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NEOTROPICAL CERAMBYCID BEETLES AND THEIR LECYTHIDACEAE HOST PLANTS:

Variations on a Theme

by

Amy Constance Berkov

A dissertation submitted to the Graduate Faculty in Biology

in partial fulfillment of the requirements for the degree of Doctor of Philosophy,

The City University of New York

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This manuscript has been read and accepted for the Graduate Faculty in Biology in satisfaction of the dissertation requirement for the degree of Doctor of Philosophy.

16 September 1998
Date

Scott Mori
Chair of Examining Committee
Dr. Scott Mori, New York Botanical Garden

September 9, 1998
Date

Richard L. Chappell
Executive Officer
Dr. Richard L. Chappell

Dwight Kincaid
Dr. Dwight Kincaid, Lehman College

Dominick V. Basile
Dr. Dominick Basile, Lehman College

David Grimaldi
Dr. David Grimaldi, American Museum of Natural History

Lee M. Herman
Dr. Lee Herman, American Museum of Natural History

Janet Morrison
Dr. Janet Morrison, The College of New Jersey

Dr. B. Meurer-Grimes, AMRAD Discovery Technologies (Reader)
Dr. G. Tavakilian, ORSTOM, Laboratoire d'Entomologie (Reader)

Supervising Committee

The City University of New York

ABSTRACT

Neotropical cerambycid beetles and their Lecythidaceae host plants: Variations on a theme

by

Amy Constance Berkov

Co-advisors: Dr. Scott Mori, Dr. Barbara Meurer-Grimes

Estimates of the total number of arthropod species in existence are based, in part, upon assumptions about both the host specificity of tropical insects and their restriction to the forest canopy. It has been difficult to evaluate these estimates because of the paucity of available data. A recently discovered association between wood-boring longicorn beetles (Cerambycidae) and their host plants in the Brazil nut family (Lecythidaceae) inspired a year-long rearing project in the lowland Neotropical rain forest of central French Guiana. Branches severed from five species of Lecythidaceae, left in the canopy or placed on the ground, yielded 1,813 cerambycids belonging to 37 species. Few cerambycid species were restricted to the canopy, although there was a seasonal shift in stratum: they reproduced at both levels during the dry season, but almost exclusively at canopy level during the rainy season.

Each potential host was associated with a distinctly different complement of cerambycids. *Couratari stellata* and *Gustavia hexapetala*, characterized by foetid odors, consistently produced few cerambycids. I hypothesize that the foul odors are oviposition deterrents to Lecythidaceae specialists. Wood samples collected from the malodorous *C. stellata*, and from two well-colonized species, *Lecythis poiteaui* and *Eschweilera coriacea*, have been analyzed for both volatile and non-volatile compounds contributing to the foetid smells.

Sulfur compounds were dominant components of *C. stellata*, while they were minor components or lacking in the two popular tree species.

Eschweilera coriacea and *Lecythis poiteaui* gave rise to large and diverse cerambycid guilds. Most species associated with *E. coriacea* demonstrated a high degree of host fidelity, while *L. poiteaui* gave rise to more species with relatively broad host ranges. Cerambycid distribution patterns are evaluated in relation to host toxicity, as revealed by antimicrobial bioassays. The results are in accord with the hypothesis that highly toxic plant species are prone to host specialized insect herbivores, but numerous factors appear to influence the predispostion towards host fidelity.

Overall, results suggest that tropical insects may show greater flexibility than some current hypotheses suggest. Many are indeed specialists, but most specialists can utilize a broader range of potential hosts under a variable range of conditions.

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CONTENTS

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

A Year in Central French Guiana: Romance versus Arduous Reality

When I precipitously decided to return to school at the ripe age of 36, there were two things I knew: I wanted to climb large tropical trees, and I wanted to spend a year living in the middle of a rain forest. I attempted to effect an improbable transformation from emphatically non-academic urban artist into... *something else*... by catapulting myself into a Ph.D. program in biology at The City University of New York and The New York Botanical Garden. The entire first year of classes passed in a haze as I shuttled among six campuses, at the very bottom of the learning curve, acquiring a scientific vocabulary, and constructing an ever-lengthening list of things I *didn't* want to do.

At the start of my second year, happy accident landed me in an entomology class at The American Museum of Natural History. Obliged to spend plenty of time outdoors, stalking and seizing insects to identify, I was irrevocably smitten. Many of my collections were made at 6 Street & Avenue B Garden, a tiny oasis in the heart of Manhattan that attracts an amazing diversity of insects. I was particularly amazed to learn about the finely tuned associations that can arise between plants and insects, and the idea that plants produced a huge variety of chemicals capable of manipulating insect behavior captured my imagination. From this point, it was not difficult to devise a thesis project specifically designed to require a year in the rain forest of central French Guiana: an investigation of a group of neotropical wood-boring beetles (Cerambycidae) that reproduced only in the very large trees belonging to the Brazil nut family (Lecythidaceae).

Flirting with domesticity

There are three ways to approach the vast roadless interior of French Guiana (one of three lesser known countries on the northern coast of South America, a bit smaller than Indiana). One may walk from the coast in approximately three weeks, take a canoe upriver for ten days and then walk for two days, or fly in a small propeller plane from the coast in less than an hour. As a solitary traveler laden with 86 pounds of supplies, I opted for the plane. My journey had thus far encompassed every conceivable mishap. Gérard Tavakilian, the entomologist I was working with in the sleepy capital of Cayenne, rapidly made the oracular assessment that I was Not Lucky. On my 40th birthday I arrived in the village of Saül in a state of intense euphoria, convinced that my luck was changing, and made the final seven kilometer hike to the homestead where I would spend the next year.

My new house, tucked amidst secondary forest but only meters from pristine old-growth forest, was enchanting. The lower walls were made of interwoven strips of wood, while billowing lace curtains sufficed as upper walls. One of the two rooms was just large enough for a built-in platform bed and a clothes rack; the second was furnished with a simple wooden table, a bench, and a set of wooden shelves. The latchable door was a mere formality: nothing hindered frogs, lizards, bats, hummingbirds, rats, opossums, columns of ants, whip scorpions, and a tremendous variety of other invertebrates from coming over, under, or through the walls. The black plastic roof was constructed with an overhang, partially protecting a clothesline and the exterior kitchen table stocked with a gas tabletop stove and miscellaneous pots and pans. My hosts had outfitted the house with all of the essentials for life without electricity or running water: a cassette player lacking a functional power source, a cantankerous gas lantern, a full-length mirror, several plastic washtubs, and a chamberpot! The house very much suited my rather stripped-down aesthetic, and best of all, it was a waterfront property.

The crystal clear stream, accessible via a short staircase carved into the bank directly outside my door, would serve as drinking fountain, dishwasher, and washing machine. This confirmed Manhattanite, accustomed to instant culinary gratification and laundry service, was clearly embarking upon an unprecedented domestic adventure. Deliberations about the relative merits of Burmese, Mexican, Polish, or Senegalese takeout a thing of the past, I would now prepare my own rice and beans or go hungry. I would launder my clothes with a scrub brush on a stone table in the middle of the stream, and scour my pans with the assistance of the ubiquitous dish-washing fishes!

Sensory deprivation in the midst of plenty

Fifteen years of life in the Big Apple had left me with a perpetual low-level craving for solitude, and I had intentionally sought out one of the lonelier spots of the world. French Guiana was the site of the famed French penal colonies, including Devil's Island. It still maintains a rather unsavory reputation and the French civil servants that brave this tropical paradise merit generous hardship pay. The majority of the Europeans and Creoles live in modern towns strung along a coastal highway, and the rivers that define French Guiana's borders serve as the transportation systems for villagers living along the banks. Currently just about one hundred souls are sufficiently hardy and / or eccentric to stake a claim in the less accessible environs of Saül.

The first week of my long-awaited year in the rain forest was an exhilarating but unnerving period of introduction to the unfamiliar. My body metabolism was undergoing its own revolution while I was adjusting to a novel quotidian routine. I investigated the local trails, attempting to grasp the spatial logic of the treefalls that often obscured them, and began to observe the remarkable profusion of plants and insects characteristic of tropical rain forests. This brief idyll came to an abrupt end with the arrival of my co-advisor Scott Mori, specialist on the local flora and expert on the ecology and systematics

of the Brazil nut family, accompanied by a coterie of assistants and colleagues. The following days were a blaze of high-energy activity as I worked with one of the world's top tree-climbers to sever branches from 25 trees (ranging from slender understory specimens to massive canopy emergents). These branches, from five different tree species, were intended to lure wood-boring beetles so that I could establish how picky different beetle species were when laying their eggs. No sooner was the project established and the crew departed than a duo of entomologists arrived, and I enjoyed a heady bit of vacation enlivened by a crash course in tropical entomology. All too soon, I was escorting them back to the airstrip-- my leaden gut reminding me that until the climber returned in the rainy season to cut a second set of branches, I was on my own.

Prior to my departure, I'd had a vague notion that it would be pretty tough to spend a year more or less alone, but I assumed I was up to the task: there was nothing in my previous life that could have prepared me for the sense of isolation I would experience. The first month had been stressful and exciting, conditions very familiar to most urban dwellers. I'd largely been among other scientists, and my sense of the passage of time had remained firmly intact. Once they departed, time slammed to a halt. There was very little to distinguish one day from the next and each seemed a vast blank slate. We had allotted the beetles three months to lay their eggs in the first set of branches. Although I'd attempted to devise projects to keep myself occupied until it was time to collect and cage the cut branches, I found myself for the first time in my life rising and setting with the sun: constantly fatigued, ravenously hungry, and disoriented. I was surrounded by an incredible profusion of visual and auditory information, but it was all of unfamiliar form. I lacked the experience that might have enabled me to interpret the overwhelming natural stimulation, my life was devoid of artificial stimulation, and the net effect was one of absolute sensory deprivation.

Each morning I was encouraged out of bed by the arrival of vicious biting tabanids. These pestiferous flies were initially detectable as an ominous buzz at 6:30 am, and by 7 am they would attack in a swarm (particularly attracted to my blue sheets). The fabulous shady waterfront house proved to be ideally situated for diurnal mosquitoes that arrived shortly after the tabanids and inspired days of perpetual, if unfocused, motion. They lazily circled me whenever I sat down, were particularly bloodthirsty whenever I was sorting or pinning insects, and eventually I would feel their persistent bites even when my eyes assured me that there was no beast to be seen.

It was a revelation to learn exactly how many hours were required to provide for one's basic needs in a non-industrial setting. In addition to the predictable domestic chores, constant vigilance was required to prevent creatures of the forest from reclaiming my small piece of turf. Unable to concentrate, I wandered about my tiny house starting first one project, then distracted by another without finishing the first. Periodic forays into the forest to search the branch samples for signs of insect attack yielded dismal results. The beetles were apparently not cooperating with my carefully designed experiment, and I suffered plagues of uncharacteristic self doubt. I was sure that, given the same opportunity, any one of my colleagues would be making amazing scientific discoveries, writing books, or creating portfolios of spectacular illustrations. I attempted to spend as much time as possible walking the trails, convinced that, if nothing else, I was at least assembling a respectable Guianan insect collection.

Throughout the remainder of the dry season, the seemingly endless succession of febrile days gave rise to an unchanging succession of languorous evenings. Although the family running the homestead had invited me to visit in the evenings, it was virtually impossible for me to remain awake until they finished dinner. I did occasionally meet for a chat with Andy, the elder son. This gentle, ethereal soul (a changeling amidst his robust and

pragmatic pioneer family) seemed profoundly depressed, and the meetings did little to elevate my spirits. Day after day passed with minimal human contact, when the only human sound I would hear was the distant wailing of the family's youngest member. When I was finally called upon to speak, my voice emerged an inharmonious croak. At the onset of the rainy season, my admittedly fragile state took a turn for the worse as I abruptly found myself with clothes and towel wet, smelly, and full of mildew. When it rained, the clear stream where I bathed would swiftly transform into a muddy torrent full of debris. The roof overhang protecting my outdoor kitchen table wasn't quite large enough, and I often prepared dinner holding an umbrella aloft. The limited amount of natural light was drastically reduced and, anxiety-stricken about the prospect of an entire year without income, I had already instituted a strict energy-rationing program: one hour each evening with the gas lantern, and a second hour of dim illumination courtesy of my precious headlamp batteries.

The insects in my prized collection began to mold, depriving me of my one consistent source of satisfaction (and the only evidence I had that my time in French Guiana had been in any way productive). Ultimately the papers lining the wooden collection boxes were completely covered with fungus, the glue holding them together started to disintegrate, and the boxes literally began to fall apart. Whenever the sun reappeared, I was faced with a host of competing demands. I attempted to wash my muddy clothes, or continued the prolonged drying process (knowing that a momentary lapse of attention, even a walk to the outhouse, might permit a passing shower to resoak the laundry that I'd been trying to dry for days). Alternately I would dash about with my insect collection, tracking the sun, trying to inhibit the fungal growth by giving my insects a dose of light (knowing that at any moment a sun shower might counteract the potential benefit of the treatment). All I really wanted to do during the sunny interludes was take advantage of the good weather to disappear into the forest.

My journal entries from this period hold a detailed account of daily activities, but assiduously avoid mention of my mental state, and thus I no longer know when the most distressing phenomenon arose. Whether it started as soon as my visitors departed, or whether it accompanied the early rains, I began to experience auditory hallucinations: repetitive noises in my head that only ceased when I was actively interacting with other people or during two brief jaunts back to the coast. I suspect that this is not an uncommon phenomenon in the rain forest, where many of the genuine sounds are repetitive and often rather mournful. Marie-Claude, the family daughter-in-law, informed me that during her first rainy season she heard the call of the screaming piha echoing ceaselessly in her head. In my case, the soundtrack was at one point stuck on a Christmas carol, but more typically restricted to Brian Eno-esque phrases. Adventurers 'lost and maddened in the rain forest' have undoubtedly endured a similar experience.

Waiting for things to fall from the sky

The one activity that provided some sense of structure to my life was a weekly jaunt to Saül, where I enjoyed a rather chaotic shopping spree. Each Friday I would pocket a few francs, latch the door of my open-air house behind me, and walk to the village on the rutted dirt road cut through pristine primary forest. The outgoing walk took, at a comfortable pace, about 2 1/2 hours, and I marked my progress by tracking landmarks associated with past visitors (knowing, for instance, that I had just passed Debbie's *Caryocar*, but had not yet reached Lee's Creek). Once in the village I scurried around collecting my mail, stocking up on tuna and chocolate, visiting the Hmong produce stand, making any essential telephone calls from the lone telephone booth, and purchasing fresh baguettes just flown in from the coast. Weather permitting, I dawdled on the return as I searched for unknown flowers or fruits and collected insects, turning the equivalent of a dash to the corner store into a full-day outing.

Flights arrived from the coast three times a week (Monday, Wednesday, and Friday) and, in addition to the baguettes, transported immense sacks of mail and cartons of supplies. Most of the villagers put in an appearance on airplane days, lending Saül an air of relative festivity. The airplane was audible in the village as it made its descent to the airstrip, and this was the cue for the entire European population of the village to materialize at the combination Air Guyane Office / Postal Bureau, waiting for things to fall from the sky. I felt sure that many of the local residents had, like myself, once nursed romantic fantasies about a flight from civilization, only to find themselves, like myself, dependent upon and desperately awaiting its products. When a flight landed the mailbags were immediately loaded, along with any newly arrived tourists, onto a truck that sped back to the village. Each precious letter or package was withdrawn from a sack by Yolanda, the combination Air Guyane employee / Post Mistress (who commuted to Saül on her bright blue tractor). She barked out the surname of the addressee, and handed it on to the waiting hordes, where it was passed from hand to hand until it reached the eager recipient.

A few other business concerns opened up for an hour or two on airplane days. A group of Hmong, relocated in French Guiana after the Viet Nam war, brought a pushcart full of delectable produce from their nearby plantation and manned a small outdoor market across from the Air Guyane Office / Postal Bureau. Two tiny grocery stores sometimes opened their doors for business. My initial reaction to these stores was one of dismay: neither was large enough to accommodate more than one or two customers, they were dimly lit by ambient light entering through the doors, the floor of the larger store was always covered with great clumps of mud left behind by the ubiquitous rubber boots, the labels of most items were covered with mildew, and the selection of non-refrigerated products was depressingly sparse. In the entire year, there were two great moments at the local groceries: I once encountered a batch of freshly laid eggs at Monsieur Agasso's, and

once Monsieur No-No took pity on me as I cast a sad eye at his empty shelves, and presented me with a gift of two ripe avocados.

The first couple of months I spent in French Guiana I could never figure out why all of the villagers left Madame Marie's on airplane days bearing armloads of baguettes, while there never seemed to be more than, at most, a single baguette for me. I eventually realized that the villagers had prepaid for their orders, and thereafter I also paid in advance and picked up two baguettes each week. These lasted for three days, after which the bread became moldy, and the remainder of the week I heaped my tuna or peanut butter onto crackers. Madame Marie was also purveyor of the telecartes required to make a telephone call from the local telephone booth. The telephone operated like a radio phone: it was possible to trade snippets of information (leaving pauses between question and response), but if one party began to respond without waiting for the current speaker to finish, the transmission would be interrupted. It was a viable method of communicating with anyone familiar with the system's peculiarities, but not especially reliable. All too often the telephone was out of order when the telecartes were in stock, and the telecartes were sold out when the telephone was functional!

Fridays in Saül were for me not simply a long walk through the forest and a few new edible treats, but also the main chance I had to try to chat with people and practice my halting French. I made friends with the Dumas, the one family in Saül that seemed to fullheartedly appreciate and enjoy their unconventional lifestyle and their motley assortment of neighbors. The Dumas had already constructed and lived in several houses since moving to French Guiana, but had ultimately decided to settle right in the middle of the village. Their house was built using natural materials, but with an airy, loft-like design. Hugette was a petite, pipe-smoking woman who worked her own small gold mining claim. She also did the cooking, painted scenes of village life on wooden panels,

and created displays of forest flowers and fruits that rivaled anything you might encounter in a toney SoHo boutique. Her husband Gérald directed the construction of nearby trails, raised poultry, maintained an extremely productive garden, and made wonderful wood carvings. I would stop by each week after finishing my errands and hang out for a while as other villagers stopped by to visit, be fed some snacks or lunch, and check out the latest changing exhibition. They offered me a much-needed opportunity to make light of my various trials and tribulations, and were interested in my small accomplishments. I began to refer to the Dumas as my Emotional Rescue, and can only suppose that I might have become completely unhinged without their kindness and humor.

I never lingered too long in town, because I wanted to get home before the sun fell promptly at 7 pm. Although mornings, even during the rainy season, typically remained clear, the afternoon rains generally caught me either as I was leaving Saül, or when I was midway home. They were often quite forceful, and would have been blinding had I not always traveled with a small folding umbrella to protect my glasses. The dirt track sometimes turned into a veritable stream, and the sound of water rushing over rocks made a melodic accompaniment as I sloshed along. I ultimately became quite fond of those long walks in the pouring rain, even though I realized that they presaged a bath in a muddy and turbulent creek.

Thanks to the unflagging efforts of family and friends, I seldom returned empty-handed from mail call. When I finally arrived home, I'd take a quick dip to rinse off the sweat, and then bolt back to my house and settle down with my haul of cookies and mail. These communiqués I devoured were virtually the only contact I had with the outside world, but they supported my sensation of having come unstuck in time. Mail sometimes traveled to French Guiana by long and circuitous routes, and was often subject to lengthy delays (due

to the propensity for either strikes or celebrations). The letters, generally mailed prior to the arrival of my latest communiqués, seldom arrived in consecutive order, and had to be accepted as a very non-linear narrative. I was nevertheless profoundly grateful for each page, and treasured each as material proof that I had not entirely ceased to exist!

The emerging of the scamps

My fears that the beetles were snubbing the cut branches proved to be totally unfounded: unobserved, they had in fact mated and laid a multitude of eggs. During the rainy season cut we finally collected the dry season branches, and as we sawed them into lengths, pupae were literally dropping out from underneath the bark. No sooner were the branch sections placed into cages I'd fashioned from plastic screen, than adult beetles began to emerge. The little scamps promptly showed themselves adept at gnawing through the screen as if it were no more than an additional layer of bark. During the next eight months much of my time was spent incessantly patrolling the cages, hoping to thwart potential escapees. Although the dreariest part of the rainy season and the year's most emotionally stressful experiences were still ahead, I now knew that I had data for my thesis, and was never again quite so demoralized.

Over the course of the year, the 400-plus branch sections ultimately gave rise to 1,813 cerambycid beetles belonging to 37 different species! Some of the beetles were clearly tourists, while other species were represented by hundreds of individuals. Every single emergence, even of yet another individual belonging to one of the most ubiquitous species, was a thrill, and I never opened a cage to extract an adult without feeling that I was unwrapping a gift. With so few external distractions, I felt uncannily attuned to my branches and beetles. Some of the scamps were extremely feisty and would stridulate like mad when handled; others were comparatively passive. I had a pretty good sense of the time of day that each species emerged (some came out during the middle of the night

and would be clinging to the tops of their cages in the morning, others emerged during the afternoon, and yet others tended to emerge shortly after dark). Even with the many cages surrounding my house, I would often just get a feeling that a particular beetle was due to emerge from a particular branch section, and these hunches almost inevitably paid off.

Hoping to figure something out about the chemical cues the beetles used to evaluate a potential host plant, I kept the adults alive for experiments with wood extracts. The experiments were frustrating and fruitless, but they did ensure that my entire table surface remained covered with a stock of cerambycids enclosed in individual plastic cups, leaving me only a small clearing for meals and specimen preparation. I also maintained a selection of living insects collected in the forest, including a succession of pet assassin bugs. I took an evil satisfaction in capturing the biting tabanids and presenting them to my pets. The assassin bugs promptly subdued the oversized flies by trapping them with their strong forelegs. They inserted their sucking mouthparts in between the sclerotized plates forming the exoskeleton, and moved from one position to another, sucking fluids, until the fly was nothing but a lifeless husk.

These assassin bugs were quite abundant, both as nymphs and as adults, and individuals often had their robust forelegs covered with some sort of sticky substance. I had found an early instar inside a fallen *Clusia* fruit and wondered if these predators covered their legs with the distinctive gooey *Clusia* resin to help entrap their prey. Although I supplied my pets with a variety of blossoms and fruits, the bugs never showed any inclination to sample resin (the fruits may already have been too old). Eventually there was an fresh fruitfall from a hemiepiphytic *Clusia* near one of my study trees. Inside almost every mature fruit I found a large assassin bug, upraised forelegs clearly coated with the

aromatic resin oozing from the fruit's central disk, awaiting insects attracted by the alluring smell.

Vertebrate visitors were attracted to my house by the abundance of dead wood piled about, the scent of overripe papaya, the easy source of insect protein, or merely to escape the rain. This resulted in a number of unsavory nocturnal surprises. One night I was abruptly woken at 4 am when a very substantial frog lost its grip on a beam supporting the roof, and landed directly upon my face. Another time, I woke up in the middle of a rainy night with the sense that *something* had just moved. I sleepily assured myself that a bat had undoubtedly flown by, when I *definitely* felt something moving towards me on the bed. I was up in a flash, and immediately turned on both of my headlamps, only to find myself face to face with a wet and indignant four-eyed possum. I promptly grabbed my insect net and chased it out of bed and out of the house, but it was to become quite the regular nocturnal guest.

I began to call the incorrigible beast Mauvaise Habitudes, because it shared most of my bad habits. Not content to raid my fruit, it would come in at night to unpack the bits of sausage that I occasionally added to my unvarying meals of rice and beans to create the illusion of meat. I once stumbled out of bed and into the other room to find the possum licking the lid it had removed from a jar of Nutella (chocolate-macadamia nut spread), so cocky that it refused to leave until finished. It would open up petri dishes to steal beetles and, after cleaning me out, return the next night, apparently expecting me to have provided a fresh supply. Desperate for company in any form, I actually began to leave Mauvaise Habitudes the occasional (non-Coleopteran) treat.

The giant wild forest pussy

Not all of my encounters with wildlife took place indoors. As a veteran of previous excursions to the tropics with avid birders, I assumed that I would see a great diversity of birds, but would rarely see mammals. I failed to anticipate the tremendous patience required to see and identify most arboreal birds. Although I periodically surprised large ground birds, including troupes of gracefully prancing trumpeters, I more frequently crossed paths with mammals as I prowled through the forest. Oddly, I seldom saw the most abundant mammals (tapirs or peccaries), but I had the good fortune to stumble upon two of the more elusive denizens of the forest: the giant anteater and the jaguar.

It took a little more than an hour to reach the trailhead to my favorite path, making it difficult for me to visit as often as I would have liked, particularly during the rainy season. On one of my eagerly anticipated outings, I noticed an alternate trail branching off to the right, and turned to explore this previously unnoticed path. After about 15 minutes, I decided to give up the exploration and return to the main path, which led to a small creek. I retraced my steps, and at the moment that I reached the intersection with the main trail, I looked ahead and saw a jaguar about 15 meters away. It was smaller than I had imagined, but whereas an ocelot has spots fused almost into stripes, the jaguar is clearly spotted. I froze, awestruck, as it strolled regally across the trail and into the forest without giving me so much as a glance. Although I had no inclination to aggravate this giant wild forest pussy, the encounter was not particularly frightening to a person raised with cats. Like other cats, the jaguar seemed profoundly interested in its own business, and domestic relations aside, humans just aren't a noteworthy part of a cat's world.

My meeting with the giant anteater was actually more unnerving. In this case I suddenly found myself facing a large animal that was completely outside of my frame of reference, and which I could only describe as looking like a cross between an Afghan hound and a

vacuum cleaner! It had a characteristic long, tubelike snout, an amazingly long and bushy tail, and each foreleg sported three oversized claws. As it lumbered towards me, I intentionally made enough noise to make sure that it didn't get any sudden surprises. It continued its approach, but then decided to surrender the path. The sides of the trail rose up about five feet and the great beast looked as clumsy as I would have had I been the one deciding to head off into the forest, as it climbed a bit but then slid partway back down, raking the bank with its claws. I subsequently learned that the giant anteater is generally fearless because it is avoided by predators, unappealing even to jaguars because of the formidable claws and its unsavory antlike flavor.

La Carte de Sejour vrai

Many of my typical minor health complaints disappeared while I was in French Guiana, where I actually led a healthy life with plenty of exercise and an incredibly low-fat diet. There were, of course, a number of distinctly tropical maladies that I hoped to avoid. My greatest fear was the flesh-eating disease leishmaniasis, caused by protists transmitted by the bite of minute blood-sucking sand flies. If treated, leishmaniasis is not one of the most dangerous tropical diseases, but it is potentially one of the more disfiguring. My other great fears were of botflies (internally feeding fly larvae hatched from eggs that could be transmitted via mosquito bites) and hemorrhagic dengue (breakbone) fever.

I didn't experience any significant or prolonged physical discomfort until I'd been away for five months. One day I noticed that one of my knees was sore, and assumed that I'd injured it while collecting branches. Within days, the pain had selectively spread to other joints, including my hips, wrists, and thumb joints. One of the Creoles in Saül diagnosed me with rheumatism, brought on either by bathing in the stream, or by overheating my feet in rubber boots. An alternate suggestion was a 'petite dengue,' and I was warned not to take aspirin, which could be fatal should a dengue enter the hemorrhagic mode. The

pain, kept under control with a few soggy Advil, was never totally debilitating. It did make it difficult to perform many of my customary tasks, including swinging my insect net, flipping the lids off of the film canisters I used when collecting my beetles from the cages, and washing my dishes crouched at the stream. About a month after the onset, I made my second brief trip back to Cayenne. No sooner had I stocked up on enough pain-killers to see me through the next six months, than the pain disappeared as precipitously as it had arrived (perhaps supporting the 'petite dengue' hypothesis)!

As the rainy season progressed, I became less and less optimistic about my chances of avoiding leishmaniasis. My dry season tree-climber had contracted such a severe case that he ended up hospitalized with 38 lesions and required a series of 28 injections. Several other visitors had developed less severe cases. Every week when I arrived in Saül, I saw yet another villager sporting the characteristic persistent ulcers (over the course of a single year, at least one in ten came down with the disease). About a month after I recuperated from the joint pain, I began to develop an unattractive facial inflammation.

One of the ongoing stressful experiences up to this point had been dealing with endless bureaucratic confusion about my 'carte de sejour,' an addendum to the special visa required for a lengthy stay in French Guiana. My occasional costly telephone calls and my two trips back to the coast had been, almost exclusively, part of a prolonged quest for this elusive document. During my recent trip to Cayenne I'd finally gotten the last paper affixed to my passport, but the official document in no way conferred residency as effectively as the facial inflammation! At last I felt truly integrated into tropical life. My lesions were not typical of those associated with leishmaniasis, and whenever I visited the Saül I was stopped by villagers offering opinions as to their source and the appropriate treatment.

France may maintain a frustrating and labyrinthine bureaucracy, but it also supports one of the most efficient medical systems. Even Saül had a small health center staffed by a doctor who flew in for two days each month. I missed the doctor's visit when the inflammation first appeared, and by the time he returned there were more than 23 lesions clustered on one side of my face. The doctor, an English-speaking dermatologist, acted quickly to minimize the chance of permanent scarring by immediately treating me for both leishmaniasis and a staph infection. The two leishmaniasis shots were anything but pleasant. Each needle was attached to a reservoir that took 15 minutes to drain (for a total of 30 minutes), and throughout the ordeal a nurse checked my blood pressure, because patients sometimes have adverse reactions to the medication. The walk back to the homestead was in fact quite surreal, as the drug kicked in. Pleasant or not, by the time the culture results came back from Cayenne positive for leishmaniasis, the lesions covering my face were already healing. It was, of course, a singularly liberating experience to withstand one's worst fear!

Seasonal change in the land of endless summer

I had decided to spend a year in the middle of the rain forest because I was eager to experience a complete annual cycle. After living in a climate with seasons well-defined by changes in daylength and temperature, I was curious about a climate with seasons differentiated by the amount of rainfall. During the dry season, when many trees and lianas were in bloom, one day had seemed so like another that when I failed to take a photograph, I assumed the subject of interest would remain intact until my return. I quickly learned that although the tropics may seem timeless, biotic interactions progress at a rapid pace and one seldom gets a second chance. The orchid spotted one day would be consumed by a caterpillar the next, the fabulous spider camouflaged on its web disappeared overnight, the tinamou eggs I'd barely restrained myself from preparing as an omelette were eagerly devoured by a less inhibited predator.

The rainy season, initially imagined as a monotonous sheet of rain lasting for nine months, proved quite variable in nature. I recorded the rainfall on a daily basis, but many patterns are not discernible because they failed to alter the total amount of precipitation. During the first few months, periods of fairly heavy rains were interspersed with days or even a week of sunny skies. There was a different complement of plants in bloom, and there was still an abundance of insects. The following month was kind of drizzly and overcast, then there was a return to alternating sun and showers. This was a good period to observe the striking assortment of fruits fallen from the forest canopy and was also the peak flowering period for many monocots, but insect populations seemed depressed. The short dry season, 'le petit été de mars' arrived in early April, and provided a welcome vacation. The final two months of the rainy season most closely approximated the stereotypical image of endless rain and mud, but the ground was covered with newly sprouted seeds taking advantage of the abundant moisture.

Signs of the impending dry season began to appear even before the rains started to let up. During the dry season I'd pulled minute ticks off of my body on a daily basis, and while it's difficult to imagine greeting a tick with joy, the first one I found on my leg near the end of the rainy season filled me with buoyancy. In the following weeks, I encountered more and more flowers and insects I'd not seen during the past eight months, and greeted each as a long-lost friend. The ticks might have returned but the tabanids and mosquitoes were on the wane, and I began to rediscover the almost forgotten pleasure of pulling a camp chair outside of my house to read during the brief tropical dusk. Emergences from my branches were quickly tapering off, and I made a final climb into one of my study trees and sawed off one last branch as a farewell gift for my beetles. I knew that the long, hot summer was coming to an end and I'd soon be back in New York, incredibly ready for autumn.

N'habite pas à l'adresse indiquée

The first thing I did when I arrived in New York was literally kiss the ground. As it turned out, I left French Guiana in the nick of time: my house was flooded by a meter of water one month after my departure. My mail support committee had continued generating letters right up to the bitter end, and those that arrived in Saül after I'd gone were returned to the senders stamped 'N'habite pas à l'adresse indiquée.' Two years later, back in New York where time once again passes in an orderly fashion and I once again firmly inhabit my person, those envelopes still grace my refrigerator, in remembrance...

BACKGROUND

Host Specificity of Cerambycid Beetles in French Guiana

Tropical rain forests are the repository for much of the Earth's biological diversity. Although a mere 7% of the land surface supports tropical rain forests (Wilson, 1988), they are home to a disproportionate number of the world's plant and animal species. Projections have been made that, given current rates of tropical deforestation, most of these forests will either have been cleared or significantly degraded by 2135 A.D. It is thus presumed that we are in the midst of a mass extinction event unparalleled within the last 65 million years (Wilson, 1988). The magnitude of this event cannot be described without a clear understanding of the rate of habitat loss, which has been the subject of varying estimates (Lugo, 1988) and the relationship between geographic area and the number of species which can be supported (Wilson, 1988).

Even should data permit the calculation of credible extinction rates (see Lugo, 1988, for a summary), it would be difficult to generate reliable figures predicting how many species might be lost, because we lack baseline documentation of many species which currently exist. Current high-end estimates of the potential number of extant species (30 - 50 million) were formulated based on the results of experiments in which insecticides were used to knock insects down from the canopies of tropical trees (Erwin, 1982, 1988). These estimates have engendered great controversy, in part due to the assumption that many tropical arthropods are dependent upon a single host plant for survival (Erwin, 1982). Subsequent studies have compared the insect faunas of conspecific trees with those of unrelated tree species and suggested that Erwin may have overestimated the host fidelity of tropical insects (Kitching et al., 1997; Mawdsley & Stork, 1997). These studies, also based on canopy-fogging experiments, do not adequately sample concealed feeders such as leaf-miners and bark or wood-borers. In

addition, due to the chaotic profusion of arthropod species and individuals harvested after the release of insecticides, very few trees can actually be sampled. The state of knowledge regarding the host specificity of tropical insects is still rudimentary, at best.

The only way to provide incontrovertible documentation of host-plant association is to actually rear an insect from an accurately identified host. Gérard Tavakilian has been gathering data regarding the systematics and host plant relationships of cerambycid (longicorn) beetles in French Guiana since 1983. Over 1,000 host-plant records (348 cerambycid species, reared from over 200 tree species belonging to 48 plant families) have been established via the arduous process of rearing adult beetles from freshly fallen wood (Tavakilian et al., 1997).

Most of these records were generated between 1991 and 1993. During this time, a massive study was conducted to document the biodiversity of an area of the Sinnamary River Basin subsequently inundated by a reservoir formed behind the Petit Saut Dam. Almost 700 trees and lianas were felled, and voucher specimens were collected from the plants, identified by specialists, and deposited in major herbaria (NY, P, CAY). Wood specimens were also collected and deposited at CTFT (the French research organization responsible for the study of wood) and the United States Forest Products Laboratory wood collection at Madison, Wisconsin. During the 1992 and 1993 field seasons, additional small wood samples were collected, preserved in methanol, and delivered to the laboratory of Barbara Meurer-Grimes (Lehman College, CUNY) for chemical analysis.

Classification of host specificity

The language used to describe feeding strategy and host specificity has been so abused (summary in May & Ahmad, 1983) that terms must be redefined with each use.

Herbivores may be broadly classified as polyphagous (generalists that attack numerous unrelated plants), monophagous (specialists restricted to a single plant species or genus), or oligophagous (specialists associated with several related genera, a plant family or closely related families). We have substituted a system in which actual host-plant records enable us to propose a host utilization strategy.

Generalists are denoted "G," and specialists are categorized according to the taxonomic level of the host plant(s) utilized. "S/ORD" indicates that a beetle species is associated with plants belonging to a particular plant order, "S/FAM," "S/GEN," and "S/SP" refer to beetle species reproductively restricted to a particular plant family, genus, or species, respectively. There is, in addition, a small group of longicorns which reproduce in trees that are not taxonomically related, but which belong to families characterized by the production of milky latex. These beetles are considered chemical specialists, and classified "S/LAT."

A longicorn has been tentatively assigned to a particular category if there are at least two host plant records directly derived from rearing experiments in French Guiana. When there are numerous host plant records, 90% of them must be in accord for a beetle to be retained in a category. For instance, if a cerambycid species has been reared from nine plant specimens belonging to the same genus, and only once from an alternate genus, that species is considered "S/GEN," or a specialist associated with the first genus. However, if the cerambycid species has been reared from eight plant specimens belonging to a single genus, and twice from an alternate genus in the same plant family, that beetle is considered "S/FAM." Should the cerambycid species be reared eight times from plant specimens belonging to a single genus, and twice from specimens belonging to a different plant family, that beetle would be downgraded to "G." These classifications are considered hypothetical, because many of them are supported by very

little data, but they nevertheless enable us to perceive meaningful trends in host plant fidelity.

Results from Tavakilian's rearing experiments

Almost half of the cerambycid species reared could not be classified as either generalists or specialists, because even after the intensive sampling, they were represented by a single host plant record. Among the remaining cerambycid species, specialists outnumbered generalists >3:1 (Figure 1), but different plant taxa gave rise to faunas with quite different ratios of specialist to generalist. The majority of the specialists successfully reproduced in related tree species belonging to a particular plant family. Only a few cerambycid species appear to depend exclusively upon a single host.

Abundantly represented plant taxa included Moraceae, Malvales, Lecythidaceae, Sapotaceae, Fabales, and Apocynaceae (Figure 1). Lecythidaceae was one of two plant families that not only gave rise to an unusually well-defined guild of specialists, but was conspicuously avoided by generalists. The other plant family associated with a similar type of cerambycid guild was Sapotaceae, apparent sister clade to Lecythidaceae (Morton et al., 1997; Morton et al., in press). The composition of the Lecythidaceae and Sapotaceae cerambycid guilds are, however, completely distinct (Tavakilian et al., 1997).

The 41 Lecythidaceae plant specimens (19 spp., 4 genera) investigated gave rise to 17 cerambycid species. Five of the cerambycid species were represented by a single host record. Of the remaining cerambycid species, only one was a generalist. Nine of the 11 specialist species, including *Neoeutrypanus incertus, Oedopeza leucostigma, Palame* spp., *Periboeum pubescens, Xylergates elaineae,* and *Xylergatina pulchra* emerged from two or more tree genera. *Neopalame* sp. 911 was reared from *Eschweilera,* and

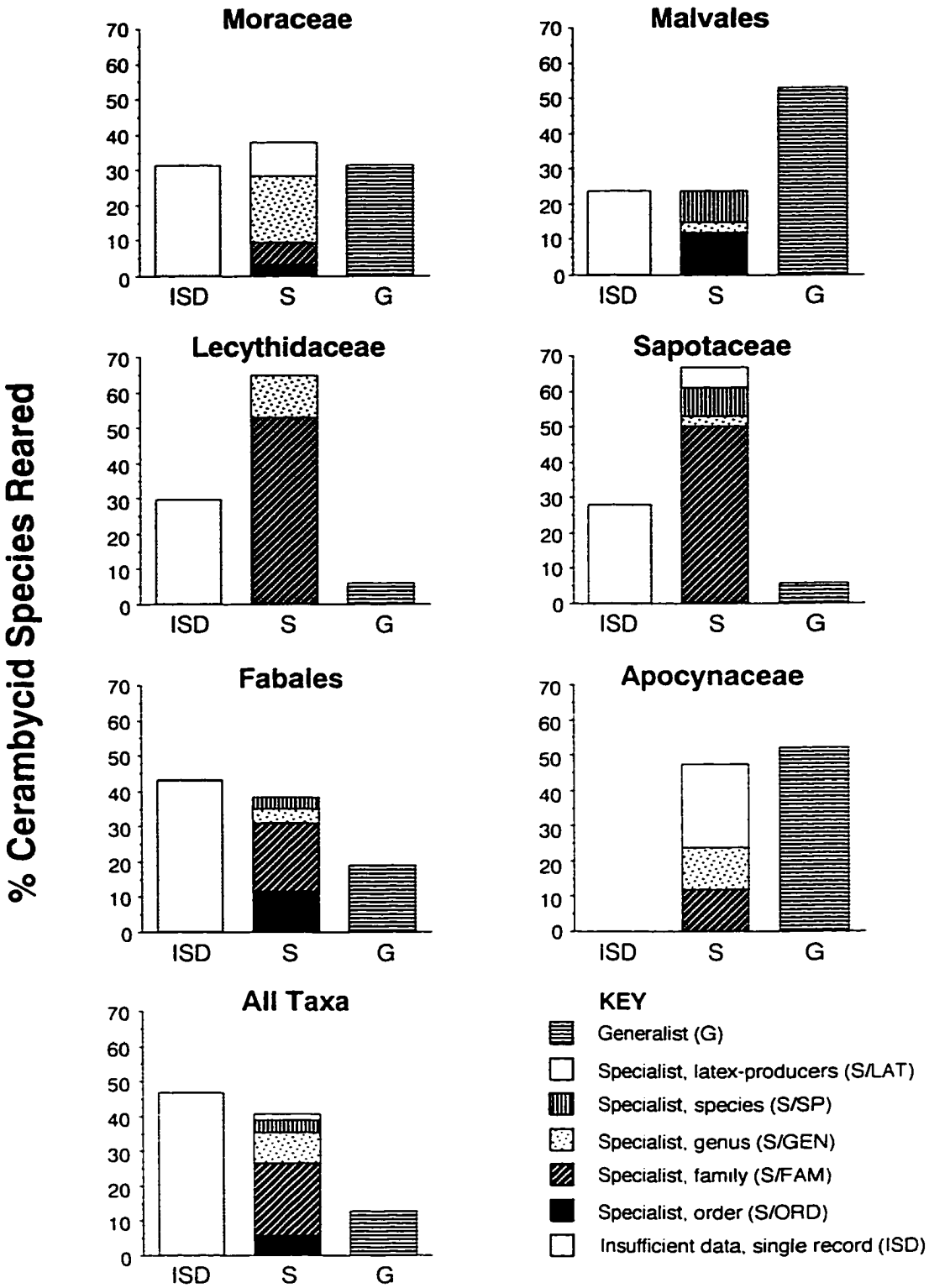


Figure 1. Host specificity of cerambycids associated with selected plant taxa. Reprinted with permission from *The Botanical Review* vol. 63 no. 4, copyright 1997, The New York Botanical Garden.

Neobaryssinus marianae was reared from *Couratari.* All of the Lecythidaceae specialists reared by Tavakilian belong to the tribe Acanthocinini in the subfamily Lamiinae, with the exception of *P. pubescens,* which belongs to the tribe Elaphidionini in the subfamily Cerambycinae.

Cerambycidae

Cerambycids (longicorns, long-horned beetles, timber beetles) constitute one of the largest groups of insects in the world, with approximately 35,000 described species (Lawrence, 1982). The family has clearly undergone a massive diversification in concert with the angiosperms (Farrell, 1998). Cerambycids have a cosmopolitan distribution, but are particularly diverse in the tropics. In 1980, only 330 species were known from French Guiana, but well over 1,400 species have now been documented (Hequet & Tavakilian, 1996). In comparison, fewer than 1,000 species of cerambycid occur in all of the United States and Canada (Arnett, 1988). Although the family Cerambycidae includes nine subfamilies, the vast majority of species belong to the subfamilies Cerambycinae and Lamiinae (Monné & Giesbert, 1994). Most of the cerambycids associated with Lecythidaceae are crepuscular species belonging to the subfamily Lamiinae (Tavakilian, 1993; Tavakilian et al., 1997).

The feeding habits of the rather short-lived adult longicorns can be quite variable. They may feed upon numerous plant parts including flowers, nectar, fruits, leaves, roots, and bark (Linsley, 1959, 1961) not necessarily belonging to the host plant in which the larvae developed. Therefore, when we discuss the host specificity of longicorns, we refer to reproductive-host specificity. The more primitive taxa, whose larvae often develop in long-dead or decomposing wood, are generally more polyphagous, while those taxa whose larvae develop in living wood are the most narrowly host specific.

The olfactory response, mediated by sensilla located on the antennae, is presumed to be critical in the location of an appropriate host tree for mating and oviposition. The females of most species oviposit their eggs into freshly killed or damaged wood with persistent bark that protects the immature stages of the beetles (Linsley, 1959, 1961). After about a week, the eggs hatch into larvae which, feeding upon the wood, gain weight and pass through five or six larval instars (Hequet & Tavakilian, 1996). As they feed, the larvae create systems of tunnels and galleries throughout the wood which may then be colonized by other animals or microorganisms. The larvae eventually excavate pupal chambers underneath the bark. After metamorphosis, the adult beetles chew exit holes through the bark of the host and commence the search for a new host.

Cerambycids play a very important ecological role in the reduction of wood to humus. Because most cerambycid species select hosts with persistent bark, they are partial to logs cut for timber but not yet processed. The galleries they create degrade the quality of the resulting lumber, and longicorns make a considerable economic impact (Linsley, 1958).

Lecythidaceae

Lecythidaceae is a comparatively small plant family (comprising about 300 woody species belonging to 20 genera) with a Pantropical distribution (Mori & Prance, 1993). Five subfamilies are currently recognized: Planchonioideae, Foetidioideae, Napoleonaeoideae, Scytopetaloideae and Lecythidoideae. The first four are restricted to the Old World tropics, with the exception of the monospecific genus *Asteranthos*, found only in the upper Rio Negro of South America (Morton et al., 1997; Morton et al., in press).

The greatest diversity is found in the Neotropical subfamily Lecythidoideae, and 52 species belonging to seven genera are found in the Guianas (Mori & Prance, 1993). Although there are some small understory trees, the majority are canopy trees or emergents, some of which reach 50 meters in height (Mori & Prance, 1993). In several lowland tropical forests, this family is extremely important, both in terms of the number of individuals and species present (Mori & Boom, 1987a; Mori & Prance, 1990). Neotropical Lecythidaceae are most easily identified in the field by the fallen androecia of their distinctive flowers, or by the presence of their conspicuous woody fruits.

The Brazil nut itself, the seed of *Bertholletia excelsa,* is one of the economically most important products in much of Amazonia. The seed is not only eaten as a snack, but oil can be extracted and used for cooking and soapmaking, or burned for illumination (Prance & Mori, 1979). One of the Brazil nut's major storage proteins is currently being cloned and expressed in other agronomically important seeds, due to its abundance of sulfur containing amino acids (Bartolome et al., 1997). Several species of *Lecythis* also yield edible seeds, but they are prohibitively difficult to harvest, and some accumulate toxic levels of selenium (Aronow & Kerdel-Vegas, 1965; Kerdel-Vegas, 1966; Prance & Mori, 1979).

The bark, roots, fruits, and seeds of some species are used in herbal remedies that most frequently function as emetics, purgatives, diuretics, or bitter tonics. *Gustavia hexapetala* (New World) and *Barringtonia acutangulata, B. asiatica,* and *B. racemosa* (Old World) yield fish poisons (Prance & Mori, 1979; Schultes & Raffauf,1990; Anonymous, 1986). The bark of *Cariniana domestica* is prepared as an arrow poison in Rondônia, Brazil (Jacobs et al., 1990), and the bark of *Couroupita guianensis* is sometimes added to psychoactive *ayahuasca* beverages in northeastern Peru (Luna, 1984). Aqueous extracts from an African species, *Petersianthus macrocarpus (=Combretodendron africanum),*

are used as contraceptives and abortifacients (El Izzi et al., 1992; Ogundain, Yisak, & Ojewolfe, 1983).

Chemical investigation of the family, and particularly of the Neotropical taxa, has been minimal. Neotropical species that have been tested for alkaloids have been negative (Schultes and Raffauf, 1990), with the exception of *Couroupita guianensis* (Bergman, at al., 1985). *Couroupita guianensis* yields several indole alkaloids including the blue dye indigotin and a related compound tryptanthrin, which is active against dermatophytes (Bergman, at al., 1985). Several other species (*Eschweilera decolorans*, *E. laevicarpa*, *Lecythis pisonis*, and *L. zabucajo*) also have flowers which stain blue when the tissues are disrupted (Mori, pers. comm.), and they are also likely to contain these alkaloids. The family is known to contain polyphenols (including tannins), triterpene saponins (considered responsible for the toxicity to fish), and cyanogenic constituents (Schultes and Raffauf, 1990). Ellagic acid and several derivatives, one with weak antifungal activity, have been isolated from *Eschweilera coriacea* (Yang et al., 1998). Saponins have been isolated and elucidated in both *Barringtonia acutangulata* and *Petersianthus macrocarpus* (Massiot et al., 1992; Pal et al., 1991). The red-colored compound associated with the anticoagulant activity of *Cariniana domestica* has been partially purified, but a structure has not yet been determined (Jacobs et al., 1990). *Lecythis ollaria* produces toxic selenium analogues of the sulfur amino acid, cystathionine (Aronow & Kerdel-Vegas, 1965; Kerdel-Vegas et al., 1965). Volatile compounds released by various Lecythidaceae flowers, including *Eschweilera coriacea* and *Couratari stellata*, have also been analyzed and discussed in relation to pollination syndromes (Knudsen & Mori, 1996).

The five species investigated in this study were *Corythophora amapaensis* Pires ex S. A. Mori & Prance, *Couratari stellata* A. C. Smith, *Eschweilera coriacea* (A. P. de Candolle)

S. A. Mori, *Gustavia hexapetala* (Aublet) J. E. Smith, and *Lecythis poiteaui* Berg. These trees, representing the five genera of Lecythidaceae commonly encountered in French Guiana, were selected because they are relatively abundant at the study site. All species are canopy trees or emergents, with the exception of *G. hexapetala*, a slender understory species. They flower profusely and leave the ground carpeted with fallen corollas, also with the exception of *G. hexapetala*, which produces relatively few flowers over a long period of time. *Lecythis poiteaui* flowers during the early rainy season, *G. hexapetala* peaks during the late rainy season, and the remaining taxa flower during the dry season. *Corythophora amapaensis* (F. G. and Amapá, Brazil) and *L. poiteaui* (F. G., Surinam, and eastern Amazonia) have somewhat restricted distributions, while *C. stellata* (Guianas, western and central Amazonia), *E. coriacea* (Guianas, the Amazon Basin, and west of the Andes in Panama and Columbia), and *G. hexapetala* (Guianas, Amazonia, and north-central Venezuela) are relatively widespread (Mori & Prance, 1990; Mori & Prance, 1993).

Field Experiments at Les Eaux Claires

Objectives

The purpose of this study was to elucidate a newly-discovered association between certain members of an ecologically and economically important family of wood-boring beetles (Cerambycidae) and their host plants in the Brazil nut family (Lecythidaceae). Cerambycids, due to the prolonged larval period spent in intimate contact with the tissues of the host plant, may be prone to the development of host-specific associations. When trees belonging to more than 45 plant families were investigated for their cerambycid associates in French Guiana, Lecythidaceae was one of two families that not only gave rise to a clearly defined guild of specialist beetles, but was conspicuously avoided by generalists (Tavakilian, 1993; Tavakilian et al., 1997). This was surprising, because the

Brazil nut family is not generally noted for its bioactive compounds, which have therefore been poorly investigated.

There were two primary objectives. The first was to analyze whether these Lecythidaceae specialists partition their potential resources by quantifying whether different cerambycid species emerged from 1) five different tree species, 2) thin or thick branches, 3) branches cut during the dry season or the rainy season, and 4) branches at canopy stratum or ground stratum. The second objective was to identify plant compounds involved in the host-selection process.

Study site in central French Guiana

French Guiana is part of the Guayana floristic province in northeastern South America (Mori, 1991), a species-rich region with between 7,000 and 10,000 angiosperms (Lindeman & Mori, 1989). Although numerous forest types are represented, including mangrove, marsh, swamp, and montane forest, much of French Guiana is covered with intact, and relatively well-investigated, seasonal evergreen forest (Granville, 1986).

This study was conducted in the lowland moist forest surrounding Les Eaux Claires, a homestead approximately seven kilometers N of the village of Saül, French Guiana (3°37-39'N, 53°12-13'W, see Figure 2). The extended population of Saül is currently about 100 individuals. The region did support a considerably larger population half a century ago, when it enjoyed a brief flicker of fame as a gold-mining center. Placer mining and associated subsistence activities have made only a slight impact upon the forest, that extends, essentially unbroken, for at least 100 kilometers in all directions. Compared with several other tropical forests, that of the nearby La Fumée Mountain incorporates the greatest number of large trees, supporting the premise that the forest surrounding Saül persists in a relatively undisturbed state (Mori & Boom, 1987a). The

flora of central French Guiana is relatively well-known (Mori et al., 1997; Mori et al., in review). Although historical and contemporary hunting undoubtedly influence the distribution and abundance of large mammals, dominant predators such as jaguars are sighted with some regularity.

The region is quite hilly, although most localities are between 200 and 400 meters above sea level (Mori & Brown, 1994). There are no navigable rivers, but the headwaters for French Guiana's major river systems arise here, and the area is dissected by many streams. The soils are generally well-drained, conditions favorable for most Lecythidaceae (Prance & Mori, 1979). The average annual rainfall for Saül has been reported to be about 2413 mm (Mori & Boom, 1987a). Measurements made at Les Eaux Claires from mid-September, 1995, through mid-August, 1996, using a Tru-Chek rain gauge, documented a cumulative rainfall of 2374 mm (Figure 3). Four years of measurements at Nouragues, a field station maintained by ORSTOM (4° 05'N, 52° 40'W), suggest an annual rainfall of about 3,000 mm (Van der Meer & Bongers, 1995), but it appears that Saül has a somewhat drier climate. There is a well-defined dry season between July and November, although the only months likely to receive less than 100 mm of rain are September and October. A second, abbreviated dry spell, locally referred to as "le petit été de mars," belatedly arrived the first two weeks of April the year of this study.

The temperature is quite equable, with greater diurnal than annual variability, and an average monthly temperature of 27.1° C (Mori & Brown, 1994). Our observations were that the chilliest times are either very early in the morning, during the clear weather of the dry season, or at dusk on the occasional totally sunless days during the rainy season. Although French Guiana is subject to the influence of either NE or SE tradewinds, depending on the time of year (Mori & Brown, 1994), the interior of the country is not

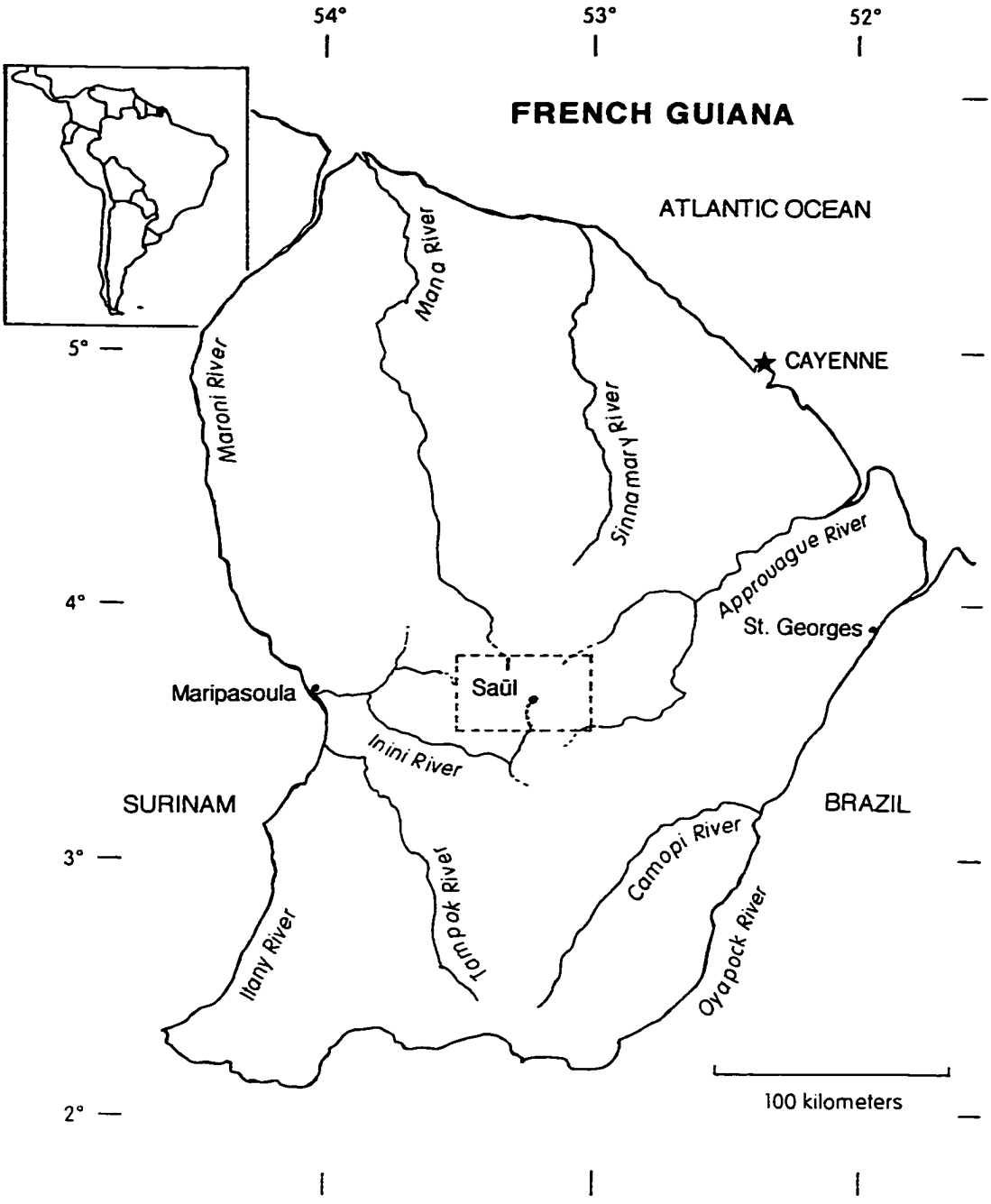


Figure 2. Map of French Guiana (adapted from Mori et al., 1997).

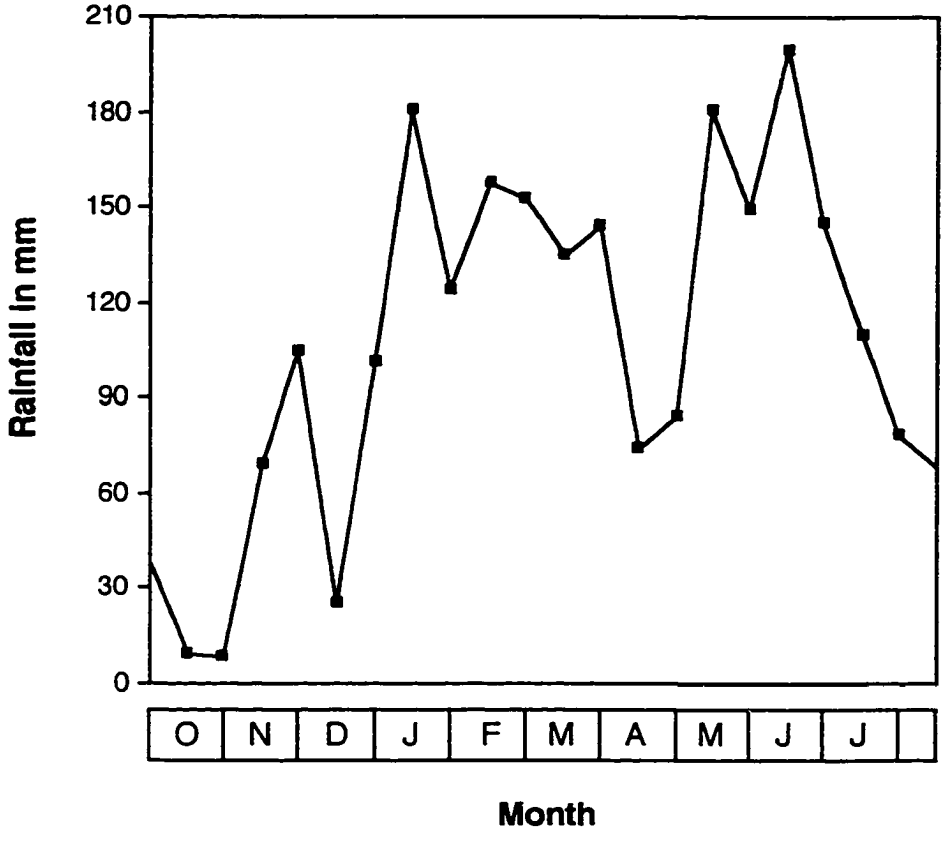


Figure 3. Rainfall at Les Eaux Claires, 1995 - 1996.

generally very windy. During the field season, the winter solstice brought one storm, that although brief, was accompanied by exceptionally high winds. The following day there were 14 fallen trees with a diameter >10 cm across the seven kilometer dirt road between Les Eaux Claires and Saül. According to our rainfall measurements (16.25 mm), there were 49 days with greater precipitation, but none of them wreaked the same sort of havoc (or provided the same potential cerambycid habitat).

Experimental protocol for the rearing experiments

Prior to the dry season cut, five trees in each of the selected species of Lecythidaceae (*Corythophora amapaensis, Couratari stellata, Eschweilera coriacea, Gustavia hexapetala,* and *Lecythis poiteaui)* were located at the study site by S. A. Mori, who has worked in the region for the past two decades and is currently completing a flora of the region's vascular plants. The cerambycids investigated in this study typically lay their eggs in freshly killed wood, and therefore branches were severed from 25 (dry season) or 20 (rainy season) trees. Two of the 25 trees were located within one kilometer of the homestead along the Route de Bélizon, the dirt road that originates in Saül and passes Les Eaux Claires. The remaining trees in the sample were located within one kilometer of the trailhead of the Sentier Botanique, a trail that ascends a ridge E of Les Eaux Claires. The trees were situated either along the crest or on the slopes of the ridge.

Each tree was assigned an identifiying letter, and its location, diameter breast height (DBH), estimated height, and fertility status were recorded (Appendix I). The tree was then flagged and marked with an aluminum tag. Herbarium vouchers collected from the study trees are on deposit at CAY and NY. Small twig samples were collected from each tree in the study, and bulk wood samples were collected from three individuals; these samples were preserved in methanol and delivered to the phytochemistry laboratory at Lehman College, CUNY.

Due to the impressive stature of many Lecythidaceae, various rope climbing technologies were used (essentially as described in Perry, 1978) to remove branches from the trees. Lead lines were placed in the trees, either by using a throwball or with the aid of a crossbow. The lead lines were used to pull climbing lines over sturdy limbs, which were then accessible with the assistance of a harness (Petzl Navaho-Vario C79), cams (CMI), and a descent device (Petzl Stop Brevete).

The first cut took place in mid dry season (September 15-24, 1995). Two individual branches (one thin, and one thick) were sawn from each sample tree approximately 60 cm from the fork. The target diameters for the branches were 2.5 cm (thin) and 10 cm (thick), but there was, of course, a limited pool of available branches on trees ranging from small understory (*G. hexapetala*) to giant emergent (*C. stellata*). The mean diameter of the thin branches turned out to be 3.21 cm (range 1.5 - 6 cm) and the mean diameter of the thick branches was 7.17 cm (range 4 - 10 cm). An effort was made to be sure that the thick branches from a tree were at least 2X the diameter of the thin branches. The two branch stubs that remained attached to the tree were girdled at the crotch to kill them. Equivalent lengths were sawn from the branches on the ground. These canopy and ground level samples, hereafter referred to as **SNACKS**, were both flagged and labeled with aluminum tags. The leftover branches, hereafter referred to as **DEBRIS**, were also flagged.

The branches prepared during the dry season were collected at the time of the second cut. All snacks were placed into individual cages constructed from plastic screen. The debris was also collected, but due to a shortage of cage materials, all branch segments from a particular tree species were consolidated in a single cage, hereafter referred to as a **BIG CAGE,** constructed of either plastic screen or no-seeum mosquito netting. The big cages therefore contained varying numbers of branch segments with mixed lengths and

diameters from several trees belonging to the same species, or segments of mixed diameters from a single tree (rainy season). Emergences from the big cages contributed additional data about associations between cerambycid species and host tree species, as well as stratum preference and seasonality.

The rainy season cut took place about six weeks after the onset of the rainy season (January 4-10, 1996). We initially followed the dry season protocol, but several modifications were made due to the time constraints of the principal tree climber and inclement weather. In addition to the reduction in sample size (all five tree species were retained but with only four replicates each), we reluctantly curtailed the canopy portion of the experiment. Canopy snacks were prepared only for *E. coriacea* and *L. poiteaui* (nocturnal observations of cerambycid visits had suggested that these two species would be the most productive). A single thick branch was severed from each of the remaining trees, and, on the ground, both thick and thin snacks were sawn from the same branch. A couple of days into the rainy season cut, we realized that many of the canopy snacks girdled during the dry season cut had not actually died, but had simply resprouted (Appendix II)! Thenceforth, the canopy snacks were prepared by completely severing thin and thick samples and rigging them upon pulleys, so that they dangled in the canopy. All of the *E. coriacea* and half of the *L. poiteaui* canopy snacks were placed on the pulleys, however *L. poiteaui* canopy snacks were left girdled on two of the four replicates.

The branches prepared during the rainy season were collected late March through April, and snacks were placed in individual cages. *Couratari stellata* and *G. hexapetala* debris was again consolidated in big cages, but the acquisition of additional cage material permitted the *E. coriacea, L. poiteaui,* and *C. amapaensis* debris to be caged by individual tree, rather than by species only. The cerambycids that emerged from the dry

season branches had proved quite capable of gnawing through plastic screen, and therefore most of the rainy season cages were constructed from no-seeum mosquito netting.

All cages were monitored continuously for the emergences of adult beetles through mid-August, 1996. The branches that still seemed productive at this time were the rainy season canopy snacks, and their cages continued to be monitored by a local assistant through November, 1996. During the field season, the newly emerged adults were sometimes retained alive in plastic cups with twigs, to be used in preference tests with various Lecythidaceae wood extracts, or quickly dispatched. Each beetle was given a preliminary identification to species, measured from the anterior portion of the scape to the tip of the elytra, and preserved in alcohol. Species were subsequently determined and individuals were sexed by G. Tavakilian (ORSTOM Cayenne, French Guiana). Some of the rarer cerambycids were retained in Cayenne, and the others were transported to the American Museum of Natural History for dry-mounting. All emergences are documented in Appendix II.

CHAPTER 1

Synopsis of cerambycid emergences from five tree species

Over the course of the year, 406 branch sections were collected from 25 trees belonging to five tree species: *Corythophora amapaensis, Couratari stellata, Eschweilera coriacea, Gustavia hexapetala,* and *Lecythis poiteaui.* These branch sections ultimately gave rise to 1813 individual cerambycid beetles belonging to 37 species (all emergences are listed in Appendix II; see also Chapter 2, Table 1). Each tree species investigated was associated with a distinctly different complement of cerambycids.

This chapter summarizes the patterns of beetle attack for each tree species using line charts showing emergences over time. Only cerambycid species represented by at least 10 individuals are included in the charts and discussions. *Eschweilera coriacea* and *L. poiteaui* were the only tree species retained in the canopy portion of the experiment during the rainy season cut. During the rainy season, canopy snacks gave rise to the vast majority of cerambycids, and these are the only tree species that show emergences from both dry season and rainy season branches. I make a few references to life history attributes of the cerambycid species reared. Size ranges reflect measurements of the individuals reared in this study. All additional host plant records cited are derived from Tavakilian et al., 1997.

Eschweilera coriacea

Dry season branches were severed from *E. coriacea* on Sept. 15 - 16, 1995. Emergences are shown in Figure 4. The branch sections left at ground level gave rise predominately to two relatively large cerambycid species: *Oedopeza leucostigma* (8 - 15 mm), belonging to the tribe Acanthocinini, and *Oreodera simplex* (9.5 - 14 mm), belonging to the tribe

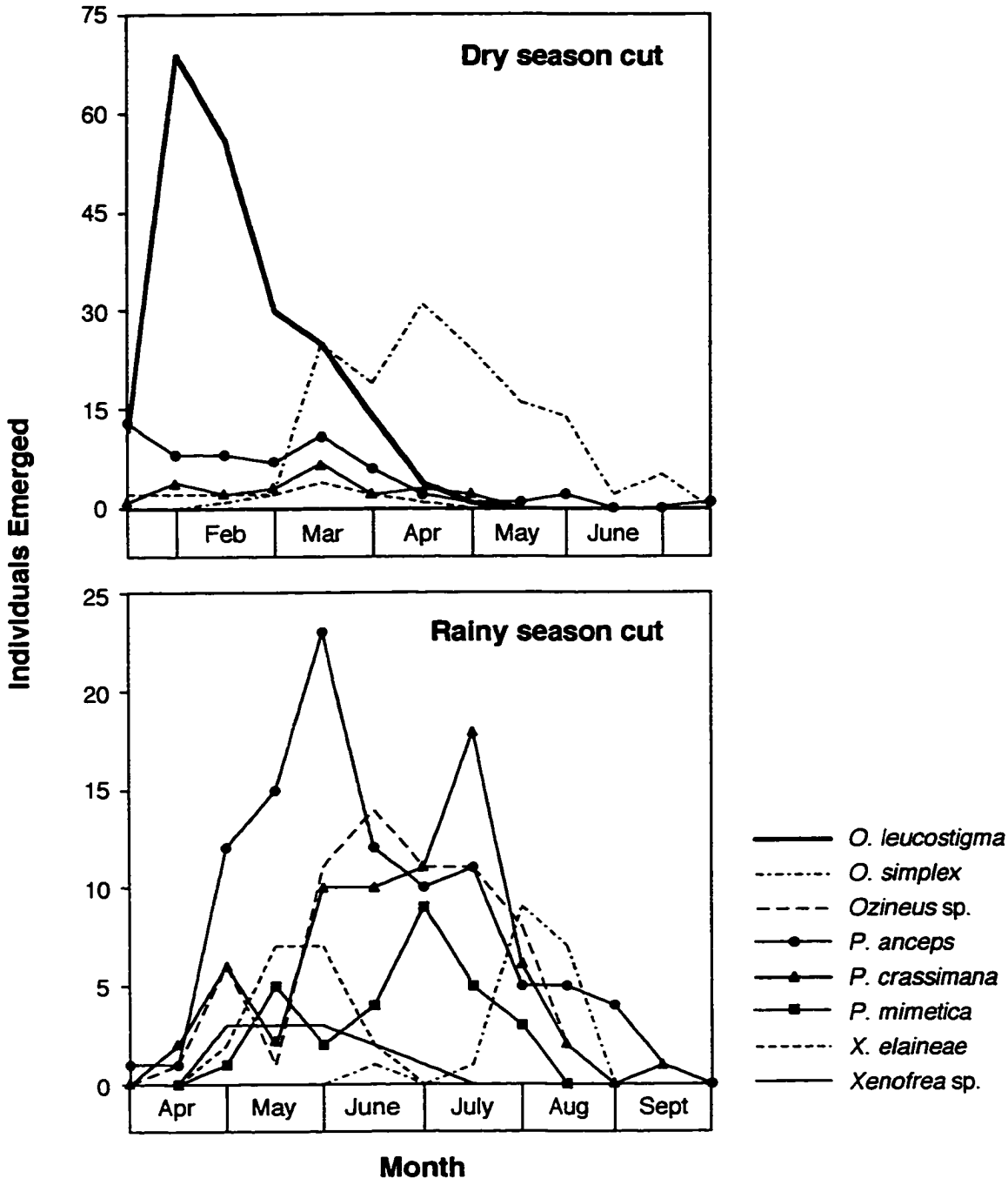


Figure 4. Cerambycids emerged from *Eschweilera coriacea* at Les Eaux Claires.

Acanthoderini. Unlike some other species associated with ground level branches, they emerged in abundance both from the debris in the big cages and most available snacks, clearly associated with almost every sample tree (Appendix II). *Oedopeza leucostigma* is a particularly feisty beetle prone to stridulate when handled. It has five additional documented host species belonging to Lecythidaceae, including *Couratari stellata* and *Lecythis poiteaui* in this study (both produced very few individuals). Emergences peaked about 4.5 - 5 months after the cut. *Oreodera simplex* was reared exclusively from *E. coriacea* in this study, and has no prior host record. Emergences peaked about 7 months after the cut.

Smaller numbers of several other cerambycid species, including *Xylergates elaineae, Palame anceps,* and *Palame crassimana* (bicolor form), all belonging to the tribe Acanthocinini, were also reared from dry season branches. These species emerged both from canopy snacks and ground level debris in the big cages. Emergences tended to straggle along at low levels, 4 - 6 months after the cut, without well-defined peaks. *Xylergates elaineae* (8.5 - 14 mm) has previously been reared from *Eschweilera* spp., *Lecythis* spp., and *Couratari guianensis*. *Palame anceps* (5.5 - 8.5 mm) was reared exclusively from *E. coriacea* in this study, but there are additional records from *Eschweilera* spp. and *Couratari guianensis*. *Palame crassimana* (5 - 9 mm), the 'least picky' cerambycid in this study (see Chapter 2), emerged from four of the five potential host plants, and has many additional host species belonging to Lecythidaceae.

Rainy season branches were severed from *E. coriacea* on Jan 4, 1996. Emergences are shown in Figure 4. Although *E. coriacea* was the only tree species to retain some portion of its ground level fauna during the rainy season (Appendix II), the canopy snacks gave rise to the vast majority of cerambycids. *Oedopeza leucostigma*, the most abundant cerambycid during the dry season, was represented during the rainy season by fewer than

ten small individuals that emerged from canopy snacks. *Oreodera simplex* emerged in reduced numbers from the ground level debris, which also gave rise to *Ozineus* sp., belonging to the tribe Acanthocinini. The diminutive *Ozineus* sp. (5 - 8 mm), represented by a single individual during the dry season, emerged exclusively from *E. coriacea*, and has no prior host record. Emergences peaked about 6 months after the cut.

The *E. coriacea* rainy season canopy snacks were very densely colonized, primarily by relatively small cerambycids (mean length < 8 mm). *Ozineus* sp. emerged from the canopy snacks as well as from the ground level debris. *Palame anceps* emerged in its greatest abundance during the rainy season, and peaked about 4.5 months after the cut. *Palame crassimana* (unicolor form, see Chapter 5), represented by only two individuals during the dry season, emerged almost exclusively from rainy season canopy snacks. Emergences peaked after about 6 months. *Palame mimetica*, associated primarily with *Lecythis poiteaui* during the dry season, made a partial host switch to *E. coriacea* during the rainy season (see Chapter 2). In addition, larger species *Xylergates elaineae* and *Xenofrea* sp. 662, both of which were present in relatively small numbers during the dry season, also emerged from canopy snacks during the rainy season.

Most cerambycids associated with *E. coriacea* seem to show a high degree of host fidelity. *Oreodera simplex*, *Ozineus* sp., and *Xenofrea* sp. 662 have no additional host records, while both *Palame anceps* and *Palame crassimana* (unicolor form) emerged exclusively from *E. coriacea* in this study. Predisposing factors for a narrow host range are discussed in Chapter 4.

Lecythis poiteaui

Dry season branches were severed from *L. poiteaui* on Sept. 22 - 24, 1995. Emergences are shown in Figure 5. The branch sections left at ground level gave rise predominately

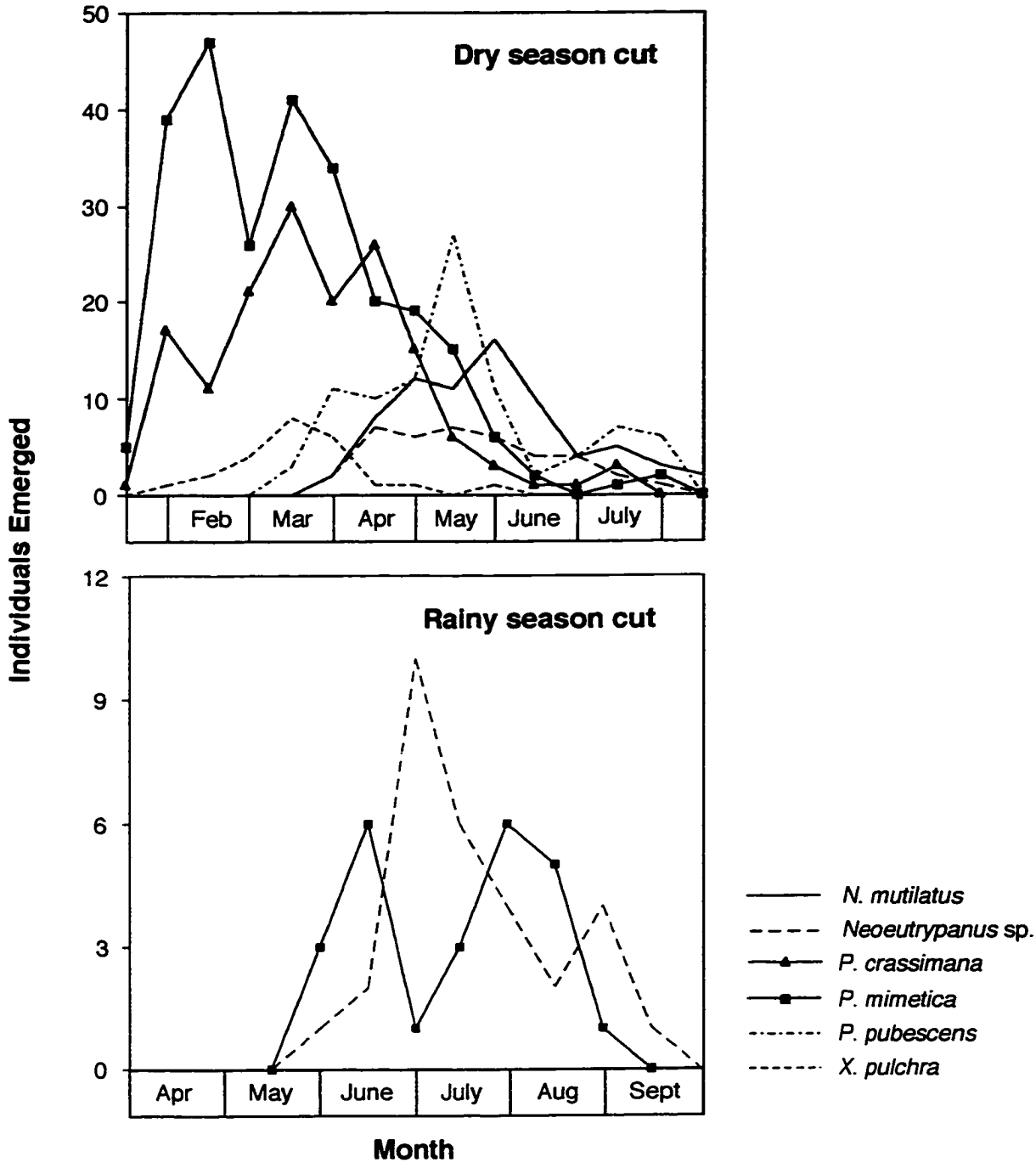


Figure 5. Cerambycids emerged from *Lecythis poiteaui* at Les Eaux Claires.

to large numbers of *Palame crassimana* (bicolor form) and *Palame mimetica* (4 - 11 mm). *Palame mimetica* was associated primarily with *L. poiteaui* in this study, although it has many other documented host species belonging to Lecythidaceae. Emergences for both of these species peaked 4 - 5.5 months after the cut. Although there were occasional emergences from ground level snacks, the vast majority of individuals were reared from ground level debris in the big cage. *Xylergatina pulchra* also peaked about 5.5 months after the cut. It emerged only from *L. poiteaui* in this study, although there are additional host records from *Couratari guianensis*, *Eschweilera* spp., and *Lecythis* spp. This is the largest Lecythidaceae specialist (14 - 18.5 mm), with a fairly long ovipositor, and it may preferentially attack trunks rather than branches.

A second group of relatively large cerambycid species emerged from *Lecythis poiteaui*, but emergences peaked about two months later, 7.5 months after the cut. *Periboeum pubescens* (7 - 15 mm), belonging to the tribe Elaphidionini in the subfamily Cerambycinae, is one of the most ubiquitous Lecythidaceae specialists. In this study it emerged primarily from *L. poiteaui* ground level branches, as did *Neoeutrypanus mutilatus* (7 - 10.5 mm), belonging to the tribe Acanthocinini. *Neoeutrypanus mutilatus*, which appears to be almost exclusively female, has few additional host records: *Couratari guianensis*, *Eschweilera congestiflora*, and *Lecythis holcogyne*. *Neoeutrypanus* sp. 915 (8 - 12 mm), associated primarily with canopy snacks, emerged only from *L. poiteaui* and has no prior host record.

Rainy season branches were severed from *L. poiteaui* on Jan. 5 - 9, 1996. Emergences are shown in Figure 5. Emergences from *Lecythis poiteaui* were drastically reduced during the rainy season. They were exclusively from canopy snacks, and the only cerambycid species represented by more than 10 individuals were *Palame mimetica* and *Neoeutrypanus* sp. 915. This reduction was probably due in part to the fact that two of

the four thick canopy snacks resprouted, and branch sections that resprouted generally produced few beetles (see branches marked with an asterisk in Appendix II). This alone was not sufficient to explain the perceived pattern, and I propose that a seasonal change in host chemistry may have caused cerambycids to shun *L. poiteaui* during the rainy season (see Chapter 3).

Corythophora amapaensis

Dry season branches were severed from *C. amapaensis* on Sept. 20 - 22, 1995. Emergences are shown in Figure 6. *Palame crassimana* (bicolor form) was the only cerambycid species that *C. amapaensis* produced in fair abundance. Individuals emerged from both canopy snacks and ground level debris in the big cage. The development time for the adults that emerged from *C. amapaensis* was about the same as for those that emerged from *Lecythis poiteaui*, and they appeared to be robust (see Chapter 4). The implication is that *C. amapaensis* is not inherently unsuitable as a host, but may be difficult for the cerambycids to locate. The only other cerambycid species represented by (exactly) ten individuals was *Neopalame* sp. 851 (6 - 8.5 mm), belonging to the tribe Acanthocinini. *Neopalame* sp. 851 has one additional host record, *Eschweilera parviflora.*

Couratari stellata

Dry season branches were severed from *C. stellata* on Sept. 17-18, 1995. Emergences are shown in Figure 7. The only cerambycid species represented by more than ten individuals was *Neobaryssinus marianae* (6.5 - 12 mm), belonging to the tribe Acanthocinini. The only additional host records for this cerambycid are *Couratari guianensis* and *C. calycina.* This suggests that *N. marianae* may genuinely be restricted to the genus *Couratari,* and the association is strong enough that adult cerambycids meet, mate, and reproduce even on a host apparently avoided by other Lecythidaceae

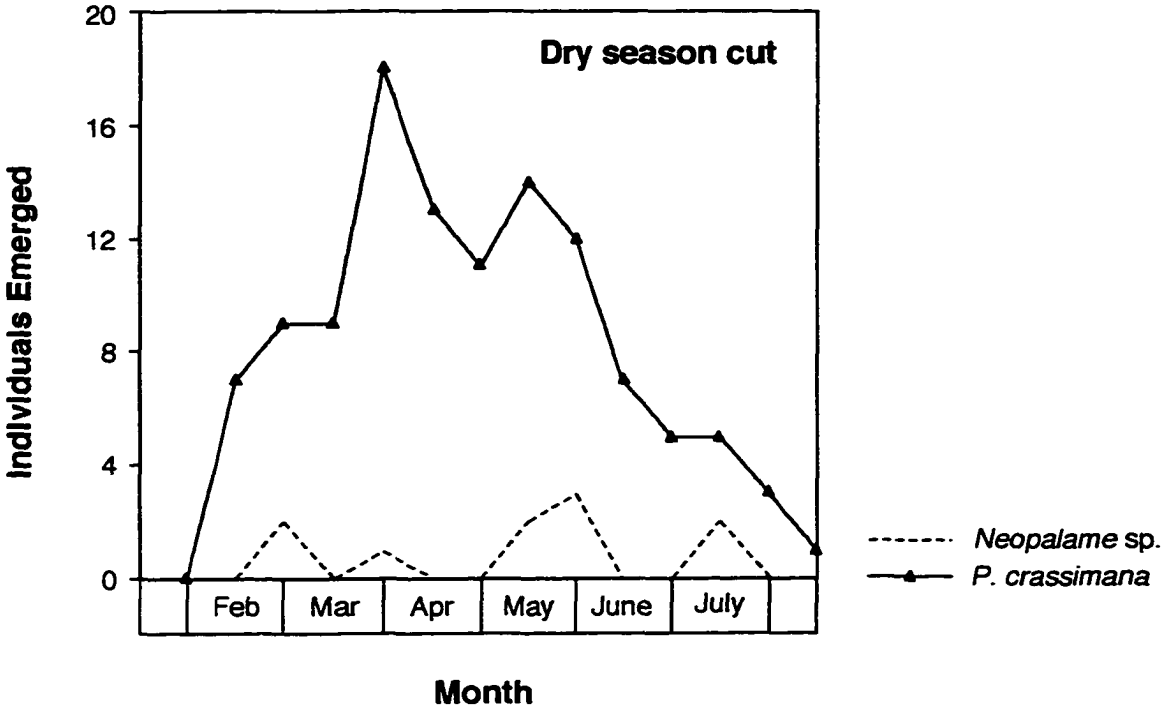


Figure 6. Cerambycids emerged from *Corythophora amapaensis* at Les Eaux Claires.

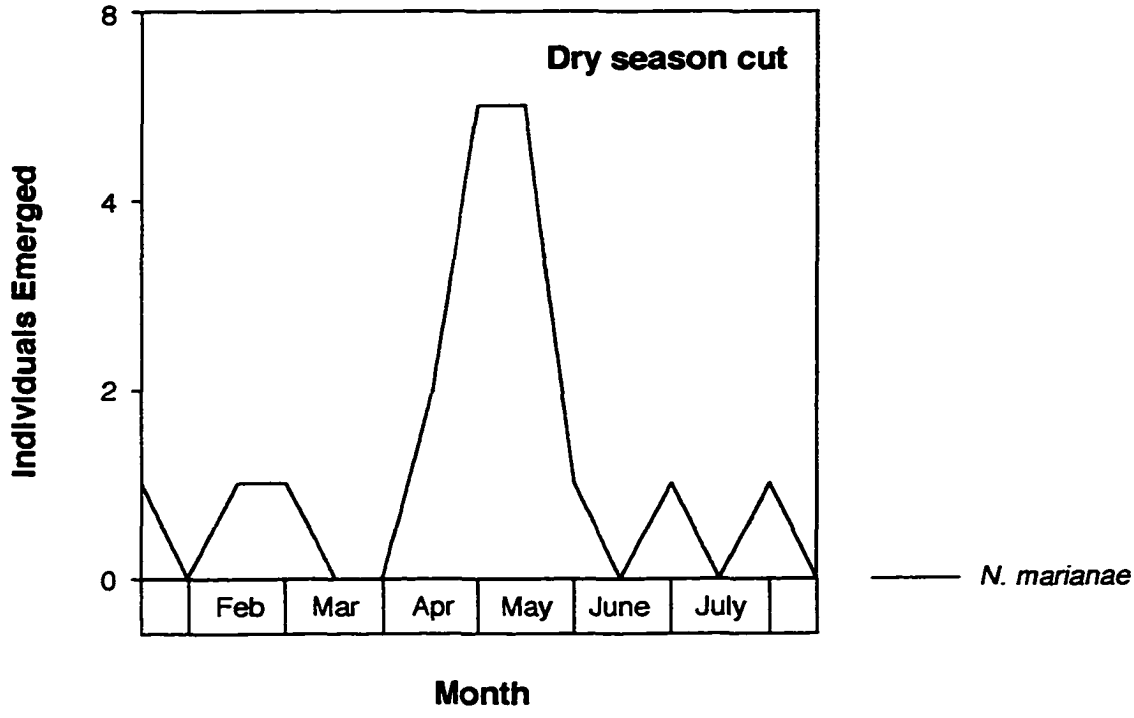


Figure 7. Cerambycids emerged from *Couratari stellata* at Les Eaux Claires.

specialists. I propose that the foul odor produced by *C. stellata*, and to a lesser degree by *Gustavia hexapetala*, may be a deterrent to cerambycids seeking oviposition sites (see Chapter 3).

Gustavia hexapetala

Dry season branches were severed from *G. hexapetala* on Sept. 18, 1995. Emergences are shown in Figure 8. *Gustavia hexapetala* actually produced quite a few different cerambycid species, but generally very few individuals per species. *Palame crassimana* (bicolor form) was the only family level Lecythidaceae specialist represented by more than ten individuals. Emergences peaked about a month later than those from the alternate host species, and the adults were quite small (see Chapter 4), implying that *G. hexapetala* may not be an optimal host for *P. crassimana.*

The other two species represented by more than ten individuals had not previously been reared from Lecythidaceae. *Taurolema bellatrix* (4.5 - 5.5 mm), belonging to the tribe Anisocerini, was one of the few cerambycids reared exclusively from canopy snacks. This tiny beetle, distinguished by the presence of tufts of pubescence on the antennae, has no prior host record and is not closely related to any other Lecythidaceae specialist. *Eupromerella clavator* (6.5 - 9 mm), belonging to the tribe Acanthoderini, emerged exclusively from ground level snacks and debris in the big cage. Its only prior host record is from *Xylopia pulcherrima* (Annonaceae), and it has therefore been classified a generalist even though it was regularly associated *G. hexapetala* in this study. It should be noted that although there were relatively few emergences from the *G. hexapetala* dry season branch sections, they had not fully tapered off when the branches were discarded in mid-August.

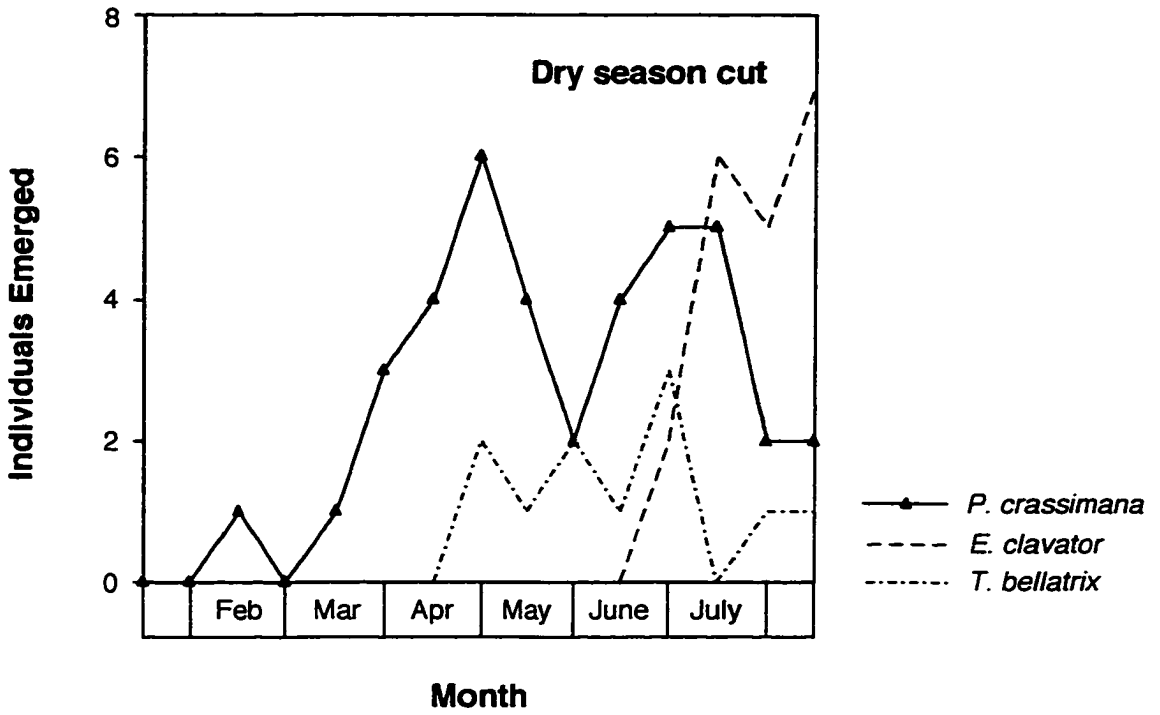


Figure 8. Cerambycids emerged from *Gustavia hexapetala* at Les Eaux Claires.

CHAPTER 2

The Private Lives of *Palame:* Host Utilization by Sympatric Species of Neotropical Wood-borers (Coleoptera, Cerambycidae, Lamiinae, Acanthocinini)

SUMMARY

Estimates of the total number of arthropod species in existence are based, in part, upon assumptions about both the host specificity of tropical insects and their restriction to the forest canopy. It has been difficult to evaluate these estimates because of the paucity of available data. A newly discovered association between wood-boring longicorn beetles (Cerambycidae) and their host plants in the Brazil nut family (Lecythidaceae) inspired a year-long rearing project in the lowland Neotropical rain forest of central French Guiana. Branches severed from five different species of Lecythidaceae yielded 1,813 cerambycids belonging to 37 species. Three cerambycid species belonging to the genus *Palame* Bates (*Palame anceps* (Bates), *P. crassimana* Bates, and *P. mimetica* Monné) accounted for almost half of the individuals reared. Each demonstrated a very different pattern of host fidelity. *Palame crassimana* emerged from four of the five potential host trees, *Palame anceps* emerged exclusively from a single host species, and *Palame mimetica* made a partial host switch during the rainy season. Although *Palame* spp. emerged from both ground level and canopy branches, they made a seasonal shift in stratum: they reproduced at both levels during the dry season, but exclusively at canopy level during the rainy season.

INTRODUCTION

Estimates of the number of arthropod species

The global insect fauna comprises close to one million described species (see references in Hammond, 1992). Various authors have proposed that if undescribed species could also be enumerated, there would prove to be between 2.5 and 10 million extant insects (Gaston, 1991a). A great controversy was instigated fifteen years ago with the publication of a brief paper speculating, based on the results of an experiment in which the canopies of 19 individuals of the tropical tree *Luehea seemanii* were fogged with insecticide, that there might actually be more than 30 million species of arthropods (Erwin, 1982).

Erwin sorted the beetles into morphospecies, and placed them in guilds (herbivore, predator, fungivore and scavenger). Faced with a lack of sufficient data on the degree of host specificity within the various guilds, he estimated percentages, and used them to calculate the number of beetles obligately dependent upon *Luehea seemanii.* He multiplied this figure by 50,000 tropical tree species, estimated that beetles constitute 40% of the total canopy fauna, and surmised that the ground fauna would contribute half as many species as the canopy. Subsequent studies convinced Erwin that he had substantially underestimated the potential number of insect species (Erwin, 1988). Other authors (Basset, 1992; Basset et al., 1996; Gaston, 1991a, 1991b; Hodkinson & Casson, 1991) maintain that his figures are seriously inflated because the premises on which they depend (the bulk of tropical insects being undescribed, often restricted to the canopy, and having a high degree of host specificity) are flawed.

The debate has continued to reverberate, with the participants (Erwin, 1991; Gaston, 1991a; May, 1988; Stork, 1988) justifying favored methods of extrapolation from limited

data sets. There are profound implications for conservation, because these same figures are used to generate hypotheses about current and projected rates of extinction as tropical forests are destroyed (Stork, 1997, and references therein). One of the points on which these authors agree is the need for empirical research, and several point out that the assumptions made about the host specificity of tropical insects compose the weakest parts of Erwin's argument. Subsequent analyses of the faunal overlaps of conspecific versus unrelated trees have suggested that Erwin may have overestimated the host fidelity of tropical insects (Kitchling et al., 1997; Mawdsley & Stork, 1997). These studies also analyzed the chaotic profusion of insects harvested after the release of insecticides into the forest canopy. Fogging experiments do not adequately sample concealed feeders including wood-borers, and cannot reveal life history attributes of the insects that are efficiently sampled.

Background: Palame Bates

Three cerambycid species belonging to the genus *Palame* Bates (*Palame anceps* (Bates), *P. crassimana* Bates, and *P. mimetica* Monné) accounted for almost half of the individual cerambycids reared at Les Eaux Claires. In French Guiana, these three species are apparently associated exclusively with trees belonging to the Brazil nut family (Tavakilian, 1993; Tavakilian et al., 1997). Like many of the beetles associated with Lecythidaceae, they are cryptic, crepuscular insects belonging to the huge tribe Acanthocinini (subfamily Lamiinae). Although *Palame* spp. can be distinguished macroscopically, their morphology is variable, and they are frequently mixed in museum collections (Tavakilian, pers. comm.).

The genus is currently delimited with five species. *Palame anceps*, *P. crassimana*, and *P. mimetica* are well documented in both Brazil and French Guiana (Monné & Giesbert, 1994; Tavakilian et al., 1997). *Palame crassimana*, which includes at least three distinct

morphological forms (Tavakilian, pers. comm., see Chapter 5), also occurs in Guyana and Peru, and *P. mimetica* also occurs in Venezuela (Martins & Monné, 1972; Monné, 1985). The genus includes two additional species, *Palame aeruginosa* and *P. vitticole*, currently known only from particular regions of Brazil (Monné, 1985).

RESULTS FROM THE REARING EXPERIMENTS

The branch segments ($N = 406$) prepared during these experiments gave rise to a total of 1813 individual cerambycid beetles, belonging to 37 species in at least 26 genera (Table 1). Three species belonging to *Palame* Bates were overwhelmingly well-represented, accounting for 48% of the individuals reared. *Palame* spp. demonstrated very different patterns of fidelity in host plant utilization, ranging from consistently restricted to widespread within Lecythidaceae (Table 2). They colonized dead branches of various diameters although, predictably, thick branches gave rise to more individuals (Table 3). Each species was present throughout the year, although there were different peaks in abundance (Table 3). (Note that in subsequent discussions of seasonality, "dry season" and "rainy season" refer to the time that the branches were cut, although most emergences from dry season branches occurred during the rainy season, and some of the emergences from rainy season branches occurred during the subsequent dry season). *Palame* spp. were present at both canopy and ground level, although there was a seasonal shift in stratum (Figure 9).

Statistical tests (contingency tables analyzed by *G*-test, using the program JMP SAS) probed for non-random associations between beetle and branch. They were run for the number of individuals reared in the following complexes: *Palame* species x 1) host plant, 2) branch diameter, 3) season, and 4) stratum. The first series of tests, which included data from both snacks and big cages, were all significant at $P \leq .0001$. A second series

Table 1

Cerambycid species reared from Lecythidaceae at Les Eaux Claires, French Guiana

Cerambycid species	TOTAL	Host Plant					H/S	Diameter		Season		Stratum		S/P
	N = 1813	CA	CS	EC	GH	LP		T	S	D	R	G	C	
Carterica sp.*	9	–	–	–	9	–	S/SP	1	4	8	1	9	–	ISD
Carterica sp.*	2	–	–	–	2	–	S/SP	–	–	1	1	2	–	ISD
Ceragenia leprieuri Buquet in Guérin- Méneville*	1	–	–	–	–	1	G	–	–	1	–	1	–	ISD
Colobothea bisignata Bates*	4	–	2	–	2	–	S/FAM	3	–	4	–	1	3	ISD
Eburodacrys sexmaculata (Olivier)*	1	–	–	–	–	1	G	1	–	1	–	–	1	ISD
Eburodacrys sp. 1282*	3	–	–	3	–	–	G	–	–	3	–	3	–	ISD
Eupromerella clavator (Fabricius)*	20	–	–	–	20	–	G	13	2	20	–	20	–	G
Hesychotypa jaspidea (Bates)*	6	–	5	–	–	1	G	–	–	6	–	6	–	ISD
Hesychotypa liturata (Bates)*	2	–	–	–	2	–	G	–	–	2	–	2	–	ISD
Mecometopus triangularis (Laporte & Gory)*	15	2	–	–	–	13	G	–	–	15	–	15	–	G
Nealcidion badium Monné & Delfino*	1	–	–	–	1	–	ISD	–	–	1	–	1	–	ISD
Neobaryssinus marianae (Martins & Monné)	18	–	18	–	–	–	S/GEN	13	1	18	–	5	13	G/C
Neoeutrypanus mutilatus (Germar)	93	9	2	2	–	80	S/FAM	7	20	84	9	67	26	G/C
Neoeutrypanus nobilis (Bates)*	5	–	–	5	–	–	ISD	5	–	–	5	–	5	ISD
Neoeutrypanus sp. 915*	69	–	–	–	–	69	S/SP	45	22	39	30	2	67	C
Neopalame sp. 851	10	10	–	–	–	–	S/FAM	6	–	10	–	4	6	G/C
Nesozineus sp.*	3	–	–	–	3	–	S/SP	3	–	3	–	1	2	ISD
Oedopeza apicale (Gilmour)*	9	–	1	–	8	–	G	3	–	9	–	9	–	ISD
Oedopeza leucostigma Bates	232	–	2	229	–	1	S/FAM	78	6	225	7	224	8	G
Oreodera melzeri Monné & Fragoso*	1	–	–	–	–	1	G	–	–	1	–	1	–	ISD
Oreodera simplex Bates*	158	–	–	158	–	–	S/SP	35	12	140	18	157	1	G
Ozineus sp*.	66	–	–	66	–	–	S/SP	3	20	1	65	43	23	G/C
***Palame anceps* (Bates)**	**160**	**–**	**–**	**160**	**–**	**–**	S/GEN	**101**	**10**	**60**	**100**	**50**	**110**	G/C
***Palame crassimana* Bates**	**402**	**114**	**–**	**93**	**39**	**156**	S/FAM	**134**	**67**	**333**	**69**	**208**	**194**	G/C
***Palame mimetica* Monné**	**316**	**3**	**–**	**29**	**2**	**282**	S/FAM	**88**	**20**	**262**	**54**	**217**	**99**	G/C
Periboeum pubescens (Olivier)	102	2	–	–	7	93	S/FAM	18	6	102	–	91	11	G/C
Plistonax albolinitus (Bates)*	1	1	–	–	–	–	ISD	–	–	–	1	1	–	ISD
Stratone rufotestacea Thompson	1	1	–	–	–	–	S/FAM	–	–	–	1	1	–	ISD
Symperasmus thoracicus (White)*	1	–	–	–	–	1	G	–	–	1	–	1	–	ISD
Taurolema bellatrix Thomson*	11	–	–	–	11	–	S/SP	7	4	11	–	–	11	C

Table 1 contd.

Cerambycid species	TOTAL	Host Plant					H/S	Diameter		Season		Stratum		S/P
	N = 1813	CA	CS	EC	GH	LP		T	S	D	R	G	C	
Xenofrea lineatipennis Zajciw*	3	–	–	–	–	3	S/SP	1	2	2	1	–	3	ISD
Xenofrea sp. 662*	16	–	–	16	–	–	S/SP	12	–	4	12	4	12	G/C
Xenofrea sp. 714*	2	–	–	2	–	–	ISD	–	2	–	2	–	2	ISD
Xylergates elaineae Gilmour	35	–	–	33	–	2	S/FAM	26	–	17	18	12	23	G/C
Xylergatina pulchra (Lane)	24	–	–	–	–	24	S/FAM	5	–	24	–	24	–	G
Genus sp. 229*	10	–	1	–	7	2	S/FAM	6	4	8	2	–	10	C
Genus sp.*	1	–	–	1	–	–	ISD	–	1	–	1	–	1	ISD

Cerambycid species are listed in alphabetical order, and those not previously reared from Lecythidaceae are marked with an asterisk. TOTAL: total number of individuals reared. Host Plant: individuals reared from each of the five host trees (CA = *Corythophora amapaensis,* CS = *Couratari stellata,* EC = *Eschweilera coriacea,* GH = *Gustavia hexapetala,* and LP = *Lecythis poiteaui*). H/S: Beetle species represented by at least two host records are classified according to their host specificity as generalists (G), or specialists associated with a single plant species (S/SP), genus (S/GEN) or family (S/FAM). There is insufficient data (ISD) to classify beetles represented by a single host record. A beetle is considered a specialist at the designated level when 90% of the host records are in accord. Each snack was considered a separate host, but all branch segments in a big cage were considered a single host because it was impossible to precisely trace the source of an emerged beetle. Data from Tavakilian et al., 1997 were included in this classification. Diameter: individuals reared from thick (T) or skinny (S) branches. Note that only emergences from snacks are included in the diameter columns, which therefore do not equal the total number of individuals reared. Season: individuals reared from branches cut during the dry (D) or rainy (R) season. Stratum: individuals reared from branches left at ground (G) or canopy (C) stratum. S/P: classification of stratum preference (G = ground, C = canopy, G/C = both strata, ISD = insufficient data). I hypothesize a stratum preference for beetles represented by at least 10 individuals from at least two hosts (determined as in the classification of specificity), when at least 95% of the individuals emerged from branches at a particular level.

Table 2

***Palame* spp. reared from five Lecythidaceae tree species**

Beetle spp.	Host Tree	TOTAL	DRY SEASON		RAINY SEASON	
			Ground	Canopy	Ground	Canopy
	C. amapaensis	0	0	0	0	—
Palame	*C. stellata*	0	0	0	0	—
anceps	*E. coriacea*	160 (111)	50 (1)	10 (10)	0	100 (100)
N = 160 (111)	*G. hexapetala*	0	0	0	0	—
	L. poiteaui	0	0	0	0	0
	TOTAL	160 (111)	50 (1)	10 (10)	0	100 (100)
	C. amapaensis	114 (64)	51 (1)	63 (63)	0	—
Palame	*C. stellata*	0	0	0	0	—
crassimana	*E. coriacea*	93 (82)	11 (0)	14 (14)	0	68 (68)
N = 402 (201)	*G. hexapetala*	39 (39)	0	39 (39)	0	—
	L. poiteaui	156 (16)	146 (6)	9 (9)	0	1 (1)
	TOTAL	402 (201)	208 (7)	125 (125)	0	69 (69)
	C. amapaensis	3 (2)	1 (0)	2 (2)	0	—
Palame	*C. stellata*	0	0	0	0	—
mimetica	*E. coriacea*	29 (29)	0	0	0	29 (29)
N = 316 (108)	*G. hexapetala*	2 (2)	0	2 (2)	0	—
	L. poiteaui	282 (75)	216 (9)	41 (41)	0	25 (25)
	TOTAL	316 (108)	217 (9)	45 (45)	0	54 (54)

TOTAL: the total number of emergences from each host plant. DRY SEASON: the number of emergences from branches cut in the dry season, left at ground or canopy stratum. RAINY SEASON: the number of emergences from branches cut in the rainy season, left at ground or canopy stratum. The number of emergences from all pertinent branches is followed, in parentheses, by the number of emergences from snacks only. — = No branches were prepared for this portion of the experiment.

Table 3

***Palame* spp. reared from various Lecythidaceae branches**

		DIAMETER		SEASON		STRATUM	
Beetle spp.	**TOTAL**	**Thick**	**Thin**	**Dry**	**Rainy**	**Ground**	**Canopy**
P. anceps	160 (111)	101 (101)	10 (10)	60 (11)	100 (100)	50 (1)	110 (110)
P. crassimana	402 (201)	134 (134)	67 (67)	333 (132)	69 (69)	208 (7)	194 (194)
P. mimetica	316 (108)	88 (88)	20 (20)	262 (54)	54 (54)	217 (9)	99 (99)
TOTAL	878 (420)	323 (323)	97 (97)	655 (197)	223 (223)	475 (17)	403 (403)

TOTAL: the total number of individuals reared. DIAMETER: the number of emergences from thick branches or thin branches. SEASON: the number of emergences from branches cut during the dry season or the rainy season. STRATUM: the number of emergences from branches at ground stratum or canopy stratum. The number of emergences from all pertinent branches is followed, in parentheses, by the number of emergences from snacks only. Note that in both diameter columns, the rainy season column, and the canopy stratum column, all emergences are from snacks.

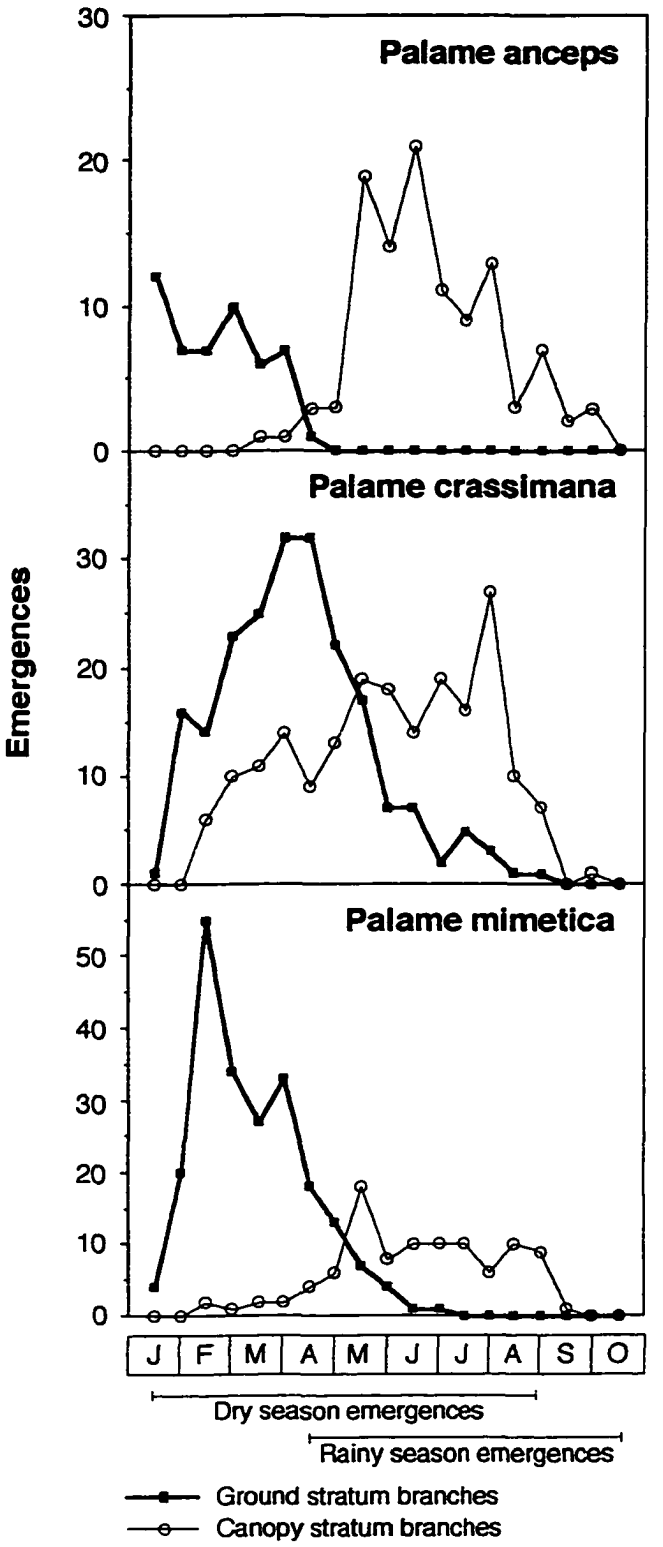


Figure 9. Emergences from ground and canopy stratum branches for three *Palame* species. The dry season branches were collected in January, and the rainy season branches were collected in April. During the dry season, *Palame* spp. reproduced at both forest strata,but during the rainy season they reproduced only at canopy stratum.

of tests was run using data from snacks only, because protocol modifications had resulted in the collection of unequal numbers of branch segments. These tests generated a less significant association ($P = .0164$) only for *Palame* species x stratum. I believe this simply reflects the paucity of individuals associated with ground level snacks (see "Ground stratum" column, Table 3). Although certain cerambycid species were as well represented in the snacks as in the debris, the vast majority of *Palame* spp. associated with ground level branches emerged from debris in the big cages.

Palame anceps (Bates), ($N = 160$, Table 2) was associated exclusively with *Eschweilera coriacea*. The thick snacks out-produced the thin snacks ten to one (Table 3), but this reflects, at least in part, the difference in available branch volume. These beetles were present throughout the year, although there was a rainy season spike (Figure 9). *Palame anceps* was associated with both forest strata, but 83% of the emergences from branches cut during the dry season were from those left at ground level. On the contrary, *P. anceps* emerged solely from canopy level snacks prepared during the rainy season (Table 2). The ground level snacks cut during the rainy season were completely devoid of beetles, and even the debris gave rise to a diminished and impoverished fauna that did not include *Palame* spp.

Palame crassimana Bates, ($N = 402$, Table 2) proved to be the only cerambycid species in this study that arose in substantial numbers from most Lecythidaceae taxa investigated (*Couratari stellata* was the lone exception). The imbalance in emergences from thick and thin snacks was less accentuated for *P. crassimana* (two to one) than for *P. anceps* (ten to one, Table 3), but this was due in part to the presence of a single thin snack, somewhat thicker than average, which was actually quite densely colonized. Like *P. anceps*, *P. crassimana* was present throughout the year, although in this case 83% of the individuals arose from dry season branches (Table 3). During the rainy season *Palame* spp., as

mentioned, reproduced exclusively at canopy level. *Gustavia hexapetala* and *Corythophora amapaenesis* were eliminated from the canopy experiment at the time of the rainy season cut, and therefore *P. crassimana* was only associated with these species during the dry season (Table 2). Total emergences from canopy and ground stratum branches were almost equally divided (Table 3), but different patterns applied for the various host plants (Table 2). Although 94% of the individuals associated with *Lecythis poiteaui* emerged from ground level branches cut during the dry season, 73% of those associated with *Eschweilera coriacea* emerged from rainy season canopy snacks. All of the individuals reared from *G. hexapetala*, and 56% of the individuals reared from *C. amapaensis*, emerged from dry season canopy snacks.

It should be noted here that there are actually several distinct morphological forms that are currently treated as *Palame crassimana* Bates. Two of these forms (bicolor and unicolor) were reared during the described experiments. Although we presently lack sufficient data to describe these forms as separate species (see Chapter 5), in this locality they are behaving as such. They are predominately reproducing at different times of the year and show different patterns of host association (Table 4). Should additional data support their delimitation as separate species, this would affect our interpretation of *P. crassimana* phenology. The bicolor form ($N = 322$) reproduced almost exclusively during the dry season, and the unicolor form ($N = 68$) almost exclusively during the rainy season. It would not, however, significantly alter our perception of *P. crassimana* (bicolor form) as the "least picky" Lecythidaceae specialist. The bicolor form did emerge from four potential hosts, although *E. coriacea* produced the fewest individuals, while the unicolor form emerged exclusively from *E. coriacea*.

Palame mimetica Monné ($N = 316$, Table 2) made a partial seasonal switch in host plant utilization. The vast majority of individuals that emerged from dry season branches

Table 4

Two forms of *Palame crassimana* reared from Lecythidaceae

		Season		Host Plant				
Morphological forms	**TOTAL**	D	R	CA	CS	EC	GH	LP
Palame crassimana (bicolor)	322	321	1	109	0	22	37	154
Palame crassimana (unicolor)	68	2	66	0	0	68	0	0

The number of emergences are listed for the *Palame crassimana* (bicolor form), and *Palame crassimana* (unicolor form). TOTAL: the total number of individuals reared. Season: the number of emergences from branches cut during the dry season or the rainy season. Host Plant: the number of emergences from each of the five potential host trees (CA = *Corythophora amapaensis*, CS = *Couratari stellata*, EC = *Eschweilera coriacea*, GH = *Gustavia hexapetala*, and LP = *Lecythis poiteaui*).

(98%) were associated with *Lecythis poiteaui.* On the contrary, 54% of the individuals that emerged from rainy season branches were associated with *Eschweilera coriacea* (which did not yield a single individual during the dry season). Once again, emergences from thick branches outnumbered those from thin branches (Table 3), at an intermediate ratio (roughly four to one). *Palame mimetica* was present throughout the year, although, like *P. crassimana,* 83% of the emergences were from dry season branches (Table 3). Like other *Palame* spp., *P. mimetica* made a seasonal shift in stratum: 83% of dry season emergences were from ground level branches, while rainy season emergences were solely from canopy snacks (Table 2).

DISCUSSION

Host Affinities of Palame spp.

In this study, *Palame anceps* ($N = 160$) was associated exclusively with *Eschweilera coriacea, P. crassimana* ($N = 402$) was associated with four of the five Lecythidaceae taxa investigated, and *P. mimetica* ($N = 316$) was primarily associated with *Lecythis poiteaui* during the dry season, but made a seasonal change in host affiliation (Table 2). It seems reasonable that the beetle species with the most restricted host range was the least abundant, while that with the widest host range was the most abundant. I believe that variability in host chemistry is most likely to account for the noted distribution patterns. Although field bioassays with Lecythidaceae wood extracts, partitions, and partially purified compounds prepared prior to the field season were not informative, I would like to propose some hypotheses.

Palame anceps was not the only cerambycid in this study that emerged solely from *Eschweilera coriacea.* Of the five tree species investigated in this study, *E. coriacea* gave rise to a complement of cerambycids showing the greatest host fidelity (Table 1;

also see Chapter 4). Although the debris in the big cages was in many cases more productive than the ground level snacks, the two cerambycid species that accounted for the majority of dry season emergences from the *E. coriacea* big cages *(Oedopeza leucostigma* and *Oreodera simplex,* Figure 4) were also quite well represented in the dry season ground level snacks (see Appendix II). *Eschweilera coriacea* was also the only tree species that consistently retained some reproductive activity in ground level branches cut during the rainy season (see Appendix II). Wood extracts and partitions analyzed by TLC (thin layer chromatography) suggest that *E. coriacea* is exceptionally rich in saponins, a class of bitter-tasting, toxic compounds prevalent in Lecythidaceae. I hypothesize that there may be a correlation between host plant toxicity and the degree of specialization demonstrated by xylophagous associates. Crude extracts derived from the wood samples collected from each tree in this study have been screened in a series of anti-microbial bioassays (see Chapter 4), and preliminary data indicate that *E. coriacea* is unusually toxic.

Four of the five Lecythidaceae taxa investigated gave rise to *Palame crassimana.* Although clearly a Lecythidaceae specialist, *P. crassimana* was the only cerambycid reared in the study that was not primarily associated with a single host species (Table 1). Of the five Lecythidaceae tree species, two *(Couratari stellata* and *Gustavia hexapetala)* have foetid odors. *Gustavia hexapetala,* somewhat less offensive, gave rise to numerous species of cerambycids but few individuals (Table 1). With the exception of *P. crassimana,* which appears to be the "least picky" of the Lecythidaceae specialists, the cerambycids most regularly associated with *G. hexapetala* were not reared from other Lecythidaceae species (see Chapter 1). *Couratari stellata,* with such a strong odor that individual trees were typically smelled before they were seen, gave rise to an even more impoverished complement of cerambycids (Table 1). Although *Palame* spp. accounted for 48% of the beetles reared during this project, not a single individual was reared from

C. stellata (Table 2). The working hypothesis is that the putrid-smelling compounds act as deterrents to Lecythidaceae specialists seeking oviposition sites. Additional support for this concept is derived from the Sinnamary rearing project, where a third malodorous Lecythidaceae species, *Gustavia augusta*, gave rise to only a very few atypical cerambycids (Tavakilian, unpubl. data). The distinctive 'bouquet' apparently comprises a combination of nitrogen and sulfur compounds, some of which are described in Chapter 3.

Palame mimetica, associated almost exclusively with *Lecythis poiteaui* during the dry season, made a partial host switch to *Eschweilera coriacea* during the rainy season. Not only did 54% of the individuals reared from rainy season branches emerge from *E. coriacea* (Table 2), but individuals were associated with three of the four sample trees (see Appendix II). *Lecythis poiteaui* was the only tree species in this study that was in bloom at the time of the rainy season cut (see Appendix I). The flowers are fairly typical of their genus in morphology: large and showy, with the androecium expanded on one side to form an open hood bearing many staminodia. They are, however, atypical in their adaptations for pollination. While many Lecythidaceae bear diurnal flowers pollinated by bees (Mori & Boeke, 1987), *L. poiteaui* anthesis is nocturnal, and the bat-pollinated flowers have the very pungent, characteristically musky odor frequently associated with this syndrome. *Palame mimetica* may simply be making a seasonal rejection of a favored host plant that no longer smells right.

Stratum Affinities of Palame spp.

Palame spp. emerged from both ground and canopy level branches cut during the dry season, and were particularly well represented at ground level. All three species emerged exclusively from canopy level snacks cut during the rainy season (Table 2). I originally believed that canopy level branches would be inherently less hospitable due to the

increased exposure to light, a greater chance of desiccation, and the reduced stability of dead branches dangling in the canopy (which, given the windier microclimate, might be prone to plummet to the ground carrying a fragile load of easily bruised larvae). Contrary to my expectations, canopy branches were well-colonized throughout the year (with the exception of those girdled branches that resprouted and yielded to vastly diminished numbers of cerambycids, see Appendix II). Canopy level was incontestably the stratum of choice during the rainy season (Figure 1), and *Palame* spp. (as well as other cerambycid species) proved quite capable of exploiting this somewhat ephemeral, but certainly renewable, resource.

The distributions of many insects are influenced by available moisture. During the extended dry season in a seasonal tropical forest, insects have proved to be more abundant and diverse in moister habitats (Janzen & Schoener, 1967). On the other hand, insects in seasonally inundated forests may need to escape the influx of water. Options for terrestrial arthropods are proposed to include 1) survival of the immersion (by egg or dormant adult) in the soil or under loose bark, 2) migration to adjacent *terra firme,* 3) wholesale death followed by recolonization, or 4) migration up the trunks or into the canopy (Adis, 1984; Irmler, 1979). The majority of beetle species investigated by Irmler (1979) did migrate to a higher forest stratum. Adis (1984) found that numerous vertical migrants made their move prior to the actual flood, apparently reacting to the increasing humidity. This study suggests that some insects living in more uniformly moist, non-inundated forests also make a seasonal migration to the treetops. Several possible explanations that may contribute to this phenomenon.

As noted, dry season canopy snacks that resprouted gave rise to very few cerambycids. It is possible that the still living branches failed to provide cues to satisfy female cerambycids seeking oviposition sites, or a persistent vascular flow through the still-

living branches might have been detrimental to larvae. Ground level branches cut during the rainy season remained in an extremely wet environment. Quite a few of these ground level snacks also sprouted new foliage; although the branch segments had no remaining connection to the parent tree, they apparently retained sufficient nutrient reserves and moisture to promote new growth. It was noted that those which did die were particularly prone to fungal attack, not likely to be advantageous for developing larvae. Finally, the atmosphere at ground level might simply be so saturated with water that the volatile molecules that initially attract a cerambycid to a potential host plant fail to circulate efficiently. Whatever the explanation, the capacity to breed even in very small dead branches at canopy level seems to assure reproductive success throughout the year.

Perceptions of host specificity

Erwin formulated his estimates about host-specificity by sorting arthropods into guilds delimited by feeding strategy (herbivore, predator, fungivore and scavenger). He suggested that herbivores would be more likely to become dependent upon specific host plants than predators, for instance, that are typically be opportunistic in their search for food. The classic explanation for the evolution of host specificity proposes that plants produce various secondary compounds to deter herbivores, some of which subsequently evolve the capacity to either detoxify the compounds, or sequester them to be utilized for defense against their own predators (Bennett & Wallsgrove, 1994; Feeny, 1980; Harborne, 1993).

If one accepts a seminal role for host plant chemistry in the development of host specificity, different types of herbivory should also predispose different insects to different degrees of host fidelity (some of the following are reviewed in Basset, 1992). One would predict that concealed feeders like leaf miners, which spend their larval period entirely surrounded by and consuming living plant tissue, would be prone to great

selectivity. Insects that feed upon plant parts harboring high levels of defensive compounds, such as seeds, should be predisposed to selective feeding strategies. Herbivores that macerate living plant tissue should show greater host fidelity than those that suck sugar-rich sap from the vascular tissue of plants. Xylophagous species that spend the larval period surrounded by freshly killed plant tissue (with the cellular contents still somewhat intact) should show greater specificity than those attacking wood in a more advanced state of decay.

Are these predictions well-supported? About 90% of the caterpillars in a Costa Rican deciduous forest seem to feed locally on either a single host plant species or on a restricted group of taxonomically or chemically related hosts (Janzen, 1988). Over half of these caterpillars are leaf-miners, leaf rollers or case-makers, but no distinction was made between the host specificity of concealed versus exposed feeders. The majority (75%) of the coleopteran seed predators at the same site appear to be locally monophagous, but polyphagous over their geographic range (Janzen, 1980; Janzen, 1981). Grasshopper species at La Selva, Costa Rica, range from being monophagous to polyphagous, but those that oviposit into or on the host plant, rather than in the soil, have the most restricted host ranges (Marquis & Braker, 1994). Leaf beetle species belonging to the chrysomelid subfamily Alticinae usually show high specificity, but may nevertheless be found feeding on completely different host plants at the end of the season (Jolivet, 1988). A variety of adult bugs that feed on floral resources including seeds are primarily associated with a single plant species or plant part at any one time, but may attack numerous unrelated hosts throughout the year (Janzen, 1981). Most species of phloem-tapping treehoppers at La Selva are indeed polyphagous (Marquis & Braker, 1994). Scolytids that feed on phloem do appear to have much narrower host ranges than those which feed on xylem (Mattson et al., 1988). Generalizations about feeding strategy

seem logical, but in the case of *Palame*, three species with similar life history attributes and some overlap in host utilization clearly showed different patterns of host fidelity.

Characteristics of host plant taxa, including the toxicity of secondary metabolites, must also be examined. Sphingids, more likely to feed on alkaloid-containing plants, are more narrowly specialized than saturniids, prone to feed on hosts rich in phenolics (Janzen, 1981; Janzen, 1984). The beetles found on a single tree species were investigated in Erwin's study, but, as noted in Basset et al., 1996, there was no way to evaluate whether this tree was in any way typical of its family (Tiliaceae) or of other trees composing tropical forests. Tavakilian's Sinnamary study (1993, 1997) made it quite clear that, although many cerambycids were so rare or poorly known that it was impossible to speculate about a feeding strategy, different plant families gave rise to vastly differently ratios of specialist to generalist cerambycids. Tiliaceae was not well-sampled at Sinnamary, but the family is part of the order Malvales, which gave rise to a cerambycid guild in which generalist species outnumbered specialist species two to one. Lecythidaceae, on the other hand, gave rise to a guild in which specialists outnumbered generalists ten to one. When all data regarding cerambycid host plant associations in French Guiana were pooled, specialists outnumbered generalists by about three to one. Specialists were, however, seldom associated with a single plant species, but were frequently able to locate and reproduce in the wood of related trees (Tavakilian et al., 1997).

Two additional variables that influence our perception of host specificity are sampling location and protocol, which can make a profound impact upon experimental results. *Neoeutrypanus incertus*, routinely associated with Lecythidaceae during the Sinnamary project (Tavakilian et al., 1997), was never encountered during this study. Several species repeatedly associated with particular Lecythidaceae taxa at Les Eaux Claires,

including *Neoeutrypanus* sp. 915, *Ozineus* sp., and *Oreodera simplex*, were never reared at Sinnamary.

These two rearing projects had different objectives and therefore, different protocols. At Sinnamary, the mission was to reveal the identities of the cerambycid species associated with as many tree species as possible. The ensuing cuts were taxonomically diverse, simulating a natural disaster such as a hurricane. Ovipositing cerambycids were able to select their hosts from a broad menu of felled trees representing many different plant families. Although entire trees were cut, it was only possible to cage a small portion of each tree. Lecythidaceae, as sampled in this scenario, gave rise predominately to family specialists, but five of the 15 species associated solely with Lecythidaceae emerged from at least three genera.

At Les Eaux Claires, the objective was to elucidate the associations between a select guild of cerambycids and their host plants in the Brazil nut family. Four or five replicates from five tree species were prepared in the ensuing cuts, which created an unnatural abundance of freshly killed Lecythidaceae. Branches were cut in lieu of entire trees, but a large portion of each branch was caged. The majority of cerambycid species reared from Lecythidaceae, as sampled in this scenario, were not family specialists, although specialist species accounted for the vast majority of individuals reared (Table 1). Those cerambycids that were clearly associated with the Brazil nut family had ample opportunity to select their favored taxon, and *Palame crassimana* was the only Lecythidaceae specialist not primarily associated with a single tree species.

The Sinnamary study (taxonomically diverse cut) presented an approximation of potential host range, while the Les Eaux Claires study (replicates of one species in each of five genera cut) gave an approximation of optimal host range. Non-numerical data from the

Sinnamary project implies that all three *Palame* species are oligophagous: *P. anceps* was associated with *Couratari* as well as *Eschweilera*, *P. crassimana* was associated with three genera, and *P. mimetica* with four genera. Data from Les Eaux Claires implies that *P. anceps* is monophagous, and, had the experiment not been repeated during the rainy season, *P. mimetica* would have appeared predominately monophagous as well. Even given seasonal repetition of the experiment, had the canopy not also been sampled, *Palame* spp. would have appeared to be absent during the rainy season. This confirms the importance of designing experiments that include seasonality and microhabitat as variables, and of analyzing insect-plant interactions at different levels of resolution.

I suspect that monophagy as most strictly defined (one insect species dependent upon a single plant species for survival) is actually a relatively uncommon phenomenon in high diversity tropical forests. At Sinnamary, Lecythidaceae specialists appeared to have broader host ranges because more species were made available but there was little replication. At Les Eaux Claires, more non-specialists oviposited in Lecythidaceae because it was abundantly available. Strict monophagy is likely to be an artifact of sampling protocol: many insects have the capacity to exploit related, if less than optimal hosts, when the need arises.

CHAPTER 3

Do Lecythidaceae Specialists (Coleoptera: Cerambycidae) Shun Foetid Tree Species?

SUMMARY

Characteristic secondary metabolites are currently acknowledged to play a pivotal role in the circumscription of a plant's insect fauna. A newly discovered association between wood-boring cerambycid (longicorn) beetles and their host trees belonging to the Lecythidaceae (Brazil nut family) inspired a year-long rearing project in the lowland Neotropical rain forest of central French Guiana. Branches severed from five different species of Lecythidaceae yielded 1,813 cerambycids belonging to 37 species. Two of the five tree species, *Couratari stellata* and *Gustavia hexapetala*, consistently yielded few cerambycids. Both are characterized by foetid odors. Wood samples collected from the malodorous *C. stellata*, as well as from two well-colonized species, *Lecythis poiteaui* and *Eschweilera coriacea*, have been analyzed for their volatile components using GC-MS. Sulfur compounds accounted for almost 15% of the volatiles detected from *C. stellata*, while they accounted for only 1.87% and 0%, respectively, of the two popular tree species. S-methylmethionine, isolated from a *C. stellata* sample and identified using ESI-MS and NMR, appears to be the major compound contributing to the distinctive foul odor, which I hypothesize is a deterrent to cerambycids seeking oviposition sites.

INTRODUCTION

Secondary metabolites and their role in the circumscription of a plant's insect fauna

Plants manufacture a vast array of chemicals that are not directly involved in the day to day business of trapping solar energy and converting it into the chemical energy that drives plant growth. Without these so-called secondary metabolites, plants would lack many of the characteristic odors, colors, and flavors that differentiate plant taxa (Bennett & Wallsgrove, 1994). Secondary compounds are frequently products of complex and metabolically costly biochemical pathways (Jones & Firn, 1991). Many have diverse roles in the life histories of plants. Some aromas and pigments are instrumental in luring animals to disperse pollen or seeds. Other compounds are primarily defensive in nature: they may absorb potentially mutagenic UV light, deter herbivores, inhibit infection by various pathogens, or inhibit the growth of competing vegetation (Bennett & Wallsgrove, 1994; Fraenkel, 1959; Harborne, 1993).

Plants live and evolve in concert with ever-changing assemblages of predators and parasites (Jones & Firn, 1991). It's advantageous for plants to produce multipurpose compounds that offer protection against a broad spectrum of adversaries, and may play additional roles (including nitrogen storage) in basic metabolism (Bennett & Wallsgrove, 1994; Feeny, 1976; Langenheim, 1984). Insects are, however, notorious in their ability to circumnavigate chemical defenses (Caprio & Tabashnik, 1992; see references in Meurer-Grimes & Tavakilian, 1997). Introduced insects quickly adapt to novel host plants (Dethier, 1954), and the application of insecticides to agricultural crops plagued by pests rapidly induces selection for resistant forms (Erlich & Murphy, 1988). Insects that do develop the capacity to detoxify or sequester plant toxins may gain access to an unexploited food supply, and ultimately require the presence of supposed 'defensive' compounds to stimulate feeding or reproductive behavior (Fraenkel, 1959; Harborne,

1993). Some specialist herbivores appear to feed preferentially upon plant tissues containing relatively high levels of their toxin of choice (Cates, 1980).

Even the least discriminating insect generalists usually show some selectivity in their choice of host plant (Dethier, 1954): gymnosperm versus angiosperm, or dicot versus monocot. On the other end of the spectrum are specialists, some so fixated upon a single preferred host that they will die (or die without reproducing) rather than switch (Craighead, 1921; Jaenike, 1990). Many specialists are able to utilize groups of plants that are taxonomically, and presumably chemically related (Feeny, 1976; Meurer-Grimes & Tavakilian, 1997; Tavakilian et al., 1997). Insects appear to have similar nutritional requirements including amino acids, a sterol, B vitamins, carbohydrates, and various minerals (Dethier, 1954; Fraenkel, 1959). Most plants provide these basic nutrients, although there may be both intra- and interspecific quantitative differences, differential distribution in various plant tissues, or seasonal changes in availability. There is little evidence that insects use nutritional cues to select a host species, although they may influence the selection of a particular plant tissue (Cates, 1980; Dethier, 1954; Fraenkel, 1969). Herbivorous insects are more likely to recognize a potential host species by the presence of characteristic secondary metabolites.

Insects appear to be the best analytic chemists, and the attempt to elicit their secrets can be tortuous. Host location frequently involves both long distance orientation (via olfactory receptors) and on-site confirmation (via gustatory receptors), and therefore both volatile and non-volatile compounds may be involved in the selection process (Fraenkel, 1969). The same compound may function as a deterrent to one insect species, and an attractant to an adapted insect species (Feeny, 1976; Harborne, 1993). The behavior elicited is not necessarily correlated with compound toxicity, and ovipositing adult insects sometimes select host plants lethal to their offspring (Fraenkel, 1969). A single

compound may function as an attractant or a deterrent to a particular insect, depending upon the concentration (Fraenkel, 1969). Even in one of the most thoroughly investigated interactions (monarch butterflies and their milkweed hosts) it's only recently been shown that the oviposition stimulants are completely distinct from the toxic cardiac glycosides sequestered by the butterflies (Haribal & Renwick, 1996).

Plants typically produce large numbers of closely related secondary compounds, most of which appear to lack biological activity (although this may be an artifact of the selected bioassay, see Jones & Firn, 1991). This chemical diversity may increase the chances of producing defensive compounds effective against a mutable group of adversaries (Jones & Firn, 1991). Minor modifications in compounds can dramatically alter insect response, and mixtures of compounds are likely to have synergistic effects, making it difficult to identify the role of an individual chemical (Fraenkel, 1969; Harborne, 1993).

In spite of the difficulties inherent in describing the precise effects of plant compounds upon herbivorous insects, many classes of compounds and individual chemical structures have been identified that can be broadly classified as attractants or deterrents to particular insect species. These include glucosinolates, cardiac glycosides, essential oils, flavonoids, alkaloids, iridoids, and triterpenoids (Harborne, 1993). In some cases, even the sensory cells stimulated by the compounds have been identified (Fraenkel, 1969). Most studies to date have investigated the responses of economically important temperate species that can be successfully reared in the laboratory.

Tropical rain forests are home to a disproportionate number of the world's plant and animal species. Exploratory studies of secondary metabolites in tropical ecosystems suggest that certain classes of compound are more frequently encountered and of greater toxicity in the moist tropics, presumably in response to the intensified pressure exerted by

insects and pathogens (Langenheim, 1984). Although there is a burgeoning interest in the medicinal properties of tropical plants, the chemicals mediating the interactions of those plants with associated insects have been poorly investigated.

In French Guiana, the majority of the cerambycid species that attack freshly felled wood appear to be specialists able to locate and successfully reproduce in the wood of related tree species, suggesting that their distribution is at least in part regulated by plant chemistry (Meurer-Grimes & Tavakilian, 1997; Tavakilian et al., 1997). Lecythidaceae is one of two plant families associated with an extremely well-defined guild of specialist cerambycids (Tavakilian, 1993; Tavakilian et al., 1997). This study represents a seminal effort to identify plant compounds from Lecythidaceae that influence host selection by Neotropical cerambycid beetles. This chapter discusses intrafamilial variability in beetle attack, and some of the intrafamilial variation in plant chemistry that I believe influences the association between cerambycid and host plant.

MATERIALS AND METHODS

Headspace analysis of three wood samples

Samples consisting of coarsely macerated bark and wood were obtained from the trunks of three trees utilized during the rearing experiments on November 15, 1997. Two of the samples were collected from trees that had produced many cerambycids (*Eschweilera coriacea* M24086 and *Lecythis poiteaui* M24176), and the third sample was collected from a tree belonging to a malodorous species that had yielded very few cerambycids (*Couratari stellata* M24094). They were shipped to Givaudan Roure Corporation in Teaneck, New Jersey. Upon receipt, the samples were stored at 4°C and returned to refrigerated storage immediately after being prepared for analysis.

Approximately 50 g of each wood and bark sample was placed in a 2 liter container equipped with an inlet and outlet. An activated charcoal filter was attached to the inlet and the outlet was sealed. The containers were equilibrated for two hours at 25°C. At the end of that time the outlet plug was replaced with a " x3" adsorption tube containing 100 mg of Tenax TAr. A 2000 ml sample was then taken at 50 ml/min. The samples were analyzed by combined thermal desorption and gas chromatography-mass spectrometry (GC-MS). Thermal desorption was done with a Perkin Elmer ATD400 Automated Thermal Desorption unit. GC-MS was with a Hewlett Packard 5890 GC on a column 60 m long, inner diameter of 250 μm, and Supelco SPB-1 100% methyl silicone stationary phase, film thickness 0.25 μm. The initial GC temperature was 50°C, held for 2 min, then increased to 240°C at 4°C/min and held at the upper temperature for 13 min. Helium was used as the carrier gas, maintained at a constant flow rate of 1 ml/min. Sample components were detected with a Hewlett Packard 5972 Mass Spectral Detector and identified by comparison with mass spectra in the Wiley Mass Spectral Database (1992), with 275,000 entries.

Purification of Isolate 4 from a Couratari stellata wood sample

Prior to the rearing experiments, a sample consisting of coarsely macerated bark and wood was obtained from the trunk of *Couratari stellata* (M23737) by S. A. Mori (31 Aug., 1994). The sample was collected in methanol at Les Eaux Claires, transported to New York, and stored in a freezer at -20°C. The methanol was drained from the wood (2 Mar., 1995), which was weighed (1.2 kg) and chipped using a Retsch SM-1 Cutting Mill. The chipped wood extracted twice with methanol for 24 hrs at room temperature. All three methanol extracts were combined, filtered, evaporated to dryness on a Savant Speed Vac Concentrator, and then stored at -20°C. Further purification took place after the field season (Sept., 1996 through Oct., 1997). The residue was reconstituted in methanol, and the crude extract was partitioned three times between 900 ml ethyl acetate and 450

ml water (2:1). The water phase was adjusted by a dropwise addition of ammonium hydroxide to pH 11-12, and partitioned three times against an equal volume of toluene.

All phases were concentrated by evaporation, and the ninhydrin-staining compounds of interest were monitored by thin layer chromatography (TLC) on 20 x 20 cm Whatman AL SIL G / UV TLC plates. The positive staining water phase was applied to a silica gel column (5 cm x 90 cm), that was eluted with 1 liter toluene/methanol (1:1), 2 liters methanol, 2 liters methanol/water (1:1), and 2 liters water. Fractions were collected in 100 ml portions, which were evaporated and reconstituted in 5 ml of the appropriate solvent. Fractions 9 - 22 were combined for subsequent purification via preparative TLC, applied to 20 x 20 cm Uniplate Silica Gel GF prep layer plates, and developed twice in n-butanol/acetic acid/water (60:20:15). Six ninhydrin-staining bands (Isolates 1 through 6) were scraped from the TLC plates. Each band was covered with 100 ml methanol, agitated for one hour, filtered, and extracted a second time with 100 ml methanol. The two extracts of each band were combined, evaporated to dryness, and reconstituted in 5 ml methanol/water (4:1).

Isolates 1 and 3 were given preliminary identifications as lysine and glutamine, respectively, based on two-dimensional chromatography in n-butanol/acetic acid/water (60:20:15) and phenol/water (75:25). No further analyses of these isolates were conducted. The remaining isolates were next applied to 20 x 20 cm Whatman AL SIL G / UV TLC plates, and developed in n-propanol/34% ammonium hydroxide (70:30).

It was noted that the characteristic odor remained in Isolate 4 (Rf value 0.5). Isolate 4 appeared to contain a mixture of two major compounds, one showing strong UV absorbance. The upper portion of the band was therefore was collected separately from the lower portion, and Isolates 4 (top) and 4 (bottom) were reextracted as described

above. Each was applied independently to an LH 20 column (2 cm x 70 cm), and eluted with 200 ml methanol, collected in 10 ml fractions. Isolate 4 (top) eluted in fractions 3-4, which were combined and evaporated. Isolate 4 (bottom) eluted in fractions 8-9, which were combined and evaporated. The residues were delivered to BMG at AMRAD Discovery Technologies PTY LTD, Australia, for further analysis.

Mass spectrometry and NMR

Isolates 4 (top) and 4 (bottom) were analyzed by electrospray mass spectrometry (ESI-MS) using a Finnigan MAT iontrap mass spectrometer (LCQ). Samples were infused in 1% acetic acid in 50% aqueous methanol at a flow rate of 3 µl per minute, with a capillary temperature of 200°C, capillary voltage of 23V, and tube lens voltage of 15V. Full mass scans were acquired in the negative ion mode.

The isolates were dissolved in water and each was applied to a 500 mg C-18 solid phase extraction column to remove some brownish residue. The column was eluted with 2 ml each of water, 20% , 40%, 60%, 80%, and 100% aqueous methanol. The fractions were dotted onto a silica gel TLC plate and sprayed with ninhydrin, and the positive fractions were recovered from the water phases. The water fractions were dried under a stream of nitrogen, and then further dried under vacuum for 24 hrs. Prior to nuclear magnetic resonance (NMR), the compounds were dissolved in dimethyl sulfoxide, and ^{1}H NMR spectra were obtained (by Dr. Jin Yu) using the 400MHz instrument at the Chemistry Department, University of Melbourne.

RESULTS

Rearing experiments

The branch segments ($N = 406$) prepared during the rearing experiments gave rise to a total of 1813 individual cerambycid beetles belonging to 37 species (Table 1). Because different numbers of branch segments were available for the five tree species investigated, the total number of emergences from each has been compared with the number that would be expected were emergences proportional to the number of available branch sections (Table 5), and analyzed by *G*-test for goodness of fit (Sokal & Rohlf, 1995). The result confirmed a highly non-random distribution of cerambycids ($G = 770$, $df = 4$, $P < .001$).

Both *Eschweilera coriacea* and *L. poiteaui* yielded at least 50% more cerambycids than expected (Table 5, column 4), although *L. poiteaui* was more densely colonized during the dry season, and *E. coriacea* during the rainy season (Table 6). They were each attacked by numerous cerambycid species either previously (Tavakilian et al., 1997) or newly identified as Lecythidaceae specialists (Table 1). Specialists were often represented by many individuals. *Eschweilera coriacea* gave rise to a cerambycid guild composed almost exclusively of specialists. *Lecythis poiteaui* was associated with numerous generalist species, although generalists were typically represented by very few individuals and made a small contribution to the total cerambycid yield (Figure 10).

Corythophora amapaensis gave rise to comparatively few beetles, just over half the number expected (Table 5). Seven of the eight cerambycid species reared were represented by ten or fewer individuals (Table 1). *Palame crassimana* appears to be the 'least picky' Lecythidaceae specialist, and this species alone arose in abundance from *C. amapaensis* (Figure 6). *Corythophora amapaensis* was the only tree species that gave

Table 5

Observed versus expected emergences from five Lecythidaceae species

Tree Species	Branch *N* (%)	Cerambycid obs. freq.	Cerambycid exp. freq.	Ratio obs. / exp.
Corythophora amapaensis	58 (14.3)	142	259	.5483
Couratari stellata	61 (15.0)	31	272	.1140
Eschweilera coriacea	116 (28.6)	797	519	1.5356
Gustavia hexapetala	62 (15.3)	113	277	.4079
Lecythis poiteaui	109 (26.8)	730	486	1.5021
TOTAL	406 (100)	1813	1813	

Branch *N* (%): the number of branch sections collected for each tree species (the percentage of all available branch sections). Cerambycid obs. freq.: the actual number of individuals emerged from branch sections belonging to each tree species. Cerambycid exp. freq.: the expected number of emergences (assumed proportional to available branch sections). Ratio obs. / exp.: the ratio of actual emergences to expected emergences. ($G = 770$, df = 4, $P < .001$).

Table 6

Seasonal change in host utilization

	Cerambycids reared		Emergences per branch	
Tree Species	Dry	Rainy	Dry	Rainy
Eschweilera coriacea	470	327	7.34	6.29
Lecythis poiteaui	664	66	11.25	1.32

Emergences are listed for the two most productive tree species: *Eschweilera coriacea* and *Lecythis poiteaui*. Cerambycids reared: The number of individual cerambycids reared from branch sections cut during the dry or rainy season ($P = 0.0000$, contingency table analyzed by Fisher's Exact Test using the program JMP SAS). Emergences per branch: the average number of individuals reared per available branch section during the dry or rainy season.

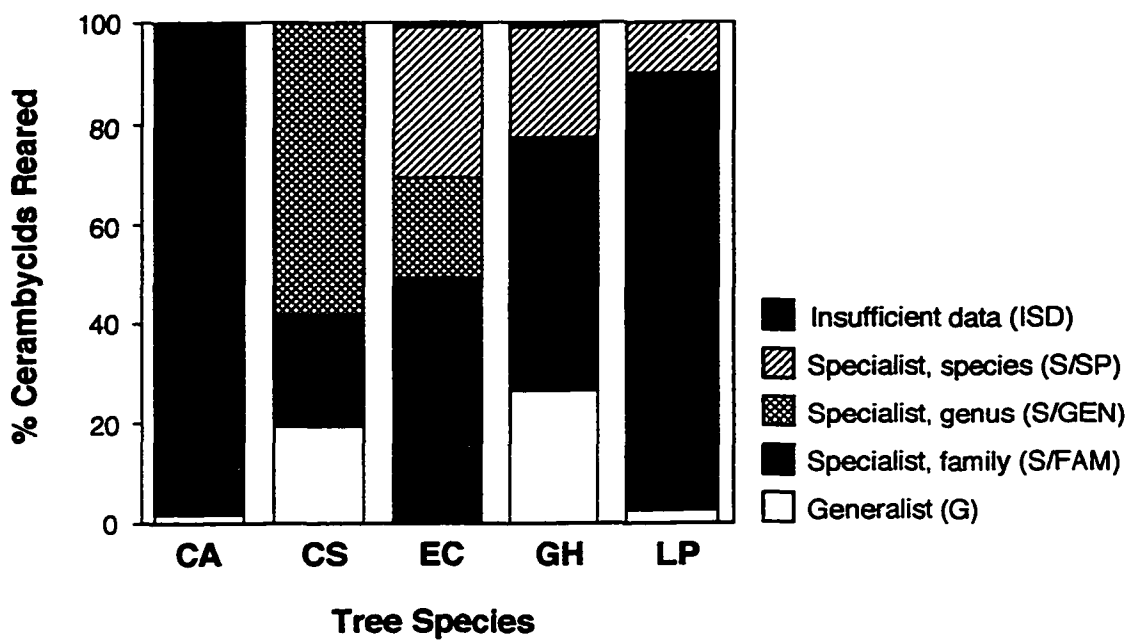


Figure 10. Host specificity of cerambycid beetles reared from five Lecythidaceae species at Les Eaux Claires. CA = *Corythophora amapaensis*, CS = *Couratari stellata*, EC = *Eschweilera coriacea*, GH = *Gustavia hexapetala*, and LP = *Lecythis poiteaui.*

rise to *Neopalame* sp. 851, a rather uncommon family specialist. A few beetles belonging to cerambycid species classified as family specialists, but more commonly associated with other tree species, were also reared.

Gustavia hexapetala, one of two foul-smelling species investigated, yielded well under half the expected number of cerambycids (Table 5). There were actually quite a few (N = 13) cerambycid species associated with *G. hexapetala*, but they were typically represented by few individuals (Table 1). *Palame crassimana* was again the cerambycid most frequently reared. With the exception of *Palame* spp. and *Periboeum pubescens*, the cerambycid species associated with *G. hexapetala* had not previously been reared from the Brazil nut family (Table 1).

The branches severed from *Couratari stellata,* an exceptionally foetid species, were practically devoid of cerambycids (Table 5). Although seven cerambycid species were reared, the only cerambycid represented by more than 10 individuals was *Neobaryssinus marianae,* which appears to be exclusively associated with the tree genus *Couratari* (Chapter 1, Tavakilian et al., 1997). Of the remaining cerambycid species reared, only *Neoeutrypanus mutilatus* and *Oedopeza leucostigma* had previously been reared from Lecythidaceae (Table 1).

GC-MS analysis of headspace samples

Each of the three samples analyzed contained at least 95 different compounds, primarily monoterpenoids and sesquiterpenoids, most of which were present in very small amounts (Appendix III). The dominant peaks detected in *Eschweilera coriacea* and *Couratari stellata* (28.11% and 19.15% peak areas, respectively) were composed of a mixture of 1,8-cineole and limonene. Both compounds are common monoterpenoids that are components of many essential oils. Limonene is a major component of orange oil, and

1,8-cineole, found in *Eucalyptus*, has a camphorous aroma (Dictionary of Natural Products, 1997). The dominant compound (19.94% peak area) detected in *Lecythis poiteaui* was α-safranal (Appendix III). Safranal is a monoterpenoid with a saffron odor, found in *Crocus* (Dictionary of Natural Products, 1997; Robinson, 1991).

I was primarily searching for compounds responsible for the foul odor characteristic of *Couratari stellata* and *Gustavia hexapetala*. Preliminary analyses (HPLC and TLC) of wood samples collected during Tavakilian's Sinnamary project (1997) and during these rearing experiments at Les Eaux Claires had convinced me to target compounds containing nitrogen and / or sulfur. Several volatile sulfur compounds were components of *Couratari stellata* and *Lecythis poiteaui*, but lacking in *Eschweilera coriacea* (Table 7). Dimethyl disulfide, dimethyl trisulfide, and methyl (methylthio)methyl sulfide were detected in both *C. stellata* and *L. poiteaui*. In addition, *C. stellata* produced 2-(methylthio)ethanol, and *L. poiteaui* produced 2,4 dithiapentane. Sulfur compounds were, however, only a minor component (1.87% peak area) of the *L. poiteaui* volatiles, while they were a much more abundant component (14.94% peak area) of the *C. stellata* volatiles. Dimethyl disulfide was particularly abundant in *C. stellata*; the only compounds that made larger contributions to the total peak area were acetic acid, which may have been a contaminant, and α-safranal.

The GC-MS protocol was not particularly sensitive to nitrogen compounds. The single nitrogen compound revealed by the GC-MS analysis, n-methyl-pyrrole, is described as having a 'moldy' smell (Fisher, pers. comm.). It was present in both *C. stellata* and *L. poiteaui*, but once again more abundant in *C. stellata*, and absent from *E. coriacea* (Table 4). This compound is likely to contribute to the distinctive foetid odor.

Table 7

Volatile malodorous compounds in three species of Lecythidaceae

TYPE	RT	COMPOUND NAME	% AREA IN 3 TREE SPP.		
			C. stellata	*L. poiteaui*	*E. coriacea*
N	5.79	N-methyl-pyrrole (91/91)	5.97	2.01	—
S	5.95	Dimethyl disulfide (91/87)	13.54	0.84	—
S	8.11	2-(methylthio)ethanol (96)	0.98	—	—
S	9.93	2,4-Dithiapentane (87)	—	0.68	—
S	14.01	Dimethyl trisulfide (*/94)	0.31*	0.29	—
S	21.26	Methyl (methylthio)methyl sulfide (91/*)	0.11	0.06*	—
% AREA ALL SULFUR COMPOUNDS			**14.94**	**1.87**	—
% AREA ALL MALODOROUS COMPOUNDS			**20.91**	**3.88**	—

Compounds likely to contribute to the distinctive foetid odor characteristic of some Lecythidaceae are listed in order of their GC retention times. TYPE: S= sulfur containing compounds, N = nitrogen containing compounds. RT: GC retention times. COMPOUND NAME (qual): the name of each compound is followed by a figure indicating how closely the observed pattern of ions matched the MS database. % AREA IN 3 LECYTHIDACEAE SPP.: relative abundance is indicated by listing the % area of the relevant peak in *Couratari stellata, Lecythis poiteaui*, and *Eschweilera coriacea.* * = the peak was composed of a mixture of compounds (therefore I lack qualitative data, and the % area was estimated).

Structural elucidation of S-methylmethionine

Although *C. stellata* lacks the 'rotten egg' or onion-like odors often associated with sulfur, the crude extract and Isolate 4 (top) smelled like the amino acid methionine, indicating the presence of reduced sulfur (SH-). The sample was a yellow-whitish powder that looked similar to Isolate 4 (bottom), and it gave a ninhydrin-positive reaction with an Rf value of approximately 0.5 in n-butanol/acetic acid/water (60:20:15). In the full mass scan (negative ion mode) signals were observed at *m/z* 161 and 163. A literature survey was conducted for compounds with a molecular weight of 164 and both sulfur and nitrogen as structural components. Possible candidates were identified: S-propenyl-cysteine, and several isomers of methylmethionine.

The ^{1}H NMR spectrum unambigously identified the compound as S-methylmethionine (Figure 11). Two large singlets, each integrating for 3 protons, were observed at 2.044 ppm and 1.889 ppm. This chemical shift is characteristic for methyl groups linked to sulfur. The methyl ester of methionine, considered one of the possible structures of the isolate, should give rise to a singlet integrating for 3 protons at approximately 3.4 to 4.0 ppm. Such a signal was not observed. In additiion, signals corresponding to two $-CH_2-$ groups were observed at 2.9 and 2.75 ppm. The ^{1}H NMR spectrum was compared to an ^{1}H NMR spectrum obtained of methionine (ALDRICH library of ^{1}H and ^{13}C NMR spectra, ID 893 C) and found to be similar except for the absence of one of the methyl signals.

The proposed structure is also supported by the mass fragmentation pattern. The MS/MS experiment on *m/z* 163 yielded a daughter ion at *m/z* 130, a loss of 33 amu. This corresponds to the loss of one methyl group (15 amu), the amino group (NH_2, 17 amu), and one proton, probably from the carboxyl function (1 amu). The second signal observed in the full mass scan was *m/z* 161. This signal could arise in the negative ion

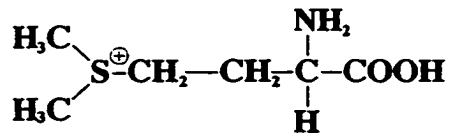


Figure 11. Structure of S-methylmethionine.

mode through the loss of 2 protons, because the molecule carries a positive charge in two positions. In the MS/MS experiment, it yielded daughter ions at *m/z* 120 and 122. The signal at *m/z* 120 corresponds to the loss of the carboxyl function (from *m/z* 164). Because the molecule carries complex charges, protons might be added or lost, and *m/z* 122 could arise from the addition of two protons to *m/z* 120. In conclusion, the mass spectra and NMR spectra support the structure of S-methylmethionine for Isolate 4-top.

Isolate 4 (bottom) also produced signals at *m/z* 161 and 163 in the full mass scan, and there was an additional set of signals at *m/z* 260 and 262. It was noted that two indole compounds isolated from *Couroupita guianensis* have a molecular weight of 262 (Bergman et al. 1985), but no further analysis of this compound mixture was conducted.

Wood extracts from each of the trees used in the rearing experiments were compared with the Band 4 isolate using co-chromatography. Extracts derived from the three tree species lacking the foul odor did produce faint bands at Rf 0.5, but these bands were consistently dominant in *Couratari stellata* and *Gustavia hexapetala.* Because there were at least two compounds with an Rf value of 0.5, it was not possible to definitively confirm which species produce S-methylmethionine. Although S-methylmethionine is not a particularly unusual plant compound (Paquet et al., 1995), it is the first intermediate in a biosynthetic pathway leading to 3-dimethylsulfoniopropionate (Hanson et al., 1994; Trossat et al., 1996), and would not ordinarily be expected to accumulate.

DISCUSSION

It is clear that, as far as cerambycids are concerned, all Lecythidaceae are not created equal. *Eschweilera coriacea* and *Lecythis poiteaui* were undoubtedly the favored tree species, while *Corythophora amapaensis, Gustavia hexapetala,* and *Couratari stellata*

were rather poorly colonized. *Corythophora amapaensis* was the only tree species lacking a conspicuous odor that gave rise to an impoverished cerambycid guild, but this might be due to non-chemical factors including its restricted geographic range (see Chapter 4).

Although I lack experimental confirmation that the foul smell (or any constituent) associated with *Gustavia hexapetala* and *Couratari stellata* is actually a deterrent to cerambycid beetles seeking oviposition sites, I feel that circumstantial evidence from the rearing experiments is convincing. These two tree species gave rise to depauperate complements of cerambycids that were rather atypical for Lecythidaceae (Figure 10). No more than 50% of the individuals reared were family level specialists. The remaining cerambycids belonged either to species with narrower host ranges, suggesting that they are particularly attuned to their host, or to generalist species that apparently tolerate variable host chemistry. A malodorous congener of *Gustavia hexapetala* (*G. augusta*) investigated in French Guiana also seems to have been avoided by cerambycids, while a non-foetid congener of *Couratari stellata* (*G. guianensis*) gave rise to many Lecythidaceae specialists (Tavakilian, 1993; Tavakilian et al., 1997).

Lecythis poiteaui, associated with a great abundance and diversity of cerambycids, also produced some of the volatile compounds contributing to the characteristic odor (Table 7). They appear to be only minor components of this species, at least during the dry season when *L. poiteaui* was especially densely colonized (Table 6). Wood samples did not have a detectable foetid odor in the field or, as extracts, in the laboratory. *Lecythis poiteaui* was, however, the only tree species in this study that was in bloom at the time of the rainy season cut, and its chemical profile may then be substantially modified. Anthesis is nocturnal, and the bat-pollinated flowers (Mori & Boeke, 1987) have the very pungent, characteristically musky odor frequently associated with this syndrome (Faegri

& van der Pijl, 1979). Headspace analyses of floral aromas from eight unrelated plant species presumed to be bat-pollinated revealed that seven of them produced sulfur compounds including dimethyl di- and trisulfides and 2,4 dithiapentane (Knudsen & Tollsen, 1995). Although the *L. poiteaui* floral scent does not resemble that of the malodorous wood (Berkov & Mori, pers. obs.), sulfur compounds were detected in the wood, and a quantitative increase may influence the reduced colonization observed during the rainy season (Table 6).

It is possible that *G. hexapetala* and *C. stellata* did not actually deter beetles at the oviposition stage, but were sufficiently toxic to prevent the development and maturation of larvae. Di- and trisulfides frequently arise as transformation products from bulkier sulfur compounds (Knudsen & Tollsten, 1995; Yu et al., 1989), have particularly offensive odors (Iberl, 1990; Robinson, 1991), and would enable an insect to quickly evaluate a potential host. I believe that while the sulfurous compounds detected in this study may indeed show some toxicity, they are chemical signals easily detected by insects and are likely to function principally as deterrents.

In general, branches severed from the tree species favored by the cerambycids in this study showed greater signs of insect activity (oviposition scars, frass, exit holes, or actual insect presence) while they remained in the forest (Berkov, unpubl. data). I made occasional diurnal and nocturnal visits to severed branches, and although I rarely managed to observe cerambycids, the majority encountered were on *Eschweilera coriacea* or *Lecythis poiteaui*. I did observe one individual on *Corythophora amapaensis*, and one on *Gustavia hexapetala*, but they belonged to species that did not emerge from the caged branch sections. *Couratari stellata* showed very few signs of insect activity while the branches remained in the forest, and the only insects regularly encountered on the branches were thrips (Thysanoptera).

Sulfur as toxin, deterrent, and attractant

Plant taxa characterized by the acrid aromas and flavors associated with sulfur include the onion family (Alliaceae) and the mustard family (Brassicaceae). Sulfurous compounds derived from these and unrelated plants can be highly irritating, and frequently do show biological activity as antimicrobials, nematicides, or larvicides (Amonkar & Banerji, 1971; Balandrin et al., 1988; Gmelin et al., 1981; Tada et al., 1988). Many insects avoid feeding on plants producing mustard oils (isothiocyanates), which are enzymatically released from glucosinolates such as sinigrin (a widepread compound found in many Brassicaceae species). Naturally occurring concentrations of sinigrin can be lethal to insects that do not normally feed upon Brassicaeae (Erickson & Feeny, 1974). Sulfur compounds are also repugnant components of both stress-induced and stress-inducing secretions released by mammals including skunks (*Mephitis mephitis*), striped hyaenas (*Hyaena hyaena*), red foxes (*Vulpes vulpes*), and weasels (Mustelidae) (Harborne, 1993).

Sulfurous odors clearly transmit some powerful messages. They often function as repellents, but can also function as lures (Harborne, 1993). Quite a few insect pests including the cabbage butterfly (*Pieris brassicae*), the cabbage aphid (*Brevicoryne brassicae*), and certain flea beetles (*Phyllotreta* spp.) specialize upon Brassicaceae spp., and recognize mustard oils as feeding or oviposition stimulants (Harborne, 1993). Several fly species (including Protophormia terraenovae and Hydrotaea anxia) are attracted to dimethyl trisulfide (Nilssen et al., 1996). Bats and other mammals also appear to respond favorably to certain sulfur compounds. Dimethyl disulfide, the dominant sulfur compound detected in the GC-MS analysis of *Couratari stellata,* has been identified as an attractant pheromone for hamsters (Singer et al., 1976)!

The malodorous lineage

Lecythidaceae is emerging as yet another plant family characterized by an unusual sulfur metabolism. References to the distinctive odors that characterize some taxa are made in anecdote, scientific names and local names. *Petersianthis macrocarpus*, belonging to the Old World Planchonioideae, has "stem bark (that) smells foetid when slashed" (Ogundain et al., 1983). The Old World subfamily Foetidioideae is composed of the single genus *Foetidia* (Bosser, 1988). Among the Neotropical taxa, *Grias foetidissima* has been synonomized with *Grias neuberthii*. *Gustavia augusta* is also known as 'stink-wood' or 'rosa de muerto' and *G. hexapetala* as 'palo de muerto' (Prance & Mori, 1979; Schultes & Raffauf, 1990). *Gustavia dubia* and *G. romeroi* are both known as 'mula muerta' (dead mule). *Gustavia romeroi* is also called 'coco hediondo' (evil-smelling coconut), as is *Couroupita guianensis* (Kerdel-Vegas, 1966; Prance & Mori, 1979).

Further study of the compounds constituting these unpleasant odors may yield insights not only into factors influencing the distribution of cerambycids, but also regarding family phylogeny. The taxa noted above are considered rather archaic, characterized by indehiscent (or functionally indehiscent) fruits and, with the exception of *C. guianensis*, actinomorphic flowers. *Couratari stellata* is the only strongly malodorous species I am aware of that has both highly modified zygomorphic flowers and dehiscent fruits.

Brazil nut seeds contain storage proteins with exceptionally high levels of sulfur containing amino acids (3% cysteine and 18% methionine) (Bartolome et al., 1997). The toxic effects of ingesting certain *Lecythis* seeds, including emesis, hair loss and nail deformation (Aronow & Kerdel-Vegas, 1965; Kerdel-Vegas, 1966), may also prove to be related to an abundance of sulfur-containing amino acids. The toxic principle is a selenium-containing analogue of the sulfur amino acid cystathionine (an intermediate in the transformation of methionine to cystine). Ingestion of this compound appears to

interfere with the formation of the disulfide cross-linkages essential to the proper structure of proteins, and therefore inhibits the normal keratinization of hair and nails. It seems that the sequestration of toxic amounts of selenium occurs when certain species of *Lecythis* are grown on soils with high selenium levels (Aronow & Kerdel-Vegas, 1965; Kerdel-Vegas, 1966; Prance & Mori, 1979).

Sulfur compounds or their analogues appear to accumulate in the seeds or fruits of *Bertholletia excelsa,* some *Lecythis* spp., and *Couroupita guianensis*. Of these, *C. guianensis* and *B. excelsa* have woody, indehiscent (or functionally indehiscent) fruits with mammal-dispersed seeds (Mori & Prance, 1990). Dimethyl disulfide, the principal volatile sulfur compound detected in *Couratari stellata,* has been verified as an attractant pheromone for one mammal (Singer et al., 1976), albeit a very small one not likely to be implicated in Lecythidaceae seed dispersal. I believe that the sulfur compounds detected in some Lecythidaceae offer some protection against herbivorous insects and may, in the case of *Lecythis poiteaui*, play a role in the attraction of bat pollinators. It is of highly speculative, but not impossible, that sometime in the family's evolutionary history the presence of sulfurous compounds in seeds or fruits may also have lured appropriate seed dispersers!

CHAPTER 4

Host Plant Toxicity and Insect Fidelity: Quantitative Association or Merely Myth

SUMMARY

The ease with which a plant can be located by potential enemies hypothetically influences the nature of its chemical defense system, thereby promoting a predisposition towards attack by either generalist or specialist herbivores. A newly discovered association between wood-boring cerambycid (longicorn) beetles and their host trees belonging to the Lecythidaceae (Brazil nut family) inspired a year-long rearing project in the lowland Neotropical rainforest of central French Guiana. Branches severed from five different species of Lecythidaceae yielded 1,813 cerambycid beetles belonging to 37 species. Each potential host was associated with a distinctly different complement of cerambycids. Two of the five tree species, *Eschweilera coriacea* and *Lecythis poiteaui*, gave rise to particularly large and diverse cerambycid guilds. Most of the species associated with *E. coriacea* demonstrated a high degree of host fidelity, while *L. poiteaui* gave rise to more species with relatively broad host ranges. Wood extracts from the five tree species have been screened as part of an ongoing investigation into the antimicrobial properties of tropical trees. *Eschweilera coriacea* consistently inhibited the growth of several microorganisms, while *Lecythis poiteaui* showed minimal antimicrobial activity. These results are in accord with the hypothesis that highly toxic plant species are prone to host specialized insect herbivores, but numerous additional factors appear to influence the predisposition towards host specificity.

INTRODUCTION

Many plant-feeding insect species demonstrate high levels of fidelity to a particular host taxon (specialists), while others apparently feed or reproduce with impunity upon an array of unrelated hosts (generalists). The classic explanation for the evolution of host specificity proposes that plants produce various secondary compounds to deter herbivores, some of which subsequently evolve the capacity to either detoxify the compounds, or sequester them to be utilized for defense against their own predators. Insects that develop the capacity to feed upon plants that other animals find toxic or distasteful may end up with a monopoly on an unexploited food supply, and eventually even require the presence of the "deterrent" compounds to stimulate feeding or reproductive activities (Bennett & Wallsgrove, 1994; Feeny, 1980; Harborne, 1993).

Actually, almost every conceivable attribute of either plant or insect has been proposed as a predictor of insect host range. Some of the plant-centric factors include plant abundance, distribution, diversity, architecture, temporal variability, and chemistry (Cates, 1980; Feeny, 1976; Futuyma, 1983; Jaenike, 1990; Langenheim, 1984). Insect-centric factors include insect size, mobility, sensory ability, feeding strategy, life span, larval performance on various hosts, dominance, density, effects of intraspecific or interspecific competition, and interactions with predators, parasites or pathogens (Bernays & Graham, 1988; Jaenike, 1990, and references therein; Mattson et al., 1988). Transitory conditions (including insect age, egg-load, and degree of host-deprivation) may influence host acceptance by individuals (Jaenike, 1990), facilitating host shifts. Many of these variables potentially alter the period of time that an insect spends searching for a suitable host (exposed, preoccupied, and vulnerable to enemy attack). It is often assumed that insect behaviors prolonging this perilous activity must confer a substantial selective advantage that justifies the increased risk.

'Apparent' versus 'unapparent' plants

Related theories linking plant (or plant tissue) availability, plant chemical defense, and insect specialization were proposed by both Feeny and Rhoades & Cates, in 1976. Feeny (1976) characterized easily located, predictable plants as apparent (typically persistent climax species) and less easily located plants as unapparent (typically ephemeral, early succession species).

Apparent plants, likely to attract and accumulate herbivores, should benefit from a defense system that offers protection against a broad spectrum of enemies. Feeny (1976) suggested that apparent plants make substantial metabolic investments in the production of large amounts of quantitative defense compounds including tannins, resins, or silica. Quantitative defenses slow insect growth by forming complexes with proteins and reducing the digestibility of plant tissues, or act as mechanical barriers to herbivory.

Unapparent plants, because they "escape in time or space," have less need for defensive compounds. In addition, because early succession species typically grow rapidly, they would be expected to allocate fewer resources to defense. Unapparent plants are proposed to rely upon the production of small amounts of qualitative defense compounds such as glucosinolates or alkaloids. Qualitative defenses are directly toxic to herbivorous insects.

Quantitative defenses theoretically hinder all insects, while qualitative defenses effectively deter nonadapted generalists, but are rather easily overcome by specialists. Specialists either detoxify the compounds or sequester them to be used for their own defense, and may ultimately recognize the defensive compounds as feeding or oviposition attractants.

Rhoades & Cates (1976) proposed a similar model, but also included plant tissues in their discussion. They elaborated a coevolutionary scenario in which predictable (= apparent) plants or plant tissues are initially expected to host specialist herbivores that select in turn for the production of digestibility-reducing (= quantitative) defenses. Predictable plants are ultimately expected to be preferentially associated with generalists. Ephemeral (= unapparent) plants or plant tissues are initially expected to be associated with generalists that select for the production of a diversity of lower molecular weight toxic molecules (= qualitative defenses). Ephemeral plants are ultimately expected to be preferentially associated with specialists.

Other researchers reject the proposed association between host plant chemistry and insect host range, in part because it has been difficult to assess the toxicity of deterrent compounds (Bernays & Graham, 1988). The concept of biochemical coevolution (Feeny, 1980; Rhoades & Cates, 1976) has also been questioned because there is little satisfactory evidence that insects do indeed promote the evolution of plant secondary chemistry (Meurer-Grimes & Tavakilian, 1997). This has led some authors to stress the importance of non-chemical variables, such as predator avoidance, in determining insect host range (Bernays & Graham, 1988).

Nevertheless, some insects are so responsive to chemical cues that they will oviposit upon pieces of filter paper treated with appropriate plant compounds (Harborne, 1993). Many insects select hosts that are taxonomically, and presumably chemically related, while other insects select unrelated hosts containing similar compounds (Barbosa, 1988; Tavakilian et al., 1997). Some insects, even in captivity and with extremely limited options, will refuse to utilize a potential host unless it provides specific chemical lures and lacks repellent compounds (broadly classified as attractants and deterrents). I agree that while insects seldom select their hosts solely on the basis of chemistry, plant

secondary metabolites indisputably play a fundamental role in determining host plant acceptability and delimiting host range (Erlich & Murphy, 1988; Schultz, 1988).

Background

In French Guiana, the majority of the cerambycid species that attack freshly felled wood appear to be specialists able to locate and successfully reproduce in the wood of related tree species, although the ratio of specialist to generalist species is very different from one plant taxon to the next. Lecythidaceae (the Brazil nut family) is one of two plant families associated with an extremely well-defined guild of specialist cerambycids (Tavakilian, 1993; Tavakilian et al., 1997).

Each of the five species of Lecythidaceae investigated in this study gave rise to a distinctly different complement of cerambycids. In this chapter I compare the specificity of intrafamilial cerambycid guilds with host plant toxicity as revealed by antimicrobial bioassays of wood extracts from the five tree species investigated. I make no assumptions about the nature of the plant chemical defense system, or the potential toxicity of the wood to either specialist or generalist insects. The antimicrobial bioassays are simply considered a gauge of general toxicity. I also avoid making assumptions about biochemical coevolution, as the insects studied attack dead wood and are not likely to be a selective force. I do assume that the cerambycids associated with the five tree species must tolerate the secondary metabolites present in the bark and wood at the time of attack. Although the rearing experiments were not originally designed to address competing hypotheses about the causes of host specificity, I use the results to discuss additional factors likely to promote a predisposition towards specialized host utilization.

MATERIALS AND METHODS

Testing for toxicity

Wood extracts from the 25 trees used in the rearing experiments were screened (July - August, 1997) as part of an investigation into the antimicrobial properties of tropical trees (Rovira et al., in review). Bioassays tested for inhibitory activity against four microorganisms: *Staphylococcus aureus* (ATCC 25923), *Candida albicans* (ATCC 60193), *Escherichia coli* (ATCC 25922), and *Enterococcus faecalis* (ATCC 29212). The organisms tested are all human pathogens, and include gram+ (*S. aureus*, *E. faecalis*) and gram– (*E. coli*) bacteria, and a yeast (*C. albicans*). Inhibitory activity in these bioassays does not necessarily predict defensive capabilities of the five tree species in the field, but does give an indication of their bioactivity.

Each small twig sample (5 - 10 cm^3, including wood and bark) from a study tree was homogenized in a blender with 150 ml methanol. The homogenate was agitated for 1 h, filtered, and the wood was extracted a second time with 100 ml methanol. The two extracts were combined and evaporated to dryness on a rotary evaporator. Dried extracts were reconstituted in 10 ml methanol and stored at -20°C. Directly prior to the bioassays, crude extracts were evaporated to dryness, and reconstituted with methanol to a final concentration of 500 mg solid : 1 ml solvent. The reconstituted extracts (20 µl) were applied to sterile disks and dried under a sterile hood, then stored at -20°C.

A sterile loop was used to obtain a small amount of stock sample of each microorganism, which was plated onto an agar plate using the four-way parallel streak method (National Committee for Clinical Laboratory Standards, 1990). *Staphylococcus aureus* and *E. coli* were plated onto Mueller-Hinton agar plates. *Enterococcus faecalis* was plated onto a Mueller-Hinton agar plate with 5% sheeps' blood, and *Candida albicans* was plated onto

a Sabouraud dextrose agar plate. The plates were incubated at 37°C for 24 h, then four or five isolated colonies were removed from each plate and inoculated into 1 ml Tryptic soy broth. Each inoculated broth was incubated at 37°C for 2-4 h, until it reached a concentration of 5 cpu (colonies per unit). A sterile cotton swab was used to transfer broth onto an agar plate by swab lawning, and the plate was allowed to dry for five minutes.

The disks prepared with 20 µl extract were placed onto the agar plates and incubated at 37°C for 24 h. During the incubation period, the bacteria grew and formed a uniform lawn. When the extract applied to a disk inhibited the growth of a particular microorganism, a clear zone (inhibition zone) surrounded the disk after the incubation period.

RESULTS

Assessment of cerambycid fidelity

The branch segments ($N = 406$) prepared during the rearing experiments gave rise to a total of 1813 individual cerambycid beetles belonging to 37 species (Table 8). When the number of documented host species is recorded for each cerambycid that emerged, there is a bimodal distribution in which there is one major group of cerambycids with 6 or fewer host species, and a second major group with 13 or more host species (Figure 12).

Eschweilera coriacea and *Lecythis poiteaui* gave rise to large and diverse cerambycid guilds. Most of the cerambycids reared from *E. coriacea* belong to the species *Oedopeza leucostigma*, *Oreodera simplex*, *Ozineus* sp., *Palame anceps*, and *P. crassimana*. With the exception of *P. crassimana*, all of these species have six or fewer documented hosts (Table 8). *Lecythis poiteaui* primarily gave rise to cerambycids belonging to the species

Table 8

The number of documented host species for Cerambycids reared from Lecythidaceae at Les Eaux Claires

Cerambycid species	*N*	Host Plant					H/S	Host spp.
		CA	CS	EC	GH	LP		
Carterica sp.	9	–	–	–	9	–	S/SP	1
Carterica sp.	2	–	–	–	2	–	S/SP	1
Ceragenia leprieuri Buquet in Guérin- Méneville	1	–	–	–	–	1	G	3
Colobothea bisignata Bates	4	–	2	–	2	–	S/FAM	2
Eburodacrys sexmaculata (Olivier)	1	–	–	–	–	1	G	4
Eburodacrys sp. 1282	3	–	–	3	–	–	G	2
Eupromerella clavator (Fabricius)	20	–	–	–	20	–	G	2
Hesychotypa jaspidea (Bates)	6	–	5	–	–	1	G	3
Hesychotypa liturata (Bates)	2	–	–	–	2	–	G	3
Mecometopus triangularis (Laporte & Gory)	15	2	–	–	–	13	G	35
Nealcidion badium Monné & Delfino	1	–	–	–	1	–	ISD	1
Neobaryssinus marianae (Martins & Monné)	18	–	18	–	–	–	S/GEN	3
Neoeutrypanus mutilatus (Germar)	93*	9	2	2	–	80	S/FAM	7
Neoeutrypanus nobilis (Bates)	5	–	–	5	–	–	ISD	1
Neoeutrypanus sp. 915	69*	–	–	–	–	69	S/SP	1
Neopalame sp. 851	10	10	–	–	–	–	S/FAM	2
Nesozineus sp.	3	–	–	–	3	–	S/SP	1
Oedopeza apicale (Gilmour)	9	–	1	–	8	–	G	8
Oedopeza leucostigma Bates	232*	–	2	229	–	1	S/FAM	6
Oreodera melzeri Monné & Fragoso	1	–	–	–	–	1	G	2
Oreodera simplex Bates	158*	–	–	158	–	–	S/SP	1
Ozineus sp.	66*	–	–	66	–	–	S/SP	1
Palame anceps (Bates)	160*	–	–	160	–	–	S/GEN	5
Palame crassimana Bates	402*	114	–	93	39	156	S/FAM	13
Palame mimetica Monné	316*	3	–	29	2	282	S/FAM	15
Peribocum pubescens (Olivier)	102*	2	–	–	7	93	S/FAM	17
Plistonax albolinitus (Bates)	1	1	–	–	–	–	ISD	1
Stratone rufotestacea Thomson	1	1	–	–	–	–	S/FAM	2
Symperasmus thoracicus (White)	1	–	–	–	–	1	G	4
Taurolema bellatrix Thomson	11	–	–	–	11	–	S/SP	1
Xenofrea lineatipennis Zajciw	3	–	–	–	–	3	S/SP	1
Xenofrea sp. 662	16	–	–	16	–	–	S/SP	1
Xenofrea sp. 714	2	–	–	2	–	–	ISD	1
Xylergates elaineae Gilmour	35	–	–	33	–	2	S/FAM	7
Xylergatina pulchra (Lane)	24	–	–	–	–	24	S/FAM	12
Genus sp. 229	10	–	1	–	7	2	S/FAM	3
Genus sp.	1	–	–	1	–	–	ISD	1
TOTAL	1813	142	31	797	113	730		

Cerambycid species are listed in alphabetical order. *N*: total number of individuals reared; an asterisk indicates a 'dominant' species (more than 50 individuals).

Legend for Table 8 contd.: Host Plant: the number of individuals reared from each of the five host species (CA = *Corythophora amapaensis*, CS = *Couratari stellata*, EC = *Eschweilera coriacea*, GH = *Gustavia hexapetala*, and LP = *Lecythis poiteaui*). H/S: Beetle species represented by at least two host records are classified according to their host specificity as generalists (G), or specialists associated with a single plant species (S/SP), genus (S/GEN) or family (S/FAM). There is insufficient data (ISD) to classify beetles represented by a single host record. A beetle is considered a specialist at the designated level when 90% of the host records are in accord. Host spp.: The total number of hosts documented to date (it is assumed that continued sampling would generate additional host records). Data from Tavakilian et al., 1997 were included in the classification of specificity and the number of documented hosts.

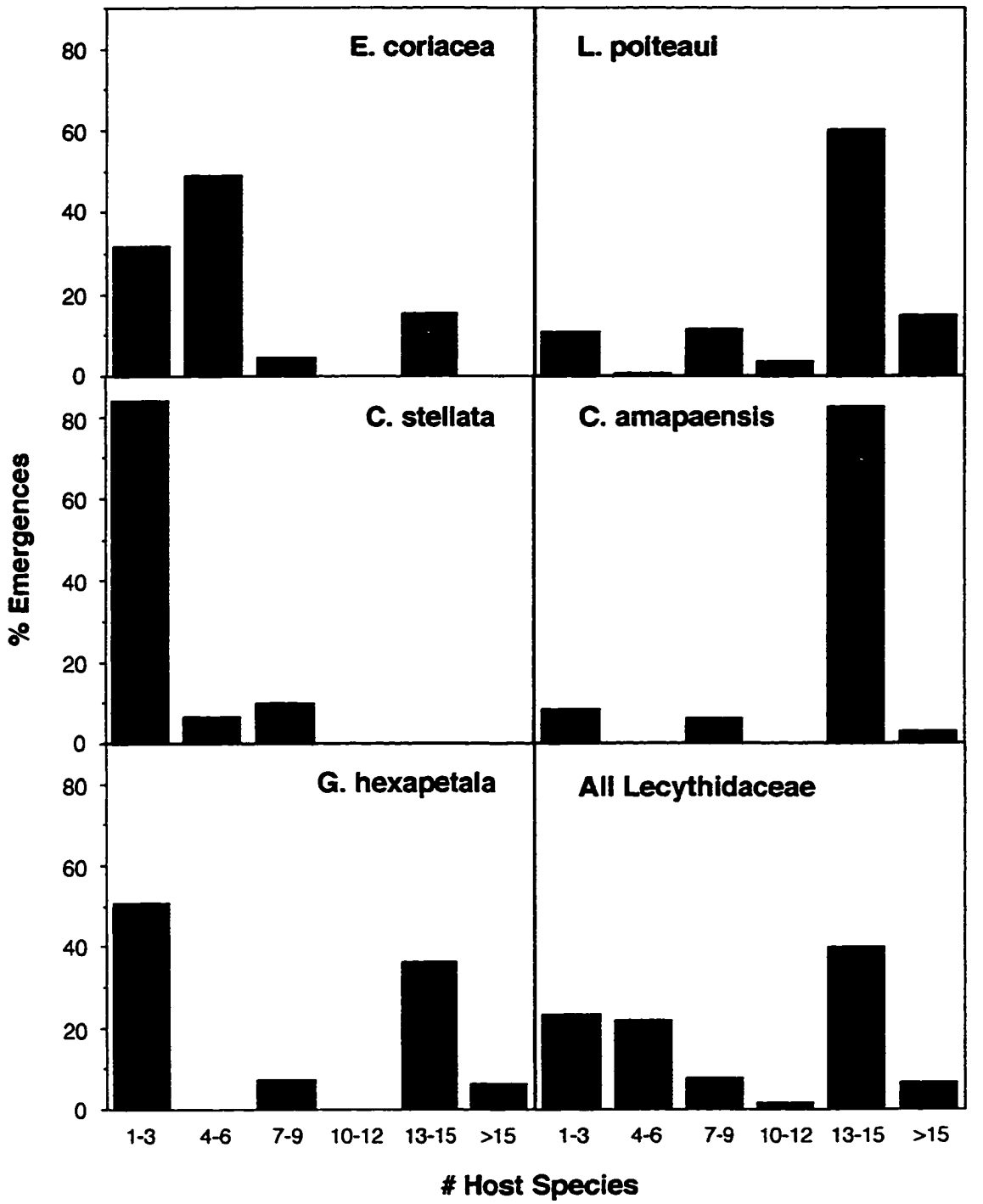


Figure 12. Host Ranges of Cerambycids Reared from Five Species of Lecythidaceae. Bar charts indicate the number of documented host species for individual cerambycids that emerged from each of the five species of Lecythidaceae, as well as from all species combined, at Les Eaux Claires.

Neoeutrypanus mutilatus, *Neoeutrypanus* sp. 915, *Palame crassimana*, *P. mimetica*, and *Periboeum pubescens*. The majority of individuals belong to the three latter species, each of which has 13 or more documented hosts (Table 8). These patterns can be clearly distinguished in Figure 12.

The remaining tree species (*Corythophora amapaensis*, *Couratari stellata*, and *Gustavia hexapetala*) were all rather poorly colonized (Table 8). *Couratari stellata* gave rise to cerambycids with relatively few hosts, *C. amapaensis* was associated with cerambycids with relatively broad host ranges, and *G. hexapetala* gave rise to some of each (Figure 12).

Although I primarily intend to search for possible explanations for the differing levels of host specialization observed in the cerambycids that emerged from *E. coriacea* and *L. poiteaui*, all five tree species are included. The following analyses record the attributes of the individual beetles that emerged from a particular host species. The results are therefore biased to reflect patterns revealed by the numerically abundant cerambycid species associated with the two tree species that produced the vast majority of individual cerambycids (Table 8).

Host plant toxicity

During a preliminary analysis of Lecythidaceae wood extracts and partitions (wood samples were collected by G. Tavakilian in French Guiana, 1992 - 1993, and analyzed in New York, 1994 - 1995) I noted that *Eschweilera coriacea* seemed exceptionally rich in saponins. The presence of saponins, a class of bitter-tasting, toxic compounds prevalent in Lecythidaceae, is easy to detect in the laboratory because saponins disrupt surface tension and prevent efficient partitioning of extracts (Berkov, pers. obs.). This was the first clue that *E. coriacea* might be more toxic than other Lecythidaceae studied. When

this tree species subsequently gave rise to numerous cerambycid species that never emerged from the four other potential hosts (Table 8), I hypothesized that there might be a correlation between host plant toxicity and the degree of specialization demonstrated by its xylophagous associates.

All five tree species showed at least occasional activity in the antimicrobial bioassays (Table 9), but *Eschweilera coriacea* extracts consistently inhibited the growth of the greatest number of pathogens: all five replicates were active against *Staphylococcus aureus* (Figure 13) and *Enterococcus faecalis*, and three showed some inhibitory activity against *Escherichia coli* (Table 9). *Lecythis poiteaui* represented the other end of the toxicity spectrum: two extracts weakly inhibited the growth of *S. aureus* (Figure 13) but there was no additional bioactivity (Table 9). While all five *Corythophora amapaensis* extracts inhibited the growth of *S. aureus*, only one replicate showed activity against additional pathogens. All *Couratari stellata* extracts inhibited the growth of *S. aureus*, two also inhibited the growth of *Candida albicans*, and one of those also showed activity against *E. faecalis* and *E. coli*. *Gustavia hexapetala* consistently inhibited the growth of *S. aureus*, three replicates were active against *E. faecalis*, and two of those also showed activity against *E. coli*.

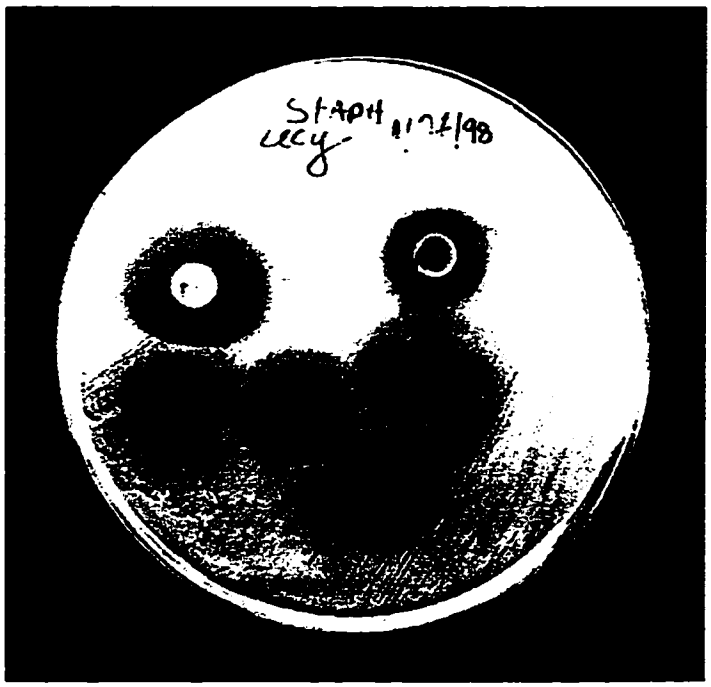
I concluded that the most informative data revealed by the antimicrobial bioassays were the number of different pathogens with growth inhibited by a particular extract (indicated by # Hits in Table 9), and the consistency of the activity. When the extracts were subject to further purification, activity against different microorganisms tended to segregate into polar or non-polar fractions, suggesting that different compounds were responsible (Rovira et al., in review). A tree species with a greater variety of biologically active compounds could certainly be considered 'more toxic' and chemical consistency should enable insects to more readily recognize a potential host.

Table 9

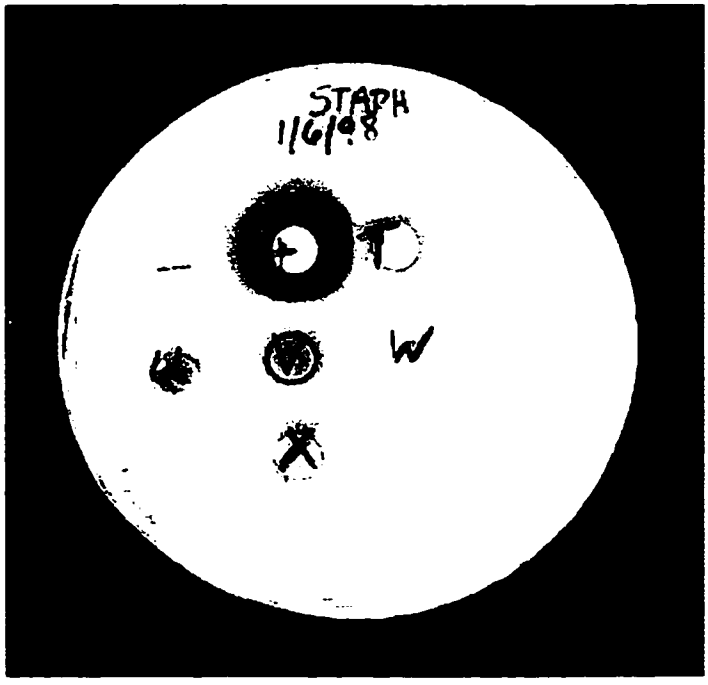
Antimicrobial activity by five species of Lecythidaceae

		Inhibition Zones				
Tree species	**Voucher #**	**S. aur**	**C. albi**	**E. faec**	**E. coli**	**# Hits**
C. amapaensis	M24145 (O)	15	—	—	—	1
	M24116 (P)	15	—	—	—	1
	M24147 (Q)	14	—	—	—	1
	M24148 (R)	15	—	12	10	3
	M24174 (S)	14.5	—	—	—	1
C. stellata	M24092 (E)	11	—	—	—	1
	M24093 (F)	13	10	—	—	2
	M24094 (G)	11	—	—	—	1
	M24095 (H)	10	—	—	—	1
	M24111 (J)	14	8	9.5	11	4
E. coriacea	M24078 (A)	14	—	12	11.5	3
	M24079 (B)	7	—	7	7	3
	M24083 (80)	11	—	8	—	2
	M24084 (C)	15	—	12	11	3
	M24086 (D)	13	—	10	—	2
G. hexapetala	M24110 (I)	16	—	12	12.5	3
	M24112 (K)	11	—	7	—	2
	M24113 (L)	20	—	11	10	3
	M24114 (M)	7.5	—	—	—	1
	M24115 (N)	10	—	—	—	1
L. poiteaui	M24175 (T)	—	—	—	—	0
	M24176 (U)	—	—	—	—	0
	M24177 (V)	9	—	—	—	1
	M24178 (W)	—	—	—	—	0
	M24179 (X)	9	—	—	—	1

Each tree species is followed by five voucher numbers, Mori et al. collections, (and code letters) specifying the tree that was the source of the extract tested. Each extract was tested against four microorganisms: S. aur = *Staphylococcus aureus*, C. albi = *Candida albicans*, E. faec = *Enterococcus faecalis*, and E. coli = *Escherichia coli.* The diameters of the inhibition zones are listed in mm, — = no growth inhibition observed. # Hits: The number of microorganisms with growth inhibited by the crude wood extract.



Eschweilera coriacea



Lecythis poiteaui

Figure 13. Growth Inhibition of *Staphylococcus aureus* by *E. coriacea* and *L. poiteaui*. Crude extracts derived from each study tree (denoted by code letter) were tested against positive (+) and negative (-) controls to document bioactivity. Clear zones around disks indicate growth inhibition.

The mean # bioassay hits (from Table 9, final column) for each tree species, along with the mean # of host species for the cerambycids reared from each tree species, is shown in Table 10. In both cases, there are significant differences among the five tree species. Tree species that produced cerambycids with relatively low host fidelity are considered Lo-Fi, while tree species that produced cerambycids with relatively high host fidelity are considered Hi-Fi. Tree species classed as 'Hi-Fi' produced significantly more bioassay hits than those classed as Lo-Fi: oneway Anova, df 1, $P = 0.0041$, using the program JMP-SAS.

The mean # of host species x the mean # of bioassay hits for each tree species (from Table 10) are plotted in Figure 14 and analyzed by linear regression ($P = 0.126$, R-sq. = .46, using the program JMP SAS). Figure 14 also includes an analysis of individual trees ($P = 0.089$, R-sq. = .13). Although the results are not statistically significant, there does seem to be a clear trend. The tree species hosting specialized cerambycids with few additional hosts had more hits in the antimicrobial bioassays than tree species hosting the less specialized cerambycids. The analysis of individual trees includes less data, because a specific host tree could not be documented for the many cerambycids that emerged in the big cages. The described trend accounts for a rather small portion of the variability among individual trees. Variability among trees could be influenced by a host of variables not presently addressed, including the effects of light, heat, and wind on branches prior to their collection.

ADDITIONAL PLANT-CENTRIC VARIABLES

Abundance, distribution, taxonomic complexity, architecture, etc.

Plant abundance is central to the concept of plant 'apparency.' I lack data from Les Eaux Claires to address the precise role of abundance, but all five tree species studied were

Table 10

A comparison of cerambycid fidelity and host plant toxicity

Tests	All Lecy	Host Plant					*P*
		CA#	LP#	GH*	EC*	CS*	
Mean # Host Species	8.95	12.09	12.6	7.23	5.42	3.55	0.0000
Mean # Bioassay Hits ±SE	1.64	1.4 ± .40	0.4 ± .24	2.0 ± .45	2.6 ± .24	1.8 ± .48	0.0142
Host Fidelity Class		Lo-Fi		Hi-Fi			
Mean # Bioassay Hits ±SE		0.9 ± .28		2.13 ± .26			0.0041

The mean # of documented host species is given for the cerambycids reared from all Lecythidaceae investigated (All Lecy) followed by the mean # of hosts for the cerambycids reared from each of the five host species. CA = *Corythophora amapaensis*, LP = *Lecythis poiteaui*, GH = *Gustavia hexapetala*, EC = *Eschweilera coriacea*, and CS = *Couratari stellata*: oneway Anova, df 4, $P = 0.0000$. The mean # bioassay hits is given for all 25 extracts tested (All Lecy) followed by the mean # of bioassay hits ±Standard Error for extracts from each of the five tree species: oneway Anova, df 4, $P = 0.0142$. # = Lo-Fi (tree species that produced ' low fidelity' cerambycids with more host species than the family mean). * = Hi-Fi (tree species that produced 'high fidelity' cerambycids with fewer host species than the family mean): Tree species classed as 'Lo-Fi' produced significantly fewer bioassay hits than those classed as Hi-Fi: oneway Anova, df 1, $P = 0.0041$.

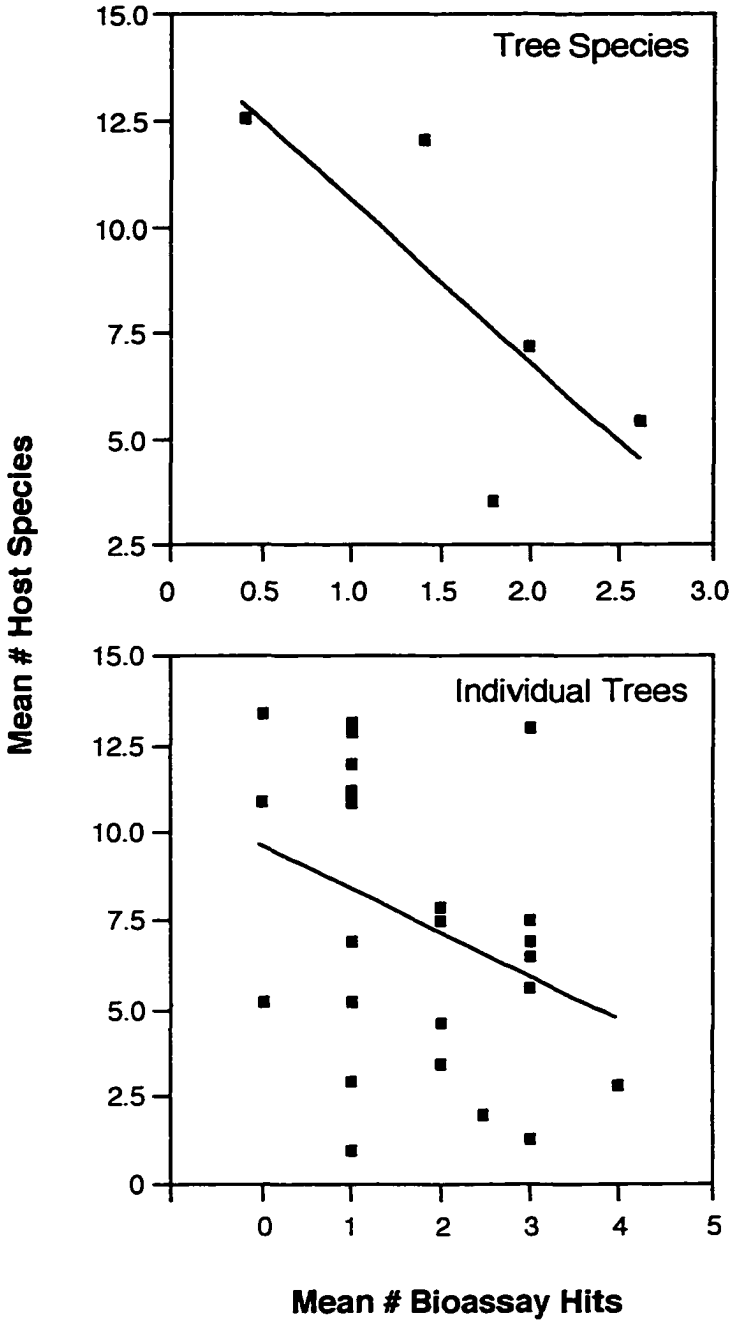


Figure 14. The trend between high host fidelity and high toxicity. Mean values for each tree species (from Table 10) are plotted and fit with a regression line: df 4, $P = 0.126$, R-sq. = .46. Mean values for individual trees are plotted and fit with a regression line: df 22, $P = 0.089$, R-sq. = .13. Only emergences from snacks are included in the analysis of individual trees (the specific host tree could not be documented for emergences in the big cages), and trees that did not produce any cerambycids were not included.

selected because they are relatively abundant at the study site. A detailed study of forest ecology at the nearby La Fumée Mountain revealed that Lecythidaceae was one of the most frequently encountered plant families. *Eschweilera coriacea*, *Couratari stellata*, and *Gustavia hexapetala* were, in that order, the most frequently encountered Lecythidaceae (Mori & Boom, 1987a). Although *C. stellata* and *G. hexapetala* were poorly colonized in this study (Table 8) they did, along with *E. coriacea*, give rise to cerambycids with relatively few additional hosts (Table 10).

Plant species with widespread distributions might be more consistently available to herbivores than those with restricted ranges. *Corythophora amapaensis* (F. G. and Amapá, Brazil) and *L. poiteaui* (F. G., Surinam, and eastern Amazonia) have relatively restricted distributions, while *C. stellata* (Guianas, western and central Amazonia), *E. coriacea* (Guianas, the Amazon Basin, and west of the Andes in Panama and Columbia), and *G. hexapetala* (Guianas, Amazonia, and north-central Venezuela) are widespread (Mori & Prance, 1993). The widespread tree species gave rise to cerambycids with a mean of 5.57 host plants, while the tree species with restricted distributions gave rise to cerambycids with a mean of 12.58 host plants (Table 11). At the generic level *Lecythis* has a widespread distribution, and only *Corythophora*, as currently delimited (Mori, pers. comm.), can be considered to have a restricted distribution. The difference in the host ranges of cerambycids reared from genera with widespread versus restricted distributions is still statistically significant, but considerably less dramatic (Table 11).

Taxonomic complexity (in this case, the number of species per genus) is more typically proposed as a predictor of the species richness of the plant's associated insect fauna than as a predictor of plant 'apparency' or insect specificity. I believe that few cerambycid species associated with Lecythidaceae are genuinely dependent upon a single host, and that documentation of a single host species is usually a sampling artifact (see Chapter 2).

Table 11

Additional factors proposed to influence insect host range

Tests	Mean # Hosts		*P*
	[redacted]		
Tree species	5.57	12.58	0.0000
Tree genus	8.68	12.09	0.0000
	[redacted]		
Spp/gen	5.64	12.27	0.0000
Spp/gen (Gu)	8.89	9.24	0.3576
	Mean Length		*P*
	[redacted]		
Beetle	9.99	7.55	0.0000
	[redacted]		
Branch	8.75	8.59	0.7003

The mean number of host species is listed for cerambycids reared from tree species with Widespread versus Restricted distributions: oneway Anova, df 1, $P = 0.0000$; and tree genera with Widespread versus Restricted distributions: oneway Anova, df 1, $P = 0.0000$. The mean number of host species is listed for cerambycids reared from tree species with Many congeners (> 35) versus Few congeners (< 35): oneway Anova, df 1, $P = 0.0000$; and from tree species with Many (> 10) versus Few (< 10) congeners present in the Guianas (Gu): oneway Anova, df 1, NS. The mean length is listed for cerambycids reared from Hi-Fi versus cerambycids reared from Lo-Fi tree species: oneway Anova, df 1, $P = 0.0000$). The mean length is listed for cerambycids reared from densely colonized branches (Dense, > 20 emerged cerambycids) versus sparsely colonized branches (Sparse, at least one, but < 5 emerged cerambycids): oneway Anova, df 1, NS.

Insects are often associated with taxonomically related plant species, and therefore a plant genus including many species might be, in effect, more frequently encountered than a plant genus with few species. For instance, a cerambycid exclusively associated with *Eschweilera coriacea* would only have access to 8.1% of the trees in a sample of 211 Lecythidaceae along the nearby La Fumée trail (Mori & Boom, 1987b). A cerambycid able to locate and successfully reproduce in any tree belonging to the genus *Eschweilera* (represented by 12 species) would have access to 46% of the Lecythidaceae in the sample.

In the Les Eaux Claires study, trees belonging to genera including many species (*E. coriacea* and *Gustavia hexapetala,* in Mori & Prance, 1993) gave rise to cerambycids with a mean of 5.6 host species, while trees belonging to genera including relatively few species (*Corythophora amapaensis*, *Couratari stellata*, and *Lecythis poiteaui*, in Mori & Prance, 1993) gave rise to cerambycids with a mean of 12.3 host species (Table 11). When the genera were categorized according to number of species present solely within the Guianas (Mori & Prance, 1993), there was no significant difference in the mean number of host species for the cerambycids reared (Table 11).

Plant architecture is also an intrinsic factor influencing 'apparency,' which categorizes plants on the basis of persistent or ephemeral growth forms. Among Lecythidaceae, the main intuitive difference in plant architecture is tree height. *Gustavia hexapetala* is a rather small understory species (< 20 m), *Eschweilera coriacea*, *Lecythis poiteaui* and *Corythophora amapaensis* are canopy species (20-35 m), and *Couratari stellata* is an emergent (> 35 m) (Mori & Boom, 1987a). There does not appear to be any relation between tree height and cerambycid specificity : each of the three tree species hosting cerambycids with relatively narrow host ranges falls into a different size class. One other conspicuous architectural difference is the nature of the trunk bark, which is relatively

smooth in all species except *L. poiteaui*, with ridged bark. This does seem potentially advantageous to the cryptic cerambycids associated with Lecythidaceae, but once again I fail to see any relation to their fidelity.

An alternate chemical hypothesis

Although the bioassays did suggest that tree species hosting specialized cerambycids contain various bioactive compounds, the wood samples are chemically complex and I lack data linking activity with compound. Wood and bark samples collected from *Eschweilera coriacea*, *Couratari stellata*, and *Lecythis poiteaui* have been analyzed by GC-MS, and each sample contained at least 95 different volatile compounds (Appendix III). Of particular interest are the compounds contributing to the foetid odors produced by the poorly colonized *C. stellata* and *Gustavia hexapetala*, proposed as deterrents to cerambycids associated with Lecythidaceae (Chapter 3). Several sulfur and nitrogen compounds were abundant in *Couratari stellata*, which has an exceptionally foul smell, and absent from *Eschweilera coriacea*. They appear to be only minor components in *Lecythis poiteaui*, which lacks the characteristic odor (Table 7). Trace quantities of these malodorous compounds may prove to be the rule, rather than the exception, within the family. Some cerambycid species clearly tolerate low levels of these compounds, and if low levels are indeed widespread within Lecythidaceae, the more tolerant cerambycid species would be able to able to utilize a broader range of hosts.

The chemical profile of *Lecythis poiteaui* may be substantially different at the beginning of the rainy season, when it bears pungent, bat-pollinated flowers. Many bat-pollinated flowers release sulfurous volatile compounds (Knudsen & Tollsen, 1995), and I suspect that an increase in sulfur compounds may have influenced the reduced cerambycid colonization noted during the rainy season (Table 6). Even if cerambycids are not

repelled by the musky smelling flowers, a radical seasonal change in the chemical signature of *L. poiteaui* would leave it less consistently recognizable to insect associates.

INSECT-CENTRIC VARIABLES

Feeding strategy, mobility, sensory capabilities

Feeding strategy determines the degree of contact an insect has with plant secondary metabolites, and therefore might influence host utilization patterns (Mattson et al., 1988; also see Chapter 2). Mobility and sensory capabilities potentially effect the amount of time an insect spends in search of food, a mate, or an oviposition site. Cerambycids are, as larvae, concealed feeders, and in French Guiana most species that attack fresh dead wood do appear to be specialists (Tavakilian et al., 1997). They have fully developed flight wings, and, presumably, a full complement of olfactory sensilla, which should facilitate host location. Feeding strategy, insect mobility, and sensory capabilities might have an impact on the host ranges used by insect taxa with vastly different life history attributes (see Chapter 2), but are unlikely to account for differences in host utilization among closely related insect species.

Size, life span, larval performance on different hosts

Insects with longer lifespans might afford to spend more time seeking an appropriate host, and this might favor the retention of specialized utilization patterns. Although I still lack complete life cycle data for the cerambycids reared from Lecythidaceae, the adults seem to be quite short-lived. Larger species were generally willing to feed in captivity and survived longer as adults (about a week), while the smaller species often expired rapidly (within a couple of days), apparently without feeding. I therefore feel that there is a relationship between beetle size and lifespan. Cerambycids reared from Hi-Fi tree

species were indeed significantly larger than those reared from Lo-Fi tree species (Table 11, oneway Anova, df 1, $P = 0.0000$, using the program JMP-SAS).

One of the principal explanations for host specialization is that insects are more successful when reared upon an optimal host, due either to differences in the nutritional quality of potential hosts, or to the detrimental effects of the various secondary metabolites. Because the major portion of the cerambycid life cycle is spent concealed under bark, I have searched for variability in insect fitness by comparing adult body lengths of the relatively few species that emerged from several hosts (Table 12).

Although there are generally very few emergences from secondary hosts (Table 8) and it is therefore difficult to quantify statistically significant differences in body length (Table 12), four of the five cerambycid species analyzed show the same pattern. *Eschweilera coriacea* and *Lecythis poiteaui* both generated similarly robust individuals. *Gustavia hexapetala* and *Couratari stellata*, characterized by foetid odors and impoverished cerambycid faunas, gave rise to diminutive individuals. *Corythophora amapaensis* is something of an enigma. This was the only poorly colonized tree species that lacked a foul odor, and the individuals reared were actually consistently larger than conspecifics that emerged from other hosts (Table 12). *Corythophora amapaensis* is clearly nutritionally suitable for the development of cerambycids associated with Lecythidaceae, but nevertheless is not a preferred host.

Interactions with predators, pathogens, and parasites

I lack rigorous data addressing the potential roles of various insect enemies. The rearing cages were checked every morning, night, and usually numerous times throughout the day, and assaults by predators upon newly emerged beetles were noted. Fifteen cerambycids were attacked by ants, one by pseudoscorpions, and one fragment of

Table 12

Mean body lengths of cerambycid species reared from at least three species of Lecythidaceae

Beetle spp.	Host Plant					*P*
	CA (*N*)	CS (*N*)	EC (*N*)	GH (*N*)	LP (*N*)	
N. mutilatus	9.22 (9)	7.75 (2)	8.75 (2)	—	8.84 (79)	0.0248
O. leucostigma	—	11.50 (2)	12.62 (218)	—	12.50 (1)	0.4257
P. crassimana	7.21 (112)	—	6.93 (90)	6.03 (37)	6.75 (152)	0.0000
P. mimetica	6.83 (3)	—	6.18 (28)	6.75 (2)	6.83 (280)	0.0698
P. pubescens	12.25 (2)	—	—	9.67 (6)	10.90 (92)	0.0923

The mean body lengths of beetles that emerged from multiple hosts are listed for each host plant: CA = *Corythophora amapaensis*, CS = *Couratari stellata*, EC = *Eschweilera coriacea*, GH = *Gustavia hexapetala*, and LP = *Lecythis poiteaui*. (Mean lengths are followed, in parentheses, by the number of individuals emerged).

exoskeleton was found in a spider web. The remains of eight additional beetles, presumably the aftermath of mortal combat, were subsequently found in rearing cages. *Lecythis poiteaui* was the most densely colonized tree species during the dry season, and *Eschweilera coriacea* was more densely colonized during the rainy season (Table 6). Of the eighteen predation events recorded in the dry season rearing cages, ten beetles emerging from *L. poiteaui*, and only two beetles emerging from *E. coriacea* were attacked. In the rainy season rearing cages, signs of predation were observed exclusively in association with *E. coriacea.* Although I lack even casual observations of predation upon immature forms, this assessment of predation upon adults is consistent with my assumption that, particularly in the under-bark community, predators and parasites are more likely to track prey than prey to avoid predators.

Competitive interactions

It is unlikely that either inter- or intraspecific interactions play an important role in determining the host ranges of cerambycids associated with Lecythidaceae. Many of these insects appear to persist at relatively low population densities (I spent three months following the dry season cut convinced that the entire rearing project would fail to yield data because I so seldom observed cerambycids on the cut branches)! On the two occasions when I did observe more than a single individual on a branch, beetles representing two or three species were present, but I did not observe any antagonistic interactions.

Nevertheless, 75% of the branch sections that gave rise to more than a single individual produced cerambycids belonging to more than one species, and a few exceptionally productive branch sections gave rise to cerambycids belonging to six or seven species (Appendix II). The majority of the branch sections were rather sparsely colonized. Although three canopy snacks did yield more than 50 individual cerambycids each, and

one of those gave rise to 99, the vast majority (83%) of the branch sections produced fewer than 10 individuals (Appendix II). Although the few very densely colonized branch sections were among those left in the canopy, which I was not able to observe, and many factors potentially influence host suitability, it seems unlikely that there was rampant competition.

Dominance, density

It has been suggested that dominant (numerically abundant) insect species might require a broader range of hosts to support their populations. I consider cerambycid species represented by more than 50 emerged beetles dominant (Table 8). Because these species are essentially responsible for the shape of the distribution seen in Figure 12, dominance alone will not account for the different patterns of host use indicated by the two peaks. Of the 1598 individual cerambycids belonging to species considered dominant, 43% have fewer than six documented host species. Of the three cerambycid species with at least 13 documented hosts, *Palame mimetica* and *Periboeum pubescens* were still primarily associated with a single host in this study. This suggests that while they may have the capacity to utilize numerous hosts, they remain selective when the preferred resource is sufficiently abundant.

A high density of attacking insects can be detrimental to insect fitness, if it results in resource deprivation, or beneficial, if the attack ultimately increases resource availability by increasing plant susceptibility. If insect density does affect fitness, there might be a corresponding impact upon host breadth (Jaenike, 1990). As a rough gauge of whether the cerambycid species reared in this study were affected by density, I compared the adult sizes of those reared from sparsely colonized branch sections (that produced < 5 cerambycids) with those reared from densely colonized branch sections (that produced > 20 cerambycids). I eliminated those species that did not occur in both sparsely and

densely colonized branch sections from the analysis. There was no significant difference in mean beetle length (Table 11, oneway Anova, df 1, $P = 0.7003$, using the program JMP-SAS).

DISCUSSION

Eschweilera coriacea, *Couratari stellata*, and *Gustavia hexapetala*, the three tree species classified as Hi-Fi, all showed unusually high levels of antimicrobial activity in the bioassays (even in comparison with numerous extracts from unrelated plants, see Rovira et al., in review). These same tree species are extremely abundant in central French Guiana, and have very widespread distributions. It may be no coincidence that tree species manufacturing compounds capable of inhibiting the growth of a spectrum of pathogens are both abundant and widely distributed.

The variables that seem to be associated with the host ranges of the cerambycids reared from *Eschweilera coriacea* and *Lecythis poiteaui* are summarized in Table 13. Many of the factors proposed to influence insect host range were not informative in our assessment of patterns demonstrated by closely related insects attacking closely related plants. Most factors that do appear to differentiate *E. coriacea* from *L. poiteaui* are related to plant 'apparency', or the ease with which a plant can be located.

Lecythidaceae are very well represented in the Guianas, both in terms of species and individuals present. The family exclusively comprises persistent woody plants, most of which are large, evergreen, forest trees (Mori et al., 1987), although the specific resource used (dead wood) is ephemeral. Of the two densely colonized tree species, *E. coriacea*, hosting the more specialized cerambycid fauna, is extremely abundant, has a widespread distribution, and belongs to a taxonomically complex genus. Although intraspecific

Table 13

Variables associated with the host fidelity of *E. coriacea* and *L. poiteaui*

Eschweilera coriacea Cerambycid fauna with high host fidelity	*Lecythis poiteaui* Cerambycid fauna with lower host fidelity
Frequently encountered at the nearby Mt. Fumée	Less frequently encountered at Mt. Fumée
Extremely widespread distribution	Restricted eastern Guayanan distribution
Many congeners (83, 21 present in the Guianas)	Fewer congeners, (25, 11 present in the Guianas)
High toxicity in antimicrobial bioassays	Low toxicity in antimicrobial bioassays
Lacked sulfur compounds (initial analysis)	Low levels of sulfur compounds (initial analysis)
No presumed seasonal change in sulfur levels	Presumed seasonal change in sulfur levels
Associated with more relatively large cerambycids	Associated with more relatively small cerambycids

chemical variability was common in preliminary analyses of wood samples (Berkov, unpubl. data), *E. coriacea* seems relatively consistent (Table 9). It also lacked any conspicuous seasonal change in odor, as noted in *L. poiteaui,* that might throw potential insect associates off track.

There does appear to be an imperfect association between host plant toxicity and beetle specificity. The pattern seems very clear when only *E. coriacea* and *L. poiteaui* are considered, but less so when the other tree species are included (Figure 14). Many variables apparently contribute to a plant species' predisposition to host a specialized fauna. Rhoades & Cates (1976) qualify their predictions about the association between resource predictability and herbivore fidelity with the caveat *"all other things being equal."* Unfortunately, other things never are equal, and it becomes increasingly difficult to perceive distinct patterns as more plant species are included in the analysis.

Corythophora amapaensis, like *L. poiteaui*, gave rise to cerambycids with a relatively broad host range (Figure 12), but very effectively inhibited the growth of *Staphylococcus aureus* in the bioassays (Table 9). Its primary cerambycid associate was *Palame crassimana* (Table 8), the 'least picky' cerambycid reared. *Corythophora amapaensis* does contain several dominant phenolic compounds that were not detected in the analyses of the other tree species (Berkov, unpubl. data), and these compounds might conceivably deter some Lecythidaceae specialists. It also has the most restricted distribution and fewest congeners (Mori & Prance, 1993) of any tree species investigated at Les Eaux Claires, and this alone may make *C. amapaensis* a less than ideal candidate to host more specialized cerambycids.

Any intermediate link between plant apparency and chemical defense system is difficult to discern. According to the theories proposed by Feeny (1976) and Rhoades & Cates

(1976), *Eschweilera coriacea* should rely heavily upon digestibility reducing compounds for defense, and, relative to *L. poiteaui,* support a generalized insect fauna (assuming that current patterns represent the endpoint of the proposed coevolutionary scenario). *Eschweilera coriacea* does appear to produce tannins, which are lacking in *L. poiteaui,* but *E. coriacea* also showed considerable toxicity in the bioassays (Table 9). Both tree species host cerambycids that are Lecythidaceae specialists, but those associated with *E. coriacea* show such high levels of fidelity that several species never emerged from an alternate host (Table 8).

I suspect that the chemical profiles of many tropical woody plants are too complex to be easily dichotomized. Digestibility reducing compounds are well represented in the family. Based on extract color, most Lecythidaceae do produce tannins, although they are occasionally lacking (for instance in *Lecythis poiteaui* and *Gustavia augusta*). The wood often contains crystal strands and / or silica bodies, although there is considerable intrageneric and even intraspecific variability, and neither predominate in *Eschweilera coriacea* or *Lecythis poiteaui* (de Zeeuw, 1993). One of the best field characters to identify Lecythidaceae is the presence of fibrous inner bark (Mori et al., 1987), and plant fiber is sometimes considered more effective at reducing digestibility than tannins (Waterman & McKey, 1983).

Toxins also appear to be well represented. Lecythidaceae appears to be rich in terpenoids, including many volatile monoterpenoids and sesquiterpenoids (Appendix III) and triterpene saponins. The dominant monoterpenoids detected from *E. coriacea* (1,8 cineole and limonene) and *L. poiteaui* (safranal) have all shown bioactivity in various bioassays (Escribano et al., 1996; Halligan, 1975; Ntiamoah, 1996; Obeng-Ofori et al., 1997). Nitrogen based toxins including indole compounds and selenium analogues of sulfur amino acids may be more widespread within Lecythidaceae than previously

supposed (Meurer-Grimes & Berkov, unpublished data). I had predicted that *E. coriacea* would be particularly toxic due to the prevalence of saponins, but variable performance in the described bioassays cannot be directly attributed to the presence of saponins, because similar compounds appear to occur in both *E. coriacea* and *L. poiteaui* (unpubl. data).

In short, each tree species investigated produces a tremendous variety of different compounds, and many, probably the majority, are not yet identified. Biological activity, even of common compounds that have been identified, has not been fully characterized. Finally, individual compounds (including saponins and tannins) may function both to reduce digestibility and as direct toxins (Rhoades & Cates, 1976; Scalbert, 1991). Perhaps it will become easier to discern patterns of allocation to either quantitative (digestibility reducing) or qualitative (directly toxic) defenses as more data are generated about the chemistry of Lecythidaceae.

Thus far I feel that there is a clear positive association between easily-located plants and the host fidelity of their insect associates. This probably extends to chemical factors as well. It may not be plant toxins *per se* that promote insect specialization, but rather the ease with which certain plant metabolites are perceived by insects, and the constancy of the chemical cues. In many cases toxins are associated with peculiar odors or bitter tastes, but the conspicuous and predictable nature of the chemical signal may be more important in influencing insect specialization than the toxicity of the compound.

CHAPTER 5

A Closer Look at Two Forms of the Enigmatic *Palame crassimana* (Coleoptera, Cerambycidae, Lamiinae, Acanthocinini)

SUMMARY

A newly discovered association between wood-boring longicorn beetles (Cerambycidae) and their host plants in the Brazil nut family (Lecythidaceae) inspired a year-long rearing project in the lowland Neotropical rainforest of central French Guiana. Branches severed from five different species of Lecythidaceae yielded 1,813 cerambycids belonging to 37 species. The most ubiquitous cerambycid reared was *Palame crassimana* Bates. *Palame crassimana* currently includes at least three distinct morphological forms, two of which were reared during this experiment. The more abundant 'bicolor' form emerged from four of the five potential host species, while the less abundant 'unicolor' form emerged exclusively from *Eschweilera coriacea*. In addition, the 'bicolor' form emerged almost exclusively from branches cut during the dry season, while the 'unicolor' form emerged almost exclusively from branches cut during the rainy season. In this chapter I discuss morphological characters in an attempt to clarify the status of these two forms.

INTRODUCTION

The quest to catch the process of speciation in the act is hard to resist. 'Incipient species' remain elusive and always slightly out of reach, ultimately circumventing a tightening grasp. The probability of observing a population as it becomes the unique entity called a species may be no greater than the probability of observing a species become extinct. Nevertheless, species do arise and they do cease to exist, these events must at some point happen, and the impulse to track the progression is strong.

While entire scientific disciplines are based upon evolutionary theory, the underlying definitions and concepts themselves continue to evolve. Ancestral species clearly give rise to divergent lineages, and the process of speciation occurs as the result of some sort of barrier to gene flow between populations of organisms. This barrier is, in many cases, intervening physical space that leaves populations out of 'cruising range' (Futuyma & Mayer, 1980). Novel plant species can arise without geographic separation, but plants have looser requirements than most animals. They regularly survive changes in ploidy (Grant, 1981; Mayr, 1970), and individuals carrying nondeliterious mutations may be able to pass them on to their progeny via vegetative reproduction or self-fertilization. There is a vast literature debating whether or not animal populations can achieve species rank without geographic separation prohibiting gene flow; whether, in effect, ecological factors alone can prevent sympatric populations from interbreeding (Diehl & Bush, 1984; Futuyma & Mayer, 1980; Jaenike, 1981; Mayr, 1970).

Of the various models that have been proposed to validate sympatric speciation of animals, the formation of host races among host specific phytophagous insects has retained the greatest credibility (Diehl & Bush, 1984; Futuyma & Mayer, 1980). It is widely acknowledged that many insect species demonstrate fairly high levels of fidelity

to a particular host plant taxon, but it is also evident that insects are capable of switching their allegiances (Diehl & Bush, 1984). If one population of an insect species becomes established on a novel host, that population, continuing to reproduce on a host not utilized by the ancestral population, could effectively become genetically isolated. Over time, the diverging population could become sufficiently distinct that it would be recognized as an independent species.

Proponents of allopatric speciation suggest that if one population successfully made the transfer to a novel host, there would be little to prevent members of another sympatric population from making the same switch, thereby keeping the paths of genetic interchange open. This would ultimately lead to a single species with a broader host range, rather than to a pair of host races (or incipient species) with narrow host ranges. They maintain that any proposed scenario of sympatric speciation can be just as easily explained as allopatric speciation followed by recolonization, and that in most cases putative host races are really closely related sibling species (Futuyma & Mayer, 1980; Jaenike, 1981; Mayr, 1970).

Rearing experiments at Les Eaux Claires, French Guiana, have indicated that two morphological forms of the cerambycid species *Palame crassimana* Bates are, at least in this locality, primarily associated with different host plants. In addition, one form reproduces primarily during the rainy season, and the other primarily during the dry season. In this chapter, I will 1) summarize pertinent results from the rearing experiments, 2) discuss the characters that have been described in prior taxonomic treatments of *Palame* species and the distribution of those characters among the species and forms reared in this study, and 3) compare the genitalia of the two forms. I will discuss whether the available data suggest that the forms are candidates for the

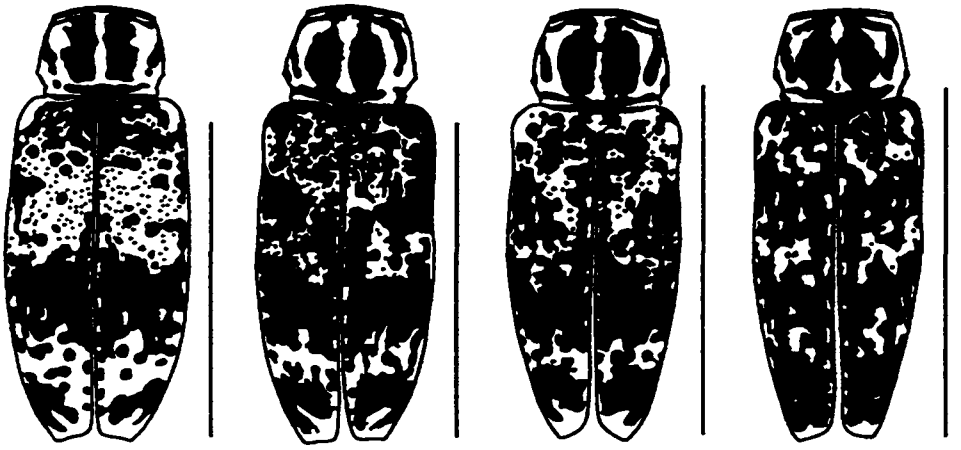
controversial designation 'host races,' or whether they should in fact be recognized as true species.

Palame Bates in French Guiana

According to the most recent generic revision (Monné, 1985), the cerambycid genus *Palame* Bates includes five species: *Palame aeruginosa* Monné, 1985; *P. anceps* (Bates, 1864); *P. crassimana* Bates, 1864; *P. mimetica* Monné, 1985; and *P. vitticole* (Bates, 1864). Three of the five species currently attributed to the genus have been documented in French Guiana: *Palame anceps*, *P. crassimana*, and *P. mimetica*. Each of these species has been reared in abundance during two cerambycid-rearing projects: one multiyear project in the Sinnamary River Basin (Tavakilian et al., 1997), and a second year-long study at Les Eaux Claires (Berkov & Tavakilian, in press). In French Guiana, all three species appear to be associated exclusively with trees belonging to the Brazil nut family (Lecythidaceae).

Although *Palame* species are quite variable (in terms of size, color of the integument and the pubescence, and the pattern of appressed pubescence on both the pronotum and the elytra), in French Guiana there do seem to be three discrete morphological forms of *Palame crassimana*. These forms, primarily differentiated on the basis of the color and pattern of the appressed pubescence on the pronotum and the elytra, will hereafter be referred to as 'olivaceous,' 'bicolor,' and 'unicolor' (Figures 15, 16).

The olivaceous form has a dark integument with appressed greenish pubescence. The bicolor form has an integument variable in color, with lighter appressed pubescence that gradates from a warm tawny color at the base of the elytra to white at the apex. The majority of the lighter appressed pubescence is in the anterior half of the elytra. The unicolor form has a dark integument and a reduction in the appressed pubescence, which



N. olivoniger
Amazonas, Brazil

X. guianensis
(British) Guyana

945 LP
French Guiana

1405 EC
French Guiana

Figure 15. Variability among forms currently included in *Palame crassimana*. *N. olivoniger* = the holotype of *Nyssoodoretus olivoniger* Gilmour, 1959 (this seems to be equivalent to the olivaceous form); *X. guianensis* = the holotype of *Xorathes guianensis* Gilmour, 1963 (both were synonomized with *P. crassimana* in Monné, 1985); 945 LP = bicolor form with some reduction in lighter pubescence, reared from *Lecythis poiteaui* at Les Eaux Claires; 1405 EC = unicolor form with minimal reduction in lighter pubesence, reared from *Eschweilera coriacea* at Les Eaux Claires. Size bars = 5 mm.

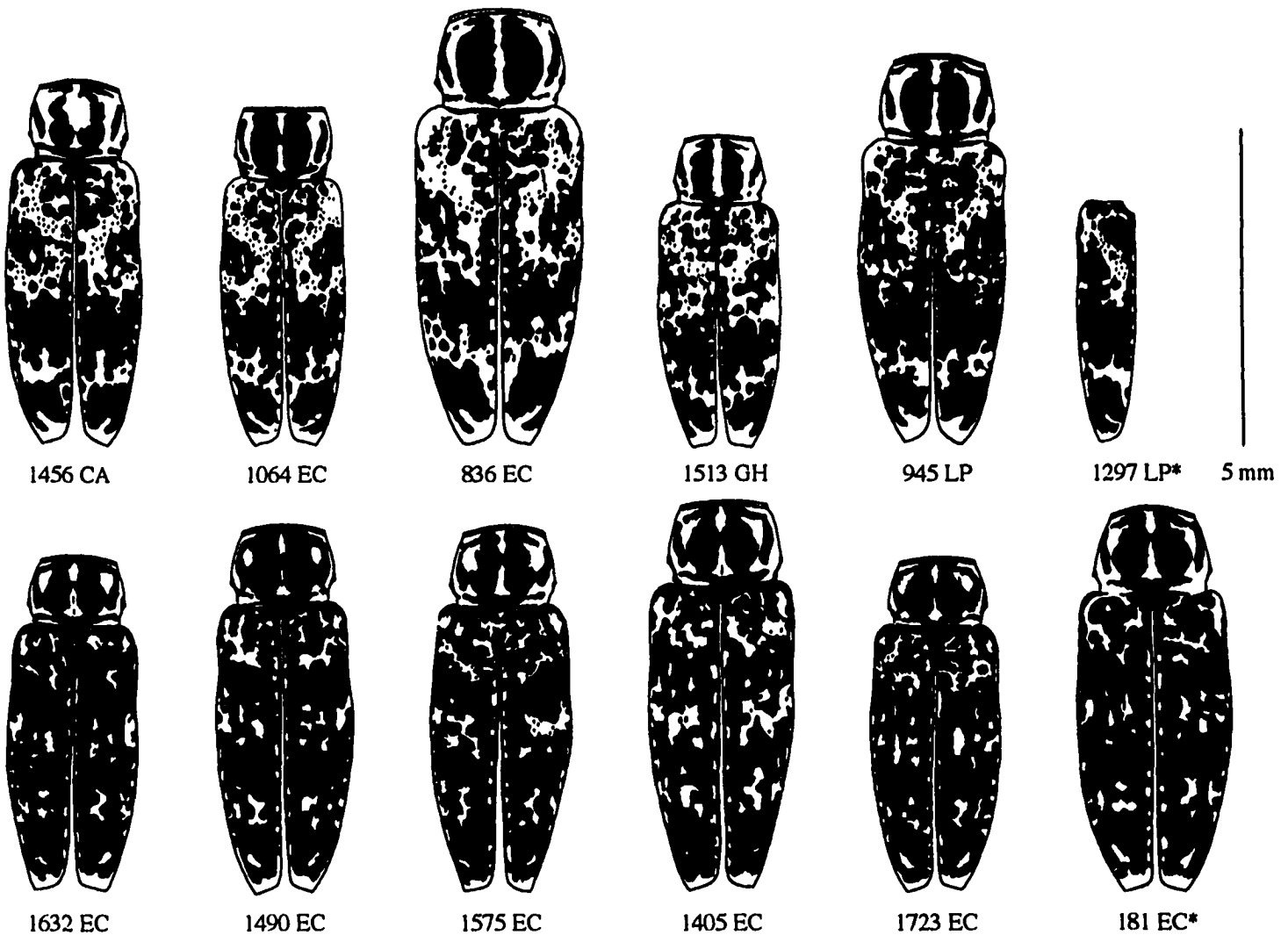


Figure 16. Pubescence patterns of *Palame crassimana*, bicolor (top row) and unicolor (bottom row) forms. Collection numbers specifying the individual beetles are followed by codes indicating the host species. CA = *C. amapaensis*, EC = *E. coriacea*, GH = *G. hexapetala*, LP = *L. poiteaui*. * = seasonal misfits: the bicolor form was reared from a rainy season branch and the unicolor form was reared from a dry season branch.

is rather evenly distributed on the elytra. Because of the reduction in the amount of the lighter pubescence, it is seldom interrupted by the dark spots surrounding punctations in the cuticle that are common in the other forms (Figures 15, 16). The pubescence lacks a conspicuous gradation in color, although this may be an artifact of the reduction in amount. All three forms were reared at Sinnamary, and the bicolor and unicolor forms were reared at Les Eaux Claires.

Palame crassimana (bicolor form) was the 'least picky' cerambycid reared at Les Eaux Claires. It emerged with some frequency from four of the five potential host trees (Chapter 2, Table 4), and was conspicuously absent only from the highly malodorous and sparsely colonized *Couratari stellata.* The tree species *Lecythis poiteaui* produced the greatest number of individuals, and all but one emerged from branches cut during the dry season. *Palame crassimana* (unicolor form) emerged exclusively from *Eschweilera coriacea* (the tree species that produced the fewest individuals of the bicolor form), and all but two individuals emerged from branches cut during the rainy season.

Taxonomic history

When Bates (1864b) described *Palame crassimanus* as the type species for the genus, he differentiated it from related genera *Sporeti* and the *Colobotheæ* (with setose elytra and other shared characters) on the basis of the dense pubescence clothing the coxae and sterna of the male, and the lack of a prolonged ovipositor in the female. In the same year, he described the new genus *Nyssodrys* (1864a), including two species currently attributed to *Palame (Nyssodrys anceps* and *Nyssodrys vitticollis*). *Nyssodrys* was characterized in part by the lack of setae on the body, and by the female having an ovipositor that extended beyond the apices of the elytra.

Gilmour (1959, 1963), apparently unfamiliar with the genus *Palame*, described two new genera based on specimens (Figure 15) that have since been synonomized with *Palame crassimana* (Monné, 1976, 1985). Gilmour (1959) described *Nyssodoretus olivoniger* after examining a single female specimen. The genus *Nyssodoretus* was differentiated from *Sporetus* Bates and *Nyssodrystes* Gilmour (*Nyssodrys* Bates, *ex parte*) by the restriction of the elytral setae to the margin. This specimen was described as having a short ovipositor extending slightly beyond the apices of the elytra. He subsequently described *Xorathes guianesis* based on two female specimens (Gilmour, 1963). Noting similarities to *Oxathres* Bates and *Sporetus* Bates, Gilmour distinguished *Xorathes* by the bispinose termination of the apical ventrite and an obtuse pygidium (extending a little beyond the apices of the elytra). *Xorathes guianensis* was described with fairly numerous, sublinear setae on the elytra.

In 1972, Martins & Monné published a paper listing additional characters to aid in the recognition of *Palame* Bates, still considered a monospecific genus, and differentiating it from the newly described genus *Neopalame* Martins & Monné. This paper was the first mention of one of the most conspicuous characteristics of the *Palame crassimana* male: the apex of the fifth antenna segment is swollen, and the apex of the sixth segment forms a small recurved hook. They also noted that the males had protuberances on the inner margin of the anterior tibiae. These, in conjunction with the ventral pubescence, and increased pubescence of the fore and mid-tarsi (males) and the lack of a prolonged ovipositor (females) were the main characters used to differentiate *Palame* Bates from *Sporetus* Bates. *Neopalame* Martins & Monné was distinguished in part by the presence of apical enlargements and hooks (males) on the fourth and fifth antenna segments, rather than on the fifth and sixth segments.

Monné (1976) realized that the males of the species originally described by Bates (1864a) as *Nyssodrys vitticollis* also had an apical hook on the sixth antenna segment. This, in conjunction with other shared attributes, convinced him to transfer the species to *Palame* Bates. He did not mention characters originally proposed to distinguish *Nyssodrys* from *Palame* (the lack of setae on the elytra and the female having an ovipositor extending beyond the apices of the elytra), although a short ovipositor is clearly visible in the supplied photograph. In the same publication he mentioned that the female holotypes Gilmour designated when he described *Nyssodoretus olivoniger* and *Xorathes guianesis* might actually represent different genotypes of *Palame crassimana.*

When Monné eventually revised the genus *Palame,* he did indeed synonomize them with *Palame crassimana* (Monné, 1985). He also transferred the species originally described as *Nyssodrys anceps* into *Palame*, and described two new species (*P. mimetica* and *P. aeruginosa*). Males of these three species all lack the apical hook on the sixth antenna segment, but according to his description all have ventral pubescence, thickened anterior femora, and dilated anterior and mid-tarsi with lateral hairs. *Palame anceps* and *P. mimetica* males have rows of teeth on the anterior and mid tibiae, and the females are described with ovipositors extending 1.5 to 2 mm beyond the apices of the elytra. *Palame aeruginosa* was described from a single male specimen, and there is no data available about the ovipositor. All five species appear to have elytral setae. The characters used to differentiate the five species in a key include the color and pattern of pubescence, the presence or lack of elytral punctations in addition to those associated with erect setae, the presence or absence of the apical hook on the males' sixth antenna segment, and the presence or absence of rows of teeth on the ventral face of the anterior and mid-tibiae.

MATERIALS AND METHODS

Body lengths of individual specimens were measured in the field from the anterior portion of the scape to the tip of the elytra. Subsequently, numerous individuals belonging to each of the three species and two morphological forms were examined for their distribution of the characters noted above. Illustrations were made of the elytra and pronotum of females (five each form, Figure 16), using a camera lucida at approximately 12x magnification. Illustrations were also made of the 'seasonal misfits' (one of the two unicolor individuals reared from a dry season branch and the sole bicolor individual reared from a rainy season branch, Figure 16). The holotypes described by Gilmour as *Nyssodoretus olivoniger* and *Xorathes guianensis* were also examined and illustrated (Figure 15). Pinned specimens from Les Eaux Claires and all illustrations were examined to search for intermediates between the two forms.

In addition, male (five each form) and female specimens (ten each form, including the five specimens illustrated in Figure 16) were dissected and examined. Drawings of the male and female genitalia were made using a camera lucida at 140x magnification. Illustrations of the spermathecae removed from the specimens illustrated in Figure 16 are shown in Figure 17. The female spermathecae were measured in both length and width (all measurements were made in cm from the illustrations). The length was measured from the apex to the point where the spermatheca begins to narrow. The width was measured at three points, and the average was taken. The spermathecae length, width, and ratio of width to length were investigated to see if there was a correlation with either body length, or with morphological form (Figure 18).

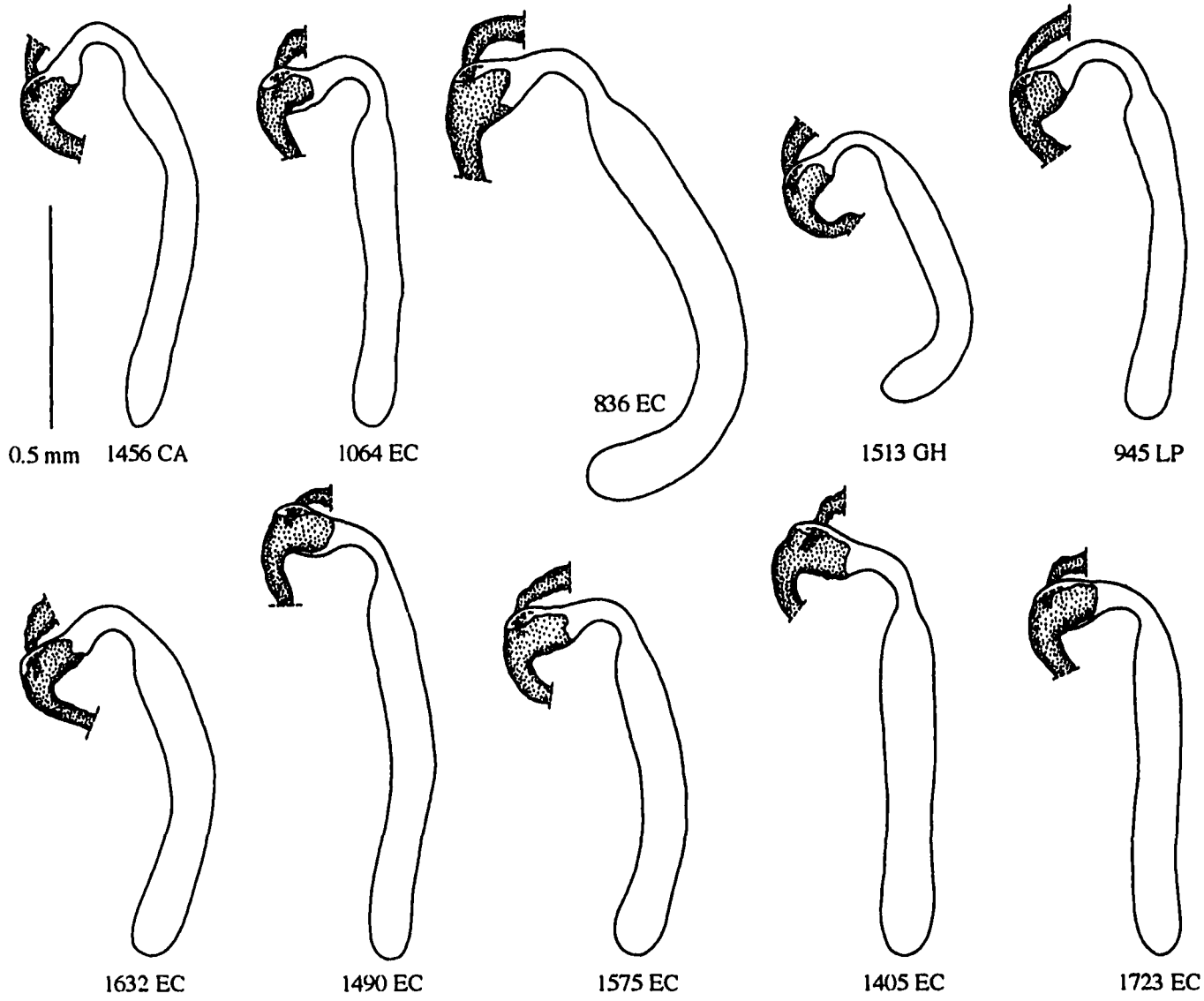


Figure 17. Spermathecae of *Palame crassimana*, bicolor (top row) and unicolor (bottom row) forms. Collection numbers specifying the individual beetles are followed by codes indicating the host species. CA = *C. amapaensis*, EC = *E. coriacea*, GH = *G. hexapetala*, LP = *L. poiteaui*.

RESULTS

The distribution of characters among Palame reared at Les Eaux Claires

One of the advantages of rearing insects is that you typically end up with many individuals, representing both genders, in fairly good condition. They do, however, represent individuals from a single locality at a single point in time. Table 14 summarizes the distribution of many of the characters noted above among the three species and two morphological forms that were reared at Les Eaux Claires. Based on a comparison with the material available at the American Museum of Natural History, *Palame* can be easily distinguished from *Nyssodrys* by the combination of the sublinear erect setae on the elytra, and the long ventral pubescence of the male. The single male specimen of *Sporetus* that I was able to observe did have erect setae, but lacked the long ventral pubescence (which is however found in other species belonging to the same tribe), and the single female specimen did have a much longer ovipositor than *Palame* spp.

The bicolor and unicolor forms of *Palame crassimana* are not immediately easy to differentiate, but can, with experience, be easily distinguished on the basis of external morphology. They appear to be more closely related to each other than to either *Palame mimetica* or *Palame anceps*. The pubescence pattern of the unicolor form can be easily derived from that of the bicolor form by a reduction in the lighter appressed pubescence (Figure 16). Males of both forms have the recurved apical hook on the sixth antenna segment that is lacking in *P. mimetica* and *P. anceps* (although this character is shared with *Palame vitticolle*, a species documented only in Brazil). In addition, the diagnostic ventral pubescence is actually much more conspicuous in both the bicolor and unicolor forms of *P. crassimana* than in the other two species (Table 14).

Table 14

The distribution of characters among *Palame* reared at Les Eaux Claires

CHARACTER	PA	PC (B)	PC (U)	PM
Elytra with sublinear erect setae	++	+++	+++	+++
Elytra with some punctations lacking setae	+++	+++	+++	+++
Male with recurved hook on antenna segment 6	—	+++	+++	—
Male with long, soft ventral pubescence	++	+++	+++	++
Male with a protuberance on anterior tibiae	+	+	+	+
Male with a row of teeth on the anterior and mid tibiae	++	—	—	—
Female with an ovipositor that extends beyond elytral apices	++	+	—	—

PA = *P. anceps*, **PC (B)** = *P. crassimana* bicolor form, **PC (U)** = *P. crassimana* unicolor form, **PM** = *P. mimetica*. +++ = character conspicuously and consistently present, ++ = character less conspicuous, + = character inconspicuous or variable, more likely to be apparent in robust individuals, — = character absent.

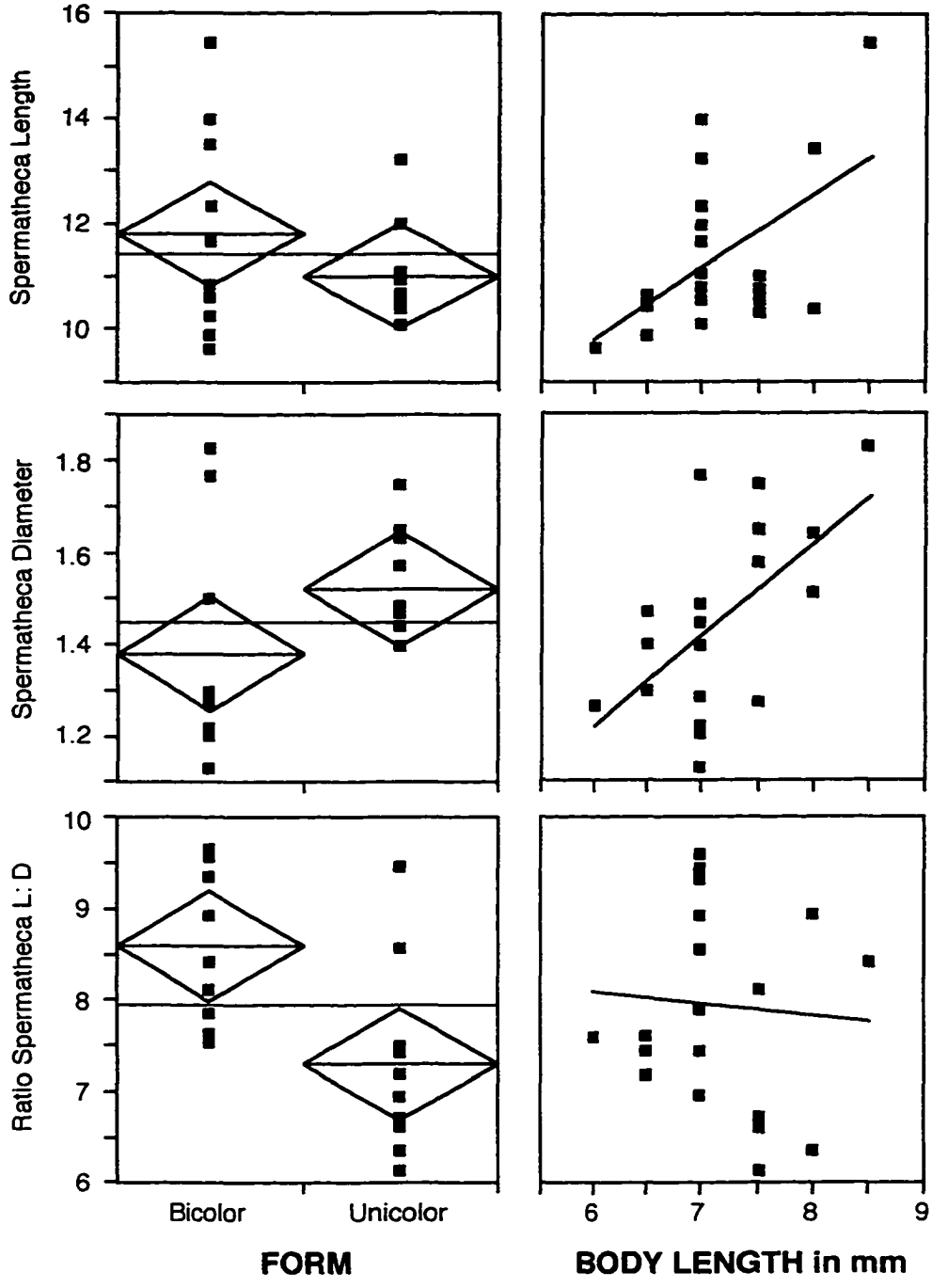


Figure 18. Comparisons between spermatheca measurements and *Palame crassimana* forms, body lengths. Spermatheca Length x Form: P = .2531, R-sq. = .02; Spermatheca Length x Body Length: P = .0179; R-sq. = .23. Spermatheca Diameter x Form: P = .1164, R-sq. = .08; Spermatheca Diameter x Body Length: P = .0067, R-sq. = .30. Ratio of Spermatheca Length : Diameter x Form: P = .0049; R-sq. = .33; Ratio of Spermatheca Length : Diameter x Body Length: P = .78, R-sq. = -.05.

Genitalia in two forms of Palame crassimana

The different patterns of host utilization and the different peaks in reproductive activity (Chapter 2, Table 4) initially suggested that the bicolor and unicolor forms might actually represent two different species. No consistent differences were observed in the male genitalia or a variety of other characters examined, including the length of the third tarsal segment on the hind leg and the number of erect setae on the elytra and antennae.

There did appear to be a subtle distinction in the shapes of the female spermathecae: the unicolor form had a spermatheca that initially looked like a regular hot dog, while that of the bicolor form looked like a foot-long hot dog! Although spermatheca length and width were each better correlated with beetle length than with morphological form, the ratio of spermatheca length to width showed no relationship at all to beetle length (Figures 17, 18). It was actually the ratio of length to width, rather than absolute length or width, that had caused me to perceive the bicolor spermatheca as a foot-long hot dog. Even in ratio, there was some overlap between forms, but the means of the two forms were significantly different (Figure 18: oneway Anova, df = 1, $P = .0049$, using the program JMP-SAS).

DISCUSSION

Conclusions based on the results from a single experiment (be it ever so long) at a single locality can only be considered preliminary. Nevertheless, some unequivocal deductions can be made. The bicolor and unicolor forms of *Palame crassimana* are sympatric at both Sinnamary and Les Eaux Claires in French Guiana. The two forms do not represent random variation within a polymorphic species, because at Les Eaux Claires they are largely associated with different host plants, and typically reproduce at different times of the year. At both sites the unicolor form can be distinguished from the bicolor form on the basis of external morphology (primarily the pattern of the appressed pubescence on

the elytra) and, at least at Les Eaux Claires, by a very subtle anatomical character (ratio of spermatheca width to length). The difference in morphology is not an artifact of the larval host plant, because both forms have been reared from *Eschweilera coriacea,* and in one case, both forms have actually been reared from branches severed from the same tree (A, voucher M24078, see Appendix II), albeit during different seasons.

Jaenike's criteria for ascertaining the existence of host races

The minimal differences distinguishing the two forms do not provide clues about physiological differences that would prevent interbreeding, and given the patterns of host utilization at Les Eaux Claires, a limited opportunity for interbreeding does exist. In order to determine whether these forms might actually qualify as host races, I have evaluated the data in light of a set of 'criteria for ascertaining the existence of host races' proposed by Jaenike, 1981. The criteria are listed and discussed below:

1. (The populations) must be sympatric...

   This is clearly the case at two localities in French Guiana.

2. There must be a statistically significant genetic difference between the populations, suggesting...that gene flow between them is not extensive.

   There are statistically significant differences in the time of emergence, in the ratio of spermatheca length to width, (and most likely in the pubescence pattern) that are probably genetic in basis.

3. The genetic difference... cannot be one that is directly related to host selection.

   The seasonal variability is not directly related to host selection (there is no reason to suppose that the host tree species preferentially yield dead wood at different times of the year), nor is the morphological variation (both forms have been reared from *Eschweilera coriacea*).

4. ...the genetic difference is not solely the result of natural selection acting on the current generation of individuals.

   Both forms have been reared at disjunct localities, during different years.

5. If the above conditions are met it should be shown, if experimentally feasible, that the genetic difference between the two populations disappears over a period of generations when they are confined to breed on a single food type.

   This would not be an easy task, given the seasonal difference in reproductive period and the short adult lifespan of *Palame crassimana.*

According to Mayr, 1970, host shifts ultimately leading to speciation would be more likely to take place among peripheral populations and that "as soon as reproductive isolation is achieved the newly evolved species can reinvade the range of the parental species and live side by side with it." This seems like a reasonable scenario to account for a hypothetical host shift from *Lecythis* to *Eschweilera*: *Lecythis* does drop off in both diversity and abundance in regions (western and southern Amazonia, southern Central America) where *Eschweilera* is still fairly common (Mori & Prance, 1990). I fail to understand, however, why reproductive isolation would be a necessary prerequisite for a population thriving on a new host to reinvade the ancestral range.

Rearing experiments at Les Eaux Claires have convinced me that host selection has the potential to be a powerful isolating mechanism (particularly among insects like cerambycids that meet and mate directly on the host plant). Although Tavakilian's data (1993, 1997) make it clear that many cerambycids have the capacity to utilize taxonomically related hosts, which would tend to break down isolation via host plant over time, those cerambycid species associated with *Eschweilera coriacea* tend to show high levels of host fidelity (see Chapter 4). *Eschweilera coriacea* was also the only tree species investigated that appears to host a distinctive rainy season fauna (all of its

relatively small cerambycid associates were more abundant at this time). These factors would increase the probability of an enduring reproductive isolation.

It seems slightly unfair that the criteria for ascertaining the existence of host races should be much more rigorous than those for ascertaining the existence of species, but Futuyma, 1980, makes it clear that the burden of proof is on the proponent of any model of sympatric speciation. According to Jaenike's criteria, the way to definitively determine the taxonomic status of *Palame crassimana* would be to interbreed the two forms and observe the fate of the subtle differences currently distinguishing them. The chance to test for the capacity to interbreed seems slender. It might be possible to rear both forms at the same time (perhaps by providing an abundance of freshly cut *Eschweilera coriacea* at the very beginning of the rainy season), but it would be difficult to maintain breeding populations. Breeding experiments might also be confounded by a potential capacity for hybridization among recognized species belonging to the genus *Palame*.

There are several other kinds of evidence that might contribute to an evaluation of the status of the two forms of *Palame crassimana*. First, it would be informative to examine material from a locality other than Les Eaux Claires to see whether the spermatheca length : width ratio remains a feasible character. It would be of particular interest to examine (or rear) specimens from peripheral areas of Lecythidaceae's range. Many studies of host races or sibling species have examined allozyme data (Emelianov, et al., 1995; Jiggins & Davies, 1998) rather than ecological data, and it might also be possible to look for molecular differentiation between the two forms.

Like all of the best arguments, the argument about the potential existence of host races may never be won. And like all of the best quests, the quest to catch the process of speciation in the act is one with its object ever elusive.

CONCLUSIONS

Of the variables investigated in this study (five tree species, stratum, season, and branch diameter) the only one that was not informative was branch diameter. Before the described cerambycid rearing experiments were designed, I perceived two patterns in the data generated by Tavakilian's rearing experiments in French Guiana (Tavakilian, 1993; and the more complete data set eventually published in Tavakilian et al., 1997):

1) There seemed to be one group of cerambycids that would reproduce in any Lecythidaceae, with the exception of a few tree species apparently avoided by all cerambycids.
2) There seemed to be a second group of beetles that emerged primarily from *Eschweilera* spp. and *Couratari* (as represented in Tavakilian's experiments by *C. guianensis).*

In the rearing experiments at Les Eaux Claires, cerambycid species belonging to the first group, including *Palame mimetica, Xylergatina pulchra,* and *Periboeum pubescens*, were associated primarily with *Lecythis poiteaui.* Many did show some flexibility in their host utilization patterns at Les Eaux Claires (Table 8), and when Tavakilian's data were merged, had a relatively large pool of potential host species (Figure 12). Most of the cerambycid species belonging to Tavakilian's *Eschweilera / Couratari* cluster, including *Oedopeza leucostigma, Palame anceps,* and *Xylergates elaineae,* were associated primarily with *Eschweilera coriacea* at Les Eaux Claires. These and other cerambycid species reared from *E. coriacea* at Les Eaux Claires do genuinely appear to be more specialized in their host utilization patterns.

At least in the case of these two major groups of cerambycids, those with more specialized patterns of host utilization are associated with the tree species currently

considered, on the basis of floral morphology, to be more highly derived. This may suggest that the pattern of host shift that appears to be taking place (or has recently taken place) within *Palame crassimana* is typical for cerambycids associated with Lecythidaceae. In general, there appear to be correlations between the abundance, distribution, and toxicity of the host plant (which may not be entirely independent), and the fidelity of the cerambycid associate.

Couratari stellata, the representative of *Couratari* sampled at Les Eaux Claires, produced the profoundly unpleasant odor that appears to be associated with diminished cerambycid yields both at Sinnamary and at Les Eaux Claires. I propose that this foul odor, also produced by *Gustavia hexapetala*, is a deterrent to Lecythidaceae specialists seeking oviposition sites, and is one of the chemical attributes characterizing some Lecythidaceae species avoided by most cerambycids.

Apart from the sulfurous compounds prevalent in *Couratari stellata*, this species does appear to share certain chemical characters with *Eschweilera coriacea*. The same dominant monoterpenoids were detected in the GC-MS analysis (1,8 cineole and limonene), and they also shared a dominant peak in the HPLC analyses (unpublished data: methanol phase, RT 47). The dominant monoterpenoid of *Lecythis poiteaui* was α-safranal, and in the HPLC analyses *L. poiteaui* was dominated by a mixture of unidentified compounds with absorption spectra atypical of any other Lecythidaceae investigated.

Although I've identified certain chemical attributes that I believe contribute to intrafamilial variability in cerambycid attack, I still lack any idea what it is that, from the cerambycids' point of view, defines Lecythidaceae as a unit. There are numerous unidentified compounds apparent in both HPLC and TLC analyses that are either

widespread or sporadically distributed within the family, but they may simply be ubiquitous plant compounds. I've clearly just touched the tip of the iceberg in this investigation into the plant metabolites influencing cerambycid attack in Lecythidaceae.

The big picture

Some of the explanations for observed phenomena proposed in this thesis are admittedly speculative, but speculations serve an important function: they can stimulate additional research. One of the most important legacies of Erwin's 1982 paper was the attention it drew to the dearth of empirical research illuminating the dynamics of plant-insect interactions in tropical forests. It is not our intention to enter the fray by generating any sort of estimate of the potential number of arthropods, but I would like to comment upon some of the assumptions made in the initial paper (that many tropical insects are restricted to the canopy and / or highly host specific) that led to the conclusion that the vast majority of tropical insects are as yet undescribed.

Only 18 of the 37 cerambycid species reared in this study (49%) were sufficiently abundant that one might draw any conclusion about stratum preference. I hypothesized a stratum preference for beetles represented by at least 10 individuals from at least two hosts, when at least 95% of the individuals emerged from branches at either ground or canopy level (Table 1). Of the 18 cerambycid species, ten (55%) were present at both ground and canopy level. Five species (28%) were associated almost exclusively with ground level branches, and only three species (17%) were restricted to the canopy level branches.

This is not consistent with the Erwin's assertion that two out of three tropical insects are restricted to the canopy, although, as with *Palame* spp., there may be a seasonal association. Our results also deviated from stratum preferences reported for cerambycids

in a lowland tropical forest in Sulawesi (Hammond, Stork, & Brendell, 1997). Hammond et al. hypothesized that although 25% of the species sampled were not sufficiently abundant to classify, 75% of the remaining cerambycids were tree-crown specialists. Although the sampling regime in Sulawesi was comprehensive, only adult cerambycids were sampled, which may have biased the results. Overall, many more beetle species were classified as ground specialists than as tree crown specialists.

Unfortunately, there are no simple generalizations to be made about host specificity. The predisposition towards host fidelity varies widely among different groups of insects associated with different groups of plants. In this study, I intentionally investigated a group of cerambycids that appeared to be family level specialists, but different sampling regimes at Sinnamary and at Les Eaux Claires provided estimations of potential host range versus optimal host range.

Erwin estimated that 20% of herbivorous insects were dependent upon a single host plant for survival. Tavakilian's data for Neotropical cerambycids suggested that overall, when a host utilization strategy could be hypothesized, specialists outnumbered generalists three to one (Figure 1). The majority of specialists were seldom restricted to a single host plant, however, and often successfully reproduced in related tree species belonging to a particular plant family. Family level specialization, a host utilization strategy that seems to be prevalent among Neotropical cerambycids, may prove to be common to other phytophagous or xylophagous insects in high diversity tropical forests.

Finally, Erwin (1982) implied that for each currently described arthropod species, at least 29 unnamed species were still waiting in the wings. In this study, five species of Lecythidaceae gave rise to 1,813 cerambycids belonging to 37 species. Of these species, 11 had not previously been described and, although 21 species of Lecythidaceae had

already been investigated for their cerambycid associates (Tavakilian et al., 1997), ten of the undescribed species had not been previously reared from Lecythidaceae. It is clear that many tropical insects do await description, but the 30% revealed in this study do not begin to approach Erwin's estimate. Cerambycids are, of course, both economically important and among the megafauna of the insect world, and therefore relatively well-investigated.

Appendix I: Twenty-five Lecythidaceae trees sampled at Les Eaux Claires, French Guiana

Tree species[a]	Code	Voucher	Ht.[b]	DBH[c]	Location[d]	Cut (D)[e]	F (D)[f]	Cut (R)[g]	F (R)[h]
C. amapaensis	O	M24145	25 m	30.1 cm	SB (L); 335° from 320-4; 3 m	20 Sept 95	B, (Fl)	7 Jan 96	Fr, IFr
	P	M24116	27 m	34.5 cm	SB (R); 238° from 340-2; 5 m	20 Sept 95	B, Fl	6 Jan 96	—
	Q	M24147	32 m	37.5 cm	SB (R); 257° from 920-4; 3 m	21 Sept 95	B, Fl	6 Jan 96	—
	R	M24148	22 m	31.8 cm	SB (R); 272° from 900-2; 3 m	20 Sept 95	—	NS	NS
	S	M24174	30 m	35 cm	SB (L); 348° from 340-1; 13 m	22 Sept 95	Fl	7 Jan 96	—
C. stellata	E	M24092	52 m	78 cm*	SB (R); 148° from 140-4; 20 m	17 Sept 95	—	10 Jan 96	—
	F	M24093	35 m	65 cm	SB (R); 142° from 240-2; 11 m	17 Sept 95	—	8 Jan 96	—
	G	M24094	47 m	66 cm*	SB (L); 21° from 240-2; 25 m	17 Sept 95	—	NS	NS
	H	M24095	30 m	35.5cm	SB (L); 247° from LP (V); 8 m	17 Sept 95	—	7 Jan 96	—
	J	M24111	30 m	36.5 cm	SB (L); 274° from 220-4; 10 m	18 Sept 95	—	9 Jan 96	—
E. coriacea	A	M24078	28 m	60 cm	RB (L); 706 m; 1 m	15 Sept 95	B	4 Jan 96	IFr, Fr
	B	M24079	20 m	37.5 cm	RB (L); 632 m; 2 m	15 Sept 95	B	4 Jan 96	IFr
	80	M24083	26 m	43 cm*	SB (L); tagged 80-1; 3 m from trail	16 Sept 95	B	4 Jan 96	IFr
	C	M24084	28 m	47 cm	SB (R); 40° from 80-2; 8m	16 Sept 95	B	NS	NS
	D	M24086	22 m	40.5 cm	SB (L); 338° from 100-3; 5 m	16 Sept 95	B	4 Jan 96	Fr
G. hexapetala	I	M24110	10 m	17 cm	SB (L); 270° from CS (G); 12 m	18 Sept 95	(IFr)	8 Jan 96	—
	K	M24112	15 m	25.9 cm	SB (R); 210° from 380-2; 3.5 m	18 Sept 95	—	7 Jan 96	—
	L	M24113	15 m	23 cm	SB (L); 117° from 380-2; 8 m	18 Sept 95	—	7 Jan 96	—
	M	M24114	12 m	21.3 cm	LC (R); 187° from 60 m; 7 m	18 Sept 95	IFr	NS	NS
	N	M24115	15 m	19 cm	SB (R); 276° from CS (H); 20 m	18 Sept 95	IFr	8 Jan 96	—
L. poiteaui	T	M24175	20 m	43.7 cm	SB (R); 134° from 860-4; 6 m	22 Sept 95	—	6 Jan 96	B
	U	M24176	26 m	40.4 cm	SB (L); 130° from 460-1; 6 m	22 Sept 95	—	5 Jan 96	B
	V	M24177	30 m	67.5 cm	SB (L); 323° from GH (I); 2.5 m	23 Sept 95	—	9 Jan 96	Fl
	W	M24178	28 m	70.5 cm	SB (L); tagged 180-3; 4 m from trail	24 Sept 95	—	5 Jan 96	B (Fl)
	X	M24179	25 m	52 cm	SB (R); 108° from 180-2; 15 m	24 Sept 95	—	NS	NS

[a] The five study tree species are listed, followed by a code designating the individual tree sampled and the collection voucher number (M = S. A. Mori).

[b] Tree heights were estimated by S. A. Mori; [c] DBH = diameter breast height, * = estimated because the tree was buttressed.

[d] The location of each tree sampled. SB = Sentier Botanique, RB = Route de Bélizon, LC = logging camp detour from SB. (L) or (R) indicates the side of the trail, leaving Les Eaux Claires. Compass readings are given from the closest tagged tree on SB, and are followed by the distance (in m) from the tagged tree. Readings are sometimes given from other sample trees (identified by initials of the tree species and code), or are simply listed as meters distant on RB and LC.

[e,g] The dates of the dry season cut and the rainy season cut, respectively; NS = Not sampled during the rainy season.

[f,h] Tree fertility status at the time of dry season cut and rainy season cut, respectively; B = bud, Fl = flower, Fr = fruit, IFr = immature fruit, () = occasional.

Appendix II

Cerambycids emerged from five species of Lecythidaceae at Les Eaux Claires, French Guiana

Cerambycids emerged from *Corythophora amapaensis*, dry season branches		
Branch[a]	Cerambycid species reared[b]	Individuals reared (collection #, gender, length, date of emergence)[c]
O-C-10*	—	—
O-C-2.5*	—	—
O-G-10	—	—
O-G-2.5	—	—
P-C-10	*Palame crassimana* (n=9)	**1084**, M, 7mm, 2 May 96; **1146**, M, 5.5mm, 6 May 96; **1215**, M, 7.5mm, 14 May 96; **1216**, F, 6mm, 14 May 96; **1255**, M, 7.5mm, 18 May 96; **1385**, F, 8mm, 2 June 96; **1541**, M, 7mm, 27 June 96; **1578**, F, 8mm, 2 July 96; **1579**, F, 8mm, 2 July 96
P-C-2.5	*Palame crassimana* (n=2)	**746**, M, 5.5mm, 30 Mar 96; **1684**, F, 6mm, 19 July 96
P-G-10	—	—
P-G-2.5	—	—
Q-C-10	*Neopalame* sp. 851 (n=6)	**391**, M, 7mm, 23 Feb 96; **407**, F, 7.5mm, 23 Feb 96; **705**, F, 6.5mm, 27 Mar 96; **1078**, F, 6.5mm, 1 May 96; **1283**, F, 7mm, 22 May 96; **1369**, M, 6.5mm, 31 May 96
	Palame crassimana (n=1)	**854**, F, 8mm, 9 Apr 96
Q-C-2.5	—	—
Q-G-10	*Periboeum pubescens* (n=1)	**1686**, F, 14.5mm, 20 July 96
Q-G-2.5	—	—
R-G-10	—	—
R-G-2.5	*Palame crassimana* (n=1)	**1254**, M, 7.5mm, 18 May 96
S-C-10	*Palame crassimana* (n=14)	**866**, M, 8mm, 11 Apr 96; **943**, M, 8mm, 19 Apr 96; **1132**, F, 9mm, 5 May 96; **1169**, F, 8.5mm, 9 May 96; **1184**, M, 8mm, 11 May 96; **1220**, F, 8mm, 14 May 96; **1311**, F, 8mm, 24 May 96; **1354**, M, 8mm, 29 May 96; **1396**, M, 8mm, 3 June 96; **1424**, F, 8mm, 7 June 96; **1425**, M, 7.5mm, 7 June 96; **1451**, M, 7mm, 11 June 96; **1618**, M, 7.5mm, 7 July 96; **1705**, M, 8mm, 23 July 96
S-C-2.5	*Palame crassimana* (n=37)	**226**, M, 6.5mm, 3 Feb 96; **227**, M, 7mm, 3 Feb 96; **228**, M, 7.5mm, 3 Feb 96; **275**, F, 8.5mm, 9 Feb 96; **294**, M, 6.5mm, 11 Feb 96; **313**, M, 7.5mm, 14 Feb 96; **333**, M, 6.5mm, 15 Feb 96; **334**, F, 8mm, 15 Feb 96; **336**, F, 8.5mm, 15 Feb 96; **341**, F, 7.5mm, 16 Feb 96; **405**, F, ±, 23 Feb 96; **406**, F, 7.5mm, 23 Feb 96; **428**, F, 8mm, 29 Feb 96; **429**, F, 8.5mm, 29 Feb 96; **443**, F, 7.5mm, 1 Mar 96; **455**, M, 7mm, 2 Mar 96; **461**, F, 8.5mm, 3 Mar 96; **485**, F, 7mm, 5 Mar 96; **554**, F, 8mm, 10 Mar 96; **584**, M, 7.5mm, 14 Mar 96; **613**, F, 7.5mm, 16 Mar 96; **630**, F, 7mm, 20 Mar 96; **683**, M, 7mm, 23 Mar 96; **684**, M, 7mm, 23 Mar 96;

Appendix II contd.

Branch	Cerambycid species reared	Individuals reared (**collection #**, gender, length, date of emergence)
S-C-2.5	*Palame crassimana* contd.	**716**, F, 6.5mm, 27 Mar 96; **737**, F, 8.5mm, 30 Mar 96; **765**, F, 8.5mm, 1 Apr 96; **906**, F, 8mm, 15 Apr 96; **918**, M, 7mm, 16 Apr 96; **940**, M, 7.5mm, 19 Apr 96; **1025**, F, 5mm, 27 Apr 96; **1083**, M, 5.5mm, 2 May 96; **1093**, M, 7mm, 2 May 96; **1099**, F, 7mm, 3 May 96; **1217**, M, 7.5mm, 14 May 96; **1368**, F, 8.5mm, 31 May 96; **1456**, F, 7mm, 12 June 96
	Palame mimetica (n=2)	**430**, F, 6.5mm, 29 Feb 96; **486**, F, 6mm, 5 Mar 96
S-G-10	—	—
S-G-2.5	—	—
BIG CAGE	*Mecometopus triangularis* (n=2)	**957**, F, 6mm, 20 Apr 96; **1250**, F, 6.5mm, 18 May 96
O,P,Q,R,S	*Neoeutrypanus mutilatus* (n=9)	**1308**, F, 10mm, 23 May 96; **1325**, F, 9.5mm, 25 May 96; **1467**, F, 9.5mm, 15 June 96; **1478**, F, 9mm, 17 June 96; **1511**, F, 9mm, 22 June 96; **1558**, F, 9mm, 29 June 96; **1627**, F, 9mm, 8 July 96; **1667**, F, 8.5mm, 15 July 96; **1714**, F, 9.5mm, 25 July 96
	Neopalame sp. 851 (n=4)	**1178**, F, 6mm, 10 May 96; **1251**, M, 6.5mm, 18 May 96; **1607**, M, 8.5mm, 6 July 96; **1665**, M, 8mm, 14 July 96
	Palame crassimana (n=50)	**240**, F, 7.5mm, 4 Feb 96; **330**, M, 7.5mm, 15 Feb 96; **436**, F, 6.5mm, 1 Mar 96; **527**, M, 7.5mm, 9 Mar 96; **586**, F, 7mm, 14 Mar 96; **620**, F, 7mm, 17 Mar 96; **628**, F, 7.5mm, 20 Mar 96; **675**, M, 7mm, 23 Mar 96; **676**, M, 7mm, 23 Mar 96; **677**, M, 7mm, 23 Mar 96; **686**, F, 5.5mm, 24 Mar 96; **707**, M, ±, 27 Mar 96; **708**, F, 8mm, 27 Mar 96; **735**, M, 7mm, 30 Mar 96; **736**, M, 5.5mm, 30 Mar 96; **756**, F, 7mm, 31 Mar 96; **795**, F, 7.5mm, 4 Apr 96; **796**, F, 6.5mm, 4 Apr 96; **804**, F, 7.5mm, 5 Apr 96; **840**, F, 7mm, 8 Apr 96; **883**, F, 7mm, 13 Apr 96; **884**, M, 6.5mm, 13 Apr 96; **901**, F, 7.5mm, 15 Apr 96; **902**, F, 7mm, 15 Apr 96; **903**, F, 7.5mm, 15 Apr 96; **909**, M, 5.5mm, 16 Apr 96; **990**, M, 7mm, 24 Apr 96; **991**, M, 5.5mm, 24 Apr 96; **1012**, M, 6.5mm, 26 Apr 96; **1033**, M, 6.5mm, 27 Apr 96; **1037**, M, 8mm, 28 Apr 96; **1055**, F, 7mm, 29 Apr 96; **1131**, M, 5mm, 5 May 96; **1154**, F, 7.5mm, 7 May 96; **1252**, F, 7.5mm, 18 May 96; **1263**, M, 5.5mm, 19 May 96; **1279**, F, 8mm, 21 May 96; **1287**, F, 7.5mm, 22 May 96; **1307**, M, 7.5mm, 23 May 96; **1331**, M, 6mm, 26 May 96; **1346**, M, 6mm, 28 May 96; **1423**, M, 7mm, 7 June 96; **1486**, M, 6mm, 18 June 96; **1512**, M, 7.5mm, 22 June 96; **1521**, F, 7.5mm, 24 June 96; **1522**, M, 7.5mm, 24 June 96; **1598**, F, 8mm, 4 July 96; **1606**, F, 7mm, 6 July 96; **1690**, M, 6.5mm, 20 July 96; **1778**, F, 7mm, 7 Aug 96
	Palame mimetica (n=1)	**763**, M, 8mm, 1 Apr 96
	Periboeum pubescens (n=1)	**1672**, M, 10mm, 16 July 96
Cerambycids emerged from *Couratari stellata*, dry season branches		
E-C-10*	*Neobaryssinus marianae* (n=2)	**1483**, F, 10mm, 17 June 96; **1721**, F, 8mm, 27 July 96
E-C-2.5*	—	—

Appendix II contd.

Branch	Cerambycid species reared	Individuals reared (**collection #**, gender, length, date of emergence)
E-G-10	*Neobaryssinus marianae* (n=1)	**908**, M, 12mm, 15 Apr 96
E-G-2.5	—	—
F-C-10	*Colobothea bisignata* (n=1)	**695**, F, 9mm, 25 Mar 96
	Neobaryssinus marianae (n=7)	**331**, M, ±, 15 Feb 96; **932**, M, 11mm, 18 Apr 96; **972**, M, 6.5mm, 22 Apr 96; **1208**, F, 9mm, 13 May 96; **1219**, F, 6.5mm, 14 May 96; **1224**, M, 8mm, 15 May 96; **1309**, M, 8mm, 24 May 96
F-C-2.5*	—	—
F-G-10	*Oedopeza apicale* (n=1)	**1310**, F, 10mm, 24 May 96
F-G-2.5	—	—
G-G-10	—	—
G-G-2.5	*Neoeutrypanus mutilatus* (n=1)	**929**, M, 7.5mm, 18 Apr 96
H-C-10*	—	—
H-C-2.5	—	—
H-G-10	—	—
H-G-2.5	—	—
J-C-10	*Colobothea bisignata* (n=1)	**687**, F, 11mm, 24 Mar 96
	Genus sp. 229 (n=1)	**833**, F, 5mm, 7 Apr 96
	Neobaryssinus marianae (n=3)	**829**, F, 10.5mm, 7 Apr 96; **919**, F, 10.5mm, 16 Apr 96; **1144**, M, 10mm, 6 May 96
J-C-2.5	*Neobaryssinus marianae* (n=1)	**970**, M, 9.5mm, 22 Apr 96
J-G-10	—	—
J-G-2.5	—	—
BIG CAGE E,F,G,H,J	*Hesychotypa jaspidea* (n=5)	**958**, M, 12.5mm, 21 Apr 96; **1130**, F, 14mm, 5 May 96; **1649**, F, 12.5mm, 12 July 96; **1713**, F, 14.5mm, 25 July 96; **1786**, F, 15.5mm, 9 Aug 96
	Neobaryssinus marianae (n=4)	**24**, M, 7.5mm, 7 Jan 96; **279**, M, 9.5mm, 10 Feb 96; **1011**, F, 10mm, 26 Apr 96; **1138**, F, 9.5mm, 6 May 96
	Neoeutrypanus mutilatus (n=1)	**915**, F, 8mm, 16 Apr 96
	Oedopeza leucostigma (n=2)	**468**, F, 10mm, 3 Mar 96; **469**, M, 13mm, 3 Mar 96
Cerambycids emerged from *Eschweilera coriacea*, dry season branches		
80-C-10	*Palame anceps* (n=2)	**699**, M, 7.5mm, 25 Mar 96; **1281**, F, ±, 21 May 96
	Palame crassimana^{U} (n=2)	**181**, F, 7.5mm, 31 Jan 96; **394**, F, 7mm, 23 Feb 96
	Xylergates elaineae (n=6)	**65**, F, 10.5mm, 20 Jan 96; **256**, M, 14mm, 6 Feb 96; **457**, F, 12.5mm, 2 Mar 96; **480**, M, 12.5mm, 4 Mar 96; **541**, M, 11.5mm, 9 Mar 96; **651**, M, 14mm, 21 Mar 96
80-C-2.5*	—	—

Appendix II contd.

Branch	Cerambycid species reared	Individuals reared (**collection #**, gender, length, date of emergence)
80-G-10	*Oedopeza leucostigma* (n=8)	**54**, F, 13mm, 18 Jan 96; **59**, F, 12.5 19 Jan; **145**, M, 12.5mm, 27 Jan 96; **161**, F, 13.5mm, 29 Jan 96; **304**, F, 14mm, 12 Feb 96; **306**, M, ±, 13 Feb 96; **321**, F, 11mm, 14 Feb 96; **444**, M, 11.5mm, 1 Mar 96
	Oreodera simplex (n=7)	**747**, F, 12.5mm, 30 Mar 96; **774**, M. 12.5mm, 2 Apr 96; **815**, ±, ±, 5 Apr 96; **923**, M, 13mm, 17 Apr 96; **987**, M. 12.5mm, 23 Apr 96; **994**, M, 11mm, 24 Apr 96; **995**, M, 11.5mm, 24 Apr 96
80-G-2.5	*Oreodera simplex* (n=1)	**1021**, F, 11mm, 26 Apr 96
A-C-10	*Oedopeza leucostigma* (n=1)	**942**, F, 12.5mm, 19 Apr 96
	Palame anceps (n=5)	**519**, M, 8mm, 8 Mar 96; **612**, M, 7.5mm, 16 Mar 96; **780**, F, 8.5mm, 2 Apr 96; **835**, F, 8mm, 7 Apr 96; **1573**, M, 6.5mm, 1 July 96
	Palame crassimana (n=11)	**432**, M, 5mm, 29 Feb 96; **505**, M, 6mm, 7 Mar 96; **517**, M, 6mm, 8 Mar 96; **518**, F, 7.5mm, 8 Mar 96; **578**, M, 5.5mm, 12 Mar 96; **596**, M, 6mm, 14 Mar 96; **777**, F, 8.5mm, 2 Apr 96; **836**, F, 8.5mm, 7 Apr 96; **837**, M, 8mm, 7 Apr 96; **1009**, F, 8.5mm, 26 Apr 96; **1064**, F, 6.5mm, 30 Apr 96
A-C-2.5	*Palame anceps* (n=3)	**941**, F, 7.5mm, 19 Apr 96; **1080**, F, 8mm, 1 May 96; **1241**, M, 7.5mm, 17 May 96
	Palame crassimana (n=1)	**1700**, F, 6.5mm, 22 July 96
A-G-10	*Oedopeza leucostigma* (n=30)	**91**, M, 11.5mm, 22 Jan 96; **99**, M, 11mm, 23 Jan 96; **100**, F, 12mm, 23 Jan 96; **101**, ±, ±, 23 Jan 96; **118**, F, 14.5mm, 25 Jan 96; **134**, F, 13mm, 26 Jan 96; **144**, M, 11mm, 27 Jan 96; **149**, F, 12mm, 28 Jan 96; **212**, M, 11.5mm, 2 Feb 96; **213**, M, 13mm, 2 Feb 96; **253**, M, 13.5mm, 5 Feb 96; **255**, M, 12mm, 6 Feb 96; **263**, F, 13.5mm, 7 Feb 96; **302**, M, 12.5mm, 12 Feb 96; **309**, M, 12mm, 13 Feb 96; **322**, M, 12.5mm, 14 Feb 96; **323**, M, 13mm, 14 Feb 96; **338**, M, 11.5mm, 15 Feb 96; **345**, F, 13.5mm, 17 Feb 96; **349**, F, 14mm, 17 Feb 96; **350**, F, 12.5mm, 17 Feb 96; **372**, F, 12.5mm, 19 Feb 96; **422**, F, 11.5mm, 25 Feb 96; **437**, F, 14.5mm, 1 Mar 96; **438**, F, 13mm, 1 Mar 96; **610**, F, 13.5mm, 16 Mar 96; **639**, F, 13.5mm, 20 Mar 96; **670**, M, 11.5mm, 22 Mar 96; **715**, F, 11.5mm, 27 Mar 96; **858**, F, 13mm, 10 Apr 96
	Oreodera simplex (n=7)	**953**, M, 10.5mm, 20 Apr 96; **1042**, M, 10.5mm, 28 Apr 96; **1183**, F, 12mm, 10 May 96; **1261**, M, 10.5mm, 19 May 96; **1303**, M, 11mm, 23 May 96; **1484**, F, ±, 17 June 96; **1536**, F, 12mm, 26 June 96
A-G-2.5	*Oedopeza leucostigma* (n=2)	**408**, M, 12.5mm, 23 Feb 96; **445**, F, 12mm, 1 Mar 96
	Oreodera simplex (n=4)	**640**, F, 11.5mm, 20 Mar 96; **1242**, M, 9.5mm, 17 May 96; **1495**, M, 9.5mm, 20 June 96; **1711**, F, 11.5mm, 25 July 96
B-C-10**	—	—
B-C-2.5**	—	—
B-G-10	*Oedopeza leucostigma* (n=10)	**117**, F, 11.5mm, 25 Jan 96; **218**, F, 13mm, 3 Feb 96; **261**, M, 11.5mm, 7 Feb 96; **270**, M, 10.5mm, 8 Feb 96; **274**, M, 10.5mm, 9 Feb 96; **351**, M, 14.5mm, 17 Feb 96; **370**, M, 11mm, 19 Feb 96; **475**, M, ±, 4 Mar 96; **512**, F, 13mm, 7 Mar 96; **526**, F, 13mm, 9 Mar 96

Appendix II contd.

Branch	Cerambycid species reared	Individuals reared (**collection #**, gender, length, date of emergence)
B-G-2.5	—	—
C-G-10	*Oreodera simplex* (n=17)	**344**, M, 12.5mm, 17 Feb 96; **431**, M, 11.5mm, 29 Feb 96; **524**, M, 11mm, 9 Mar 96; **560**, F, 12.5mm, 11 Mar 96; **585**, F, 12mm, 14 Mar 96; **597**, F, 12.5mm, 14 Mar 96; **601**, F, 13mm, 15 Mar 96; **714**, M, 11mm, 27 Mar 96; **718**, M, 12mm, 28 Mar 96; **719**, M, 12mm, 28 Mar 96; **776**, F, 12.5mm, 2 Apr 96; **821**, M, 12.5mm, 6 Apr 96; **852**, M, 11.5mm, 9 Apr 96; **1085**, F, 11.5mm, 2 May 96; **1120**, M, 12.5mm, 4 May 96; **1155**, F, 11.5mm, 7 May 96; **1207**, F, 11mm, 13 May 96
	Palame anceps (n=1)	**290**, M, 7mm, 11 Feb 96
C-G-2.5	*Oedopeza leucostigma* (n=1)	**60**, F, 12.5mm, 19 Jan 96
	Oreodera simplex (n=6)	**503**, M, 11.5mm, 7 Mar 96; **504**, F, 12mm, 7 Mar 96; **598**, ±, 13mm, 15 Mar 96; **599**, F, 10.5mm, 15 Mar 96; **600**, M, 11mm, 15 Mar 96; **689**, M, 11mm, 24 Mar 96
D-C-10	—	—
D-C-2.5*	—	—
D-G-10	*Oedopeza leucostigma* (n=22)	**38**, F, 13.5mm, 14 Jan 96; **66**, M, 13.5mm, 20 Jan 96; **76**, F, 13.5mm, 21 Jan 96; **77**, F, 14mm, 21 Jan 96; **130**, M, 12.5mm, 26 Jan 96; **131**, F, 13mm, 26 Jan 96; **132**, F, 13.5mm, 26 Jan 96; **133**, M, 13.5mm, 26 Jan 96; **169**, F, ±, 29 Jan 96; **187**, F, 13.5mm, 1 Feb 96; **198**, M, 10.5mm, 1 Feb 96; **211**, F, 11.5mm, 2 Feb 96; **250**, M, ±, 5 Feb 96; **251**, F, 14mm, 5 Feb 96; **252**, F, 11.5mm, 5 Feb 96; **369**, M, 11mm, 19 Feb 96; **393**, F, 12.5mm, 23 Feb 96; **446**, M, 10mm, 1 Mar 96; **476**, F, 10.5mm, 4 Mar 96; **483**, M, 11.5mm, 5 Mar 96; **624**, F, 11mm, 17 Mar 96; **778**, F, 11mm, 2 Apr 96
	Oreodera simplex (n=3)	**577**, M, 12.5mm, 12 Mar 96; **877**, M, 12mm, 12 Apr 96; **1119**, M, 11.5mm, 4 May 96
D-G-2.5	*Oedopeza leucostigma* (n=2)	**775**, F, 11.5mm, 2 Apr 96; **838**, F, 11mm, 7 Apr 96
	Oreodera simplex (n=1)	**748**, F, 11.5mm, 30 Mar 96
BIG CAGE	*Eburodacrys* sp. 1282 (n=3)	**1373**, F, 14.5mm, 31 May 96; **1519**, M, 16mm, 23 June 96; **1767**, F, 16.5mm, 6 Aug 96
80,A,B,C,D	*Oedopeza leucostigma* (n=146)	**11**, M, 13mm, 2 Jan 96; **12**, M, 13.5 2 Jan 96; **14**, F, 13mm, 3 Jan 96; **19**, F, 14mm, 5 Jan 96; **21**, M, 13.5mm, 7 Jan 96; **25**, F, 13mm, 9 Jan 96; **27**, F, 14.5mm, 11 Jan 96; **1794**, F, 14mm, 11 Jan 96; **28**, F, 12.5mm, 11 Jan 96; **29**, M, 13mm, 12 Jan 96; **30**, F, 14mm, 12 Jan 96; **31**, F, 14mm, 12 Jan 96; **32**, F, 13mm, 12 Jan 96; **1795**, M, 13.5mm, 13 Jan 96 **34**, M, 14mm, 14 Jan 96; **35**, M, 13.5mm, 14 Jan 96; **36**, M, 13mm, 14 Jan 96; **37**, F, 13.5mm, 14 Jan 96; **39**, M, 12mm, 15 Jan 96; **40**, M, 14mm, 15 Jan 96; **41**, M, 9.5mm, 15 Jan 96; **44**, F, 14mm, 16 Jan 96; **45**, M, 13.5mm, 17 Jan 96; **46**, F, 14mm, 17 Jan 96; **47**, M, 12.5mm, 17 Jan 96; **49**, M, 11.5mm, 18 Jan 96; **50**, M, 12mm, 18 Jan 96; **51**, F, 14mm, 18 Jan 96; **52**, M, 13.5mm, 18 Jan 96; **55**, F, 13mm, 18 Jan 96; **56**, F, 13.5mm, 19 Jan 96; **57**, F, 14mm, 19 Jan 96; **58**, M, 12.5mm, 19 Jan 96; **63**, F, 13.5mm, 19 Jan 96; **71**, F, 13.5mm, 21 Jan 96; **72**, M, 13mm, 21 Jan 96; **73**, F, 14.5mm, 21 Jan 96; **84**, M, 13mm, 21 Jan 96; **85**, M, 12mm, 21 Jan; 96; **86**, F, 12mm, 21 Jan 96; **87**, F, 13mm, 21 Jan 96;

Appendix II contd.

Branch	Cerambycid species reared	Individuals reared (**collection #**, gender, length, date of emergence)
BIG CAGE 80,A,B,C,D	*Oedopeza leucostigma* contd.	**88**, ±, ±, 21 Jan 96; **89**, M, 12mm, 21 Jan 96; **95**, F, 12.5mm, 23 Jan 96; **96**, F, 13mm, 23 Jan 96; **97**, F, 12.5mm, 23 Jan 96; **103**, F, 14mm, 24 Jan 96; **104**, M, 13mm, 24 Jan 96; **105**, M, 12.5mm, 24 Jan 96; **106**, M, 13mm, 24 Jan 96; **107**, F, 13mm, 24 Jan 96; **109**, F, 13.5mm, 24 Jan 96; **114**, F, 14mm, 25 Jan 96; **115**, F, 14mm, 25 Jan 96; **116**, M, ±, 25 Jan 96; **128**, M, 10mm, 26 Jan 96; **129**, F, 13.5mm, 26 Jan 96; **139**, M, 11.5mm, 27 Jan 96; **140**, F, 13mm, 27 Jan 96; **141**, M, 12.5mm, 27 Jan 96; **148**, M, 13.5mm, 28 Jan 96; **166**, M, 12.5mm, 29 Jan 96; **170**, F, 14.5mm, 30 Jan 96; **176**, M, 12mm, 31 Jan 96; **177**, F, 11mm, 31 Jan 96; **178**, F, 12.5mm, 31 Jan 96; **179**, F, 12.5mm, 31 Jan 96; **180**, ±, ±, 31 Jan 96; **186**, M, 11mm, 1 Feb 96; **195**, M, 11.5mm, 1 Feb 96; **197**, F, 13.5mm, 1 Feb 96; **199**, M, 11mm, 2 Feb 96; **200**, M, 14mm, 2 Feb 96; **201**, F, 12mm, 2 Feb 96; **202**, M, 13.5mm, 2 Feb 96; **222**, M, 11.5mm, 3 Feb 96; **230**, M, 12mm, 4 Feb 96; **231**, M, 12.5mm, 4 Feb 96; **241**, F, 15mm, 5 Feb 96; **243**, M, 12.5mm, 5 Feb 96; **244**, F, 12.5mm, 5 Feb 96; **245**, M, 12.5mm, 5 Feb 96; **254**, M, 12.5mm, 6 Feb 96; **258**, F, 13mm, 7 Feb 96; **259**, F, 13.5mm, 7 Feb 96; **260**, F, 13mm, 7 Feb 96; **271**, M, 13mm, 9 Feb 96; **272**, F, 13mm, 9 Feb 96; **273**, F, 12.5mm, 9 Feb 96; **278**, F, 13mm, 9 Feb 96; **280**, M, 11.5mm, 10 Feb 96; **281**, M, 12.5mm, 10 Feb 96; **282**, F, 14mm, 10 Feb 96; **286**, F, ±, 11 Feb 96; **298**, F, 14.5mm, 12 Feb 96; **299**, F, 13mm, 12 Feb 96; **305**, F, 14mm, 13 Feb 96; **310**, F, 12.5mm, 14 Feb 96; **311**, M, 13mm, 14 Feb 96; **312**, F, 14.5mm, 14 Feb 96; **318**, M, 13.5mm, 14 Feb 96; **320**, F, 13.5mm, 14 Feb 96; **324**, F, 14.5mm, 15 Feb 96; **325**, M, 12.5mm, 15 Feb 96; **339**, F, ±, 16 Feb 96; **353**, M, 13mm, 17 Feb 96; **354**, M, 13mm, 17 Feb 96; **355**, M, 12mm, 17 Feb 96; **356**, F, 13mm, 18 Feb 96; **357**, F, 12.5mm, 18 Feb 96; **363**, F, 13.5mm, 19 Feb 96; **376**, M, 12.5mm, 21 Feb 96; **377**, F, 12.5mm, 21 Feb 96; **385**, F, 13mm, 22 Feb 96; **388**, M, 12.5mm, 23 Feb 96; **389**, F, 14.5mm, 23 Feb 96; **410**, M, 12.5mm, 24 Feb 96; **411**, M, 13.5mm, 24 Feb 96; **433**, F, 12.5mm, 29 Feb 96; **434**, F, 12.5mm, 29 Feb 96; **435**, F, 13.5mm, 29 Feb 96; **439**, M, 11.5mm, 1 Mar 96; **447**, F, 14mm, 1 Mar 96; **449**, M, 12.5mm, 2 Mar 96; **458**, M, 14mm, 3 Mar 96; **459**, F, 13mm, 3 Mar 96; **460**, M, 11.5mm, 3 Mar 96; **470**, M, 12mm, 3 Mar 96; **472**, F, 13mm, 4 Mar 96; **496**, F, 13.5mm, 6 Mar 96; **516**, M, 12.5mm, 8 Mar 96; **542**, M, 11.5mm, 9 Mar 96; **543**, M, 12.5mm, 10 Mar 96; **582**, F, 13mm, 13 Mar 96; **583**, F, 12mm, 13 Mar 96; **594**, F, 12mm, 14 Mar 96; **607**, F, 13mm, 16 Mar 96; **618**, F, 12.5mm, 16 Mar 96; **652**, F, 13.5mm, 21 Mar 96; **662**, F, 13mm, 22 Mar 96; **672**, F, 13mm, 22 Mar 96; **694**, F, 12.5mm, 24 Mar 96; **724**, F, 13.5mm, 28 Mar 96; **728**, F, 13mm, 29 Mar 96; **754**, M, 10mm, 31 Mar 96; **1753**, M, 11.5mm, 2 Aug 96
	Oreodera simplex (n=94)	**296**, F, 12mm, 11 Feb 96; **448**, F, 12mm, 2 Mar 96; **473**, M, 11.5mm, 4 Mar 96; **497**, F, 13mm, 6 Mar 96; **498**, F, 13mm, 6 Mar 96; **499**, M, 12mm, 6 Mar 96; **500**, M, 12.5mm, 7 Mar 96; **501**, M, 12.5mm, 7 Mar 96; **502**, M, 12mm, 7 Mar 96; **544**, F, 14mm, 10 Mar 96; **559**, F, 14mm, 11 Mar 96; **571**, F,

Appendix II contd.

Branch	Cerambycid species reared	Individuals reared (**collection #**, gender, length, date of emergence)
BIG CAGE 80,A,B,C,D	*Oreodera simplex* contd.	13mm, 12 Mar 96; **572**, F, 13.5mm, 12 Mar 96; **595**, F, 12.5mm, 14 Mar 96; **602**, M, 11.5mm, 15 Mar 96; **608**, F, 13mm, 16 Mar 96; **649**, M, 10.5mm, 21 Mar 96; **663**, F, 12mm, 22 Mar 96; **664**, M, 12.5mm, 22 Mar 96; **678**, F, 13mm, 23 Mar 96; **698**, F, 13mm, 25 Mar 96; **734**, F, 13mm, 29 Mar 96; **749**, F, 13mm, 31 Mar 96; **750**, F, 12mm, 31 Mar 96; **751**, F, 12.5mm, 31 Mar 96; **752**, F, 12mm, 31 Mar 96; **753**, F, 12.5mm, 31 Mar 96; **759**, M, 11mm, 1 Apr 96; **760**, M, 12mm, 1 Apr 96; **761**, F, 12.5mm, 1 Apr 96; **762**, F, 11.5mm, 1 Apr 96; **781**, F, 13mm, 2 Apr 96; **782**, F, 13mm, 2 Apr 96; **784**, M, 11.5mm, 3 Apr 96; **785**, F, 13mm, 3 Apr 96; **786**, F, 13.5mm, 3 Apr 96; **787**, M, 13mm, 3 Apr 96; **794**, M, 12mm, 4 Apr 96; **814**, M, 11.5mm, 5 Apr 96; **828**, F, 13mm, 7 Apr 96; **839**, M, 13mm, 8 Apr 96; **844**, M, 12.5mm, 9 Apr 96; **845**, M, 12.5mm, 9 Apr 96; **846**, M, 12.5mm, 9 Apr 96; **847**, M, 11.5mm, 9 Apr 96; **857**, F, 12mm, 10 Apr 96; **859**, M, 12.5mm, 11 Apr 96; **887**, F, 13mm, 13 Apr 96; **896**, F, 13mm, 14 Apr 96; **897**, F, 12.5mm, 14 Apr 96; **904**, F, 13mm, 15 Apr 96; **905**, F, 13.5mm, 15 Apr 96; **920**, F, 12.5mm, 16 Apr 96; **937**, F, 12mm, 18 Apr 96; **948**, F, 12.5mm, 19 Apr 96; **949**, M, 12mm, 19 Apr 96; **950**, M, 12mm, 20 Apr 96; **951**, F, 13mm, 20 Apr 96; **952**, M, 11.5mm, 20 Apr 96; **986**, M, 13mm, 23 Apr 96; **996**, F, 14mm, 24 Apr 96; **997**, F, 12.5mm, 24 Apr 96; **1006**, M, 11.5mm, 25 Apr 96; **1007**, M, 12.5mm, 25 Apr 96; **1010**, F, 12mm, 26 Apr 96; **1035**, M, 12mm, 28 Apr 96; **1036**, M, 12.5mm, 28 Apr 96; **1059**, F, 12mm, 29 Apr 96; **1063**, M, 11.5mm, 30 Apr 96; **1077**, F, 13.5mm, 1 May 96; **1094**, M, 10.5mm, 2 May 96; **1095**, M, 11mm, 2 May 96; **1125**, M, 12.5mm, 5 May 96; **1126**, M, 11.5mm, 5 May 96; **1152**, M, 11mm, 7 May 96; **1153**, M, 11.5mm, 7 May 96; **1164**, F, 12mm, 9 May 96; **1189**, F, 11mm, 12 May 96; **1206**, F, 11mm, 13 May 96; **1234**, F, 11mm, 17 May 96; **1249**, F, 12mm, 18 May 96; **1292**, M, 10mm, 22 May 96; **1293**, F, 13mm, 22 May 96; **1304**, F, 12.5mm, 23 May 96; **1305**, F, 10.5mm, 23 May 96; **1321**, F, 11mm, 25 May 96; **1328**, F, 12mm, 26 May 96; **1337**, M, 10mm, 27 May 96; **1338**, M, 11.5mm, 27 May 96; **1372**, M, 9.5mm, 31 May 96; **1446**, F, 10.5mm, 10 June 96; **1461**, F, 11mm, 14 June 96; **1488**, F, 10mm, 19 June 96; **1494**, F, 10mm, 20 June 96
	Ozineus (n=1)	**471**, F, 6.5mm, 3 Mar 96
	Palame anceps (n=49)	**3**, M, 7mm, 31 Dec; **4**, F, 7mm, 31 Dec; **5**, F, 7mm, 31 Dec; **6**, F, 7.5mm, 1 Jan 96; **7**, M, ±, 1 Jan 96; **8**, M, 5.5mm, 1 Jan 96; **10**, M, 8mm, 1 Jan 96; **13**, M, 8mm, 2 Jan 96; **16**, M, 8mm, 3 Jan 96; **18**, F, 8mm, 4 Jan 96; **20**, M, 7.5mm, 5 Jan 96; **23**, M, 7.5mm, 7 Jan 96; **33**, F, 7.5mm, 14 Jan 96; **61**, F, 7.5mm, 19 Jan 96; **74**, M, 6.5mm, 21 Jan 96; **93**, M, 7.5mm, 22 Jan 96; **94**, M, 7.5mm, 22 Jan 96; **102**, M, 7mm, 23 Jan 96; **127**, M, 7mm, 25 Jan 96; **167**, F, 8mm, 29 Jan 96; **168**, M, 7mm, 29 Jan 96; **188**, M, 7mm, 1 Feb 96; **189**, M, 7mm, 1 Feb 96; **210**, M, ±, 2 Feb 96; **269**, M, 8mm, 8 Feb 96; **283**, M, 7mm, 10 Feb 96; **287**, F, 7.5mm, 11 Feb 96; **301**, M, 7.5mm, 12 Feb 96; **348**, M, 7.5mm, 17 Feb 96; **358**, M, 8mm, 18 Feb 96; **374**, F, 8mm, 20 Feb 96; **381**, F, 8mm, 21 Feb 96; **390**, M, 7.5mm, 23 Feb 96; **404**, M, 8.5mm, 23 Feb 96; **412**, F, 7.5mm, 24 Feb 96;

Appendix II contd.

Branch	Cerambycid species reared	Individuals reared (**collection #**, gender, length, date of emergence)
BIG CAGE 80,A,B,C,D	*Palame anceps* contd.	**478**, F, 7.5mm, 4 Mar 96; **484**, F, 7.5mm, 5 Mar 96; **488**, F, 7.5mm, 5 Mar 96; **515**, M, 7.5mm, 8 Mar 96; **528**, M, 7.5mm, 9 Mar 96; **529**, F, 8mm, 9 Mar 96; **558**, F, 8.5mm, 11 Mar 96; **568**, F, 8mm, 11 Mar 96; **570**, M, 7mm, 12 Mar 96; **573**, M, 7.5mm, 12 Mar 96; **621**, M, 7.5mm, 17 Mar 96; **665**, M, 7.5mm, 22 Mar 96; **666**, F, 8.5mm, 22 Mar 96; **725**, M, 7.5mm, 28 Mar 96
	Palame crassimana (n=11)	**26**, F, 5.5mm, 9 Jan 96; **81**, F, 7mm, 21 Jan 96; **1796**, M, 6.5mm, 27 Jan 96; **142**, F, 7.5mm, 27 Jan 96; **196**, F, 6.5mm, 1 Feb 96; **297**, F, 7mm, 11 Feb 96; **403**, F, 7.5mm, 23 Feb 96; **530**, M, 8mm, 9 Mar 96; **580**, F, 7mm, 12 Mar 96; **627**, F, 7.5mm, 17 Mar 96; **648**, M, 7.5mm, 21 Mar 96
	Xenofrea sp. 662 (n=4)	**78**, F, 10mm, 21 Jan 96; **79**, M, 10.5mm, 21 Jan 96; **80**, M, 10.5mm, 21 Jan 96; **362**, F, 10mm, 18 Feb 96
	Xylergates elaineae (n=9)	**2**, F, 13mm, 31 Dec; **22**, F, 13mm, 7 Jan 96; **138**, F, 12mm, 27 Jan 96; **242**, F, 13.5mm, 5 Feb 96; **383**, F, 12.5mm, 22 Feb 96; **384**, F, 13mm, 22 Feb 96; **569**, M, 11mm, 11 Mar 96; **693**, F, 13mm, 24 Mar 96; **856**, M, 11mm, 10 Apr 96
Cerambycids emerged from *Gustavia hexapetala*, dry season branches		
I-C-10	Genus sp. 229 (n=5)	**603**, F, 4.5mm, 15 Mar 96; **779**, M, 4mm, 2 Apr 96; **788**, F, 4.5mm, 3 Apr 96; **789**, F, 5.5mm, 3 Apr 96; **876**, F, 4.5mm, 12 Apr 96
	Nesozineus sp. (n=2)	**793**, M, 6.5mm, 4 Apr 96; **1020**, F, 7.5mm, 26 Apr 96
	Palame crassimana (n=6)	**992**, M, 7mm, 24 Apr 96; **1096**, M, 6.5mm, 2 May 96; **1161**, M, 5.5mm, 8 May 96; **1395**, F, 5mm, 3 June 96; **1572**, F, 6mm, 1 July 96; **1685**, F, 5mm, 19 July 96
	Tauralema bellatrix (n=4)	**1282**, F, 5mm, 22 May 96; **1353**, F, 5.5mm, 29 May 96; **1403**, F, 5.5mm, 4 June 96; **1479**, F, 5mm, 17 June 96
I-C-2.5	Genus sp. 229 (n=2)	**717**, M, 4.5mm, 28 Mar 96; **758**, ±, 5mm, 31 Mar 96
	Palame crassimana (n=7)	**673**, ±, ±, 23 Mar 96; **822**, M, 5mm, 6 Apr 96; **927**, F, 6mm, 18 Apr 96; **928**, M, 7mm, 18 Apr 96; **1260**, M, 5mm, 19 May 96; **1532**, F, 5mm, 25 June 96; **1567**, F, 6mm, 30 June 96
	Tauralema bellatrix (n=4)	**1003**, M, 5.5mm, 25 Apr 96; **1480**, F, 5.5mm, 17 June 96; **1481**, F, 5.5mm, 17 June 96; **1687**, ±, 4.5mm, 20 July 96
I-G-10	*Nesozineus* sp. (n=1)	**851**, M, 6.5mm, 9 Apr 96
	Oedopeza apicale (n=2)	**1157**, M, 10mm, 7 May 96; **1284**, M, 10 22mm, May 96
I-G-2.5	—	—
K-C-10	*Palame crassimana* (n=10)	**308**, F, 8mm, 13 Feb 96; **540**, F, 6.5mm, 9 Mar 96; **819**, F, 6.5mm, 6 Apr 96; **979**, F, 6mm, 23 Apr 96; **1040**, F, 5mm, 28 Apr 96; **1452**, F, 6mm, 11 June 96; **1468**, M, 5.5mm, 15 June 96; **1619**, M, 5.5mm, 7 July 96; **1620**, M, 5.5mm, 7 July 96; **1790**, F, 6mm, 10 Aug 96
	Tauralema bellatrix (n=3)	**964**, M, 5 21mm, Apr 96; **1168**, F, 4.5mm, 9 May 96; **1791**, F, 5mm, 10 Aug 96
K-C-2.5	*Palame crassimana* (n=1)	**1482**, F, ±, 17 June 96

Appendix II contd.

Branch	Cerambycid species reared	Individuals reared (**collection #**, gender, length, date of emergence)
K-G-10	*Eupromerella clavator* (n=7)	**1596**, F, 9mm, 4 July 96; **1605**, M, 8mm, 6 July 96; **1646**, M, 8mm, 11 July 96; **1688**, M, 9mm, 20 July 96; **1699**, M, 7.5mm, 22 July 96; **1733**, F, 6.5mm, 29 July 96; **1772**, F, 7.5mm, 6 Aug 96
K-G-2.5	—	—
L-C-10	*Palame crassimana* (n=1)	**1185**, M, 5.5mm, 11 May 96
L-C-2.5	—	—
L-G-10	*Eupromerella clavator* (n=1)	**1773**, M, 6.5mm, 6 Aug 96
L-G-2.5	—	—
M-G-10	*Carterica* sp. (n=1)	**619**, M, 7mm, 17 Mar 96
M-G-2.5	*Carterica* sp. (n=4)	**679**, M, ±, 23 Mar 96; **680**, ±, ±, 23 Mar 96; **925**, F, 7.5 18 Apr 96; **926**, F, ±, 18 Apr 96
N-C-10	*Colobothea bisignata* (n=1)	**1174**, F, 9mm, 10 May 96
	Palame crassimana (n=10)	**629**, M, 6.5mm, 20 Mar 96; **641**, F, 6mm, 21 Mar 96; **805**, M, 7mm, 5 Apr 96; **1066**, F, 6.5mm, 30 Apr 96; **1160**, F, 6.5mm, 8 May 96; **1352**, F, 7mm, 29 May 96; **1513**, F, 6mm, 22 June 96; **1571**, F, 5mm, 1 July 96; **1647**, F, 6.5mm, 11 July 96; **1764**, F, 5mm, 4 Aug 96
	Palame mimetica (n=1)	**420**, F, 7mm, 24 Feb 96
	Peribоeum pubescens (n=7)	**999**, F, 9.5mm, 25 Apr 96; **1143**, M, 9.5mm, 6 May 96; **1156**, M, 11mm, 7 May 96; **1173**, F, 10mm, 10 May 96; **1531**, M, 9mm, 25 June 96; **1580**, ±, ±, 2 July 96; **1698**, F, 9mm, 22 July 96
N-C-2.5	*Palame crassimana* (n=4)	**803**, M, 6.5mm, 4 Apr 96; **1409**, M, 6.5mm, 5 June 96; **1520**, M, 6.5mm, 23 June 96; **1712**, F, 6.5mm, 25 July 96
	Palame mimetica (n=1)	**757**, F, 6.5mm, 31 Mar 96
N-G-10	*Eupromerella clavator* (n=5)	**1524**, M, 7mm, 24 June 96; **1597**, M, 7.5mm, 4 July 96; **1660**, M, 7mm, 13 July 96; **1765**, F, 8mm, 4 Aug 96; **1771**, M, 7.5mm, 6 Aug 96
N-G-2.5	*Eupromerella clavator* (n=2)	**1540**, F, 7.5mm, 27 June 96; **1774**, F, 9mm, 6 Aug 96
BIG CAGE	*Colobothea bisignata* (n=1)	**514**, M, 10mm, 8 Mar 96
I,K,L,M,N	*Carterica* sp. (n=3)	**674**, M, 6mm, 23 Mar 96; **706**, M, 7.5mm, 27 Mar 96; **827**, F, 6mm, 7 Apr 96
	Carterica sp. (n=1)	**1533**, M, 5mm, 25 June 96
	Hesychotypa liturata (n=2)	**989**, M, 13.5mm, 24 Apr 96; **998**, M, 14mm, 25 Apr 96
	Nealcidion badium (n=1)	**867**, F, 7.5mm, 12 Apr 96
	Oedopeza apicale (n=6)	**1330**, M, 9mm, 26 May 96; **1408**, F, 10mm, 5 June 96; **1557**, M, 9.5mm, 29 June 96; **1650**, F, 10.5mm, 12 July 96; **1737**, M, 10mm, 30 July 96; **1759**, M, 10mm, 3 Aug 96
	Eupromerella clavator (n=5)	**1583**, M, 8.5 2 July 96; **1731**, M, 7.5 29 July 96; **1743**, M, 8 31 July 96; **1770**, F, 7.5 6 Aug 96; **1780**, F, 8.5 8 Aug 96

Appendix II contd.

Branch	Cerambycid species reared	Individuals reared (**collection #**, gender, length, date of emergence)
Cerambycids emerged from *Lecythis poiteaui*, dry season branches		
T-C-10	*Neoeutrypanus* sp. 915 (n=9)	**931**, F, 12mm, 18 Apr 96; **1098**, M, 11mm, 3 May 96; **1192**, F, 11mm, 12 May 96; **1367**, M, 11.5mm, 31 May 96; **1410**, M, 11mm, 5 June 96; **1469**, F, 12mm, 15 June 96; **1556**, F, 11.5mm, 28 June 96; **1561**, M, 10mm, 29 June 96; **1595**, M, 9mm, 3 July 96
	Palame crassimana (n=2)	**239**, F, 7mm, 4 Feb 96; **1637**, M, 6mm, 9 July 96
	Palame mimetica (n=1)	**238**, F, 6.5mm, 4 Feb 96
T-C-2.5	*Neoeutrypanus mutilatus* (n=17)	**917**, F, 9mm, 16 Apr 96; **1024**, ±, 9mm, 27 Apr 96; **1065**, F, 10mm, 30 Apr 96; **1081**, F, 9mm, 1 May 96; **1191**, F, 9mm, 12 May 96; **1225**, F, 8.5mm, 16 May 96; **1259**, F, 10.5mm, 19 May 96; **1285**, F, 8.5mm, 22 May 96; **1302**, F, 9mm, 23 May 96; **1349**, F, 9.5mm, 28 May 96; **1350**, F, 8.5mm, 28 May 96; **1380**, F, 9mm, 1 June 96; **1455**, F, 9mm, 12 June 96; **1554**, F, 9mm, 28 June 96; **1555**, F, 8mm, 28 June 96; **1666**, F, 9mm, 14 July 96; **1710**, F, 9mm, 25 July 96
	Neoeutrypanus sp. 915 (n=22)	**732**, M, 8.5mm, 29 Mar 96; **801**, F, 9.5mm, 4 Apr 96; **806**, F, 10.5mm, 5 Apr 96; **820**, M, 9mm, 6 Apr 96; **831**, M, 9.5mm, 7 Apr 96; **874**, M, 8.5mm, 12 Apr 96; **875**, M, 10mm, 12 Apr 96; **895**, F, 10mm, 14 Apr 96; **922**, M, 10.5mm, 17 Apr 96; **980**, F, 9mm, 23 Apr 96; **1041**, M, 9.5mm, 28 Apr 96; **1053**, F, 10mm, 29 Apr 96; **1097**, M, 9.5mm, 3 May 96; **1158**, F, 9.5mm, 7 May 96; **1162**, F, 10mm, 8 May 96; **1186**, F, 10mm, 11 May 96; **1239**, F, 10mm, 17 May 96; **1258**, F, 10mm, 19 May 96; **1365**, F, 10mm, 30 May 96; **1431**, M, 9mm, 8 June 96; **1523**, F, 9.5mm, 24 June 96; **1701**, M, 9.5mm, 22 July 96
	Palame crassimana (n=2)	**653** ±, ±, 21 Mar 96; **1351**, F, ±, 28 May 96
	Palame mimetica (n=6)	**229**, F, 7.5mm, 3 Feb 96; **574**, M, 6mm, 12 Mar 96; **701**, F, 8mm, 26 Mar 96; **738**, M, 5.5mm, 30 Mar 96; **790**, M, 6.5mm, 3 Apr 96; **880**, F, 7mm, 13 Apr 96
	Periboeum pubescens (n=4)	**879**, F, 11mm, 13 Apr 96; **1581**, F, 11mm, 2 July 96; **1638**, M, 9.5mm, 9 July 96; **1720**, F, 13mm, 27 July 96
T-G-10	—	—
T-G-2.5	*Palame crassimana* (n=1)	**53**, F, 7.5mm, 18 Jan 96
U-C-10	*Neoeutrypanus* sp. 915 (n=3)	**611**, F, 11.5mm, 16 Mar 96; **1487**, F, 10mm, 18 June 96; **1604**, M, 9mm, 6 July 96
	Palame mimetica (n=25)	**685**, F, 9mm, 23 Mar 96; **834**, M, 8.5mm, 7 Apr 96; **843**, M, 8.5mm, 8 Apr 96; **885**, M, 9.5mm, 13 Apr 96; **886**, M, 8.5mm, 13 Apr 96; **962**, M, 8.5mm, 21 Apr 96; **971**, M, 8.5mm, 22 Apr 96; **993**, F, 8.5mm, 24 Apr 96; **1000**, M, 9.5mm, 25 Apr 96; **1001**, F, 9mm, 25 Apr 96; **1002**, M, 9mm, 25 Apr 96; **1008**, F, 9mm, 26 Apr 96; **1022**, F, 9mm, 27 Apr 96; **1023**, M, 9mm, 27 Apr 96; **1034**, F,
	Palame mimetica contd.	9.5mm, 27 Apr 96; **1101**, M, 9mm, 3 May 96; **1117**, F, 8.5mm, 4 May 96; **1133**, M, 8mm, 5 May 96;**1145**, M, 9mm, 6 May 96; **1218**, F, 9.5mm, 14 May 96; **1223**, M, 8.5mm, 15 May 96; **1240**, M, 9.5mm, 17 May 96; **1334**, F, 9.5mm, 27 May 96; **1348**, M, 8.5mm, 28 May 96; **1366**, F, 8.5mm, 30 May 96

Appendix II contd.

Branch	Cerambycid species reared	Individuals reared (**collection #**, gender, length, date of emergence)
U-C-2.5	*Palame crassimana* (n=4)	**668**, M, 6mm, 22 Mar 96; **669**, M, 6.5mm, 22 Mar 96; **1043**, M, 5mm, 29 Apr 96; **1639**, F, 7.5mm, 9 July 96
	Palame mimetica (n=5)	**832**, F, 6.5mm, 7 Apr 96; **1044**, F, 6.5mm, 29 Apr 96; **1100**, F, 6mm, 3 May 96; **1118**, M, 6.5mm, 4 May 96; **1603**, M, 5mm, 6 July 96
U-G-10	*Xylergates elaineae* (n=2)	**352**, M, 11mm, 17 Feb 96; **873**, M, 9.5mm, 12 Apr 96
	Xylergatina pulchra (n=2)	**327**, F, 14.5mm, 15 Feb 96; **671**, M, 14.5mm, 22 Mar 96
U-G-2.5	*Oedopeza leucostigma* (n=1)	**479**, F, 12.5mm, 4 Mar 96
V-C-10*	*Neoeutrypanus* sp. 915 (n=2)	**963**, M, 8.5mm, 21 Apr 96; **1429**, F, 10.5mm, 7 June 96
V-C-2.5*	*Palame crassimana* (n=1)	**1079**, F, 6.5mm, 1 May 96
	Xenofrea lineatipennis (n=2)	**1102**, M, 7.5mm, 3 May 96; **1370**, F, 7.5mm, 31 May 96
V-G-10	*Palame mimetica* (n=5)	**319**, F, 9.5mm, 14 Feb 96; **631**, M, 8.5mm, 20 Mar 96; **642**, F, 9.5mm, 21 Mar 96; **688**, M, 7.5mm, 24 Mar 96; **1054**, M, 8.5mm, 29 Apr 96
	Periboeum pubescens (n=10)	**830**, F, 12mm, 7 Apr 96; **894**, F, 10.5mm, 14 Apr 96; **916**, F, 10.5mm, 16 Apr 96; **930**, F, 11.5mm, 18 Apr 96; **1253**, F, 9.5mm, 18 May 96; **1560**, F, 10.5mm, 29 June 96; **1566**, F, 11mm, 30 June 96; **1709**, F, 12.5mm, 25 July 96; **1719**, M, 11mm, 27 July 96; **1734**, M, 11.5mm, 29 July 96
V-G-2.5	*Palame mimetica* (n=4)	**392**, M, 7.5mm, 23 Feb 96; **667**, ±, ±, 22 Mar 96; **700**, F, 8.5mm, 26 Mar 96; **713**, F, 8mm, 27 Mar 96
	Periboeum pubescens (n=2)	**1113**, M, 10.5mm, 3 May 96; **1582**, M, 8.5mm, 2 July 96
W-C-10*	*Eburodacrys sexmaculata* (n=1)	**1441**, M, 19.5mm, 9 June 96
	Neoeutrypanus sp. 915 (n=1)	**1347**, M, 10mm, 28 May 96
	Palame mimetica (n=4)	**1286**, F, 9mm, 22 May 96; **1453**, F, 9.5mm, 11 June 96; **1680**, M, 7.5mm, 17 July 96; **1682**, M, 8mm, 18 July 96
W-C-2.5*	—	—
W-G-10	*Palame crassimana* (n=3)	**853**, M, 8mm, 9 Apr 96; **933**, F, 8.5mm, 18 Apr 96; **1661**, ±, ±, 13 July 96
W-G-2.5	*Palame crassimana* (n=2)	**681**, F, 8mm, 23 Mar 96; **682**, F, 8mm, 23 Mar 96
X-G-10	*Xylergatina pulchra* (n=3)	**632**, F, 16mm, 20 Mar 96; **727**, M, 18.5mm, 28 Mar 96; **855**, F, 15.5mm, 9 Apr 96
X-G-2.5	—	—
BIG CAGE T,U,V,W,X	*Ceragenia leprieuri* (n=1)	**1651**, M, 22.5mm, 12 July 96
	Hesychotypa jaspidea (n=1)	**1167**, F, 14.5mm, 9 May 96
	Mecometopus triangularis (n=13)	**744**, F, 6.5mm, 30 Mar 96; **771**, M, 8mm, 2 Apr 96; **864**, F, 9.5mm, 11 Apr 96; **869**, M, 7.5mm, 12 Apr 96; **969**, F, 8.5mm, 21 Apr 96; **1076**, M, 7.5mm, 1 May 96; **1090**, M, 5.5mm, 2 May 96; **1108**, F, 7.5mm, 3 May 96; **1238**, M, 7.5mm, 17 May 96; **1291**, F, 8mm, 22 May 96; **1324**, M, 8mm, 25 May 96; **1355**, F, 8.5mm, 29 May 96; **1493**, M, 5.5mm, 20 June 96

Appendix II contd.

Branch	Cerambycid species reared	Individuals reared (**collection #**, gender, length, date of emergence)
BIG CAGE T,U,V,W,X	*Neoeutrypanus mutilatus* (n=56)	**626**, F, 9mm, 17 Mar 96; **692**, F, 8.5mm, 24 Mar 96; **766**, F, 9.5mm, 2 Apr 96; **772**, F, 8.5mm, 2 Apr 96; **797**, F, 9mm, 4 Apr 96; **823**, F, 9mm, 7 Apr 96; **860**, F, 8mm, 11 Apr 96; **861**, F, 8.5mm, 11 Apr 96; **865**, F, 9mm, 11 Apr 96; **924**, F, 8.5mm, week of 10 Apr 96; **936**, F, 9mm, 18 Apr 96; **954**, F, 9.5mm, 20 Apr 96; **965**, F, 8.5mm, 21 Apr 96; **1013**, F, 8.5mm, 26 Apr 96; **1016**, F, 9mm, 26 Apr 96; **1017**, F, 9mm, 26 Apr 96; **1038**, F, 8mm, 28 Apr 96; **1039**, F, 8.5mm, 28 Apr 96; **1057**, F, 9.5mm, 29 Apr 96; **1071**, F, 9.5mm, 1 May 96; **1128**, F, 7.5mm, 5 May 96; **1137**, F, 9mm, 6 May 96; **1166**, F, 8.5mm, 9 May 96; **1202**, F, 9mm, 13 May 96; **1203**, F, 10mm, 13 May 96; **1210**, F, 9mm, 14 May 96; **1211**, F, 9mm, 14 May 96; **1212**, F, 9.5mm, 14 May 96; **1235**, F, 9mm, 17 May 96; **1236**, F, 7.5mm, 17 May 96; **1247**, F, 9.5mm, 18 May 96; **1288**, F, 9mm, 22 May 96; **1289**, F, 9.5mm, 22 May 96; **1316**, F, 9mm, 24 May 96; **1322**, F, 8.5mm, 25 May 96; **1323**, F, 9mm, 25 May 96; **1345**, F, 8mm, 28 May 96; **1356**, F, 8.5mm, 29 May 96; **1393**, F, 9mm, 3 June 96; **1394**, F, 9mm, 3 June 96; **1402**, F, 9mm, 4 June 96; **1414**, F, 9mm, 6 June 96; **1430**, F, 9mm, 8 June 96; **1447**, F, 9mm, 10 June 96; **1454**, F, ±, 12 June 96; **1462**, F, 9.5mm, 14 June 96; **1491**, F, 9mm, 20 June 96; **1559**, F, 7mm, 29 June 96; **1584**, F, 8.5mm, 2 July 96; **1585**, F, 7.5mm, 2 July 96; **1586**, F, 7.5mm, 2 July 96; **1636**, F, 9mm, 9 July 96; **1716**, F, 7.5mm, 26 July 96; **1732**, F, 8mm, 29 July 96; **1769**, F, 8.5mm, 6 Aug 96; **1792**, F, 9mm, 10 Aug 96
	Neoeutrypanus sp. 915 (n=2)	**1182**, M, 10mm, 10 May 96; **1230**, F, 12mm, 16 May 96
	Oreodera melzeri (n=1)	**1014**, F, 8.5mm, 26 Apr 96
	Palame crassimana (n=140)	**43**, F, 8.5mm, 15 Jan 96; **48**, M, 7.5mm, 17 Jan 96; **62**, F, 7mm, 19 Jan 96; **64**, M, 6mm, 20 Jan 96; **68**, M, 6.5mm, 20 Jan 96; **98**, M, 6mm, 23 Jan 96; **119**, F, ±, 25 Jan 96; **121**, F, 8mm, 25 Jan 96; **123**, F, 6.5mm, 25 Jan 96; **126**, F, 8mm, 25 Jan 96; **143**, F, 7mm, 27 Jan 96; **146**, M, 6mm, 27 Jan 96; **151**, F, 7.5mm, 28 Jan 96; **152**, M, 5.5mm, 28 Jan 96; **154**, M, 6.5mm, 28 Jan 96; **164**, F, 6.5mm, 29 Jan 96; **172**, F, 6mm, 30 Jan 96; **192**, M, 6.5mm, 1 Feb 96; **205**, M, 6.5mm, 2 Feb 96; **214**, M, 6.5mm, 3 Feb 96; **217**, M, 6mm, 3 Feb 96; **232**, F, 8mm, 4 Feb 96; **233**, M, 6.5mm, 4 Feb 96; **267**, M, 6.5mm, 7 Feb 96; **293**, M, 6mm, 11 Feb 96; **300**, F, 7.5mm, 12 Feb 96; **316**, M, 7mm, 14 Feb 96; **328**, F, 6mm, 15 Feb 96; **346**, F, 5.5mm, 17 Feb 96; **347**, F, 7mm, 17 Feb 96; **359**, F, 5.5mm, 18 Feb 96; **361**, M, 6mm, 18 Feb 96; **366**, M, 5.5mm, 19 Feb 96; **373**, M, 6mm, 20 Feb 96; **378**, F, 7.5mm, 21 Feb 96; **380**, M, 6mm, 21 Feb 96; **386**, F, 7.5mm, 22 Feb 96; **395**, F, 6.5mm, 23 Feb 96; **396**, M, 6.5mm, 23 Feb 96; **398**, F, 8mm, 23 Feb 96; **399**, M, 6.5mm, 23 Feb 96; **413**, F, 7.5mm, 24 Feb 96; **414**, M, 7mm, 24 Feb 96; **415**, M, 6.5mm, 24 Feb 96; **421**, F, 7mm, 25 Feb 96; **423**, F, 6.5mm, 25 Feb 96; **425**, M, 6mm, 25 Feb 96; **427**, M, 6.5mm, 25 Feb 96; **442**, M, 5.5mm, 1 Mar 96; **451**, F, 6mm, 2 Mar 96; **453**, F, 6.5mm, 2 Mar 96; **477**, M, 5.5mm, 4 Mar 96; **481**, F, 7mm, 5 Mar 96; **482**, M, 7mm, 5 Mar 96; **489**, F, 7mm, 5 Mar 96; **490**, M, 7mm, 5 Mar 96; **491**, F, 6mm, 5 Mar 96; **493**, M, 6.5mm, 6 Mar 96; **495**, M, 6.5mm, 6 Mar 96; **506**, M, 6.5mm, 7 Mar 96; **507**, M, 6mm, 7 Mar 96; **511**, F, 7.5mm, 7 Mar 96; **520**, F, 6.5mm, 8 Mar 96; **525**, M, 7.5mm, 9 Mar 96; **533**, M, 7.5mm, 9 Mar 96;

Appendix II contd.

Branch	Cerambycid species reared	Individuals reared (**collection #**, gender, length, date of emergence)
BIG CAGE T,U,V,W,X	*Palame crassimana* contd.	**539**, M, 7.5mm, 9 Mar 96; **546**, F, 6.5mm, 10 Mar 96; **547**, F, 7.5mm, 10 Mar 96; **548**, M, 5.5mm, 10 Mar 96; **549**, M, 7mm, 10 Mar 96; **550**, F, 6mm, 10 Mar 96; **551**, F, 7mm, 10 Mar 96; **553**, M, 6mm, 10 Mar 96; **563**, M, 5.5mm, 11 Mar 96; **564**, F, 8mm, 11 Mar 96; **591**, F, 6.5mm, 14 Mar 96; **592**, F, 6mm, 14 Mar 96; **604**, M, 7.5mm, 15 Mar 96; **614**, F, 7mm, 16 Mar 96; **616**, M, 6mm, 16 Mar 96; **623**, F, 7.5mm, 17 Mar 96; **634**, M, 6.5mm, 20 Mar 96; **645**, F, 7.5mm, 21 Mar 96; **646**, M, 6.5mm, 21 Mar 96; **654**, F, 6mm, 22 Mar 96; **659**, F, 7mm, 22 Mar 96; **660**, F, 8mm, 22 Mar 96; **704**, F, 7mm, 26 Mar 96; **711**, M, 6.5mm, 27 Mar 96; **733**, M, 6mm, 29 Mar 96; **742**, F, 7.5mm, 30 Mar 96; **743**, F, 5.5mm, 30 Mar 96; **755**, M, 7.5mm, 31 Mar 96; **764**, F, 6.5mm, 1 Apr 96; **767**, M, 5mm, 2 Apr 96; **769**, F, 7mm, 2 Apr 96; **773**, M, 6.5mm, 2 Apr 96; **783**, M, 5.5mm, 2 Apr 96; **792**, M, 7.5mm, 3 Apr 96; **799**, F, 8mm, 4 Apr 96; **802**, F, 7mm, 4 Apr 96; **808**, M, 6mm, 5 Apr 96; **809**, M, 5mm, 5 Apr 96; **810**, F, 8mm, 5 Apr 96; **811**, F, 7mm, 5 Apr 96; **812**, F, 7mm, 5 Apr 96; **813**, M, 5.5mm, 5 Apr 96; **816**, F, 7mm, 6 Apr 96; **817**, F, 7mm, 6 Apr 96; **818**, M, 7mm, 6 Apr 96; **826**, F, 6.5mm, 7 Apr 96; **842**, F, 8.5mm, 8 Apr 96; **848**, F, 7.5mm, 9 Apr 96; **870**, F, 7.5mm, 12 Apr 96; **872**, M, 5mm, 12 Apr 96; **891**, F, 7mm, 14 Apr 96; **898**, M, 5mm, 15 Apr 96; **899**, M, 7.5mm, 15 Apr 96; **914**, F, 7mm, 16 Apr 96; **945**, F, 7.5mm, 19 Apr 96; **946**, F, 6.5mm, 19 Apr 96; **947**, F, 6.5mm, 19 Apr 96; **956**, F, 7.5mm, 20 Apr 96; **968**, M, 7mm, 21 Apr 96; **976**, M, 7mm, 22 Apr 96; **977**, F, 7.5mm, 22 Apr 96; **978**, M, 7mm, 22 Apr 96; **985**, F, 7.5mm, 23 Apr 96; **1015**, M, 7.5mm, 26 Apr 96; **1030**, M, 7mm, 27 Apr 96; **1032**, M, 7mm, 27 Apr 96; **1074**, F, 7mm, 1 May 96; **1107**, M, 5.5mm, 3 May 96; **1115**, F, 7mm, 4 May 96; **1204**, F, 7mm, 13 May 96; **1205**, F, 7mm, 13 May 96; **1237**, M, 7.5mm, 17 May 96; **1371**, F, 8mm, 31 May 96; **1466**, F, 7mm, 15 June 96; **1504**, F, 6.5mm, 21 June 96
	Palame mimetica (n=207)	1, M, 11mm, 31 Dec; **9**, M, 9mm, 1 Jan 96; **15**, M, 10mm, 3 Jan 96; **17**, M, 9mm, 4 Jan 96; **42**, M, 9mm, 15 Jan 96; **67**, F, 7.5mm, 20 Jan 96; **69**, F, 8.5mm, 20 Jan 96; **70**, F, 6.5mm, 20 Jan 96; **75**, F, 8.5mm, 21 Jan 96; **82**, M, 6mm, 21 Jan 96; **83**, F, 9mm, 21 Jan 96; **90**, F, 7.5mm, 22 Jan 96; **92**, F, 7.5mm, 22 Jan 96; **108**, M, 9.5mm, 24 Jan 96; **110**, M, 8.5mm, 24 Jan 96; **111**, M, 9mm, 24 Jan 96; **113**, F, 6mm, 25 Jan 96; **120**, F, 7.5mm, 25 Jan 96; **122**, M, 5.5mm, 25 Jan 96; **124**, F, 8mm, 25 Jan 96; **125**, M, 8.5mm, 25 Jan 96; **135**, F, 6.5mm, 26 Jan 96; **136**, M, 5.5mm, 26 Jan 96; **137**, M, 5.5mm, 26 Jan 96; **147**, F, 7.5mm, 28 Jan 96; **150**, F, 6.5mm, 28 Jan 96; **153**, F, 6.5mm, 28 Jan 96; **155**, M, 6mm, 28 Jan 96; **156**, M, 7mm, 28 Jan 96; **157**, F, 8mm, 28 Jan 96; **158**, F, 6mm, 28 Jan 96; **159**, F, 7.5mm, 29 Jan 96; **160**, F, 6mm, 29 Jan 96; **162**, F, 8.5mm, 29 Jan 96; **163**, F, 6mm, 29 Jan 96; **165**, F, 8mm, 29 Jan 96; **171**, M, 8.5mm, 30 Jan 96; **173**, F, 8.5mm, 30 Jan 96; **174**, M, 5mm, 30 Jan 96; **175**, M, 5mm, 30 Jan 96; **182**, F, 6mm, 31 Jan 96; **183**, M, 5.5mm, 31 Jan 96; **184**, F, 6mm, 31 Jan 96; **185**, M, 6mm, 31 Jan 96; **190**, M, 6.5mm, 1 Feb 96; **191**, M, 5.5mm, 1 Feb 96; **193**, M, 6mm, 1 Feb 96; **194**, M, 6.5mm, 1 Feb 96; **203**, M, 9mm, 2 Feb 96; **204**, F, 7.5mm, 2 Feb 96; **206**, M, 8.5mm, 2 Feb 96; **207**, F, 7mm, 2 Feb 96; **208**, F, 8.5mm, 2 Feb 96; **209**, M, 7mm, 2 Feb 96; **215**, F, 7.5mm, 3 Feb 96; **216**, M, 6mm, 3 Feb 96; **219**, F, 6.5mm, 3 Feb 96; **220**, M, 7.5mm, 3 Feb 96;

Appendix II contd.

Branch	Cerambycid species reared	Individuals reared (**collection #**, gender, length, date of emergence)
BIG CAGE T,U,V,W,X	*Palame mimetica* contd.	**221**, M, 8mm, 3 Feb 96; **223**, M, 6mm, 3 Feb 96; **224**, M, 6mm, 3 Feb 96; **225**, F, 6.5mm, 3 Feb 96; **234**, M, 6mm, 4 Feb 96; **235**, M, 7.5mm, 4 Feb 96; **236**, F, 6mm, 4 Feb 96; **237**, M, 5.5mm, 4 Feb 96; **246**, F, 7.5mm, 5 Feb 96; **247**, F, 8mm, 5 Feb 96; **248**, M, 5.5mm, 5 Feb 96; **249**, F, 7.5mm, 5 Feb 96; **257**, F, 5.5mm, 6 Feb 96; **262**, F, 8.5mm, 7 Feb 96; **264**, M, 6mm, 7 Feb 96; **265**, F, 7mm, 7 Feb 96; **266**, F, 5.5mm, 7 Feb 96; **268**, F, 6.5mm, 7 Feb 96; **277**, F, 8mm, 9 Feb 96; **284**, F, 8mm, 10 Feb 96; **285**, F, 6mm, 10 Feb 96; **289**, F, 6.5mm, 11 Feb 96; **291**, F, 6.5mm, 11 Feb 96; **292**, F, 6.5mm, 11 Feb 96; **295**, M, 6.5mm, 11 Feb 96; **303**, F, 8.5mm, 12 Feb 96; **307**, F, 6.5mm, 13 Feb 96; **314**, F, 6mm, 14 Feb 96; **315**, M, 6mm, 14 Feb 96; **317**, M, 7.5mm, 14 Feb 96; **329**, F, 6mm, 15 Feb 96; **332**, M, 5.5mm, 15 Feb 96; **335**, F, 6mm, 15 Feb 96; **337**, M, 6mm, 15 Feb 96; **340**, M, 6.5mm, 16 Feb 96; **342**, F, 7.5mm, 16 Feb 96; **360**, F, 5.5mm, 18 Feb 96; **364**, M, 7mm, 19 Feb 96; **365**, F, 7mm, 19 Feb 96; **367**, F, 6.5mm, 19 Feb 96; **368**, M, 6mm, 19 Feb 96; **375**, M, 5.5mm, 20 Feb 96; **379**, M, 6.5mm, 21 Feb 96; **387**, F, 6mm, 22 Feb 96; **397**, F, 7.5mm, 23 Feb 96; **400**, M, 5.5mm, 23 Feb 96; **401**, M, 6mm, 23 Feb 96; **402**, M, 6mm, 23 Feb 96; **409**, F, 9.5mm, 23 Feb 96; **416**, M, 6.5mm, 24 Feb 96; **417**, F, 7mm, 24 Feb 96; **418**, M, 5.5mm, 24 Feb 96; **419**, F, 6.5mm, 24 Feb 96; **424**, M, 5.5mm, 25 Feb 96; **426**, F, 6mm, 25 Feb 96; **440**, F, 6.5mm, 1 Mar 96; **441**, M, 5mm, 1 Mar 96; **450**, M, 5.5mm, 2 Mar 96; **452**, M, 6mm, 2 Mar 96; **454**, M, 5mm, 2 Mar 96; **456**, M, 6.5mm, 2 Mar 96; **462**, F, 6.5mm, 3 Mar 96; **463**, M, 6mm, 3 Mar 96; **464**, M, 6mm, 3 Mar 96; **465**, M, 6mm, 3 Mar 96; **466**, M, 5.5mm, 3 Mar 96; **467**, F, 7mm, 3 Mar 96; **487**, M, 6.5mm, 5 Mar 96; **494**, F, 6.5mm, 6 Mar 96; **508**, M, 6.5mm, 7 Mar 96; **509**, F, 6.5mm, 7 Mar 96; **510**, M, 6mm, 7 Mar 96; **521**, M, 5mm, 8 Mar 96; **531**, M, 5.5mm, 9 Mar 96; **532**, M, 5.5mm, 9 Mar 96; **534**, M, 7.5mm, 9 Mar 96; **535**, F, 7mm, 9 Mar 96; **536**, M, 5.5mm, 9 Mar 96; **537**, F, 6mm, 9 Mar 96; **538**, M, 6.5mm, 9 Mar 96; **545**, F, 6mm, 10 Mar 96; **552**, M, 6.5mm, 10 Mar 96; **557**, M, 6mm, 11 Mar 96; **562**, F, 7mm, 11 Mar 96; **565**, M, 5.5mm, 11 Mar 96; **566**, F, 7mm, 11 Mar 96; **567**, F, 7.5mm, 11 Mar 96; **575**, M, 6mm, 12 Mar 96; **579**, F, 6.5mm, 12 Mar 96; **581**, F, 6.5mm, 13 Mar 96; **588**, F, 6mm, 14 Mar 96; **589**, M, 7mm, 14 Mar 96; **590**, M, 6.5mm, 14 Mar 96; **593**, F, 6mm, 14 Mar 96; **605**, M, 4.5mm, 15 Mar 96; **615**, F, 6mm, 16 Mar 96; **617**, M, 6mm, 16 Mar 96; **622**, M, 5.5mm, 17 Mar 96; **633**, F, 6.5mm, 20 Mar 96; **635**, M, 6mm, 20 Mar 96; **637**, F, 6.5mm, 20 Mar 96; **638**, F, 7mm, 20 Mar 96; **643**, M, 6mm, 21 Mar 96; **647**, F, 5.5mm, 21 Mar 96; **650**, F, 7mm, 21 Mar 96; **655**, M, 5.5mm, 22 Mar 96; **656**, F, 5.5mm, 22 Mar 96; **657**, F, 6.5mm, 22 Mar 96; **658**, F, 6.5mm, 22 Mar 96; **661**, M, 7mm, 22 Mar 96; **690**, F, 6.5mm, 24 Mar 96; **697**, M, 5.5mm, 25 Mar 96; **703**, F, 7mm, 26 Mar 96; **710**, M, 6.5mm, 27 Mar 96; **722**, F, 5.5mm, 28 Mar 96; **723**, M, 4.5mm, 28 Mar 96; **726**, F, 7.5mm, 28 Mar 96; **731**, M, 7mm, 29 Mar 96; **741**, M, 6mm, 30 Mar 96; **745**, M, 8.5mm, 30 Mar 96; **770**, M, 5.5mm, 2 Apr 96; **791**, F, 6.5mm, 3 Apr 96; **798**, F, 6mm, 4 Apr 96; **800**, M, 6mm, 4 Apr 96; **824**, M, 7mm, 7 Apr 96; **825**, F, 7.5mm, 7 Apr 96; **849**, M, 5.5mm, 9 Apr 96; **850**, M, 6.5mm, 9 Apr 96; **862**, M, 6mm, 11 Apr 96; **871**, F, 5.5mm, 12 Apr 96; **882**, F, 6.5mm, 13 Apr 96; **892**, M, 8mm, 14 Apr 96; **900**, F, 6.5mm, 15 Apr 96;

Appendix II contd.

Branch	Cerambycid species reared	Individuals reared (**collection #**, gender, length, date of emergence)
BIG CAGE T,U,V,W,X	*Palame mimetica* contd.	**910**, F, 6mm, 16 Apr 96; **912**, M, 6mm, 16 Apr 96; **913**, M, 8mm, 16 Apr 96; **921**, M, 8mm, 17 Apr 96; **966**, F, 6.5mm, 21 Apr 96; **1018**, F, 7mm, 26 Apr 96; **1062**, M, 5.5mm, 30 Apr 96; **1069**, M, 4.5mm, 1 May 96; **1075**, M, 5mm, 1 May 96; **1088**, M, 8mm, 2 May 96; **1147**, M, 6mm, 6 May 96; **1150**, M, 4.5mm, 7 May 96; **1181**, F, 4mm, 10 May 96; **1201**, F, 6.5mm, 13 May 96; **1329**, M, 5.5mm, 26 May 96; **1386**, M, 5.5mm, 2 June 96
	Peribocum pubescens (n=77)	**561**, F, 9.5mm, 11 Mar 96; **576**, F, 8.5mm, 12 Mar 96; **606**, F, 11mm, 15 Mar 96; **636**, M, 11.5mm, 20 Mar 96; **644**, M, 9.5mm, 21 Mar 96; **691**, F, 11.5mm, 24 Mar 96; **702**, M, 10mm, 26 Mar 96; **709**, M, 12.5mm, 27 Mar 96; **712**, F, 10.5mm, 27 Mar 96; **721**, M, 8mm, 28 Mar 96; **729**, M, 12mm, 29 Mar 96; **730**, F, 11mm, 29 Mar 96; **739**, M, 11mm, 30 Mar 96; **740**, M, 7mm, 30 Mar 96; **768**, M, 10mm, 2 Apr 96; **807**, F, 10.5mm, 5 Apr 96; **841**, F, 9mm, 8 Apr 96; **863**, F, 10mm, 11 Apr 96; **868**, F, 12.5mm, 12 Apr 96; **881**, M, 9.5mm, 13 Apr 96; **893**, M, 11.5mm, 14 Apr 96; **911**, M, 11.5mm, 16 Apr 96; **934**, M, 8mm, 18 Apr 96; **935**, M, 9.5mm, 18 Apr 96; **944**, M, 8mm, 19 Apr 96; **955**, F, 11mm, 20 Apr 96; **983**, F, 9.5mm, 23 Apr 96; **984**, F, 10mm, 23 Apr 96; **1031**, F, 8mm, 27 Apr 96; **1058**, F, 10mm, 29 Apr 96; **1061**, F, 13mm, 30 Apr 96; **1070**, M, 11.5mm, 1 May 96; **1072**, F, 14mm, 1 May 96; **1073**, M, 11mm, 1 May 96; **1089**, M, 9.5mm, 2 May 96; **1091**, M, 11.5mm, 2 May 96; **1092**, F, 11mm, 2 May 96; **1109**, F, 13.5mm, 3 May 96; **1110**, M, 12mm, 3 May 96; **1111**, M, 9mm, 3 May 96; **1112**, M, 10mm, 3 May 96; **1114**, M, 9.5mm, 4 May 96; **1116**, F, 11.5mm, 4 May 96; **1127**, F, 13mm, 5 May 96; **1129**, F, 10.5mm, 5 May 96; **1135**, F, 11mm, 6 May 96; **1136**, F, 11mm, 6 May 96; **1151**, F, 14mm, 7 May 96; **1165**, F, 10.5mm, 9 May 96; **1179**, F, 10mm, 10 May 96; **1180**, M, 9mm, 10 May 96; **1188**, M, 10mm, 11 May 96; **1190**, F, 12.5mm, 12 May 96; **1200**, M, 11mm, 13 May 96; **1213**, F, 11mm, 14 May 96; **1214**, M, 8.5mm, 14 May 96; **1221**, F, 10mm, 15 May 96; **1229**, M, 9.5mm, 16 May 96; **1248**, M, 10mm, 18 May 96; **1264**, F, 12.5 19 May 96; **1265**, ±, ±, 20 May 96; **1266**, M, 11.5mm, 20 May 96; **1290**, F, 14.5mm, 22 May 96; **1306**, M, 11mm, 23 May 96; **1314**, F, 14mm, 24 May 96; **1315**, F, 11.5mm, 24 May 96; **1364**, F, 15mm, 30 May 96; **1379**, M, 14.5mm, 1 June 96; **1413**, F, 12mm, 6 June 96; **1492**, F, 10mm, 20 June 96; **1505**, F, 13mm, 21 June 96; **1570**, M, 9mm, 1 July 96; **1608**, F, 11mm, 6 July 96; **1621**, F, 13mm, 7 July 96; **1622**, M, 12.5mm, 7 July 96; **1689**, F, 11.5mm, 20 July 96; **1704**, F, 11.5mm, 23 July 96
	Symperasmus thoracicus (n=1)	**1768**, F, 15mm, 6 Aug 96
	Xylergatina pulchra (n=19)	**112**, M, 18.5mm, 25 Jan 96; **276**, F, 15mm, 9 Feb 96; **288**, F, ±, 11 Feb 96; **326**, F, 15.5mm, 15 Feb 96; **343**, F, 16.5mm, 17 Feb 96; **371**, M, 16.5mm, 19 Feb 96; **474**, F, 14.5mm, 4 Mar 96; **492**, F, 15.5mm, 5 Mar 96; **513**, F, 15.5mm, 7 Mar 96; **522**, M, 18mm, 8 Mar 96; **523**, F, 14.5mm, 9 Mar 96; **555**, M, 17mm, 10 Mar 96; **556**, F, 16.5mm, 11 Mar 96; **587**, M, 14mm, 14 Mar 96; **609**, F, 17mm, 16 Mar 96; **625**, F, 15.5mm, 17 Mar 96; **696**, M, 16.5mm, 25 Mar 96; **967**, M, 16.5mm, 21 Apr 96; **1280**, F, 14.5mm, 21 May 96

Appendix II contd.

Branch	Cerambycid species reared	Individuals reared (**collection #**, gender, length, date of emergence)
Cerambycids emerged from *Corythophora amapaensis*, rainy season branches		
R-O-G-10	—	—
R-O-G-2.5	—	—
R-P-G-10	—	—
R-P-G-2.5	—	—
R-Q-G-10	—	—
R-Q-G-2.5	—	—
R-S-G-10*	—	—
R-S-G-2.5	—	—
BIG CAGE		
Rainy O	—	—
Rainy P	—	—
Rainy Q	*Plistonax albolinitus* (n=1)	**1648**, M, 14mm, 11 July 96
	Stratone rufotestacea (n=1)	**1645**, F, 10mm, 10 July 96
Rainy S	—	—
Cerambycids emerged from *Couratari stellata*, rainy season branches		
R-E-G-10*	—	—
R-E-G-2.5*	—	—
R-F-G-10*	—	—
R-F-G-2.5	—	—
R-H-G-10*	—	—
R-H-G-2.5*	—	—
R-J-G-10	—	—
R-J-G-2.5*	—	—
BIG CAGE E,F,H,J	—	—
Cerambycids emerged from *Eschweilera coriacea*, rainy season branches		
R-80-C-10	*Neoeutrypanus nobilis* (n=5)	**1811**, ±, ±, 18 Sept 96; **1814**, ±, ±, 25 Sept 96; **1817**, ±, ±, 4 Oct 96; **1818**, ±, ±, 5 Oct 96; **1820**, ±, ±, 16 Oct 96
	Oedopeza leucostigma (n=6)	**1195**, F, 11mm, 12 May 96; **1440**, ±, ±, 8 June 96; **1463**, F, 9.5mm, 14 June 96; **1470**, M, 9mm, 15 June 96; **1496**, M, 8.5mm, 20 June 96; **1508**, M, 8mm, 22 June 96

Appendix II contd.

Branch	Cerambycid species reared	Individuals reared (**collection #**, gender, length, date of emergence)
R-80-C-10	*Palame anceps* (n=35)	**1029**, M, 7.5mm, 27 Apr 96; **1103**, M, 7.5mm, 3 May 96; **1104**, M, 7.5mm, 3 May 96; **1121**, M, 7mm, 4 May 96; **1196**, M, 7.5mm, 12 May 96; **1197**, M, 7mm, 12 May 96; **1232**, F, 7.5mm, 17 May 96; **1233**, F, 7.5mm, 17 May 96; **1244**, F, 7mm, 18 May 96; **1267**, F, 8mm, 20 May 96; **1268**, M, 6.5mm, 20 May 96; **1270**, M, 7mm, 20 May 96; **1312**, M, 7mm, 24 May 96; **1319**, M, 7mm, 25 May 96; **1320**, ±, ±, 25 May 96; **1335**, F, 7mm, 27 May 96; **1339**, F, 7mm, 28 May 96; **1359**, M, 7.5mm, 29 May 96; **1374**, M, 6.5mm, 31 May 96; **1375**, M, 5.5mm, 31 May 96; **1382**, F, 7.5mm, 1 June 96; **1389**, M, 8mm, 2 June 96; **1390**, M, 7mm, 2 June 96; **1400**, M, 7mm, 3 June 96; **1401**, M, 7mm, 3 June 96; **1421**, F, 8mm, 6 June 96; **1427**, F, 6.5mm, 7 June 96; **1428**, M, 7.5mm, 7 June 96; **1509**, M, 6mm, 22 June 96; **1525**, F, 6mm, 24 June 96; **1569**, M, 6mm, 30 June 96; **1574**, F, 6.5mm, 1 July 96; **1630**, F, 6mm, 8 July 96; **1729**, M, 5.5mm, 28 July 96; **1798**, ±, ±, 19 Aug 96
	Palame crassimana[U] (n=40)	**1222**, M, 7mm, 15 May 96; **1231**, F, 8mm, 17 May 96; **1245**, M, 7mm, 18 May 96; **1246**, M, 7mm, 18 May 96; **1262**, M, 7.5mm, 19 May 96; **1269**, F, 8mm, 20 May 96; **1299**, F, 8.5mm, 23 May 96; **1340**, F, 8mm, 28 May 96; **1383**, F, 7.5mm, 1 June 96; **1405**, F, 7.5mm, 4 June 96; **1420**, F, 7.5mm, 6 June 96; **1444**, F, 7mm, 9 June 96; **1458**, M, 7mm, 13 June 96; **1459**, M, 7mm, 13 June 96; **1497**, F, ±, 20 June 96; **1498**, M, 7mm, 20 June 96; **1515**, M, 6mm, 23 June 96; **1539**, F, 7mm, 26 June 96; **1544**, M, 6.5mm, 27 June 96; **1551**, M, 7mm, 28 June 96; **1564**, F, 7mm, 29 June 96; **1575**, F, 7mm, 1 July 96; **1590**, F, 7mm, 3 July 96; **1592**, M, 6.5mm, 3 July 96; **1599**, M, 6mm, 4 July 96; **1601**, F, 7mm, 5 July 96; **1612**, M, 7mm, 6 July 96; **1624**, M, 7mm, 7 July 96; **1625**, M, 6.5mm, 7 July 96; **1626**, M, 6.5mm, 7 July 96; **1629**, M, 6.5mm, 8 July 96; **1631**, M, 6mm, 8 July 96; **1632**, F, 6.5mm, 8 July 96; **1656**, M, 7.5mm, 13 July 96; **1657**, F, 7.5mm, 13 July 96; **1669**, M, 6mm, 15 July 96; **1718**, M, 7mm, 26 July 96; **1736**, F, 7mm, 29 July 96; **1748**, M, 7mm, 31 July 96; **1808**, ±, ±, 3 Sept 96
	Palame mimetica (n=10)	**1464**, M, 5.5mm, 14 June 96; **1499**, M, 6mm, 20 June 96; **1516**, M, ±, 23 June 96; **1543**, F, 6mm, 27 June 96; **1552**, F, 6.5mm, 28 June 96; **1591**, M, 5.5mm, 3 July 96; **1641**, M, 6mm, 9 July 96; **1663**, F, 7mm, 14 July 96; **1664**, M, 5.5mm, 14 July 96; **1668**, F, 5.5mm, 15 July 96
	Xenofrea sp. 662 (n=2)	**1332**, F, ±, 26 May 96; **1507**, M, 10mm, 22 June 96
	Xylergates elaineae (n=1)	**1460**, M, 10.5mm, 13 June 96
R-80-C-2.5	*Palame anceps* (n=1)	**1357**, M, 6mm, 29 May 96
R-80-G-10	—	—
R-80-G-2.5	—	—
R-A-C-10	*Neoeutrypanus mutilatus* (n=1)	**1815**, F, 8.5mm, 30 Sept 96
	Oreodera simplex (n=1)	**1725**, M, 11.5mm, 27 July 96

Appendix II contd.

Branch	Cerambycid species reared	Individuals reared (**collection #**, gender, length, date of emergence)
R-A-C-10	*Palame anceps* (n=25)	**1193**, F, 8.5mm, 12 May 96; **1296**, M, 7mm, 22 May 96; **1301**, F, 7.5mm, 23 May 96; **1327**, F, 7.5mm, 25 May 96; **1360**, M, 7mm, 29 May 96; **1391**, F, 6.5mm, 2 June 96; **1404**, M, 8.5mm, 4 June 96; **1436**, M, 7mm, 8 June 96; **1471**, M, 6.5mm, 15 June 96; **1485**, M, 7mm, 18 June 96; **1510**, F, 7mm, 22 June 96; **1514**, F, 7mm, 23 June 96; **1545**, M, 7mm, 27 June 96; **1548**, M, 6.5mm, 28 June 96; **1549**, M, 7mm, 28 June 96; **1588**, M, 6.5mm, 3 July 96; **1589**, F, 6.5mm, 3 July 96; **1600**, M, 7mm, 5 July 96; **1609**, F, ±, 6 July 96; **1610**, M, 7mm, 6 July 96; **1611**, M, 7mm, 6 July 96; **1623**, M, 7mm, 7 July 96; **1708**, M, 7.5mm, 24 July 96; **1717**, M, 6.5mm, 26 July 96; **1752**, M, 6.5mm, 1 Aug 96
	Palame crassimana[U] (n=2)	**1442**, M, 7mm, 9 June 96; **1457**, M, 7.5mm, 13 June 96
	Palame mimetica (n=17)	**973**, F, 6mm, 22 Apr 96; **1087**, F, 6.5mm, 2 May 96; **1106**, F, 6.5mm, 3 May 96; **1159**, M, 6.5mm, 7 May 96; **1175**, F, 6.5mm, 10 May 96; **1275**, F, 6.5mm, 21 May 96; **1418**, M, 6.5mm, 6 June 96; **1443**, M, 6mm, 9 June 96; **1472**, F, 6mm, 15 June 96; **1501**, F, 7.5mm,20 June 96; **1503**, F, 6mm, 21 June 96; **1538**, M, 5.5mm, 26 June 96; **1547**, M, 6mm, 28 June 96; **1550**, F, 6mm, 28 June 96; **1674**, M, 5.5mm, 16 July 96; **1678**, F, 7mm, 17 July 96; **1702**, ±, 6.5mm, 22 July 96
	Xylergates elaineae (n=15)	**988**, F, 11mm, 23 Apr 96; **1068**, F, 11mm, 30 Apr 96; **1122**, M, 10.5mm, 4 May 96; **1123**, M, 11mm, 4 May 96; **1124**, F, 12mm, 4 May 96; **1176**, M, 11.5mm, 10 May 96; **1177**, F, 10.5mm, 10 May 96; **1194**, M, 10mm, 12 May 96; **1256**, F, 13mm, 18 May 96; **1271**, F, 10.5mm, 20 May 96; **1272**, F, 10mm, 20 May 96; **1300**, F, 10mm, 23 May 96; **1333**, F, 11mm, 26 May 96; **1377**, M, 11mm, 31 May 96; **1392**, F, 11mm, 2 June 96
R-A-C-2.5	Gen. sp. (n=1)	**1653**, F, 4.5mm, 12 July 96
	Ozineus sp. (n=5)	**1046**, F, 6mm, 29 Apr 96; **1047**, M, 6mm, 29 Apr 96; **1048**, F, 6mm, 29 Apr 96; **1052**, F, 7mm, 29 Apr 96; **1735**, F, 6mm, 29 July 96
	Palame anceps (n=2)	**1051**, F, 6.5mm, 29 Apr 96; **1082**, M, 7mm, 1 May 96
R-A-G-10	—	—
R-A-G-2.5	—	—
R-B-C-10	*Oedopeza leucostigma* (n=1)	**1148**, M, 8mm, 6 May 96
	Palame anceps (n=11)	**1028**, M, 7mm, 27 Apr 96; **1614**, M, 5.5mm, 6 July 96; **1722**, M, 5.5mm, 27 July 96; **1740**, M, 6.5mm, 30 July 96; **1754**, F, 7.5mm, 2 Aug 96; **1758**, M, 7mm, 2 Aug 96; **1777**, M, 5.5mm, 6 Aug 96; **1799**, ±, ±, 21 Aug 96; **1802**, ±, ±, 25 Aug 96; **1807**, ±, ±, 31 Aug 96; **1809**, ±, ±, 5 Sept 96
	Palame crassimana[U] (n=13)	**1172**, M, 6.5mm, 9 May 96; **1273**, F, ±, 20 May 96; **1276**, F, 7.5mm, 21 May 96; **1399**, M, 6.5mm, 3 June 96; **1419**, M, 6mm, 6 June 96; **1535**, F, 7mm, 25 June 96; **1613**, F, 6.5mm, 6 July 96; **1670**, M, 7mm, 15 July 96; **1723**, F, 6.5mm, 27 July 96; **1724**, M, 6mm, 27 July 96; **1749**, M, 7mm, 31 July 96; **1776**, M, 6mm, 6 Aug 96; **1789**, M, 6.5mm, 9 Aug 96
	Xylergates elaineae (n=2)	**1199**, F, 10mm, 12 May 96; **1326**, M, 8.5mm, 25 May 96

Appendix II contd.

Branch	Cerambycid species reared	Individuals reared (**collection #**, gender, length, date of emergence)
R-B-C-2.5	*Ozineus* sp. (n=10)	**1313**, M, 6mm, 24 May 96; **1336**, F, 6.5mm, 27 May 96; **1398**, F, 6.5mm, 3 June 96; **1477**, M, 5.5mm, 17 June 96; **1577**, M, 6mm, 1 July 96; **1642**, M, 6mm, 10 July 96; **1643**, F, 6.5mm, 10 July 96; **1673**, M, 5mm, 16 July 96; **1706**, M, 5mm, 23 July 96; **1707**, ±, ±, 23mm, July 96
	Palame anceps (n=3)	**1187**, M, 7.5mm, 11 May 96; **1228**, M, 7.5mm, 16 May 96; **1489**, F, 6.5mm, 19 June 96
	Palame crassimana[U] (n=4)	**1490**, F, 7mm, 19 June 96; **1518**, M, 6mm, 23 June 96; **1534**, F, 7mm, 25 June 96; **1576**, M, 6mm, 1 July 96
R-B-G-10	—	—
R-B-G-2.5	—	—
R-D-C-10	*Ozineus* sp. (n=3)	**878**, M, 8mm, 12 Apr 96; **939**, F, 7.5mm, 19 Apr 96; **1439**, M, 6mm, 8 June 96
	Palame anceps (n=22)	**720**, M, 7mm, 28 Mar 96; **890**, F, 8mm, 13 Apr 96; **960**, M, 8mm, 21 Apr 96; **961**, F, 8mm, 21 Apr 96; **974**, M, 7.5mm, 22 Apr 96; **975**, F, 8mm, 22 Apr 96; **1005**, M, 8mm, 25 Apr 96; **1019**, M, 7mm, 26 Apr 96; **1027**, M, 8mm, 27 Apr 96; **1045**, F, 8mm, 29 Apr 96; **1067**, M, 8.5mm, 30 Apr 96; **1086**, M, 7.5mm, 2 May 96; **1105**, F, 8mm, 3 May 96; **1134**, M, 8mm, 5 May 96; **1139**, F, 7.5mm, 6 May 96; **1140**, M, 7mm, 6 May 96; **1198**, M, 8mm, 12 May 96; **1294**, M, 6mm, 22 May 96; **1295**, M, 7.5mm, 22 May 96; **1376**, M, 5.5mm, 31 May 96; **1658**, M, 7.5mm, 13 July 96; **1782**, F, 7mm, 8 Aug 96
	Palame crassimana[U] (n=9)	**888**, F, 7.5mm, 13 Apr 96; **907**, F, 7mm, 15 Apr 96; **938**, F, 7mm, 19 Apr 96; **959**, F, 7mm, 21 Apr 96; **982**, F, 7.5mm, 23 Apr 96; **1004**, F, 7mm, 25 Apr 96; **1026**, M, 6.5mm, 27 Apr 96; **1056**, F, 7.5mm, 29 Apr 96; **1227**, M, 6mm, 16 May 96
	Palame mimetica (n=2)	**1141**, F, 6mm, 6 May 96; **1341**, F, 6.5mm, 28 May 96
	Xenofrea sp. 662 (n=10)	**981**, F, 10mm, 23 Apr 96; **1793**, ±, ±, 24 Apr 96; **1049**, F, 10mm, 29 Apr 96; **1163**, M, 9.5mm, 8 May 96; **1171**, M, 10mm, 9 May 96; **1209**, F, 9.5mm, 13 May 96; **1243**, F, 9mm, 18 May 96; **1257**, M, 9.5mm, 18 May 96; **1438**, M, 9mm, 8 June 96; **1450**, F, 9mm, 11 June 96
R-D-C-2.5	*Neoeutrypanus mutilatus* (n=1)	**1812**, F, 9mm, 21 Sept 96
	Ozineus sp. (n=5)	**1358**, F, 6mm, 29 May 96; **1565**, M, 5.5mm, 29 June 96; **1644**, F, 6.5mm, 10 July 96; **1727**, F, 6mm, 28 July 96; **1784**, M, 5mm, 8 Aug 96
	Palame anceps (n=1)	**1142**, F, 8mm, 6 May 96
	Xenofrea sp. 714 (n=2)	**1378**, F, 4mm, 31 May 96; **1445**, M, 4.5mm, 9 June 96
R-D-G-10	—	—
R-D-G-2.5	—	—
BIG CAGE Rainy 80 Rainy A	*Ozineus* sp. (n=6)	**1342**, M, 6.5mm, 28 May 96; **1343**, M, 6.5mm, 28 May 96; **1435**, M, 5.5mm, 8 June 96; **1448**, F, 6mm, 10 June 96; **1465**, F, 6mm, 14 June 96; **1617**, F, 6mm, 6 July 96
	Oreodera simplex (n=9)	**1411**, M, 11mm, 5 June 96; **1662**, F, 12mm, 14 July 96; **1683**, F, 12.5mm, 19 July 96; **1730**, M, 12.5mm, 28 July 96; **1742**, F, 12.5mm, 30 July 96; **1750**, F, 13mm, 1 Aug 96; **1751**, M, 12mm, 1 Aug 96; **1757**, M, 11.5mm, 2 Aug 96; **1788**, F, 12.5mm, 9 Aug 96

Appendix II contd.

Branch	Cerambycid species reared	Individuals reared (**collection #**, gender, length, date of emergence)
Rainy A	*Ozineus* sp. (n=30)	**1050**, M, 7.5mm, 29 Apr 96; **1170**, M, 6.5mm, 9 May 96; **1226**, M, 7.5mm, 16 May 96; **1278**, M, 7mm, 21 May 96; **1317**, F, 7mm, 25 May 96; **1318**, F, 7mm, 25 May 96; **1363**, M, 7mm, 30 May 96; **1381**, M, 6mm, 1 June 96; **1412**, F, 7mm, 5 June 96; **1415**, F, 6mm, 6 June 96; **1416**, F, 7mm, 6 June 96; **1417**, F, 7mm, 6 June 96; **1426**, F, 7mm, 7 June 96; **1432**, F, 6.5mm, 8 June 96; **1433**, M, 6mm, 8 June 96; **1434**, M, 6.5mm, 8 June 96; **1476**, M, 7.5mm, 17 June 96; **1528**, F, 6mm, 24 June 96; **1529**, F, 6mm, 24 June 96; **1530**, F, 7mm, 24 June 96; **1542**, M, 6mm, 27 June 96; **1562**, F, 5.5mm, 29 June 96; **1587**, M, 6mm, 2 July 96; **1616**, M, 6.5mm, 6 July 96; **1628**, M, 6.5mm, 8 July 96; **1652**, F, 5.5mm, 12 July 96; **1681**, F, 6.5mm, 18 July 96; **1715**, M, 5.5mm, 25 July 96; **1741**, F, 6mm, 30 July 96; **1787**, F, 5.5mm, 9 Aug 96
Rainy B	—	—
Rainy D	*Oreodera simplex* (n=8)	**1675**, M, 11.5mm, 16 July 96; **1692**, M, 12.5mm, 20 July 96; **1693**, F, 12mm, 20 July 96; **1746**, F, 13mm, 31 July 96; **1747**, M, 12mm, 31 July 96; **1760**, F, 12.5mm, 3 Aug 96; **1766**, M, 13.5mm, 4 Aug 96; **1785**, M, 12mm, 8 Aug 96
	Ozineus sp. (n=6)	**1344**, M, 6.5mm, 28 May 96; **1506**, F, 7.5mm, 22 June 96; **1527**, M, 7.5mm, 24 June 96; **1563**, F, 7.5mm, 29 June 96; **1640**, F, 6.5mm, 9 July 96; **1659**, M, 6mm, 13 July 96
Cerambycids emerged from *Gustavia hexapetala*, rainy season branches		
R-I-G-10	—	—
R-I-G-2.5	—	—
R-K-G-10	—	—
R-K-G-2.5	—	—
R-L-G-10	—	—
R-L-G-2.5	—	—
R-N-G-10	—	—
R-N-G-2.5	—	—
BIG CAGE	*Carterica* sp. (n=1)	**1756**, F, 5mm, 2 Aug 96
I,K,L,N	*Carterica* sp. (n=1)	**1679**, F, 5mm, 17 July 96
Cerambycids emerged from *Lecythis poiteaui*, rainy season branches		
R-T-C-10	*Neoeutrypanus mutilatus* (n=4)	**1739**, F, 10.5mm, 30 July 96; **1801**, F, 9mm, 23 Aug 96; **1803**, F, 9.5mm, 27 Aug 96; **1813**, F, 9mm, 22 Sept 96
	Neoeutrypanus sp. 915 (n=19)	**1274**, F, 12mm, 20 May 96; **1473**, F, 10mm, 16 June 96; **1474**, F, 10mm, 16 June 96; **1475**, M, 10.5mm, 16 June 96; **1517**, F, 10.5mm, 23 June 96; **1526**, F, 10mm, 24 June 96; **1537**, F, 10mm, 26 June 96; **1546**, F, 9mm, 27 June 96; **1553**, M, 8.5mm, 28 June 96; **1568**, F, 11mm, 30 June 96; **1615**, F, 11mm, 6 July 96; **1634**, M, 10.5mm, 8 July 96; **1635**, F, 11mm, 8 July 96; **1655**, M, 8.5mm, 13 July 96;

Appendix II contd.

Branch	Cerambycid species reared	Individuals reared (**collection #**, gender, length, date of emergence)
R-T-C-10	*Neoeutrypanus* sp. 915 contd.	**1691**, M, 10.5mm, 20 July 96; **1695**, F, 10mm, 21 July 96; **1703**, F, 10mm, 22 July 96; **1755**, M, 8mm, 2 Aug 96; **1806**, ±, ±, 30 Aug 96
	Palame mimetica (n=1)	**1277**, F, 6mm, 21 May 96
R-T-C-2.5	Genus sp. 229 (n=2)	**1676**, F, 4mm, 17 July 96; **1677**, F, 3.5mm, 17 July 96
	Neoeutrypanus mutilatus (n=1)	**1783**, F, 9mm, 8 Aug 96
	Palame mimetica (n=2)	**1502**, F, 6mm, 20 June 96; **1694**, M, 6.5mm, 21 July 96
R-T-G-10	—	—
R-T-G-2.5	—	—
R-U-C-10*	*Palame mimetica* (n=10)	**1726**, M, 5.5mm, 27 July 96; **1738**, M, 5.5mm, 30 July 96; **1744**, F, 6mm, 31 July 96; **1745**, M, 5mm, 31 July 96; **1762**, F, 6mm, 3 Aug 96; **1763**, F, 6mm, 3 Aug 96; **1775**, F, 6.5mm, 6 Aug 96; **1779**, F, 5.5mm, 7 Aug 96; **1781**, F, 5.5mm, 8 Aug 96; **1800**, ±, ±, 21 Aug 96
R-U-C-2.5*	—	—
R-U-G-10	—	—
R-U-G-2.5	—	—
R-V-C-10	*Neoeutrypanus mutilatus* (n=2)	**1816**, F, 8.5mm, 30 Sept 96; **1819**, F, 9mm, 8 Oct 96
	Neoeutrypanus sp. 915 (n=10)	**1388**, M, 9.5mm, 2 June 96; **1397**, M, 9mm, 3 June 96; **1500**, M, 8.5mm, 20 June 96; **1654**, M, 8.5mm, 12 July 96; **1671**, M, 8.5mm, 15 July 96; **1696**, F, 10mm, 21 July 96; **1761**, M, 8mm, 3 Aug 96; **1797**, ±, ±, 17 Aug 96; **1804**, ±, ±, 29 Aug 96; **1805**, ±, ±, 29 Aug 96
	Palame crassimana (n=1)	**1297**. M, 6mm, 22 May 96
	Palame mimetica (n=12)	**1298**, M, 5.5mm, 22 May 96; **1361**, M, 5.5mm, 29 May 96; **1384**, M, 6mm, 1 June 96; **1387**, ±, 6mm, 2 June 96; **1406**, F, 7mm, 4 June 96; **1407**, M, 6mm, 4 June 96; **1422**, M, 6mm, 6 June 96; **1437**, M, 6.5mm, 8 June 96; **1593**, M, 7mm, 3 July 96; **1602**, M, 6mm, 5 July 96; **1633**, F, 7mm, 8 July 96; **1728**, F, 5.5mm, 28 July 96
	Xenofrea lineatipennis (n=1)	**1697**, M, 8mm, 21 July 96
R-V-C-2.5	—	—
R-V-G-10	—	—
R-V-G-2.5	—	—
R-W-C-10*	*Neoeutrypanus* sp. 915 (n=1)	**1810**, ±, ±, 9 Sept 96
R-W-C-2.5	—	—
R-W-G-10	—	—
R-W-G-2.5	—	—

Appendix II contd.

Branch	Cerambycid species reared	Individuals reared (**collection #**, gender, length, date of emergence)
BIG CAGE		
Rainy T	—	—
Rainy U	—	—
Rainy V	—	—
Rainy W	—	—

Emergences are listed first from branches cut from each of the five tree species during the dry season, then from branches cut from each of the five tree species during the rainy season. Within each section, emergences from snacks are listed before emergences from big cages.

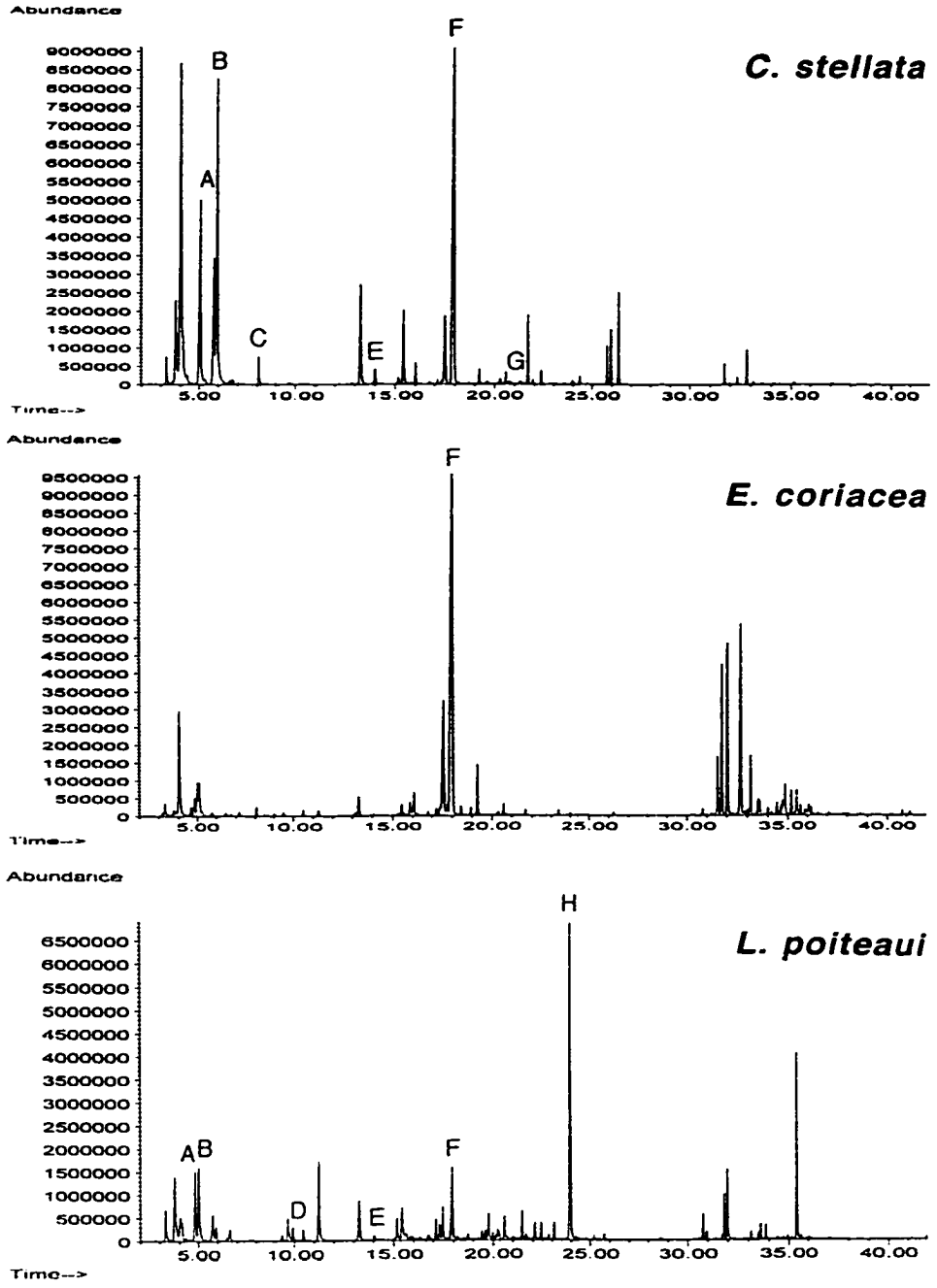
[a] SNACKS prepared during the dry season are identified with three-part codes. The first letter indicates the individual tree sampled (see Appendix I). The second letter, C or G, indicates that the branch was left at canopy or ground stratum. The following number, 10 or 2.5, indicates whether the branch was considered thick or thin. The letter R precedes the code of snacks cut during the rainy season. * = branch section resprouted. BIG CAGES included branches of mixed lengths and diameters. In some cases branches cut from different trees belonging to the same species were included in a Big Cage, in other cases only branches cut from the same tree were included.

[b] Each cerambycid species reared from a particular branch section (or group of branch sections) is listed, followed by the number of individuals that emerged; — = no emergences from the branch section or group of branch sections.

[c] For each cerambycid species reared, individuals are listed by their **collection number**, gender (M or F), length measured from the tip of the scape to the apex of the elytra, and date of emergence; ± = missing data.

Appendix III

Headspace analysis of three Lecythidaceae wood samples (2000 ml)



( ) = Retention time. A (5.79) = N-methyl-pyrrole; B (5.95) = dimethyl disulfide; C (8.11) = 2-(methylthio)ethanol; D (9.93) = 2,4-dithiapentane; E (14.01) = dimethyl trisulfide; F (17.98) = a mixture of 1,8-cineole and limonene; G (21.26) = methyl (methylthio)methyl sulfide; H (24.01) = α-safranal.

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IMAGE EVALUATION
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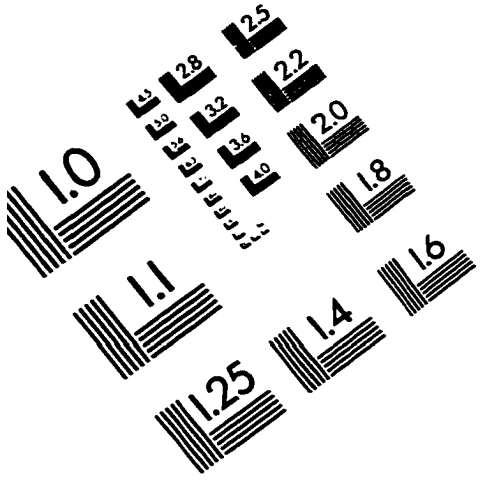

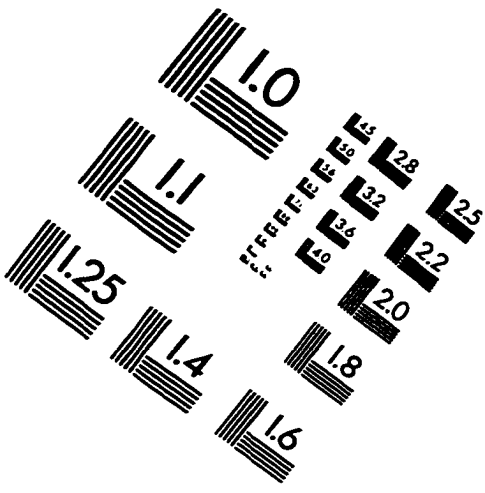

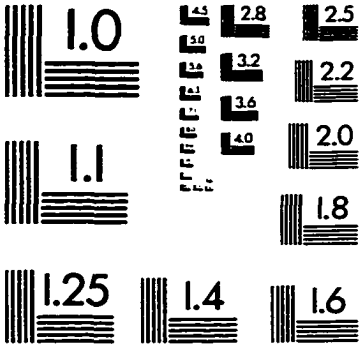

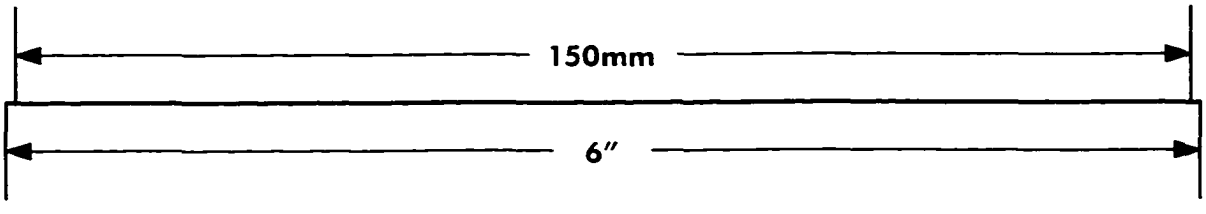

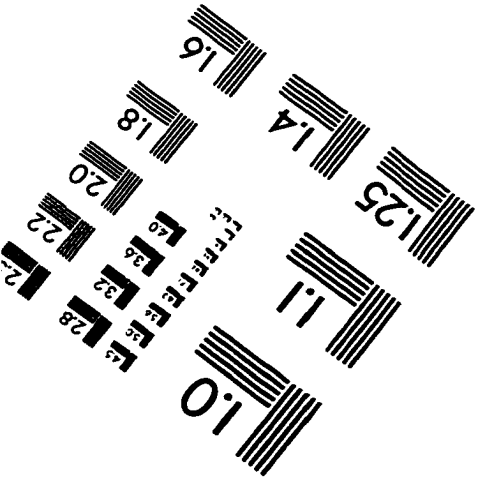

APPLIED IMAGE, Inc
1653 East Main Street
Rochester, NY 14609 USA
Phone: 716/482-0300
Fax: 716/288-5989