

BEHAVIOURAL ECOLOGY OF COCKROACHES*

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I. INTRODUCTION

In the introduction to their treatise on the biotic associations of cockroaches, citing 1700 references, Roth & Willis (1960) concluded that: "Our detailed knowledge of cockroaches is based on studies of a 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 appeared, 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

* Dedicated to Dr Louis M. Roth, a pioneer in every aspect of cockroach biology.

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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 and psychological, reports and papers dealing primarily with other animal groups, comprise the bulk of the remaining 17 papers. With few exceptions, the behavioural 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 species that 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 behaviour, neurophysiology, and endocrinology (see Bell & Adiyodi, 1981a), and yet our understanding of their natural habitats and ecological associations is limited to vague geographical distribution data.

Nevertheless, recent research in field biology of cockroaches has provided a solid basis on which to compile this review. Of the several useful reasons for doing so, perhaps most important is the opportunity to integrate and synthesize different conceptual approaches by different researchers and to offer specific questions for future research. This work demonstrates that cockroaches, in addition to being inexpensive and expendible models for physiological and behavioural studies, are rewarding subjects for field investigations. We hope that the ease of studying cockroaches in the field will stimulate further research with these insects.

II. CLASSIFICATION OF COCKROACHES

Cockroaches are placed in five families comprising two major phyletic lines (Blattoidea, Blaberoidea) separated on the basis of reproductive strategies and morphology (McKittrick, 1964) (Fig. 1). Females of the Blattoidea species (families Cryptocercidae, Blattidae) are oviparous, producing hard, rigid egg cases which are dropped shortly after their formation; embryogenesis proceeds in the discarded oötheca. Several different oviposition mechanisms characterize the Blaberoidea. Females in the Polyphagidae rotate the oötheca and then carry it externally attached at the genital vestibulum. In 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 reproductive mode within the Blaberidae. Family Blattellidae contains both oviparous and ovoviviparous species, and some carry their oöthecae externally throughout embryogenesis in an intermediate condition between the two modes. The implications of these reproductive tactics will be discussed in relation to mating systems, communication, and social behaviour.

III. HABITAT TYPES

Cockroaches are ubiquitous in almost all habitat types where insects occur. Roth & Willis (1960), Princis (1962-1971) and Kumar (1975) list cockroach species with their respective geographical distributions. Several other works (e.g. Rehn & Hebard*, 1914; Bey-Bienko, 1950; Kevan & Chopard*, 1954; Ragge, 1965) describe local distributions

* Numerous references cited in this review appear in Roth & Willis (1960); they are marked with an asterisk and do not appear in the reference section of the present paper.

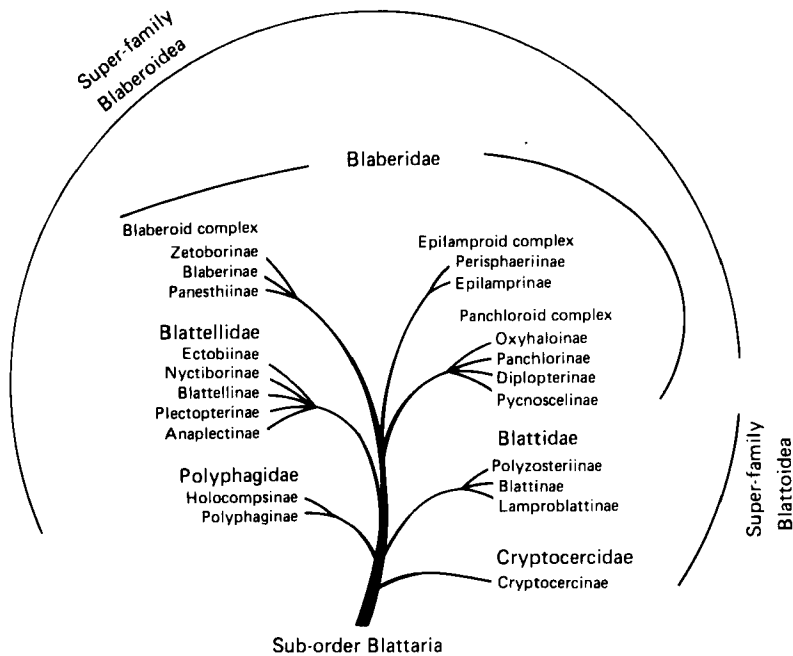


Fig. 1. Phylogenetic relationships of major cockroach families (from McKittrick, 1964).

in different habitat types. Cockroach fauna is most diverse in warm, humid regions of Africa and tropical America (Guthrie & Tindall, 1968).

Many of the Polyphagidae (*Arenivaga*, *Polyphaga*) inhabit desert regions of North Africa, Asia (Bey-Bienko, 1950) and the U.S. Southwest (Hebard*, 1917). Edney (1966), Edney, Haynes & Gibo (1974), Hawke & Farley (1973) and Cohen & Cohen (1981) investigated behavioural and physiological strategies adopted by desert species to maintain water balance. These findings are discussed in the context of habitat preferences and microhabitat selection. Aquatic species are the least studied of all cockroaches. Anecdotal reports of epilamprine (Blaberidae) nymphs and adults comprise the bulk of our knowledge about amphibious species. Shelford* (1907–1909) and Takahashi* (1926) conducted the most thorough studies of cockroaches in streams, pools, and in ephemeral water-filled bromeliads. Albuquerque *et al.* (1976) emphasize microhabitat chemistry in studies of semi-aquatic nymphs in streams and flood plains in Brazil.

Of more than 50 species recorded in man-made habitats (Roth & Willis, 1960; Vargas & Fisk, 1973), four *Periplaneta*, two *Blatta*, *Blattella* and several blaberid genera (*Blaberus*, *Eublaberus*, *Leucophoea* and *Nauphoeta*) are most commonly given a domiciliary status. Only those studies dealing with the ecology of these species will be discussed in this review. Most domiciliary cockroaches are of African or Indo-Malayan origin (Rehn*, 1945). Cornwell (1968) presents a concise review of the presumed trade routes taken in the spread of several species through commerce. Dissemination and range extension through local trade is common for the domiciliary species (e.g. *Mallis*, Esterline & Miller, 1961). International dissemination of tropical cockroaches continues as trade, especially by air and sea, with tropical regions proliferates.

In a series of papers between 1919 and 1950, Chopard constructed a solid foundation for future investigations of cavernicolous cockroach species (see Roth & Willis, 1960, for these and other references). Gautier (1974*a, b*, 1978, 1980), Deleporte (1976) and R. Brossut (personal communications) studied the social interactions, mating systems, and natural history of cave dwelling cockroaches. Caves, in some ways similar to man-made structures, are ecologically stable habitats, and in fact, Chopard* (1938) hypothesized that the association between cockroaches and man originated when cockroaches followed man's food into caves. Because cavernicolous cockroaches (and domiciliary species) associate with man's shelter and food even when man is not present, it seems more likely that caves were already inhabited by cockroaches when man abandoned his arboreal habits. Associations with other cavernicolous animals (e.g. bats, porcupines, opossums) may have preadapted cockroaches to later associations with man.

The degree of specialization to cave habitats varies in cockroaches from accidental habitation of caves by outdoor or domiciliary species to restriction to such habitats accompanied by adaptations that may be morphological (loss of vision and wings), behavioural (no circadian rhythmicity), or physiological (narrow range of temperature or humidity tolerance). The reader should keep in mind that broad definition of this habitat may include hollow trees, man-made mines, nests of social insects, burrows of vertebrates, and excavated logs.

All except the more specialized species discussed above are included in the category of outdoor habitats. Many of the domiciliary cockroaches (e.g. *P. americana*) may occur and breed in outdoor habitats if temperature and humidity are favourable. Cavernicolous species (e.g. *Blaberus craniifer*) may be found outdoors in specific dispersal or migration phases.

The majority of studies on outdoor cockroaches are results of systematic collection, thus providing excellent distribution data but little behavioural information. As illustrated by this review, however, our knowledge of the behavioural ecology of cockroaches in forests and grasslands has vastly increased over the past decade. Studies of tropical habitats where cockroaches are most diverse and abundant indicate a large variety of habitats where cockroaches are found, including leaf litter, dead leaves trapped above ground, in caves, in hollow trees, rotting logs, pools and streams, in nests of other animals, flowers, at various altitudes and of course in homes.

IV. HABITAT PREFERENCES AND MICROHABITAT SELECTION

Few studies deal with cockroach habitat preferences under natural conditions, although laboratory investigations document preferences for temperature (review: Cornwell, 1968; Edney, Franco & Wood, 1978; Coenen-Stass, 1976), humidity (review: Cornwell, 1968; Edney *et al.*, 1978), light conditions (review: Cornwell, 1968; Crawford & Cloudsley-Thompson, 1971), types of shelters (Berthold & Wilson, 1967; Mizuno & Tsuji, 1974) and substrate (Takagi, 1979; Crawford & Cloudsley-Thompson, 1971).

Gautier (1974*a, b*) studied the spatial distribution of burrowing blaberid nymphs in caves by counting the number of cockroaches in 50-cm-square samples to a depth of 15 cm. The number of nymphs found in each sample, ranging from 0 to 47 individuals, correlated positively with both the depth and quality of organic matter. Nymphs concentrate in zones where bat guano, fruit, and twigs dropped by bats accumulate, and are absent from zones of dry soil, stones or pebbles. Therefore, the positions of bats

in the cave which determine the placement of guano (and other organic material) are related to the horizontal distribution of nymphs. Female blaberids hatch nymphs near or on the substratum (Gautier, 1974a). *P. americana* deposit oöthecae primarily in thick and moist guano (60%) or dry guano (21%); few are deposited in dry clay containing little or no guano (Deleporte, 1976). Hence, the distribution of first instar nymphs is in part determined by preferred oviposition sites of females, and the nymphs remain at these moist sites where nutritional resources are abundant.

R. Brossut (personal communication) marked individual males, females and nymphs in four aggregations of cavernicolous *Eublaberus distanti* (Blaberidae) and found that 90% of individuals remained in their group during a 30-day period. Site constancy also characterizes a large proportion of marked *P. americana*; Deleporte (1976) found large groups of males, females and nymphs in particular crevices, even though similar nearby sites were uninhabited. Examples of non-homogeneous groupings in cave habitats may in part be due to structural heterogeneity, but aggregation pheromones probably also play a role in stimulating and maintaining aggregations (review: Brossut, 1975).

Abiotic factors, particularly light, also influence cockroach distribution: zones directly in sunlight at cave entrances are strongly avoided. Darlington (1968) noted that *E. posticus* and *E. distanti* may segregate in caves according to moisture requirements. The former prefers moist inner sections of caves, whereas the latter is common in drier guano and occasionally in rotting logs.

As with other insects, cockroaches employ behavioural 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 & Willis, 1960). The relative humidity inside kangaroo rat burrows, for example, is several-fold higher than that recorded on the desert surface (Schmidt-Nielsen*, 1949). Desiccated *A. investigata* can absorb water vapour from the surrounding air at relative humidities of 82% or above (Edney, 1966), a condition available 45 cm below the ground 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 & Farley, 1973; Edney *et al.*, 1974). Mycorrhizae that coat adventitious roots of desert shrubs, 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.

Cohen & Cohen (1981) compared the microclimates and physiological tolerance of *Arenivaga investigata* and *A. apacha*. The former is a free-ranging desert species and thus it is exposed to more stressful conditions; it has a higher temperature tolerance, and lower rates of water loss and oxygen consumption. *A. apacha* is an inhabitant of rodent burrows which provide for a less harsh environment.

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 (1967) summarizes 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 *P. bolliana* was strictly a grassland cockroach species in Kansas, and *P. lata* was taken frequently in 'open woodlands'. Gorton, on the basis of two 'nonforest' and twelve 'forest' sightings, considers *P. bolliana* 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) have been observed by Morvan (1972) in Brittany: *E. lapponicus* on mesophilous heathlands under pine trees, *E. lividus* and *E. sylvestris* 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 localize *E. lapponicus* and *E. panzeri* in deciduous forests in Europe and *E. duskei* to grasslands on Russian steppe. Strict relationships between a given habitat and any one species of *Parcoblatta* or *Ectobius* are not evident.

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 (Cleveland *et al.*, 1934*b*; Nalepa, 1982, and unpublished data; Seelinger & Seelinger, 1983). Family groups of a male, female, and nymphs excavate fallen rotting logs which are used as food. Other congeners occur in similar habitats in the Far East (Bobyleva, 1975). Extensive work of Cleveland *et al.* (1934) on the 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* (Blaberidae) (see Roth & Willis, 1960). C. Schal & G. Seelinger (unpublished data) noted that *Capucina patula* (Blaberidae) juveniles in Costa Rica were restricted to these habitats, whereas adults were occasionally seen on nearby foliage. Being cryptically coloured and dorso-ventrally depressed, *C. patula* is well adapted for burrowing in crevices. Nothing is known about its specificity to particular tree species or its preferences for trees of particular age groups.

Other reports of microhabitat selection include investigations of specialized niches. Roth & Willis (1960) reviewed associations of cockroaches with termites, ants, bees, wasps and birds. Although no studies attempt to delineate the preferences of commensal cockroaches, 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 have been reported (Roth & Willis, 1960). Commensal associations are no doubt the result of ecological convergence of unrelated species on similar microhabitats (Chopard*, 1924).

V. VERTICAL STRATIFICATION

An evolutionary consequence of microhabitat preferences, predation and competition may be the vertical stratification of species. Sexual and life-stage (demographic) selection of microhabitats may result in intraspecific stratification. Vertical stratification varies temporally as individuals migrate from refugia to activity sites. Seasonal shifts of individuals from layer to layer may affect the rigidity of classification into vertical strata. Biotic associations, such as perch type and size (leaf, trunk), predator or parasite pressure, and competition within or between species, are important variables in determining the deviation of stratification from what might be expected on the basis of habitat preferences.

Hawke & Farley (1973) and Edney *et al.* (1974) documented a circadian and seasonal vertical migration of *Arenivaga* sp. through desert sand dunes, a behaviour that enables it to avoid extreme high and low temperatures (Fig. 6 shows seasonal distributions). Light, temperature, vapour pressure deficit and energetic factors are important variables controlling migration (Hawke & Farley, 1973; Edney *et al.*, 1974). Evaporative water loss is reduced by selecting appropriate microhabitats.

Sexual and demographic differences in migration are also documented. During the day *Arenivaga* sp. nymphs and adult females burrow year-round within the sand at a depth of 20–60 cm. At night in the spring, summer and autumn they burrow within 1–3 cm of the surface. Adult males are either on the surface or at 30–60 cm. Hawke & Farley (1973) suggest that vertical stratification may be related to communication between males and females, but data are lacking to support this idea or to exclude strategies that would be equally as efficient.

By contrast, Edney *et al.* (1974) found adult male *A. investigata* perching on bushes at night rather than burrowing below the surface in the Colorado Desert. The results suggest a life-stage stratification with older nymphs and adult females ranging deeper in the sand than younger nymphs (Edney *et al.*, 1974). Unfortunately no data are available on their relative water requirements. Cohen & Cohen (1981) showed that although less stressful conditions are available deeper in the sand, *A. investigata* is restricted to the upper layers because of the almost toxic carbon dioxide concentrations below. *A. apacha*, a closely related species occurs in deeper regions because of the enhanced air circulation in rodent burrows.

Williams* (1941), in analysing the floor fauna of the Panamanian rain-forest noted that "there are two possible explanations for... [the decrease in population densities at night], either the animals retreat into the soil, or they move up into the trees and shrubs." Although vertical stratification of arthropod forest communities is well known, few studies address questions regarding the vertical separation of forest cockroaches.

Dreisig (1971) used the upward migration in the vegetation of *Ectobius lapponicus* adults during the active phase as a relative measure of activity. Low night time temperatures (less than 12 °C) shift the locomotory activity of males from late to early afternoon. Females become active shortly after sunset, overlapping only slightly with males. Dreisig (1971) attributes these differences to differential susceptibility to low temperatures, but does not discuss the implications on mate finding.

Gorton (1980) found differences in perching heights within and between six species of cockroaches in Kansas (Fig. 2). Males are good fliers and are active at night on trees and bushes, whereas females do not fly and, except for *Parcoblatta pennsylvanica*, all

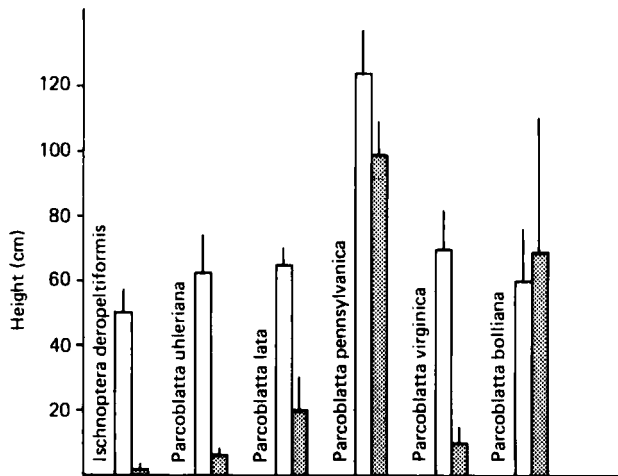


Fig. 2. Vertical distributions of *Parcoblatta* and *Ischnoptera* species in temperate grassland and oak-hickory forest in Kansas (means and standard errors) (Gorton, 1980).

have reduced wings. Most females remain on or near the ground. The brachypterous state of female *Parcoblatta* (Gorton, 1980) and *Ectobius* (Dreisig, 1971) is probably responsible in part for the unusually large sexual differences in their vertical distributions. Although Gorton (1980) suggests that "intersexual, interspecific and probably inter-lifestage competition" are factors influencing community structure, the evidence he cites is primarily that of species overlap with respect to diets and habitat-specific differences in vertical distributions. Alternative mechanisms (e.g. physiological specialization) which may be as important in regulating vertical distributions are ignored. Gorton (1980) demonstrates habitat *distribution* (as discussed by Partridge, 1978), and not vertical habitat *preference* or *choice*. Dreisig's (1971) laboratory studies show that subtle temperature and humidity *preferences* affect habitat *selection* in *E. lapponicus*, indicating that the habitat-specific vertical distributions in *Parcoblatta* species (Gorton, 1980) may be unrelated to competition. Neither investigation considers mate-finding mechanisms of ecologically stratified sexes.

Schal (1982) and Schal & Bell (1984a) conducted similar investigations on the vertical distributions of cockroaches in a Costa Rican rain-forest utilizing the 'conspicuousness' of perching insects as a relative measure of activity. They document significant differences in the height distributions of species, sexes and nymphs within 2 m above the ground (Figs. 3 and 4), and diel vertical migrations from resting to activity sites.

Adults and nymphs of some species (e.g. *Epilampra involucris*, *E. unistilata*, *E. rothi*, *Xestoblatta cantralli*, *X. hamata*, *Nesomylacris* sp. and *Hyporhichnoda reflexa*) retreat to diurnal leaf-litter or subterranean refugia. At night, adults walk or fly to above ground perches. In general, young nymphs occupy leaf litter habitats and are rarely seen above ground, whereas older nymphs occur higher in the foliage, approaching the mean perching heights of the adults. Interestingly, in nymphs this can be a sex-specific process. Whereas older nymphs of some species perch higher than younger nymphs, regardless of sex, the largest nymphs of *E. involucris* and *E. rothi* (for which information is available) are all juvenile females and occur mostly on the ground. Their vertical distribution corresponds to or approaches that of adult females. Late instar male nymphs may perch significantly higher than adult females. Assuming that these distributions

represent species-, sexual-, and age-specific preferences in the absence of competition, this example demonstrates a possible genetic basis of habitat selection. This daily vertical migration is probably related to differential predation and parasitism in the leaf-litter and on foliage (see Section XIII), and to foraging (Section IX).

A second activity pattern is that of species of *Imblattella*, *Cariblatta* and *Nahublattella* (Blattellidae) which rest diurnally in above-ground refugia such as rolled dead leaves and loose bark, or among roots and leaves of epiphytes. Adults and nymphs of these species share common diurnal shelters, as well as nocturnal activity strata (Schal, 1983; Schal & Bell, 1984*a*). Fisk (1983) using pyrethrum fogging techniques concludes that members of the subfamily Plectopterinae are truly arboreal with all life stages found in trees both day and night.

As in Gorton's (1980) temperate study (Fig. 3), Schal & Bell (1984*a*) demonstrated intersexual separation among several tropical species (Fig. 3). Differences in vertical distributions between conspecific sexes, in addition to reflecting trophic, morphological, and physiological sexual dimorphism, may enhance mate finding. Males occupy higher perches than their potential mates (Fig. 3). One explanation for this phenomenon is that volatile pheromones emitted by females ascend in thermal convective air flow reaching the males above (Schal, 1982). In the forest, the vertical profiles of temperature and wind favour this mechanism at night. Laboratory experiments with *P. americana* and its synthetic sex pheromone confirmed upward movement of pheromone in an identical thermal gradient, releasing courtship behaviour in males stationed above the pheromone source.

A different type of vertical distribution has been observed in the blaberid *Gyna maculipennis* in caves and abandoned mine galleries in Gabon (Gautier, 1980). Most adult females (68%) are found above 1 m on the walls, 9% between 0 and 1 m, and 23% on the ground. Most pregnant females are found high on the walls or on the ceiling, although some females carrying oöthecae occur on the ground. Near the end of pregnancy females move down to the substratum where nymphs hatch. The majority of adult males (90%) live on or near the ground; the remaining 10% occur on the walls with vertical movements linked to the activity of the females (Gautier, 1980).

Sexual vertical stratification is not evident in *P. americana*, *B. colosseus* or *B. atropos* in caves in Trinidad. As shown in Figs. 5 and 6, vertical cross-sections of the Lopinot Cave reveal vertical, horizontal and sloping surfaces, and most types of surfaces are inhabited at least transiently by a group of *B. colosseus* adults (Gautier, 1974*a, b*). The sex ratio favours males on both vertical walls 0.5–5 m above the ground (84% males) and on horizontal shelves 1.5 m above the ground (78% males). It is possible that sexual vertical differences are less evident in caves than in forests because of the patchy distribution of food (trapped guano) on horizontal surfaces. It is also possible that the key abiotic factors that may regulate height preferences in tropical and temperate forests (e.g. humidity gradients) are less pronounced in caves. Interestingly, Silverman & Bell (1979) showed that male *P. americana* perch higher in chambers in the laboratory than conspecific females. Deleporte (1982) showed that males spent more time on the upper parts of walls than on the ground.

The studies of blaberid populations in caves showed significant ontogenetic differences in vertical distributions (Gautier, 1974*a*), corroborating laboratory investigations of Crawford & Cloudsley-Thompson (1971). Nymphs of *B. colosseus* and *E. distanti* burrow in organically rich soil on the floor of the cave until the 6th or 7th

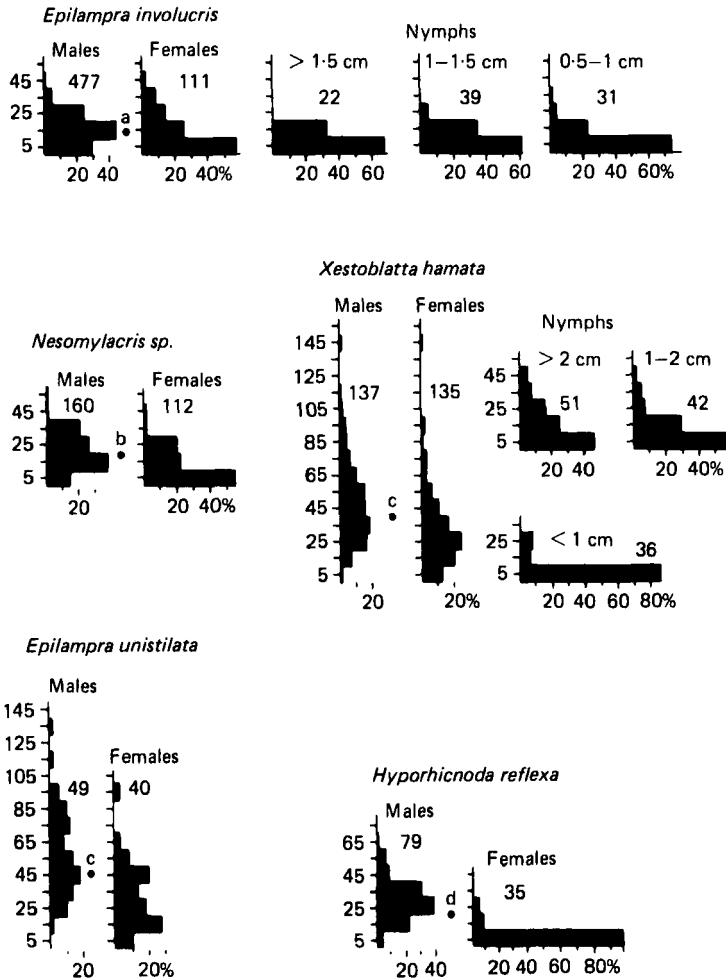


Fig. 3. For legend see facing page.

instar, and then climb onto the rocky walls where they complete their development (Gautier, 1947a; R. Brossut, personal communication). Darlington (1968) studied the metabolism of *Eublabeus posticus* nymphs in Tamana cave in Trinidad, and found that the transition from rapid to slow development takes place at about the same time that the change occurs from living in guano to climbing on the walls.

VI. DIEL ACTIVITY PATTERNS

Partridge (1978) states that "It is debatable whether the time of day at which an animal is active should be regarded as part of its habitat, but there are instances where differences in time of activity contribute to ecological segregation." From the few studies of habitat selection in cockroaches, we conclude that time is a major niche axis in this group. It is not known whether this is due to circadian periodicity of micrometeorological events, or to internal clocks which the animals obey, without regard to environmental changes. In caves in Trinidad, *Blaberus colosseus* and *P.*

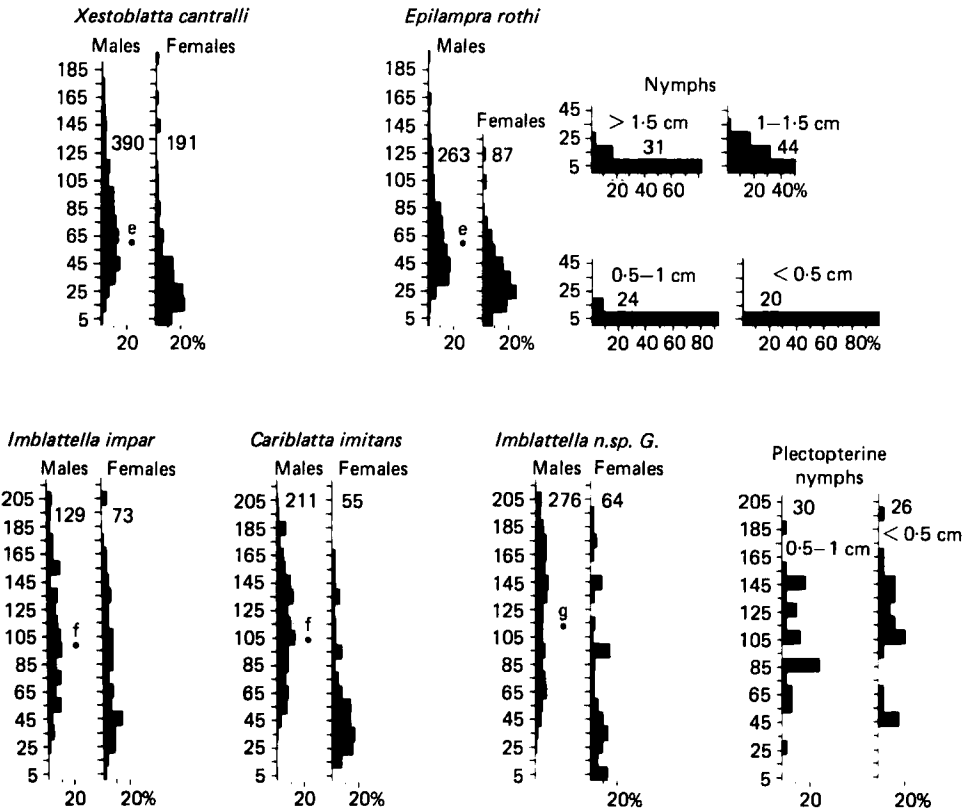


Fig. 3. Vertical distributions of species, sexes, and life-stages of Costa Rican rainforest cockroaches. The ordinates give perch height in cm. The sample size for each group is stated next to the respective histogram. The mean perch heights for the species are graphed between the distributions of the males and females. Statistically different ($P < 0.05$, Student's t -Test of log transformed data and Wilcoxon Rank Sum Test) species distributions are labelled with different letters (above species mean). *Imblattella* and *Cariblatta* nymphs are grouped together (plectopterines) because we could not identify the species (Schal, 1983; Schal & Bell, 1984a).

americana adults and older nymphs emerge from their shelters and younger nymphs crawl onto the surface of the cave floor at about 1845 h (Gautier, 1974a; Deleporte, 1976). Males are active during the first 2 to 4 h of the scotophase, exploring and feeding with pauses of varying lengths between these activities. Pregnant females emerge from their resting sites at nightfall (1845 h) and move onto the walls of the cave where they feed on guano. Non-pregnant females are more active, often covering distances greater than 10 m per night. These observations agree with the laboratory results of Leuthold (1966) and Engelmann & Rau (1965) on the blaberid *Leucophaea maderae* in which little activity was noted during pregnancy, a rapid and significant increase in activity about 8 d before parturition, and an intermediate level of activity at the beginning of oögenesis. Parallel to the progressive development of the eggs, daily activity decreases gradually until the level characteristic of pregnancy is reached. In caves, the increase in activity prior to parturition correlates with activity of females searching for a site where the nymphs may hatch.

Animals near cave entrances are exposed to temperature and light fluctuations,

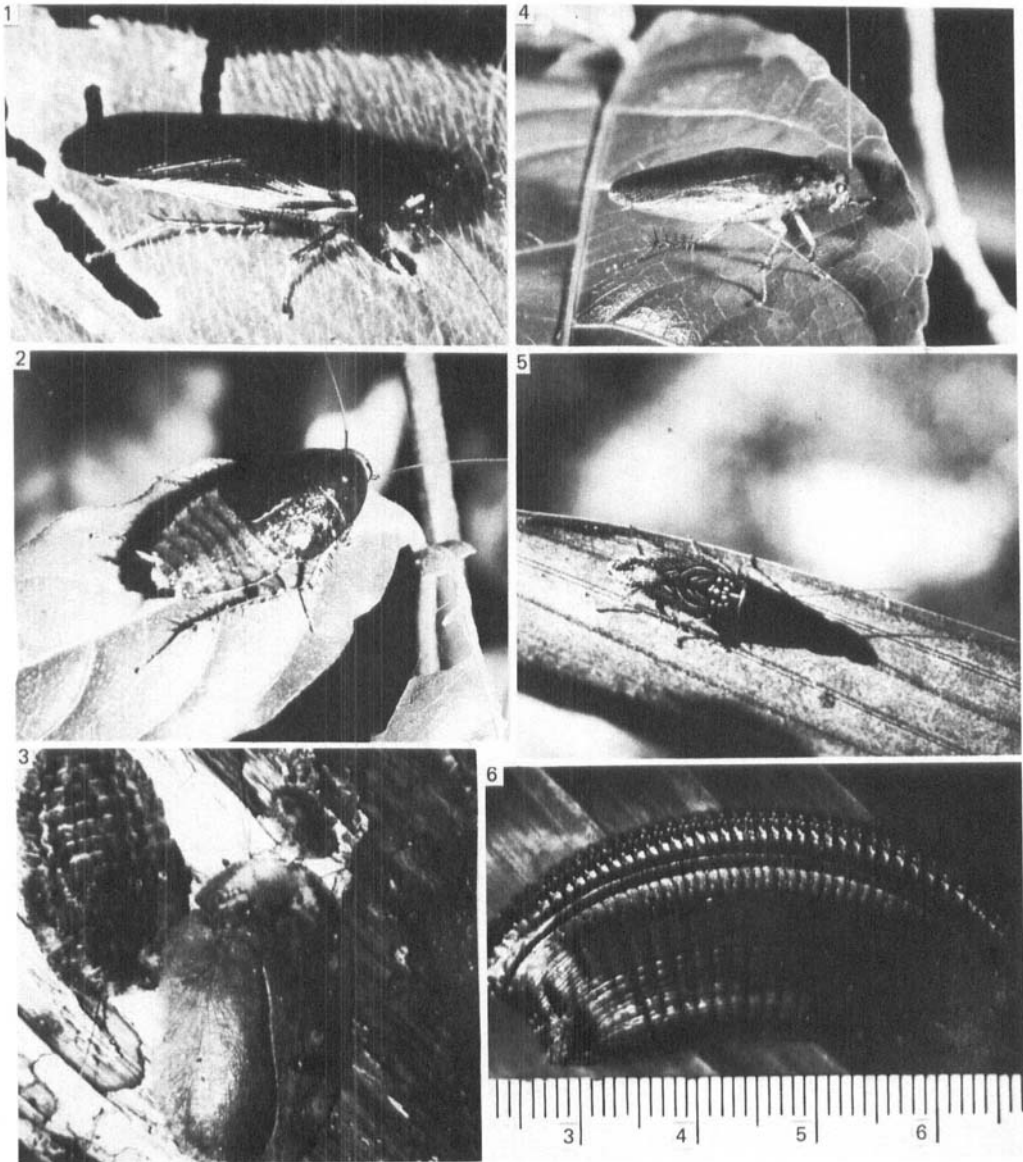


Fig. 4. Perching tropical cockroaches. (1) *Ischnoptera* sp., (2) *Epilampra involucris*, (3) *Capucina patula* adult and nymphs, (4) *Imblattella* sp., (5) *Euphyllodromia angustata*, a diurnal cockroach, (6) ootheca of *Megaloblatta blaberoides*, scale in cm.

whereas animals further from the entrance are not exposed to these potential synchronizers of circadian activity. Adult *B. colosseus* and *B. atropos* close to the entrance, where sunlight may be perceived, become active when the light intensity in this area falls below 0.7 Lux (Gautier, 1974b). Most likely, even daily variations of a few tenths of one Lux are sufficient to entrain the activity rhythm. Wobus (1966) showed in the laboratory that an intensity change of 1 Lux influenced the rhythm of *B. craniifer*.

Changes in temperature of several degrees occur at the cave entrance, whereas the temperature further from the entrance remains relatively stable (typical daily fluctuations of 1 or 2 °C) and probably limits its potential synchronizing role. In the deepest parts



Fig. 5. *Blaberus colosseus* on walls and in crevices of Lopinot cave in Trinidad (Gautier, 1974a).

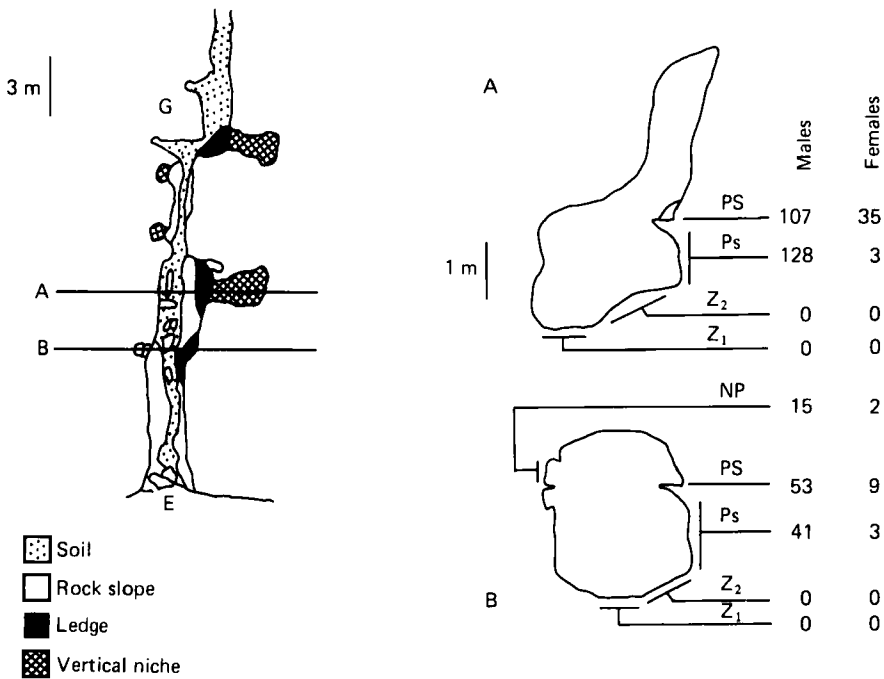


Fig. 6. Diagram of Lopinot cave in Trinidad. Two cross-sections are depicted (A and B). Numbers in the right margin are for male and female cockroaches collected at each site. Adults were observed only transiently on substratum sites Z₁ and Z₂, PS, ledge; Ps, wall under ledge; NP, wall in niche (Gautier, 1974a).

of caves, where complete darkness is permanent and relative humidity remains constant, wind disturbances or increase in temperature at the beginning of bat activity could be important factors for setting the circadian rhythm of cockroaches. Darlington (1968) recorded a 2.5 °C increase in temperature in the evening when bats become active in the deep part of Tamana cave (Trinidad), and Roberts (1960) showed that a thermo-period with variations of 5 °C was sufficient to set the rhythm of *L. maderae* in continuous darkness in the laboratory.

In the deepest parts of caves in Trinidad, species of *Blaberus* and *P. americana* remain on the walls and rocks both day and night rather than resting in crevices and clefts. Similarly, a well defined circadian rhythm was not observed in *G. maculipennis* in mine-galleries in Gabon (Gautier, 1980). Uniform environmental conditions deep in the 220-m-long mine, where the cockroaches were observed, is probably responsible for the absence of rhythms.

Sexual differences in activity are better documented than interspecific differences (*Arenivaga* sp. – Hawke & Farley, 1973; *E. lapponicus* – Dreisig, 1971; species of *Blaberus* – Gautier, 1974*a, b*; several tropical rain-forest species – Schal, 1983; Schal & Bell, 1984*a*). Diel shifts between sexes, as for those between species, may be due to physiological, morphological, or behavioural dimorphism which result in different trophic or microclimatic requirements, different predator avoidance strategies, or most likely, different roles in the mate-finding process (Schal, 1982). Adult *Hyporhichoda reflexa* males illustrate both the importance of time as a habitat dimension and potential problems with the methodologies of the studies cited above. The 'conspicuousness' count indicates that adult males move upward onto vegetation early after sunset (18 h), but return to the leaf litter 2–3 h later. Yet both in laboratory experiments and in field observations *H. reflexa* males remain active for several hours after they return to the leaf litter (Schal & Bell, 1984*a*). Hence, the 'locomotory rhythm' or 'activity' counts of Dreisig (1971) and of Gorton (1980) may represent only a small portion of the potential activity period. It is not known whether (i) this activity pattern is used to avoid predators, (ii) males choose microenvironmental regimes which change over time, or (iii) a form of mate searching is followed by ranging in the leaf-litter. We also do not know if the role of perching serves different functions in different species or subgroups within species.

VII. SEASONAL ACTIVITY PATTERNS

Tsuji & Mizuno (1972) and Takagi (1978*a, b*) found a 2-year cycle in over-wintering populations of *P. fuliginosa* living outdoors in Japan. As in studies in domestic dwellings (Takagi, 1974), the rate of nymphal growth (Takagi, 1978*a* – in Japan) and activity (Fleet, Piper & Frankie, 1978 – in Texas) in the field correlates positively with temperature. At low temperatures young nymphs experienced greater mortality than did older nymphs, and adult *P. fuliginosa* females have a higher winter survivorship than males (Takagi, 1978*b*). Based on relative capture rates, more eggs and nymphs overwinter successfully than adults in Japan (Tsuji & Mizuno, 1972) and in Texas (Fleet *et al.*, 1978).

Arenivaga sp. avoids the desert heat during the spring, summer, and autumn by migrating vertically on a diel basis. Between November and March, when nocturnal temperatures are lower they excavate among the roots of shrubs and do not appear on

the desert surface (Hawke & Farley, 1973). The time of first visible subsurface burrowing activity at night is dependent on the season. From March to September *Arenivaga* sp. emerged about 2 h after darkness, possibly because of the delayed cooling of the surface. In winter, early activity (soon after darkness) corresponded to peaks in the night-time surface temperature (Hawke & Farley, 1973). Edney *et al.* (1974) found similar patterns and also recorded seasonal distributions of *A. investigata*. In a vertical distribution profile in July, all life-stages (adult males not included) ranged from 2.5 to 30 cm below the surface, with a mode at 12.5 cm. In November the profile extended to a depth of 15 cm with most insects occurring at 5 cm below the surface (Edney *et al.*, 1974).

Neither study provides details on seasonal population fluctuations, absolute abundances, or demographic seasonal changes. July samples showed a larger number of young nymphs, whereas older nymphs predominated in the November samples (Edney *et al.*, 1974). However, as sampling was done in different years it is not known whether the results demonstrate demographic seasonal changes or other factors, e.g. catastrophic or unfavourable conditions in a particular year, or both.

The most thorough work on seasonality in cockroaches began with a paper by E. B. Brown* (1952) and continued with a series of papers by V. K. Brown (1973*a, b*, 1980) on three species of *Ectobius* (Blattellidae) in Britain. *E. panzeri* is a univoltine species; adult eclosion occurs during a short period in late July (Brown*, 1952) and both sexes die off by mid-October. Only oöthecae were collected during February, indicating that the egg stage overwinters in this species (Brown*, 1952). Two other species of *Ectobius* are semivoltine, overwintering as eggs and intermediate nymphal instars (Brown, 1980). Fourth instar nymphs of *E. lapponicus* enter a definite diapause, whereas other instars overwinter in a quiescent state, and moulting proceeds whenever conditions are favourable for growth (Brown, 1973*a, b*). Six developmental pathways are possible in *E. pallidus* (Brown, 1980). Quiescent overwintering by any of the second to fifth instars accounts for four of the pathways, and diapause in 3rd and 4th instar nymphs accounts for the other two. Because moulting ceases in September and does not resume until April, the autumn and winter demographic composition is predominated by young nymphs; the proportion of later instars and adults increases in spring and summer (Brown, 1980). Both *E. pallidus* and *E. lapponicus* have long adult seasons. *E. lapponicus* adult males die off in early August, as do males of species of *Parcoblatta* (Gorton, 1980), but adult *E. lapponicus* females continue to emerge. Such incomplete seasonal overlap of the sexes may explain the evolution of parthenogenesis in *E. lapponicus* and *E. pallidus* and not in *E. panzeri* (where a short adult emergence season and complete sexual overlap occurs) (Brown*, 1952).

Wolda & Fisk (1981) examined seasonal variations in abundance of cockroaches in seasonal and non-seasonal localities in Panama. On the basis of catches in light-traps, Wolda & Fisk (1981) conclude that in both climatically seasonal and non-seasonal localities in Panama cockroach adults were most common between April and July, corresponding to the beginning of the rainy season. However, it is not known whether these trends represent absence or inactivity of adults. In a relatively aseasonal rain-forest in Costa Rica we (C. Schal & W. J. Bell, unpublished observations) found active adults throughout the year.

VIII. INTERSPECIFIC ASSOCIATIONS

(1) *Predation*

Roth & Willis (1960) review numerous records of predation on cockroaches, but most recent reports employ cockroaches as experimental prey in laboratory studies (e.g. Camhi, Tom & Volman, 1978; Wourms, 1981). Of all arthropods, ants and spiders are the most important predators of cockroaches, particularly in tropical habitats. Records of predation on cockroaches by the army ant *Eciton burchelli* are most common (Bates*, 1863; Wallace*, 1891; Johnson*, 1954; Schneirla*, 1956). In Costa Rica we observed several large swarms raiding the inside walls of hollow trees (*Pentaclethra* sp. – Leguminosae) and emerging with adults and nymphs of *B. colosseus*.

Ctenid and lycosid spiders perch on leaves or on the ground and take cockroaches as they walk or fly onto the leaf. Orb-weaving spiders (Araneidae) prey on flying cockroaches (Barth & Seyfarth, 1979). Blattellid cockroaches comprise 23% and 92% of the respective diets of the Australian net-casting spiders *Dinopis* and *Menneus* (Austin & Blest, 1979). Scorpions take cockroaches along with other surface dwelling insects (Brownell & Farley, 1979). *Arenivaga* cockroaches in the Colorado Desert in California comprise 15% of the diet of the scorpion *Paruroctonus* sp. (Hawke & Farley, 1973). Roth & Willis (1960) cite observations of the centipede *Scolopendra* taking the cockroach *E. panzeri* in Britain and other cockroaches in Hawaii. They also review the predatory habits of mites (Acarina) on cockroaches.

Cockroach parts have been found in stomachs of fish (Beebe*, 1925), salamanders, toads, frogs, turtles, geckos and lizards (review: Roth & Willis, 1960). H. Hespeneide & T. Sherry (personal communication) "found cockroaches with some regularity in stomachs of pauraques (Caprimulgidae, night hawk/goatsucker family)." Pauraques are crepuscular (sometimes nocturnal) hunters, capturing insects in flight. The nunbird, and probably most puffbirds, are regular predators on Blattaria and related groups. They follow large flocks of birds which stir up cockroaches from bromeliads, dead leaves and tree bark (T. Sherry, personal communication). We have observed ant-birds (Formicariidae) feed on nymphs and adults of species of *Xestoblatta* and *Epilampra* which were flushed from the leaf-litter by army ants. Tschudi* (1847) described a wren *Troglodytes audax* (called 'cucarachero' by Peruvian Indians), which apparently specializes on cockroaches. In enclosure experiments in a moist tropical forest in Panama, Gradwohl & Greenberg (1982) demonstrated a reduction in the cockroach population in dead leaves trapped in above-ground foliage when the antwren *Myrmotherula fulviventris* was present. Cockroaches comprised 44% of the potential arthropod prey items.

The daily vertical migrations of cockroaches upward into the vegetation at night and into aerial and ground leaf-litter during the day are probably related to predation. At night, spiders, ants, and other arthropods are active on the ground. Moreover, both feeding and mate-finding in most cockroaches occur above ground (Schal & Bell, 1984a). During the day, visual predators (birds, lizards) are active, forcing cockroaches to take cover.

In caves in Trinidad, terrestrial crabs, *Anolis* geckos, *Tarantula* spiders, *Morion* beetles, *Bufo* toads, and *Phyllostomus* bats all prey on cockroaches (Brossut, 1983). Mammalian predators on cockroaches include opossums (Beebe*, 1925; Gautier,

1974a – in caves), porcupines (C. Schal, unpublished data – in hollow trees), as well as monkeys, rodents, and cats (Roth & Willis, 1960).

(2) Parasitism

For associations of cockroaches with viruses, bacteria, protozoa, fungi and various helminths, see Roth & Willis (1960) and Roth (1981a). We briefly review behavioural and ecological studies of parasitism of cockroaches.

Schaefer & Peckham (1968) showed that specific olfactory cues emanating from the cockroach *G. portentosa* are used by the ectoparasitic mite *Androlaelaps* to orient in a Y-maze. Egan (1976) and Egan, Barth & Hanson (1975) isolated 'nauphoetamine', an odour specific to *N. cinerea*, which is utilized by the mite *Proctolaelaps nauphoetae* in orienting to the cockroach over distances of up to several centimetres. Behavioural host preferences were corroborated with electrophysiological experiments. Other mite-cockroach associations are reported by Lindquist (1975).

Representatives of Hymenoptera, Diptera and Coleoptera are major insect parasitoids of cockroaches. All of the Evaniidae (ensign wasps), for which hosts are known, are parasitic on cockroach eggs (Townes*, 1951) in both urban (Edmunds*, 1953) and natural habitats (Edmunds*, 1952, 1954; Cameron*, 1955, 1957; Deleporte, 1976). These studies document the oviposition behaviour and development of several wasp species, but information regarding their ecological impact on the host population is lacking.

Roth & Willis* (1954a, b) provide information on distribution, development, behaviour, and sex ratios of several Chalcidoidea species parasitic on cockroach eggs. The dipteran families Phoridae and Muscidae also have representative species which parasitize cockroach eggs.

Parasitoids on nymphal and adult cockroaches include hymenopteran species in the Pompilidae, Ampulicidae and Sphecidae, the dipterous families Conopidae, Tachinidae and Sarcophagidae, and Ripiphoridae in the Coleoptera (Roth & Willis, 1960). Species of *Ampulex* and *Polichurus* (Ampulicidae) provision their nests exclusively with cockroaches. Typically, the female wasp stings the cockroach in the thorax, cuts off a distal section of its antennae, and pulls and leads the cockroach by its antennae to a convenient resting site, oviposits an egg on its mesocoxa, and closes the nest with debris (e.g. Kamo*, 1957; Williams*, 1929).

C. Schal & R. Coville (unpublished data) examined the foraging biology of the wasp *Tachysphex blatticidus* on *Chorisoneura* (Blattellidae) and other species of the subfamily Plectopterinae, members of which are either rare or occur in the canopy. The wasp's oblique burrows occur in gregarious nesting sites. A nest may contain one or two cells and each cell may hold one to five individual cockroaches (adults and nymphs); one egg is attached to a coxa of the largest cockroach in the cell. Provisions of cells designed to support female wasps are larger than those for male wasps.

Flies are important parasitoids of cockroaches. *Stylogaster* (Conopidae) and *Calodexia* (Tachinidae) parasitize hosts that are flushed out by swarm raids of the army ant *Eciton burchelli*, such that "50–90% of cockroaches and crickets that escape the ants are parasitized by *Calodexia* alone" (Rettenmeyer, 1961).

The beetle family Ripiphoridae is believed to have been dispersed geographically, largely through the cosmopolitan transport of its cockroach host (Roth & Willis, 1960).

Riek* (1955) noted host specificity in Australian species: *Riekella* on the subfamily Blattinae, *Rhipidioides* on Ectobiinae and Pseudomophinae, and *Paranephrites* on Panchlorinae. *Ripidius pectinicornis* may attack a variety of cockroach species, but the only substantiated records involve adult females and nymphs of *B. germanica* (Barbier*, 1947). Oviposition and development of this fly suggest a dependence of early larval stages on aggregations of the cockroach host. The eggs are oviposited in a cluster; the first instar larvae crawl up the host's legs and penetrate its abdomen. Nothing is known of the host-seeking behaviour or the effect of host population structure and density on the parasite's search strategies.

(3) Defence

Cockroaches may employ any one or a combination of the following proximate and evolutionary defensive tactics: concealment, evasive behaviours, protective or aposematic colouration, chemical defence, disturbance sound production, and fighting.

Species of *Pycnoscelus* (Reser*, 1940) *Arenivaga* (Hawke & Farley, 1973), *Epilampra* and *Geoscapheus* (Tepper*, 1893), *Macropanesthia* (Henson in Day, 1950), *Blaberus* (Gautier, 1974a), *Hyporhichnoda*, *Eublaberus*, *Byrsotria*, and others (C. Schal, unpublished data) burrow into the substratum during this inactive period or in response to disturbance. *Arenivaga* sp. "can detect an approaching scorpion and avoid capture by burrowing deeper into the sand, or by ceasing all movements. . ." (Brownell & Farley, 1979). Other cockroaches actively conceal themselves in folded dead leaves (e.g. species of *Imblattella*, *Cariblatta* – Schal & Bell, 1984a), in the roots of trees (e.g. *Therea* – Annandale in Chopard*, 1924), among sharp spines on the trunks of trees (e.g. *Eurycotis* sp. – C. Schal, unpublished data), and in crevices in and between trunks of trees (e.g. species of *Blaberus* – Gautier, 1974a).

Young blaberid nymphs escape from predators in caves (e.g. bats, ants, toads) by burrowing in the guano, and older nymphs and adults by running into crevices. Adults and older nymphs emit an alarm pheromone when attacked by a predator and individuals in the vicinity quickly scatter (Crawford & Cloudsley-Thompson, 1971; Gautier, 1974a). The alarm pheromone, a biproduct of benzoquinone, ethyl phenol and 2-decenal, is emitted by tracheal glands associated with the second abdominal spiracle in *E. distanti* (R. Brossut, personal communication).

Sensitive mechanoreceptors on the cerci can detect slight acceleration of air as a predator approaches (review: Seelinger & Tobin, 1981). Camhi *et al.* (1978) have studied the evasive responses of cockroaches to vertebrate predators. Although the role of the cerci in evading flying predators and parasites has not been explored, it is possible that flies and wasps may be perceived by the low frequency sound produced by the wings in flight. Other evasive tactics include rapid running and flight in many of the tropical species. Immobility is employed by all life stages of *H. reflexa* in response to approaches by spiders (C. Schal, unpublished data).

Roth & Alsop (1978) review the morphology and chemistry of defensive glands and secretions of cockroaches. Ventral intersegmental glands are common, especially in the Polyzosteriinae. Aliphatic compounds, notably trans-2-hexenal, are the most common defensive secretions and they are forcibly sprayed upon disturbance (Roth & Alsop, 1978). Observations of their effectiveness in nature are rare, but Blum (1964) reports that ants are repelled and that *Anolis* lizards are not. In contrast, Brossut (1983) observed *Anolis* sp. strongly deterred by the secretion of *E. decipiens* at the entrance to a cave in

Trinidad. Laboratory investigations support the effectiveness of these secretions as repellents against man (*Eurycotis floridana* – Roth & Willis*, 1957; *Ischnoptera* sp. – C. Schal, unpublished observations) and ants (*Eurycotis decipiens* – Dateo & Roth, 1967; Eisner, McKittrick & Payne, 1959; species of *Platyzosteria* – Waterhouse & Wallbank, 1967; Wallbank & Waterhouse, 1970).

Meinwald *et al.* (unpublished data, cited in Roth & Alsop, 1978) describe a dorsal gland in *Deropeltis* (Blattidae) which secretes benzoquinone, toluquinone, terpineol, and sugar. *Diploptera punctata* secretes benzoquinones from paired tracheal glands (Roth & Stay, 1958). Eisner* (1958) and Eisner *et al.* (1959) showed that, in the laboratory, these secretions effectively repel ants, beetles, and spiders. However, Brossut (1983) demonstrated in field and laboratory experiments that quinones and other secretions of the second abdominal spiracle of *Eublabeas distanti* did not repel predators but acted as alarm pheromones and resulted in rapid disruption and escape behaviour in cockroaches.

Roth & Alsop (1978) summarize observations on the occurrence of a sticky secretion on the dorsum of some cockroaches. Roth & Stahl (1956), Plattner *et al.* (1972), and Schal, Fraser & Bell (1982) report that the secretion is mainly proteinaceous in *Blatta orientalis*, *Megaloblatta blaberoides*, *Nyctibora noctivaga* and *N. lutzi* and acts as a mechanical deterrent to ants and beetles in the laboratory (Naylor, 1964; Schal *et al.*, 1982).

Platyzosteria reficeps, a diurnally active cockroach, exposes bright orange markings when disturbed; further irritation results in discharge of a defensive secretion (Waterhouse & Wallbank, 1967). *E. decipiens* also has bright yellow and black aposematic colours and a secretion of trans-2-hexenal (Dateo & Roth, 1967). Schal *et al.* (1982) hypothesize that aposematic colouration (bright orange spots and an orange venter), acoustic aposematism, and a sticky proteinaceous secretion combine in *M. blaberoides* nymphs to deter or repel predators.

Warning colouration involving mimicry is common in tropical cockroaches, but the role of mimicry in predator-prey relationships has not been studied. Species of *Paratropes* and *Archiblatta* resemble lampyrid beetles (C. Schal, unpublished data), *Prosoplecta* resembles coccinellid beetles (Shelford*, 1912), and diurnal *Euphyllodromia angustata* may mimic wasps morphologically and behaviourally (Williams*, 1928; W. J. Bell & C. Schal, unpublished data).

Roth & Hartman (1967) reviewed the evolution and roles of sound production in cockroaches and concluded that disturbance stridulation in adult males evolved a dual role in courtship and defence. Because the structures occur in both sexes, Roth & Hartman (1967) proposed that courtship stridulation is a more derived behaviour; stridulation then, evolved primarily as a defensive mechanism. In *M. blaberoides*, where nymphs stridulates, specialized abdominal organs generate loud, broad-frequency-band sound which may function to startle predators (Schal *et al.*, 1982). Interestingly, *M. blaberoides* adults possess the structures, but have not been observed to stridulate. Many blaberid cockroaches utilize pronotum-tegmina stridulatory structures (Roth & Hartman, 1967).

A less common acoustic defensive mechanism is expulsion of air through the spiracles. *Gromphadorhina portentosa* and *G. chopardi* nymphs and adults hiss in response to disturbance (Roth & Hartman, 1967). Nelson & Fraser (1980) showed that nymphs and

adults produce different hisses in response to different stimuli (contexts). Little direct evidence is available to link disturbance sounds with survivorship in cockroaches. However, Masters (1979, 1980) has shown with other insects that 'noisy' amplitude-modulated acoustic signals do in fact deter predators.

Agonistic encounters and fighting are common among conspecifics (see Section XI(3)(b)). In *Cryptocercus*, adults respond to alarm behaviour of nymphs and fight unfamiliar intruders (Seelinger & Seelinger, 1983). Interspecific fighting in cockroaches has not been documented in nature, but no doubt occurs, especially around food.

IX. NUTRITION

Cockroaches have been used as model organisms in studies of insect digestive physiology (review: Bignell, 1981). Numerous papers discuss nutritional requirements, metabolic processes and reproductive cycles in *P. americana*, *B. orientalis*, *B. germanica*, and *L. maderae*. The ease with which these species can be maintained has encouraged extensive physiological work, but so little is known about the botanical associations of cockroaches that the number of speculative papers regarding such relationships in fossil cockroaches rivals that for modern cockroaches. Citing the coexistence of fossil cockroaches and palms in the same geological strata and the occurrence of long ovipositors in fossil cockroaches, researchers have suggested that cockroaches either fed on the plants (e.g. Scudder*, 1879) or oviposited into them (e.g. Zaleskii*, 1953). A few publications on ecological distributions of cockroaches list the botanical species composition of the habitat (e.g. Cantrall*, 1943; Friauf*, 1953); this is the extent of our knowledge about the botanical associations of cockroaches in the temperate zone.

Reports of cockroaches feeding on plants (references in Roth & Willis, 1960) are usually related to damage of agricultural or ornamental plants (e.g. *Pycnoscelus surinamensis* and *P. americana* on palms, ferns, roses, lilies, poinsettias, orchids, cucumbers, potatoes, pineapples, chrysanthemums and tobacco). Most reports are either from tropical regions (such as Hawaii and Haiti) or in transport of bananas and other fruit. *D. punctata* feeds on the bark of cypress trees in Hawaii and *P. americana* nymphs damage up to 30% of planted seeds of *Cinchona pubescens* in Puerto Rico.

Cockroaches inhabiting caves feed on guano, fruits and seeds that bats bring back to the cave, and on the larvae of Diptera and Lepidoptera living in guano (Gautier, 1974a). Cockroaches also feed on dead animals (bats and many invertebrates). *G. maculipennis* was seen feeding on *Isopoda* and on conspecific nymphs (Gautier, 1980). Cannibalism is common in many species, but it is not clear whether younger instars are captured by older nymphs and adults or if only injured or sick individuals are eaten.

Temperate *Parcoblatta* and *Ischnoptera* adults feed on mushrooms, mammalian and bird faeces, sap and cambium of trees, flowers and mosses (Gorton, 1980). Analysis of its gut contents showed that *Arenivaga* sp. consumes decaying leaf matter and root tissue with mycorrhizae, both of which are located at depths in the desert sand to which the cockroach burrows (Hawke & Farley, 1973). On the other hand, *A. apacha* feeds on materials stored underground by desert rodents (Cohen & Cohen, 1981). Unfortunately, nothing is known about the diet of *E. lapponicus* for which other ecological data are available.

The wood-feeding cockroaches, *C. punctulatus* and *Panesthia*, harbour cellulose-digesting bacteria and protozoa in their hind-guts (Cleveland *et al.*, 1934; Bobyleva,

1975). Sexual cycles in many gut protozoans are induced by hormones produced by the cockroach during its moult (Cleveland *et al.*, 1934), suggesting a coevolutionary relationship rather than accidental infection and reinfection of moulting nymphs.

Qualitative correlations of crop contents and trapped faecal material of cockroaches in a Costa Rican wet-forest showed that nearly 50% of the females and nymphs of several species captured during the scotophase had maximally filled crops, whereas only 7% of males were collected in this condition (W. J. Bell & C. Schal, unpublished data). Within 24 h food material is absent from guts of cockroaches maintained without food.

Gut contents were analyzed for 400 individuals captured during the scotophase (W. J. Bell & C. Schal, unpublished data). Gut contents of adults which forage in leaf-litter or low vegetation (*E. involucris*, *H. reflexa*, *Nesomylacris* sp.) and of nymphs of nearly all species contained almost exclusively chips of decaying leaf materials. Minor items in gut contents of these species include arthropod cuticle, algae and fungi.

Guts of winged species that migrate onto foliage at night (e.g. *X. hamata*) contain woody chips, leaf chips, arthropod cuticle, fungi and algae in their crops. Guts of species that live relatively high in the vegetation (e.g. species of *Imblattella*, *Cariblatta*, *Euphyllodromia*) contain algae (especially blue-green), leaf trichomes, moss, liverwort, fungi and occasionally leaf chips. These species spend most of the day and night in the shrub layer, and graze epiphylls. Several species regularly feed on fallen fruits on or near the ground. *Capucina patula*, which forages primarily on and beneath tree bark, contains a large proportion of woody chips and fungi in its gut.

Experiments were performed on preferences for living or dead leaves with *Euphyllodromia angustata*, *Epilampra rothi* and *E. involucris*. In no case was living leaf tissue consumed; in fact, cut leaf surfaces were repellent to all three species. *E. involucris* males, females and nymphs readily fed on dead, rotting leaves (taken from litter); the same was true for *E. rothi* nymphs. *E. rothi* females fed on epiphylls taken from plants on which they commonly perched at night, and showed a preference for older, epiphyll-covered leaves rather than those with 'clean' surfaces. *Euphyllodromia* males and females grazed on hairs coating leaves of several plant species, and on epiphylls.

Finer vertical definition of feeding preferences has not been carried out. We do not know, for instance, whether trophic differences exist between species that overlap significantly in their vertical distributions (e.g. *X. hamata* vs. *E. unistilata*). Epiphylls are restricted to 1–2 m above the forest floor with greatest densities at about 1.5 m (B. Bentley, personal communication). However, the importance of environmental gradients at this stratum (0–2 m) suggests that thorough vertical sampling of epiphyll loads and compositions will reveal differences in the availabilities of various food items to cockroaches.

X. MOVEMENT PATTERNS

Interest in cockroaches as vectors of enteric diseases stimulated research in the early 1950s on their movement and dispersal. Schoof & Siverly (1954) showed in a 60-day study of a Phoenix, Arizona, sewerage system that radioactively labeled *P. americana* superimposed on a resident population do not disperse to adjacent sewer manholes or residential yards. However, problems such as the relatively low recapture rate and low incidence of unmarked individuals at the release sites were not addressed. Comparison of numbers of unmarked cockroaches trapped at the release sites and at adjacent

manholes suggests that dispersal from the release sites did occur (perhaps and cockroaches dispersed, but not sufficiently to traverse the 219 m between adjacent manholes). Finally, the incidence of above-ground dispersal was not adequately tested.

A subsequent study (Jackson & Maier, 1955) of the Phoenix system concluded that during the summer, when 1200 marked cockroaches were superimposed on a resident manhole population of approximately 300 individuals, emigration was stimulated from the release site, but when only the resident population was marked, little dispersal occurred. Note that Schoof & Siverly (1954) released 1625 individuals at each manhole with no resultant emigration. Of the six manholes sampled by Jackson & Maier (1955), 95% of the recaptured cockroaches (3.4% of total) were in two manholes within 56 m of the release site. In another experiment, three marked individuals were recaptured in manholes (0.6% of marked individuals), but only one manhole was within 52 m of the release site. A difference of 2.8% in recapture rate is probably insignificant because the design in the former experiment allowed for upstream and downstream movement, whereas the latter experiment restricted movement to only one direction.

In winter, little movement occurred when 1500 individuals were introduced into a manhole, whereas in late spring, superimposition of marked cockroaches on stable populations resulted in dispersal of marked individuals into adjacent manholes and apartments (Jackson & Maier, 1961). *P. americana* was most prevalent in manholes and the number trapped peaked in the spring in twelve towns in Georgia (Haines & Palmer*, 1955).

In all of the dispersal studies in sewerage systems, a basic supposition is that resident manhole populations are at carrying capacity and that introduction of foreign individuals results in 'population stress'. To our knowledge, no studies have examined growth parameters of natural populations of urban cockroaches.

More recent investigations of foraging ranges of cockroaches have employed individual tagging methods. Fleet & Frankie (1974) and Fleet *et al.* (1978) conclude from studies of *P. fuliginosa* around a house in Texas that (i) more females are multiply recaptured than males, (ii) most movements (75% and 70% of captures, respectively for the two studies) are of less than 3 m, (iii) females account for 73% and 60% of all movements, respectively, (iv) the longest movement was 37 m and 109 m, respectively, and (v) adults move longer distances than do nymphs. Using the mean distance moved by females and males, Fleet & Frankie (1974) calculated that the mean circular home range for females is 2.3 times as large as that for males. It is doubtful, however, that this assumption is justified in such an asymmetrical and heterogenous environment; no information is provided on the directions of movements. In their 1978 study the calculated home range for females would have been 75% of that calculated in 1974; the home range for males is 169% the area of the 1974 calculation. Clearly, the length and direction of movement depends upon the distribution of resources (food, shelters) and is probably asymmetrical about any focal trap.

In *Blattella germanica*, the only other domiciliary cockroach in which movement patterns have been investigated, Keil (1981) showed that in two shipboard populations adult females were most common (trapped most frequently). Somewhat conflicting results were obtained by Ross & Wright (1977). The former study reports more adults than nymphs and a bias toward larger nymphs. Ross & Wright (1977) found that, in homes, nymphs are more common than adults, and that the age distribution of nymphs

is uniform. Bakonyi (1978) showed that first instar *B. germanica* nymphs are more than twice as common as any other instar. However, so little is known about the nutritional and physical relationships of cockroaches with the environment, that invoking 'carrying capacity' and growth parameters (see Keil, 1981) may be premature.

Qualitative analysis of movement patterns of *B. germanica* on ships indicates that dispersion from groups is largely nymphal (Ross, Keil & Cochran, 1981). This is opposite to the findings of Fleet *et al.* (1978) in outdoor populations of *P. fuliginosa* where nymphs are more common in harbourages and adults move in the open more commonly.

Our observations in Costa Rica indicate that female gonadotrophic cycles are important in determining movement of *X. hamata* in forest habitats. *X. hamata* females feed mainly on plant materials (fruits, flowers, epiphylls). They are relatively uncommon along random line transects through the forest (*ca.* one adult per 10 m), where large aggregations of both sexes occur near food plants. For females, the average volume of terminal oöcytes (an indicator of reproductive stage) at any particular feeding site is related to the nutritional properties of the predominant food item. Thus, females in the vicinity of foods with high lipid content are predominantly in the early stages (post-oviposition) of their ovarian cycle.

A mark-recapture study (C. Schal, unpublished data) with individually marked adults monitored each night (without utilizing traps), showed that *X. hamata* females return to the study site to feed at periodic intervals corresponding to the length of the gonadotrophic cycle. As in Fleet *et al.* (1978), although equal numbers of both sexes were marked, three times as many female recaptures were recorded because of more multiple visits by marked females than by males. Concurrent with this study but 600 m removed, a second mark-recapture programme indicated that *X. hamata* can fly over 600 m in 55 days (C. Schal, unpublished data). It is not known, however, if such distances are flown routinely during foraging bouts or while seeking mates. That many species are capable of extended flight is corroborated by the arrival of forest cockroaches at isolated lights hundreds of metres away.

By contrast, in some species (myrmecophyles, cavernicolous) movement is restricted to several centimetres. *Cryptocercus* is apterous and the extent of dispersal is probably limited. Whereas *Arenivaga investigata* ranges freely through the desert sand dunes, (Fig. 7), highly clumped groups of *A. apacha* are found in rodent mounds; the latter moves little in its search for food (Cohen & Cohen, 1981).

XI. COMMUNICATION AND BEHAVIOUR

(1) Chemical communication

Chemical communication in cockroaches is important in most phases of mate-acquisition, including long-distance attraction of males to females by volatile pheromones (reviews: Barth, 1968; Bell, 1981; Breed, 1983). Female as well as male secretions may operate as short-range attractants. Species and sexual recognition are most commonly accomplished by means of cuticular pheromones (Roth & Willis, 1952; Bell & Schal, 1980; Schal & Bell, 1983; Schal *et al.*, 1983).

Long-range pheromonal attraction is best documented in *P. americana*. Virgin females expand their genital chamber, presumably releasing the sex attractant (Schal

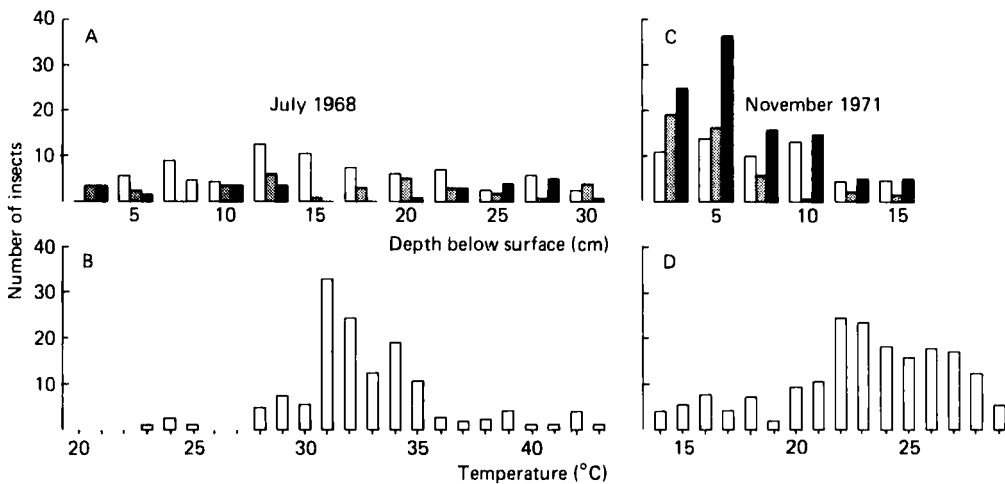


Fig. 7. Distribution of *Arenivaga* in relation to depth below the surface (A and C) and temperature (B and D). A, B, distribution in July 1968; C, D, distribution in November 1971. (In November samples were taken down to 15 cm only.) In A and C the insects are scored according to size: open columns = 1st-3rd instars; stippled columns = 4th-6th instars; solid columns = 7th-9th instars and adults. Adult males were rarely found below the surface and have not been included. In July there was a preponderance of young stages, and in November of old stages (but the records were made in different years, and their significance with regard to phenology is not clear). In July the main concentration of insects was at 12.5 cm and between 30° and 35 °C; in November, at 5.0 cm and at 23 °C (Edney *et al.*, 1974).

& Bell, 1984*b*). Males are attracted to receptive females and to a synthetic component of the sex pheromone in the laboratory (reviews: Barth, 1968; Bell, 1981) and in the field (Bell *et al.*, 1983). Unfortunately, observations of males orienting to sex pheromone in wind tunnels (Tobin, 1981) or in still-air arenas (Bell & Tobin, 1981) do not clarify orientation mechanisms of cockroaches in structurally complex natural habitats. Silverman & Bell (1979) report the only data that may provide ecological correlates to pheromone orientation in *P. americana*: males occupy perches higher than females in large (1.2 × 1.2 × 1.2 m) chambers. When exposed to female sex pheromone in an air stream, males run downward (where females would be located); clean air alone stimulates upward running (away from predators generating wind currents). Appel & Rust (1983) report on the effect of acclimation temperature on the production of an response to sex pheromone by *P. americana*.

Willis (1970) reported that females of three *Latiblattella* species from Honduras assumed 'calling' postures in the laboratory, but he was unable to detect any behavioural differences in males encountering these females. Schal & Bell (1984*b*) and Hales & Breed (1983) observed similar behaviours in several species, both in laboratory cultures and in the rain-forest in Costa Rica (Fig. 8). Females raise their wings and expose intertergal membranes (e.g. *Capucina patula*), expand their genital chambers (e.g. *P. americana*, *Supella longipalpa*), or combine both behaviours (e.g. *Nyctibora noctivaga*, *Xestoblatta cantralli*). In the laboratory, calling females are more attractive to males than are non-calling females. In the field, the density of male cockroaches near calling females on leaves is higher than around non-calling females. Calling female *P. americana* in small cages attract males from distances up to ca. 30 m outdoors in Jamaica (G. Seelinger, personal communication). Schal (1982) proposed a model interpreting sexually dimorphic vertical distributions (see above) as a mate-finding

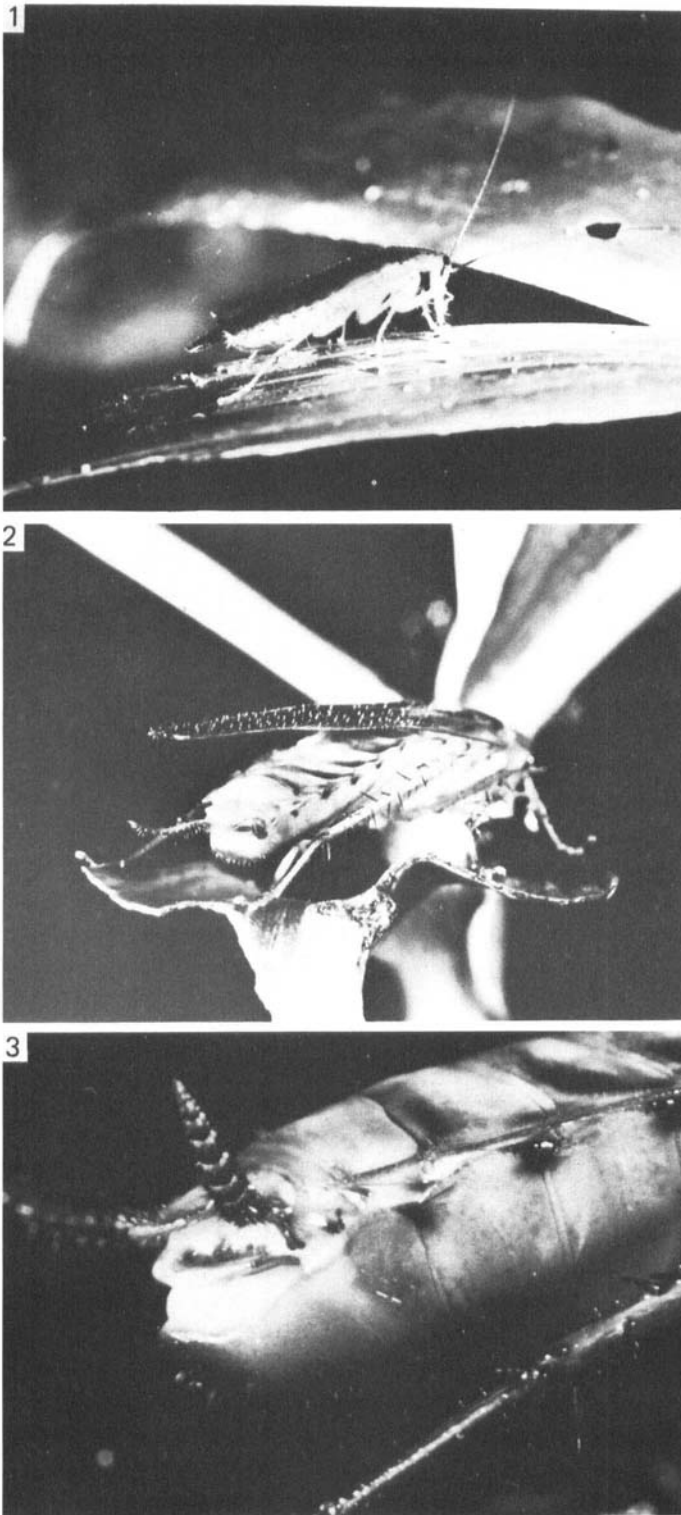


Fig. 8. Calling behaviour of perching females of *Xestoblatta cantralli* (Schal & Bell, 1984*b*). (1) Perching female in non-calling position. (2-3) Calling female.

mechanism, which operates at night when the predominant meteorological conditions are favourable for convective transport of pheromones.

Based on this meagre survey, calling by females seems not to follow a phylogenetic pattern. Although calling is most common in the Blattellidae, the behaviour has also been observed in blattids (e.g. *P. americana*) and blaberids (e.g. *C. patula*).

A second common mechanism for bringing the sexes together is the 'resource-based aggregation' (Alexander, 1975). Adult males and females orient independently to a common site. Once there, either pheromones or random encounters mediate sexual recognition and courtship. The 'resource' for *B. germanica* in domiciliary habitats is sheltered moist sites to which adults and nymphs are attracted and where they emit an aggregation pheromone (Ishii & Kuwahara, 1967, 1968). Males employ a conditional search strategy which depends on the elapsed time since their last encounter with a female (Schal, *et al.*, 1983); no volatile signals are exchanged during the search (Roth & Willis, 1952). Female cuticular pheromones arouse courtship in the male upon contact (Nishida, Fukami & Ishii, 1974; Bell & Schal, 1980).

In the rain-forest, *X. hamata* and *X. cantralli* males and females are independently attracted to common feeding sites (C. Schal, unpublished data). The reproductive status of *X. hamata* may be predicted from the type of resource visited (see Section X). Hence, operational mating assemblies are formed near foods that attract sexually receptive females mid-way through their ovarian cycles. The reproductive readiness of males in such aggregations may be related to the status of accessory glands, secretions of which are transferred to the female during or after mating (Schal & Bell, 1982; see below).

Male sex pheromones may function as volatile attractants at close range (e.g. *N. cinerea* in Roth & Dateo, 1966) or, more commonly, as contact releasers of mounting and feeding behaviour in receptive females (e.g. *B. germanica* – Roth & Willis, 1952). These secretions are produced by specialized abdominal glands as in *L. maderae*, or exuded through cuticular micropore canals as in *N. cinerea* (Barth, 1968; Brossut & Roth, 1977), but Sreng (1979) reported that in *N. cinerea* the sternal and tergal glands secrete attractant and arrestant pheromones, respectively. Tergal abdominal glands are presumed to function in defence, aggregation, mate attraction, species and sexual recognition, and mating behaviour (Roth & Alsop, 1978; Brossut & Roth, 1977). When present only in males their most common role is to orient the female into an appropriate precopulatory position and to arrest her long enough for the male to establish genital contact (Roth, 1970*a*). Tergal glands are most common in the Blattellidae (Roth, 1969).

(2) *Visual and auditory communication*

Roth & Willis (1952) concluded that vision plays no significant role in sexual recognition, courtship, and copulatory behaviour in *B. germanica*. This is presumed to be the case for other species of Blattaria. Vision has little if any role in the vertical selection of perches in *E. involucris* (Schal & Bell, 1983). Yet, many cockroaches, especially diurnally active species (e.g. *Euphyllodromia angustata*), have large well developed and highly pigmented eyes, and respond visually to moving objects in the field (C. Schal, unpublished data). Electrophysiological evidence indicates that *P. americana* possesses two receptor groups most sensitive at 500–520 nm and at 365 nm, and although behavioural and morphological studies show little sensitivity for red light or polarized light, respectively (review: Seelinger & Tobin, 1981), the role of polarized

light in cockroach orientation has not been examined and no work has been done on diurnally active cockroaches.

Long-range auditory stimuli are not known to function as orientation cues in cockroaches. Many blaberid species and at least one blattellid genus possess sound-producing structures (Roth & Hartman, 1967; Schal *et al.*, 1982), but their role in sexual behaviour has not been studied experimentally. Only one report (Nelson & Fraser, 1980) includes playback of recorded male *Gromphadorhina portentosa* hisses to show that short range or contact auditory signals release sexual receptivity in females. As we stated previously, nothing is known of the physical and biotic associations of this species.

As part of the courtship or agonistic repertoire in some species, the male vibrates rapidly up and down or forward and back (Roth, 1970*a*). In some cases (e.g. *X. hamata*) faint air-borne sound is produced, and the substratum (leaf) is vibrated vigorously (C. Schal, unpublished data). This behaviour may be important in mate selection by females when the male's material contribution to the female is significant.

(3) Mating systems

Calling or searching by both sexes is redundant and inefficient. Darwin (1871) first posed the question: "why should the male almost always be the seeker?" In the Blattaria, only females emit long distance sex attractants; male pheromones and acoustic stimuli function at close range or in contact with the female during courtship. This is consistent with the notion that pheromone emission is a relatively low-risk activity (compared to acoustic signalling, e.g. Cade, 1979), and that males experience greater sexual competition than do females. Long gestation in the ovoviparous Blaberidae reduces the number of receptive females at any point in time, thus increasing intrasexual competition among males. For example, a female blaberid *N. cinerea* produces approximately six broods during her adult life. At most she remates once between successive ovipositions. On the other hand, females of the blattellid *X. hamata* deposit an egg case every 8–9 days and remate every second to fourth ovarian cycle (Schal & Bell, 1982). Because remating is more frequent in *X. hamata*, the operational pool of receptive females over time is greater than in *N. cinerea*. It follows that whereas females encounter little difficulty in obtaining mates, most blaberid males realize low mating success.

Greater competition among blaberid males would be expected to select for (i) early recognition by males of virgin females, (ii) greater material contribution by males to females and their young, or control by males of resources (food, shelter, oviposition sites, protection) which females require for successful reproduction, and (iii) control by males of females through various pre- and post-copulatory behaviours. A mechanism to accomplish these ends (and enhanced mating success) is likely to be increased aggression among males for control of resources or to establish dominance in a social hierarchy.

(a) Early recognition

Schal & Bell (1983) noted that male courtship of newly ecdysed adult females is common in laboratory studies of the Blaberidae, whereas sexual recognition and courtship in most blattids are delayed for several days after the adult moult (e.g. *P. americana* – Hawkins, 1978). The blaberid pattern is best documented for *Diploptera punctata*, a viviparous cockroach. Adult females mate upon emergence from the

nymphal cuticle, in some cases without preliminary male courtship (Stay & Roth, 1958). In Hawaii, males are commonly found on plants waiting next to moulting females; they copulate with teneral females (A. Woodhead, personal communication). Mated females average three broods during a one-year adult life (Willis* *et al.*, 1958), and one mating at emergence is necessary and sufficient for the production of up to five broods (Stay & Roth, 1958). Stay & Roth (1958) report only a slight, probably insignificant, increase in the number of broods in females that mated twice, but nothing is known regarding the interactions of spermatozoa from the two copulations. Clearly, virgin females of this species are a limited resource for males. Once discovered by a male, a virgin female is guarded until she is receptive or copulated with without prior courtship. Unfortunately, we know of no field observations of male post-copulatory behaviour.

In many blattids and blattellids, shorter reproductive cycles, repeated matings by females, and greater material contribution by males (in blattellids) may have selected for the evolution of volatile pheromones and delayed sexual recognition. Chemical signals and female receptivity became independent of the imaginal moult. Receptive females assume calling postures, presumably when depleted of spermatozoa or other male-derived materials. By advertising her receptivity rather than relying on chance encounters, the female can attract several males simultaneously and exercise choices in mate selection (as well as feed on tergal secretions from several males). Also, during their short ovarian cycles, oviparous females have a narrow time window in which to copulate. Since failure to acquire a spermatophore during this time may result in resorption of the maturing oöcytes or production of a non-viable egg case (review: Bell & Bohm, 1975), strong selective pressure may operate on females to evolve efficient (yet possibly costly) sexual communication mechanisms.

The classification of sexual communication and recognition systems and their underlying control mechanisms are poorly understood. We presented a seemingly clear distinction between oviparous and ovoviviparous tactics. Yet, females of *B. germanica*, an oviparous cockroach, produce contact sex pheromones, and females of *Byrsotria fumigata* and *Pycnoscelus surinamensis*, which are ovoviviparous, emit short range volatile attractants (review: Barth, 1968). *Capucina patula*, a blaberid, assumes calling stances in the forest. Clearly, there are many exceptions to these patterns and the few ecological observations reported indicate that modes of sexual communication in cockroaches correlate more with habitat features than with phylogenetic classification. Taxonomic correlations may be explained by the fact that most of the blaberids examined presumably live in closed habitats (e.g. caves) whereas the majority of the blattellid species inhabit 'open' forests. Volatile pheromones are more important communicants in the latter habitat.

(b) *Resource manipulation by males*

Two factors influence male strategies: (i) differences between males in agonistic interactions, and (ii) differences in the structures of resources (Borgia, 1979). Mating systems based on manipulation of resources by males are best documented for the blaberids, *N. cinerea*, *G. portentosa*, and species of *Blaberus*. Investigations of the first two have been performed entirely in the laboratory, whereas species of *Blaberus* have been studied both in the laboratory and in caves in Trinidad. *G. portentosa* males establish hierarchies and territories (Ziegler, 1972), and possess morphological

specializations (horns), apparently for agonistic encounters, but nothing is known of their ecology.

Social organizations of male *N. cinerea* (Ewing, 1972, 1973) and species of *Blaberus* (Gautier, 1974*a, b*, 1976, 1978, 1979; Gautier & Forasté, 1982) are density-dependent and develop as a result of agonistic interactions among males. Individual *B. colosseus* males hold territories at low densities (1.0–2.0 m²/male) in caves. Preferred sites are horizontal ledges with an overhang, providing both protection from light and a surface upon which bat guano accumulates. The area of a territory depends on physical features of the site and on overall male density, but usually varies from 0.5 to 2.0 m² (Gautier, 1974*a*). Males at low density are site-specific for up to 45 d, teneral males remaining on their larval sites or finding and maintaining one that is unoccupied. Ewing (1973) found that at low densities (0.5 m²/male), some *N. cinerea* males were not territorial. Rather, they remained inactive much of the time and were not site-specific, as were top-ranking territorial males.

At intermediate densities in terraria (0.0245 m²/male), the hierarchical dominance order of male *N. cinerea* determines the territorial organization (Ewing, 1972). High ranking males acquire permanent territories through agonistic contests, and territories are lost after the territory holder loses his rank (Ewing, 1972). Top-ranking males consume less food and water than males of lower rank, perhaps because of extended periods patrolling their territories. In Ewing's (1972, 1973) experiments the resources (food and water) were clumped so that usually one male controlled them. But, food and water deprivation by other territorial males is probably insignificant in hierarchy formation, as *N. cinerea* is able to withstand deprivation for up to 60 days (Cafferty, 1969, in Ewing, 1972), and the rank order, though stable, changes eventually (Ewing, 1972; Bell & Gorton, 1978; Schal & Bell, 1983).

In intermediate densities (0.4 m²/male) several *B. colosseus* males inhabit a site of 1–3 m², an area similar to that held by one male in the low density situation (Gautier, 1974*a*). Whereas some males were observed on the same site for up to 27 d, most were site-specific for only 3–5 d. Of 38 marked males, 31 moved from one site to another during a 30-day period (Gautier, 1974*a*). Male-male interactions are of short duration and most encounters terminate in the departure of one or both interacting individuals. When males were removed from the cave and isolated for up to 15 d, they were more aggressive and became dominant over individuals they encountered upon being returned to the original site. These experiments confirm that low levels of aggressiveness might be related to frequent encounters in highly overlapping home ranges.

At higher densities (0.005 m²/male and 0.0005 m²/male), hierarchy plays an increasingly more important role in the social organization of *N. cinerea* males (Ewing, 1972; Bell & Gorton, 1978). Only the top-ranking male and the owner of the food and water territory control permanent areas on which they also rest (Ewing, 1972). The hierarchical type of organization also characterized highest densities (0.125 m²/male) of *B. colosseus* (Gautier, 1974*a*), and experiments in the laboratory confirmed that this species and *B. craniifer* establish dominance hierarchies at high densities (Gautier, 1974*a*, 1976, 1978; Bell *et al.*, 1979).

In each of the three types of social organizations the presence of sexually receptive females alters the male-male behaviour of *B. colosseus* (Gautier, 1978). In low density, males follow a receptive female, fighting other males as the female moves from one

territory to another. Males were observed 'herding' a female by orienting in front of her, thus preventing the female from leaving the territory. Territorial males enjoy the advantage of undisturbed courtship and mating without expending much time and energy chasing intruding males and keeping females or a female group on his site. Other males may establish territories peripheral to the top-ranking male or rest on or between territories of other males, and may intercept receptive females who have parted from the female group at parturition (Ewing, 1973). At high densities, receptive females bring about reversals in rank order of *N. cinerea* males (Ewing, 1973).

When food and water are clumped, the male controlling this territory has greater access to the resources and limits their availability to other males (Ewing, 1972). At high densities, only the individual controlling food and water holds a permanent territory and is site-specific (Ewing, 1972). Cudlip (unpublished data, in Breed, 1983) observed that the preferred resource of *N. cinerea* males was shelter rather than food or water, but no details are given of the duration of such preferences nor of the experimental conditions. Clearly shelters were not preferred territories in Ewing's (1972) experiments where *N. cinerea* males aggregated within some shelters and left others unoccupied, but limited shelters were preferred territories of males of *Eublaberus posticus*, *E. distanti*, *Blaberus craniifer*, and *P. americana* (Gorton *et al.*, 1979; Gautier & Forastè, 1982; Deleporte, 1982). *N. cinerea* males prefer raised objects which they patrol regularly (C. Schal, unpublished data), and their preference for shelter over food might be because the shelters provided a more suitable perch.

The territorial male may also control resources to which females may be attracted. After parturition and prior to maturation of terminal oöcytes and mating, *L. maderae* females eat large amounts of food (Engelmann & Rau, 1965), and *N. cinerea* and *B. colosseus* females are more active (Ewing, 1973; Gautier, 1974a). Though feeding is depressed during pregnancy, *L. maderae* females nonetheless ingest some food (Engelmann & Rau, 1965). Hence, a male that controls clumped food and water is able to provide material goods for his mate and her young. Receptive newly emerged and post-parturition females may be attracted to these territories. Moreover, since *N. cinerea* females move about in groups (Ewing, 1973), the territorial male may attract receptive females simply by monopolizing a few (unreceptive) females. Indeed, Schal & Bell (1983) suggest that by courting and immobilizing newly moulted males, which dominant males cannot distinguish from teneral females, dominant males may lure lone females.

Males control oviposition sites in some insect species (e.g. dragonflies – Campanella & Wolf, 1974; flies – Parker, 1970). They guard adequate sites against other males, capture females, copulate, and guard them during oviposition. This strategy has not been observed in cockroaches, probably because of the long delay between copulation and oviposition. In some blaberid cockroaches this period may be as long as 3 months. Moreover, no special substrate is required for embryogenesis (as fresh cow dung is required for *Scatophaga* flies) and the fully mobile nymphs can select suitable microhabitats for nymphal development. C. Schal (unpublished data) observed that in pairs of *N. cinerea* males, the patrolling range of the dominant and the resting site of the subordinate male could be determined by experimentally controlling the distribution of faeces in the cage. It is possible that females stay within an area marked by the territorial male. The male in turn herds and immobilizes females by tapping their

pronotum with his antennae as in species of *Blaberus* (Gautier, 1974a). Thus, by protecting females during their long gestation period (ca. 40 d), the blaberid male may both protect his progeny and increase the probability of access to post-parturient females. This is the only known case of noncopulatory male control of females in Blattaria.

The ultimate question is: Does the territorial/dominant male have greater mating success? At intermediate densities with clumped food and water resources, Ewing (1972) found that dominant male *N. cinerea* did not mate more often than other males. However, she examined only the effects of hierarchy (not territory) on mating success of three groups of males to each of which three females were added. At this density, the top-ranking males do not necessarily patrol the food and water territories. At much lower densities (eight males, 0.5 m²/male) a territorial male may encounter intruding males, but has exclusive mating rights with females on his territory (Ewing, 1973). Breed, Smith & Gall (1980) showed that the top ranking *N. cinerea* male in a laboratory group of four males (0.0063 m²/male) mated successfully in 46% of all matings. An average of 5.2 females were presented to each group of males, with introductions separated by 24 h. They showed further that in olfactometer tests females chose the odour of a dominant male over that of a sub-dominant male. Dominant males were similarly more attractive to female *G. portentosa* (L. Leibensperger, personal communication).

Gorton *et al.* (1979) found that the dominant *E. posticus* male mated with an introduced virgin female in 100% of tests at a density of 0.03–0.1 m²/male, whereas at a density of 0.02 m²/male the dominant male mated in only 58% of tests. This effect of density on the success of the dominant male is reflected by the findings of Breed *et al.* (1980) that a female mated readily with a subordinate if no dominant male was present. Schal & Bell (1983) reported that introduction of *N. cinerea* females to pairs of males (0.01 m²/male) may result in rank reversals, but it is difficult to force successive reversals; the new dominant maintains his rank for several days. In the latter study 81% of the dominant males mated successfully when only one female was introduced to each pair of males.

Rivault (1984) observed hierarchies in *P. americana*, similar to those noted by Bell & Sams (1973), and found that receptive females mated indiscriminantly with males of varying social rank.

(4) Reproductive tactics

(a) Females

We divide post-copulatory female strategies into three phases: (i) utilization of male contributions (spermatozoa, accessory gland secretions), (ii) gestation, and (iii) parturition and maternal care. The first phase will be discussed in the context of paternal investment (Section XI(4)(b)).

The gestation period in Blattaria varies from several hours prior to oviposition in oviparous species to several months of internal incubation of the eggs in viviparous species. The female's contributions in all forms of oviparity are restricted to preovulation materials transferred to the oöcytes (vitellogenins, water, symbiotic bacteria – see Bell & Adiyodi, 1981b), a scleroprotein protective covering (oötheca) secreted during oviposition, selection of an appropriate microhabitat for embryogenesis (oviposition site), and in some species, protection of the extruded oötheca. In addition, gestating

females of ovoviviparous species provide the eggs with water and protection through internal incubation; viviparous females also transfer nutrients to ovulated eggs.

As might be expected, blattid oöthecae have relatively high water content (Roth, 1970b). In oviparous species with less than 50% water in the oötheca (e.g. *Ectobius*), water must be gained from the substrate during embryogenesis. In most ovoviviparous blaberids the egg cases contain less than 50% water at oviposition, since the embryos absorb water after the oötheca is retracted into the brood sac. Similarly, *B. germanica* females transfer water through the attached end of the extruded oötheca. The eggs of viviparous *D. punctata* contain 65% water at the time of oviposition, but they increase in dry weight during embryogenesis, suggesting intrauterine material exchange (Roth & Willis, 1955; Ingram, Stay & Cain, 1977). Roth & Hahn (1964) showed that by reducing the number of embryos in the uterus of *D. punctata* they could increase the size of developing embryos, indicating competition among embryos for nutrients; space is not limiting, since the size of embryos is not reduced by this procedure in larger ovoviviparous species.

No information is available on the ecological significance of internal incubation in Blattaria, nor are data available to assess the interplay between greater viability of young due to increased protection during embryogenesis and the reduced fecundity of viviparous females.

Three parturition and maternal-care patterns occur in females that carry the oötheca externally. In the Blattoidea (Cryptocercidae and Blattidae), where the oötheca contains sufficient water for embryogenesis, the female deposits the oötheca soon after its formation (first pattern). Some species cement the egg case to the substrate and cover it with debris, others conceal or bury it (see Cornwell, 1968). It is unknown whether, by covering the oötheca with debris and saliva, the female masks a kairomone that may be utilized by parasitoids or perhaps introduces one. In the Blattoidea, in which the egg case is attached with the keel pointing dorsally, the oötheca is rotated 90° and then either dropped as in some blattellids (second pattern), or carried externally until the eggs hatch (Roth, 1970b) as in *B. germanica* (third pattern). Roth (1970b) suggested that "rotating the oötheca (usually taller than wide) probably allows the female to crawl into narrow crevices while carrying it, and reduces the possibility of accidental or premature dislodgement." Though not examined experimentally, females that carry the oötheca externally until the young hatch probably afford it more protection from predators and parasites than do females that deposit the oötheca soon after oviposition. Breed, Hinkle & Bell (1975) showed that *B. germanica* females with egg cases are more aggressive.

After oviposition in oviparous species, the oöthecae are not cared for by females. However, egg cases of most oviparous species contain calcium oxalate crystals which contribute to their hardness (Rajulu & Rengenathan, 1966), and also may render them unpalatable to predators as they do in tissues of aeroid plants. With increased female guarding of embryos (ovoviviparity or carrying the oötheca externally during embryogenesis), the number of calcium oxalate crystals decreases.

The simplest post-parturition mother-offspring relationship in oviparous and in ovoviviparous species is brood care. For example, nymphs of the ovoviviparous Cuban burrowing cockroach *B. fumigata* aggregate under the female until their cuticle hardens (Roth & Willis, 1960; Liechti & Bell, 1975). Nymphs of *N. cinerea* and other blaberid species crawl under the female's wings (Willis *et al.**, 1958), but again, only for a short

time. In *Phlebotomus*, *Thorax* and *Phoraspis* the female's tegmina are large and arched; in the former, the wings are reduced, the abdominal terga are depressed forming a chamber, and maternal care is known to occur (see Roth, 1981*b* for references).

The most advanced specializations for maternal care occur in the blaberids *Perisphaerus* and *Pseudophoraspis* in which young nymphs cling to the undersurface of the mother. Young *Perisphaerus* nymphs lack eyes, but have elongate, proboscis-like mouthparts which are inserted into intercoxal openings in the female (Roth, 1981*b*). However, since these findings are based on preserved specimens, it is not known whether this is merely a case of phoresy or if the young are nourished by the female. When disturbed, the female rolls up into a spherical ball resembling a pillbug (Isopoda). Roth concludes from analysis of labels on museum specimens that the nymphs can remain attached to a rolled-up female and thereby be protected from potential predators. As in the highly evolved viviparous *D. punctata*, the number of eggs is reduced in *Perisphaerus*, as compared to other ovoviviparous species (Roth, 1981*b*). Interestingly, male *Perisphaerus* are winged and do not roll up into a ball.

Cryptocercus punctulatus is a monogamous, wood-feeding cockroach that is morphologically, behaviourally and physiologically related to the lower termites. Seelinger & Seelinger (1983) and C. Nalepa (1982, personal communication) showed that in rotting logs the basic social group consists of one female, one male and up to 75 nymphs of similar size. A pair of adults found and excavate a small gallery which is greatly enlarged through the development of a single brood (Seelinger & Seelinger, 1983). Nymphal development is slow and the female does not oviposit for at least 3 years while a brood matures. Parental care consists of nymphs feeding by trophallaxis on adult proctodeum materials, and protection of the nymphs. Small nymphs probably acquire protozoans, which are required for cellulose digestion, by surrounding the adults and feeding on anal secretions. Since small nymphs seem to have an incomplete symbiotic fauna, and no overlap occurs between successive broods, the adults are the exclusive source for this transfer (Seelinger & Seelinger, 1983). Kin recognition in *Cryptocercus* is highly developed. Nymphs exhibit a rapid rocking or jerking behaviour in response to foreign individuals; the adults are readily alarmed by this behaviour, fight intruders, and are stimulated to mend the gallery system (Seelinger & Seelinger, 1983; Ritter, 1964).

Trophallaxis, protection of nymphs through development, other advantages of group feeding, and reproductive arrest for several years are highly evolved tactics indicating that parental care in Blattaria is not related strictly to phylogeny as might be expected from a survey of the reproductive modes. Habitat complexity and physiological requirements (e.g. transfer of symbionts) are important in shaping the social organization.

(b) Males

In addition to materials transferred during copulation, male cockroaches can influence the fate of their progeny in the following ways: (i) resource holding before and/or after copulation, (ii) pre- or post-copulatory material contribution to the female, and (iii) paternal care of the young. The occurrence of male territories was discussed in Section XI (3)(b), but it is not known if male territories are utilized by gestating females and, if so, how they influence the male's reproductive fitness.

The evolution of male strategies involving material contributions and resource

manipulation depends largely on the spatial distributions of resources and of females. Thus, in caves, resource patchiness probably resulted in both resource and female control (e.g. territoriality). On the other hand, when resources are more dispersed, as in forests, males can affect the female's reproductive output by gathering needed resources and offering them to the females (as in many blattellids).

Pre-copulatory material contributions by males involve tergal gland secretions, which in some species attract females from relatively short distances (Roth & Dateo, 1966). In most species the female feeds on or palpates the male's dorsum and thus is manoeuvred into a copulatory position. Many species that lack specialized tergal glands possess dorsal cuticular pores and glandular openings, which may be palpated by the female during courtship (Brossut & Roth, 1977). In one blattid, two blattellid and two blaberid species that have been examined, the tergal secretions were mixtures of proteinaceous and volatile substances, but apparently their use is mainly defensive (Brossut *et al.*, 1975). However, nymphs, males and females feed on male tergal glands (e.g. *B. germanica* – Roth & Willis, 1952), suggesting that these materials may be general attractants as well. In some blattellid males (e.g. *Xestoblatta cantralli*), the large quantities of secreted materials stored in tergal depressions appear to have no defensive function and are in excess of what a female would utilize in the few seconds of courtship.

These observations suggest that tergal secretions may be nutritional contributions to the female. In the Blattellidae, with relatively short vitellogenic cycles and little nutrient storage for successive cycles (Kunkel, 1966), a proteinaceous paternal contribution would be significant to the maturation of oöcytes.

In insects, the spermatozoa and associate accessory secretions may serve multifunctional roles (Leopold, 1976): (i) facilitation of sperm transfer, (ii) activation of nonmotile spermatozoa, (iii) cementing the mating pair together, (iv) formation of mating plugs to block the genital opening of the female, (v) barriers to interspecific insemination, (vi) inhibition of sexual receptivity in females, (vii) nutritional contribution to the female (more or larger eggs), (viii) accelerated egg maturation, and (ix) stimulation of oviposition. Of these functions, (i), (ii), (iv), (vi)–(ix) have been documented in Blattaria. Roth & Dateo (1964) added the elimination of end products of protein metabolism (uric acid) in males as an additional function.

Proteins are the most common constituents of accessory gland secretions of *P. americana* males (Vijayalekshmi & Adiyodi, 1973*a*). Qualitative analyses also indicate the presence of carbohydrates (mainly the non-reducing inositol, but some glycogen and glucose), neutral lipids, phospholipids and sterols in the male accessory glands of *P. americana* (Vijayalekshmi & Adiyodi, 1973*a, b*), and uric acid and inorganic ions in those of *B. germanica* (Ballan-Dufrancais, 1970).

Of these chemicals, only uric acid has been shown, through radiolabelling experiments, to be involved in paternal investment. Mullins & Keil (1980) and Schal & Bell (1982) injected ¹⁴C-labelled uric acid precursors into blattellid males (*B. germanica* and *X. hamata*, respectively) and traced labelled uric acid into mated females and their oöthecae. Both studies conclude that since nitrogen-deficient females acquire more label and because urates can be mobilized as a nitrogen source (employing symbiotic bacteria), the accessory gland secretion is probably an important contribution. Schal & Bell (1982) relate this male strategy to a nitrogen-poor environment and to the substantial risks associated with foraging. They also indicate that the preoviposition period is longer in the absence of sexual transfer of urates in *X. hamata*.

Pre-copulatory transfer of tergal gland secretions and copulatory and post-copulatory contributions of accessory gland secretions are areas that merit further study, especially with regard to the physiology of synthesis, transfer, and utilization, the significance of these secretions in the reproductive biology of cockroaches, and the ecological (nutritional) conditions selecting for the persistence of these behaviours.

If accessory gland secretions constituted an important paternal contribution, it might be expected that sexual selection would result in females discriminating among males, preferring those with the greatest offering. Choice of mates has been documented in only three cockroach species (see Section XI(1)). It is probable that mate choice, particularly in blattellid females, involves correlated criteria. For example, the mate's tergal offering during courtship may provide the female with an adequate assessment of the probability of accruing other nutrients during or after copulation. This is a fascinating possibility, which recently has been suggested for other insects (review: Thornhill & Alcock, 1983).

Extended paternal care of the young has not been documented for Blattaria. The closest association of adult males and nymphs is trophallaxis in *Cryptocercus punctulatus* (see Section XI(4)(a)). No experimental manipulation of colony composition has been performed to elucidate the nutritional role of adult male contributions.

(c) Life-history patterns

As noted in several previous sections, behavioural (e.g. parental care), ecological (e.g. habitat choice), and physiological (e.g. diapause) patterns in cockroaches are closely related to a variety of life-history (and reproductive) tactics. The following general questions are posed (see Stearns, 1976): (i) how many times should a cockroach reproduce, (ii) when should an adult begin reproducing, (iii) how many young are appropriate per oötheca, (iv) should it produce a few large or many small young, (v) how much effort (in time and energy) should be allocated to reproduction? In order to focus on the major traits, this section excludes diapausing species and outdoor temperate zone species. Also, no relationship with ephemeral resources will be introduced (*cf.* Southwood, May & Conway, 1974).

Three major models attempt to explain the evolution of life history tactics (review: Tallamy & Denno, 1981). (i) r and K selection (MacArthur & Wilson, 1967): Pianka (1970) suggested an r - K continuum leading to high productivity (r) as a consequence of "no density effects and no competition", and increased efficiency (K) in a competitive environment, respectively. A basic tenet of this model is its determinism; mortality and fecundity do not fluctuate. (ii) Bet-hedging model (Stearns, 1976): fluctuating mortality schedules of juveniles and adults due to environmental stability and predictability patterns select traits of r or K selection. (iii) Balanced-mortality model (Price, 1974): high mortality rates favour high fecundity.

Thus far, no life table data are available for cockroach species in their natural habitats, and variations in age distribution, mortality and fecundity schedules are poorly understood even in the laboratory. For example, in the laboratory, *P. brunnea* produces an average of 32 oöthecae per female life-time (Wright, 1973). In the same study, however, only ten egg cases were viable. Hence, inferences on mortality in cockroaches are based on observations that oviparous, forest-inhabiting species experience high mortality throughout development, and that ovoviviparous species reduce egg and juvenile mortality with internal incubation, parental care and relatively short nymphal

Table 1. *Life history traits of cockroaches*¹

	Blattidae		Blattellidae		Blaberidae		
	<i>Periplaneta americana</i>	<i>Periplaneta brunnea</i>	<i>Blattella germanica</i>	<i>Supella longipalpa</i>	<i>Nauphoeta cinerea</i>	<i>Pycnoscelus surinamensis</i>	<i>Diploptera punctata</i>
1. Habitat	urban	urban tropical	urban	urban temperate	tropical-outdoor temperate-urban	tropical-outdoor temperate-urban	tropical-outdoor temperate-urban
2. No. of eggs per ootheca	16	24	37.6	15.5	32.8	26.4	11.4
3. No. of oothecae per female	21	10	6.6	10.8	6.2	3.4	3.0
4. Fecundity ²	336	240	242	167	203	90	34
5. Eggs hatched per ootheca	11.2	9.6	27.8	12.2	31.1	20.7	9.8
6. Percent hatch ³	70	40	76	79	95	78	86
7. Percent hatch that mature	84	78	85	85	99	86	90
8. Eggs per female per day ⁴	0.75	1.00	1.60	1.85	0.59	0.29	0.10
9. No. of adults per female ⁵	197	75	156	112	191	60	26
10. Preoviposition period (days)	13	9.5	7.8	10.4	13.4	7.3	—
11. Interval between oothecae (days)	6	3.8	22	6.4	51	48	—
12. Incubation period (days)	34	39.5	17.2	39.9	35.5	35.2	68
13. Age at first reproduction (days) ⁶	185	207	65	65	123	181	124
14. Adult female longevity (days)	450	241	153	90	344	307	355
15. Adult male longevity (days)	—	293	128	115	365	parthenogenetic	442
16. Nymphal development (days)	165	187	40	55	78	140	46
17. No. of moults	9-13	9-13	5-7	6-8	7-9	8-10	3-4

¹ Means of ranges of values at 30 °C for all data, except 24° for items 1-15 and 36° for item 16 in *D. punctata*. Data obtained from Cornwell (1968), Rau* (1924), Gould & Deay* (1938), Griffiths & Tauber* (1942), Roth & Willis* (1955), Willis *et al.* (1958), Engelmann (1970), Bell (1969), and W. J. Bell (unpublished data).

² Fecundity = item 2 × item 3.

³ Percent hatch = item 5 ÷ item 2.

⁴ Eggs per female per day = item 4 ÷ item 14.

⁵ No. of adults per female = item 5 × item 3 × item 7 ÷ 100.

⁶ Age at first reproduction = item 10 + item 12 + item 16 or item 16 + time to first brood.

development. Nonetheless, it is surprising that to date no attempt has been made to examine correlations between life-history traits and reproductive modes in Blattaria.

Traits associated with three major reproductive modes (discussed in Sections II and XI) in Blattaria seem only partially to correlate with predicted traits of r and K selection (Table 1). Most oviparous females appear to achieve high fecundity by reproducing soon after adult emergence, (Table 1, item 10), and by maximizing the rate of oötheca production (Table 1, item 4). Their apparent intrinsic rate of increase per day, r , is high (Table 1, items 8 and 9). Also consistent with r -selected traits, most oviparous species occur in variable, less predictable environments, they experience high mortality, and parental and social behaviours are poorly developed. However, contrary to predictions of r -selection, blattids are long-lived and invest relatively little in each reproductive effort. Moreover, if the age at which reproduction first takes place is taken as age since hatching rather than age since adult eclosion, oviparous females appear to delay reproduction. Assuming greater juvenile than adult mortality (Table 1, items 6 and 7), the bet-hedging hypothesis correctly predicts delayed reproduction, small reproductive effort, long life, and the production of many small clutches.

As predicted by MacArthur & Wilson (1967), species exhibiting r -selected traits are good colonizers. In the Blattidae, parthenogenesis probably evolved several times in response to a demand for high fecundity. *B. orientalis*, *P. americana*, and *P. brunnea* are facultative parthenogens (Willis* *et al.*, 1958). It is probable that the predictability of human-associated habitats facilitated the evolution of the parthenogenetic strains in Blattaria. Interestingly, *Pycnoscelus surinamensis*, a pan-tropical blaberid, is a multi-clonal form composed of many genotypes that are successful invaders of domicile habitats (Parker *et al.*, 1977). Its presumed ancestor, *P. indicus*, is bisexual, but is restricted to outdoor tropical habitats. Parker *et al.* (1977) suggest that multi-clonal forms are phenotypically more flexible than bisexual forms, thus increasing the probability of colonizing areas where several habitat types are available.

Many Blaberid cockroaches inhabit stable, predictable environments (e.g. caves, hollow trees, logs) and would be expected to respond to K selection. Competition is intense in cave-inhabiting *Blaberus*, and they are long-lived. There is a delay between adult emergence and production of the first brood (Table 1, item 10). Parental care and social grouping are more developed than in oviparous species. Although K selection predicts few offspring, most blaberids produce more young per clutch than do blattids (Table 1, item 2). Nevertheless, in extreme K -selected species with high levels of parental care (e.g. *Diploptera*, *Perisphaerus*), a reduction does occur in number of offspring per clutch.

Juvenile mortality in blaberids is relatively low. (Table 1, items 6 and 7). A large percentage of the eggs hatch because of the protection provided by internal incubation, and a large percentage ($\sim 99\%$) of hatched nymphs mature to adults in laboratory conditions (Willis *et al.*, 1958). Adult mortality is probably more variable than juvenile mortality. The bet-hedging model predicts small reproductive effort and few offspring. Blaberids span the range from few to many offspring, but in all cases, reproductive effort per clutch is relatively high. For example, juveniles of *Panchlora nivea*, a blaberid, are found under bark (low mortality) whereas adults fly in the forest (high mortality). Yet, in a remarkable reproductive effort, *P. nivea* females internally incubate more than 100 embryos per clutch. This example illustrates the difficulties encountered when the

environment of a species is classified as 'stable' or 'fluctuating', without regard to ontogenetic habitat shifts and concomitant changes in the mortality schedules. Moreover, it points out the lack of a general relationship between size and reproduction in cockroaches, opposite to the predictions of r - K selection. *Panchlora*, a relatively small cockroach produces larger broods than species of *Blaberus* which may be up to five times its size and mass.

D. punctata is a long-lived viviparous cockroach with few offspring per clutch. The meagre available ecological information indicates that its outdoor habits may expose juveniles to greater mortality. The bet-hedging model predicts more broods, *D. punctata* females average only three broods. *Epilampra involucris*, on the other hand, produces large clutches in a similar forest environment.

The predictions of the balanced mortality model seem to be only partially supported in cockroaches. In agreement with predicted traits, oviparous *Cryptocercus* which inhabits rotting logs (stable environment, probably low mortality) has reduced fecundity. Forest-dwelling blaberids (*Epilampra*, *Panchlora*) tend to have larger clutches than other blaberids, possibly in response to increased mortality. However, other outdoor-dwelling blaberids (e.g. *Diploptera*) have evolved parental care of few offspring, few nymphal moults, and short nymphal development in response to similar pressures.

From the interaction of traits across models, it is clear that the reproductive biologies of cockroaches have evolved in response to various interacting selective pressures; alternative adaptive responses may evolve in a particular environment (see Tallamy & Denno, 1981, for a similar conclusion with lacebugs). The occurrence of relatively advanced paternal care (material contribution) in blattellids seems to be a response to rapid reproductive cycles and resource limitation in variable or patchy environments, rather than to K -selected factors. In *X. hamata*, resorption of proximal oöcytes (hence fewer eggs per clutch), and extension of the interval between oöthecae, are common in the field and result from unsuccessful foraging (Schal & Bell, 1982; C. Schal unpublished data). Persistence and clumping of resources in caves, hollow trees, logs, nests of social insects, and leaf-litter have probably selected for increased reproductive efforts, parental care, less locomotion, and ultimately for the brachypterous or apterous condition of many blaberid cockroaches, particularly females.

Predation pressure on cockroaches may select different tactics in different habitats. Chemical defence is a common response in cockroaches. Hard oöthecae are a form of defence in oviparous species that lack maternal care of oöthecae. Blaberids seem to have responded to predation (and other pressures) with internal egg incubation, greater parental care, and burrowing habits.

The occurrence (and success) of ovoviviparous colonizers (e.g. *P. surinamensis*) further supports the conclusion that various conglomerates of life-history traits may evolve under similar environmental conditions (*cf.* Tallamy & Denno, 1981).

XII. CONCLUSIONS

Based on habitat selection, modes of communication, social organization, and reproductive tactics in cockroaches, we conclude that no general phylogenetic pattern is evident, but the following relationships (with some exceptions) are clear: (i) ovoviviparous species (Blaberidae) tend to occur in stable habitats such as caves, hollow trees and rotting logs, where long-range chemical communication is not necessary.

Males of these species engage in agonistic interactions to control territories at low male densities and to assert dominance in a social hierarchy at high male densities. Dominant males have higher reproductive success than do subdominants. Internal incubation and extended maternal care protect the developing embryos from predators, parasites and desiccation. (ii) Cockroaches inhabiting forest habitats usually have oviparous reproduction. Maternal contribution consists of the eggs and their contents, a hard oötheca, and selection of a substrate for embryogenesis. Rapid gonadotrophic cycles have probably favoured contribution of collected resources by males rather than male control of resources as in blaberids. In forest environments, daily vertical migration between the leaf-litter and nocturnal activity sites in the foliage is probably a multi-functional response to predation in the litter at night and above ground during the day, the need to feed on foliage, the enhancement of mate-finding above ground, and preferences along micrometeorological gradients. In these species, long-range chemical communication becomes more important.

A notable exception to these patterns is *Cryptocercus*, an oviparous species, which lives in monogamous family units. Oviposition is followed by several years of reproductive arrest while the current brood matures. Highly evolved parental care is exhibited. *Arenivaga apache*, an oviparous desert species, evolved a colony organization in response to clumping of its preferred microhabitat (rodent burrows) and food.

A general conclusion is that both reproductive modes and habitats are important in determining the life-history patterns of cockroaches.

To date, work on cockroaches has been mainly physiological. Behavioural research is almost exclusively conducted in laboratories, and ecological information on cockroaches is largely rudimentary and anecdotal. For instance, the findings that *Blaberus* females release volatile sex pheromones in the laboratory, and that males are territorial in the field, seem inconsistent, unless territories enhance pheromone reception by males. More thorough field and laboratory work is needed to resolve these questions. Cockroaches offer an excellent system for studies of (i) microhabitat selection and the effect of predators on activity patterns, (ii) the relations between major reproductive modes (oviparity, ovoviviparity) and stability of the environment, (iii) parental tactics and life-history patterns, (iv) social organization and communication, and (v) tactics of colonization and synanthropy. It is hoped that this review stimulates research in these areas, as well as the naming and describing of the focal species.

XIII. SUMMARY

1. Cockroaches are ubiquitous in most habitats where insects occur. Although most reports on cockroaches are physiological in nature, sufficient information is available to indicate that forest, desert, and cave-dwelling cockroaches select microhabitats on the basis of finely resolved environmental preferences. This is particularly true for oviparous females which select specific substrates for oviposition and embryogenesis. Selection and diel movements between microhabitats are related to diel changes in micrometeorological profiles and predation, feeding, and enhancement of sexual communication.

2. With some exceptions oviparous species live in wooded habitats; ovoviviparous species tend to occur in protected environments such as caves and logs. Oviparous species are exposed to greater predation, parasitism, and environmental pressures

during embryogenesis than are ovoviviparous species, where internal incubation and some parental care reduce these risks. Most ovoviviparous species produce larger clutches, but the interval between broods is significantly longer than in oviparous species. Long gestation, clumping of food resources, and relatively little movement probably selected for male control of resources as a mate-attraction tactic in ovoviviparous species; agonistic interactions, and in some cases morphological specializations for fighting, and highly ritualized behaviours are common. In most oviparous species, volatile pheromone communication and resource-based aggregations are common. Rapid ovarian cycles and patchily distributed nutritional resources result in the need for greater mobility, and hence adults encounter greater risks.

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