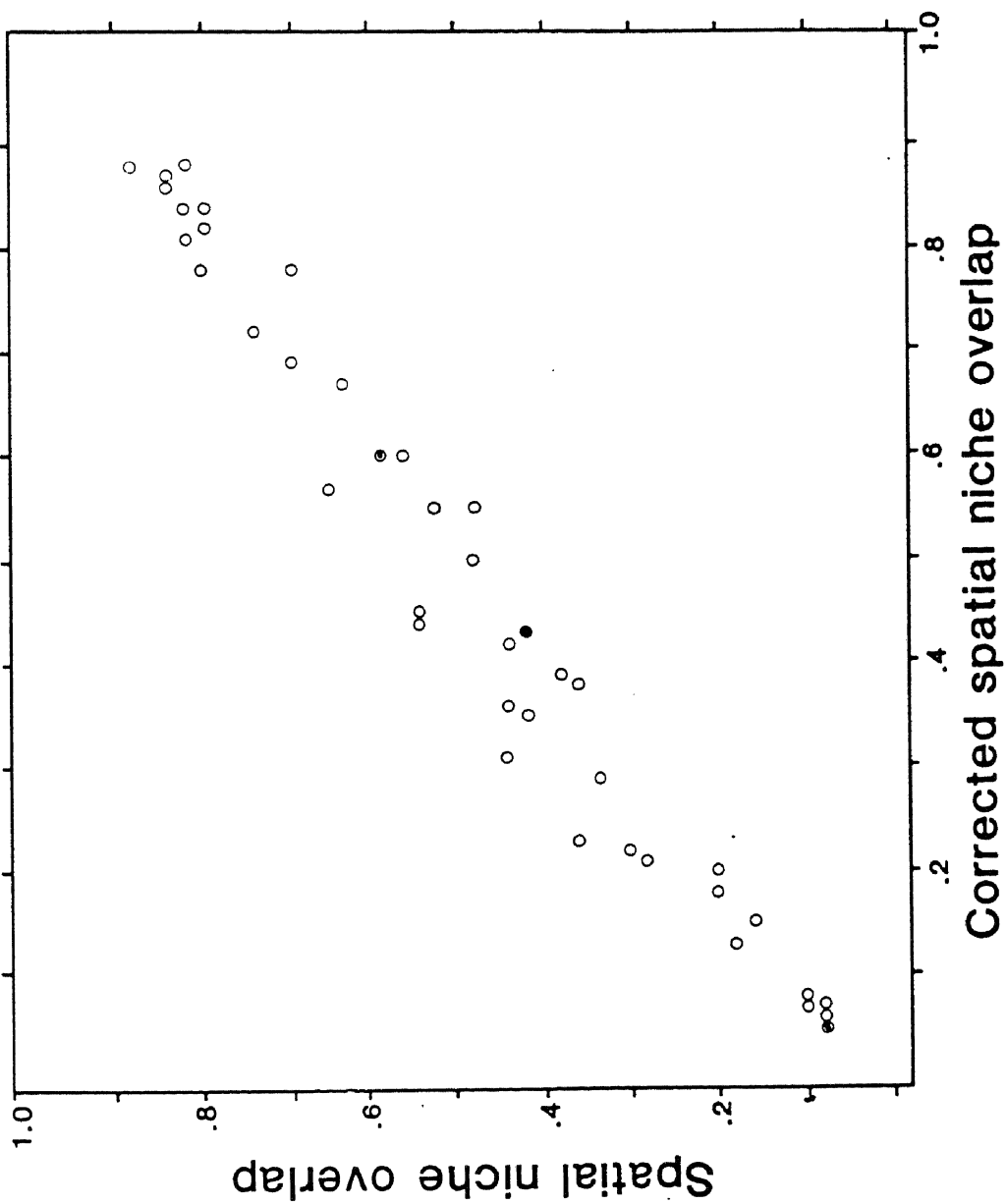
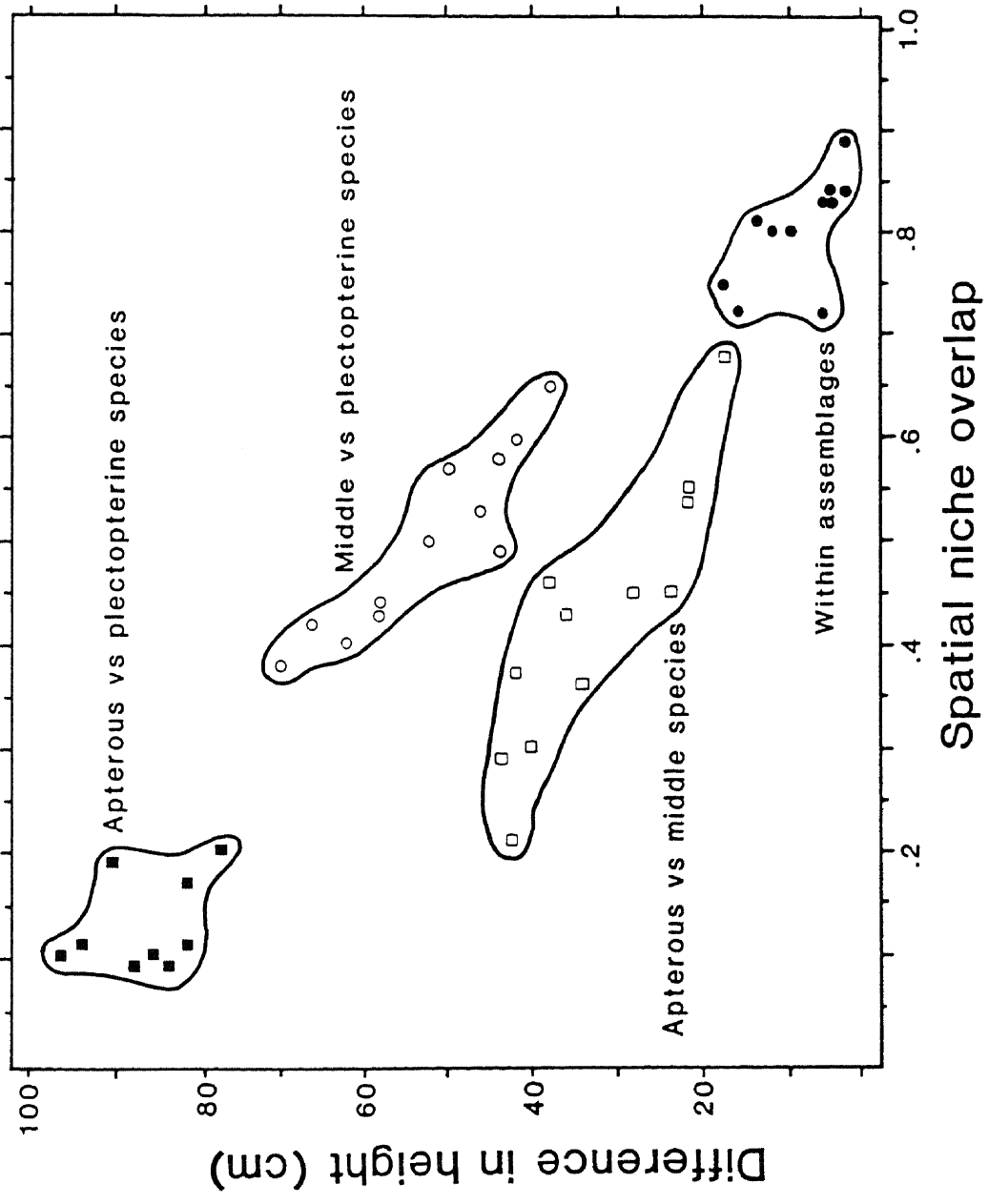


Figure 3-4. Relationship between differences in species mean height and vertical overlap. middle species are X. hamata, X. cantralli, E. unistilata, and E. rothi. Within assemblages are comparisons of species within each assemblage (e.g., E. unistilata vs. Nesomylacris, E. rothi vs. E. unistilata).



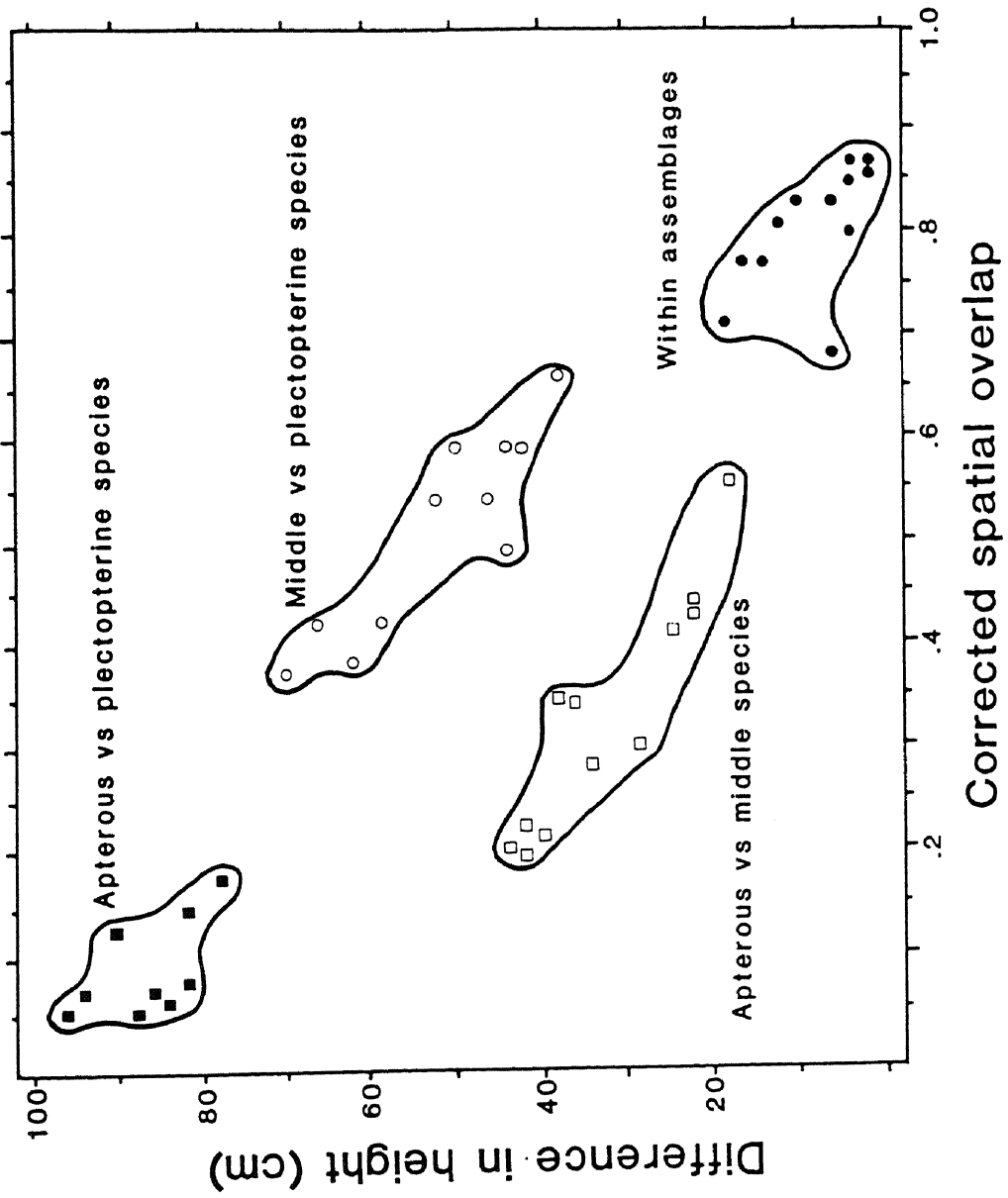


Figure 3-6. Dendrogram of ecological similarity of species and consexuals, based on overlaps in vertical distributions. Overlaps within clusters were averaged in the amalgamation procedure.

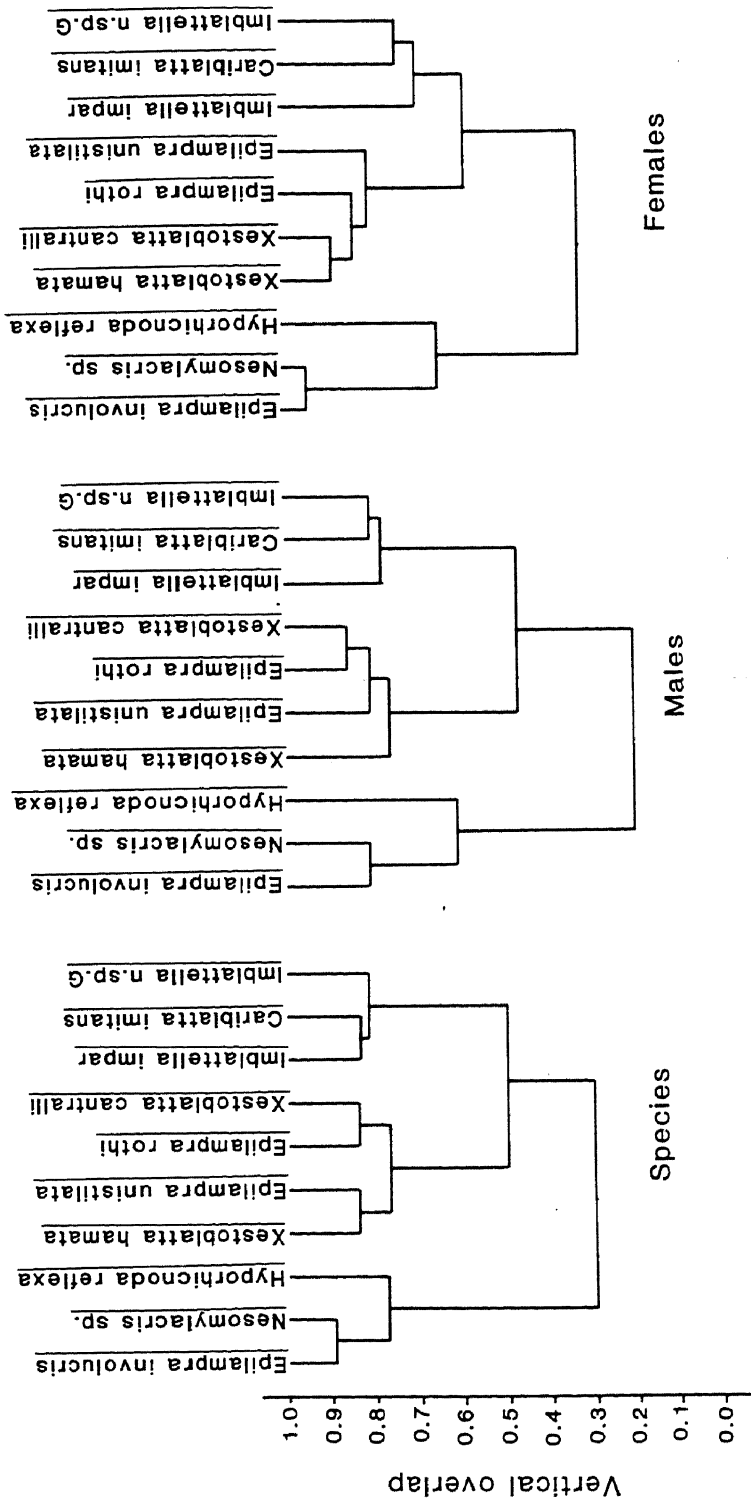


Figure 3-7. Relation between mean height and vertical breadth for species and sexes. Boundaries for groups were drawn to delimit the three assemblages; no statistical procedure was used to do so.

□ = species,

○ = females,

● = males.

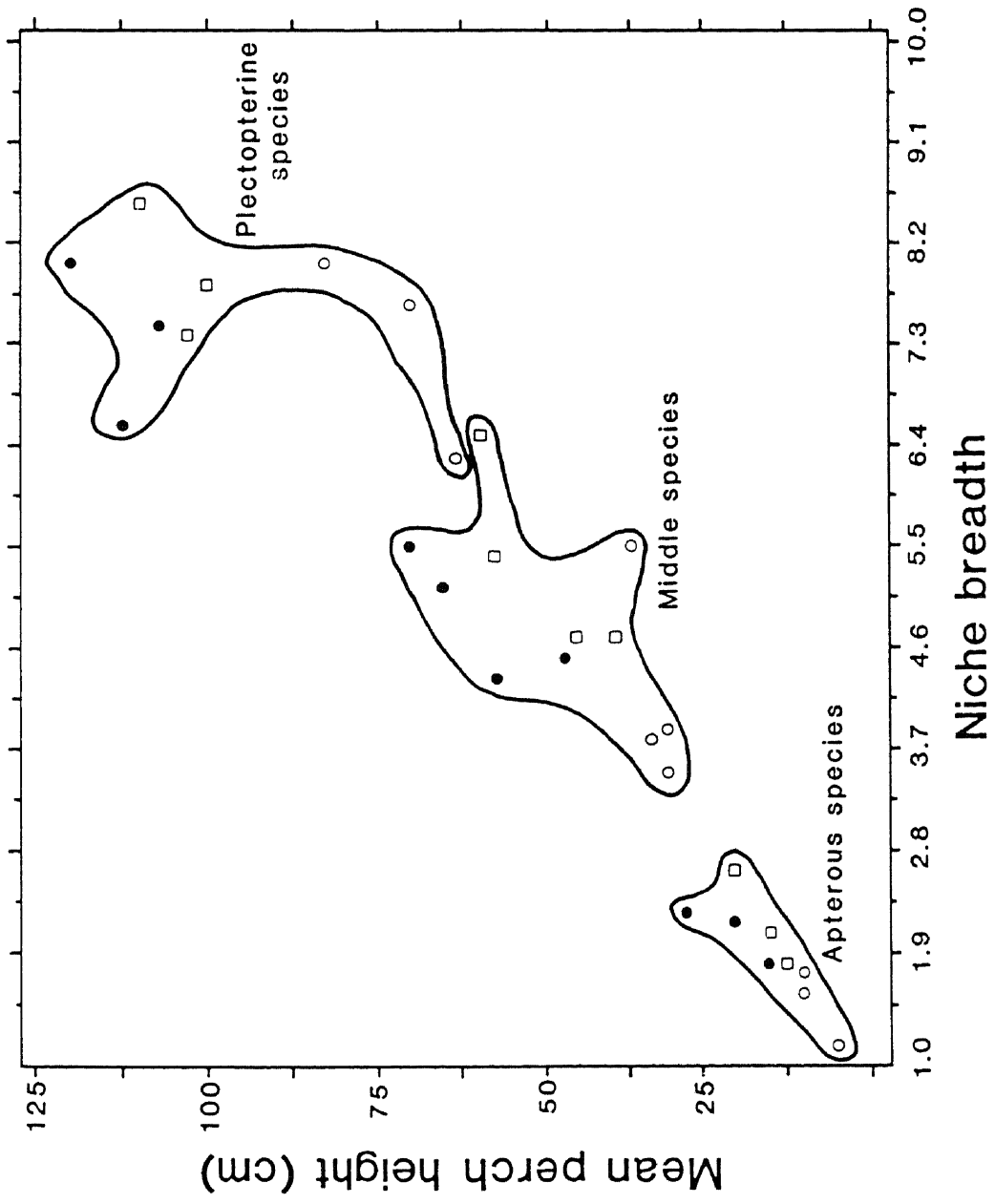


Figure 3-8. Relation between mean height and the difference in mean heights of conspecific males and females.

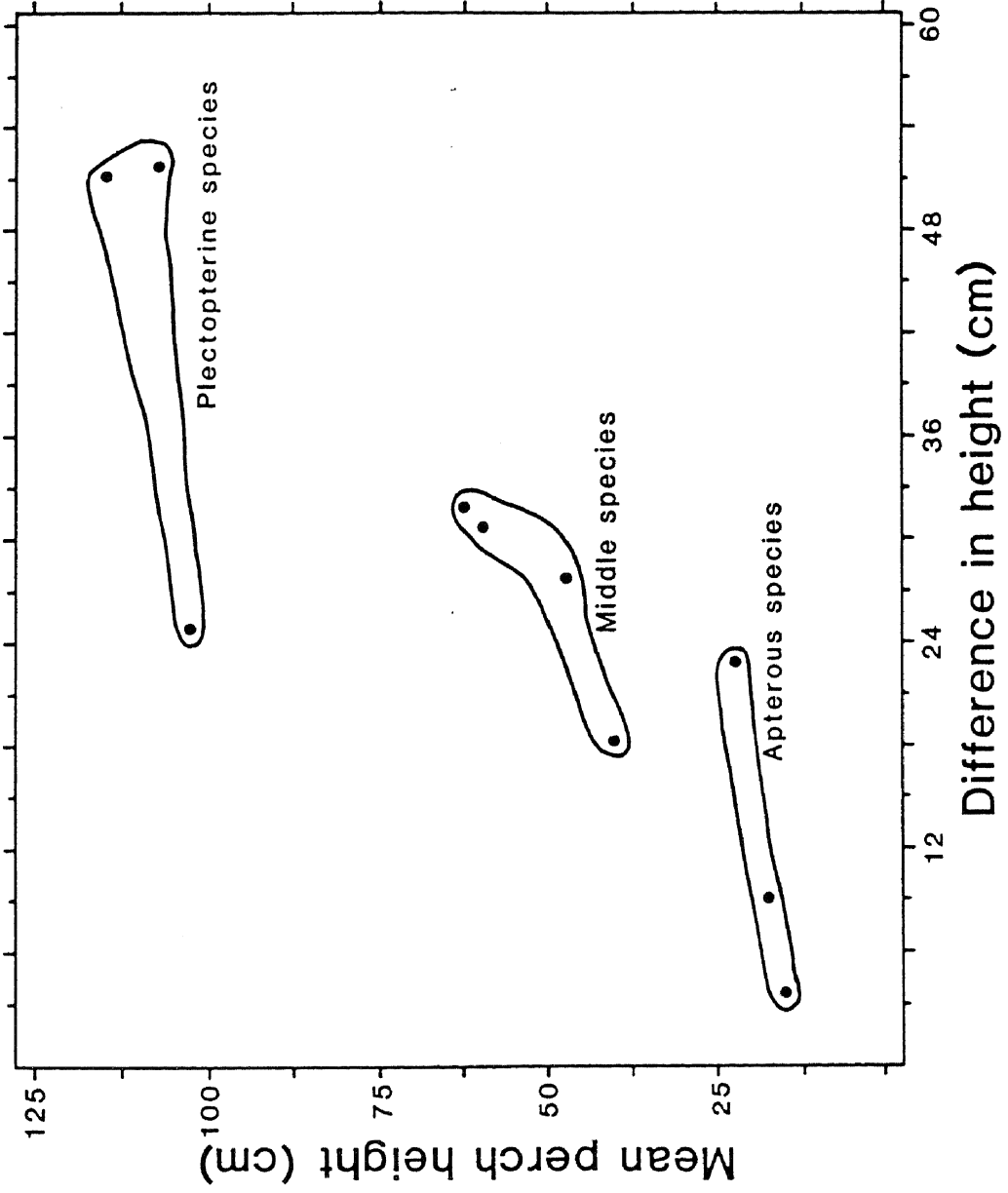


Figure 3-9. Diel activity of cockroaches. Comparison of activity (conspicuousness) in the field and locomotory activity in an outdoor insectary.

CHAPTER 4

Intraspecific Vertical Stratification as a Mate-Finding
Mechanism in Tropical Cockroaches

Cockroaches in a tropical forest stratify vertically both inter- and intraspecifically along micrometeorological gradients. At night, low wind speeds and unstable atmospheric conditions result in efficient mixing of air near the ground. Convective ascent of warm air imparts directionality to the pheromone dispersion process. The occurrence of males at greater heights than pheromone-emitting conspecific females appears to be a mate-finding strategy.

INTRODUCTION

For airborne chemicals to be effective signals in communication, their release and reception must correlate with favorable micrometeorological conditions. To enhance their efficiency in finding pheromone-emitting females, males should occupy ranges above, overlapping, or below the females' vertical ranges, depending upon the prevailing atmospheric conditions. Because meteorological patterns exhibit circadian cycles, they couple the orientation behavior to specific times during the day or night. If, for example, buoyant (temperature decreases with height above the ground) atmospheric conditions prevail at night, males should occupy perches at greater heights than females. Conversely, under stable (temperature increases with height) atmospheric conditions with temperature inversion, males should overlap with the vertical distribution of the females or range below them.

Dispersion models (e.g., Sutton, 1953; Bossert and Wilson, 1963; review: Elkinton and Carde, 1983) describe plumes with center lines parallel to the ground and remaining at the height of the point source. The vertical and horizontal profiles of the plumes at any given point along this line correspond to Gaussian distributions. These models predict that the optimal vertical distribution for males should completely overlap the range of pheromone-emitting females. An exception is a study by Fares et al. (1980) who discuss the influence of micrometeorological conditions on concentration profiles at different emission heights. They conclude that "pheromone communication appears

to be ineffective under buoyant atmospheric conditions." However, they limit their data analysis to daytime patterns and to diurnally active insects. Also, flight of diurnal insects may be related to thermal stress in mid-day resulting in early and late (bimodal) flight activity, which happens to correlate well with stable conditions. Fares et al. (1980) do not address this problem.

With increased interest in behavioral and biological control and management of forest insects, it is important to describe the transport mechanisms which operate in olfactory communication. I report spatial distribution data for forest cockroaches with micrometeorological profiles and show that vertical stratification is important in mate-finding.

RESULTS and DISCUSSION

I found that the cockroach community at Finca La Selva in Costa Rica (see Holdridge et al., 1971 for site description) stratified vertically both inter- and intraspecifically. Interspecific and demographic separation was discussed in Chapter 3. Resource partitioning due to sexual dimorphism is likely to occur in several species (e.g., Epilampra involucris, and Hyporhicnoda reflexa), where the females are either larger than the males or are wingless. However, this mechanism does not account for the consistent occurrence of males higher than conspecific females regardless of the morphology or size of the sexes.

I hypothesize that sexual stratification enhances the efficiency of males in orienting to pheromone-emitting females. This mechanism will

operate best when temperature lapse profiles result in convective ascent of air (and airborne chemicals) near the ground.

Contrary to what is expected in the canopy and above the forest (Richards, 1952), daytime temperature inversion is followed by nighttime temperature lapse within 2 m above the ground (Fig. 4-1, see also Melpar, 1969). The wind profile (Fig. 4-2) is similar to results obtained by other researchers (Evans, 1939; Geiger, 1965; Allen et al., 1972), but the wind speeds recorded in the tropical forest at night are at least an order of magnitude smaller than those reported from other forest types.

The interaction of vertical thermal gradients and mechanical aspects of the wind profile is described by the Richardson number, R (e.g., Thom, 1975). It is a measure of the stability of the atmosphere near the ground. In the present study, temperature lapse and low wind speeds near the ground at night result in large negative R values. Free convection predominates close to the ground; buoyant air of relatively low density moves vertically into denser, cooler air resulting in efficient vertical mixing. Higher above the ground free convection and wind-generated eddies coexist to form a hybrid turbulence regime called mixed convection.

The driving force of the nighttime thermal convection is directly proportional to the difference in temperature between the two mixing layers of air. As air rises, its temperature excess over that of its new environment increases, and therefore the buoyant driving force increases. Hence, a convective plume will accelerate upward until slowed by entrainment (mixing) or until it meets a layer of stable air.

The observed temperature differences decrease per unit distance of ascent (Fig. 4-1). Therefore, both entrainment and stability at higher levels decrease the rate of upward movement of the plume.

Visual representations of plumes from point sources of artificial, nonbuoyant smoke (Fig. 4-3) indicate that the vertical component is frequently more significant close to the ground where large temperature differences and low wind speeds predominate. At higher levels the horizontal component accounts for most of the air movement as entrainment, increased wind speeds, and a shift to thermal stability interact to reduce the vertical flow.

If relatively small vertical temperature gradients impart directionality to air movement, then a behavioral response which does not occur under vertically isothermal conditions (that is, subthreshold pheromone concentrations) ought to be elicited in males downwind in a temperature gradient. I installed a 1 centigrade degree vertical gradient over a distance of 60 cm with resistance wire and two temperature regulators (Yellow Springs Instruments models 71 and 73). A continuous output of the temperatures was provided by a two-channel strip chart recorder (Esterline-Angus Speed Servo 2). I used 5×10^{-6} μg of synthetic (+/-) Periplanone B (Adams et al., 1979) adsorbed onto a 1 cm^2 Whatman number 1 filter paper to elicit sexual responses in P. americana males in a screen cage above the pheromone source. The test recorded the number of times in 30 second intervals that the males crossed a line bisecting the floor of the cage. Each test was 4 minutes. I performed 10 tests in isothermal and ten in temperature lapse conditions.

In isothermal (neutral) conditions the Periplaneta americana sex pheromone did not elicit searching in males; no courtship responses were observed. However, when temperature was made to decrease with height, and the pheromone was introduced below the males, their locomotion increased significantly ($P < 0.01$), and the complete courtship sequence of rapid antennal movement, stilt walking, wing raising, and wing fanning was elicited. Clearly, the thermal gradient imparts a new directionality to the air flow. The 360° emission angle of Fickian diffusion decreases to a narrow vertical plume in the direction of the males. Hence, more molecules per unit volume of air impinge on the male antennae, and threshold concentrations are more likely to be reached.

Silverman and Bell (1979) found that P. americana males tethered on a vertical surface responded to sex pheromone delivered perpendicularly to the vertical surface. Air without pheromone caused the males to run up, whereas air currents with sex pheromones caused them to run down. These data are consistent with my convective model for volatile pheromones.

In conclusion, the vertical distribution data, predictable nocturnal micrometeorological profiles, pheromone dispersion models, male orientation behavior, and laboratory experiments suggest that intraspecific height stratification in these species of cockroaches is a mechanism that enhances the efficiency of the mate-finding process.

ACKNOWLEDGEMENTS

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Figure 4-1. Temperature profiles for a typical 24 hour period in the dry season (10 April 1980). Mercury thermometers were positioned at four heights in the understory. Measurements were recorded every 2 hours along with climatological conditions. The stippled area represents nighttime.

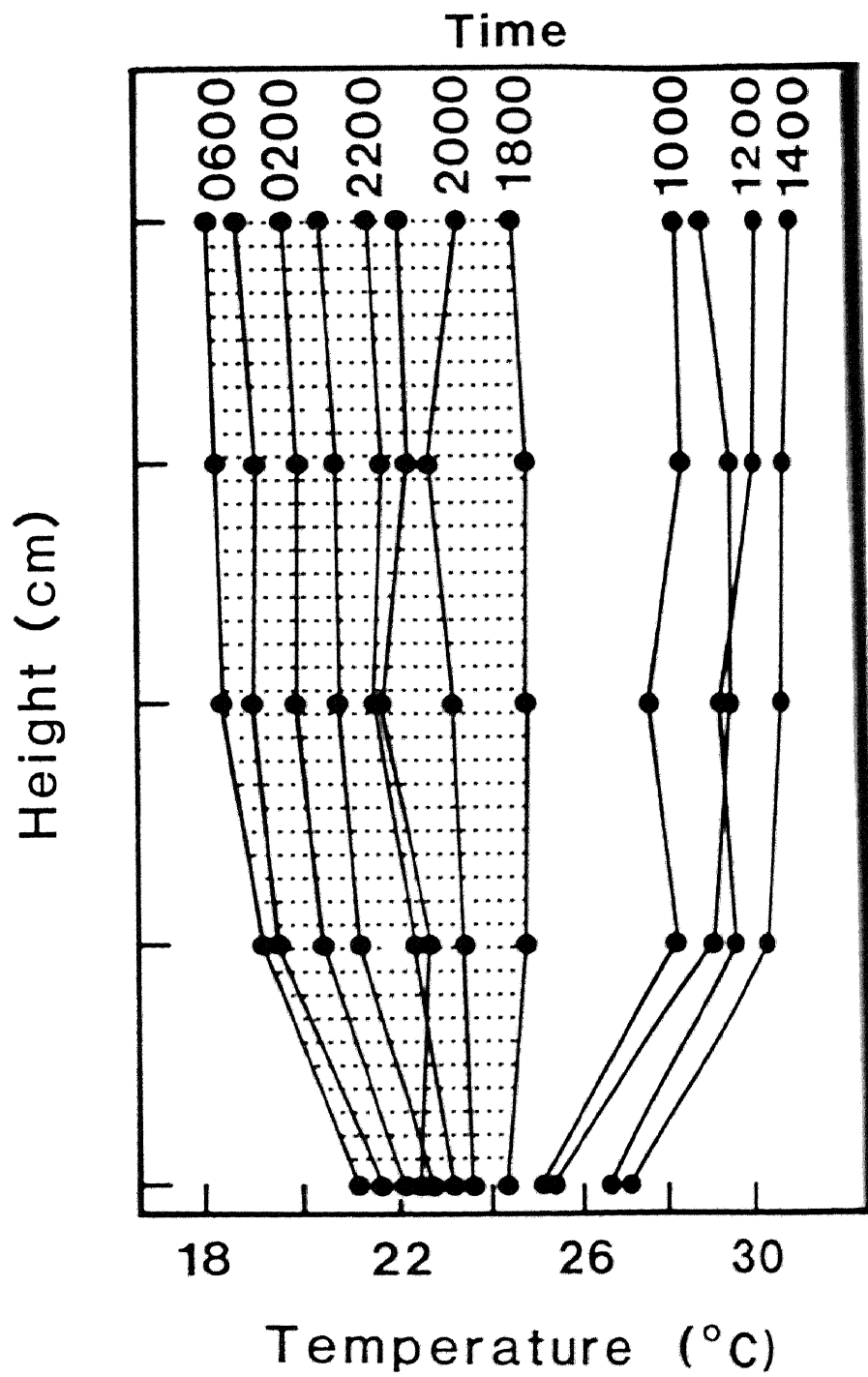


Figure 4-2. Wind profile for day and night conditions in the dry season. Instantaneous readings with an Alnor type 8500 Thermo-anemometer were taken every 15 seconds for 4 minutes at each of three heights, followed by eight additional readings at each height. The sampling order of the three heights was randomized; 96 instantaneous readings taken over 4 days were averaged (\pm standard error) for each height.

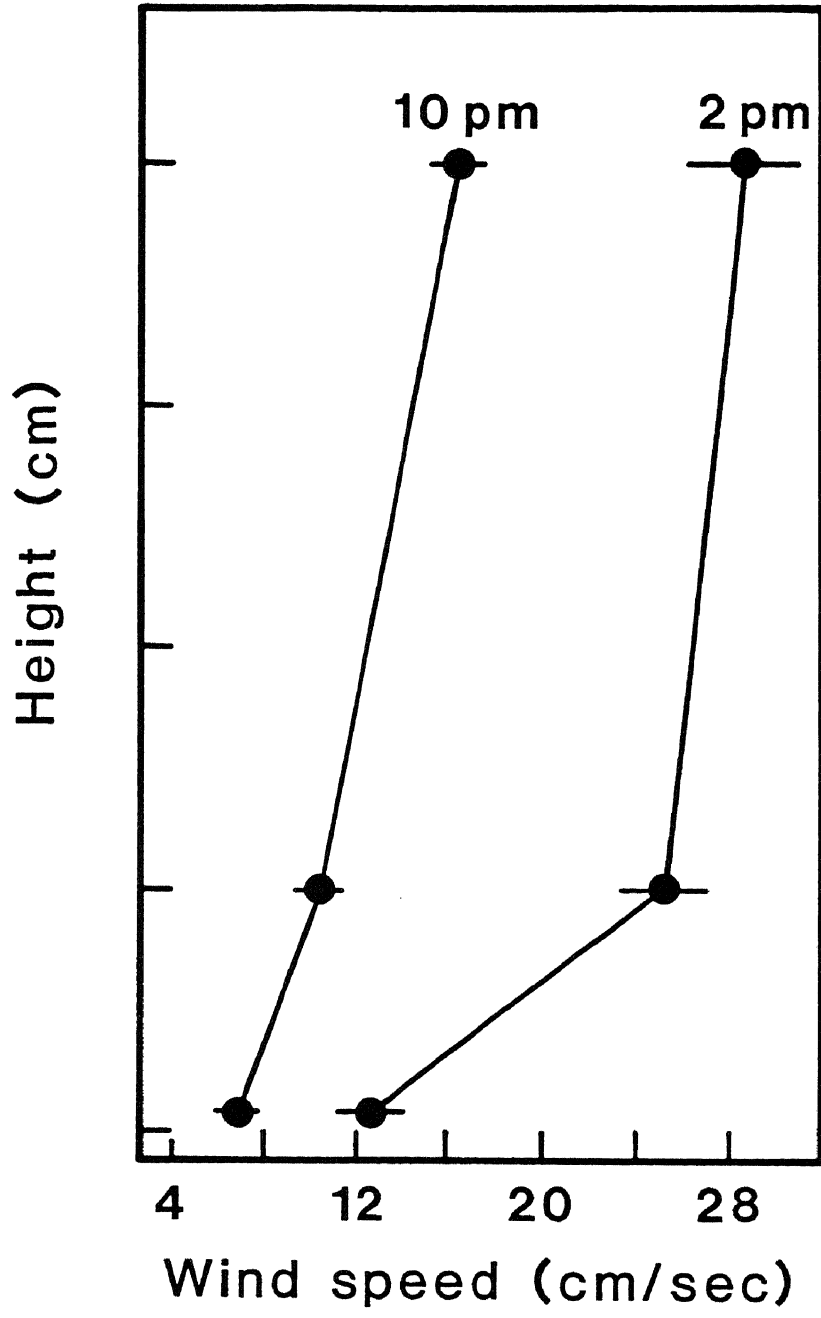
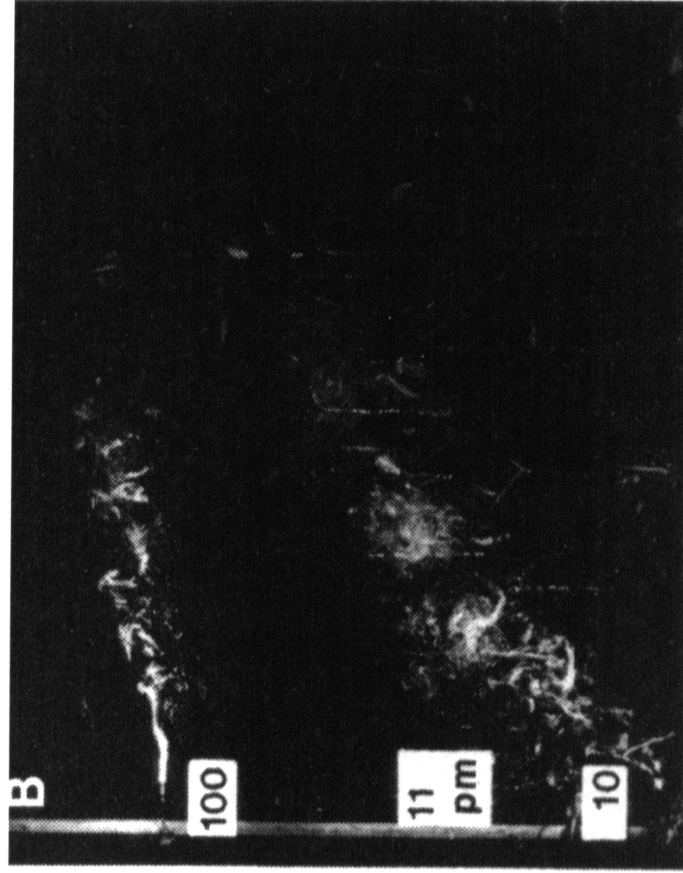


Figure 4-3. Titanium tetrachloride was used as point sources for smoke plumes. The photograph (A) was taken at 2 p.m. Note the predominantly horizontal flow at both point sources. The photograph (B) was taken at 11 p.m. Nighttime unstable conditions result in vertical ascent from the lower source (10 cm.).



CHAPTER 5

Ecological Correlates of Paternal Investment of Urates
in a Tropical Cockroach

Females of the tropical cockroach Xestoblatta hamata feed on urates offered by the male after copulation. Females on nitrogen-deficient diets ingest and transfer to their maturing oocytes more male-derived uric acid than do females on high-protein diets. In isolated females, the greatest uptake of uric acid by the ovaries occurs during the mating stage in the reproductive cycle. Uric acid from males contributes significantly to the female's nitrogen pool and may help shorten the time between mating and oviposition. In both field and in laboratory experiments males choose high-protein foods and dietary uric acid.

INTRODUCTION

Cockroaches, unlike many terrestrial insects, void little uric acid (Mullins and Cochran, 1972). Instead, they store urates in specialized cells of the fat body or secrete them into accessory glands in males of some species. In three subfamilies of cockroaches the male coats his sperm package with uric acid after inserting it into the female (Roth and Dateo, 1964, 1965). Roth (1967, 1970c) suggested that uric acid might protect the spermatophore from being prematurely consumed by the female or by other insects, and Cornwell (1968) suggested that it might act like a plug to prevent females from mating repeatedly. Mullins and Keil (1980) reported, however, that the spermatophore-urate complex sometimes disappeared shortly after mating and that male uric acid could be recovered from mated Blattella germanica females and their oothecae. The transfer of urates was related to the nutritional state of the female: those on a low-protein diet transferred more to oothecae than did those on a high-protein diet. Mullins and Keil (1980) suggested that the transfer of urates might represent "paternal investment of a nitrogen resource from which the female and her progeny might benefit."

I report a post-copulatory behavior in the tropical rain-forest cockroach Xestoblatta hamata that supports the paternal investment proposal. After copulation the male raises his wings, telescopes his abdomen, widens the genital chamber exposing a white urate secretion, and directs it toward the female (Fig 5-1), who ingests the secretion. This behavior supports the nutritional investment hypothesis and Mullins and Keil's (1980) suggestion that the male urates are ingested by the

female (B. germanica in their report, subfamily Blattellinae, as is X. hamata). This cockroach species is one of few for which sufficient ecological data are available (see Chapters 3,4) to directly assess the significance of male dietary contributions to the female's nitrogen budget.

RESULTS and DISCUSSION

Both the size of the male's uricose glands and the dietary nitrogen status of the female determine the duration of feeding and the quantity of uric acid ingested by the female. I maintained some females on an 8 percent casein protein diet, and others on a 64 percent casein diet: in males the result was small (mean \pm S.E.M., 13.0 ± 1.5 mg; N=9) and large (27.4 ± 1.2 mg; N=11) uricose glands, respectively, after 20 days. Long, uninterrupted post-copulatory feeding was common when the male had large stores of urates regardless of the nutritional condition of the female (pooled data for both female groups: 216.5 ± 19.23 seconds, 2.3 ± 0.33 pauses; N=11). Females deficient in dietary nitrogen (N=5) continued to palpate the male and attempted to feed after his small gland was depleted. Hence, their cumulative feeding periods were significantly longer than those of females with high dietary nitrogen (N=7): 128.0 ± 22.73 seconds, 4.0 ± 0.45 pauses, versus 76.4 ± 12.66 seconds, 2.9 ± 0.40 pauses ($P < 0.05$, Mann-Whitney U-test).

Females maintained on the low-protein diet incorporated and transferred to their egg-cases large quantities of label which had been injected into males as [8 - 14 C]-hypoxanthine, whether the males had

small or large uricose glands (Table 5-1). Females on a high-protein diet acquired significantly less label from males with large uricose glands ($t=3.53$, $P=0.008$) and consequently incorporated less label into their oothecae ($t=8.67$, $P=0.003$). Some label was lost in the transfer of uric acid. I did not quantify the conversion of hypoxanthine to uric acid nor measure urate metabolism to $^{14}\text{CO}_2$. In Parcoblatta the amounts of $^{14}\text{CO}_2$ evolved are related to nitrogen content in the diet (D.G. Cochran, personal communication).

Transfer of uric acid into the terminal oocytes begins after the third night of an 8- to 9-day ovarian cycle; mating usually occurs on the fourth night. As both the protein content (due to uptake of blood vitellogenin) and the mass of the ovaries increase, the percentage of nitrogen content remains relatively constant (8.47 ± 0.51 percent). Yet, ovarian uric acid (uricase assay) increases from $3.4 \mu\text{g}$ per milligram of dry ovarian tissue early in the cycle to $61.7 \mu\text{g}$ per milligram of dry tissue when ovulation begins (Fig. 5-2). Hence, the percentage of total ovarian nitrogen attributed to uric acid increases from 1.0 percent immediately after deposition of an egg case (day 1) to 27.7 percent in mature oocytes (Fig. 5-2).

A similar pattern was observed by incorporation of labeled hypoxanthine in the ovaries. I injected $1 \mu\text{l}$ of $[8 - ^{14}\text{C}]$ -hypoxanthine into females on the first day of the ovarian cycle (postoviposition) and assayed the radioactivity of paired ovaries on subsequent days. The radioactivity was 352 ± 32 dpm on day 2 ($N=3$), 5170 ± 1200 dpm on day 4 ($N=4$), and $10,479 \pm 1148$ dpm ($N=3$) on day 6. The females were maintained on a 25 percent protein diet.

Females mate repeatedly throughout their adult lives either because of sperm shortage or because of urate deficiency. The latter is implicated by the following data: females maintained on a high-protein diet produced egg cases containing significantly more uric acid than females on an 8-percent protein diet ($7.6 \pm 1.01 \mu\text{M}$ and $4.8 \pm 1.00 \mu\text{M}$ per egg case, corresponding to 2.58 and 1.52 percent of the dry weights, respectively; $N=8$, $P=0.01$). Two freshly deposited oothecae collected in the field yielded an average of $7.3 \mu\text{M}$ uric acid, suggesting that, in the forest, females may feed on high-protein foods, on uric acid, or on both. Yet, field evidence indicates that females feed on nitrogen-deficient foods and rarely forage on uric acid. In choice experiments in the laboratory high-nitrogen diets were consumed mainly on nights 3 and 4 of the ovarian cycle. Foods (mainly plant material; Chapter 3) ingested at this stage in the field contained more nitrogen than did foods consumed during earlier and later stages, but the nitrogen content was not sufficient to produce the $7 \mu\text{M}$ of uric acid found in egg cases collected in the field (data not shown).

As in the German cockroach, but unlike the American cockroach, X. hamata females use most of the food consumed before oviposition for a single egg case; little nutrient storage occurs (B. germanica females use 90 percent of the food gained in the preovipositional period for the production of a single egg case [Kunkel, 1966]). Moreover, in the field, the uric acid content (ovaries and stomachs excluded) of postoviposition females did not differ from females midway through the ovarian cycle ($11.51 \pm 4.75 \mu\text{M}$ and $12.23 \pm 3.91 \mu\text{M}$ per female, which represent 1.54 and 1.16 percent of the total dry weight, respectively;

N=10, P=0.89), and some females in both groups had low uric acid reserves. An increase in uric acid content through the first 4 days of the ovarian cycle should occur if females ingested foods high in nitrogen.

The percent uric acid values which I report are significantly lower than the 18 to 87 percent values reported for female B. germanica (Valovage and Brooks, 1979), and the 8 to 31 percent reported for various species maintained in the laboratory (Mullins and Cochran, 1976). Potrikus and Breznak (1980) reported that freshly collected termites contained approximately 2 percent uric acid; the amount increased to 45 percent for those in captivity, indicating that levels of uric acid might generally be higher in captive cockroaches as well.

The average dry weight of uricose glands in a natural population was 17.6 ± 1.2 mg (N=45) which, if one assumes a urate content of $4.3 \mu\text{M}$ per milligram of dry gland as reported for B. germanica and Nyctibora lutzi (Mullins, 1979), corresponds to $75.7 \mu\text{M}$ of uric acid. I did not determine the urate content of Xestoblatta uricose glands. The average male has sufficient uric acid in his uricose gland to supply enough for 10 egg cases, if there is no loss during transfer and uptake by the female. Since oothecal uric acid is related to dietary nitrogen, and if embryonic uric acid increases the fitness of the young, females would have to forage for high-nitrogen foods to obtain adequate quantities of uric acid in the absence of males.

My data indicate that if females have access to uric acid after mating, the preovipositional period may be shortened. Since delaying oviposition may result either in resorption of oocytes if essential

nutrients are not available (Bell and Bohm, 1975) or in re-mating, or both, the male should minimize the time between mating and oviposition. In B. germanica when two males mate with a female before she oviposits, mixing of the two ejaculates (that is, sperm competition) may occur (Cochran, 1979).

Presumably, these consequences of deficiency in nitrogenous foods, short reproductive cycles, a concurrent demand by females for other nutrients, and the relative scarcity of foods high in nitrogen would select for male urate contribution to females. Although males have relatively low nitrogen requirements, they feed on bird and reptilian droppings (Fig. 5-1C) which are largely uric acid. In choice experiments in the laboratory, males consume large percentages of uric acid and high-protein food which results in rapid enlargement of their uricose glands. Yet, if sexually receptive females are not available to accept the accessory secretion, accumulation of extracellular uric acid results in increased mortality (Haydak, 1953). Mullins and Cochran (1973) reported that mutagenic and carcinogenic tryptophan metabolites increase as dietary nitrogen increases, and they suggested that the quinoline compounds contributed to the increased mortality of P. americana on high-protein diets.

Pressures on the male to accumulate and void stored urates and his enhanced fitness when uric acid is successfully transferred to the female may have contributed to the evolution of a relatively protracted copulation (248.3 ± 18.5 minutes; $N=9$). Other species of cockroaches copulate for about 20 to 120 minutes (e.g., Stay and Roth, 1958). This period in X. hamata approximately corresponds to the time required for

the crop to empty following feeding. In the forest, females feed on plant material starting at approximately 1900 hours and couple with males at midnight, allowing for only one mating per night. Hence, the male may be delaying the deposition of a spermatophore until the female's crop is empty and she can accommodate his urate secretion. Parker (1970) suggests that long mating sequences may be a form of mate-guarding (and paternity assurance) whereby the female is unavailable to other males when she is most receptive.

On the basis of significant urate accumulation in aposymbiotic cockroaches, and mobilization of urates by cockroaches deficient in nitrogen, researchers have implicated bacteria in the degradation of uric acid (review: Mullins and Cochran, 1975). Specialized cells harboring symbiotic bacteria are also found in the ovaries of cockroaches (Brooks and Richards, 1966) and are transferred to oocytes during their maturation. If, in fact, trans-ovarial transmission of uricolytic bacteria occurs in X. hamata (as it does in the other cockroach species examined thus far), then nitrogen and carbon may be gained from metabolism during embryogenesis of paternally derived uric acid.

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Table 5-1. Fate of labeled hypoxanthine injected into males.

Males with empty uricose glands were injected with 1 μ l [8-¹⁴C]-hypoxanthine and maintained on 8 or 64 percent protein diets for 8 to 30 days. The ¹⁴C-labeled urates were traced in males, mated whole females, and in egg cases by the extraction and counting procedures of Mullins and Keil (1980). The amount of label incorporated into the accessory gland increased with time ($y = 6900 + 3000x$). Only copulations occurring 20 to 25 days after injection are reported. Uricose glands of unmated males averaged $114,606 \pm 19,207$ degradations/min per male (N=7); the average for the rest of the body was $11,327 \pm 588$ dpm (N=7) after 20 to 25 days. The relatively large variance in the radioactivity of females in the group on the 64-percent protein diet with access to large uricose glands was in part due to defecation of uric acid shortly after ingestion. Two white fecal pellets from two females in this group contained 25,817 and 33,511 dpm per insect.

Each entry represents a mean, standard error of the mean, number of observations, and coefficient of variation.

Significance values are based on t-tests.

Radioactivity in cockroach tissues (d.p.m. X 10³)

Female diet	Mated Females				Mated Males		
	Male glands	Whole females*	First ootheca	Second ootheca	Uricose gland	Rest of body	
8% protein	small	77.2±5.9(5) (17.2%)	22.5±2.7(3) (20.9%)	15.8±1.7(2) (15.4%)	12.4±3.1(5) (56.1%)	14.7±1.2(5) (18.8%)	
	large	73.1±5.0(5) (15.2%)	16.9±2.1(4) (24.7%)	9.3±2.0(2) (29.8%)	20.4±4.5(5) (49.8%)	15.1±1.2(5) (17.4%)	
		P=0.618	P=0.156		P=0.184	P=0.816	
64% protein	small	59.3±10.2(5) (38.5%)	8.7±0.6(2) (9.1%)	3.0 (1)	45.4±7.0(5) (34.6%)	14.9±1.2(5) (18.1%)	
	large	19.5±4.7(5) (54.4%)	2.5±0.4(3) (30.8%)	**	88.7±6.0(5) (15.2%)	14.3±1.6(5) (25.7%)	
		P=0.008	P=0.003		P=0.002	P=0.762	
8% vs 64%		P=0.001	P<0.001		P<0.001	P=0.825	

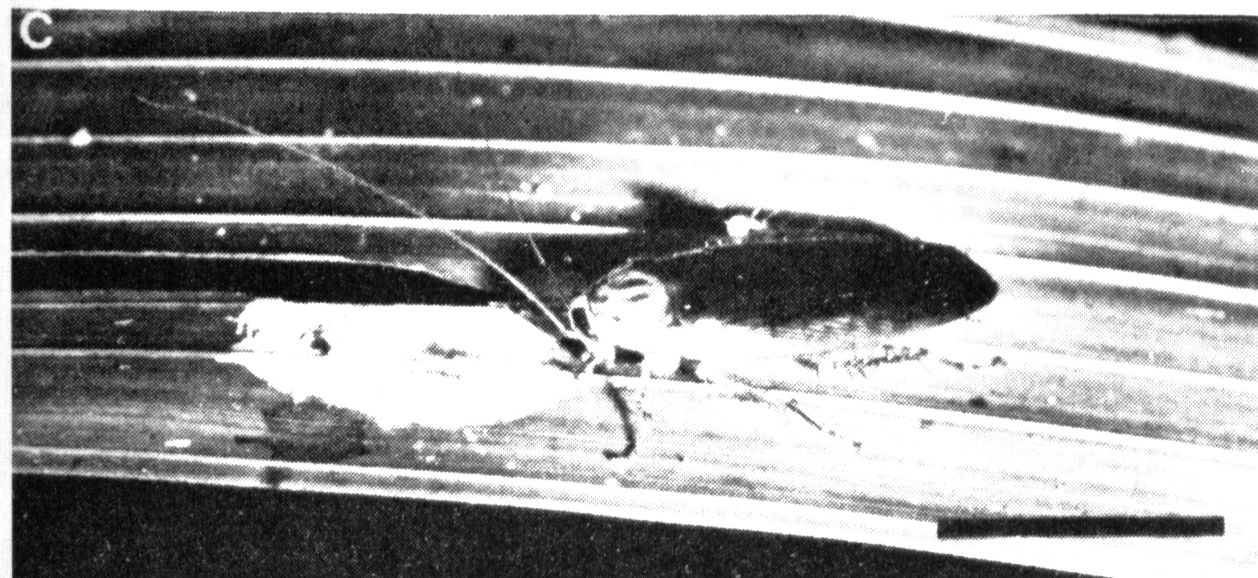
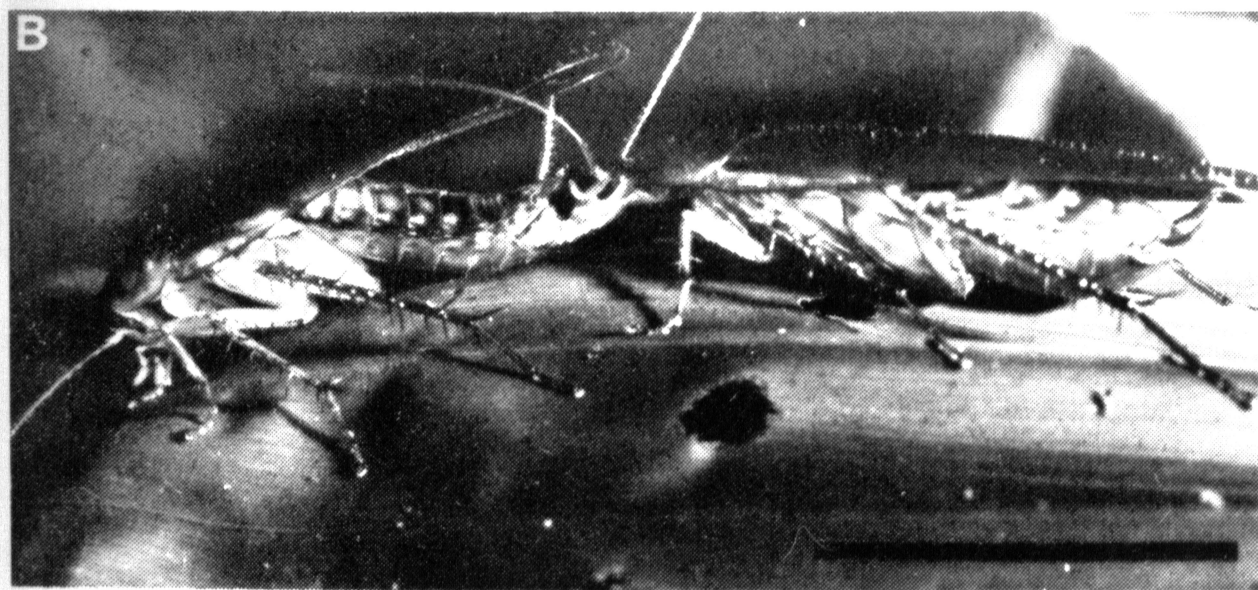
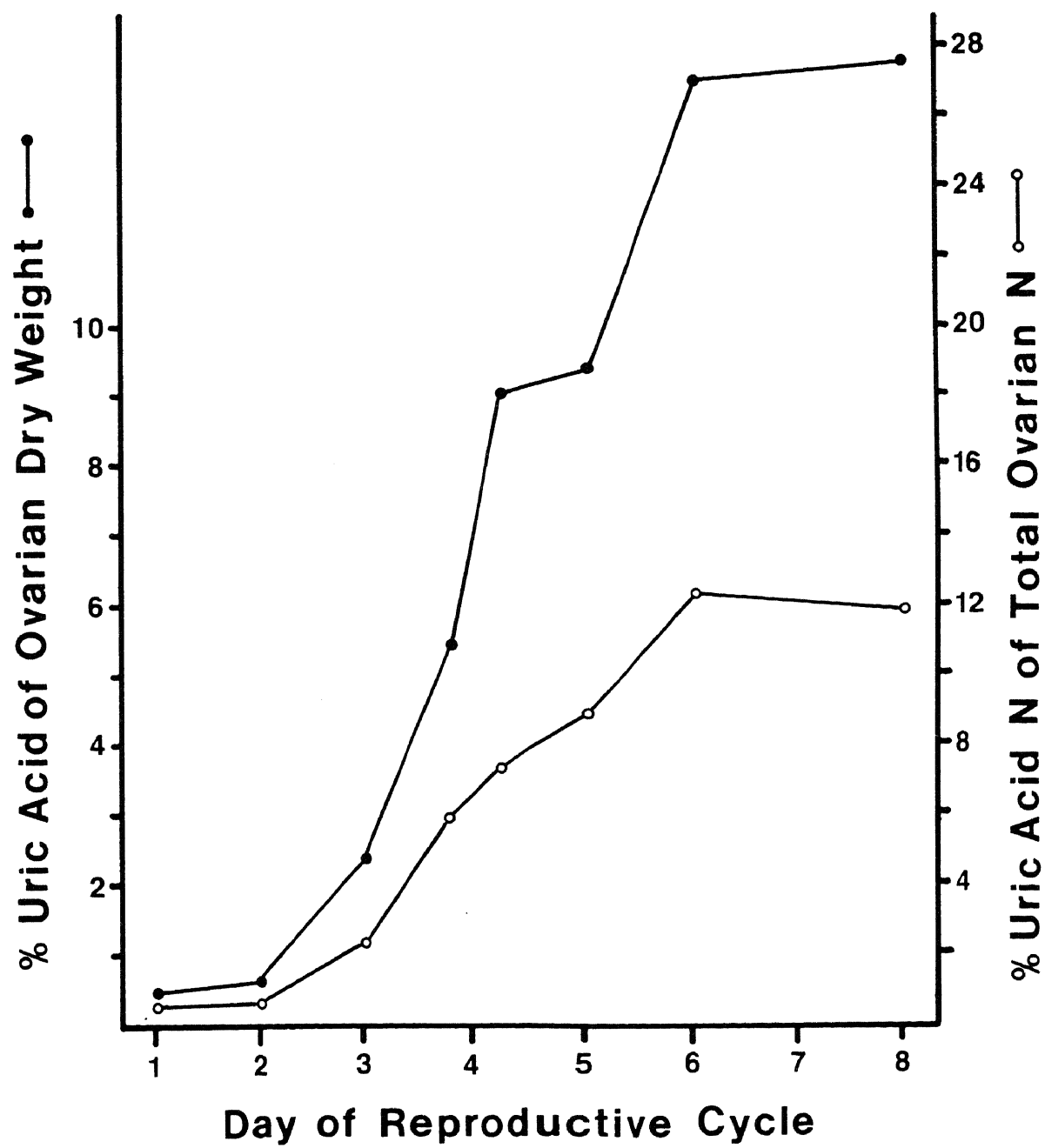


Figure 5-2. To evaluate the time-course of the uptake of uric acid, the ovaries of field captured females were assayed enzymatically (uricase test) for uric acid content. Percent nitrogen attributed to uric acid was calculated on the basis of 33.3 percent nitrogen in uric acid. Points represent the average of two replicates of several ovaries each.



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