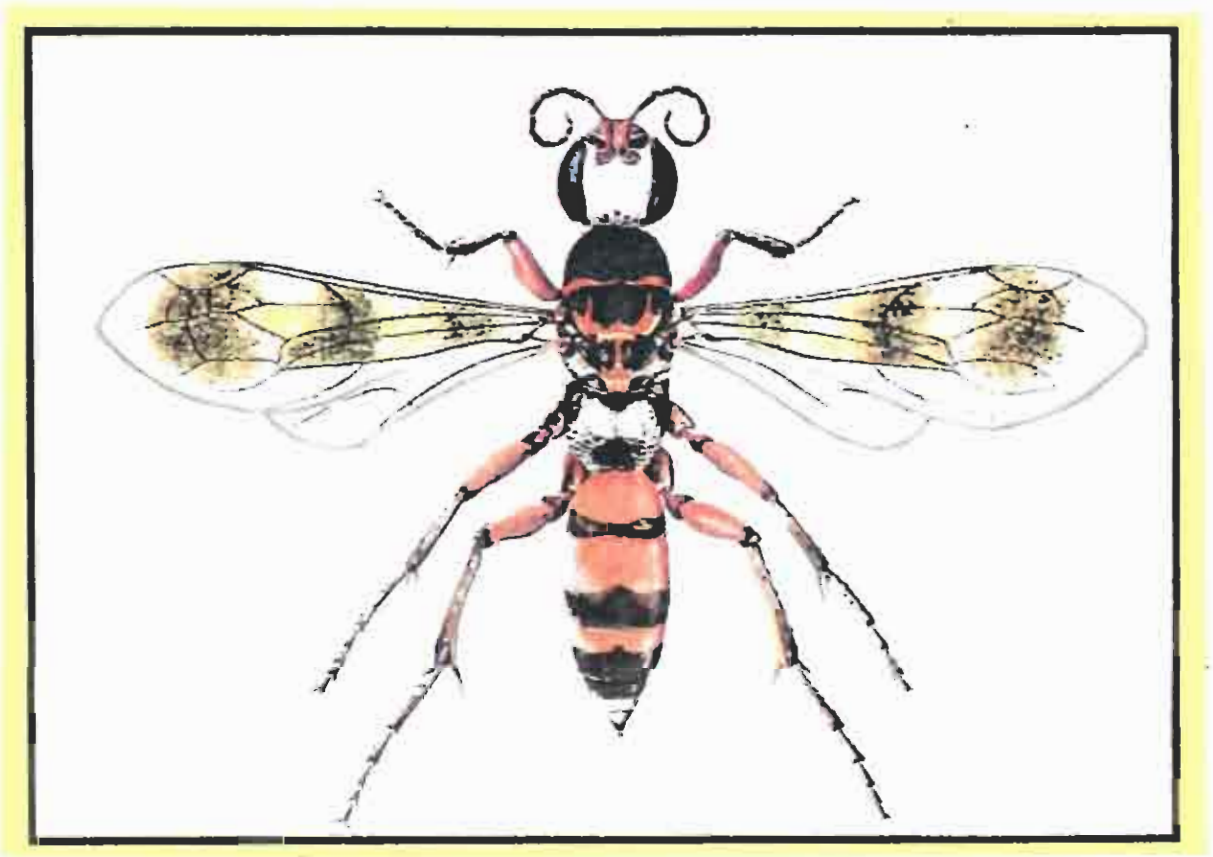
GUANA



Psorthaspis gloria

1995

The Conservation Agency

Exploration, Education, and Research

President
James D. Lazell, Ph.D.
401-423-2652

6 Swinburne Street
Conanicut Island
R.I. 02835 U.S.A.

10 Nov. '95

Dr. Henry Jarecki
10 Timber Trail
Rye, NY 10580

Dear Henry:

Well, it was certainly a very different sort of scientists' month!

The first week, with the whole island rental, was quite unpleasant, but there were only a few of us present. There were several members of the rental gang who were very interested in what we were doing. One, Jode Edmunds, works at the Buffalo, NY, Museum of Science, and has followed up on our contact. Still, we hope that either nothing like that ever happens again, or that utterly different ground rules are established.

Then ,the loss of seven (7!) of my participants was tough. The entire termite crew of four (Thorne and her student; Haverty and his assistant Nelson -- the latter scheduled to present spectrometry at the symposium) was wiped out by USDA's financial restructuring. Entomologist Bartlett and photographer/radio-tracker Green found they simply could not come up with the airfare. Writer/radio-tracker Pollard had a death in the family.

Gary and his crew turned out to be a very positive experience for me, and for most of the others too, I believe. Not only did I enjoy hamming for the camera, but the whole process made me concentrate on and articulate goals, plans, and motivations. Even if they did not like it (e.g. Gaddy), I was glad the others had to go through the process. Also, the crew was four real characters -- all most enjoyable and worth our time to get to know. Claudia was a real help to me.

For me the highlight of this year was radio-tracking tortoises. For two weeks little three-year-old "Sparky" did nothing much (two young iguanas, also radio-tracked, were equally dull). Then we got a ten-year-old, now adult, male, and things got interesting. He led us to a 21-plus-year-old female, one of the original colonists, and we got terrific data. Fortunately, two enthusiastic and well-trained volunteers from St. Croix -- Kim and James -- came over on 23 October and took over the hard work. Mike Ivie, the beetle man, had found them and told them about us. Numi now has all the data and the three of them (Numi, Kim, and James) are planning a great paper combining home ranges, activity, and successful restoration aspects.

Sparky, after removal of his radio and in response to feeding, developed strong positive anthropotrophy: stand still and he will come right to you. Jon, Catherine, Shelley, and Lynford all were enthusiastic to keep him and raise him up for guests to see. I hope that works.

Meantime, material keeps flooding in. I am whipping this into shape now, even though new stuff keeps arriving.

Here is a sketch, by page numbers:

1-3: Hand-written notes left by me at the end of October, with update annotations.

4-7: Reptiles and our study center. Reptiles, especially lizards, are by far the most abundant and conspicuous terrestrial vertebrates on Caribbean islands. Their amazing species diversity continues to be chronicled. We still have one unnamed species - the Carrot Rock skink - in the BVI. Careful studies of ground lizards and sphere-toed geckos might reveal other undescribed forms. By contrast, there is virtually zero probability of finding new mammals (no native species except bats), birds, or fishes. Further, reptiles -- especially lizards -- are model organisms for physiological and ecological studies. The Caribbean is the realm of reptiles. If you do not love reptiles, you should not go near the Caribbean.

8-63: Gad Perry's is the third doctoral dissertation to include Guana data (Scott Miller and Greg Mayer preceded him). Perry's is the first to utilize Guana extensively. I have excerpted his 304-page tome herein to provide most of Guana component and the overview general picture. The comparisons to economic theory are interesting but not developed.

Similarly, the phylogenetic component is very superficial because Gaddy did not consider any of the more adaptively deviant members of the larger families -- for example, gecko-like anoles or anole-like geckos. Gad's work corroborates my comments on reptiles, above.

64-67: Razi will be writing up our evaporative water loss data more fully for publication. This year the Anolis cristatellus populations about flat-lined. We await rainfall correlations. Next year we plan an elaborate "common garden" experiment with anoles from Sage Mountain, Necker, and Guana kept under identical conditions on Guana. A trial run with Guana anoles this year was wholly successful. This is a perfect example of the sort of research that can really only be efficiently done with reptiles like anole lizards. We have been concerned about drought-induced population declines, so Greg Mayer has looked over the data, with equivocal results. We will expand this to a real analysis. Numi will follow up on the iguana poster.

68-74: Jaquette's ECOTRAVELER note got us Dr. Betty Anne Schrieber and her husband/assistant Gary Schenk. I believe getting them on our long-term team will be a huge benefit because the birds are so popular, the issues -- like global warming, pollution, and illegal slaughter -- are so timely, and there is so much opportunity for local involvement.

75-77: Jim Ortiz's preliminary report came too late to include in last year's report, for some of the reasons mentioned in his first paragraph. He got more and better stuff this year, because of the rain, and is writing it up.

78-82: Certainly a high point for 1995 was Roy's description of our cover species, P. gloria. You have seen it already, but I include the text for completeness.

83-93: Wenhua has pretty much taken over the Tumbling Flower Beetles from Mike Ivie. He began the project and will still be second author. Wenhua has done the illustrations, but the text is really rough and needs massive editing. Wenhua got a small grant independently to finish this project.

94-99: Three small entomological contributions -- one actually published. I have illustrated them, with pictures from other sources, with generic representatives.

100-101: Scott Miller's note on the exotics that came in on Dillingham's Florida plants should provide a cautionary tale. Although he did not list the fire ant, Solenopsis envicta, it is now established on Guana (report of 1993). This is not at all the species locally called "fire ant," which causes a nippy sting. Real fire ants produce large, inflamed, pus-filled blisters that go right on hurting. They can be controlled by pouring "Lemon Fresh Joy" on their mounds. The mounds look like sand piles about a foot in diameter. Touched, the ants swarm up and out of them. The Surinam cockroach is far more of a household pest than any native species. We already had introduced, exotic, pest roaches on Guana. Now we have one more.

102-114: Barbara Thorne proposes bringing students next year, and I have agreed to consider it. I doubt H.L.S.C.C./BVI students could participate much, because most of them have jobs. However, maybe on a weekend. The UMD students will have to have real research projects to satisfy me re the use of bed nights. Barbara also has a nice paper accepted. MS follows, and another in press. She is prodding Margaret, gently (as am I), to finish up her MS.

115-159: Mike Haverty might have been shot down for 1995, but he keeps on producing. Here is his latest version of the extended hydrocarbon analysis of termites. The long paper is just a little dry, but the correspondence is pretty good. This is excellent research and I hope he gets it back on the front burner. He, too, is prodding Margaret to finish up.

160-161: I close with an article from Trends in Ecology and Evolution, a flashy "impact" journal. I call attention to the snake, but far more important is the overview provided of biodiversity studies. True, we are not looking for cancer cures on Guana, but someone might one day. In this connection, and re your mysterious fax of 9 November. "We do science on GI...," it is demeaning to perpetually refer to us as "misanthropes" because we understand that human overpopulation threatens most of life on earth.

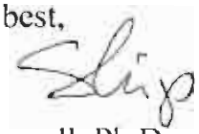
"Are scientists doing it to help the world? No." What a silly thing to write!

What do you mean by that? The "World" of Manhattan and high finance? Or the real world? We are people too. We live on this planet. We cannot, perhaps, stop our species from committing suicide and trying to exterminate as

many other species as possible, but we can try. We can speak up. We do not want everything we care about -- the real world -- wrecked in our time. We would like to have a healthier planet. I bet you would too. That means having fewer people. Get realistic!

More later....

All the best,



James Lazell, Ph.D.

"SPARKY"

TORTOISE ("MOROCOY") CARE

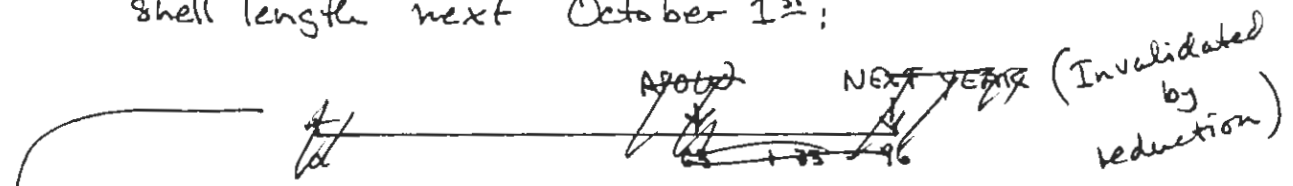
He loves Hibiscus and Tabebuia flowers, but needs a more varied diet including grapes, plums (prunes), melon bits, and lettuce. Also banana, including the peels.

He probably will not eat citrus. Some flowers - like ~~Oleader~~ Oleander and Frangipani — are poisonous. He probably won't eat them, but don't take a chance.

You might try a little tinned cat or dog food, say, once a week. I believe he needs some protein, but he wouldn't eat mealworms or caterpillars for me.

Growth:

From 60 mm shell ~~leg~~ length and 48 grams on 2 Oct to 63 mm and 58 grams on 29 Oct. At this rate of growth, he should be 96 mm shell length next October 1st:



He needs water and shelter. A sea shell of water, plus a hose sprinkle if it doesn't rain. A slab of coral, blocked up, is fine shelter.

Dear Mike -

Salt Pond:

Don't put any water in it at all unless it drops way down - so the island is a foot out of water.

Don't put RO water in it ever, because it is too salty. If you have to prevent it drying up, pump in sea water.

Ideally, water should go in at the extreme east end - foot of the concrete road. Ideally, there should be a culvert under road at this end, and another under the Bar → Dock road. Then, if the pond gets stinky, we could flush it out.

It is good for the Pond and its life to go through fluctuations of high and low water, and high and low salinity.

Brush:

In the good old days, when there was a "golf course," the White Bay Flat was kept open under the trees and park-like. There were rides and driving ranges. Now it is a jungle.

It would be especially helpful to us (for lizard and bird censusing) if the area east of the badminton court,

westward to the Sabal palm tree (big, gray, bulbous trunk) was cleared. Of course, leave all the real trees, even those that were blown down if they are still alive. Dead trees and limbs can go. It will be tough, but if we wait another year it will be nearly impossible....

Thanks!

Skip

* * * * *

Note, added 9 Nov. '95:

We asked Mario to clear out this brush - mostly "crown-of-thorns" acacia - last year. He did exactly what we asked him not to do: mowed down all the palm seedlings around the big Sabal palm, but did nothing in the main grove of regular trees. Typical Mario.

WE'RE A REPTILE STUDY CENTER

1.	Lizard Phys	129	
2.	Iguanas	6	
3.	Frogs	36	← Not reptiles! Amphibians...
4.	Snakes	9	
5.	Tortoises	24	
6.	Reptile Total	~~204~~	168
7.	Entomologists	83	
8.	Ornithologists	45	
9.	Other Total	~~28~~	61
10.	Overall Total	357	

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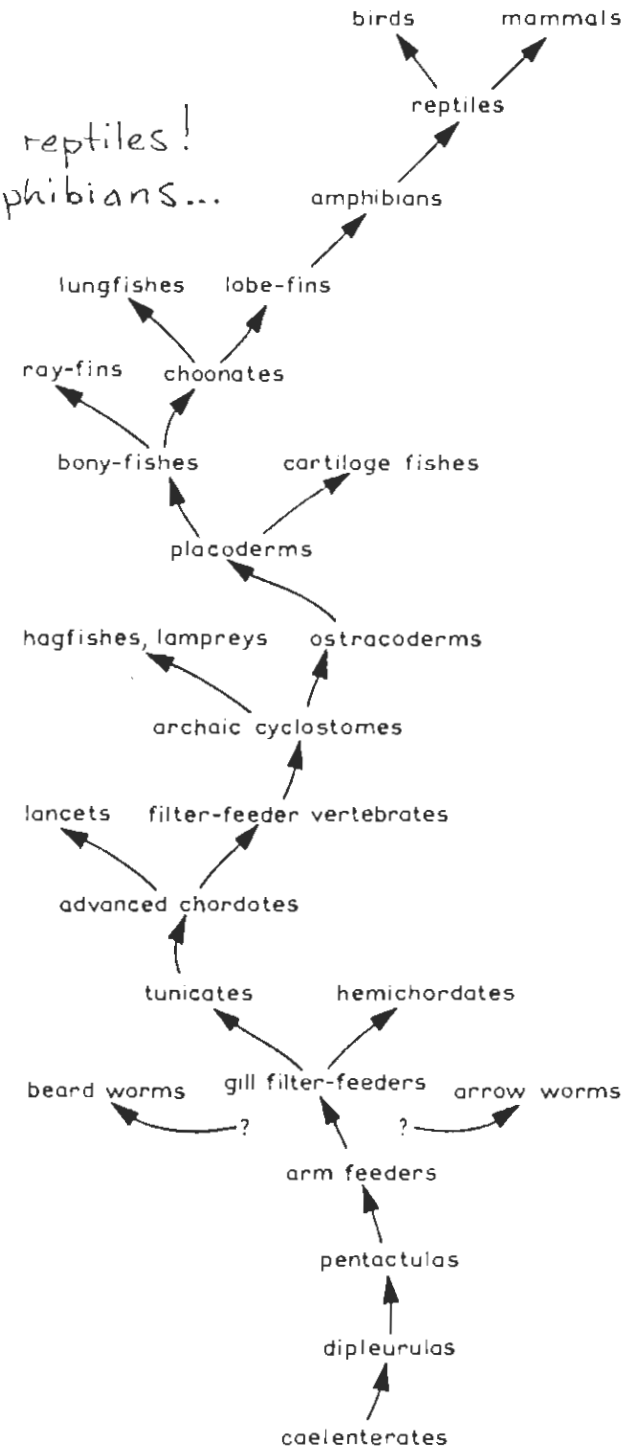

Figure 16.1 The family tree of the Chordata as related to probable evolution of an echinoderm–chordate line.

LIZARD ECOLOGY
A SYMPOSIUM

University of Missouri at Kansas City

June 13-15, 1965

William W. Milstead
Editor

Preface

STUDIES on the ecology of lizards have increased vastly both in number and in importance over the past 15 years. This is partially because the number of workers in the fields of ecology and herpetology has increased since 1950, and partially because lizards have proved to be highly suitable animals to use for studying a number of problems in ecology and basic biology. Lizards occur in nature in populations that are perhaps more easily studied than the populations of any other animal; they are clean, easily-cared-for laboratory animals; and their relatively short life span, with the accompanying potential for rapid genetic change, is a particularly useful feature in both laboratory and field studies. Among the many topics to be considered in the following pages are: how the study of a population of lizards has provided enough field data to test a theoretical mathematical formula, how social behavior in lizards has evolved to a high degree, how heat regulation in reptiles is dependent upon many internal and external factors, and how one may build a useful physiological model of a lizard out of a metal cylinder. Perhaps the most interesting point that manifests itself in the following pages is the degree of careful thought that has gone into both the formulating of hypotheses and the probing of these and older hypotheses. In this age of advanced technology and gadgetry, one tends to lose sight of the fact that the most useful tool of the scientist is, as always, the human mind.

Chapter

10

1993

Summary: Future Research on Snakes, or How to Combat "Lizard Envy"

Richard A. Seigel

Introduction

During the American Society of Ichthyologists and Herpetologists meetings at the University of Victoria in 1986, I was asked to give the summary address at the first-ever symposium on snake ecology and behavior. This excellent symposium, organized by Neil Ford and Patrick Gregory, brought together an impressive group of researchers, including Richard Shine, Patrick Gregory, Neil Ford, Henry Fitch, William Brown, Hubert Saint Girons, Charles Peterson, Thomas Madsen, and many others. I recall vividly listening to their talks, and wondering what I could possibly say that would add to what these distinguished biologists had already discussed.

Just a few hours before I was scheduled to speak, it finally struck me that I had heard a recurring theme throughout many of the papers. A frequent comment was "well, in comparison to lizards my data are meager, but...." This apologetic tone led me to the main theme of my talk in 1986, and the main message for this chapter, i.e., how do we combat what I termed "lizard envy"?

Roots of Lizard Envy

The idea that snakes are poor research animals in comparison to so-called model organisms (Huey et al., 1983) is probably a long-standing tradition, but recent ideas may stem from a frequently cited paper

7

by Turner (1977), which reviewed studies of reproduction and demography of lizards, snakes, crocodilians, and tuataras. The low recapture rate among most of the studies on snakes (especially for juveniles), combined with high variability in density and survival estimates, led Turner to conclude that "one is left with distinct reservations about the suitability of snake populations for this sort of ecological endeavor" (Turner, 1977, p. 228).

Later authors seconded Turner's view. For example, Parker and Plummer (1987) noted that "no single study on snake populations measures up to numerous studies on lizards or mammals." Vitt (1987) suggested that despite considerable effort, studies on snakes have contributed little to our understanding of community ecology. Considering that both of these papers were in the original *Snakes: Ecology and Evolutionary Biology* volume (coedited by Joseph T. Collins, Susan S. Novak, and myself), it seems that even specialists who work with snakes have accepted Turner's conclusions.

be

I do not dispute the specific problems identified by these workers; snakes can (and often are) difficult to work with. However, this is not the issue; as I argue below, all species are difficult to work with for some kinds of studies but are ideally suited for others. The real problem with lizard envy stems from the mindset that such statements engender. For example, when I was a new graduate student at the University of Kansas, Henry Fitch encouraged me to make the transition from studying turtle ecology to working with snakes. Having just read Turner's (1977) paper, I asked Fitch "can you really do good science with snakes?" Obviously, Fitch convinced me that you can (rather quickly, I might add), but I wonder how many young biologists have been turned away from imaginative research on snakes by the negative attitude described above.

Combating Lizard Envy

Here, I argue that lizard envy results from (1) not recognizing the limitations of snakes for certain kinds of studies, (2) not using different and innovative techniques when it is apparent that traditional techniques are inadequate, (3) not properly matching question, study animal, and technique, and (4) not focusing on the aspects of snake biology that make them "model" organisms for certain kinds of research.

The truth is, lizards are just better....

12

THE EVOLUTIONARY ECOLOGY OF LIZARD FORAGING: A COMPARATIVE STUDY

by

GAD PERRY, B.Sc., M.Sc.

DISSERTATION

Presented to the Faculty of the Graduate School of

The University of Texas at Austin

in Partial Fulfillment

of the Requirements

for the Degree of

DOCTOR OF PHILOSOPHY

THE UNIVERSITY OF TEXAS AS AUSTIN

August 1995

Dedication

To the Golux and the March Hare,

for their impeccable logic

Acknowledgments

The help of many people was important in the success of this work.

Insightful comments on various parts of the manuscript were provided by E.R. Pianka, R.A. Anderson, R.M. Andrews, E.J. Censky, L.E. Gilbert, K.R. LeVering, T.B. Rowe, M.J. Ryan, M.C. Singer and L.J. Vitt. They helped improve this manuscript greatly. I also thank Y.L. Werner for many fruitful discussions of lizard foraging. For introducing me to the various study sites I thank L.E. Gilbert (Corcovado), J. Lazell (BVI), ...

... the Conservation Agency through a grant from the Falconwood Foundation, by a grant from the Institute of Latin American Studies at the University of Texas, by an NSF grant DEB-9307804 to M.C. Singer, and by personal funds.

Vita

Gad Perry was born in Tel Aviv, Israel, on July 20th, 1963. He is the son of Moshe and Zippora Perry. After graduating from the High-school for Environmental Education in Sede Boqer, Israel, he served in the IDF from 1981 until 1984, when he was given an honorable discharge. He received a B.Sc. in Biology from Tel Aviv University in 1987 and an M.Sc. in Zoology from Tel Aviv University in 1990. He entered the Graduate School of The University of Texas at Austin in 1990.

Perry's work experience includes being Tel Aviv University's Curator of Herpetology (1987-1990), a consultant to several zoos and museums in Israel (1989-1993) and various teaching and research assistant positions from the elementary school to the university level. His scientific publications appeared in Amphibia-Reptilia, Biotropica, Herpetological Journal, Israel Journal of Zoology, International Zoo Yearbook, Journal of Arid Environments, and The Snake, and his work has been presented at over ten national and international scientific meetings. He has also published over 20 popular articles and has been a judge for the Texas State Science and engineering Fair, an evaluator for Mensa (Austin) Research Fund grants and a reviewer for several scientific journals.

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This dissertation was typed by the author

THE EVOLUTIONARY ECOLOGY OF LIZARD FORAGING: A COMPARATIVE STUDY

Publication No. _____

Gad Perry, Ph.D.

The University of Texas at Austin, 1995

Supervisor: Eric R. Pianka

Obtaining nourishment is one of the most essential activities engaged in by organisms, and has therefore attracted much interest. Despite this, some of the most basic claims and assumptions made in ecology regarding it have not been adequately tested. In particular, many of our perceptions of how animals forage are based on assumptions regarding the importance of historical processes outside of natural selection. In this dissertation I examine several such questions and reevaluate existing paradigms in the light of additional information and the insights provided by incorporating a phylogenetic perspective and the comparative method.

The questions I ask range from the intraspecific to the order level and use lizards as a model system for understanding issues of wide relevance in ecology. Specifically, I ask:

1) Is sexual size dimorphism a result of intraspecific niche divergence or of sexual selection?
2) What are the forces that structure ecological communities, and how important is foraging behavior in this process?
3) Are predator and prey behaviors inversely correlated?
4) How did foraging behavior in squamates evolve?

The answers to these questions were then used to reevaluate some of the common paradigms in the field.

Contrary to the view that foraging behavior is a highly labile trait that can change rapidly under selection pressures, I found that closely related species tend to have highly similar foraging behaviors. Ecologically similar species that are not closely related are likely to be less similar than closely related species inhabiting radically different habitats.

Thus, ignorance of historical processes in general and phylogenetic conservatism in particular has had a confounding influence on previously accepted interpretations of processes at all levels. My findings strongly suggest that invoking optimality in the context of foraging behavior may be unwarranted.

Chapter 1: Introduction

"From the least to the greatest in the zoological progression, the stomach sways the world" (Fabre, 1913).

1.1 Introduction

Obtaining nourishment has often been considered the most important activity of living organisms (e.g. O'Brien et al., 1990). To reproduce successfully, an organism must survive, attain suitable size, attract a mate, and produce offspring. All of these activities require that the individual obtain considerable amounts of energy, and there is often a correlation between feeding success and reproductive ability (Travers and Sih, 1991; Bernardo, 1994; Nilsson, 1994). Important ecological variables, such as population stability and species diversity, ultimately reflect such behavioral choices made by individuals (Krebs and Kacelnik, 1991). In fact, knowledge of foraging behavior can be used to calculate critical ecological parameters such as carrying capacity and density-dependent mortality (Goss-Custard et al., 1995).

Since foraging success can strongly impact reproductive success - the material natural selection

works upon (Darwin 1859, 1871) - evolutionary biologists have shown a considerable amount of interest in behaviors associated with food acquisition in the past two decades. Among the many factors that appear correlated with feeding are morphology, physiology and ecology (reviewed in Huey and Pianka, 1981), as well as sensory capabilities (Martin and Katzir, 1995).

Two general approaches have emerged since MacArthur and Pianka (1966) and Emlen (1966) pioneered the study of foraging. Some researchers have taken a theoretical approach, attempting to predict phenomena associated with foraging by use of mathematical models (e.g. Pianka, 1966; Schoener, 1971; and see Stephens and Krebs, 1986, for a recent compilation of such efforts). Others (e.g. Huey and Pianka, 1981; Perry et al., 1990) have preferred to derive general patterns by observing the behavior of model organisms in the field. Yet our knowledge of how free-ranging animals obtain nourishment is still limited. Much of our understanding stems from occasional observations and theoretical analyses. Attempts to study the foraging behavior of organisms in an evolutionary context (e.g. Singer and Parmesan, 1993) have been few.

Both theoretical and empirical approaches have had their successes in analyzing and predicting the behaviors of free-ranging organisms. Unfortunately, an alarmingly wide gulf has opened between proponents of these two approaches in ecology (Kareiva, 1989; Lawton, 1991; Weiner, 1995), and this is also true for studies of foraging. As a consequence, many assumptions and predictions of foraging theory have not been adequately tested. We now have very sophisticated foraging models at our disposal, but they are often based on previous models, rather than on empirical data. At the same time, processes suggested by field studies have not all been incorporated into the theoretical framework. Like all models, those at the heart of foraging theory are by definition simplifications and therefore less than perfect representations of the real world (Levins, 1966; Pease and Bull, 1992). Testing of models, preferably under natural conditions, is therefore critical (e.g. MacArthur and Pianka, 1966; Bernardo, 1993; Orzack and Sober, 1994).

My goal in choosing the topic of this dissertation was to address this gap between theoretical and empirical work. I was especially motivated to closely examine some of the fundamental theories regarding the

relationships between foraging behavior and other ecological and evolutionary phenomena. Rather than concentrate on the newer and more derived models available, I chose to concentrate on older, simpler models: the more enduring and well-accepted a statement is, the more likely it is to be the basis for newer work. Surprisingly, many of these foundations have still not been sufficiently tested empirically.

Another choice I faced was whether to use a variety of organisms to explore a single question, or to use a single group of animals as a model for addressing a wide range of questions. I chose the second approach because it is more time-efficient. By centering on a single group I could simplify the methodologies needed and elucidate the role of phylogenetic history (Harvey and Pagel, 1991) in producing observed patterns of foraging behavior.

Having a historical perspective is another uniting theme of this dissertation. Many of the issues I studied have previously been asked in a non-historical manner, yet recent advances (e.g. Harvey and Pagel, 1991) suggest important information may be obscured unless phylogenetic history is explicitly studied in conjunction with ecology or behavior. The "null

hypothesis" of ecology has long been explicitly evolutionary, in the sense of expecting adaptations to result from natural selection. One of the most prevalent approaches in behavioral ecology, optimality modeling, takes this to the extreme by predicting traits to be optimally suited to their function. Yet ecology has also been strongly non-evolutionary, because it consistently ignored other historical processes (Alley, 1982; Losos, 1992; Inchausti, 1994). As Culver et al. (1995) point out, "the fundamental problem in evolutionary biology [is] distinguishing patterns that are a consequence of common descent from patterns that are the result of natural selection". In effect, our null hypothesis must now be the absence, rather than the presence, of adaptation. The recent spate of research on phylogenetic reconstruction and the phylogeny of various organisms now often provides ecologists with an invaluable hypothesis of historical events that allows this hypothesis to be tested. Whenever possible, I provide an this additional dimension by combining such an approach with more traditional ones.

Lizards were chosen as the main study group for two main reasons. First, lizards have repeatedly been utilized as model organisms in ecology (Huey et al.,

1983) and a relatively good database exists on various aspects of their natural histories. A large percentage of previous field studies of foraging behavior centered on lizards, and this meant that I would not have to start working in a vacuum. Second, some of the causes of this popularity, namely the wide distribution and large population sizes typical of lizards, were highly useful in answering the questions posed. A third reason was the understanding of lizard biology and the acquaintance with the methodology used for studying them that my previous work with reptiles in general and lizards in particular has given me. These would take a long time to duplicate.

Though they arose from lizards, snakes were not included in the analysis for three reasons. First, they are difficult to observe because of their secretiveness. Second, few data are available about their foraging behavior to compare to. Third, it is unclear precisely where in lizard evolution they arose, nor what the relationships of modern snake genera are.

Finally, I had to choose parameters for describing and comparing foraging behavior. Whereas many authors have been content with qualitative descriptions (e.g. Cooper, 1994), I felt a more quantitative approach was

needed, if only because use of qualitative labels tends to mask important methodological differences between studies (Biro and Ridgway, 1995). Additionally, I was concerned because of the extensive argument regarding the number of existing foraging modes (Perry et al., 1990; Mac Nally, 1994). Pianka et al. (1979) provided three such numerical parameters, all of them commonly reported in later studies: velocity, the number of moves/minute (MPM) and the percent of the time spent moving (PTM). However, subsequent work has shown that velocity is not a good parameter (see Perry et al., 1990). I therefore omitted measurements of velocity and used MPM and PTM throughout this work.

As Perry et al. (1990) have shown, MPM and PTM are highly positively correlated. McLaughlin (1989) used MPM exclusively. Why then use both? Like Perry at al. (1990), I consider the two to be complementary measures. An animal may spend all of its time moving (PTM=100%) and never pause (producing a low MPM value), but an animal which made one brief move (low PTM) would produce similar MPM measurements. Additionally, similar PTM values can mask biologically important differences between animals that never pause and ones that do so frequently. Thus, the combination of the two parameters

provides a more complete understanding of the biology of an organism than either alone.

1.2 Preview

The organization of this dissertation follows a growing level of phylogenetic complexity, beginning with questions regarding a single species and culminating with ones spanning the evolutionary sequence of events in lizards in general. Throughout it, however, I have concentrated on testing existing theories and predictions regarding foraging behavior and its correlates.

In many species, male and females are significantly different in size (Fitch, 1981; Shine, 1988). Two main explanations, intraspecitic niche divergence and sexual selection, have been proposed to explain this phenomenon (Stamps, 1983; Hedrick and Temeles, 1989; Shine, 1991). These can be used to produce mutually exclusive hypotheses regarding present-day feeding ecology and behavior. I contrasted these hypotheses by studying the ecology, feeding behavior, and diet of Anolis polylepis in a Costa Rican rain forest. The first chapter shows how information on intraspecific variation in the

foraging behavior of a single species can be used to gain insight into the causes for sexual size dimorphism.

The mechanisms structuring ecological communities are still being hotly debated. Whereas some authors have concluded that interspecific competition for resources is important in structuring communities (Schoener, 1983,1984; Pianka, 1986; Petren et al., 1993), others disagreed (Strong et al., 1979; Strong, 1984). Unfortunately, little experimental work has been carried out on this topic (Connor and Simberloff, 1986; Petren et al., 1993). Dietary differences are one of the three main mechanisms for reducing competition proposed by Pianka (1973). Several authors have suggested that differences in foraging behavior can allow otherwise ecologically similar species to coexist (Echternacht, 1967; Pianka et al., 1979; Perry et al., 1990; Peres, 1993; Schall, 1993; Klein and Bay, 1994), and in chapter two I use two tropical lizard communities to test this hypothesis. Following recent work on the importance of phylogeny (Cadle and Greene, 1993; Cooper, 1994; Losos, 1994), I pose the alternative hypothesis that phylogenetic history may be a sufficient explanation for the foraging behaviors observed in extant species.

Originally suggested by Huey and Pianka (1981) and supported by theoretical models (e.g. Gerritsen and Strickler, 1977), the suggestion that sit and wait predators should mainly feed on widely foraging organisms and wide foragers should prey on stationary prey has been widely accepted and cited (e.g. Perry et al., 1990; Pianka, 1993; Cooper, 1994), but never thoroughly tested. In chapter 3, data on the behavior of both predator and prey are used to test this hypothesis. Whereas most work on foraging presents qualitative statements, I used quantitative data for my analysis, as well as a novel technique for quantifying prey behavior.

Without a historic perspective, discussions of the evolutionary significance of foraging behavior lack a critical dimension. The possible confounding effects of phylogeny, as recently iterated by Harvey and Pagel (1991), Brooks and McLennan (1991) and others (e.g. Eggleton and Vane-Wright, 1994) are first examined in chapter 2. In chapter 4 I use a phylogenetic hypothesis for all lizards and quantitative data on the foraging behavior of diverse lizard species to develop a scenario for the evolutionary sequence of events that led to the present distribution of foraging behaviors in lizards. I then use this historical perspective to re-examine one

of the most troublesome issues in the study of foraging behavior, its possible bimodality (Pianka, 1966). This issue has been widely debated (Regal, 1978; McLaughlin, 1989; Perry et al., 1990; Pianka, 1993; Cooper, 1994), with little consensus emerging. However, Cooper's (1994) recent phylogenetic analysis of qualitative information on family-typical foraging modes has provided a new insight into this question. I extend it to look at quantitative data for representative species.

Foraging theory now forms an extensive body of literature encompassing many thousands of pages. Much of it currently consists of applying optimality approaches to foraging behavior (e.g Stephens and Krebs, 1986). This approach has engendered much dissent and left few people indifferent; assessments of its success have also been conflicting (Parker and Maynard Smith, 1990). Recent work suggests most such attempts to test the assumptions and predictions of optimality models have been flawed (Orzack and Sober, 1994). One of the most basic assumptions of optimality theory is that behavioral and ecological traits are highly labile and can be locally optimized (Orzack and Sober, 1994). This supposedly allows organisms to conform to a changing environment without long evolutionary time lags and is

the basis for expecting optimality in traits such as clutch size and foraging behavior. However, a growing body of evidence suggests that this assumption is not true, and that adaptation may sometimes be constrained by history (e.g. Losos, 1994).

Another implicit assumption is that, by optimizing their feeding behavior, organisms also maximize their fitness (Parker and Maynard Smith, 1990). In applying optimality theory to life history modeling, however, the existence of adaptive compromises, often termed trade-offs, is generally acknowledged (e.g. Schwarzkopf, 1994; Sinervo, 1994). This limitation is only gradually penetrating into optimal foraging theory, and is currently mostly limited to taking risk of predation into account (e.g. Sih, 1992). Thus, foraging theory currently does not take into account the need for compromise between many competing needs. Unfortunately, feeding success probably does not equal fitness in many cases.

In view of these problems, and in light of my empirical findings, the final chapter is devoted to re-examining foraging theory. I give particular attention to reevaluating some of the assumptions built into it and its success in predicting the behavior of organisms

under realistic conditions. I use several well-studied groups such as lizards and honey-bees to identify under what conditions existing theory provides meaningful insights.

1.3 References for chapter 1

Alley, T.R. 1982. Competition theory, evolution, and the concept of an ecological niche. Acta Biotheoretica 31:165-179.

Bernardo, J. 1993. Determinants of maturation in animals. Trends in Ecology and Evolution 8:166-173.

Bernardo, J. 1994. Experimental analysis of allocation in two divergent, natural salamander populations. American Naturalist 143:14-38.

Biro, P.A. and M.S. Ridgway. 1995. Individual variation in foraging movement in a lake population of young-of-the-year brook charr (Salvelinus fontinalis). Behaviour 132:57-74.

Brooks, D.B. and D.A. McLennan. 1991. Phylogeny, ecology, and behavior: a research program in comparative biology. University of Chicago Press, Chicago.

Cadle, J.E. and H.W. Greene. 1993. Phylogenetic patterns, biogeography, and the ecological structure of neotropical snake assemblages. Pp. 281-293 in: Ricklefs, R.E. and D. Schluter (Eds). Species diversity in ecological communities. University of Chicago Press, Chicago.

Connor, E.F. and D. Simberloff. 1986. Competition, scientific method, and null models in ecology. American Scientist 74:155-162.

Chapter 3: Foraging behavior, interspecific competition, and community structure in two tropical lizard guilds

3.1 Introduction

Much of ecological research involves assemblages containing species which interact with one another, and with their common abiotic environment. Such species assemblages are termed ecological communities, and are traditionally considered to be limited by availability of resources and therefore structured by interspecific competition. Through coevolutionary processes, assemblage rules presumably arise that limit the amount of similarity between component species (Rand, 1964; MacArthur and Levin, 1967; Schoener, 1974; Toft, 1985; Alley, 1982; Wiens, 1993; Inchausti, 1994; Pianka, 1994a). Rummel and Roughgarden (1983, 1985) named this theoretical model "coevolution-structured communities" and proposed an alternative, "invasion structured communities". However, little has been done to determine which of the two is at work in real assemblages, and the nature of ecological communities is still being debated. The factors that structure them are considered unclear,

(G. Perry and K.M. Warkentin, unpublished), but not all are common or available for study. The 12 species observed intensely (Teiidae: Ameiva festiva, A. quadrilineata, A. leptophrys; Corytophanidae: Basiliscus basiliscus; Iguanidae: Ctenosaura similis, Iguana iguana; Polychridae: Anolis aquaticus, A. capito, A. limifrons, A. polylepis; Scincidae: Mabuya unimarginata, Sphenomorphus cherriei) represent all common species except for Leposoma southi, which is active almost exclusively in the leaf litter. Corytophanes cristatus has been studied by Andrews (1979), and only a single individual was quantitatively observed in this study. Talbot (1979) has reported on foraging in A. limifrons, but his methodology differs and his data are inconsistent with those used here, which follow the format of Huey and Pianka (1981) and Perry at al. (1990).

Guana Island is located in the British Virgin Islands (18°20' latitude, 64°40' longitude). The entire island is a private wildlife sanctuary whose area is approximately 340 hectares. Altitudes range from sea level to 250 m. The habitat is typically scrub, and much effort has gone into restoring the damage feral livestock have caused to the vegetation. The foraging

behaviors of none of the eight species found on Guana (Lazell, 1989) have been observed there previously, though Lewis and Saliva (1987) reported on Ameiva exsul and Reagan (1986) studied Anolis stratulus on Puerto Rico.

3.2.2. Field observations. Study sites were surveyed on foot and animals were located visually. As previously noted (Perry et al., 1990; Anderson, 1993), many lizards appear undisturbed by human proximity. Observation distance ranged from 20 m for species that reacted strongly to human presence (e.g. B. basiliscus) to less than one meter (individuals of Ameiva quadrilineata and Anolis polylepis regularly approached motionless observers) but was usually around five meters. All observations in which individuals appeared to react to my presence were dropped from the analysis. Animals displaying agonistic or courtship behaviors were also excluded. To avoid confounding thermoregulation with foraging, observations were not conducted within three hours of sunrise or two hours of sunset. For each species observed I also collected information on time allocation, habitat and microhabitat selection. . . . Following previous workers (Huey and Pianka, 1981, Perry

3.3 Results

A total of 66.5 observation hours, encompassing 479 individuals from 12 species, were obtained at Corcovado (Table 3.1). These include all common and many uncommon lizard species at the site. Additional preliminary data for single individuals of two species, Leposoma southi and Corytophanes cristatus, are also presented in Table 3.1. Leposoma southi, though common, spends most of its time in leaf litter, and was only observed once for more than a few seconds; only this observation, which was congruent with the many brief ones, is given. One Corytophanes cristatus was also observed.

At Guana I studied 142 individuals from seven species in five families, and obtained a total of 24.75 observation hours (Table 3.2). This includes all lizard species found on the island except Sphaerodactylus macrolepis, which is impossible to observe for more than a few seconds at a time in the leaf litter it inhabits. Although some of the sample sizes are small, the foraging indices for Guana are very similar to those obtained elsewhere in the BVI (G. Perry, unpublished data).

Table 3.2. Observation times and foraging parameters for Guana Island lizards.

Species	n	Observation time (min)	MPM avg	MPM SD	PTM avg	PTM SD
Ameiva exsul	9	75.8	0.28	0.25	5.11	5.36
Anolis cristatellus	84	887.9	0.37	0.60	0.96	1.70
Anolis pulchellus	5	36.0	0.64	1.18	1.34	2.53
Anolis stratulus	19	192.4	0.70	0.55	1.42	1.09
Hemidactylus mabouia	15	147.2	0.44	0.70	1.76	4.68
Iguana pinguis	6	98.0	0.20	0.25	5.11	5.36
Mabuya sloanii	4	49.2	1.28	1.41	14.00	19.37

Table 3.4. Typical microhabitat and diet for lizards observed on Guana. Microhabitat: C- in human habitations, D- disturbed habitat, G- ground, P- mature forest, R- rocky outcrops, V- on vegetation. Diet: H- herbivorous, I- insectivorous, O- omnivorous.

Species	Microhabitat		Diet	Comments
Ameiva exsul	D	G	I	
Anolis cristatellus	D,P	V	I	very abundant
Anolis pulchellus	D	V	I	
Anolis stratulus	D,P	V	I	very abundant
Hemidactylus mabouia	D	C	I	nocturnal
Iguana pinguis	P	G	H	introduced in 1984
Mabuya sloanii	D,P	V,R	I	uncommon

~~Five pairs of ecologically similar species were~~ identified at Corcovado (Table ~~3.5~~). Ameiva festiva and A. leptophrys often occur together in sunny spots in the forest and dry stream beds; Anolis capito and A. polylepis could both be found at similar heights in ~~primary forest habitats; Anolis limifrons and A.~~

Table 3.6. Absolute difference in MPM and PTM between ecologically similar and randomly chosen species pairs from Guana Island. AC- Anolis cristatellus, AP- Anolis pulchellus, AS- Anolis stratulus, HM- Hemidactylus mabouia.

Ecologically similar		Difference in		Random pairs		Difference in		Average	difference in	
1st	2nd	MPM	PTM	1st	2nd	MPM	PTM	1st	MPM	PTM
AC - AS		0.33	0.46	AC - AP		0.27	0.38	AC	0.30	4.50
				AS - HM		0.26.	0.34	AS	0.36	3.47

(p≥0.1, t-test), but differences between similar pairs were significantly smaller than those between each species and the average of all other species in its guild (p=0.007, t-test). However, this result becomes less significant when the Bonferroni correction (Holm, 1979) is employed to correct for the multiple comparisons conducted (0.01<adjusted p<0.05). A similar analysis is not possible for the Guana guild, where only one ecologically-similar species pair was found (Table 3.6).

Chapter 4: Are predator and prey foraging behaviors inversely correlated?

4.1 Introduction

What is the most profitable way of searching for a resource? Despite the critical importance this question has in many biological contexts (e.g finding mates or food; Bell, 1991), this question was first mathematically studied in the context of military operations (Koopman, 1956, cited in Gerritsen and Strickler, 1977). In biology, this issue was not quantitatively addressed until two decades later: studying zooplankton, Gerritsen and Strickler (1977) asked what tactics would best allow predators to obtain nourishment. Two optimal strategies emerged from their model, a stationary predator feeding on roving prey, and a mobile predator that specialized on slow-moving prey (Gerritsen and Strickler, 1977).

Apparently unknown to Gerritsen and Strickler (1977), these same strategies (now commonly termed "sit-and-wait" (SW) and "widely foraging" (WF)) were first introduced by Pianka (1966), ~~based on observations of~~

p=0.002 for males and females only, x^2 test). Because the number of items per stomach (23.7 items/lizard on average in males, 16.2/lizard in females) was not normally distributed, I used a non-parametric test to compare males to females. Despite the small sample size (9 males and 10 females), the difference between the sexes was nearly statistically significant (p=0.08, Mann-Whitney U-test).

4.3.2. Diet of Anolis cristatellus. A total of 40 A. cristatellus were examined, yielding 468 items (Table 4.4). None of the stomachs dissected was empty, and ants accounted for 73% of all food items. In addition to the items listed below, ten individuals (three males, four females and three juveniles) had sloughed skin in their stomachs and 10 (six males, three females and one juvenile) contained plant material.

Table 4.4. Diet of Anolis cristatellus on Guana Island. Sample sizes are given in parentheses.

Prey category	Items taken		# of items taken by		
	number	%	males	females	juveniles
	(40)		(14)	(13)	(13)
Araneae	11	2.4	1	7	3
Blattidae	15	3.2	4	3	8
Coleoptera	13	2.8	5	6	2
Diplopoda	9	1.9	0	4	5
Diptera	3	0.6	0	3	0
Hymenoptera					
(unwinged ants)	341	72.9	40	153	148
(other)	18	3.9	10	6	2
Hemiptera and Homoptera	10	2.1	5	2	3
Orthoptera	6	1.3	1	2	3
Vertebrates	2	0.4	1	1	0
All larvae	18	3.9	2	8	8
Other invertebrates	10	2.1	1	1	8
Unidentified	9	1.9	3	3	3
Other matter	3	0.6	1	0	2
Total items	468	100.0	74	199	195

→ Guana & BVI ←

Table 4.5. Food movement index (H_j) and average foraging parameters of 37 lizard species. See Table 4.1 for sources of data on foraging behavior and diet.

Species	MPM	PTM	H_i
Corytophanidae			
Corytophanes cristatus	0.01	0.5	240
Iguanidae			
Iguana iguana	0.40	2.8	0
→ I. pinguis	0.20	5.1	3 ←
Lacertidae			
Acanthodactylus schreiberi	1.54	30.5	340
A. scutellatus	1.01	7.7	327
Heliobolus lugubris	2.97	57.4	255
Ichnotrophis squamulosa	3.10	54.6	267
Meroles suborbitalis	1.83	13.5	293
Mesalina guttulata	0.46	35.1	307
Nucras tessellata	2.90	50.2	270
Pedioplanis lineoocellata	1.54	14.3	304
P. namaquensis	2.78	53.5	267

(Table 4.5 continued)

Phrynosomatidae			
Phrynosoma mcallii	--	32.0	359
P. modestum	0.12	--	359
Sceloporus graciosus	1.31	5.8	354
Uma inornata (male)	--	2.4	169
(female)	--	1.9	201
Polychridae			
Anolis auratus	0.01	--	340
A. cristatellus (male)	0.43	1.5	382
(female)	0.45	0.9	353
(juvenile)	0.21	0.5	339
A. limifrons	0.09	--	352
A. oculatus	0.20	--	344
A. polylepis			
male	0.24	1.0	320
female	0.42	1.1	362
juvenile	0.43	1.5	356
A. punctatus	0.14	--	370
A. stratulus (wet season)	0.72	--	318
(dry season)	1.16	--	328

(Table 4.5 continued)

Scincidae			
Ctenotus taeniolatus	--	79.0	300
Mabuya acutilabris	0.29	--	323
Tiliqua rugosa	--	10.4	0
Teiidae			
Ameiva ameiva	0.64	26.7	292
A. exsul	--	41.2	205
A. quadrilineata	1.26	18.0	359
Cnemidophorus deppii	--	62.8	342
C. lemniscatus	0.51	--	315
C. sexlineatus (adult)	--	47.9	348
(juvenile)	--	67.7	346
C. tigris	1.62	87.0	239
Kentropyx calcarata	0.86	--	383
K. striatus	0.24	--	296
Tropiduridae			
Plica umbra	0.19	--	372
Uranoscodon superciliosa	0.02	--	329

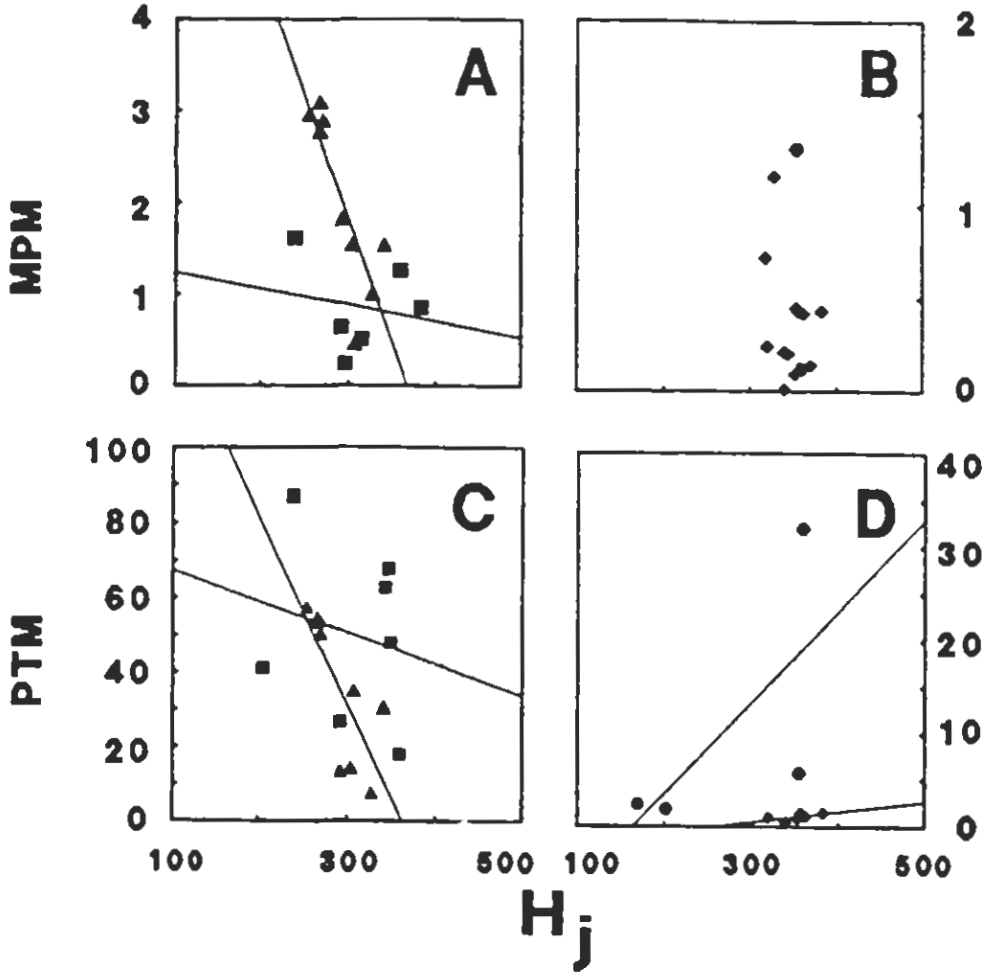

Figure 4.1. Relationship between movement indices of foragers (MPM, PTM) and prey (H_j). A,C: Lacertidae (triangles) and Teiidae (squares). B,D: Polychridae (diamonds) and Phrynosomatidae (circles). Lines represent a linear trend for each family, but only for Lacertidae are the correlations statistically significant.

4.4 Discussion

Pianka (1993) explicitly summarized the economics of the accepted crossover hypothesis: "In order for the sit-and-wait tactic to pay off, prey must be relatively mobile and prey density must be high". The data obtained to test this hypothesis encompass 37 species in eight lizard families, thus providing a broad perspective. Although MPM and PTM varied greatly in the sampled species, H_j values were relatively constant. Except in herbivorous species, H_j rarely exceeded 400 or fell below 200. In Anolis, no H_j values outside the 300-400 range were noted. Thus, no predaceous species specialized on truly sedentary or highly mobile prey.

Applied to the predator-prey locomotory crossover hypothesis (Huey and Pianka, 1981), these data only provide statistically significant support in one case. In Lacertidae, the family for which this hypothesis was originally proposed, more active species apparently specialize on less active prey, whereas sedentary species prefer prey that move more. Though not statistically significant, the trend exhibited by Teiidae is similar to that of Lacertidae. ~~With~~

Chapter 5: The evolution of foraging behavior in squamates: historical and ecological aspects

5.1 Introduction

Beginning with Pianka (1966), many authors have recognized two basic modes of foraging, commonly called "sit-and-wait" (SW) and "widely foraging" (WF). These terms have never been quantitatively defined (McLaughlin, 1989), and the assignment of a species to either category is, therefore, subjective. Although many organisms seem to fit in either of these categories (Vitt and Congdon, 1978; Huey and Pianka, 1981; McLaughlin, 1989; Helfman, 1990; Pianka, 1993; Angilletta, 1994; Biro and Ridgway, 1995; Secor and Nagy, 1995; and references in Pietruszka, 1986 and McLaughlin, 1989), some authors have realized that they are "somewhat artificial" (e.g. Pianka, 1986,1993), and have suggested alternative views. These include assuming three or more categories (Regal, 1978; Robinson and Holmes, 1982; Gatz, 1983; Cooper, 1994) or a continuum (Pianka, 1973; Regal 1978, 1983; Taigen and Pough, 1983; Magnusson et al., 1985; Cooper and Alberts, 1990; Bell,

→ Guana & BVI ←

185

Table 5.3. Foraging behavior indices of lizard species observed for this study.

Species	MPM		PTM		Location
	mean	SD	mean	SD	
Corytophanidae					
Basiliscus basiliscus	0.27	0.40	0.78	1.26	Corcovado
Corytophanes cristatus	0.01		0.54		Corcovado
Gekkonidae					
Gonatodes albogularis	0.81	0.77	2.03	2.08	Costa Rica, Panama
Hemidactylus frenatus	0.75	0.81	2.66	4.01	Costa Rica
→ Hemidactylus mabouia	0.44	0.70	1.76	4.68	BVI ←
Hemidactylus turcicus					
1. Israel	0.20	0.16	1.01	1.91	
2. Texas	0.41	0.70	1.23	2.19	
Iguanidae					
Ctenosaura similis	0.53	0.59	7.73	11.1	Corcovado
Iguana iguana	0.40	0.51	2.81	4.44	Corcovado
→ Iguana pinguis	0.28	0.25	5.11	5.36	BVI ←

(Table 5.3 continued)

Gymnophthalmidae					
Leposoma southi	0.91		10.7		Corcovado
Phrynosomatidae					
Cophosaurus texanus	2.83	3.06	4.98	3.05	Texas
Sceloporus graciosus	1.31	1.13	5.84	5.28	California
Sceloporus merriami	1.07	0.88	2.51	2.08	Texas
Sceloporus olivaceus	0.62	0.48	1.98	1.33	Texas
Sceloporus undulatus	0.29	0.33	0.81	0.93	Texas
Urosaurus ornatus	1.33	0.50	3.41	1.08	Texas
Polychridae					
Anolis aquaticus	0.08	0.07	0.23	0.18	Corcovado
Anolis carolinensis	0.86	0.83	7.04	8.50	Texas
Anolis capito	0.01	0.03	0.07	0.14	Corcovado
Anolis cristatellus	0.36	0.53	0.83	1.35	BVI
Anolis ernestwilliamsi	0.60	0.69	1.21	1.48	BVI
Anolis limifrons	0.61	0.74	1.59	1.51	Corcovado
Anolis polylepis	0.36	0.36	1.20	1.20	Corcovado
Anolis pulchellus	0.65	0.74	1.78	2.31	BVI
Anolis startulus	0.54	0.49	1.09	0.99	BVI

(Table 5.3 continued)

Scincidae						
→	Mabuya sloanii	1.28	1.41	14.0	19.4	BVI ←
	Mabuya unimarginata	0.89	0.70	10.8	10.9	Corcovado
	Sphenomorphus cherriei	1.69	1.83	11.3	15.8	Corcovado
Teiidae						
→	Ameiva exsul	2.18	1.41	32.1	25.8	BVI ←
	Ameiva festiva	1.06	0.84	34.5	24.6	Corcovado
	Ameiva leptophrys	0.58	0.51	26.8	25.9	Corcovado
	Ameiva quadrilineata	1.56	1.08	31.9	23.6	Corcovado

MPM data from Tables 5.2 and 5.3 are summarized in Fig. 5.1 using the categories of McLaughlin (1989). The observed distribution is significantly non-even ($D=0.41$, $p<0.01$, one-sample Kolmogorov-Smirnov test; $x^2=108.1$, $p<0.001$, x^2 test). PTM data were even less evenly distributed (Fig. 5.2; $D=0.58$, $p<0.01$, one-sample Kolmogorov-Smirnov test; $x^2=179.4$, $p<0.001$, x^2 test). In both cases, a large preponderance of relatively stationary species is evident.

5.4.4. A caveat. Anderson (1993) raised an important problem in interpreting observations of foraging behavior which was also evident in this study. Do similar behaviors necessarily imply a similar internal state ("motivation")? Having discounted thermoregulation and social interactions as possible causes, Perry et al. (1990) stated they had "no evidence that all locomotion was related to feeding". Anoles typically hunt from ambush. Is their lack of movement really equivalent to that of an active forager that has stopped to thermoregulate? If each behavior only had one utility, the answer would be a definite "no". However, I repeatedly observed active foragers catching food while sedentary. Moreover, a motionless sedentary predator may well not be searching for prey: obtaining mates and maintaining vigilance for competing males are just two of the many alternative (and probably not mutually exclusive) motivations ("making time"; Pianka, 1976). Even when obvious bouts of thermoregulation and social interactions are excluded, there observed behaviors are may not actually be attributable to the motivation applied by the observer. Thus, "time allocation" may be more appropriate than "foraging behavior" for describing these behavioral suites.

Chapter 6: Foraging theory and foraging behavior: never the twain shall meet?

6.1 Introduction

"The starting point for much [of] behavioural ecology is that animals are maximizers" (Grafen, 1991). Thus, the optimality criterion is the basis for much of modern behavioral ecology theory. To a degree, this is a natural extension of Darwin's (1859) ideas on natural selection: organisms that are better adapted to their environment produce more offspring than ones that are not, and those offspring are likely to also be superior competitors. Despite this, optimality theory first explicitly emerged in the field of economics, where it was initially used to describe the outcome of consumer decision-making. Once explicitly adopted by biologists, however, it was immediately applied to evolutionary analyses of foraging behavior and life history variations.

In its simplest form, optimality is the expected result of selection over evolutionary time for ever more efficient organisms. Applied to foraging theory, the argument becomes that competition for resources benefits

those organisms that are best able to procure them, and this selection pressure eventually leads to the evolution of organisms highly adept at acquiring resources (Emlen, 1966; MacArthur and Pianka, 1966; Schoener, 1971; MacArthur, 1972, p. 61; Pyke et al., 1977; Stephens and Krebs, 1986; Grafen, 1991; Speakman and Bryant, 1993). Almost since its inception, however, use of optimality criteria in biology has been highly controversial, engendering heated debate (e.g. Pierce and Ollason, 1987; Parker and Maynard Smith, 1990; Orzack and Sober, 1994a,b). MacArthur and Pianka's (1966) cautious "such `optimum theories' are hypotheses for testing rather than anything certain" was soon replaced by a less conscientious attitude. While optimal foraging theory (OFT) has been highly influential (e.g. Stephens and Krebs, 1986; Mangel and Clark, 1988), many authors have found it unsatisfactory (e.g. Gould and Lewontin, 1979; Heinrich, 1983; Orzack and Sober, 1994a,b); those who find it a useful tool for understanding evolutionary processes are balanced by others, who think it unproductive or misleading.

Recently, economists have begun to question the wisdom of the optimality approach openly (Arthur, 1989,1993; Rapport, 1991; Waldman, 1994). Moreover, a

growing body of evidence exists to suggest that some traits are unable to change as OFT assumes because of phylogenetic conservatism (e.g Harvey and Pagel, 1991; Eggleton and Vane-Wright, 1994). Unless a genotypic response can follow, selection on phenotype will not cause evolution. Thus, if phylogenetic history is a powerful constraint, historical processes are likely to be an important confounding factor in understanding the function of extant feeding phenotypes. It may, therefore, be time for biologists to re-evaluate the utility of the optimality approach in general, and OFT in particular.

In this concluding chapter I ask whether OFT is indeed a useful tool. By necessity, this is a highly selective compendium. Such an effort is both aided and hindered by the large amount of data collected in the past decades. It is no longer possible to cover every published manuscript dealing with this topic, or even to cite the hundreds of papers whose title includes the word "optimal" I reviewed for this synthesis. Instead, I will list the main assumptions underlying OFT, types of models and predictions that have emerged from them, and major criticisms levelled at this approach. I will briefly review what we know of factors affecting

decisions made by foragers under natural situations and concentrate on the ability of OFT to predict the behavior of real organisms in the field. Finally, I will attempt to map future directions for research based on present knowledge.

6.2 The optimality approach to foraging behavior

OFT has become ubiquitous. In some cases, a detailed analysis of mechanisms leading to optimality is used, but sometimes the claim of optimality is made with no clear justification. Yet use of OFT (and other optimality criteria) involves a common language and accepted rules. As these have been discussed before in detail (e.g. Schoener, 1971; Pyke et al., 1977; Stephens and Krebs, 1986; Bell, 1991), in this section I will only briefly summarize the types of questions and assumptions commonly encountered in OFT.

6.2.1 Defining optimality in a biological context is not a simple task. Stephens and Krebs (1986) never define the term. They come closest when citing Bellman's principle of optimality: "an optimal policy has the property that, whatever the initial state and initial

decision are, the remaining decisions must constitute an optimal policy with regard to the state resulting from the first decision (Bellman, 1957; in Stephens and Krebs, 1986, p. 155). This definition is so circular and vague that is of little practical use. Mangel and Clark (1988, p. 227) come closer to a working definition: "the optimally fit animal must maximize its total lifetime fitness".

For adaptationists, underlying this is the belief that "natural selection is a sufficient explanation for most nonmolecular traits, and these traits are locally adaptive" (Orzack and Sober, 1994a). Few biologists now take the extreme view (termed here 'naive optimality') this means all traits are optimal (Parker and Maynard Smith, 1990; Orzack and Sober, 1994a). More commonly, an optimal phenotype is considered one that "outperforms the other phenotypes and thereby results in a higher fitness" (Orzack and Sober, 1994a).

From the definitions above, costs, benefits and the relationship between the two clearly must play a role in any solution coming from such an approach. Perhaps the best way to define it is to expand on Pianka's (1994, p. 90) view of an optimal foraging behavior. An optimal behavior, then, maximizes the long-term difference

between profits and the costs associated with obtaining them.

6.2.2 What is OFT? Before I discuss what its rules are, it is necessary to more precisely define what is meant by foraging in optimality analyses. Classically, optimality has been defined in OFT as "that complex of behavior and morphology best suited to gather food energy in a particular environment" (Schoener, 1971). Though energy is still the most commonly-used index of foraging success (e.g Stephens and Krebs, 1986; Parker and Maynard Smith, 1990), OFT has expanded to include maximization of nutrient intake and avoidance of toxins and predators. I will therefore use the definition given by Pianka (1994, p. 90): "an optimal foraging tactic maximizes the differences between foraging profits and their costs". The ultimate goal of OFT, like that of other theoretical analyses "is to understand and predict real phenomena" (Mitchell, 1990), based on the view "an optimal consumer should opt to pursue an item only when it cannot expect to locate, catch, and eat a better item" (Pianka, 1994, p. 91).

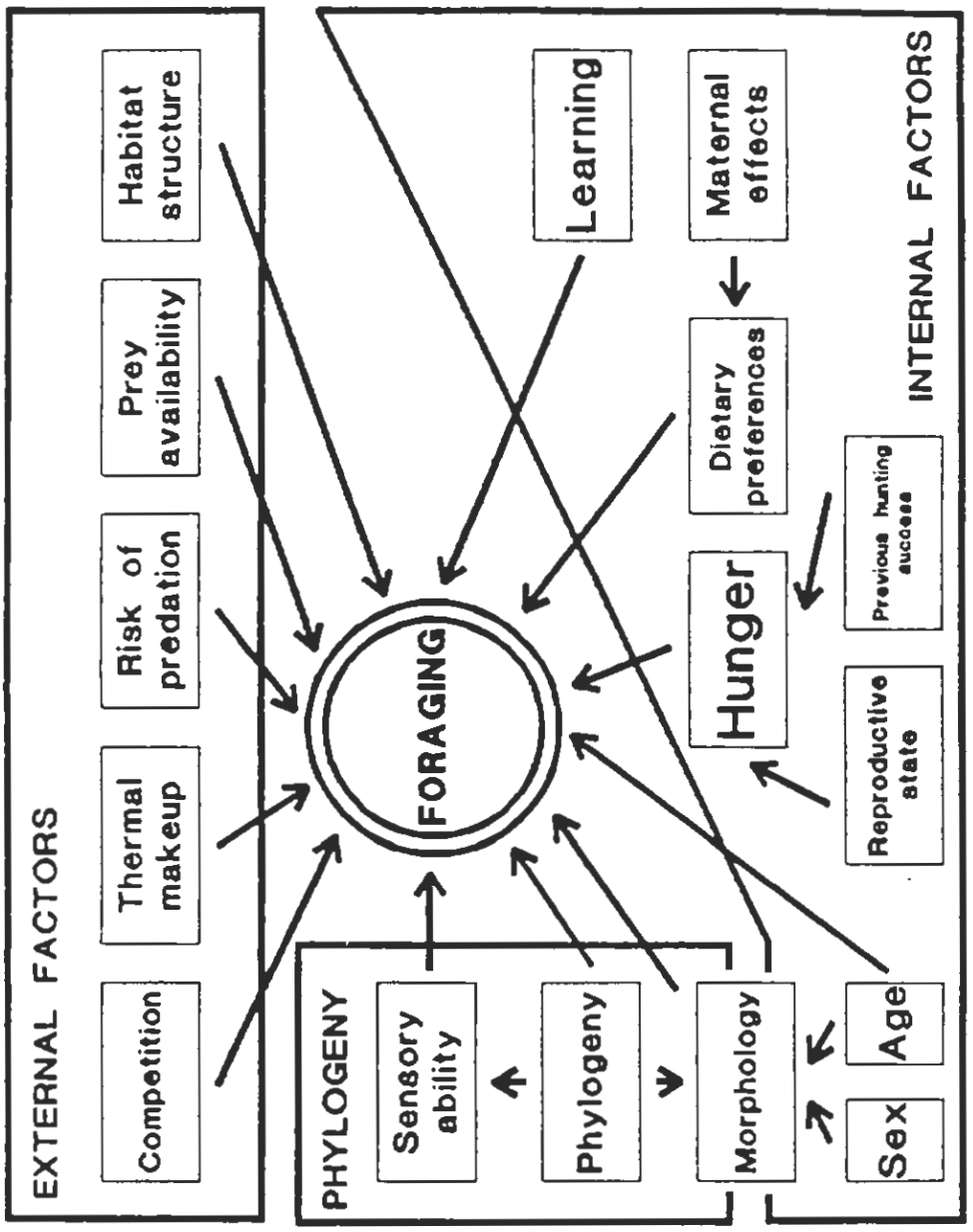

Figure 6.1. Factors affecting foraging behavior.

(see e.g. Loeschke, 1987; reviewed in Gray, 1987). It is now beyond question that selection has led to some exceptionally complex adaptations. Regardless of whether these are "optimal" of not, they plainly indicate that organisms can be efficient foragers. Yet the previous chapters show just as clearly that many instances of phylogenetic conservatism exist that prevent adaptation. Thus, I agree with Orzack and Sober (1994b): though optimality may occur, there is no reason to expect it to be the norm.

6.6 Conclusions and future directions

Initially, OFT appeared to be provide important insights (e.g. Pyke et al., 1977; Stephens and Krebs, 1986). The pattern that emerges from the many different types of OFT models and variety of testing methodologies reviewed above, however, is clear: real support for OFT is meager, because many of the studies used to bolster OFT suffer from serious flaws that make their conclusions doubtful. Even if those are accepted at face value, however, OFT has failed much more often than it has succeeded. In the words of Gray (1987): "the more

OFT sticks its head out, the more its head is chopped off".

When an OFT model fails, two reasons are possible. On the one hand, the model may have been wrong, in which case it needs to be improved. On the other hand, the model may have been correct, and the discrepancy is due to the non-optimal nature of the organism studied. Unfortunately, the second possibility is generally ignored by OFT proponents. Suggesting a trait is not optimal "is tantamount to an admission of defeat for the modeling project ... in many cases the greater truth lies in recognizing that the model is inadequate" (Mangel and Clark, 1988). "Many adaptationists emphasize the success of optimality hypotheses to the detriment of awkward facts that refute them" (Kacelnik, 1993).

Roughgarden (1995, p. 1) rightly distinguished "the ecological theory of optimal foraging" from evolutionary theory. Naive OFT equates natural selection with evolution, a clearly unjustified approach. This non-evolutionary nature is one main reason why OFT fails. Animals often have deeply-rooted behavioral or physiological limitations, and these can prevent them from behaving optimally. Attempts to "explain" biological traits without first regarding historical

factors fail to address this issue (e.g. Harvey and Pagel, 1991; Eggleton and Vane-Wright, 1994; Losos and Miles, 1994) and are therefore doomed to fail explaining real-world phenomena.

6.6.1 Null models in evolutionary biology. In the adaptationist view, an evolutionary biologist "must first attempt to explain biological phenomena and processes as the product of natural selection. Only after all attempts to do so have failed, is he justified in designating the unexplained residue tentatively as a product of chance" (Mayr, 1983, p. 326). However, with our current knowledge of the effects of historical events, the fundamental goal of evolutionary biology should be "distinguishing patterns that are a consequence of common descent from patterns that are the result of natural selection" (Culver et al., 1995).

If we cannot use adaptationism as our null model, what should we use? Instead, our null hypothesis should be absence of adaptation (e.g. Ward, 1993), and natural selection should only be invoked when this null model is rejected. Recent advances in phylogeny reconstruction and the appearance of the comparative method (e.g. Harvey and Pagel, 1991; Eggleton and Vane-Wright, 1994)

allow us to define the appropriate null model in any ecological endeavor more precisely: unless shown otherwise, any current trait must be considered due only to historical events. Yet rejection of the historical null hypothesis should not be taken to indicate acceptance of optimality. As shown above, other, sometimes simpler, explanations often also fit. Those too must be considered.

6.6.2 Redefining optimal foraging. Under most circumstances, organisms are engaged in multiple activities simultaneously, and obtaining food is but one of them. Though ability to obtain food is often correlated with reproductive success, that is not always the case. Certainly, the common tendency to use energy intake as the optimized criterion (e.g. Roughgarden, 1995) is often unjustified, and fitness should be more directly incorporated. As more constraints are incorporated into OFT models, the definition of what comprises optimal foraging appears to be shifting towards "the best strategy to acquire dietary input available under the cumulative set of needs, constraints and competing demands".

Yet is using such a definition really useful? "It seems to me that such a broad prediction is of dubious value ... I want it to help me predict what is not intuitively obvious," complained Heinrich (1983). Indeed, optimality is often invoked to make qualitative predictions that require no complicated theory. Using this definition makes any trait optimal, simply because it cannot be otherwise. OFT thus "essentially predicts that animals feed on what gives them a good meal, and they forage so that they get a good deal, but if they do not do either, then it is because of limitations in their genetic makeup, or because they have other things to do to stay alive and reproduce" (Heinrich, 1983).

The key to appropriate use of OFT lies in defining the question more carefully. Having discounted adaptation as a null model, we can now attempt to "understand specific examples of adaptation, in terms of the selective forces and the historical and developmental constraints operating" (Parker and Maynard Smith, 1990). In this way, optimality need no longer be assumed. A modified OFT, acknowledging that the selected solution (e.g. sickle-cell anemia) may not be an ideal one (Parker and Maynard Smith, 1990), can thus provide insight into specific questions and allow us to ask

whether certain features of observed behaviors or structures can be ascribed to specific functions.

6.6.3 Conclusions. Hall (1988) concluded that where predictions made by theoretical models have been tested, they have been rejected, and his view was applied to OFT by Weiner (1995). Pyke (1984) and Gray (1987) were both dubious of OFT's success, and Rapport (1991) concluded optimality rests on "tenuous grounds ... it may be necessary to forego some of the elegance of the mathematical constructs to obtain descriptions of resource allocation behaviour that are better grounded in the real world". Similar conclusions have emerged regarding other applications of optimality such as life-history evolution (Rose et al., 1987) and symmorphosis (optimality in design; e.g. Garland and Huey, 1987; Dabrowski, 1993). These findings strongly suggest that the adaptationist approach (sensu Mayr, 1983) should be reexamined. What few valid data are available (Orzack and Sober, 1994a; Singer et al., 1994) do not provide strong support for hyper-adaptationist views (selection is sufficient and optimality ubiquitous), yet they do not fully disprove them either. Though data remain

scant, they suggest strong adaptationism may be well need to be abandoned.

Clearly, phylogenetic inertia can affect foraging "decisions" at almost any stage, and inclusion of historical factors is essential in any ecological and evolutionary study. In practical terms, this means we must stop using adaptation as our null model; before we ask "Is it adaptive?" we should first inquire "Can the trait be explained in historical terms?" If above work is any indication, the answer to the latter question will frequently be "yes", and many of our current notions about ecological processes will need to be reevaluated.

Evolution is not synonymous with natural selection (e.g. Srb et al., 1965; Pianka, 1994, p. 133). In fact, natural selection is not even a sufficient explanation (Orzack and Sober, 1994b), since historical constraints clearly influence the outcome greatly in at least those cases I studied, as well as some other, non-related cases (e.g. Fleishman et al., 1995, for visual adaptations in anoles). Like every other scientific endeavor, ecology needs to have multiple hypotheses (Chamberlin, 1897; Belovsky et al., 1989; Ward, 1993).

6.6.4 Future directions. Existing empirical tests of the models are essential for future development of theory (Kacelnik and Todd, 1992; Kacelnik, 1993), yet are almost invariably seriously flawed (Pyke, 1984; Orzack and Sober, 1994a,b). Like any theory, however mathematically elegant, OFT remains of dubious value without constant validation from real organisms. Unfortunately, the gap between theory and empirical work is growing, instead of shrinking (Lawton, 1991).

Is OFT "a complete waste of time" (Pierce and Ollason, 1987)? Certainly not. No longer using OFT as a null model does not require the loss of the concept of adaptation, an end to finding and elucidating adaptive patterns, or even use of optimality models. However, theory does not appear to hold the key for the near future. Production of ever more elaborate models has not generally rendered OFT more predictive so far, even in well-studied systems (e.g. Heinrich, 1983; Grantham et al., 1995). "Whether the incorporation of all these factors [will] produce a progressive research programme ... or a degenerative one ... remains an open question (Kennedy and Gray, 1993). Moreover, quantifying all the variables needed to create a valid projection for the lifetime of even a single species could be an enormous

task. Since addition of variables is associated with additional uncertainty that may actually decrease a model's predictive power (Hakanson, 1995), creating even more complex models may not be a solution. Also, the more elaborate and specific the model is, the less useful it becomes for producing general predictions (Holling, 1966). By the time we understand all factors affecting organism X, of what utility will a mathematical model to predict its actions (that will not work for any other species) be?

"Foraging ecology must not seek a single model (or several) and its solution(s) as a general 'optimal foraging theory'. Rather, foraging ecology must employ appropriate models based on given food distributions observed in the field" (Belovsky et al., 1989). Incorporation of lifetime reproduction instead of feeding success as the optimized parameter (e.g. Schmitz and Ritchie, 1989) is likely to produce more realistic models, as is experimental information on nutrient and energy intake of real organisms in complex feeding situations (see Simpson and Raubenheimer, 1993, for a promising approach). Surprisingly similar dietary requirements are apparently shared by fish from different taxa possessing different foraging behaviors

(Dabrowski, 1993). Realistic assumptions about perceptual constraints of foragers are also essential (Kacelnik and Todd, 1992). These approaches may initially be most useful when applied to the least complicated systems. Birds furnishing food for their offspring, one of the classical systems in which foraging behavior has been studied, seem like the ideal place to start. They embody the perceptual, nutritional, and risk-aversion aspects of the problem, yet phylogeny can be factored out by comparing individual within the same species, competing activities are often relatively few during the height of provisioning, and decisions are made at the individual level, unlike the case for two other classical systems, bees and ants. Central place foraging theory (Orians and Perason, 1979) appears to be a good theoretical basis. However, extreme care will be needed before such studies can be extended beyond this scale, and deviations from optimality should be embraced, rather than explained away or ignored.

Only when theoreticians leave their armchairs and empiricists appropriately test theories in the real world will the potential of OFT and similar approaches be fulfilled. I have shown that knowing a lizard's phylogenetic position provides excellent predictive

power regarding its foraging behavior. Only when such historical aspects are explicitly incorporated into our analyses via modern comparative methods will we be able to provide intelligent interpretations (and consequently predictions) of actual behaviors.

6.7 References for discussion

Altbäcker, V., R. Hudson and A. Bilkó. 1995. Rabbit-mothers' diet influences pups' later food choice. Ethology 99:107-116.

Arnold, S.J. 1981. The microevolution of feeding behavior. Pp. 409-453 In: Kamil, A.C. and T.D. Sargent (Eds). Foraging behavior: ecological, ethological and psychological approaches. Garland Press, New York.

Arnold, S.J. 1993. Foraging theory and prey-size - predator-size relations in snakes. Pp. 87-115 In: Seigel, R.A. and J.T. Collins (Eds). Snakes: ecology and behavior. McGraw-Hill, New York.

Arthur, W.B. 1989. Competing technologies, increasing returns, and lock-in by historical events. Economic Journal 99:116-132.

Arthur, W.B. 1993. Why do things become more complex. Scientific American 268(5):144.

Auffenberg, W. 1988. Gray's monitor lizard. University of Florida Press, Gainsville. 419 pp.

Auffenberg, W. and T. Auffenberg. 1988. Resource partitioning in a community of Philippene skinks (Sauria: Scincidae). Bulletin of the Florida State Museum, Biological Sciences 32:151-219.

October 1995. Body size, evaporative water loss (EWL), and integumentary resistance (R) of A. cristatellus ♂♂. N (number of specimens from each locality) = 6. Values are mean ± S.D.

Locality	T_a* °C	RH* %	Body size, mass, g	Body size, surface, cm^2	EWL $mgg^{-1}h^{-1}$	R $s\,cm^{-1}$
Tortola, Sage Mt.	29.2	70	7.77	53.8	2.78	83.2
	0.8	1	0.97	3.9	0.61	17.2
Virgin Gorda, G. Peak	28.4	75	5.84	44.5	3.42	81.4
	0.7	2	0.99	6.1	0.72	11.3
Tortola, Bridge	30.8	64	8.48	47.9	2.23	88.7
	0.3	2	1.51	8.5	0.33	15.3
Beef Isl	32.1	68	8.47	53.7	2.54	113.0
	0.2	2	0.94	5.8	0.71	36.7
Guana Isl	29.0	74	7.43	50.8	1.44	126.8
	0.6	2	0.71	3.6	0.34	28.9
Norman Isl	30.6	68	6.27	46.1	1.65	116.6
	0.6	3	0.84	8.5	0.45	15.9
Necker Isl	29.0	74	8.82	58.2	2.60	77.6
	0.2	1	1.08	8.0	0.26	10.2
Anegada	31.4	68	7.55	47.6	2.19	83.8
	0.8	3	1.82	7.5	0.32	8.5

* Field conditions

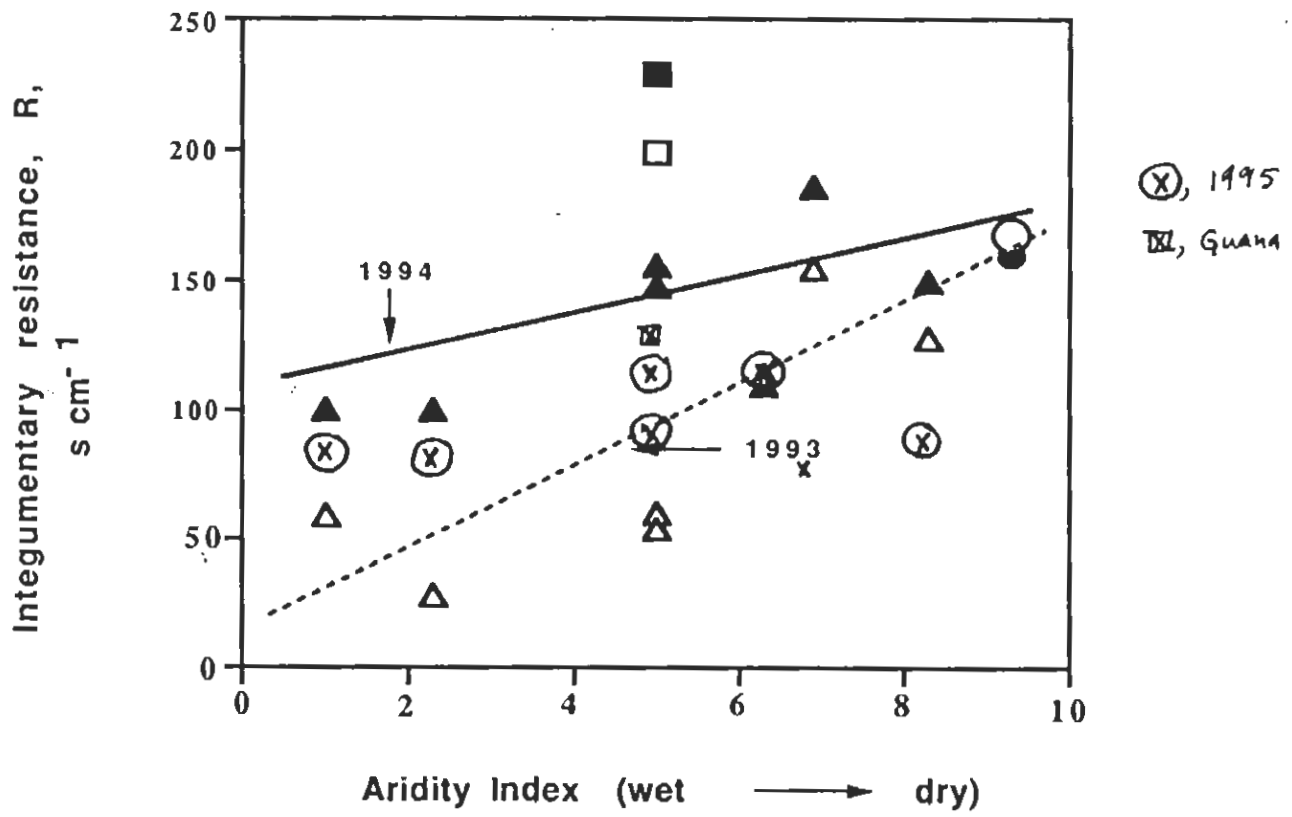

Figure 2. The relationship between habitat aridity and integumentary resistance in *Anolis cristatellus* (triangle) and *Anolis ernestwilliamsi* (circle); Guana is represented by a square. The regression line is based on data for *Anolis cristatellus* only. Hollow symbols and dashed line represent 1993 values.

66

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24 October 1995

Dr. James D. Lazell, Jr.
Guana Island Club
British Virgin Islands

Dear Skip:

The 1994 White Bay Flat Lizard Plot numbers for cristatellus are as follows:
20 October: marked--9
22 October: total--25; recaps--5
N=(9)(25)/5=45 or 170/ha

The 1984 White Bay Flat Lizard Plot numbers for cristatellus are as follows:
7 July: marked--17
9-10 July: total--10; recaps--3
N=(17)(10)/3=56.7 or 226.7/ha

You have the 1993 data, and I will look up the earlier data and send you the numbers. Note that the 12 year trend is down only slightly, and probably not significantly. On the other hand, it took us less time to catch a sample in the old days. But three things have happened since 1984 which would make it harder to get a large sample, even if the lizard numbers were constant: 1) the acacias make it tough to encircle a tree, reducing our capture efficiency; 2) there's only you and me catching, without Bill, Joe, Zonker, Nan, and/or Elayne as well; and 3) we're both slower and don't see as well as we used to (the Richard Thomas effect). Stratulus, however, have undoubtedly declined: the per ha estimate for 1984 is 246.9, now down to maybe 50 or so, and perhaps as little as 16!

There were no problems filing the 3-177 in San Juan with Customs. They actually were interested in herps, and were asking me about the species that lived in their homes and gardens. If you have mealworms to spare, you might want to give some to the lizards that are to be brought back, as they'll be in transit from yesterday to at least next week. Jim made it successfully as far as Miami with me, and I assume he got to LA. Give my regards to Fred and Peggy.

Best wishes,

Gregory C. Mayer
Assistant Professor
Biological Sciences

fort worth zoo

DATE: 21 October 1995

TO: Iguana specialists

FROM: Rick Hudson RH

RE: West Indian rock iguana poster

Recently I was approached by the company that produced the Jamaican iguana poster for the Fort Worth Zoo with an offer to print a second poster. This time, rather than doing a poster limited to one species, I would like to produce something with more versatility and a wider application.

My initial thoughts are to produce a comprehensive West Indian rock iguana poster that includes all Cyclura plus Iguana delicatissima. The poster would carry a strong conservation message concerning the status and plight of this group, and would feature a high-quality photograph of each taxon. To the best of my knowledge this will be the first format to feature a color layout of all the West Indian iguanas.

This poster would serve two primary purposes: education and fund-raising. First, the poster could be used by many of us during our work with iguanas in the West Indies, or distributed through the relevant conservation agencies in those countries. Second, the poster would become a powerful fund-raising tool to help support some of our in-situ projects. The Jamaican iguana poster generated thousands of dollars through sales that went directly to support that recovery effort.

In order to pull this off, I'm going to need help. I want to compile a collection of good quality slides from which to choose. This will likely prove a challenge; however, with each of your assistance I think we can cover each taxa. I will give photo credit if you request. With that in mind, would you consider providing slides of the following iguanas:

C. pinguis

Also if you have any suggestions regarding the text or format I would appreciate your input. I would like to get the slides compiled by the end of November 1995. Hope to hear from each of you soon.

Thanks!

fort worth zoo association
1989 colonial parkway, fort worth, texas 76110 • 817-871-7000 • fax 817-871-7012

Test Tube Holidays

DURING SCIENTISTS MONTHS on Guana Island in the British Virgin Islands, scientists from all over the world spend days collecting data and evenings sharing information while sequestered in five-star luxury. At the invitation of the island's owners, Henry and Gloria Jarecki of New York, and under the aegis of the Conservation Agency, scientists mix work and play at one of the Caribbean's oldest and most exclusive resorts.

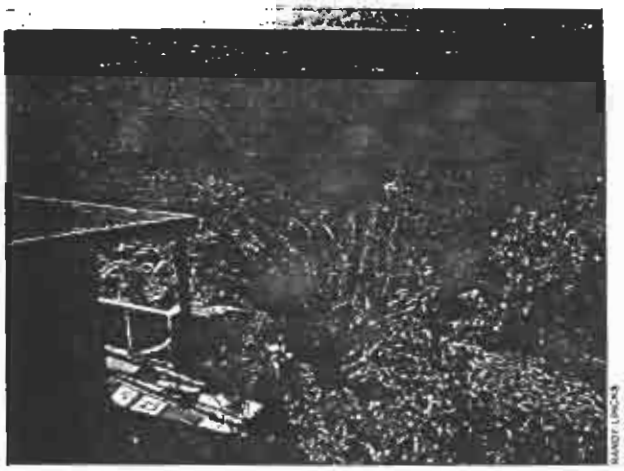
A wildlife sanctuary with the richest fauna of any West Indian island its size, Guana Island provides a beautifully preserved, natural "lab." Each year for the past 15, the Jareckis have invited the likes of the "Termite Lady," Margaret S. Collins, a research associate from the Smithsonian Institute, to conduct studies on the 850-acre island.

During October, the elegant, 15-room Guana Island Resort is dedicated completely to land-based scientific research. Every July, half of the resort's rooms are available to guests, and the other half are open to scientists studying marine topics such as reef dynamics and salt pond biology.

All manner of research transpires on this private paradise. In October, "Guana Island Gang" member Collins can be seen cutting open papier-mâché-like termite nests with her tiny hacksaw. In order to cultivate these helpful creatures that add nitrogen to the soil and might eventually act as a meat substitute, she's trying to describe the factors that determine where they live.

Another regular during Scientists Month, University of Tel Aviv Professor Razi Dmi'el, studies moisture retention in lizards. "Spider Man" Jim Ortiz, trustee of the Orange County Natural History Museum, has discovered 40 species of spiders new to Guana Island, several of which probably never have been described before. Last October, the two Canadian "Frog Ladies," Kristiina Ovaska and Jeanine Calbeck from the University of Victoria, British Columbia, spent every rainy night in the field observing female piping frogs "stalk" their mates during a noisy courtship ritual.

The island's most spectacular preservation accomplishments is followed by a number of visiting scientists. James "Skip" Lazell, Conservation Agency president and director of Guana Island Wildlife Sanctuary, says most of the Anegada rock iguanas were killed off centuries ago by the Spanish. Only on remote Anegada Island in the BVIs could a few of the huge, brown iguanas, some weighing 40 pounds and living to the age of 60, be found. In 1980, the Conservation Agency transplanted five females and three males from Anegada to Guana. These days, a population of more than 100 plump lizards thrive on the east-facing slopes of Guana, enough to transplant to other suitably protected Caribbean islands eventually.



(Above) Dr. James Lazell scrutinizes a young Anegada rock iguana. (Below) The view from Guana Island Resort.

For more information, contact Guana Island Resort—Guana Island Office, 10 Timber Trail, Rye, NY 10580, or phone 914-967-6050. —*Leslee Jaquette*

70

The
Ornithological
Council

SCIENTIFIC
INFORMATION
ABOUT BIRDS

American Ornithologists' Union
Association of Field Ornithologists
Colonial Waterbird Society
Cooper Ornithological Society
Pacific Seabird Group
Raptor Research Foundation
Wilson Ornithological Society

8 August 1995

Guana Island Resort
Guana Island Office
10 Timber Trail
Rye, New York 10580

Dear Sirs:

I read with interest, the article in EcoTraveler concerning your resort and the research conducted there. I am an ornithologist specializing in studying the ecology and breeding biology of tropical seabirds. I worked on brown pelicans in Florida for 5 years. For the past 18 years, while a research curator at the LA County Museum of Natural History, I have been working on Christmas Is (Pacific Oc.) and Johnston Atoll studying the pelecaniforms (boobies, tropicbirds, frigatebirds) and terns.

I have recently moved to the east coast and would like to continue studying pelecaniforms and terns, now in the Caribbean, for comparative purposes. These species have been little studied due to their often remote nesting locations, so that little is known about subspecific relationships, population status, conservation status, or the breeding biology. Thus, I am very interested to know if any of these species nest on or around Guana Island and what the possibilities for studying there might be. There is a small island near Guana called Great Bird Island which I suspect may have boobies and terns nesting, but I cannot find anything in the literature about it.

I have enclosed a couple articles about our work in the Pacific.

Thanks very much.

Sincerely,

Betty Anne Schreiber

Betty Anne Schreiber

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74

The Ornithological Council

SCIENTIFIC INFORMATION ABOUT BIRDS

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Wilson Ornithological Society

2 September 1995

Dr. James D. Lazell
The Conservation Agency
6 Swinburne Street
Conanicut Is, RI 02835

Dear Skip,

I am writing as a follow-up on our conversation concerning conducting research on the seabirds of Guana Island. As I mentioned, for the past 18 years, while a research curator at the LA County Museum of Natural History, I have been working on Christmas Is (Pacific Oc.) and Johnston Atoll studying the breeding biology and ecology of pelecaniforms (boobies, tropicbirds, frigatebirds) and terns. Prior to that I studied pelicans in Florida.

I have been looking for an island in the Caribbean which has several nesting seabird species in order to begin comparative studies with what we have learned in the Pacific. There are several questions in which I am interested. The subspecies of brown pelicans, brown boobies, red-footed boobies, magnificent frigatebirds and tropicbirds are poorly described and in need of revision. I would like to examine morphometric and plumage differences, and eventually take tissue biopsies or blood samples for DNA analyses.

I have also been studying the energetics of breeding and time budgets of adults in several of these species and would like to look at this in the Caribbean. Birds in the central Pacific are severely affected by El Niño - Southern Oscillation events. These events are much less severe in the Caribbean. How are the same species of birds adapting their breeding biology to dramatically different oceanographic conditions? What is occurring energetically? How are evolutionary patterns affected?

Additionally, in over 20 years of studying seabirds, I have not found supporting data for the Lack and Ashmole hypotheses regarding energy limitation in seabirds. Part of my research in the Pacific has been setting up and running experimental procedures to test these hypotheses. With the very different oceanographic conditions in the Caribbean, I would like to examine this problem further.

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Conservation is a problem for these species also. Little is known about many of them due to their remote nesting locations and yet, over the past 50 years the populations of many of them have declined primarily because of human interference. ICBP Technical Publication No. 2, "Status and Conservation of the World's Seabirds", summarizes the problems around the world, including in the Caribbean. We know too little to even determine the population sizes of many of the species, but we do know that introduced cats, rats, goats and other predators are destroying many colonies. We desperately need more information on these species in order to draw attention to the problem and to begin an active conservation program.

Initially I would like to make a visit to Guana Island for about 4-5 days in October 1995 to assess the possibilities of working there on these questions. During a 4 day visit I would visit the colony areas, catch, measure and weigh adult birds for those species present, determine what equipment would be needed to work on the nesting species in May (access to cliff nesting birds, need for blinds, etc.). I would also like to try to get to some other nearby seabird colony areas if possible.

Thanks very much for your assistance in this project.

Sincerely,

Betty Anne Schreiber

The Ornithological Council

SCIENTIFIC INFORMATION ABOUT BIRDS

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Cooper Ornithological Society
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Raptor Research Foundation
Wilson Ornithological Society

1 November 1995

Dr. James D. Lazell
The Conservation Agency
6 Swinburne St.
Conanicut Is., RI 02835

Dear Skip,

I can't thank you enough for the opportunity to come and look at the research possibilities on Guana Island and in the surrounding British Virgin Islands. And thank you for taking the time to assist us in getting around, etc. I am working on a summary of what we found with the seabird populations of the area, which I will send along soon. The hurricanes this year had obviously destroyed earlier nesting attempts of some species.

A couple things strike me immediately as real needs for research in this area. First of all, we do not know the populations sizes of any of the breeding seabird species, or even if they are breeding successfully. We do know that populations are reduced from what they used to be due to introduced predators (including humans). I serve on the BirdLife International working group on the Brown Pelican, and we are very concerned about their populations in the Caribbean. (Guana Is. is providing one of the last safe nesting sites for them.) There is a need for preliminary surveys of these colonies during the main breeding season to document what is happening. This should include banding a series of birds, if possible, for future tracking. And I definitely would like to look at the subspecific differentiation between the Pacific and Caribbean by measuring and weighing a series of birds.

Secondly, there is a need for training and education with the local wildlife people. We spent a day with Nick Drayton, Director of the National Parks Trust, and some of his staff. They are very capable and enthusiastic people, but are unfamiliar in many cases, with what needs to be done to preserve their natural resources. They seemed very amenable to having some outside input on what to do. I am putting together a package of information for the Natl. Parks Trust which

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703 768-6726

addresses the issues and problems peculiar to islands. But there is lot more which could be done. I would like to set up with Nick to visit all the colonies with his staff and train them in how to handle the birds, how to census (what to record, etc.), how to set up a long term monitoring program. They could easily do some monitoring of seabirds while patrolling the areas. With some background data, they could also apply to BirdLife International, Cambridge, or other conservation organization for funding for further programs.

Ideally we would need to visit the islands in the May-June period, when most nests should have chicks present. I'm on my way to a meeting tomorrow, but will give you a call about this later.

Thanks again for all your help.

Best regards,

Betty Anne Schreiber

Mr. & Mrs. James Ortiz
31162 Boca Raton Place
Laguna Niguel, CA 92677

April 12, 1995

Dear Skip,

Well, Carol and I survived the bankruptcy in Orange County, The fires in Laguna Beach, the floods in the canyons, the earthquake in L.A., the flesh eating bacteria, and the local man-eating mountain lions in our hills. You must come and visit us ! Guana Island seams like a pretty safe place compared to Southern California. Thanks for the sympathetic postcard at Christmas .

I finally compiled a list of the spiders on Guana Island and some of the nearby islands that I visited last October. I found 22 Families, 39 Genera, and 47 species. The list below has some notes on habitat and habits for some of the species. Mike Ivie is sending me some more specimens, but they have not yet arrived.

Key to numbers found - C = common , O = occasional , R = rare

Theraphosidae

C #1 - ***Cyrtopholis bartholomei*** (large "tarantula" - in burrows, open areas)
C #2 - Smaller than above, Dark, (low carapace) - under logs in damp areas
R #3 - Arboreal - hirsute carapace, obvious double tarsal pads-scopulae
R #4 - Small - Chevrons on back of abdomen

Araneidae

C ***Argiope argentata*** - smaller than most neotropical specimens , lateral projections of abdomen not prominent
C ***Gasteracantha tetracantha*** - (4 spines on abdomen) - 2 color phases on island
C ***Neoscona moreli*** - sweeping tall grass and shrubs in plantation area
C ***Eustala sp.*** - in tall shrubs and trees
C ***Cyclosa walchenaeri*** - in low shrubs - looks like debris in web
R ***Nephila clavipes*** - Reported but not found at this time
C ***Metepeira labyrinthea*** - in shrubs and low trees - also on docks (communal)
O ***Ocrepeira serrallesi***
C ***Leucauge argyra*** - in horizontal webs , sheltered areas
R ***Tetragnatha sp.*** (immature) -
R ***Agalostichus sp.*** (tubercles on carapace)
R ***Acacesia hamata***

Uloboridae

R ***Miagraminops sp.*** - web a single thread

Scytodidae

R *Scytodes sp.* - in termite nests , under rocks

Lycosidae

R *Trochosa sp.* (immature)

Mimetidae

R *Mimetus sp.*

Clubionidae

R *Trachelas borinquensis*
O *Micaria sp.*

Theridiidae

O *Argyrodes sp.* (kleptoparasite)
R *Achaearanea sp.*

Caponiidae

O *Orthonops sp.*

Oecobiidae

R *Oecobius concinnus*

Dinopidae

R *Dinopis sp.*

Gnaphosidae

R *Drassyllus sp.*

Anyphaenidae

C *Aysha sp.* - (near A. velox - female only)

Linyphiidae - Erigininae (3 species) - O

Oonopidae

R *Oonops sp.*

Loxoscelidae

C ***Loxosceles virgina*** - in buildings and under rocks that have hollow area below

Selenopidae

C ***Selenops lindborgi*** - in buildings and on Agave leaves at night

Pholcidae

R #1
C #2
C #3

Oxyopidae

R ***Hamataliwa sp.*** - on Great Caminoe only at this time
C ***Oxyopes salticus*** - in open areas on grass and low shrubs

Heteropodidae (Sparassidae)

O ***Olios sp.*** - large
O ***Pseudosparianthis antiguensis***

Salticidae

C ***Metaphidippus sp.*** #1 - green irridescence
C ***Metaphidippus sp.*** #2 - chevrons on abdomen
R ***Metaphidippus*** sp. #3 - similar to #2
O ***Hentzia sp.***

I'm working on some keys and illustrations of the above specimens at this time. I'll send them to you when they are finished. I only have 9 days available this October to visit the Island. Carol can"t come due to a new job; if I'm still welcome after last years problems with the Island owners let me know. Hope to see you soon.

(714) 495-9231

Your Friend,

James L. Ortiz

Acta Científica 6(1-3):103-108,(1992) 1995

78

A NEW SPIDER WASP OF THE GENUS *PSORTHASPIS* FROM THE GREATER ANTILLES (HYMENOPTERA; POMPILIDAE; POMPILINAE)

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ABSTRACT

A new species of spider wasp is described from specimens of both sexes collected in the British Virgin Islands (Guana I.), the American Virgin Islands (St. Croix), and Puerto Rico (Desecheo I.). Morphologically, this species is most similar to *Psorthaspis variegata* (F. Smith), a Central American species. The characters of both morphology and color that will distinguish between the new species and other known *Psorthaspis* are delineated. The female of this new species is depicted in a color habitus figure, male terminalia are illustrated and compared to those of *P. variegata*.

RESUMEN

Una nueva especie de avispa atacante de arañas es descrita utilizando especímenes de ambos sexos coleccionados en las Islas Vírgenes Británicas (Isla Guana), Islas Vírgenes Estadounidenses (Santa Cruz) y Puerto Rico (Isla Desecheo). Morfológicamente esta especie es más parecida a *Psorthaspis variegata* (F. Smith), una especie de América Central. Las características morfológicas y color que distinguen esta especie de las otras especies de *Psorthaspis* son mostradas. La hembra de esta nueva especie es presentada en una ilustración a color, los segmentos genitales del macho son ilustrados y comparados con los de *P. variegata*.

INTRODUCTION

The following new species of *Psorthaspis* is described in order that the name may be available for use by other scientists. The Antillean spider wasps of the tribe Aporini, to which *Psorthaspis* belongs, were last reviewed by Bradley (1944). The more recent work by Evans (1966), dealing with the Pompilinae of México and Central America refined some of the generic concepts put forth by Bradley, largely by lumping several of Bradley's genera within the genus *Psorthaspis*.

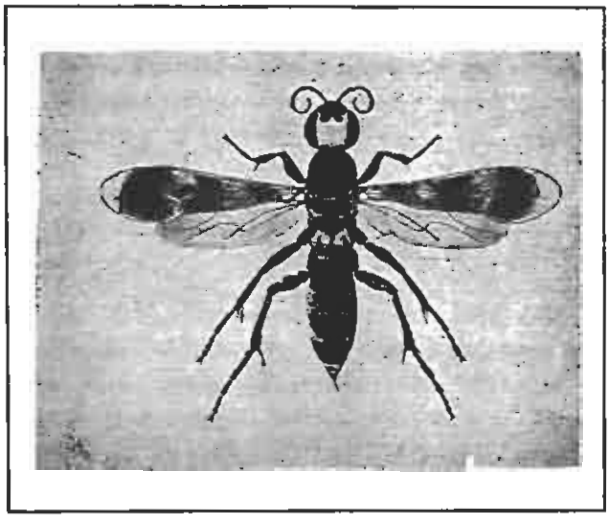
The Antillean spider wasp fauna remains poorly known. While it is not all surprising that species remain to be described, it does seem somewhat surprising that such a handsome species as the one described below has remained unknown for so long.

The following description is patterned after those of Evans (1966) to facilitate comparison with his descriptions of mesoamerican species. Abbreviations used in the description are as follows: **IOD** (Interocellar Distance), the distance between the ~~lower~~ inner margins of the lateral (posterior) ocelli; **LID** (lower Interocular Distance) the minimum distance between the lower inner margis of the compound eyes (slightly above level of base of clypeus); **MID** (Middle Interocular Distance) the **maximum** distance between the inner margins of the compound eyes; **OD** (Ocellar Diameter), the transverse diameter of the anterior (middle) ocellus; **OOD** (Ocellocular Distance), the **minimum** distance between the outer margin of a lateral ocellus and the adjacent inner margin of the compound eye; **OVD** (Ocellovertexal Distance), with the head **in full frontal view**, the distance between the upper margins of

82

the lateral ocelli and the top of the vertex; **UID** (Upper Interocular Distance), the **minimum** distance between the upper inner margins of the compound eyes.

Psorthaspis gloria, new species
(cover illustration, Figs. 1-3)



DIAGNOSIS

Females may be separated from all other species by the distinctive color pattern (Fig. 1, see cover); ~~diagram);~~ additionally, the clypeofrontal bridge is not depressed, but is narrow, the portion between the antennal sockets less than 0.50 times the diameter of the sockets; the metatibia is without spines above; the outer ray of the tarsal claw is strongly curved and nearly parallel to the subbasal tooth. Males are recognizable by the banded wings, the short antennae (segments 4 to 12 about as long as wide), the presence of tomentose metasomal bands, and the red femora, as well as the genitalic features described below.

DESCRIPTION

Female. Length 12.4 to 19.4mm; forewing length 8.6 to 11.5mm. Head and body largely black; clypeus, mandibles (except blackish teeth) and scape bright reddish, underside of flagellum duller reddish; coxae (except meso- and metacoxae ventrally), femora (except brownish apices), inner side of protibiae, approximately proximal 0.66 of mesotibia, proximal 0.80 of metatibia; transverse preapical bands on metasomal terga 1 to 3, all distinctly pink, remainder of legs dull reddish; tibial spurs dull reddish.

Face (except clypeus), vertex, underside of head, most of dorsum of propodeum (and extending down along sides of disc), exposed portions of metasomal terga 5 to 6 (except apex of 6), completely hidden beneath flattened and appressed white hairs. Mesosomal pubescence dense and largely concealing surface, in most areas reflecting dull bluish to purple; side and posterior margin of pronotum, posterior margin of mesoscutum, anterior and posterior margins and narrow median stripe of scutellum, disc of metanotum (paler laterad), all with reddish golden pubescence. Mesepisternum with large patch of yellowish pubescence posteriorly along oblique suture and an irregular area of yellowish to golden pubescence ventrally that may extend over most of mesepisternum below suture. Metasomal terga 1 to 3 with broad apical bands of dark pubescence (bluish to purplish, depending on viewing angle), bands on 2 and 3 slightly expanded in middle, band of 2 slightly shorter and band of 3 slightly longer than basal pink band, segment 4 entirely dark pubescent; sterna 5 and 6 with very fine yellowish pubescence; pink basal bands with extremely fine, whitish tomentum. Most body areas with scattered short, erect hairs.

Forewings dark, with bluish reflections from dark pubescence, but with two areas of mostly yellowish pubescence: near apex of median and submedian cells; near midlength of first submarginal and first discoidal cells, most of apical area beyond apex of marginal cell with distinctly whitish pubescence. Hindwing transparent, slightly brownish, apical and posterior margins broadly darker.

Clypeus about 1.6 times as wide as long, separated from inner eye margin by less than OD; apical margin evenly rounded. Clypeo-frontal bridge well developed and not depressed below level of clypeus and frons. Inner eye margins weakly curved, UID and LID about equal, MID about 1.3 x UID; vertex flat and passing straight across slightly above level

of tops of eyes. In frontal view, IOD 2.2 to 2.3 x OD; OOD 2.7 to 3.0 x OD; OVD 1.3 to 1.4 x OD.

Dorsal surface of pronotum continuous with collar. Mesepisternum posteriorly with band of short, longitudinal rugae. Apicolateral angles of propodeum with 6 to 10 very coarse, conspicuous rugae than extend nearly to base and across summit of declivity, basal area separated from declivity by transverse ridge.

Tarsal claws not strongly curved, tooth erect and widely separated from apical ray. Metasoma weakly compressed.

Male. Length 6.8 to 9.5mm, forewing length 4.9 to 6.3mm. Black, some areas of meso- and metasoma with weak bluish reflections from minute appressed tomentum. Mandibles and meso- and metafemora red; meso- and metacoxae duller reddish and meso- and metatibiae dull brownish red; posterior face of profemur with reddish median blotch in one specimen. Tibial spurs dark. The following with appressed whitish pubescence (longest and shaggiest on propodeum): entire head; mesosoma except medially interrupted preapical band on pronotal disc; most of mesoscutum; disc of scutellum; irregular posterior area on mesepisternum; anterior band on basal area of propodeum, continued more broadly down side; metasomal terga, but terga 1 to 3 with broad distal bands of dark pubescence and tergum 4 dark at sides.

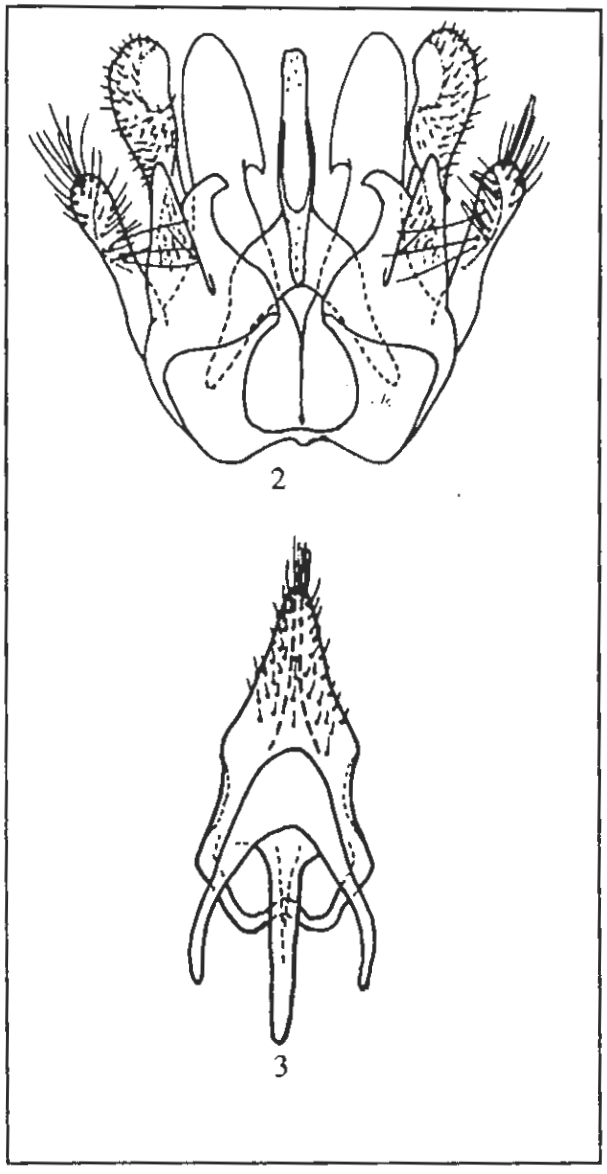
Distal 0.33 of forewing brownish and brownish blotch also present along veins M and cu-v, wing membrane otherwise clear. Hindwing clear, distal 0.25 brownish.

Head subcircular, only slightly broader than long; vertex forming an even arc above tops of eyes. Clypeus about 1.6 times as broad as long, apical margin evenly rounded. Antennal segment 4 about 1.3 times as long as thick.

Posterior margin of mesepisternum with short, widely spaced longitudinal rugae. Propodeal declivity well defined and marked on each side by a short ridge that extends partly down apicolateral angle (absent in one specimen), but propodeum otherwise devoid of rugae.

Inner claw of protarsus strongly curved and deeply bifid, with lobiform inner ray; outer claw of protarsus almost bifid; claws of meso- and metatarsi dentate.

Subgenital plate (Fig. 3) strongly beveled, profile convex, about as in *P. variegata;* in ~~vertical~~ view, sides distinctly angulate. Genital aedeagus elongate, about equal to parapenial lobe and digitus, distal, mesal area of digitus with semicircular asetose area (Fig. 2).



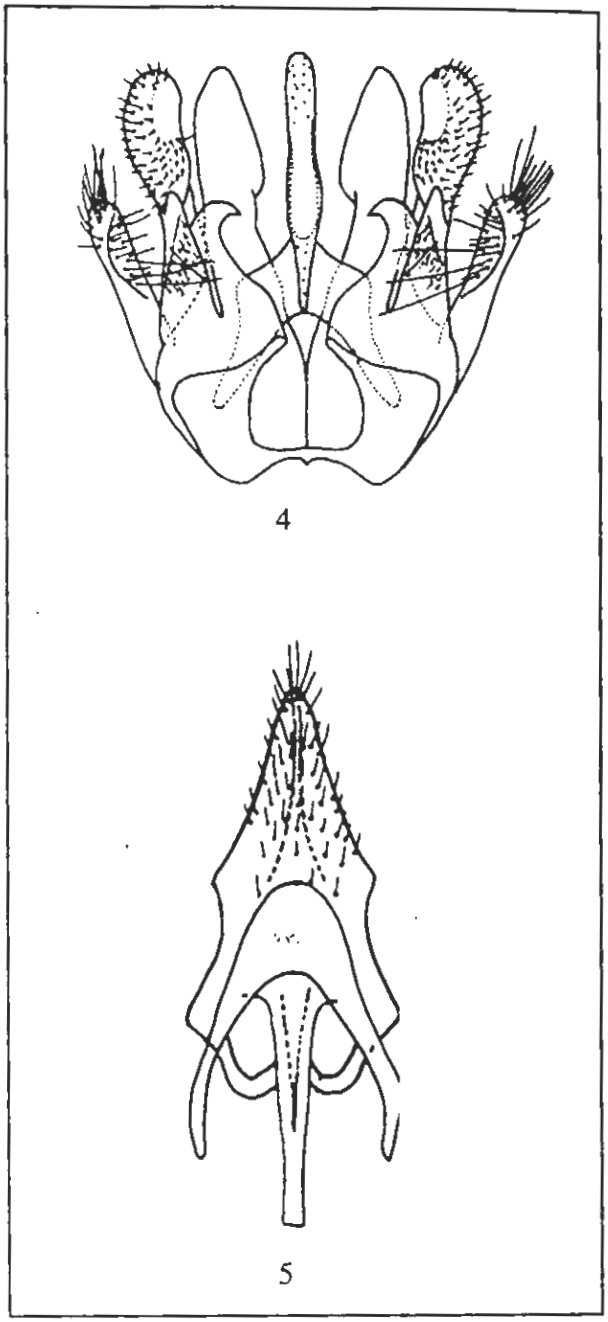
Figures 2-5. Genitalic capsule and subgenital plate, respectively of *Psorthaspis gloria* (2-3) and P. variegata (4-5; after Evans 1966).

TYPE MATERIAL

Holotype female, Long Man's Point trail, Guana Island, BRITISH VIRGIN ISLANDS, 24 October 1992, (R.R. Snelling) deposited in LACM. Paratypes (All from Guana Island): 3 ♂♂. 15 to 20 April 1993 (R.R. Snelling; LACM); 3 ♂♂, 20 to 25 April 1993 (R.R. Snelling; LACM); 1 ♀, 26 June, 1993 (R.R. Snelling; LACM); 1 ♀, 3 July 1993 (R.R. Snelling, LACM), 1 ♂, 7 July 1993 (R.R. Snelling; LACM; 1♂, 1 to 7 July 1993 (R.R. Snelling; LACM); 1 ♀, 4 to 10 July 1988 (S.E. Miller and C. O'Connell; BPBM); 1 ♂, 7 October 1992 (R.R. Snelling LACM), on flowers of *Capparis cynophallophora*; 1 ♀, 14 October 1992 (J. Stark; AMNH); 1 ♀, 16 October 1991 (R.R. Snelling; LACM); 2 ♂♂, 16 to 20 October 1992 (R.R. Snelling; LACM), ex malaise trap; 4 ♂♂, 19 October 1992 (M.A. and L.L. Ivie MSUC). Additional paratypes: 4 ♂♂, Estate North Star, St. Croix, AMERICAN VIRGIN ISLANDS, 15 Nov. to 18 Dec. 1992 (J. Keularts; MSUC); 1 ♂, Estate North Hall, Creque Gut, 19 May to 18 June 1993 (J. Keularts; MSUC); 1 ♀. Desecheo Island, PUERTO RICO, 13 July 1968 (S. Medina Gaud, PRAES). Paratypes in AMNH, BPBM, PRAES, LACM, and MSUC.

ETYMOLOGY

This species in named *gloria* because it truly is a thing of beauty and also in appreciation of the support and encouragement rendered by Gloria Jarecki to the biologists who have visited Guana Island. The name is to be treated as a noun in apposition.



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DISCUSSION

The male terminalia of this species are very suggestive of those of the mainland species, *P. variegata* (F. Smith 1862) as defined by Evans (1966). Especially similar are the keeled and angulate subgenital plate and the presence of a semicircular asetose area near the apex of the mesal margin of the digitus. The range of *P. variegata*, including that of its putative subspecies *impudica* (Cameron 1893), extends from central México to Panamá, according to Evans.

The male of *P. variegata* differs from that of *P. gloria* in the proportionately shorter fourth flagellar segment, the more sharply angulate subgenital plate (Fig. 5) and the rounded or obtuse ventral angle of the parapenial lobes. The several males of *P. variegata* that I have seen all have uniformly black legs. The color of the vestiture of the two species is similar, but the males of *P. gloria* have long distal bands of dark hairs on metasomal terga 2 and 3; in *P. variegata* the distal band of tergum 2 is shorter

than the basal pale band and tergum 3 is almost wholly pale pubescent.

In the key to the then known species of *Psorthaspis* by Bradley (1944) the male of *P. gloria* will fail at couplet 11, separating *P. mariae* (Cresson) and *P. australis* (Banks), two species of the United States. The shape of the subgenital plate (= "sternite 9" of Bradley) and of the paramere does not accord with either alternative.

Females of *P. gloria* and *P. variegata* differ dramatically in the color of the metasomal terga: in *P. variegata* tergum 3 has a yellow-orange band (*P. variegata variegata*) or a pair of spots (*P. variegata impudica*) *versus* the broad pinkish bands on terga 1 to 3 of *P. gloria*. In *P. variegata* the coarse pale pilosity of the head and mesosomal dorsum is yellowish (white in *P. gloria*) and the side of metasomal tergum 1 is entirely covered by coarse whitish hairs that extend across the summit as a broad distal band (entirely lacking in *P. gloria*). The most obvious morphological difference between the two species may be seen in the propodeal sculpture: *P. variegata* lacks the distinct ridge or crest at the summit of the declivity that is present in *P. gloria*; the lateral rugae are finer and more regular in appearance.

Nothing is known of the biology of *P. gloria*. Guana Island is mostly covered by the dry evergreen forest common to many of the Virgin Islands. Most of the female specimens of *P. gloria* have been collected along the ridge leading to Long Man's Point. This ridge traverses the more xeric portions of Guana Island, an area with considerable cacti and other succulents amidst many rocks and boulders. The females run very rapidly over the surface and will run under the rim of a net dropped over them. Although the prey of this species is unknown, P. *gloria* may be a predator of some species of burrowing spider; Evans (1966) has suggested, probably correctly, that all species of this genus "attack ctenizids or at least some type of burrowing spider."

Except for the individual collected on flowers of *Capparis*, most males were collected in Malaise traps situated in densely wooded areas. Three males were collected by the Ivies while beating shrubbery at night. According to Dr. Ivie (personal communication) these were part of a persistent cluster of males, presumably similar to sleeping clusters of male *Pepsis rubra* (Fabricius) that I observed on Guana Island.

ACKNOWLEGMENTS

Most of all, I must express my profound gratitude to Henry and Gloria Jarecki whose interest, enthusiasm, and financial support made possible my visits to Guana Island. Thanks, too, to James "Skip" Lazell, for being the "middle man" who made it happen. Important specimens were made available by S.P. Cover, Museum of Comparative Zoology, Harvard University (MCZ), M.A. Ivie, Montana State University (MSUC), S. Medina Gaud, Puerto Rican Agricultural Experiment Station, Río Piedras, Puerto Rico (PRAES), S.E. Miller, Bernice P. Bishop Museum (BPBM), and J. Stark, American Museum of Natural History (AMNH). For the splendid color habitus figure I am greatly indebted to Marianne D. Wallace. The Spanish summary was prepared by Juan Torres, to whom I remain grateful for many kindnesses. ¡Mil gracias, amigo!

LITERATURE CITED

Bradley, J.C. 1944. A preliminary revision of the Pompilinae (exclusive of the tribe Pompilini) of the Americas (Hymenoptera: Pompilidae). American Entomological Society Transactions 70:23-157.

Cameron, P. 1891-1893. Pompilidae. Biologia Centrali-Americana, Hymenoptera 2:158-223.

Evans, H.E. 1966. A revision of the Mexican and Central American spider wasps of the Subfamily Pompilinae (Hymenoptera: Pompilidae). American Entomological Society Memoirs no. 20, 442 p.

Smith, F. 1862. Descriptions of new species of Mexican Pompilidae belonging to the genera *Pompilus, Agenia, Priocnemis, Notocyphus* and *Ferreola*. Journal of Entomology 1:395-399.

Family **Mordéllidae**—Tumbling Flower Beetles: These beetles have a rather characteristic body shape (Figure 310); the body is somewhat wedge-shaped, humpbacked, the head is bent down, and the abdomen is pointed apically and extends beyond the tips of the elytra. Most mordellids are black or mottled gray in color, and the body is covered with a dense pubescence. Most of them are 3–7 mm in length, but some reach a length of 14 mm. These beetles are common on flowers, especially the composites. They are quite active and run or fly quickly when disturbed; their common name is derived from the tumbling movements they make in attempting to escape capture.

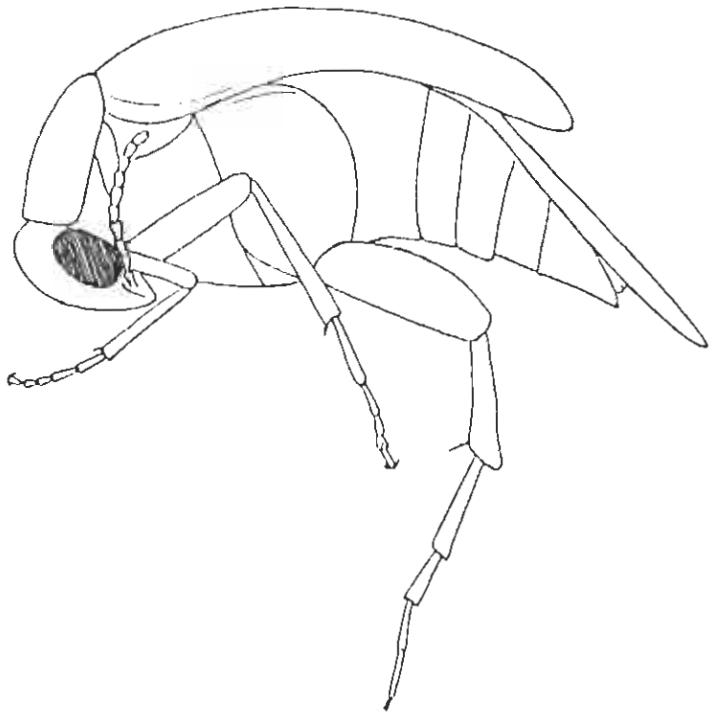

Figure 310. A tumbling flower beetle, *Mordélla marginàta* Melsheimer, 15 ×.

The larvae live in decaying wood and in plant pith; some are predaceous.

Tumbling Flower Beetles of the Virgin Islands (Coleoptera: Mordellidae)

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Bozeman, MT 59717

Introduction

Fabrician Names probably originating from the Virgin Islands:

Mordella vittata Fabricius Syst. El. II 124. 14. "in America meridionali D. Smidt (3 specimens)not in Blackwelder under Mordellidae

Mordella haemorrhoidalis Fabricius Syst. II El. 124. 15 "in America meridionali D. Smidt (1 specimen). remains in this genus in Blackwelder 1945: 476]

Mordella bifaciata Fabricius Syst. El. II 124. 16 "in America meridionali D. Smidt (2 specimens). [remains in this genus in Blackwelder 1945: 475]

Mordella ferruginea Fabricius Syst. El. II 124. 17 "in America meridionali D. Smidt (2 specimens). Placed in Mordellistena by Quedenfeldt 1886: 127, Ray 1937: 391; Blackwelder 1945: 478]

This is a junior homonym of Mordella ferruginea Fabricius Syst. Ent. 1775 262. 1 "in India orientali Koenig" (1 specimen) (moved to Rhipiphorus by Fabricius).

Current Names used in the Virgin Islands:

Mordellistena ferruginea (Fabricius)

Type locality to be narrowed to St. Thomas

Recorded from St. Thomas (Leng and Mutchler 1914: 466, Wolcott 1950: 317, Blackwelder 1945: 478); St. Croix (Miskimen and Bond 1970: 86). A record for the USA (Blackwelder 1945: 478) has no known source.

Methods and Materials

Length of a species is given by a range between the smallest and the biggist (eye sighted) in the specimens, measuring from the side view of the front edge of pronotum to the tip of elytrum in unaltered specimen condition.

Results

Mordellistena fabrici Lu and Ivie, REPLACEMENT NAME

Mordellistena ferruginea (Fabricius)

Mordella ferruginea Fabricius, Systema eleutheratorum. , 2: 124, 1801.

Mordellistena ferruginea (Fabricius), Quedenfeldt, Berliner Ent. Zeitschr. , 30: 127, 1886.

Mordellistena ferruginea Quedenfeldt, Ray, Proceedings of U. S. N. M. , 84(3020): 391, 1937.

Mordellistena ferruginea (Fabricius), Ray, Proceedings of U. S. N. M. , 84(3020): 391, 1937.

Form elongate, narrow, sides subparalell, attenuate and rounded gradually caudad from apical 4th of elytra. Derm ferrugineous; head with sometimes fuscous clouds; antennae, maxillary palpi, anterior and middle legs lighter (flavoferruginous), underside darker; eyes black with silvery reflection. Surface covered with fine pubescence partaking of ground color.

Head small and convex; eyes large, hairy, and coarsely granulated, reaching occiput, emarginate behind antennae.

Antennae filiform, long and slender, reaching base of thorax; segments 1 and 2 subequal, 3 and 4 shorter and narrower, 3 slightly shorter than 4; 5 almost as long as 3 and 4 combined or at least 1/4 longer than 4; 5-10 slightly decreasing in length and increasing in width; 11 1/4 longer than 10, side straight, apex rounded.

Distal segment of maxillary palpi enlarged, scalene triangle, inner side a little longer than apical edge and shorter than outer side, apical side and angle rounded.

Pronotum a little broader than long, broadest at base; basal angles acute, base arcuate, basal lobe short and broadly rounded or truncated.

Scutellum triangular, sides straight, apical angle rounded. Elytra at least 2. 5 as long as broad, sides subparalell on basal 3/4, thence broadly rounded to apex; apices individually rounded.

Middle tibiae as long as their tarsi; next to the last segment of anterior and middle tarsi emarginate or notched at apex. Posterior tibiae with 2 long, oblique ridges, each extending half way across outer surface, and a short subapical ridge; basitarsi with 3, second with 2 short oblique ridges, each extending less than half way across outer surface; basal ridge on basitarsi sometimes rudimentary. Outer spur of posterior tibiae 1/4 of inner one.

Anal style long, at least 2. 5 length of hypogyium, conical, slender, and attenuate to apex.

Length: 2. 1-3. 3mm, specimens from Dominican Republic can reach 3. 5mm.

PREVIOUS RECORDS. -Puerto Rico;

MATERIAL EXAMINED. -Puerto Rico; Tortola, Guana Island, Necker Island, Jost Van Dyke, Anegada, St. John, St. Thomas, St. Croix, Virgin Gorda, British Virgin Islands; Dominican Repiblic;

TYPE LOCALITY. -.

TYPE. -.

REMARKS. -The ridges on posterior tibiae and tarsi vary a lot among individuals. Basitarsi rarely show a rudimentary 4th ridge and sometimes have only two ridges. Second ridge on posterior tibiae sometimes is less than half way across outer surface. extremely small individual from St. John has only one long oblique ridge on posterior tibiae, other than the short subapical on; it has two ridges on basitarsus and one on second segment of the right tarsi, a rudimentary second on second segment of the left tarsi.

Rarely a rudimentary third is observed on the posterior tibiae other than the two long oblique ridges. However, one large individual from Dominican Republic has three oblique long ridges on its left posterior tibiae instead of two only, obviously a rudimentary

one (which showed on the right tibiae) become dominant because it was not as long as the second ridge, which is half way across the outer surface.

There are two types of antennae within a large population (more than 50 individuals). One is slender, often longer beyond base of thorax, segment 5 shorter than 3 and 4 combined. The degree of degreasing in length of 5-10 is less, each segment ranging from 2.5 to 2 as long as broad. The other is stouter, segment 5 as long as 3 and 4 combined. The degree of decrease in length and increase in width of 5-10 is obvious, each segment ranging from 2 to 1 as long as broad. At this time we could not associate this variation in antennae with sex or size, and we doubt that the variation is because of the tension in antennae.

All specimens (4) from Jost Van Dyke are entirely fuscous-headed, and segments 3 and 4 of the antennae are distinctly shorter and narrower so that 5 is as long as 3 and 4 combined. Such a form is also collected from St. John and Guana Island. However, there is a whole range of color variation in the head from flavoferruginous to entirely fuscous with the same type of antennae.

We also observe variation in elytral color in the population from Puerto Rico. Basal margin and basal sutural area are rather fuscous than ferruginous in a few specimens.

Mordellistena lineata Ray

Mordellistena lineata Ray, Proceedings of U. S. N. M. , 84(3020): 395, 1937.

Form elongate, narrow, sides subparalell, attenuate and rounded gradually caudad from apical 3rd of elytra. Derm black; front of head, basal 4 segments of antennae, maxillary palpi, anterior and middle legs, and posterior trochanters, tibiae and tarsi flavocastaneous; a broad median stripe on elytra flavocastaneous, reaching base at humeri, narrowing within 2/4 of elytra, and extending to apex, leaving a black narrow line on each margin and a black sutural line in the middle. Surface covered with fine, cinereous pubescence, except on flavocastaneous area, where it partaking of ground color.
Head convex, eyes moderately granulated, reaching occiput,
emarginate behind antennae, and hairy.

Antennae filiform, long, reaching base of thorax; segments 1 and 2 subequal, 3 and 4 subequal, shorter, and narrower; 5-10 each as long as 3 and 4 combined, each slightly broader apically; 11 1/4 longer than 10, rounded.

Distal segment of maxillary palpi enlarged, isosceles triangle.

Pronotum a little broader than long, narrowest behind head; basal angles abtuse, base arcuate, basal lobe short and subtruncate. Scutellum small, triangular. Elytra 2. 5 as long as broad, sides subparalell on basal 2/3; apices individually rounded.

Middle tibiae as long as their tarsi; next to the last segment of anterior and middle tarsi emarginate or notched at apex. Posterior tibiae with 2 long, oblique ridges, each extending half way across outer surface, and a short subapical ridge; the basal ridge usually longer than the second, sometimes extending entirely across outer surface to genu; basitarsi with 2, second with 1 short oblique ridges; basal ridge on basitarsi sometimes rudimentary. Outer spur of posterior tibiae 1/3 of inner one.

Anal style long, almost 3 time as long as hypogyium, conical, attenuate to apex.

Length: 1. 6-2. 2mm.

PREVIOUS RECORDS. -Guanica, Puerto Rico.
MATERIAL EXAMINED. -Mona Island, Puerto Rico; Guana Island, Buck Island, St. Croix, St. Thomas, St. John, Virgin Islands.
TYPE LOCALITY. -Guanica, Puerto Rico.
TYPE. -U. S. N. M. no. 51601.
REMARKS. -In his original description, Ray stated that "seven apical segments of antennae" were flavocastaneous, lighter than basal segments. This is not true to all specimens we have examined from the Virgin Islands, as well as to the type specimen (Waren Steina, March 23, 1995; personal communication). Ray also stated that the basal oblique ridge on posterior tibiae was "entirely across out face". We find this character is variable. Less than half of the specimens examined are of that type. Most specimens have the basal ridge on posterior tibiae only half way across the outer surface or more, but not entirely. This is a very abundant species.

Mordellistena danforthi Ray
Mordellistena danforthi Ray, Proceedings of U. S. N. M. 84(3020): 392-393, 1937.

Form elongate, sides subparalell. Derm flavous; elytra fuscous with a flavous, broad, humerous spot along base to suture, narrowing caudad to basal 1/3 of elytra; eyes, apical 7 segments of antennae, ventral abdominal segments, anal style, and ridges and apical setae fuscous. Surface densely covered with fine golden pubescence.

Head large; eyes hairy, and moderately granulated, reaching occiput, emarginate behind antennae.

Antennae filiform, long, reaching base of thorax; segments 1 and 2 subequal, 3 and 4 subequal, shorter and narrower; 5-10 equal, each 1/3 longer and slightly broader than 4; 11 rounded, slightly longer than 10.

Distal segment of maxillary palpi enlarged, elongate-triangular, apical side short.

Pronotum slightly broader than long, sides rounded; basal angles acute, base arcuate, basal lobe short, rounded. Scutellum small, triangular. Elytra at most 2. 5 as long as broad, sides parallel on basal 3/4, broadly rounded to apex; apices individually rounded.

Middle tibiae as long as their tarsi; next to the last segment of anterior and middle tarsi emarginate or notched at apex. Posterior tibiae with 2 long, oblique ridges, each extending half way across outer surface, and a short subapical ridge; basitarsi with 3, second with 2 short oblique ridges, each extending less than half way across outer surface; basal ridge on basitarsi sometimes rudimentary. Outer spur of posterior tibiae 1/4 of inner one.

Anal style long, from 2. 5 to 3 times as long as hypogyium, conical, slender, and attenuate to apex.

Length: 2. 0-2. 8mm.
PREVIOUS RECORDS. -Villalba, Puerto Rico;
MATERIAL EXAMINED. -Guana Island, St. John, Great St. James, British Virgin Islands.
TYPE LOCALITY. -Villalba, Puerto Rico.
TYPE. -U. S. N. M. no. 51599.

REMARKS. -One specimen from St. John has a additional rudimentary ridge each on posterior tibiae and basitarsus. According to Ray (1937), the scutellum, apical 2/3 of anal style, and only three abdominal ventral segments were fuscous, but he also stated that " the abdominal segments of the female (except anal style) lack the fuscous coloration of the male, and the general castaneous color is lighter. " We have observed variation in abdominal ventral segments from total fuscous to total flavocastaneous, as well as in anal style from total fucous to what he described. We see no variation in the color of scutellum, which is as flavous as the front part of the body and the basal part of the elytra. We have also observed variation in elytral color in one specimen from Guana Island. The basal flavous spot on the elytra is extending narrowly to 1/2 of the elytra, then widening all the way to apex.

Mordellistena pseudolineata Lu and Ivie, NEW SPECIES.

Form elongate, sides subparalell. Derm black; basal 4 segments of antennae, anterior legs, tibiae and tarsi of middle and posterior legs testaceous except ridges and apical setae. Surface densely covered with coarse whitish pubescence, underside longer; a broad median vitta of testaneous setae on elytra, touching margin and suture at humeri, extending caudad to apex, narrowed slightly within basal 2/4 of elytra, leaving margin and suture piceous slightly beyond basal 1/10 of elytra.

Head small; eyes hairy, and moderately granulated, reaching occiput, suboval. Antennae filiform, long, reaching base of thorax; segments 1 and 2 subequal, 3 and 4 subequal, shorter and narrower, 5 equal to 3 and 4 combined; 5-10 equal, 11 rounded, 1/4 longer than 10.

Distal segment of maxillary palpi enlarged, elongate-triangular, apical side short.

Pronotum slightly broader than long, sides rounded; basal angles acute, base arcuate, basal lobe conspicuous, rounded. Scutellum small, triangular. Elytra at most 2. 5 as long as broad, sides parallel on basal 3/4, broadly rounded to apex; apices individually rounded.

Middle tibiae as long as their tarsi; next to the last segment of anterior and middle tarsi emarginate or notched at apex. Posterior tibiae with 2 long, oblique ridges, basal one extending entirely across outer surface, and a short subapical ridge; basal and second tarsal segments with 2 short oblique ridges. Outer spur of posterior tibiae 1/4 of inner one.

Anal style long, 3 times as long as hypogyium, conical, slender, and attenuate to apex.

Length: 2. 2mm.

MATERIAL EXAMINED. -British Virgin Islands. St. John: East Hope, Bordeaux Mt. , 900 feet, 2-24. vii. 1994. , flight intercept trap, M. Becker & S. Bucklin

TYPE LOCALITY. -Same as above.

HOLOTYPE. -U. S. N. M.

REMARKS. -Only one specimen from St. John has been collected.

Mordella atrata Melsheimer

Mordella atrata Melsheimer, 1846, p. 313. Liljeblad, 1922, p. 53.

Mordella scutellaris of authors, not Fabricius 1801.

Cuneiform, more robust in female than in male. Derm entirely black; pubescence on upper surface brownish, on scutellum cinereous; underside and basal anal style with longer cinereous hairs.

Head small, 3/4 as broad as pronotum; eyes suboval, reaching occiput, finely granulated with sparse short hairs.

Antennae shorter than head and pronotum combined; segments 1 to 4 slender, 3 and 4 shorter and narrower, subequal, 4 apically broader than 3; 5 triangular, 1/3 longer than 3 and twice as broad at apex; 6-10 of uniform width, serrate, about as broad as long, each 1/4 shorter than 5, 11 rounded on inner side and on apex, 1/3 longer than 10.

Distal segment of maxillary palpi scalene triangular in male, inner angle rounded in female; second segment stouter than usual.

Pronotum convex, 1/3 broader than long, a little broader than elytra at base, widest a little before base, then evenly rounded to apex; basal angles abtuse, base arcuate, basal lobe short, broadly rounded. Scutellum triangular, broadly rounded at apex. Elytra twice as long as broad, widest at base, attenuate apically; apices individually rounded with fine but distinct margin.

Middle tibiae as long as their tarsi; next to the last segment of anterior and middle tarsi notched at apex, two and third segments straight-truncate. Posterior tibiae with a short subapical ridge, parallel to apical margin, no dorsal carina ridge but with small carinated granules scattered in an irregular line on dorsum; the same dorsal granules weakly indicated on basitarsi, much less so on second segment of posterior tarsi. Outer spur of posterior tibiae 1/4 shorter than inner one.

Anal style long, twice as long as hypopygium, rather stout at base, attenuate to apex; hypopygium about twice as long as penultimate segments in male, shorter in female.

Length: 3. 2-4mm.

PREVIOUS RECORDS. -North, Central, and South America.

MATERIAL EXAMINED. -British Virgin Islands: Guana Island; Cuba, Haiti, Dominican Republic.

REMARKS. -In descriptions by Champion (1889) and Liljeblad (1945), both mentioned that the third segment was a little longer than the forth of antennae. We find sometimes that the 2 segments are of the same length. They didn't mentioned the carinated granules on dorsum of the posterior tibiae either. The three specimens collected on October 1994 were on sea grape flowers.

Mordella summermanae Ray

Mordella summermanae Ray, Proceedings of U. S. N. M. 87(3075): 283-284, 1939.

Fore short, broad, subovate, broadest near base of pronotum. Derm black, apical segments of antennae and legs fuscous, spurs of posterior tibiae flavous, basal 4 segments of antennae less so. Upper surface covered with yellowish brown pubescence; underside hairs whitish.

Head big, about as broad as pronotum; eyes oval, reaching occiput, finely granulated with sparse short hairs.

Antennae shorter than head and pronotum combined, scarcely reaching base of pronotum; segments 3 and 4 shorter and narrower, equal; 5 triangular, 1/3 longer than 4

and 3 times as broad at apex; 6-10 strongly serrate, twice as broad as long, each 1/4 shorter than 5; 11 rounded on sides and apex, a little longer than 10.

Distal segment of maxillary palpi enlarged, isosceles triangular with outer side longer, almost equilateral in male.

Pronotum broader than long, widest subbasally, evenly rounded to apex; basal angles almost right angles, base arcuate, basal lobe short, but rounded. Scutellum small, broadly triangular, apical angle rounded. Elytra about twice as long as broad, widest subbasally, attenuate apically; apices individually rounded with fine but distinct margin.

Middle tibiae as long as their tarsi or slightly longer; next to the last segment of anterior and middle tarsi notched at apex. Posterior tibiae with a short subapical ridge, parallel to apical margin. Outer spur of posterior tibiae 1/4 of inner one.

Anal style flat, short, but 1/4 longer than hypopygium, very broad at base, but 1/3 longer than broad from a dorsal view; sides strait, apex rounded; hypopygium 1. 5 of penultimate segments.

Length: 1. 7-2. 2mm

PREVIOUS RECORDS. -South America.

MATERIAL EXAMINED. -British Virgin Islands: Guana Island; St. Thomas. Jamaica. Dominican Republic.

REMARKS. -In Ray's description (1939) the lighter color of the basal 4 segments of antennae was not mentioned, and the width of 5-10 segments were only "as broad as long. " We also observe that the front, mouth except tips of mandibles, and anterior femora sometimes flavous.

Tolidomordella discoidea

Form elongate, subparalell, broadest at middle of pronotum. Dermal color greatly variable from fulvous to black; elytra with two yellow transverse spots, one before middle, reaching neither suture nor side margin, another behind middle, not reaching suture but often touching side margin. Surface covered with pubescence partaking distinctly of ground color, which usually cinereous under certain light on darker surface.

Head regularly convex; eyes oval, reaching occiput, moderately granulated with setae-like hairs.

Antennae shorter than head and pronotum combined, not reaching base of pronotum; segments 3 distinctly small, triangular, not much longer than broad; 4-7 subserrate, increasing in width and length, 4 about 1/3 wider at apex and slightly longer than 3, 5 twice as long and broad as 3; 8-10 equal, each as long as 7 and 1/3 longer than broad; 11 suboval, 1/3 longer and slightly broader at middle than 10.

Distal segment of maxillary palpi boat-shape or hammer-shape in male, often chitinized heavily on outer half, scalene triangular in female, with outer side longer and rounded, apical side barely shorter than inner side.

Pronotum 1/4 broader than long, widest at middle, evenly rounded to apex; basal angles obtuse, base arcuate, basal lobe broadly rounded. Scutellum small, triangular, broadly rounded to apex. Elytra more than twice as long as broad, scarcely narrower at base than pronotum, subparalell on basal 2/3, then attenuate apically; apices individually rounded with fine but distinct margin. Middle tibiae as long as their tarsi; next to the last segment of anterior and middle tarsi dilated. Posterior tibiae with a subapical ridge,

halfway across outer face and parallel to apical margin; a fine carinated ridge along dorsal outer edge on posterior tibiae, interrupted halfway to genu, another on basi tarsi. Outer spur of posterior tibiae 1/5 of inner one. Anal style slender, 2. 5 of hypopygium, attenuate to apex. This is an exceedingly variable species, as regards the dermal color, and the form of yellow spots on elytra. Four marked forms occur:

a. Dermal color black with regular elytral spots; basal 10 segments of antennae, distal segment of maxillary palpi, anterior and middle legs except femora, distal segments of posterior tarsi, spurs of posterior tibiae testaceous.

b. Dermal color castaneous with regular elytral spots; antennae except a few apical segments, distal segment of maxillary palpi, legs except posterior femora, spurs of posterior tibiae testaceous.

c. Dermal color black or castaneous with anterior elytral spots broken into two small spots; head except front, sometimes semicircularly anterior part of pronotum as yellow as the elytral spots. Others variable corresponding in color to forms a and b.

d. Dermal color black or castaneous with regular elytral spots; head, sometimes semicircularly anterior part of pronotum ferruginous. Others variable corresponding in color to forms a and b. Dermal color castaneous with regular elytral spots; front of head, sides and basal part of pronotum yellow or ferruginous, color of antennae, maxillary palpi, and legs corresponding. In all cases, color of ventral segments and pygydium variable.

Length: 1. 9-2. 7mm.

PREVIOUS RECORDS. -South America.

MATERIAL EXAMINED. -British Virgin Islands: Guana Island; St. Thomas. Jamaica. Dominican Republic.

REMARKS. -In descriptions by Champion (1889) and Liljeblad

Introduction, methods and materials -- Ivie
Edit species treatments -- Ivie
Key -- Ivie, checked by Lu
Bibliography -- both

References

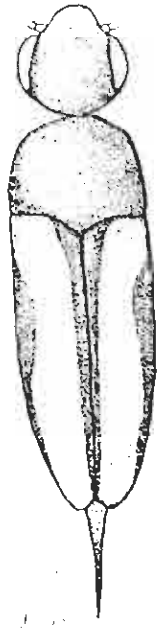
Fabricius, J. C. 1775. Systema Entomologiae, 30 + 832pp. Lipsiae.

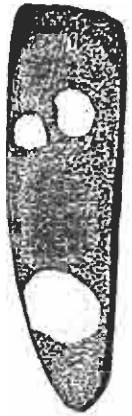
Fabricius, J. C. 1801. Systema Eleutheratorum, vol. 2, 687p. Kiliae.

Liljeblad, E. 1945. Monograph of the family Mordellidae (Coleoptera) of North America, North of Mexico. Misc. Pub. Museum of Zoology, University of Michigan 62: 1-229.

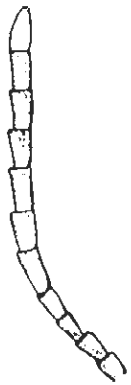
Quedenfeldt, G. 1886. Neue und seltnere Kfer von Portorico. Belriner Entomol. Zeitschr. 30: 119-128.

Ray, E. 1937. Synopsis of the Puerto Rican Beetles of the genus Mordellistena, with descriptions of new species. Proc. U. S. National Museum 84 (3020): 389-399.





Nauheimeria Lineata



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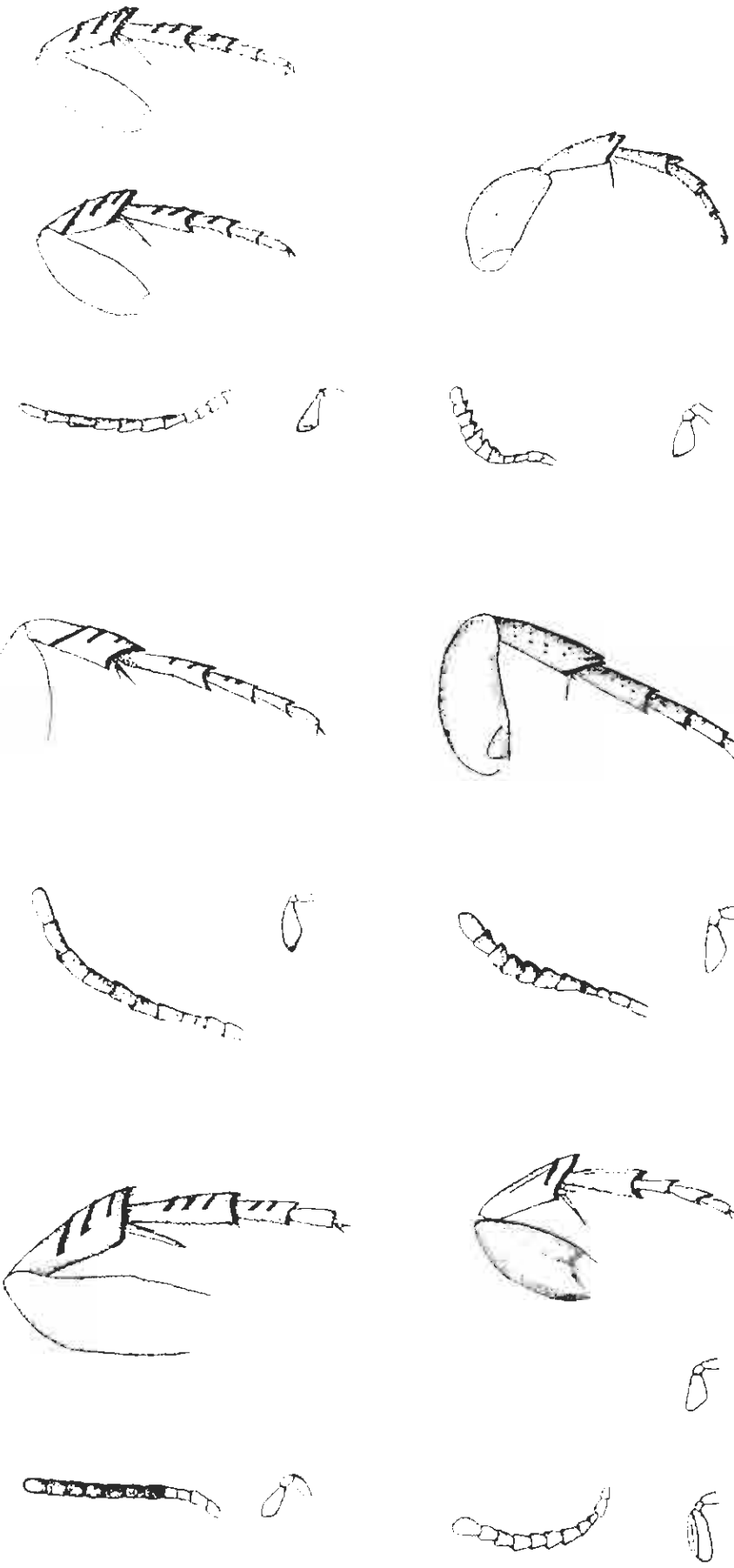

The World *Blaesoxipha* Loew, 1861 (Diptera: Sarcophagidae)

THOMAS PAPE

Pape, Th.: The World *Blaesoxipha* Loew, 1861 (Diptera: Sarcophagidae).
Ent. scand. Suppl. 45:1–247. Lund, Sweden 2 December, 1994. ISSN 0105-3574.

The flesh fly genus *Blaesoxipha* Loew, 1861 is redefined and synonymized with the clade Protodexiini + Impariini. A cladistic analysis outlines possible inter- and infrageneric phylogenetic relationships of *Blaesoxipha* and serves as a basis for a division into 10 subgenera. A catalogue of the world species is provided, giving exhaustive information on distribution, biology, and bibliographical information for 242 valid species. Within *Blaesoxipha*, a total of 15 new generic synonyms and 39 new specific synonyms are proposed. 53 new species are described: *B. aix* sp. n., *B. akrolophos* sp. n., *B. aldrichi* sp. n., *B. angul* sp. n., *B. apoxa* sp. n., *B. arizona* sp. n., *B. arktotophos* sp. n., *B. atrox* sp. n., *B. boreas* sp. n., *B. brazil* sp. n., *B. butte* sp. n., *B. cactus* sp. n., *B. calliste* sp. n., *B. casuarius* sp. n., *B. cerkyma* sp. n., *B. diloboderi* sp. n., *B. ejuncida* sp. n., *B. enotah* sp. n., *B. falx* sp. n., *B. gibberis* sp. n., *B. gongros* sp. n., *B. gracilis* sp. n., *B. ibe* sp. n., *B. inagua* sp. n., *B. karnataka* sp. n., *B. kivu* sp. n., *B. kyrton* sp. n., *B. kyrtonidion* sp. n., *B. laguna* sp. n., *B. lapidosa* sp. n., *B. likros* sp. n., *B. lillooet* sp. n., *B. lingua* sp. n., *B. melanderi* sp. n., *B. mona* sp. n., *B. mystica* sp. n., *B. occidens* sp. n., *B. oriens* sp. n., *B. ragg* sp. n., *B. saccata* sp. n., *B. sagittarius* sp. n., *B. santafe* sp. n., *B. spiniger* sp. n., *B. steyskali* sp. n., *B. taiwanensis* sp. n., *B. tingomaria* sp. n., *B. torreya* sp. n., *B. tricuspis* sp. n., *B. tunisia* sp. n., *B. uncatoides* sp. n., *B. utah* sp. n., *B. vesper* sp. n., *B. virgo* sp. n. 4 new names are proposed to replace secondary junior homonyms: *B. kazak* n. nov. for *Agriella grunini* Verves, 1985 (preocc. *B. grunini* Rohdendorf & Verves, 1977); *B. mex* n. nov. for *Kurtomyia mexicana* Lopes, 1976 (preocc. *Acanthodotheca mexicana* Lopes & Downs, 1951); *B. mongol* n. nov. for *Agriella mongolica* Verves, 1985 (preocc. *B. mongolica* Rohdendorf & Verves, 1978); and *B. spina* n. nov. for *B. spinosa* Lopes, 1990 (preocc. *Acridiophaga spinosa* Lopes, 1978). Twenty lectotypes are designated. Extensive annotations deal with nomenclatural issues, revised identities and new or dubious host records. The monotypic genus-group taxa *Conomya* Robineau-Desvoidy, 1830 and *Myorhina* Robineau-Desvoidy, 1830 are revised and shown not to be members of the genus *Blaesoxipha*.

Thomas Pape, Zoological Museum, Universitetsparken 15, DK- 2100 Copenhagen, DENMARK

Introduction

The focus of the present catalogue is a group of flesh flies (Diptera: Sarcophagidae), here considered under the generic name *Blaesoxipha* Loew. The scope is to redefine the genus, analyse infra- and intergeneric phylogenetic relationships, and present a catalogue of the species of the world, correcting and adjusting the nomenclature where necessary, and include data on taxonomy, biology and distribution in an easily extractable form.

Blaesoxipha was erected by Loew (1861) as a monotypic genus, based on a female specimen caught during a sunny spell on an otherwise rainy day in the Austrian Alps. Impressed by the protruding, swordlike larvipositor, unique within the Sarcophagidae, Loew aptly named the genus by combining the Greek words *blaisos* [= bandy-legged, bent] and *xiphos* [= sword, saber].

Blaesoxipha is interesting for biological reasons as the genus in the present definition contains the large majority of obligate insect parasites within the Sarcophagidae. Hosts are mainly acridid grasshoppers and darkling beetles, although many other insect host taxa are involved. Many species are parasites of locusts, and species of *Blaesoxipha* have received some attention from applied entomologists although the few attempts of biological control apparently have been unsuccessful (e.g., Clausen 1978).

Blaesoxipha is generally considered as one of the more prolific taxa within the Sarcophagidae in terms of numbers of species and assumed speciation rate.

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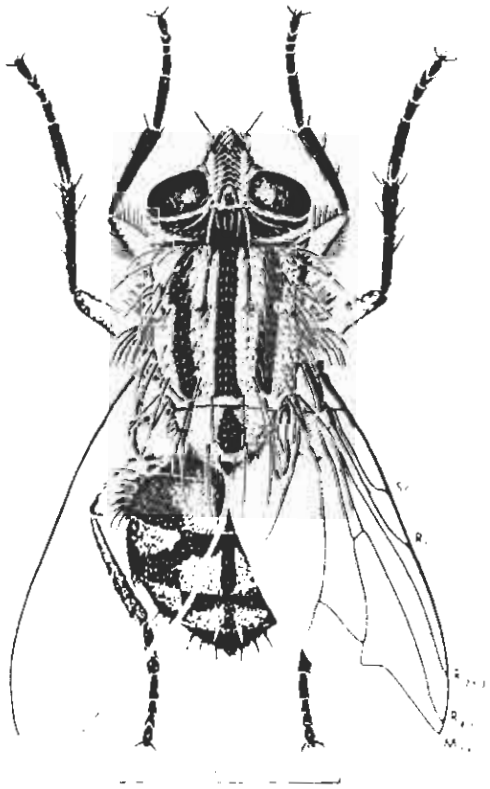
43. *Blaesoxipha (Gigantotheca) virgo* sp. n.
Figs. 395–398.

Type material. Holotype ♂, BRITISH VIRGIN ISLANDS: Necker Island, 21.vii.1987, S.E. Miller (BPBM). — *Paratypes.* 1♂, data as holotype (ZMUC); British Virgin Islands, Guana Island, 1♂, 12.viii.1988, S.E. Miller & C. O'Connell (BPBM). *Etymology.* A noun in apposition. From the Latin, *virgo* = virgin; the name refers to the type locality.



Description

Male

Head. Narrowest part of frons 0.21x head width. Outer vertical bristle not differentiated. Posterior 0.3 of gena with white setae, other genal setae black. Postgenal and occipital setae white except for black postocular setae. Row of parafacial setae close to eye and consisting of short, hairlike setae. Palpus black.

Thorax. Proanepisternum bare; acr = 0 + 1, dc = 0–1 + 2, ia = 2–3 + 1, sa = 1–2 + 2, pa = 2. Scutellum with marginals: 2, discals: none, and apicals: 1.

Legs. Hind trochanter with 1–3 posteromedian spines, which are much shorter but of only slightly greater diameter than adjacent setae. Hind tibia with numerous elongated pv and v setae. Ventral surface of proximal 0.3 of fore femur as well as entire ventral surface of mid and hind femur with elongated setae with wavy tip.

Wing. Costal spine very short.

Abdomen. T1+2–T3 without median marginal bristles, T4 without or with a pair of weak marginals, T5 with a row of fully developed marginals. Lateral (= ventral) margins of tergites with some elongated setae with wavy tip. Lateral margins of T5 meeting ventrally, completely covering ST5 and forming moderately spinose, elongate pads slightly extending posteriorly beyond ST5. ST5 with a pair of slender, posteriorly directed lobes curving ventrally at an almost right angle and with a slightly swollen, setose tip.

Terminalia. Colour red. Cercal prong largely straight. Surstylus large and with a narrow 'handle' at base. Gonostyle with a long subapical bristle, gonocoxital lobe with a basal hump. Phallus with a large, bilobed and swollen juxta. Median stylus with a large opening and margins thickened and densely covered with denticles.

Length. 11.0–11.5 mm.

Female. Unknown.

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May 17, 1995

Drs. James Lazell & Wenhua Lu
The Conservation Agency
1140 Monroe Street
Jackson, Mississippi 39202

Dear Skip & Wenhua;

I hope all is well with you both and Mississippi meets your every expectation. I greatly appreciate you sending me specimens from your travels in the Caribbean. Much of the Jamaican material is new to me. I hope that you will collect some in Mississippi and have some material to pass along eventually [most fulgoroids are not out until the fall].

This morning Jason passed his thesis seminar and defense. He officially has a masters degree now, although there are still some details to attend to. There always are.

I would like to go to Guana again this year if possible. I suspect that this year may be my last opportunity for a few years. I understand that Mike Ivie has been sending BVI fulgoroids to Lois O'Brien over the years. He sent some to me that were collected last year and much to my annoyance there was something I hadn't seen before from Guana. In any case, I anticipate that Lois O'Brien's material, plus the material that I have collected and have on loan from the Bishop Museum should be sufficient for me to work with for a monograph on the Lesser Antilles fulgoroids.

My goals this year are:

1). Collect fulgoroids on as many different islands as possible, collecting host plant data where possible.

2). Collect any Membracids that I can find into 95% ETOH for molecular systematics. Both Jason and T.K. Wood (U. of Delaware) need material for their respective projects. Last year I collected *Deiroderes inermis* on Virgin Gorda and *Monobelus* sp. on Tortola. I still have not found nymphs of *Deiroderes*. Jason tells me that the holotype of *D. inermis* was collected from *Capparis nitida*, so at least I can concentrate my efforts on *Capparis* sp. for this species. *Monobelus* was collected near the highest point marker on Sage Mountain. *Monobelus* is interesting in terms of biogeography because it is a member of the subfamily Centrotinae, which includes all of the old world treehoppers.

Regarding specimens that have already been collected, mounted and processed (about 2,000 specimens donated to NCSU museum) I have a number of irons in the fire, but no new species lists yet. Bob Blinn has been keeping a list of Hemiptera, however, and I will include a working list with this letter as it currently stands. He hasn't worked with the new material yet.

I had set out last year to find kinnarid nymphs (which have not been described), a fulgoroid that had been reported to feed on roots. Last year kinnarids were abundant and I believe I have some, but I need to submit them to Lois O'Brien for her opinion to be sure.

The most convenient dates for me to go to Guana would be Oct. 11-22. Thank you for your consideration and look forward to hearing from you again.

Sincerely,

Charles R. Bartlett

Hemiptera from the BVI

Lygaeidae

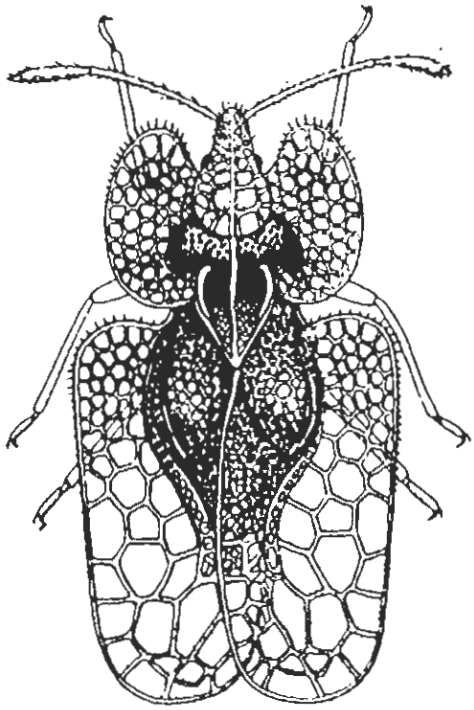
Ozophora divaricata Barber
Ozophora quinquemaculata Barber
Pseudopachybrachis vinctus (Say)

Nabidae

Arachnocoris berytoides (Uhler)

Tingidae

Corythaica carinata Uhler



A lace bug, family Tingidae

Date: Tue, 18 Apr 1995 16:19:58 +22305714 (HST)
From: Scott Miller <scottm@bishop.bishop.Hawaii.Org>
To: "Daniel E. Perez" <PEREZ@FCRFV2.NCIFCRF.GOV>
Cc: Scott Miller <scottm@bishop.bishop.Hawaii.Org>,
Keith Arakaki <karakaki@bishop.bishop.Hawaii.Org>,
Gordon Nishida <gordo@bishop.bishop.Hawaii.Org>
Subject: Caribbean Grasshoppers

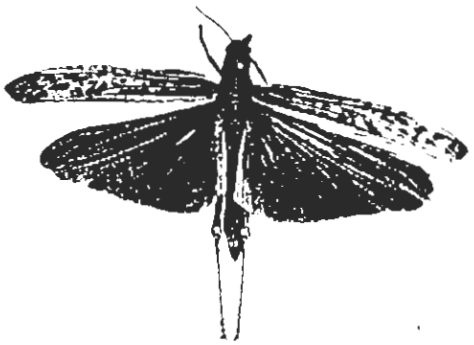
I have made a quick check of the collection, but did not find much from the Caribbean: 14 of my specimens from the British Virgin Islands and 1 from the Dominican Republic. These specimens are being sent on loan. It looks like the material from one of my BVI trips did not make it into the Orthoptera collection, so it must be off in the unsorted somewhere.

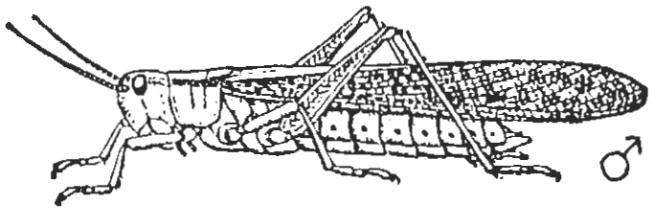
We do have a few drawers of unsorted grasshoppers from Central America (Mexico, Guatemala, etc.), and another few from South America (esp. Brazil), in case anyone is interested.

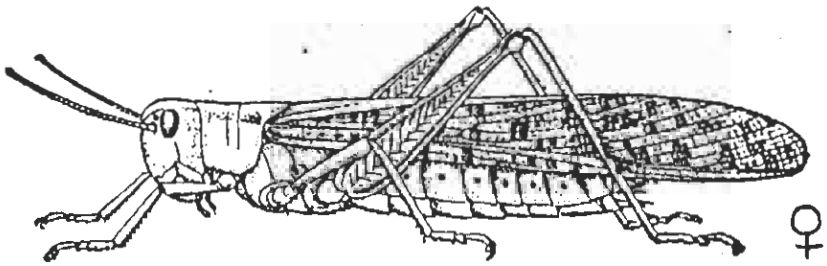
Over the next couple of years, we will be sorting and curating the grasshoppers as part of an NSF curatorial project. I'm alerting Gordon Nishida of your interest in any further Caribbean grasshoppers that may turn up.

I hope that the BVI material is of some interest.

Scott Miller
Bishop Museum







Schistocerca

Orthoptera: Acrididae (grasshoppers) from British Virgin Islands in Bishop Museum
Identified by Daniel E. Perez, July 1995

Rhammatocerus cyanipes Fabricius
Guana Island, 11-vii-1988, S.E. Miller & C.E. O'Connell (1)
Virgin Gorda, Biras Hill, 22-vii-1988, Miller & O'Connell (1)

Schistocerca serialis Thunberg
Great Camanoe, 15-vii-1988, S.E. Miller & C.E. O'Connell (2)
Guana Island, 4-14-vii-1988, Miller & O'Connell (2)
Guana Island, 0-80 m, 9-23-vii-1987, S.E. Miller & V.O. Becker (3)
Marina Cay, 5-vii-1988, Miller & O'Connell (3)

Schistocerca pallens (?)
Great Camanoe, 15-vii-1988, Miller & O'Connell (1)

Also 1 small unidentifiable nymph, Guana Island, 14-vii-1988

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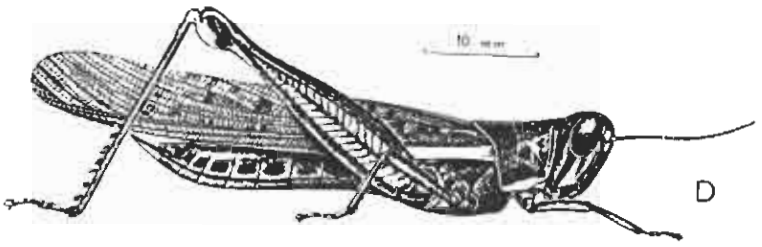

Schistocerca, called "bird grasshoppers" because of their strong flight, are the plague locusts of the Old World.

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DISPERSAL OF PLANT PESTS INTO THE VIRGIN ISLANDS

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On 26 October 1990, Greg Mayer, Tina Kuklenski, and Scott Miller sampled invertebrates from a large shipment (an entire barge) of potted plants being unloaded at Guana Island, British Virgin Islands (BVI). Becker & Miller (1992) provide background on Guana Island. The plants, including many specimens of several species of palms, were being imported from nurseries in southern Florida for landscaping. The importers had apparently met all BVI regulations and had checked in with government authorities in Tortola before the barge proceeded to Guana Island. The shipment was infested with large numbers of insects and snails, most of which have been identified as follows. A millipede, an isopod, and several beetle larvae were not identified.

Cockroach (Blattodea: Blaberidae)
Pycnoscelus surinamensis (Linnaeus), Surinam cockroach
Mealybug (Homoptera: Pseudococcidae)
Dysmicoccus brevipes (Cockerell), pineapple mealybug
Ants (Hymenoptera: Formicidae)
Brachymyrmex obscurior Forel
Hypoponera opaciceps (Mayr)
Odontomachus ruginodis Wheeler
Paratrechina longicornis (Latreille), crazy ant
Paratrechina pubens (Forel)
Pheidole morerens Wheeler
Snails (Mollusca)
Lamellaxis gracilis (Hutton)
Polygyra cf. *P. cereolus* (Muhlfeld)
Praticolella griseola (Pfeiffer)
Succinea cf. *S. luteola floridana* Pilsbry

Although some of these species are native to the Puerto Rican Bank, most are immigrant species that are now widespread in the Caribbean region, including southern Florida (Godan 1983, Roth 1994). Most are known from the Puerto Rican Bank (Wolcott 1950-1951). Several major agricultural pests are included, such as those with common names listed. The presence of this many invertebrates on this shipment indicates the ease of dispersal of agricultural pests.

Non-indigenous pests are a major problem for North American agriculture (Dowell & Krass 1992, Sailer 1978, 1983, U.S Congress 1993). In addition to being agricultural pests, non-indigenous insects and snails appear to be the primary cause of extinction for native invertebrates on islands (e.g., Howarth 1990, Howarth & Ramsay 1991). Vectors of human disease, such as *Aedes albopictus* (Skuse) (Asian tiger mosquito), can also be spread by commerce (e.g., Francy et al. 1990, Mitchell et al. 1992). The recent spread of two giant African snails, *Achatina fulica* Bowditch and *Limicolaria aurora* (Jay), to Martinique is a stark example of the problem of continued pest dispersal (Mead & Palcy 1992).

Given the threat that non-indigenous insects and snails present to agriculture, human health, and conservation management, and potential economic consequences of such introductions, island governments should create and implement policies for the

inspection of agricultural materials, including provisions for fumigation and quarantine as necessary.

Identifications were made by K. Emberton (Academy of Natural Sciences of Philadelphia, snails), D.R. Miller (Systematic Entomology Laboratory, U.S. Dept. of Agriculture, mealybug), R.R. Snelling (Natural History Museum of Los Angeles County, ants), and J. Strazanac (Bishop Museum, cockroach). Voucher specimens were retained by specialists, except snails.

SUMMARY

A large shipment of potted plants from Florida to the British Virgin Islands included live cockroaches (1 species), mealybugs (1 species), ants (6 species), and snails (4 species) on arrival at the destination, Guana Island. Several major agricultural pests were included, emphasizing the need for more effective measures to prevent continued spread of non-indigenous invertebrates.

REFERENCES CITED

BECKER, V.O., AND S.E. MILLER. 1992. The butterflies of Guana Island, British Virgin Islands. Bull. Allyn Mus. 136: 1-9.

DOWELL, R.V., AND C.J. KRASS. 1992. Exotic pests pose growing problem for California. California Agr. 46(1): 6-8, 10-12.

FRANCY, D.B., N. KARABATSOS, D.M. WESSON, C.G. MOORE, JR., J.S. LAZUICK, M.L. NIEBYLSKI, T.F. TSAI, AND G.B. CRAIG, JR. 1990. A new arbovirus from *Aedes albopictus*, an Asian mosquito established in the United States. Science 250: 1738-1740.

GODAN, D. 1983. Pest slugs and snails: biology and control. Springer-Verlag, Berlin. x + 445 pp.

HOWARTH, F.G. 1990. Hawaiian terrestrial arthropods: An overview. Bishop Museum Occ. Pap. 30: 4-26.

HOWARTH, F.G., AND G.W. RAMSAY. 1991. The conservation of island insects and their habitats, pp. 71-107 *in* N.M. Collins and J.A. Thomas [eds.], The conservation of insects and their habitats. Academic Press, London.

MEAD, A.R., AND L. PALCY. 1992. Two giant African land snail species spread to Martinique, French West Indies. Veliger 35: 74-77.

MITCHELL, C.J., M.L. NIEBYLSKI, G.C. SMITH, N. KARABATSOS, D. MARTIN, J.-P. MUTEBI, G.B. CRAIG, JR., AND M.J. MAHLER. 1992. Isolation of Eastern Equine Encaphalitis Virus from *Aedes albopictus* in Florida. Science 257: 526-527.

ROTH, L.M. 1994. Cockroaches from Guana Island, British West Indies (Blattaria: Blattellidae: Blaberidae). Psyche 101: 45-52.

SAILER, R.I. 1978. Our immigrant insect fauna. Bull. Entomol. Soc. America 24: 3-11.

SAILER, R.I. 1983. History of insect introductions, pp. 15-38 *in* C.L. Wilson and C.L. Graham [eds.], Exotic plant pests and North American agriculture. Academic Press, New York.

UNITED STATES CONGRESS, OFFICE OF TECHNOLOGY ASSESSMENT. 1993. Harmful non-indigenous species in the United States. U.S. Government Printing Office, Washington, D.C. (OTA-F-565). viii + 391 pp.

WOLCOTT, G.N. 1950-1951. The insects of Puerto Rico. J. Agr. Univ. Puerto Rico 32: 1-975.

UNIVERSITY OF MARYLAND AT COLLEGE PARK

COLLEGE OF LIFE SCIENCES • DEPARTMENT OF ENTOMOLOGY

12 October 1995

Dr. James D. Lazell
The Conservation Agency
6 Swinburne Street
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Dear Skip,

I still have deep regrets that the termite team could not travel to Guana Island this Fall. Apologies to you and all impacted by our sudden, last minute withdrawl. Had the cancellation come just a week earlier I could have regrouped and bought a ticket for a student to go in place of Mike and we could have re-directed our research efforts, but as it happened the timing was just too tight. I hope that we can realign and participate next year.

In discussing this upheaval with one of the faculty in my department, we came up with an idea that I would like to present to you for comment and consideration. What would you think about the possibility of having 3-5 graduate students from Maryland plus 2 faculty (myself and ecologist Bob Denno) come to Guana Island for 7 days to do a short but intensive field course for the Maryland students plus 6-10 students from the Community College on Tortola? The graduate students from Maryland would be relatively clueless about the tropical biota, but they would know general organismal biology, ecology, evolution, behavior, sampling methodology, etc. The undergraduates from the Community College would be more comfortable with the habitat and the local flora and fauna. Both groups would hopefully benefit from a close peer relationship. We as faculty would prepare specific field problems and exercises having to do with insects, plants, and maybe even reptiles, each designed to address different types of questions and to use different field techniques and analytical methods.

I realize that the bed night quota is limited and may be an issue. For full participation and integration into the group it would be best to have the Tortola students also living on the Island during the course. The Maryland students could be shoehorned into 1-2 rooms, but I know that they would each still take up bed nights.

Well, it's an idea that I thought I would pitch to you for consideration, and there is certainly no rush in rendering any decision. If you think that the general concept has merit I am flexible about the details. I remain idealistic enough to think that educating students about tropical biology and field methods is a very high priority. I also feel that there is nothing like the synergism of a field station atmosphere, and it is a real treat for students to get to absorb a few days of that kind of energy.

Enjoy your month on Guana,

Barbara

Barbara L. Thorne

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SUBMITTED, BIOTROPICA 11/5/95

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Associations Between Termites and Bromeliads in Two Dry Tropical Habitats

Key words: Isoptera; Nasutitermes; *Bromeliaceae,* Tillandsia; *Guana Island; British Virgin Islands; symbiosis, Minas Gerais, Brazil; fire protection*

The ecologically and numerically prominent termite *Nasutitermes acajutlae* (Holmgren) occurs through the Caribbean from Puerto Rico south to Trinidad, possibly extending into South America (Thorne *et al.* 1994). This species builds arboreal nests that are among the largest known for any termite, measuring up to 2 m in height and 1 m in diameter (Thorne *et al.* 1994, 1995). Like other *Nasutitermes*, these termites build extensive networks of covered tunnels connecting the nest to distant foraging sites in the tree crown and ground below. Workers and soldiers, numbering well over a million individuals in mature colonies, travel within these "carton" tunnels which consist of partially digested wood, fecal material, soil, and water (Light 1933). We discovered an association between *N. acajutlae* termites and the bromeliad *Tillandsia utriculata* on Guana Island, British Virgin Islands (B.V.I.), during October, 1994. *T. utriculata* is the largest of the local tank-forming or phytotelm bromeliads, that by definition impound water and litter among inflated, tightly overlapping leaf bases.

Guana Island, a wildlife sanctuary which lies directly north of the eastern end of the island of Tortola, B.V.I., covers about 340 hectares and rises to about 246 m at maximum elevation. Guana Island is volcanic and supports a rich diversity of flora and fauna due to habitat variation and a history of minimal disturbance (Lazell 1989). Dry lowland scrub forest predominates, while abundant cacti characterize scattered, drier sites. Wet areas are confined to the few ghuts on the island. *T. utriculata* occurs abundantly in some of the drier woodlands, but they were not surveyed comprehensively.

The association between the termites and bromeliads on Guana Island was particularly easy to document because *N. acajutlae* build distinctive and conspicuous trails, and *T. utriculata* often grows in relatively low canopies. We inspected every tree and large cactus that we could readily see along four transects in four locations on the island. Only trees and cacti that had both active termite foraging tunnels and at least one *T. utriculata* plant were examined.

Termite tunnels intersected a bromeliad in 97.4% of the 115 possibilities (Table 1; Figure 1). Usually, *N. acajutlae* tunnels went to the root system or above to the water-filled leaf axils. Often tunnels continued into the shoots to cover impounded water. Some hung suspended for short distances (4-12 cm) between adjacent bark and the plant. A few tunnels led only to the moist area where the bromeliad rooted, but usually at least one leaf axil was accessed.

Each tree was counted only once in a transect, but many trees hosted more than one *T. utriculata* plant, and termite trails intersected up to eight bromeliads on a single tree. We were unable to determine the extent of a complete network, i.e. how many bromeliads were tapped by a given *N. acajutlae* colony, in part because *N. acajutlae* foragers also travel within decayed wood. Quite likely, termites inconspicuously tap bromeliads from inside supporting trunks and branches. *N. acajutlae* may also tap *T. utriculata* rooted on the ground. Hence, our data probably presents a conservative measure of the termite / bromeliad association.

Although diverse invertebrates occupy bromeliad tanks (e.g.. Picado 1911, Pittendrigh 1948, Laessle 1961, Fish 1983, Benzing 1990, Nadkarni & Longino 1990), this is the first report

of an association with termites. Most likely the termites are visiting *T. utriculata* to obtain water, a scarce commodity given the xerophytic vegetation and porous soils of Guana Island. No formal weather records exist, but longtime residents and scientific researchers agree that the two years prior to our study were uncharacteristically dry in the Virgin Islands. Drought was particularly acute where aridity generally prevails as on Guana Island. Our related studies of termites on Guana Island (1989-1994), suggest diminished populations of *Nasutitermes* and other termites caused by abnormally low rainfall in 1993 and 1994, but more extensive records are needed to assess the magnitude and rarity of this presumed stress.

Organic matter suspended in the water impounded by *Tillandsia* shoots is a potential source of termite nutrients (Huxley 1980, Benzing 1981, 1990). However, preliminary bioassays using disks of saturated Whatman #1 filter paper and several hundred termite foragers indicated no preferences between bromeliad extracts and tap water. We do not know if termites feed on tank debris as the water level recedes.

The symbiosis between *N. acajutlae* and *T. utriculata* is exploitative. The termites visit primarily to collect moisture otherwise available to the bromeliad. The bromeliad receives no benefit, and may lose needed moisture during dry weather. Plants are denied additional water by the wicking action of the termite trails that contact the reservoirs. Up to 35 cm of carton tunnel was saturated with moisture siphoned from leaf axils or the areas of seepage around the bromeliad roots. Although termites deny the bromeliad some impounded water through the wicking action of tunnels and by drinking, carton built over shoot reservoirs may offer limited desiccation protection to the plants. Thus the relationship may shift according to local circumstances from weakly mutualistic through commensalistic to parasitic if the water lost to termites and their tunnels causes plant stress.

Tillandsia utriculata possess considerable desiccation-tolerance, enough to survive weeks or perhaps months with little or no impounded water (Benzing 1990). Erratic rains and prolonged dry seasons force plants to accomodate extended drought (Madison 1977, Benzing 1981, 1990,

Nadkarni 1984). Gas exchange or acid rhythms associated with CAM (Crassulacean Acid Metabolism) must be monitored to determine whether bromeliads supporting termites experience greater drought stress than those without termites.

Termites are ill-suited to match certain ants as plant mutualists. Termites typically remain confined to tunnels unavailable, even if disposed, to deter plant predators. Some ants deposit nutritive materials in bromeliad shoots, thus contributing to plant welfare (reviewed in Huxley 1980, Benzing 1990). An occasional termite may die or drown in a leaf axil, but probably not often enough to significantly promote plant nutrition. Termite tunnel carton that ends up in the tanks is also unlikely to constitute much of a nutritional supplement for the bromeliad.

The termite diet precludes bromeliad seed dispersal, a phenomenon known from several ant / epiphyte relationships (reviewed in Huxley 1980, Benzing 1990; Yu 1994). Only once did we observe a juvenile *T. utriculata* rooted in a termite tunnel or a bromeliad growing adjacent to a termite nest. Furthermore, a number of the termite trails turned toward a bromeliad, suggesting that the plant had arrived first and had been subsequently located by exploring termites.

A heavy rain in October 1994, the first following a prolonged drought, provided an opportunity to observe termite trail construction. As is typical for arid-land *Nasutitermes*, trail building escalated because workers need moisture to masticate and manipulate materials used for tunnel construction. Trails were rapidly laid down on four trees which supported bromeliads that *N. acajutlae* had only recently discovered. In each case, the termites first lay a trail of fecal deposits and secretions on the tree bark, typical of their normal building behavior (Jones 1980). Tunnel construction then began at the junction with the bromeliad, proceeding down the tree. By working from the bromeliad down instead of from the base of the tree up, the termites had ample moisture for their work.

Do termites use trees with bromeliads for *both* food and water, or are they exploring some supports only to obtain moisture from the attached epiphytes? Host trees we examined were generally mature with apparent or probable zones of dead wood. In addition to the tunnels

leading to the bromeliad, usually one or more of the trails led to a feeding site through a knothole or dead branch. However, young trees with no dead wood would, because of their age, also be the trees least likely to support epiphytes. If one found a case in which the termites appeared to be occupying the tree only for access to the bromeliad, the carton tunnels should be scraped away to confirm presence or absence of any covered access holes into the tree wood.

Although *N. acajutlae* appears to be remarkably drought tolerant, probably more so than other *Nasutitermes* species in the Caribbean, bromeliads may at least occasionally provide essential moisture. *N. acajutlae* workers possess comparatively large water sacks, sufficient to store enough water for prolonged dry weather (M.S. Collins, pers. comm.). *N. acajutlae* is clearly not a specialist on trees with bromeliads, but linking to one or more tank reservoirs may enable these termites to thrive or survive in an otherwise inhospitable season or habitat. To further understand the ecological dynamics of this association, we plan to seek comparative data on intersections between *N. acajutlae* foraging trails and *T. utriculata* plants on wetter islands in the Virgin Islands cluster, and on Guana Island in times of heavier rainfall.

Alerted by the Caribbean findings, the third author subsequently discovered evidence of associations between an unidentified, locally abundant termite and diverse bromeliads in the rocky, semiarid "campos rupestres" of Minas Gerais state in southeastern Brazil near the city of Diamantina. Covered trails in some instances traversed large rocks to reach reservoirs provided by usually lithophytic *Aechmea phanerophelbia*, a large phytotelm bromeliad that sometimes also harbors ant nests among the older foliage (Fig. 2A). Much more common, however, were mounds of termite carton built around terrestrial bromeliads of the related, non-water impounding genera *Dyckia* and *Encholiirioum* (Fig. 2B). Virtually every large plant exhibited some sign of adjacent termite construction. Companion flora of similar low stature (e.g., Cyperaceae, Vellosiaceae, and a variety of shrubs) were also providing superstructures for termite nests. Inspection of the plants indicated no damage from the insects. Root systems tended to be below

rather than within surrounding carton material. This is to be expected if termites build around established plants rather than synthesizing the association by providing seed beds.

Drought may occasionally render bromeliad phytotelmata an important termite resource in the high rocky grasslands of southeastern Brazil as on Guana Island, but another phenomenon at the first location more likely benefits flora. Abundant, charred vegetation and the well-insulated herbaceous stems and thick bark of the endemic flora testify to frequent natural fire through the campos rupestres. Some of the more exposed bromeliads had been seriously burned in recent months, but others, within larger termite nests, had survived unscathed. Termite nest material may provide insulation and thus promote heat-tolerance for flora in this fire-prone region (Morison *et al.* 1948, Harris 1961). Absorptive termite carton may also enhance plant water balance. The survivorship and fecundity of bromeliads among other low-growing vegetation would also be improved if these insects increase plant access to nutrients or deter herbivores. Conversely, spiny-leafed *Dyckia* and *Encholiirium* may discourage large, local ant-eaters seeking termites as food.

Termites consititute prominent components in diverse ecosystems, particularly in the tropics, where they substantially enhance nutrient cycles. Observations reported here indicate that termite colonies in some habitats may establish long-term relationships with bromeliads for access to their water reserves. These interactions may have varying consequences for the plants. Some of these relationships seem pervasive enough to warrant further inquiry.

Sincere thanks to Henry and Gloria Jarecki and the staff of The Guana Island Club for their support and hospitality during the course of this project. We gratefully acknowledge constructive input and productive discussions with Drs. Margaret S. Collins, James D. Lazell, and Nalini M. Nadkarni. This research was funded by a grant from The Conservation Agency, through a grant

from the Falconwood Foundation, and by a cooperative agreement between the University of Maryland and the Pacific Southwest Research Station, U.S. Department of Agriculture.

BENZING, D.H. 1981. Mineral nutrition of epiphytes: an appraisal of adaptive features. Selbyana 5: 219-223.

BENZING, D.H. 1990. Vascular epiphytes. Cambridge University Press, Cambridge, England.

FISH, D. 1983. Phytotelmata: flora and fauna. *In* J.H. Frank and L.P. Lounibos (Eds.) Phytotelmata: terrestrial plants as hosts for aquatic insect communities, pp. 1-27. Plexus, Medford, New Jersey.

HARRIS, W.V. 1961. Termites: Their Control and Recognition. Longmans Green & Co., London.

HUXLEY, C. 1980. Symbiosis between ants and epiphytes. Biol. Rev. 55: 321-340.

JONES, R. 1980. Gallery construction by *Nasutitermes costalis*. Insectes Sociaux 27: 5-28.

LAESSLE, A. 1961. A microlimnological study of Jamaican bromeliads. Ecology 42: 499-517.

LAZELL, J. 1989. Guana: A Natural History Guide. The Conservation Agency, Jamestown, R.I.

LIGHT, S.F. 1933. Termites of Western Mexico. Univ. Calif. Pub. Entomol. 6: 79-164.

MADISON, M. 1977. Vascular epiphytes: their systematic occurrence and salient features. Selbyana 2: 1-13.

MORISON, C.G.T., A.C. HOYLE, AND J.F. HOPE-SIMPSON. 1948. Tropical soil-vegetation catenas and mosaics. A study in the south-western part of the Anglo-Egyptian Sudan. J. Ecol. 36: 1-84.

NADKARNI, N.M. 1984. Epiphyte biomass and nutrient capital of a neotropical elfin forest. Biotropica 16: 249-256.

NADKARNI, N.M. AND J.T. LONGINO. 1990. Macroinvertebrate communities in canopy and forest floor organic matter in a montane cloud forest, Costa Rica. Biotropica 22: 286-289.

PICADO, C. 1911. Les Bromeliacees epiphytes comme milieu biologique. Bull. Sci. France Belg. 45: 215-360.

PITTENDRIGH, C.S. 1948. The bromeliad - *Anopheles* - malaria complex in Trinidad. I. The bromeliad flora. Evolution 2: 58-89.

THORNE, B.L., M.S. COLLINS, AND K. BJORNDAL. (1995) Architecture and nutritional analysis of arboreal carton nests of two Neotropical *Nasutitermes* species (Isoptera; Termitidae), with notes on embedded nodules. Submitted, The Florida Entomologist.

THORNE, B.L., M.I. HAVERTY, AND M.S. COLLINS. 1994. Taxonomy and biogeography of *Nasutitermes acajutlae* and *N. nigriceps* (Isoptera; Termitidae) in the Caribbean and Central America. Ann. Ent. Soc. Am. 87: 762-770.

YU, D.W. 1994. The structural role of epiphytes in ant gardens. Biotropica 26: 222-226.

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TABLE 1. Transect survey of the association between active trails of the termite *Nasutitermes acajutlae* and the bromeliad *Tillandsia utriculata* in four locations on Guana Island, British Virgin Islands. Only trees (including cacti) that contained both termite trails and at least one bromeliad were included in the study.

LOCATION TRANSECT ON GUANA ISLAND	NUMBER OF TREES WITH TERMITE TRAILS INTERSECTING THE BROMELIAD	NUMBER OF TREES WITH TERMITE TRAILS NOT INTERSECTING THE BROMELIAD
"Garden of Eden" nr. Guana Island Club	11	1
Trail to Longman's Point	75	2
White Bay Beach	17	0
Wei Ping Liao Trail	12	0
Total	**115 (97.4%)**	**3 (2.6%)**

112

[FIGURE CAPTION]

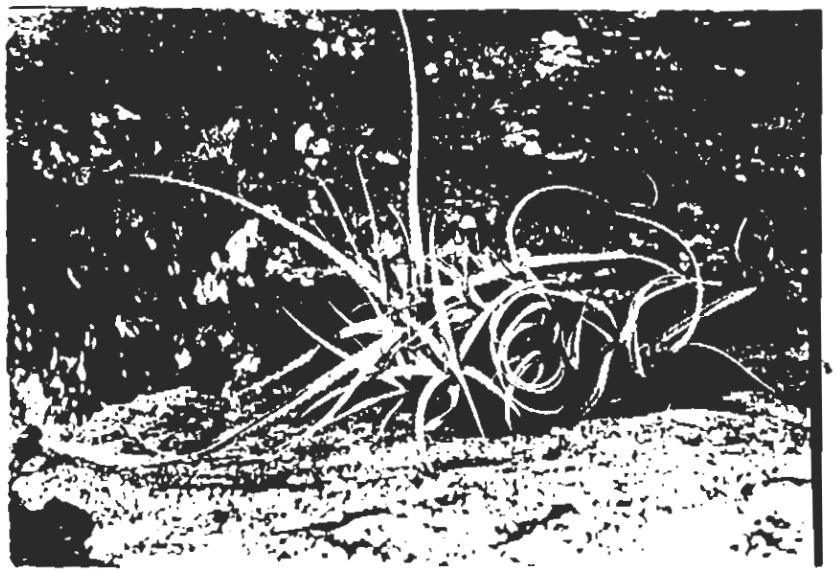
FIGURE 1. Photographs of tunnels built by the termite *Nasutitermes acajutlae* intersecting leaf base chambers of the bromeliad *Tillandsia utriculata* on Guana Island, British Virgin Islands. **A**. *N. acajutlae* trail built up to the the moist root cluster and leaf base reservoirs of *T. utriculata*. **B**. *N. acajutlae* trail built over leaf bases of a *T. utriculata* plant.

FIGURE 2. Photographs of termite tunnels and nest material associated with bromeliads in the Minas Gerais state of southeastern Brazil. **A**. Termite trail leading to an *Aechmea* plant growing on a rock. **B**. Group of *Encholiirium sp.*, also growing on a rock, surrounded by termite nest carton.

FIGURE 1.

FIGURE 2.

A



B

United States Department of Agriculture | Forest Service | Pacific Southwest Forest and Range Experiment Station | P.O. Box 245 Berkeley, CA 94701 U.S.A.

Reply to: 4500

Date: September 26, 1995

Dr. James D. Lazell, President
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6 Swinburne Street
Conanicut Island, RI 02835

Dear Skip:

I can't really express the emotions I that have been feeling over the cancellation of my trip to Guana Island. There are many factors involved; some are determined by the general political and budgetary climate in the Forest Service and the country. Apparently of immediate concern to our Station Director was the appearance of spending government dollars to go to a "resort area" when Forest Service Research is closing locations, extinguishing Research Work Units, discontinuing lines of research, and telling people that they no longer have a job. I think that he simply did not want the unfunded people to have a reason like this to complain about as they were leaving. I think we can all appreciate his concern.

I had contemplated simply taking annual leave and going on my own money. This would not have really been a financial hardship on me, but it seemed like a futile effort given some of the other information that I was given while discussing this trip with my Station Director and Assistant Station Director. I got a pretty clear message that research on termites is not a high priority for the upper level managers in the Forest Service. In fact, I was told that this area of research has one of the lowest priorities as viewed by these same top managers. This is why I finally decided it might be wisest to not gather any additional samples/data and focus on finishing the work that I have started under the sponsorship of the Conservation Agency.

Barbara, Lori and I will move forward on the paper that I recently sent to you. Any comments you have would be appreciated. I guess you'll have to send them by mail or by phone (best to fax rather than try to catch me in my office). I think that this paper should serve as the baseline for additional papers on using cuticular hydrocarbons for taxonomy of the termites of the Caribbean Basin. We have a reasonable "library" of characterizations of hydrocarbons of termites from locations ranging from Trinidad, through the Lesser Antilles, Puerto Rico, and the Cayman Islands. I hope to somehow group these together and report on them on the basis of higher taxa. We will also be writing several additional papers on subjects like inter-nest variation in cuticular hydrocarbons, association of foragers with nests on the basis of cuticular hydrocarbons, and behavior associated with building foraging tunnels (one of BLT's projects).

Amidst all of this writing, I need to begin educating my immediate supervisors on my current research program and discuss where I should be going next. Year after year I have taken heat about working on termites. I do not think that my managers realize that a huge majority of my work is not termite control research; rather my program encompasses taxonomy, biogeography, foraging and population ecology, and social and feeding behavior. Somehow I need to impress on them that this new knowledge will form the basis for forest ecology, biodiversity, as well as termite control. Wish me luck!

In closing, I just want to apologize for the late withdrawl from the Terrestrial Ecology/Scientist Month on Guana Island. I know this is a major inconvenience for you, especially the planned presentation that Lori Nelson was going to make at the community college on Tortola and the 21 wasted bed-nights. For that I am truly sorry. Along with an apology, I have to admit that I am very embarrassed by this entire episode. I think that it reflects badly on my employer and me. It probably boils down to that famous quote from the movie *Cool Hand Luke*: "What we have here is a failure to communicate." I will try to do a better job of keeping my managers informed and hope that they can do the same for me.

If I'm still in the business in the future, I hope that I haven't lost too many points for me or my colleagues and can look forward to visiting Guana Island again. Best of luck tracking the iguanas and tortoises this year. When you have time, I'd like to hear how the flamingos did on Guana and Anegada.

Sincerely,

Michael I. Haverty

MICHAEL I. HAVERTY
Chief Research Entomologist

cc Barbara L. Thorne, Lori Nelson

[redacted]

United States Department of Agriculture | Forest Service | Pacific Southwest Forest and Range Experiment Station | P.O. Box 245 Berkeley, CA 94701 U.S.A.

Reply to: 1630

Date: October 27, 1995

Dr. James L. Nation, Editor
Journal of Chemical Ecology
c/o Department of Botany
220 Bartram Hall
University of Florida
Gainesville, FL 32611-8526

Dear Dr. Nation:

Enclosed you will find the original and two copies of a manuscript entitled, "Comparison of methodologies for sampling cuticular hydrocarbons of Caribbean termites for taxonomic and ecological studies," by Michael I. Haverty, Barbara L. Thorne, and Lori J. Nelson. We are submitting it to you for publication in the Journal of Chemical Ecology.

This manuscript was reviewed in an earlier draft by Drs. Gary J. Blomquist, Department of Biochemistry, University of Nevada, Reno, NV; Coby Schal, Department of Entomology, North Carolina State University, Raleigh, NC; and James Lazell, The Conservation Agency, Conanicut Island, RI. I have incorporated their suggestions, as appropriate, into the version of the manuscript that I am submitting now. If you would like to see their reviews and my specific response to each comment, I can easily supply them. I would suggest the following as potential additional reviewers: Ralph W. Howard, ARS/USDA, Manhattan, KS; Steven J. Seybold, Dept. of Biochemistry, Univ. of Nevada, Reno, NV; or Dennis R. Nelson, ARS/USDA, Fargo, ND.

One of my co-authors, Lori Nelson, discussed with you the possibility of publishing several of the figures as fold-outs. She told me that you were interested in considering this format. Therefore, we have prepared most of the figures in this format. If you or the reviewers feel that a different format is preferable, we can easily change the illustrations. We can also supply an electronic copy of the figures.

Thank you for considering this manuscript and the different format for the figures.

Sincerely,

MICHAEL I. HAVERTY
Chief Research Entomologist
Chemical Ecology of Western Forest Insects

Enclosures

cc B.L. Thorne, L.J. Nelson, V. Dong, & G.N. Mason

Journal of Chemical Ecology

Send Galley Proofs to:

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COMPARISON OF METHODOLOGIES FOR SAMPLING CUTICULAR HYDROCARBONS OF CARIBBEAN TERMITES FOR TAXONOMIC AND ECOLOGICAL STUDIES

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Abstract – Using the arboreal nesting *Nasutitermes acajutlae* (Holmgren), we propose standard collection and extraction methodology for characterization of cuticular hydrocarbons of termites under field conditions in the tropics. The methodology described here should be applicable to most termites in the 2.6 mg to 7.1 mg (wet weight) range. Specifically, we evaluated (1) the effect of the duration and the number of extractions; (2) the effect of the condition of the termite specimens (live or dried); (3) the effect of group/sample size; and (4) the effect of solvents (ethanol vs. hexane) on the similarity or reproducibility of cuticular hydrocarbon profiles. Olefins comprise *ca.* 70 percent of the total hydrocarbon fraction of *N. acajutlae*. Hydrocarbons consist of two distinct groups: early eluting components, primarily normal alkanes and methyl-branched alkanes, and late-eluting compounds, which consist almost exclusively of unsaturated components with one to five double bonds. Soldiers have considerably greater quantities of the early-eluting compounds than do workers. Nests of this species from the same island had qualitatively similar (not identical), but quantitatively dissimilar hydrocarbon mixtures. Rinses of 300 live workers in 10 ml of hexane for only 20 seconds produced chromatograms equivalent to a 10-minute extraction. Holding 300 workers in hexane for 2 years resulted in different mixtures of hydrocarbons. Hydrocarbon mixtures extracted from live or dried workers were different; drying tended to enhance extraction of the less abundant unsaturated compounds such as C41:4 and C41:5. Extractions of a minimum 100 workers (live or dried), with hexane for 20 seconds to 10 minutes is best for characterizing cuticular hydrocarbons. For quantitative comparisons, hydrocarbon mixtures extracted from dried samples should not be compared to those extracted from live samples. For several logistical reasons we obtain the best results by drying at least 100 termites before extraction. Storage in ethanol caused numerous unidentified, non-hydrocarbon compounds to be extracted either from the cuticle or from internal tissues.

Key Words – Chemotaxonomy, Isoptera, Termitidae, tropical termites, *Naustitermes acajutlae* (Holmgren), gas chromatography, cuticular hydrocarbons, olefins

INTRODUCTION

Termites play an essential role in the ecological dynamics of many tropical ecosystems, recycling nutrients and aerating soils in forests, mangroves and grasslands. Some species of termites are also economically important as structural pests in urban, as well as rural, areas of the tropics. The termite fauna of tropical regions is known to be diverse, but species diagnosis remains equivocal in many groups. Cuticular hydrocarbons have been found to be useful for discriminating termite species in both tropical and temperate regions. Species sorting and diagnosis based on such chemical separation may then be used to facilitate discovery of morphological criteria for discriminating species (Haverty et al., 1988; Thorne and Haverty, 1989) and delimiting geographic distributions (Thorne et al., 1993).

Comparative research for characterizing cuticular hydrocarbons for both taxonomic and/or ecological studies will necessitate uniform protocols among investigators. Field circumstances must also be considered. In the tropics, termites are usually collected far from laboratory facilities. Hydrocarbon extractions must therefore be delayed until well after the insects have been collected. Standard preservation techniques, such as freezing, are usually impractical. Keeping subcolonies, groups, or samples of a specific size alive and healthy for more than a few hours is very difficult. Hot sun and predacious ants usually render field samples unusable, and live cultures are prone to humidity problems, food stress, and pathogenic fungi. Collection of specimens directly into 70% or 85% ethanol may partially extract hydrocarbons or include some debris and potential contaminants. Long-term retention of specimens in ethanol or in a solvent such as hexane for extended periods, although potentially quite convenient, may also extract internal hydrocarbons and confound the characterization of cuticular hydrocarbons.

We have been collecting termites from the islands in the Caribbean, and have also been receiving specimens collected by colleagues, for characterization of

cuticular hydrocarbons. The method of collection has varied among these efforts. To interpret these data we must know if different collection/extraction regimes are equivalent or comparable. We also want to recommend the most appropriate technique for a given taxon to collaborating scientists.

In the earliest studies that introduced the concept of species specificity of cuticular hydrocarbons, it was not specified how the insects were handled before extraction (Howard et al., 1978, 1982a). In later studies of chemical mimicry by termitophilous staphylinids Howard et al. (1980, 1982b) separated beetles from the termites and froze them at -20°C before extraction. Haverty et al. (1988) froze *Zootermopsis* spp. individuals, then subsequently thawed them to room temperature before extraction. The termites for the study of *Zootermopsis* were brought from the field to the laboratory alive. However, after extracting a few live termites one of us (LJN) noticed that the termites convulsed and emptied their gut contents into the hexane during the process. Freezing the insects, followed by extraction of the specimens at ambient temperature, prevented this possible source of contamination.

Subsequent studies of cuticular hydrocarbons of termites have used live termites extracted in the field or in the laboratory (Howard et al., 1988 [for *Nasutitermes*]; Haverty et al., 1990b [for *Nasutitermes*], 1991, unpublished [for *Reticulitermes*]), or termites dried in the field and later extracted in the laboratory (Haverty et al., 1990a, 1996b [for *Coptotermes*], 1991, 1992 [for *Reticulitermes* and *Coptotermes*]). Our preliminary results comparing extraction of live vs. dried *Nasutitermes acajutlae* (Holmgren) indicated that resulting chromatograms were not equivalent.

Many of our colleagues find it difficult to dry termites in the field while working in the tropics because of logistical problems. Ovens, heating lamps, or even electricity are not always available. Since drying is often impractical, many

researchers prefer to collect termites directly into alcohol or hexane. Detailed comparisons of cuticular hydrocarbon patterns derived from extractions of live or dried termites or termites stored for extended periods in alcohol or hexane is thus warranted and is one focus of this study.

Another factor affecting the quality of cuticular hydrocarbon assessments is the number of insects that are extracted, or quantity of "wax" extracted. In some studies a variable number of individuals (and mixture of castes) was included. Haverty et al. (1991) used anywhere from 15 to 200 *Reticulitermes* spp. workers per sample in their preliminary study of this genus. In most of our studies an exact number of termites is extracted: individual *Zootermopsis* spp. pseudergates, nymphs, soldiers or alates (Haverty et al., 1988); 100 *Coptotermes formosanus* Shiraki workers or soldiers (Haverty et al., 1990a); 200 *C. formosanus* workers or 50 soldiers (Haverty et al., 1996b); and 100 *Nasutitermes costalis* (Holmgren) or *N. ephratae* (Holmgren) large workers (Haverty et al., 1990b)

Extraction of too few individuals can result in a diluted extract and will require concentration of the extract and a deviation from a standard technique. Characterization of hydrocarbons from dilute extracts would likely underestimate or eliminate the less abundant compounds and over-estimate the proportions and importance of the abundant compounds. We know of no published studies to determine the minimum number of individuals necessary to characterize the cuticular hydrocarbons of any termite taxon.

Preliminary observations of Seybold and Nelson (pers. comm.) indicate that ethanol (EtOH) will extract cuticular hydrocarbons of adult *Ips pini* (Say)(family Scolytidae). Also, the longer beetles are in EtOH, the greater the extraction efficiency. Their work showed (1) that the EtOH-extracted insects can be further extracted with hexane, (2) that the EtOH extract can be dried and the lipids re-eluted in hexane, and (3) that the EtOH extract and the EtOH-extracted-insect extract can be

recombined to provide a reconstituted extract for characterization. It is not clear whether the resulting chromatogram is comparable to an extract gathered by the standard 10-minute extraction of live or dead insects with hexane.

In the present study we attempted to define a standard methodology for collecting and extracting termites under "field" conditions. Our field work was based at our research site on Guana Island, British Virgin Islands (Thorne et al., 1994; Collins, 1996 or Scheffrahn et al., 1994; Haverty et al. 1996a). This island has a diverse termite fauna consisting of nine species in three families. The most conspicuous, and apparently abundant, species is the arboreal nesting *Nasutitermes acajutlae* (Holmgren) (Thorne et al., 1994; Collins, 1996 or Scheffrahn et al., 1994). This species, as well as a closely related species, *N. nigriceps* (Holmgren), is numerically and ecologically conspicuous on many of the Caribbean islands (Thorne et al., 1994). A better understanding of the appropriate procedure(s) for sampling and extracting cuticular hydrocarbons of *N. acajutlae* is important to our understanding of the taxonomy, ecology, and biogeography of this and other *Naustitermes* species. The methodology described here is optimal for sampling and extracting cuticular hydrocarbons for this species and should be applicable to most termites in the 2.6 mg to 7.1 mg (wet weight) range.

In this paper we report the results of a sequence of studies, conducted in 1989 and 1993, to compare and improve our sampling and extraction techniques for the characterization of cuticular hydrocarbons of tropical termites. In 1993 we tried to design studies that would ultimately provide us with the "best" field method(s) for characterizing both the composition and relative abundance of the cuticular hydrocarbons of *N. acajutlae*. We compare methodologies and suggest standard and alternative, acceptable methodologies for both chemotaxonomic and ecological studies of this termite. Specifically, we evaluate (1) the effect of the duration and the number of extractions; (2) the effect of the conditions of the termite specimens (live or

dried); (3) the effect of group/sample size; and (4) the effect of solvents (ethanol vs. hexane) on the quality and similarity or reproducibility of cuticular hydrocarbon profiles.

METHODS AND MATERIALS

Collecting and Processing Termite Specimens. We collected workers and soldiers of *Nasutitermes acajutlae* during two separate trips to Guana Island, British Virgin Islands. During each trip different collection techniques were used. In 1989 two nests were sampled near White Sands Beach. Portions of nest material containing workers and soldiers were returned to the laboratory. Nest material was placed in pans and folded index cards (cardboard) were placed on top of this material. Workers and soldiers climbed onto the cards and then were tapped off into trays, where they were sorted, counted, and prepared for hydrocarbon analyses.

In 1993 we selected 13 colonies from the same area. That year we used a modification of a technique demonstrated to us by Dr. Jan Krecek. This is the best technique for collecting large numbers of workers and soldiers with the least effect on nest structure. A tangential slice, 2 to 3 cm deep and 15 to 20 cm in diameter, was removed from the more fragile exterior portion of a nest and discarded. Over this breach we placed one or two 20 cm X 20 cm squares of moist corrugated cardboard. If we were able to cut the slice from the top of a nest, the corrugated cardboard squares were secured against the surface of the nest with a stone. If the slice was taken from the side of the nest (often we could not reach the top of the nest) the corrugated cardboard squares were secured to the nest with 7.5 cm, galvanized, finishing nails.

As soon as the slice of nest was removed and the corrugated cardboard squares put in place, soldiers swarmed out of the breach and covered the squares; workers immediately retreated into the nest. In less than 60 seconds the squares were

removed and a collection of nearly pure soldiers was tapped into a collection pan. To readily obtain a nearly clean sample, hundreds to thousands of soldiers, this process can be repeated several times. We then visually scanned all individuals in the collection pan and removed the few workers in the sample.

Workers were collected by leaving the moist squares of corrugated cardboard on the nest for up to 60 minutes. Once the alarm reaction of the soldiers began to dissipate, workers ventured to the underside of the squares and began to repair the breach. When the cardboard was gently removed a dense sample of workers adhered to the surface. Contrary to the technique for collecting soldiers, the squares of corrugated paper containing the workers (and relatively few soldiers) were placed in a collection pan and returned to the field laboratory for sorting, counting, and preparation of workers for hydrocarbon analyses.

Since soldiers squirt glue over the containers and themselves, they were difficult to count individually. For the purposes of cuticular hydrocarbon analyses, we measured ca. 5 to 8 ml of soldiers in 20-ml scintillation vials for extraction or drying. Workers were separated and individually counted into 20-ml scintillation vials for extraction or drying of the appropriate number of individuals.

Additional termites from each of the sampled colonies (with soldiers and alates, when available, as diagnostic castes) were placed in 80 percent ethanol to serve as voucher specimens. These voucher specimens are kept at the Pacific Southwest Research Station, Albany, California, and the Department of Entomology, University of Maryland, College Park, Maryland.

Standard Sample Processing. Cuticular lipids were extracted by immersing termites in *n*-hexane. Our usual procedure has been a 10-minute rinse of 100 termites in 10 ml of *n*-hexane. In this study, we used this procedure as the standard to evaluate the various extraction regimes described in the following sections. The lipid extracts resulting from each of the various methods were pipetted through 4 cm

of activated BioSil-A in Pasteur pipette mini-columns in order to isolate the hydrocarbon components. The resulting hydrocarbon extracts were evaporated to dryness under nitrogen and re-dissolved in 60 µl of *n*-hexane for gas chromatography-mass spectrometry (GC-MS) analyses.

Duration and Number of Extractions. One of the primary reasons we began our studies of extraction methodology was to remedy a problem encountered during studies of the cuticular hydrocarbons of *N. corniger* (Motchulsky), *N. ephratae*, and *N. costalis* (Haverty et al., 1990b; Howard et al., 1988). Haverty et al. (1990b) experienced difficulty obtaining a sufficiently large hydrocarbon sample by extracting 100 large workers of *N. costalis* or *N. ephratae* in the field in Trinidad. The samples taken during that study were barely sufficient to allow quantification of the hydrocarbon mixtures. Thus, we designed a first set of experiments in 1989 to better understand the difficulties experienced with the characterization of cuticular hydrocarbons from *N. costalis* and *N. ephratae*.

In 1989 we evaluated the following extraction regimes using *N. acajutlae* from Guana Island, British Virgin Islands, to determine whether we could improve upon rinsing 100 live workers in 10 ml of hexane for 10 minutes:

A. Rinse 300 workers in 10 ml hexane for 10 minutes (standard technique with an increased sample size).

B. Sequentially rinse 300 workers three times in 10 ml of hexane for 10 minutes, keeping each extract separate to determine if the standard technique left significant quantities of hydrocarbon on the sample.

C. Rinse 300 workers in 10 ml of hexane for 20 seconds followed by a 10 minute rinse in 10 ml of hexane, keeping each extract separate to determine whether a quick rinse would produce an acceptable chromatogram.

D. Rinse 300 workers in 10 ml of hexane for 20 seconds followed by soaking for 24 hours in 10 ml hexane, keeping each extract separate (same as "b" with an extended

post-rinse extraction) to determine whether an extended soaking would remove additional hydrocarbons from the cuticle or from other tissues.

E. Soak 300 workers in 10 ml of hexane for 24 hours to allow for a less stringent extraction schedule.

F. Soak 300 workers in 10 ml of hexane for 2 years to allow field collection with subsequent laboratory storage for an extended period.

G. Isolate 300 workers (alive) from soldiers for 24 hours, then rinse in hexane for 10 minutes to allow time for defense secretions that might have contaminated the sample to evaporate or be groomed off one another by the nestmates in the sample.

Condition of the Termites: Live vs. Dried. We used six samples of 100 workers from each of 13 nests. Live termites were extracted at the field laboratory on Guana Island. Live termites from three samples from each colony were placed directly into separate 20-ml scintillation vials and extracted in 10 ml of hexane for 10 minutes. The hexane from each of 39 vials was then decanted into a separate 20-ml scintillation vial and was subsequently returned to our laboratory in California for characterization of cuticular hydrocarbons.

The other three samples of *N. acajutlae* workers from each of 13 colonies were dried by placing 20-ml scintillation vials, each containing 100 individuals, in a wire box over a single 75-watt, reflecting, incandescent light. The amount of time required to completely dry termites varied slightly as a function of the position of the vials over the bulb. The position of the vials over the bulb was changed in an attempt to make the drying time similar for each sample. Once termites were completely dried, we kept them dry by tightly sealing the vials. The vials were returned to our laboratory in California for extraction and characterization of cuticular hydrocarbons.

Effects of Group/Sample Size. Samples of 25, 50, 100, or 200 *N. acajutlae* workers from 5 different colonies were extracted either live or dried as described

above. Each combination (sample size X live vs. dried X colony) was replicated 3 times.

Effects of Solvent. For each of 5 colonies, 3 replicates of 200 workers were placed in 20 ml of 100% ethanol and left in the solvent for 60 days. The ethanol extract was decanted and evaporated to dryness under nitrogen. The extract was then re-dissolved in 10 ml of hexane and processed by the standard procedure. After the ethanol was drained from the termites, the insects were dried and extracted with hexane following the standard procedure.

Characterization of Cuticular Hydrocarbons. GC-MS analyses were performed on a Hewlett-Packard 5890 gas chromatograph equipped with a Hewlett-Packard 5970B Mass Selective Detector interfaced with a Hewlett-Packard Chemstation computer. The GC-MS was equipped with an HP-1, fused silica capillary column (30 m x 0.2 mm ID) and operated in split mode (with a split ratio of 8:1). A 3 µl aliquot was injected into the GC/MS. Each mixture was analyzed by a temperature program from 200°C to 320°C at 3°C/minute with a final hold of 16 minutes. Electron impact (EI) mass spectra were obtained at 70 eV. *n*-Alkanes were identified by their mass spectra. Mass spectra of methylalkanes were interpreted as described by Blomquist et al. (1987) to identify methyl branch locations. Alkenes were tentatively identified by their mass spectra and retention times relative to *n*-alkanes. A typical alkene mass spectrum shows a molecular ion and a series of fragments at 14-mass unit intervals (69, 83, 97), similar to those displayed by *n*-alkanes, less 2 mass units. Interpretation of the mass spectra of dienes and polyunsaturated hydrocarbons was extrapolated from this pattern, i.e. for each double bond, the molecular ion is decreased by 2 mass units.

Integration of the total ion chromatogram was performed by the data analysis software (HP59974J Rev. 3.1.2) in the Hewlett-Packard Chemstation. GC-MS peak areas were converted to percentage of the total hydrocarbon fraction. These

percentages for each hydrocarbon peak were the response variables used to make statistical comparisons among extraction/collection techniques.

Statistical Analyses. The response variables for all statistical tests were the percentages of each cuticular hydrocarbon peak. The effect of the condition of the termites before extraction (live vs. dead and dried) was assessed by a *t*-test of the differences between the means (3 replicates or subsamples from each nest or colony) of each of two conditions for each of 13 colonies. The significance of the calculated *t*-value was tested at $\alpha = 0.05/32$, the number of hydrocarbon peaks for workers. Our null hypothesis was that the 10-minute extraction of 100 dried termites was not significantly different from the standard 10-minute extraction of 100 live termites.

The effect of group size was tested with an analysis of variance for each hydrocarbon. Each treatment combination (group size X colony) was replicated 3 times. The four sample sizes were compared separately for termites extracted live or dried. Our null hypothesis was that all group sizes provide chromatograms with the same relative quantities of each hydrocarbon.

The significance of the F-statistic was tested with $\alpha = 0.00147$ (0.05/35, the number of hydrocarbons from workers). Significant differences among means for each hydrocarbon were determined by Tukey's honestly significant difference (hsd) procedure. We were looking for the smallest group size that results in a hydrocarbon profile equivalent in resolution to those of the next greatest group size. A group size was considered inadequate if they yield hydrocarbon mixtures that are significantly different in quantity from those of a larger size.

RESULTS AND DISCUSSION

Cuticular Hydrocarbon Mixtures of N. acajutlae. We identified 36 hydrocarbons from workers and 43 from soldiers (Figure 1 and Haverty et al., 1996a). The hydrocarbons found in these chromatograms can be seen in two distinct groups.

The early eluting components are primarily normal alkanes, methyl-branched alkanes, and a few normal alkenes in the 23 to 31 carbon range. The second group of later-eluting compounds consists almost exclusively of unsaturated components with one to five double bonds, in the 37 to 45 carbon range, and two monomethyl alkanes in trace amounts. Soldiers have more of the earlier-eluting compounds than do workers (Figure 1). By far, the predominant class of hydrocarbons is the alkenes, comprising greater than 70 percent of the total hydrocarbon component in workers (Haverty et al., 1996a).

Duration and Number of Extractions. Early in our research on the chemotaxonomy of termites we extracted live or recently frozen individuals. The standard 10-minute rinse of 300 live workers of *N. acajutlae* (Figure 2A) allowed us to resolve and characterize most of the components identified for this species (Haverty et al., 1996a). We also discovered that different nests of this species from the same island produced qualitatively similar (not identical), but quantitatively dissimilar hydrocarbon mixtures (Figure 1). Furthermore, these colony-specific profiles are repeatable; when a second group of 300 live workers was extracted the chromatograms for each colony were qualitatively identical and quantitatively quite similar (Figure 2A,B1; Table 1). A second extraction of the same 300 workers resulted in a hydrocarbon mixture that was quite similar to the mixture from the first extraction (Figure 2B2). A third 10-minute extraction resulted in chromatograms that did not resemble those from either of the first two extractions; only the predominant peaks (C25, C27, C39:1, and C41:1) were detected (Figure 2B3). We conclude that subsequent extractions did not change the relative proportions of the cuticular hydrocarbons of *N. acajutlae* .

A very brief rinse of 300 live workers in 10 ml of hexane for only 20 seconds produced chromatograms equivalent to a 10-minute extraction (Figure 2A,C1,D1; Table 1). Furthermore, the 20-second rinse was repeatable. A subsequent 10-minute

extraction of the same workers produced a chromatogram similar to that of a 20-second rinse (Figure 2C1,C2; Table 1). Soaking 300 workers for 24 hours after a 20-second rinse resulted in a chromatogram that was different from the standard extraction (10 ml for 10 minutes) or a 20-second rinse. Proportional relationships change dramatically: C25 and C27 were much more prominent as were C41:4 and C41:5 (Figure 2A,D1,D2; Table 1).

Extraction of 300 workers for 24 hours results in a chromatogram that appears similar to the standard 10-minute extraction (Figure 2A,E; Table 1). Holding a sample of 300 workers in hexane for a period of 2 years provided a radically different mixture of hydrocarbons than the standard 10-minute extraction (Figure 2F; Table 1). Many hydrocarbons that we rarely see in *N. acajutlae* workers (such as C22, C23:1, C24:1, C25:1 [an additional isomer], C26:1, 11,13-MeC25, C27:2, 2-MeC26, C29:2, 5-MeC29, C31:1, C43:5, and C43:2) were present in quantities exceeding trace amounts. Furthermore, some compounds (C25, C27, C41:5, and C41:4) were present in much greater proportions. As a result of these qualitative and quantitative differences, we do not consider the hydrocarbon mixtures from lengthy extractions to be comparable to the standard 10-minute extraction.

When a nest is breached or a large group of termites in a pan is disturbed, soldiers congregate at the site of the disturbance and discharge large quantities of defense secretions or glue. The effect of these defense secretions on extraction of worker hydrocarbons was unknown. We isolated 300 workers from each of two colonies for 24 hours to allow time for these secretions to degrade or for the workers to groom one another to remove these compounds. The resulting chromatograms did not appear to differ from the standard (Figure 2G; Table 1).

Condition of the Termites: Live vs. Dried. Mixtures of cuticular hydrocarbons extracted from live or dried workers were quantitatively different from one another. Of the 32 hydrocarbon peaks, the percentages of 20 of them were significantly

different (Table 2). The most striking differences were exhibited in the late-eluting alkenes (Figure 3). Drying the workers before extraction resulted in highly significant increases in the relative amounts of C41:4 and C41:5. Related to the apparent increased efficiency of the extraction of these compounds was the apparent decrease in the relative amounts of the most abundant compounds, C39:1, C41:1, and C43:1.

In general, drying workers first tended to enhance extraction of the less abundant unsaturated compounds. Extraction of 100 dried workers did not result in equivalent mixtures of hydrocarbons when compared to extraction of 100 live workers, and may not be comparable for taxonomic purposes. However, either technique would suffice for characterization of cuticular hydrocarbons for ecological studies.

There is the possibility that these differences are due to the extraction of hydrocarbons from internal tissues. By definition, these hydrocarbons are not cuticular lipids, though the components may be the same (deRenobales et al., 1991). Dried termites are more fragile and often lose legs, antennae, or even heads during shipment. Also, the cuticle can become cracked. These conditions could allow the hexane to penetrate and extract lipids from the inner layers of cuticle and internal tissues. It is conceivable that some of the hydrocarbons extracted from our dried samples are not surface hydrocarbons, but those deposited on the external surface of the cuticle of the next instar (Howard et al., 1995). We found no evidence that any abundant hydrocarbons (with the possible exception of C41:2 or C43:2) were unique to dried samples.

After examining hundreds of samples of termites extracted live or after drying it appears to us that the chromatograms from dried individuals are sharper and have a flatter base line than those from live, field-extracted individuals. Three possible reasons are: (1) live termites void gut contents when placed in hexane and thus

introduce contaminants, (2) live insects have a higher water content in the cuticle and less hydrocarbon is extracted because hexane is hydrophobic, or (2) hexane in a vial extracts contaminants from the vial lids during transit from the field to the laboratory. When we stored clean hexane in vials that were upside down, the resulting chromatogram had an uneven baseline similar to that resulting from extraction of live termites, however, no peaks were seen. Further study of this phenomenon is warranted.

Effects of Group/Sample Size. Statistically significant differences (α=0.00147) in the percentage of hydrocarbon components among sample sizes were found for 22 hydrocarbon peaks from workers extracted live (Table 3). The most abundant components, C39:1 and C41:1, were not significantly different among sample sizes. Groups of 25 or 50 workers were found to be significantly different in only three cases: C26, C28, and C29. Groups of 25 workers produced hydrocarbon proportions significantly different from groups of 100 workers in 14 cases and from groups of 200 workers in 20 cases (Table 3.) Groups of 50 workers produced hydrocarbon proportions significantly different from groups of 100 workers in 7 cases and from groups of 200 workers in 13 cases. Groups of 100 and 200 workers were found to be significantly different in only 3 cases. If workers were extracted while alive, it appears that the cuticular hydrocarbon mixtures change the least in samples of 100 or more.

Statistically significant differences (α=0.00147) in the percentage of hydrocarbon components among sample sizes were found for 20 hydrocarbon peaks when workers were extracted after drying (Table 4). Contrary to the results of extracting live workers, the most abundant hydrocarbons, C39:1 and C41:1, did display statistically significant differences among sample sizes. Groups of 25 or 50 workers were found to be significantly different for only one hydrocarbon, 2-MeC27. Groups of 25 workers produced hydrocarbon proportions significantly different from

groups of 100 in 13 cases and from 200 workers in 14 cases. Groups of 50 workers produced hydrocarbon proportions significantly different from groups of 100 in only 2 cases and from groups of 200 workers in 6 cases (Table 4). Groups of 100 and 200 workers were found to be significantly different in only 4 cases. Similar to the result of extracting live workers, extracting workers after drying changes the least when sample sizes are 100 or more.

The less abundant compounds, or those that are present only in trace amounts from extractions of the standard group size (100), are either missing or infrequently recorded (with a lower mean value resulting) in samples of 25 or 50 workers (Tables 3 and 4, Figures 4 and 5). The most abundant compounds, such as C39:1 and C41:1, have a lower mean value in groups of 100 or 200 workers (Tables 3 and 4; Figure 5). This undoubtedly results from the greater contribution of the minor compounds to the total hydrocarbon mixtures in the larger sample sizes; many of these trace compounds are not recorded in the groups of 25 or 50 workers and they do not add to the total hydrocarbon (Figure 5). Thus, for workers of *N. acajutlae*, 100 appears to be the minimum acceptable sample size for adequately characterizing the cuticular hydrocarbons for quantitative comparisons, regardless of whether the workers are extracted while alive or after drying. If the goal is to characterize all hydrocarbon components, even though they might be present in trivial amounts, then a larger sample (200 to 300 workers) should be taken or the extracts should be concentrated beyond our standard 60 µl.

It is likely that our earlier problem with quantifying hydrocarbons from *N. costalis* and *N. ephratae* (Haverty et al., 1990b) resulted from three confounding problems. First, the workers were extracted live, in the field, which resulted in a less efficient extraction of the hydrocarbons, especially the less abundant components. Second, only 100 workers were used in the extractions; therefore, these collections could very well have been below an acceptable size. Large workers of *N. ephratae*

(dry weight = 0.6 mg) are considerably smaller than large workers of *N. acajutlae* (dry weight = 1.31 mg) (Thorne, 1985); 100 large workers of the former species may not have had sufficient surface lipids to provide an adequate chromatogram. Third, in our earlier studies of *N. costalis* and *N. ephratae* we used a flame ionization detector (FID) to quantify hydrocarbon peaks. Even though we used the same type of column, the resolution of that earlier chromatographic scheme (Haverty et al., 1990b) did not resolve peaks as well as the equipment we currently use. Since the study of *N. costalis* and *N. ephratae*, we have had better results with a FID and a different gas chromatograph.

Effects of Solvent. For field entomologists working in the tropics it would be convenient if storage of termites in 100 percent ethanol allowed for equivalent extraction of hydrocarbons. Unfortunately, the resulting chromatograms for both workers and soldiers were not comparable to those where the standard technique was utilized. Storage in ethanol caused numerous, hexane soluable, unidentified, non-hydrocarbon compounds to be extracted or these non-hydrocarbon peaks were in the ethanol as denaturing components (Figure 6). These compounds were not removed after evaporating the ethanol under nitrogen, re-dissolving in hexane, and pipetting through activated BioSil-A. Furthermore, enormous amounts of nitrogen and time were required to dry the ethanol samples. Therefore, unless a different cleanup procedure is developed, storage in ethanol is unacceptable for characterizing the hydrocarbons from *Nasutitermes*.

CONCLUSIONS

Different colonies of *N. acajutlae* produce qualitatively similar, but quantitatively dissimilar hydrocarbon mixtures. These colony-specific profiles are reproducible; multiple chromatograms from separate samples of each colony are qualitatively identical and quantitatively quite similar. Only one extraction of a

group of workers is necessary. A very brief rinse (in 10 ml of hexane for only 20 seconds) of live workers produces a chromatogram equivalent to a 10-minute extraction. Holding a sample of workers (or soldiers) in hexane for a period of 2 years results in a radically different mixture of hydrocarbons than the standard 10-minute extraction, and is not recommended.

Drying workers of *N. acajutlae* before extraction results in highly significant increases in the relative amounts of C41:4 and C41:5 and an apparent decrease in the relative amounts of the most abundant compounds, C39:1, C41:1, and C43:1. In general, drying workers first tends to enhance extraction of the less abundant unsaturated compounds and does not result in equivalent mixtures of hydrocarbons when compared to extraction of live workers. Extracting a minimum of 100 workers (live or dried) with hexane for 20 seconds to 10 minutes seems to be the best method for characterizing cuticular hydrocarbons of *N. acajutlae*. For smaller species, groups of 200 would probably guarantee a satisfactory chromatogram.

For quantitative comparisons, the extraction technique should ideally be the same for all samples, i.e. hydrocarbon mixtures extracted from dried samples should not be compared to those extracted from live samples. Extraction of either live or dried termites would suffice for characterization of cuticular hydrocarbons for ecological studies, but may not be comparable for taxonomic purposes. For quality of chromatograms and for several logistical reasons, we obtain the best results by drying at least 100 termites then extracting them by the standard technique (10 minutes in 10 ml hexane). Extraction of live termites in the field requires twice the number of vials and transportation of flammable liquids. Even with the potential logistical difficulties involved with drying termites in the tropics, we recommend this as the optimal technique to use.

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REFERENCES

Blomquist, G.J., Nelson, D.R., and de Renobales, M.. 1987. Chemistry, biochemistry, and physiology of insect cuticular lipids. *Arch. Insect Biochem. Physiol.* 6: 227-265.

Collins, M.S. 1996. The termites of Guana and other British Virgin Islands. *Florida Entomol.* (to be submitted).

deRenobales, M., Nelson, D.R., and Blomquist, G.J. 1991. Cuticular lipids, pp. 240-251 in K. Binnington and A. Retnakaran (eds.). Physiology of the Insect Epidermis, CSIRO, Australia.

Haverty, M.I., Collins, M.S., Nelson, L.J., and B.L. Thorne. 1996a. Cuticular hydrocarbons of the termites of the British Virgin Islands. *Florida Entomol.* (in preparation)

Haverty, M.I., Grace, J.K., Nelson, L.J., and Yamamoto, R.T. 1996b. Intercaste, intercolony, and temporal variation of cuticular hydrocarbon mixtures of *Coptotermes formosanus* Shiraki from Oahu, Hawaii. *J. Chem. Ecol.* (submitted soon!).

Haverty, M.I., Nelson, L.J., and Page, M. 1990a. Cuticular hydrocarbons of four populations of *Coptotermes formosanus* Shiraki in the United States: Similarities and origins of introductions, *J. Chem. Ecol.* 16: 1635-1647.

Haverty, M.I., Nelson, L.J., Page, M. 1991. Preliminary investigations of the cuticular hydrocarbons of North American *Reticulitermes* and tropical *Coptotermes* (Isoptera: Rhinotermitidae) for chemosystematic studies. *Sociobiology* 19: 51-76.

Haverty, M.I., Nelson, L.J., Thorne, B.L., Collins, M.S., Darlington, J.P.E.C., and Page, M. 1992. Cuticular hydrocarbons for species determination of tropical termites, pp. 58-66 *in* C.E. Conrad and L.A. Newell (tech. coords.). Proceedings of the session on Tropical Forestry for People of the Pacific.

Pacific Science Congress, Honolulu, Hawaii, May 22-28, 1991. USDA Forest Service Gen. Tech Report PSW-129.

Haverty, M.I., Page, M., Nelson, L.J., and Blomquist, G.J. 1988. Cuticular hydrocarbons of dampwood termites, *Zootermopsis*: intra- and intercolony variation and potential as taxonomic characters. *J. Chem. Ecol.* 14: 1035-1058.

Haverty, M.I., Thorne, B.L., and Page, M. 1990b. Surface hydrocarbon components of two species of *Nasutitermes* from Trinidad, *J. Chem. Ecol.* 16: 2441-2450.

Howard, R.W., Howard, C.D., and Colquhoun, S. 1995. Ontogenetic and environmentally induced changes in the cuticular hydrocarbons of *Oryzaephilus surinamensis* (L.) (Coleoptera: Cucujidae). *Ann. Entomol. Soc. Amer.* (In press).

Howard, R.W., McDaniel, C.A., and Blomquist, G.J. 1978. Cuticular hydrocarbons of the eastern subterranean termite, *Reticulitermes flavipes* (Kollar) (Isoptera: Rhinotermitidae). *J. Chem. Ecol.* 4: 233-245.

Howard, R.W., McDaniel, C.A., and Blomquist, G.J. 1980. Chemical mimicry as an integrating mechanism: cuticular hydrocarbons of a termitophile and its host. *Science* 210: 431-433.

Howard, R.W., McDaniel, C.A., and Blomquist, G.J. 1982b. Chemical mimicry as an integrating mechanism for three termitophiles associated with *Reticulitermes virginicus* (Banks). *Psyche* 89: 157-167.

Howard, R.W., McDaniel, C.A., Nelson, D.R., Blomquist, G.J., Gelbaum, L.T., and Zalkow, L.H. 1982a. Cuticular hydrocarbons of *Reticulitermes virginicus* (Banks) and their role as potential species- and caste-recognition cues. *J. Chem. Ecol.* 8: 1227-1239.

Howard, R.W., Thorne, B.L., Levings, S.C., and McDaniel, C.A. 1988. Cuticular hydrocarbons as chemotaxonomic characters for *Nasutitermes corniger* (Motschulsky) and *N. ephratae* (Holmgren) (Isoptera: Termitidae). *Ann. Entomol. Soc. Amer.* 81: 395-399.

Scheffrahn, R.H., Darlington, J.P.E.C., Collins, M.S., Krecek, J., and Su, N.-Y. 1994. Termites (Isoptera: Kalotermitidae, Rhinotermitidae, Termitidae) of the West Indies. *Sociobiology* 24: 213-238.

Steel, R.G.D., and Torrie, J.H. 1960. Principles and Procedures of Statistics. McGraw-Hill Book Co., Inc., New York, 481 pages.

Thorne, B.L. 1985. Numerical and biomass caste proportions in colonies of the termites *Nasutitermes corniger* and *N. ephratae*. *Insectes Sociaux* 32: 411-426.

Thorne, B.L. and Haverty, M.I. 1989. Accurate identification of *Zootermposis* species (Isoptera: Termopsidae) based on a mandibular character of nonsoldier castes. *Ann. Entomol. Soc. Amer.* 82: 262-266.

Thorne, B.L., Haverty, M.I., and CollinsM.S. 1994. Taxonomy and biogeography of *Nasutitermes acajutlae* and *N. nigriceps* (Isoptera:Termitidae) in the Caribbean and Central America. *Ann. Entomol. Soc. Amer.* 87: 762-770.

Thorne, B.L., Haverty, M.I., M. Page, and Nutting, W.L. 1993. Distribution and biogeography of the North American termite genus *Zootermopsis* (Isoptera: Termopsidae). *Ann. Entomol. Soc. Amer.* 86: 532-544.

Table 1. Relative abundance (mean value from two colonies) of cuticular hydrocarbons of workers of *Nasutitermes acajutlae* (Holmgren) from Guana Island, British Virgin Islands, resulting from different extraction regimes.

	Mean percent from each chromatogram [a]									
Hydrocarbon[b]	A	B1	B2	B3	C1	C2	D1	D2	E	G
C23	0.3	0.4	0.0	0.0	0.2	0.0	0.3	1.5	0.6	0.4
C24	0.3	0.3	0.0	0.0	0.2	0.0	0.2	0.5	0.3	0.2
C25	4.7	4.7	5.3	18.4	3.5	4.9	3.9	7.5	5.6	3.6
11-MeC25	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.3	0.2	0.1
C26	0.9	1.0	0.9	0.0	0.7	0.9	0.7	1.4	1.1	0.2
2-MeC26 + C27:1	0.4	0.3	0.0	0.0	0.1	0.0	0.2	1.2	0.5	0.8
C27	5.1	6.1	7.5	20.1	4.2	7.5	4.3	9.5	6.7	4.2
11-MeC27	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.1
2-MeC27	0.0	0.2	0.0	0.0	0.1	0.0	0.0	1.1	0.3	0.2
C28	0.4	0.6	0.8	0.0	0.4	0.8	0.4	1.3	0.7	0.4
C29	1.0	1.3	1.8	0.0	0.9	1.8	0.8	3.0	1.7	0.8
C30	0.1	0.1	0.0	0.0	0.1	0.0	0.0	0.3	0.1	0.1

C31	0.1	0.2	0.0	0.0	0.1	0.0	0.1	0.8	0.3	0.1
C37:1	0.2	0.2	0.2	0.0	0.3	0.0	0.3	0.0	0.3	0.4
C38:1	0.4	0.6	0.7	0.0	0.8	0.0	0.6	0.2	0.4	0.8
C39:4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.5	0.0	0.3
C39:1	32.0	30.0	31.7	34.3	31.3	32.6	31.4	23.0	28.4	30.2
15-MeC39	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1
C40:1	2.7	2.9	2.4	0.0	2.9	1.6	3.0	1.8	2.5	3.0
C41:4	0.9	0.9	2.4	0.0	0.9	2.3	1.5	8.0	0.7	3.3
C41:5	0.7	0.7	1.6	0.0	0.7	1.2	0.7	3.9	0.7	1.8
C41:1	37.1	35.4	35.9	27.2	37.7	38.2	37.2	25.9	35.3	34.3
15-MeC41	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2
C42:1	0.9	1.1	0.4	0.0	1.2	0.0	1.2	0.0	1.0	1.2
C43:5	0.0	0.1	0.0	0.0	0.0	0.0	0.4	2.0	0.0	1.1
C43:1	11.2	11.2	8.0	0.0	11.8	8.3	11.3	6.3	10.9	11.1
C45:1	0.6	1.5	0.4	0.0	1.6	0.0	1.7	0.1	1.4	1.4

[a] Extraction regimes A-G are outlined in the methods and in Figure 2. Extraction procedure F was not included because of numerous extraneous peaks.

[b] This shorthand uses a descriptor for the location of the methyl group (X-Me), the total number of carbons (CXX) in the hydrocarbon component, excluding the methyl branch(es), and the number of double bonds following the colon (CXX:Y).

Table 2. Relative quantities of cuticular hydrocarbons (mean percent and standard deviation) from samples of workers of *Nasutitermes acajutlae* (Holmgren) from Guana Island, British Virgin Islands, extracted alive or after drying.

	Extracted Live[b]		Extracted Dry[b]		
Hydrocarbon[a]	Mean	Std. Dev.	Mean	Std. Dev.	*t* value[c]
C23:1	0.41	0.32	0.32	0.30	0.819
C23	0.80	0.29	0.97	0.33	-3.029
C24	0.45	0.27	0.22	0.22	3.348
C25:1	0.36	0.35	0.68	0.27	-4.445
C25	2.64	0.95	3.05	1.14	-2.618
13-; 11-MeC25	0.04	0.10	0.16	0.17	-4.361
C26	0.53	0.32	0.26	0.27	4.453
C27:1	0.34	0.33	0.86	0.42	-6.610
C27	1.40	0.95	1.90	1.60	-2.706
13-; 11-MeC27	0.03	0.09	0.07	0.11	-1.747
2-MeC27	0.00	0.00	0.15	0.13	-4.944
C28	0.37	0.22	0.15	0.19	3.251
C29	0.53	0.34	0.73	0.56	-2.438
C31	0.16	0.20	0.06	0.15	2.394
C33	0.01	0.04	0.00	0.00	1.000
C37:1	0.45	0.22	0.40	0.17	1.724
C38:1	0.63	0.25	0.53	0.20	3.537
C39:5	0.03	0.09	0.36	0.33	-4.439
C39:4	0.54	0.40	2.00	0.73	-7.526
C39:2	0.08	0.36	0.43	0.48	-3.272

C39:1	28.12	2.49	20.01	2.20	17.314
15-MeC39	0.03	0.09	0.04	0.12	-0.380
C40:1	2.84	0.27	2.51	0.42	3.928
C41:4 + C41:5	6.23	3.61	18.77	3.81	-16.929
C41:2	0.01	0.05	1.21	0.63	-8.168
C41:1	33.77	2.73	24.43	2.74	15.720
15-MeC41	0.07	0.17	0.13	0.23	-1.302
C42:1	1.46	0.50	1.60	0.65	-1.650
C43:5	1.01	1.13	4.35	1.37	-9.746
C43:2	0.04	0.12	0.83	0.52	-5.876
C43:1	13.15	1.41	10.40	1.61	11.519
C45:1	3.44	0.66	2.41	0.82	6.233

[a] This shorthand uses a descriptor for the location of the methyl group (X-Me), the total number of carbons (CXX) in the hydrocarbon component, excluding the methyl branch(es), and the number of double bonds following the colon (CXX:Y).

[b] Three subsamples of one hundred workers from 13 colonies were either placed in a scintillation vial alive then extracted for 10 minutes with 10 ml of hexane or placed in a vial, dried over an incandescent light, then extracted for 10 minutes with 10 ml of hexane.

[c] The critical $t_{12,.995} = 3.055$.

Table 3. Relative quantities of cuticular hydrocarbons (mean percent and standard deviation) from four sizes of groups of workers from five nests of *Nasutitermes acajutlae* (Holmgren) from Guana Island, British Virgin Islands, extracted live.[a]

	25 workers		50 workers		100 workers		200 workers	
Hydrocarbon	Mean	Std Dev	Mean	Std Dev	Mean	Std Dev	Mean	Std Dev
C23:1	0.00a	0.00	0.00a	0.00	0.33b	0.31	0.00a	0.00
C23	1.33a	0.50	1.26a	0.40	0.85ab	0.20	0.74b	0.14
C24	1.18a	0.59	0.99a	0.25	0.41b	0.18	0.41b	0.09
C25:1	0.00a	0.00	0.01ab	0.05	0.33c	0.30	0.25bc	0.13
C25	4.73a	1.31	4.05ab	1.15	2.84b	0.48	2.78b	0.44
13-; 11-MeC25	0.00a	0.00	0.02a	0.05	0.05ab	0.14	0.16b	0.10
C26:1 + 3-MeC25	0.00a	0.00	0.00a	0.00	0.00a	0.00	0.01a	0.03
C26	1.49a	0.53	1.01b	0.24	0.49c	0.18	0.45c	0.13
C27:1	0.14a	0.44	0.11a	0.21	0.42a	0.31	0.36a	0.15
C27	2.48a	1.23	1.97a	0.73	1.59a	0.65	1.44a	0.66
13-; 11-MeC27	0.00a	0.00	0.00a	0.00	0.05a	0.14	0.11a	0.08
2-MeC27	0.00a	0.00	0.00a	0.00	0.00a	0.00	0.00a	0.00
C28	1.17a	0.41	0.75b	0.19	0.32c	0.21	0.25c	0.10
C29	1.18a	0.39	0.73b	0.15	0.46bc	0.26	0.35c	0.10
C31	0.45a	0.34	0.31ab	0.14	0.08b	0.14	0.13b	0.06
C33	0.02a	0.09	0.02a	0.05	0.00a	0.00	0.02a	0.04
C37:1	0.07a	0.18	0.14a	0.22	0.50b	0.18	0.48b	0.15
C38:1	0.21a	0.38	0.33ab	0.27	0.68bc	0.23	0.80c	0.16
C39:5	0.00a	0.00	0.03a	0.09	0.04a	0.10	0.27b	0.26
C39:4	0.10a	0.22	0.15a	0.27	0.73b	0.34	0.81b	0.38

C39:2	0.00a	0.00	0.00a	0.00	0.00a	0.00	0.08a	0.16
C39:1	29.2a	2.47	28.7a	1.62	27.9a	2.70	26.4a	1.32
15-MeC39	0.00a	0.00	0.00a	0.00	0.00a	0.00	0.13b	0.11
C40:1	2.01a	0.85	2.47ab	0.40	2.87b	0.13	3.23b	0.52
C41:4 + C41:5	5.47a	2.51	6.43a	2.44	7.92a	4.12	9.27a	2.52
C41:2	0.00a	0.00	2.34a	8.96	0.00a	0.00	0.70a	1.15
C41:1	35.5a	2.79	32.2a	8.88	32.4a	2.90	30.4a	1.98
15-MeC41	0.00a	0.00	0.01a	0.04	0.00a	0.00	0.26b	0.16
C42:1	0.99a	0.78	1.50ab	0.77	1.54ab	0.58	2.12b	0.66
C43:5	0.23a	0.50	0.94ab	0.97	1.49ab	1.44	2.20b	0.71
C43:2	0.00a	0.00	0.02a	0.08	0.03a	0.11	0.33b	0.11
C43:1	10.7a	1.26	11.5ab	0.87	12.5b	1.48	12.4ab	1.11
C45:1	1.29a	1.10	1.96ab	0.84	3.21b	0.59	2.70b	0.98

[a] Means are from 3 subsamples from each of 5 separate nests. Means for a given hydrocarbon followed by the same letter are not significantly different at the α=0.00147 level.

Table 4. Relative quantities of cuticular hydrocarbons (mean percent and standard deviation) from four sizes of groups of workers from five nests of *Nasutitermes acajutlae* (Holmgren) from Guana Island, British Virgin Islands, extracted after drying.[a]

	25 workers		50 workers		100 workers		200 workers	
Hydrocarbon	Mean	Std Dev	Mean	Std Dev	Mean	Std Dev	Mean	Std Dev
C23:1	0.00a	0.00	0.00a	0.00	0.24b	0.28	0.05ab	0.06
C23	1.20a	0.38	1.08a	0.28	0.93a	0.20	1.12a	0.26
C24	0.34a	0.34	0.39a	0.28	0.24a	0.23	0.36a	0.20
C25:1	0.24a	0.41	0.40a	0.27	0.64a	0.21	0.59a	0.19
C25	5.25a	2.44	3.83ab	1.09	3.04b	0.77	3.69ab	0.81
13-; 11-MeC25	0.13a	0.23	0.20a	0.15	0.17a	0.16	0.29a	0.10
C26:1 + 3-MEC25	0.00a	0.00	0.00a	0.00	0.00a	0.00	0.05b	0.06
C26	0.41a	0.35	0.41a	0.31	0.35a	0.29	0.41a	0.26
C27:1	0.33a	0.43	0.58ab	0.22	0.89b	0.56	0.74ab	0.25
C27	2.75a	1.62	2.49a	1.47	2.13a	1.44	2.65a	1.46
13-; 11-MeC27	0.03a	0.13	0.09ab	0.11	0.09ab	0.11	0.20b	0.07
2-MeC27	0.00a	0.00	0.15b	0.11	0.13b	0.11	0.23b	0.08
C28	0.05a	0.13	0.25a	0.20	0.26a	0.22	0.29a	0.17
C29:1	0.00a	0.00	0.00a	0.00	0.00a	0.00	0.14b	0.10
C29	0.62a	0.50	0.69a	0.42	0.84a	0.52	0.85a	0.50
C31	0.00a	0.00	0.03ab	0.07	0.04ab	0.09	0.13b	0.09
C33	0.00a	0.00	0.00a	0.00	0.00a	0.00	0.02a	0.04
C37:1	0.12a	0.22	0.22ab	0.15	0.47b	0.07	0.43ab	0.15
C38:1	0.26a	0.35	0.45ab	0.16	0.57ab	0.10	0.63b	0.21
C39:5	0.04a	0.16	0.19ab	0.14	0.36b	0.20	0.36b	0.13

C39:4	0.97a	0.75	1.30ab	0.43	2.00b	0.68	1.91ab	0.92
C39:2	0.00a	0.00	0.00a	0.00	0.67b	0.46	0.69b	0.28
C39:1	22.6a	1.99	21.3ab	1.57	19.6b	1.97	19.6b	1.79
15-MeC39	0.00a	0.00	0.00a	0.00	0.06a	0.16	0.22b	0.17
C40:1	1.90a	0.29	2.05a	0.33	2.41a	0.19	2.27a	0.55
C41:4 + C41:5	18.6a	4.60	18.9a	3.05	19.4a	3.39	17.4a	2.43
C41:2	0.05a	0.20	0.61ab	0.51	1.21bc	0.59	1.58c	0.54
C41:1	28.7a	2.20	26.3ab	1.85	23.1b	1.77	23.4b	3.16
15-MeC41	0.00a	0.00	0.01a	0.05	0.11a	0.21	0.34b	0.17
C42:1	1.33a	1.02	1.75a	0.80	1.72a	0.52	1.44a	0.49
C43:5	3.10a	1.58	4.17a	0.98	4.25a	1.92	4.40a	1.09
C43:2	0.12a	0.47	0.48ab	0.32	0.91b	0.63	0.94b	0.37
C43:1	9.58a	1.01	9.84a	0.76	10.0a	1.77	10.3a	1.30
C45:1	1.35a	0.72	1.89ab	0.54	2.47b	0.55	2.26ab	0.83

[a] Means are from 3 subsamples from each of 5 separate nests. Means for a given hydrocarbon followed by the same letter are not significantly different at the α=0.00147 level.

Figure Legends

Fig. 1. Total ion chromatogram of the cuticular hydrocarbons of workers and soldiers of *Nasutitermes acajutlae* (Holmgren) from two colonies (A & B) from Guana Island, British Virgin Islands. These chromatograms were derived from dried samples of 100 workers and ca. 8 ml of soldiers collected in October 1993.

Fig. 2. Chromatograms of cuticular hydrocarbons extracted from 300 live workers from a nest of *N. acajutlae* from Guana Island, B.V.I. A = Extraction with 10 ml hexane for 10 minutes (standard); B1 = First extraction a separate group with 10 ml hexane for 10 minutes (equivalent to the standard); B2 = Second extraction of the same termites as B1 with 10 ml hexane for 10 minutes; B3 = Third extraction of the same termites as B1 with 10 ml hexane for 10 minutes; C1 = First extraction of a different group with 10 ml hexane for 20 seconds; C2 = Second extraction of the same termites as C1 with 10 ml hexane for 10 minutes; D1 = First extraction a third group with 10 ml hexane for 20 seconds (equivalent to C1, but with a different group of 300 workers); D2 = Second extraction of the same termites as D2 with 10 ml hexane for 24 hours; E = Extraction with 10 ml hexane for 24 hours; F = Extraction with 10 ml hexane for 2 years; G = A group of 300 workers that was isolated from other colony mates for 24 hours before extraction with 10 ml hexane for 10 minutes (equivalent to the standard extraction technique).

Fig. 3. Chromatograms of cuticular hydrocarbons from 100 workers from two nests (A & B) of *N. acajutlae* from Guana Island, British Virgin Islands. Workers were extracted with 10 ml of hexane for 10 minutes either live or after drying.

Fig. 4. Chromatograms of cuticular hydrocarbons from four sizes of groups (25, 50, 100, and 200) workers from one colony of *N. acajutlae* from Guana Island, British Virgin Islands, extracted after drying with 10 ml hexane for 10 minutes.

Fir. 5. Log (mean percent + 1) of 34 cuticular hydrocarbon components for groups of 25 and 200 workers extracted either alive (A) or after drying (B). Most of the less abundant components fall below the line of equality (dashed line). Note: transformation was not done for statistical purposes, but to spread out the points for the less abundant components.

Fig. 6. Chromatograms of cuticular hydrocarbons (and other compounds) from 200 workers (A) or 200 soldiers (B) collected into 100 percent ethanol. For each caste the first chromatogram (A1 or B1) represents the pattern of compounds that were extracted by the ethanol. The second chromatogram for each caste (A2 or B2) represents the pattern of compounds extracted from the termites after they were stored in ethanol for 60 days, subsequently dried, then extracted with 10 ml of hexane for 10 minutes.

Figure .

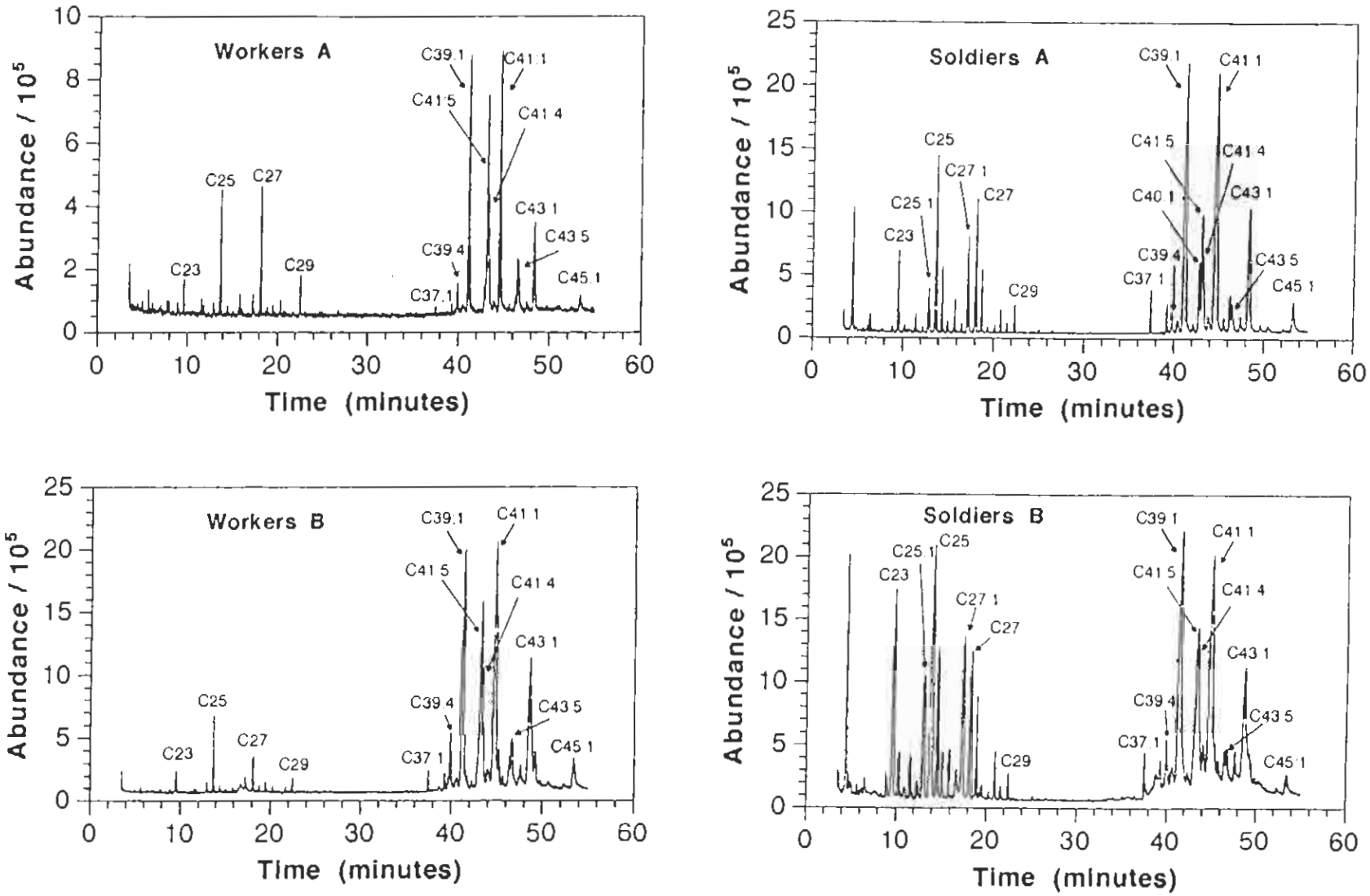
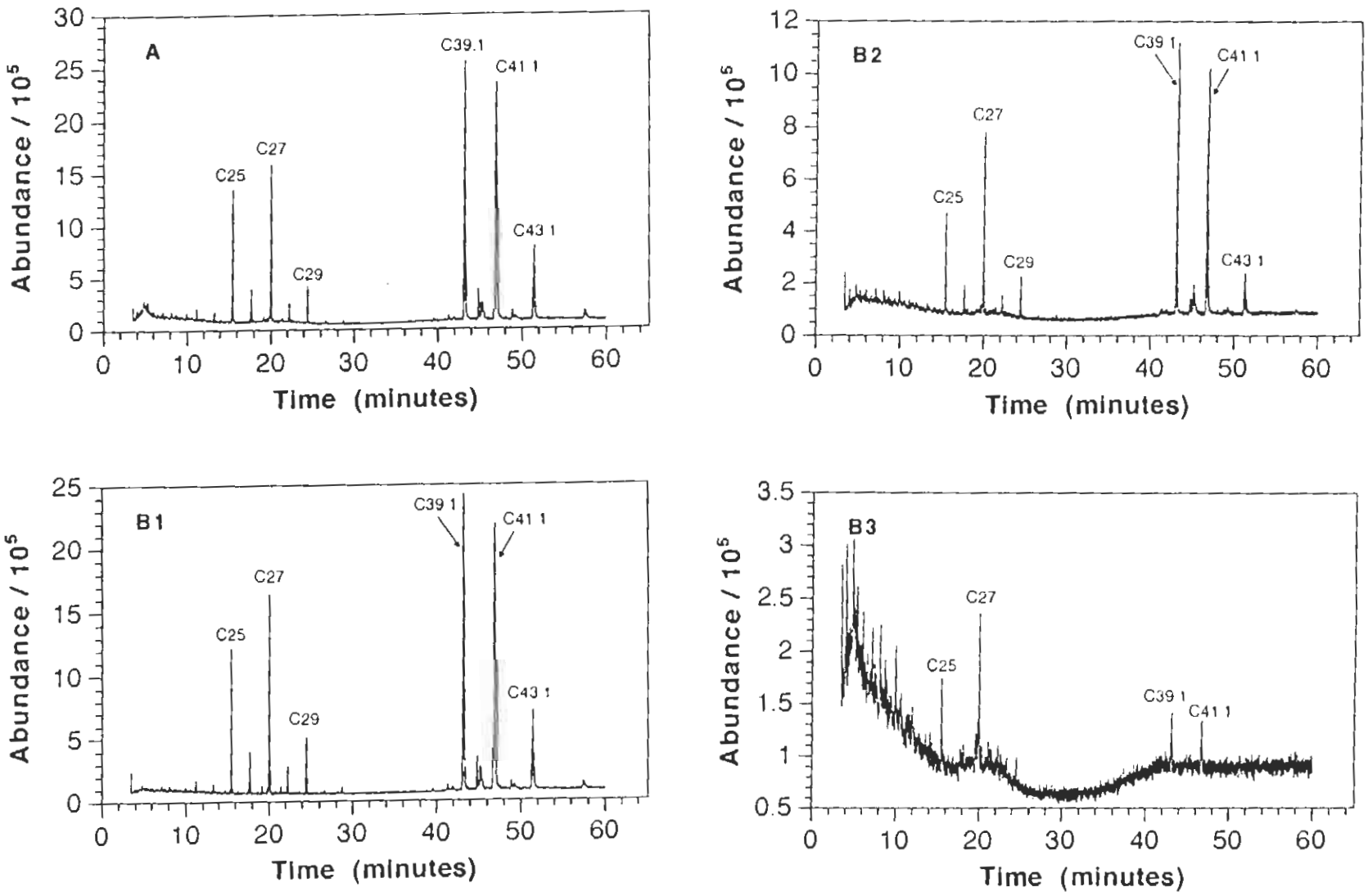

Workers A
Soldiers A
Workers B
Soldiers B
Abundance / 10^5
Time (minutes)
C23
C25
C25 1
C27
C27 1
C29
C37 1
C39 1
C39 4
C40 1
C41 1
C41 4
C41 5
C43 1
C43 5
C45 1

Figure .


A
B1
B2
B3
C25
C27
C29
C39.1
C39 1
C41 1
C43 1
Abundance / 10^5
Time (minutes)

157

Figure 2

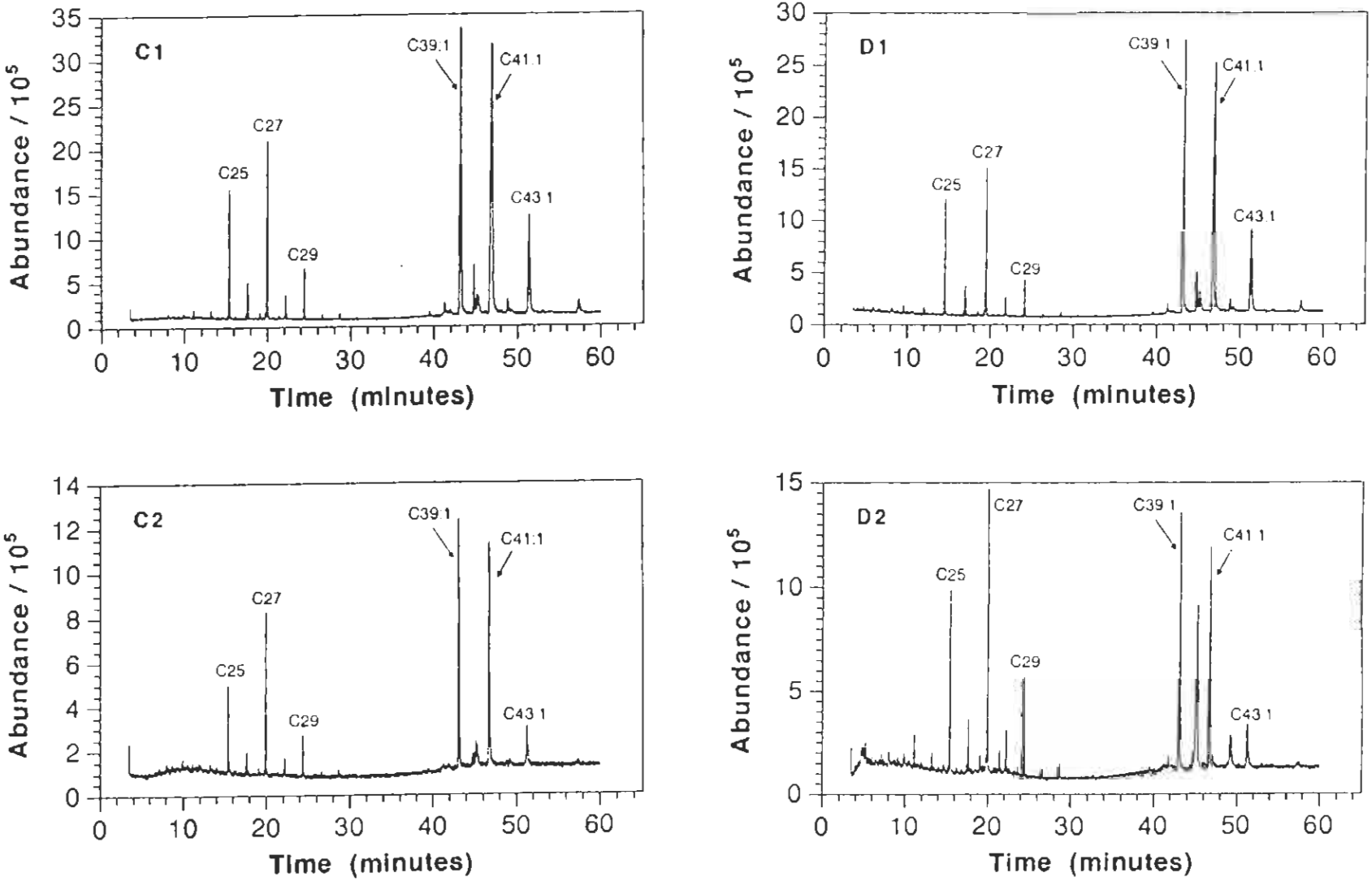
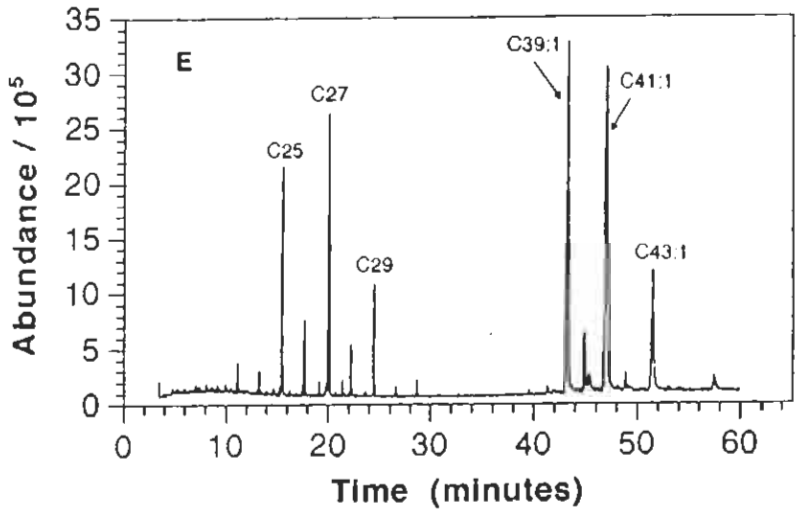
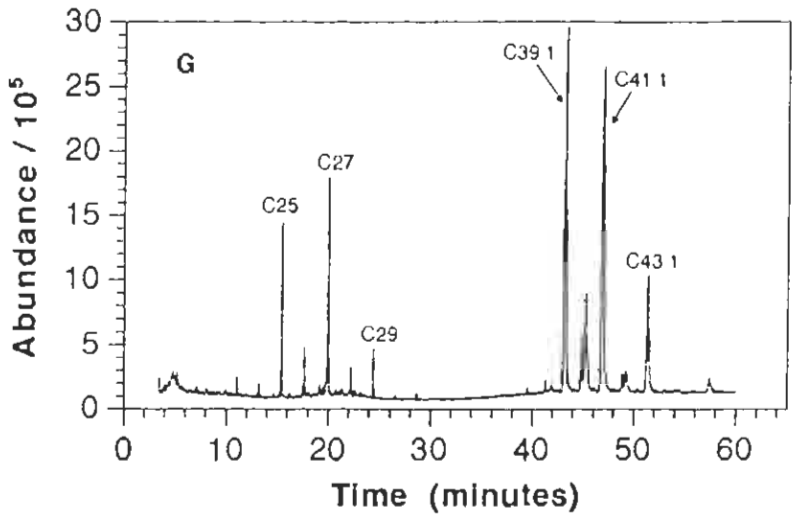

C1
C25
C27
C29
C39:1
C41:1
C43:1
Abundance / 10^5
Time (minutes)
D1
C25
C27
C29
C39:1
C41:1
C43:1
Abundance / 10^5
Time (minutes)
C2
C25
C27
C29
C39:1
C41:1
C43:1
Abundance / 10^5
Time (minutes)
D2
C25
C27
C29
C39:1
C41:1
C43:1
Abundance / 10^5
Time (minutes)

Figure 2


E
C25
C27
C29
C39:1
C41:1
C43:1
Abundance / 10^5
Time (minutes)


G
C25
C27
C29
C39:1
C41:1
C43:1
Abundance / 10^5
Time (minutes)

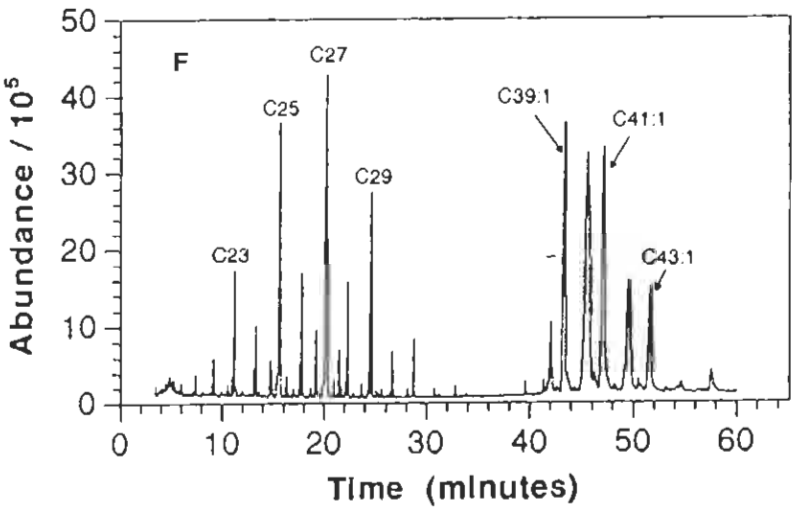

F
C23
C25
C27
C29
C39:1
C41:1
C43:1
Abundance / 10^5
Time (minutes)

Figure 3

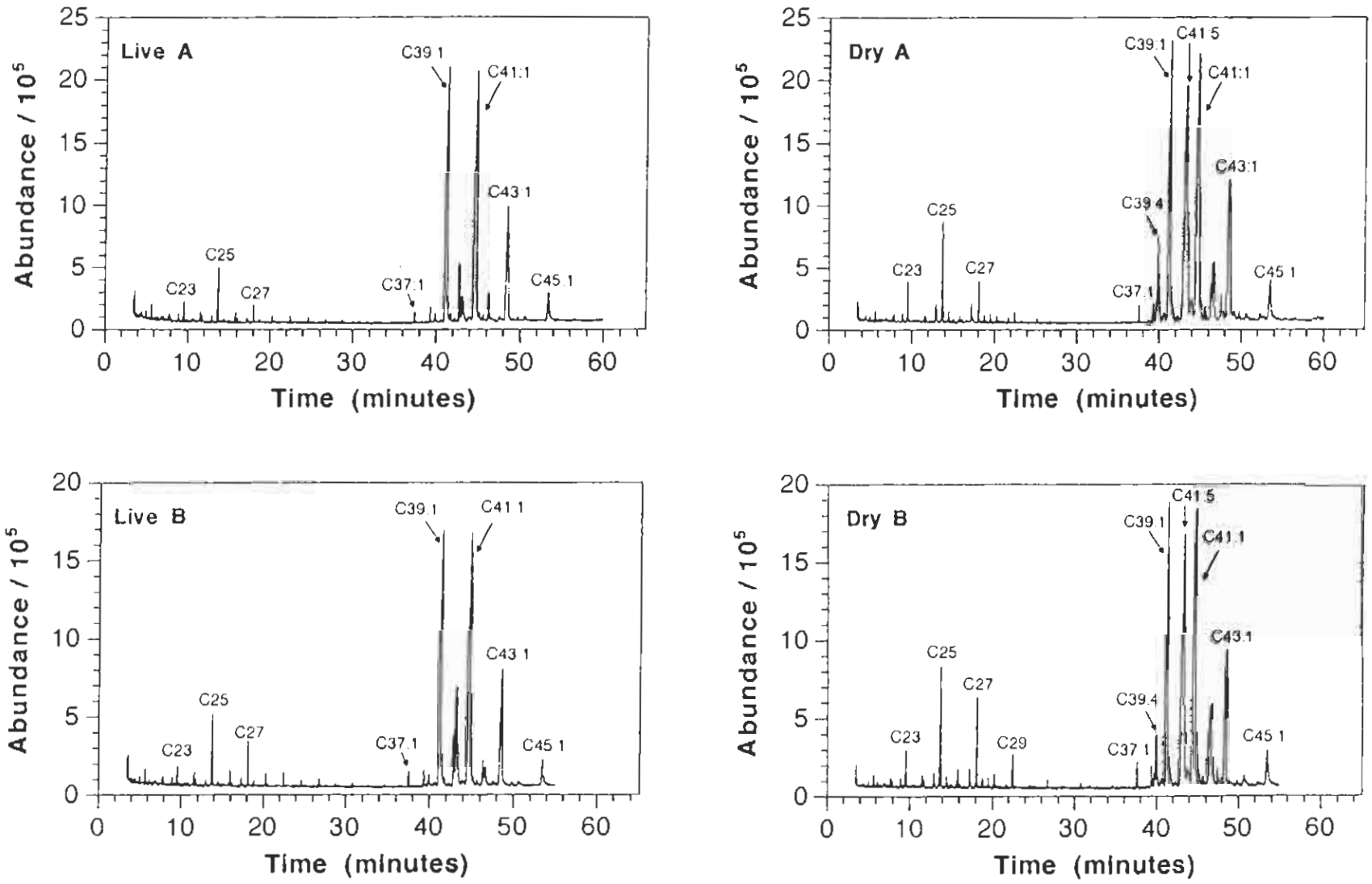

Live A
Dry A
Live B
Dry B
Abundance / 10⁵
Time (minutes)
C23
C25
C27
C29
C37:1
C39:1
C39:4
C41:5
C41:1
C43:1
C45:1

Figure 4

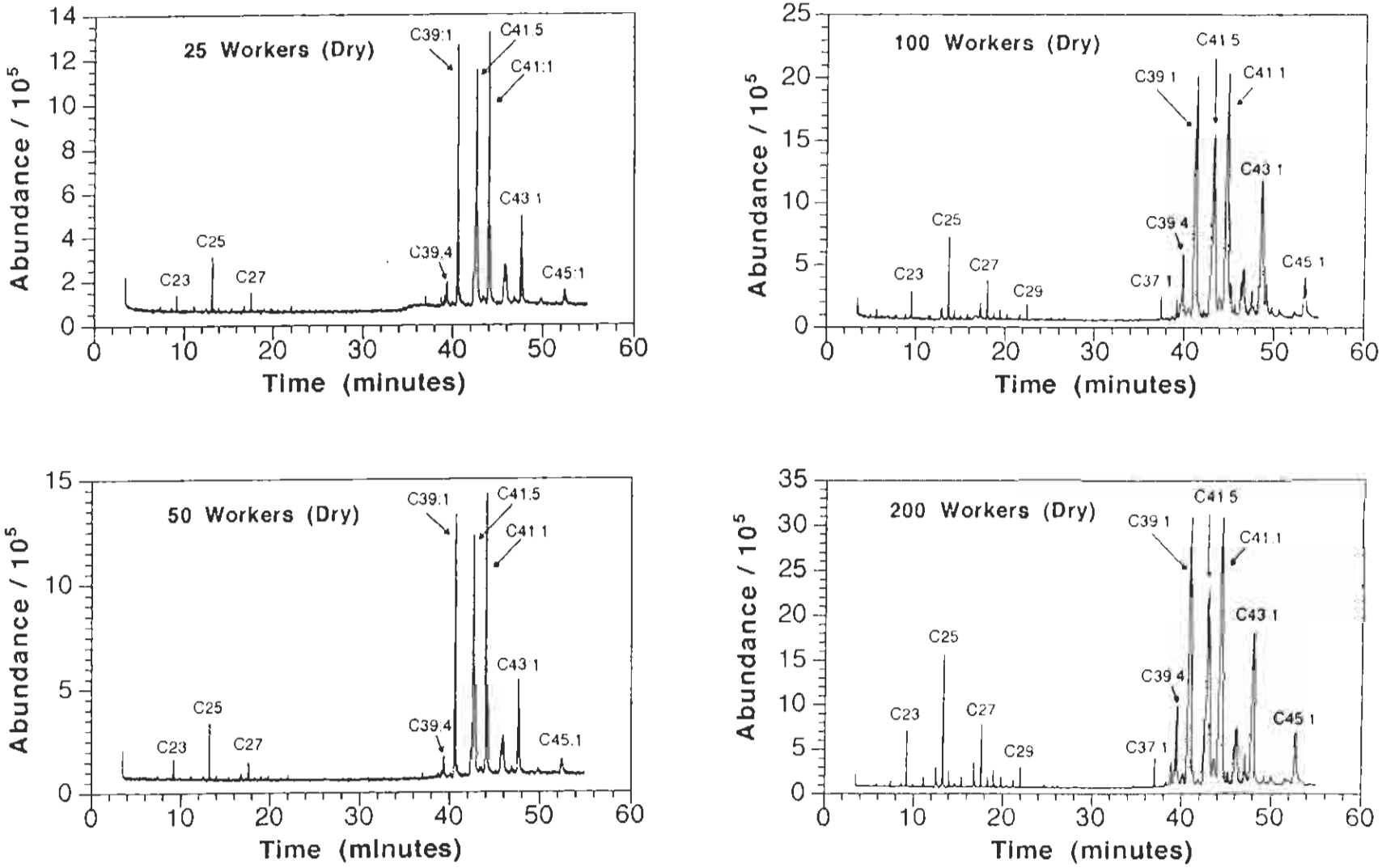
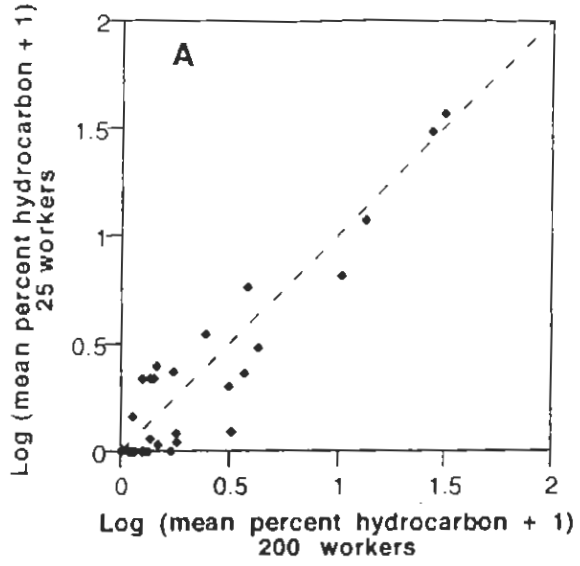

25 Workers (Dry)
100 Workers (Dry)
50 Workers (Dry)
200 Workers (Dry)
Abundance / 10^5
Time (minutes)
Time (mInutes)
C23
C25
C27
C29
C37:1
C39:1
C39:4
C41:5
C41:1
C43:1
C45:1

Figure 5


A
Log (mean percent hydrocarbon + 1)
25 workers
Log (mean percent hydrocarbon + 1)
200 workers
0
0.5
1
1.5
2

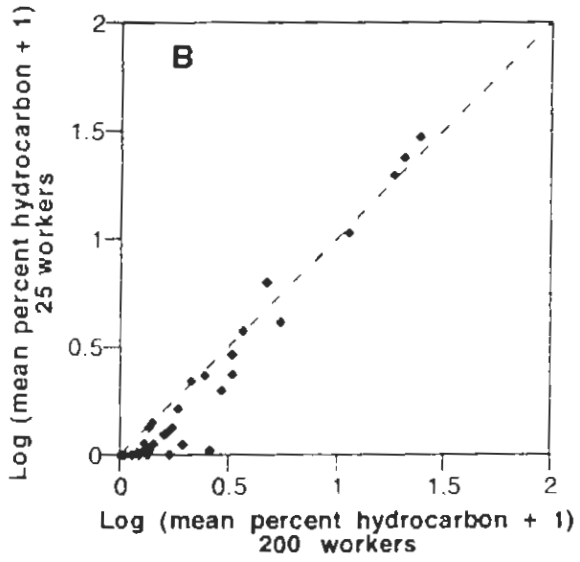
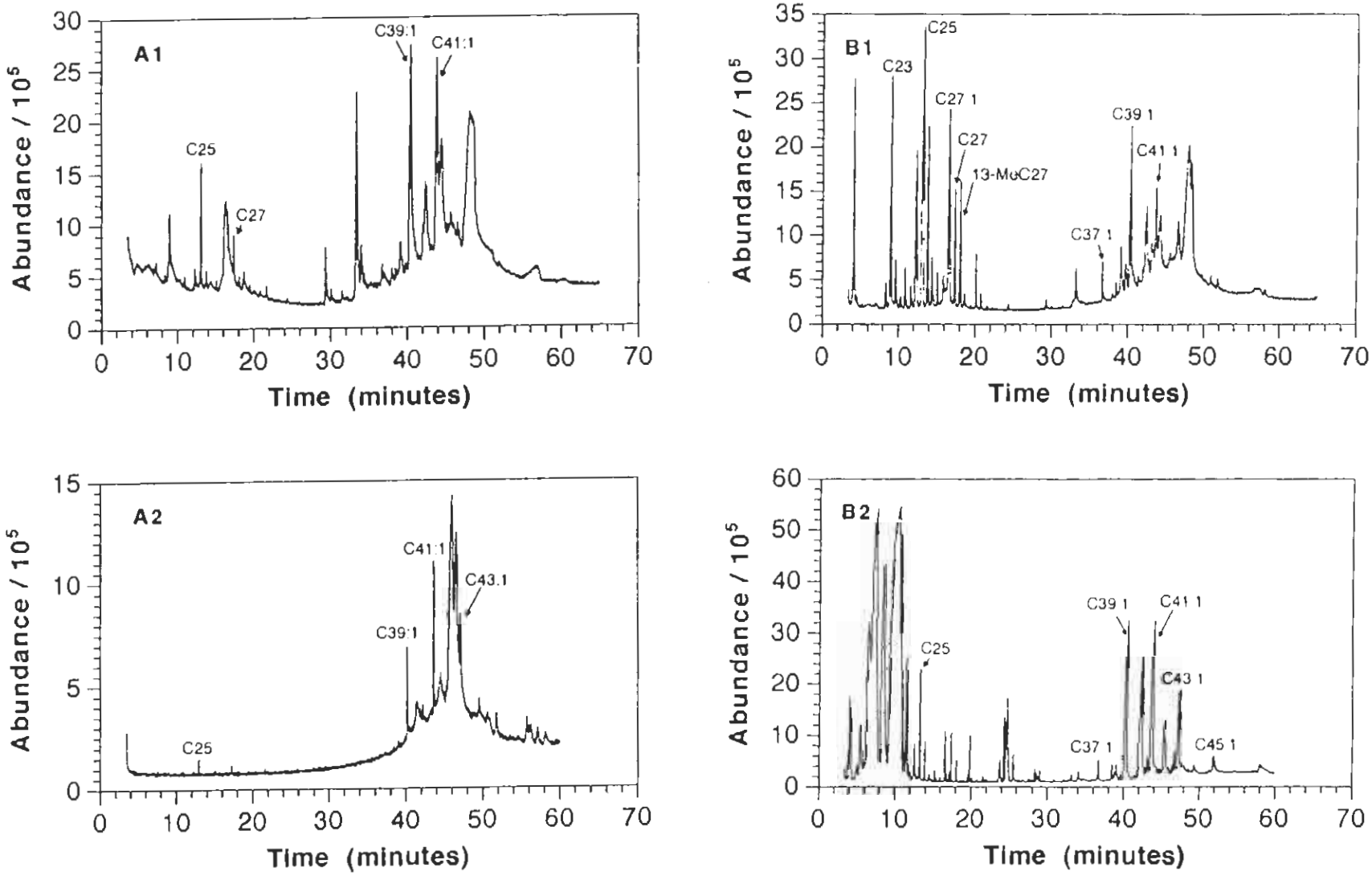

B
Log (mean percent hydrocarbon + 1)
25 workers
Log (mean percent hydrocarbon + 1)
200 workers
0
0.5
1
1.5
2

Figure 6


A1
C25
C27
C39:1
C41:1
Abundance / 10^5
Time (minutes)
B1
C23
C25
C27 1
C27
13-MeC27
C37 1
C39 1
C41 1
Abundance / 10^5
Time (minutes)
A2
C25
C39:1
C41:1
C43.1
Abundance / 10^5
Time (minutes)
B2
C25
C37 1
C39 1
C41 1
C43 1
C45 1
Abundance / 10^5
Time (minutes)

Biodiversity and human health

The recent outbreak of Ebola virus in the town of Kikwit in Zaire claimed over a hundred human victims. The current epidemic of HIV/AIDS[1] and the resurgence of tuberculosis (TB) remind us just how susceptible we are to infectious diseases and underline the complacent attitude towards infectious diseases that operates in the health care systems of many developed and developing countries[2]. In our continued assault on natural habitats through population expansion and economic exploitation, humans are not only creating a less healthy environment, but are consequently being exposed to a variety of new pathogens[3,4,23]. This is occurring at a time when global climate change may lead to expansions in the range of a number of infectious diseases[5,6] and when resistance is evolving to the antibiotics used to cure many common ailments[7,8]. A recent meeting at the Dillon Ripley Center of the Smithsonian Institute in Washington on 'Biodiversity and Human Health' highlighted the potential interactions between human health, the destruction of tropical forests, the emergence of new pathogens and the loss of natural products with therapeutic potential that could be used to treat new and existing diseases. The April meeting was organized by the National Institutes of Health, the National Science Foundation and the Smithsonian Institute. The talks at the Conference highlighted the potential dangers to human health of the continued assault on the environment, particularly the destruction of tropical forests.

Just how big is the potential for tropical (and temperate) forests to supply agents with medicinal value that might be used to treat infectious and congenital diseases? Robert McCaleb (Herb Research Foundation, Boulder, CO, USA) gave some important statistics on this. So far, one out of every 125 plant species studied has produced a major drug. The market value of these drugs in the US is at least $200 million per year. If we estimate that we lose one tree species a day, then we lose three to four potentially valuable new drugs every year, at a total cost of around $600 million. If we contrast this with the production of new drugs from synthesized chemicals, the potential for finding major new drugs is in the order of one in 10 000 for each compound tested. The difference in the success rate between screening programs and looking for natural products from plants is patentability. Pharmaceutical companies have a much harder time patenting natural products than ones they have synthesized, and their potential profits are thus diminished when they attempt to market natural compounds over which they have only a limited monopoly. This is in part because of the litigation associated with the potential misuse of drugs in the US, but it is also because of the trade barriers and tariffs that the pharmaceutical industry has lobbied for to prevent the import of drugs based upon plant products. Much of President Bush's reluctance to sign the Rio biodiversity treaty was based on pressure from pharmaceutical companies that felt their 'competitiveness' might be threatened by a treaty that acknowledged the potential use of plant-based drugs with a tropical origin.

Despite significant trade and legislative barriers, the overwhelming majority of prescription drugs used at present in the US are based on natural products. In a fascinating review of the top prescription drugs in the US, Francesca Grifo (American Museum of Natural History, New York, USA)[9] showed that 118 out of the top 150 prescription drugs, 74% are based on plants, 18% on fungi, 5% on bacteria and 3% on vertebrates (indeed all are from one species of snake *Bothrops asper*). If we look at the top ten prescription drugs in the US, nine out of the ten are based on natural plant products. The figures are likely to significantly underestimate the use of natural products as drugs in other parts of the world as the US is particularly conservative in terms of its pharmaceutical diversity. The World Health Organization estimates that more than 80% of the world's population relies upon traditional plant medicine for primary health care.

Many drugs and herbal remedies that are widely used in Europe aren't even for sale in the US. For example, a plant derivative based on the leaves of the *Ginkgo* tree is now used by 80% of Europeans older than the age of 45 (Ref. 10). The species escaped extinction in the wild when preserved in monastery gardens where they were tended by Chinese monks for many centuries[11]. Compounds distilled from leaves of the *Ginkgo* tree increase rates of cerebral blood flow and have major effects in preventing senile dementia. Other compounds that are widely available in Europe, but that are not available in the US, include (1) an extract of mistletoe, which laboratory tests have shown doubles the survival time of women suffering from breast cancer[10]; (2) Theokal, a hawthorn extract, which is now widely used as an anti-arrhythmic and is much safer to use than digitalis (itself an extract of foxgloves), having fewer side effects on people with heart problems[10]; and (3) Thisilyn, a derivative of milk thistles, that is now kept on hand in all hospitals in Europe and is used widely for liver damage (particularly from alcoholism!) – it can also provide very effective relief for sufferers from hepatitis[10]. Garlic-based compounds provide the finest irony. Although Americans can buy as much garlic as they like in their supermarkets, only recently have drugs derived from garlic appeared on the shelves of herbalists and pharmacies in the US. This is despite garlic's proven qualities in reducing cholesterol through its action as an anti-oxidant.

As a mere 1100 of the world's 365 000 known species of plants have been examined

for their medicinal properties[12], how can we focus our search for potentially useful species? Katy Moran (Healing Forest Conservancy, Washington, DC, USA) pointed out that indigenous cultures are the *in situ* protectors of >90% of the world's remaining diversity. Their knowledge of medicinal plants and their uses is of incalculable value to human health. At present, one indigenous culture goes extinct in the Amazon basin every year[13]. Every time one of the shamans of these tribes dies, significant amounts of scientific information on tropical plants and their medicinal properties are lost. This information is potentially of huge value to the medical and pharmaceutical industry throughout the world. However, it is important that if tropical rain forest's products are used to put a value on preserving biodiversity, then intellectual property rights agreements have to be set up to ensure that a significant proportion of the financial benefit goes back into protecting the habitat and the indigenous tribes that are the source of this potential wealth. The Rio Convention on Biological Diversity laid down important guidelines for biodiversity prospecting. Unfortunately, although over 106 countries have ratified this convention, the US has not yet ratified the convention. Given the 103rd Congress's attitude towards the Endangered Species Act, it seems unlikely that it will be ratified in the near future.

Why do we need these new drugs? There are four main reasons for this: (1) the increasing widescale development of resistance to many antibiotic and anthelmintic compounds currently in use[7,8]; (2) the emergence of new human diseases[4,14], particularly HIV/AIDS[1]; (3) the resurgence of older diseases such as TB[2]; and (4) changes in the geographical distribution of older diseases owing to increased human movement and global climate change[5,6]. Furthermore, conservation biologists are desperately searching for examples of human benefits that result from conserving biodiversity. Pharmaceutical products from rain forest plants may provide an excellent justification for rain forest protection in a world where we are beginning to lose the present round of our long-term battle with infectious diseases. In this light, it is ironic that most conservation and development programs ignore the importance of parasitic helminths and other infectious diseases as major components of health and welfare of people in the tropical countries where most of the world's biodiversity lies. A recent paper by Chan *et al.*[15] suggests that, at present, many hundreds of millions of children continue to suffer the impact of parasitic helminth diseases. In countries where these problems are also chronic in the adult population, they lead to significant levels of debilitation that in turn have significant impacts on industrial productivity and economic growth[16]. Few things will convince people more of the value of biodiversity, than if it can be shown to provide cures and treatments for many of the ailments that place a major constraint on human health and economic development in areas with significant amounts of tropical biodiversity.

The recent movie *Outbreak* and a best-selling book *The Hot Zone*[17] have concentrated the public's mind on the fact that new pathogens continue to emerge. Increases in human population growth are probably the main determinants of when new pathogens emerge and establish in humans. Essentially the more humans that are out there sampling the environment, the greater the chance that some of them will pick up a new pathogen that they transport to a sufficiently populous area to cause an epidemic outbreak. However, it is likely that parasites and pathogens that have been with us for a long time still maintain the greatest threat to the welfare of human populations. This particularly will be the case in a world where a changing climate may allow pathogens to establish either in areas where they had previously been eradicated, or in areas that have become noticeably warmer and damper[5,18]. Furthermore, resistance has evolved to many of the manufactured compounds used to control these pests and their vectors, the search for new compounds will become increasingly frantic. Particularly in cases where the production of new synthetic drugs is constrained to variations of compounds that are similar in chemical structure to those to that are already in use, but for which resistance has already evolved. A significant number of 'new' drugs are produced in this way, unfortunately they tend to select for resistance fairly rapidly[8,19,20]. In contrast, drugs derived from natural products are likely to have novel properties to which the pathogens are unlikely to have much resistance. Furthermore, as many natural products consist not of one but of a large number of active compounds, this will be like using more than one drug to treat an outbreak and may considerably reduce the rate at which resistance evolves[19,21,22].

The meeting was held within a mile of Capitol Hill during the week when the new Congress in the US were celebrating the first hundred days of Contract with America and building up to rewriting the Endangered Species Act. Many of the new members of Congress regard the ESA as an impediment to development and would like to see it eviscerated. It is ironic that politicians that rose to fame through their defeat of Clinton's health-care package are now developing environmental policies that will make comprehensive health-care an even more formidable challenge. Weakening the Endangered Species Act in the US and failing to ratify the Rio convention will send an importunate message to tropical countries that will now have even less of an incentive to discourage further losses of biodiversity. With it will go a huge reduction in the potential for the discovery of new drugs from plants in the rain forest. As Paul Cox (Brigham Young University, Provo, UT, USA) astutely pointed out, 'weakening the Endangered Species Act is tantamount to declaring a war on Creation!'. It is a salient point that many children and immunologically compromised adults are likely to sharply appreciate as their chances recede of receiving drugs for potentially curable ailments.

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References

1 Garnett, G.P. and Anderson, R.M. (1993) *Trans. R. Soc. Trop. Med. Hyg.* 87, S19–S22
2 Bloom, B.R. and Murray, C.J.L. (1992) *Science* 257, 1055–1063
3 Chivian, E., McCally, M., Hu, H. and Haines, A. (1994) *Critical Condition: Human Health and the Environment*, MIT Press
4 Morse, S.S. (1995) *Emerging Infect. Dis.* 1, 7–15
5 Dobson, A.P. and Carper, R.J. (1992) In *Global Warming and Biodiversity* (Peters, R. and Lovejoy, T., eds), pp. 201–217, Yale University Press
6 Last, J.M. (1993) *Annu. Rev. Publ. Health* 14, 115–136
7 Cohen, M.L. (1992) *Science* 257, 1050–1055
8 Neu, H.C. (1992) *Science* 257, 1064–1073
9 Grifo, F. in *Biodiversity and Human Health* (Rosenthal, J. and Grifo, F., eds), Island Press (in press)
10 McCaleb, R.S. in *Biodiversity and Human Health* (Rosenthal, J. and Grifo, F., eds), Island Press (in press)
11 Stebbins, G.L. (1979) *Mem. Great Basin Nat.* 3, 87–93
12 Bell, E.A. (1993) *Parasitology* 106, S47–S53
13 Durning, A.T. (1992) *Worldwatch Pap.* 112, 1–62
14 Krause, R.M. (1992) *Science* 257, 1073–1078
15 Chan, M.S., Medley, G.F., Jamison, D. and Bundy, D.A.P. (1995) *Parasitology* 109, 373–387
16 Warren, K.S. (1988) in *The Biology of Parasitism* (Englund, P.T. and Sher, A., eds), pp. 3–12, Alan R. Liss
17 Preston, R. (1994) *The Hot Zone*, Scribners
18 Dobson, A.P. and Carper, E.R. (1993) *Lancet* 342, 1096–1099
19 Mallet, J. (1989) *Trends Ecol. Evol.* 4, 336–340
20 Pankavich, J.A., Berger, H. and Simkins, K.L. (1992) *Vet. Rec.* 130, 241–243
21 Callaghan, A., Pourie, M. and Raymond, M. (1990) *Trends Ecol. Evol.* 5, 164
22 Johnson, R. and Adams, J. (1992) *Trends Ecol. Evol.* 7, 295–299

Reference added in proof

23 Schrag, S.J. and Wiener, P. (1995) *Trends Ecol. Evol.* 10, 319–324